THE ECOLOGY OF THREE SANDY BEACHES ON THE WEST COAST OF SOUTH AFRICA

by

R. Bally

Submitted in fulfilment of the requirements
for the Degree of Doctor of Philosophy at
The University of Cape Town

August 1981

CORRIGENDA

Page	Paragraph	Correction
12	3	Samples were collected from a quadrat measuring 50 x 50 cm and were excavated to a depth of 35 cm using a spade.
12	2	The longshore length of the sampling grid was 150 m except at Rocherpan where this was occasionally reduced to 80 m when the beach was cusped.
14		These dendrograms were constructed from a Bray-Curtis similarity matrix (Bray and Curtis, 1957; Lance and Williams, 1967).
36		Fig. 3.7b shows spread of points in Fig. 3.7a. Symbols refer to tidal levels and are explained in Fig. 3.7a.
42		Fig. 3.13 is plot of Sorting (QD) and Fig. 3.14 of Skewnwss (Sk).
43		Figs 3.16 and 3.17 are plots of % organic carbon and % calcium carbonate.
50		Table 3.4: the units for mean and median diameters are in phi.
58		Fig. 3.25: the reference is Tankard (1976). Scale of map is 1 : 1 500 000.
63		Table 3.7: units are : Mean (phi), Median (phi), Sorting (QD), Skewness (Sk) and Kurtosis (KG).
71	2	References are: Bray and Curtis (1957) for similarity matrix, Kruskal (1964) for multidimensional scaling and Levine (1978) for determination of stress acceptability.
	3	Reference for information statistic program is Field (1971).
77		Fig. 4.4: A,B,C and D are replicates along a given tidal level.
84		This whole page is a duplicate of p 84* and should be ignored.
111		Scales of x and y axes are 150 and 54 m respectively.
112		" " " " " " " 78 " 42 m "
113		" " " " " " " 150 " 66 m "
117	2	Last line should read "interstitial harpacticoids".
119	2	Line 12: "porosity" should read "permeability".
134	2	Equilibration was for 2 hours.
139	1	The programme for calculating regressions is called REGRESS and was written by L. De Re for the Zoology Dept., University of Cape Town.
140		Reference to equations is Newell (1979).
168	3	Random samples were selected by choosing two sets of random numbers from tables and pacing these out first in the x and then in the y directions from the previous stations.
170		All biomass values on contour plots are in $g.m^{-2}$.
231		Table 8.1: for "weight" read "mass".

Page	Paragraph	Correction
276	1	The information analysed by the similarity analysis consists of environmental data from the distribution ranges of the genera being studied.
295		Fig. 9.5: see pp. 275 and 276 for information on data matrix.

Meyer-Reil has been misspelt throughout the thesis (i.e. on pp. 53, 62, 122 and 391).

Additional References

Bray, J.R. and Curtis, J.J. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* *27*: 325-349.

Field, J.G. 1971. A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa. *J. exp. mar. Biol. Ecol.* *7*:215-253.

Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* *29*: 1-27.

Lance, G.N. and Williams, W.T. 1967. A general theory of classification programs I. Hierarchical systems. *Comput. J.* *9*: 373-380.

ABSTRACT

The ecology of three sandy beaches on the west coast of South Africa is examined in this thesis. The first chapter constitutes an introduction to the subject and presents a brief review of studies carried out on beaches in South Africa in order to place this thesis into its proper context. In the second chapter, methods of sampling sandy-beach macrofauna (in particular sampling strategies) are briefly reviewed and discussed. For this study it was decided to adopt a grid sampling strategy, and the value of this strategy was tested.

In the third chapter the sedimentological characteristics of the beach were examined in considerable detail in order to determine whether these differed between beaches, between zones and seasons on individual beaches. Characteristic differences were found for all the above categories, and the reasons for these are discussed in detail.

Two zonation classificatory schemes for intertidal sandy-beach fauna have been proposed: that of Dahl (1953) and that of Salvat (1964). The zonation of organisms on west coast beaches is described in chapter 4, and the results obtained are discussed in the light of the above zonation schemes. Using cluster analysis, ordination and information statistic techniques, Salvat's zonation scheme was found to best describe the situation on the west coast, and its advantages over Dahl's scheme are discussed.

Chapter 5 deals with the biomass and densities of macrofauna and meiofauna on the three beaches studied and discusses these results in relation to season and results obtained on beaches elsewhere. On a very broad basis, it is found that the results from west coast beaches fall within the range of results obtained elsewhere, although they rank among the higher values. The results also show that mean individual mass of organisms is related to beach exposure - the mean mass increases with increasing exposure.

The respiratory metabolisms of the three dominant isopod species are examined in chapter 6. Using multivariate analysis, the effects of mass, temperature and activity on respiratory rates were determined for each species. Analysis of the results showed that the activity potential of each species differed, and this was correlated with the degree of exposure of the zone inhabited by each species. Thus the species living at the top of the shore showed a high activity potential while that living at the bottom of the shore had the lowest activity potential. The results and the reason for these differences are discussed and related to the differences in the conditions pertaining in each species' environment.

Traditionally, sandy beaches are investigated by means of one or two transects across the beach, and the results extrapolated to the remainder of the beach. The results obtained in chapter 2 show that there is considerable variation in biomass and density values along the beach, but a special study of this was made in chapter 7. This showed that all species in fact have an irregular distribution both along and across the beach. These distribution patches are described for all species on all three beaches in this chapter. In addition, interspecific competition and predator-prey relationships were investigated, to determine whether these had any influence on the distributions of the species concerned.

Animal-sediment relationships are investigated in chapter 8 and two major types of relationship are described. The first or gross type occurs where species are excluded from a beach due to unfavourable grain size, or where the intertidal position of all the species is affected by the sediment coarseness. The second type is where species or size-classes within species select particular grades within a particular intertidal zone. Animal-sediment relationships are discussed for each species, although these were not detected in all cases.

In chapter 9 the biogeography of the sandy beach genera occurring on west coast beaches is investigated. It was found that genera generally made up of intertidal species consisted of fewer species, with generally larger distribution ranges, than genera that tended to consist mainly of sub-tidal species. Of the 15 genera investigated in this chapter, almost all had a greater percentage of species occurring tropically than in temperate and arctic and antarctic climatic zones. When these percentages were corrected for coastline length or oceanic area, however, the concentrations of species were found to be highest in temperate zones, in all cases. The reasons for these findings are discussed in the light of Bretsky and Lorenz's (1970) theory pertaining to genetic-adaptive strategies and mass extinctions.

Finally, in chapter 10, the results of this thesis are synthesized and placed into the context of existing knowledge on sandy beach ecology. In addition, trends in sandy beach studies are discussed and future fields of research outlined.

ACKNOWLEDGEMENTS

I would firstly like to thank Professor A.C. Brown and Dr C.L. Griffiths for their patient help and supervision of this thesis, and for their encouragement.

The field work which formed the basis of this study could not have been undertaken without the help of a large number of volunteers, to whom my thanks are due. Among the most steadfast of these, were Catharine Carr, Kate Davies, Juanita Koop, Karin Koop, Anne Linley, Christopher McQuaid and Dave Muir, and I owe them an especial debt of gratitude. In addition I would like to thank Leonora Fox for her patience in typing this thesis.

My greatest debt of gratitude, however, is to Klaus Koop, not only for his unfailing assistance in the field, but also for the many hours of discussion and constructive criticism he has devoted to me.

Finally, I would like to thank my parents, Mrs H. Bally and the late Dr P.R.O. Bally for their support, as well as Professor J.U.M. Jarvis for hers.

This thesis was undertaken with grants and bursaries from S.A.N.C.O.R., the C.S.I.R. and the University of Cape Town.

CHAPTER 1

INTRODUCTION

The intertidal zone has long been of great interest to biologists for it is in this region that the two principal life-supporting media (i.e. the terrestrial and aquatic environments) meet, creating a complex range of intermediate conditions. In this zone, organisms that are essentially marine have entered the terrestrial environment to varying degrees, although all either depend upon a regular resubmergence by the tides or depend on a localized environment created by the tidal cycle. In a similar manner some terrestrial organisms have entered the marine environment. For certain marine groups, the intertidal zone has been a route for colonizing the terrestrial environment (Brusca, 1966; Hurley, 1968).

Because the intertidal zone encompasses a set of conditions ranging from almost permanent submergence to almost permanent emergence, individual groups of plants and animals have adapted to specific zones of exposure within the intertidal area. The resulting zonation has been very well documented on rocky shores (e.g. Stephenson and Stephenson, 1972) and extensive studies have been undertaken on the morphological, physiological and behavioural adaptations of intertidal organisms (see Newell, 1976 and 1979 for recent reviews).

The intertidal zone of sandy beaches has been studied much less extensively for a number of reasons. Firstly the fauna is specially adapted to burrow into the substrate, and is therefore usually invisible at low tide, the time when it is most convenient for biologists to sample. Secondly, the beach fauna has less spectacular adaptations to survive periods of emersion since the sand confers considerable protection against heat and desiccation to intertidal organisms.

Nevertheless, zonation classificatory systems for beaches have been proposed (Dahl, 1952; Salvat, 1964) and discussed (Pichon, 1967; Withers, 1977). In addition, a considerable body of literature on beaches and their fauna does exist, but these studies are only rarely as refined and conclusive as similar studies undertaken on the rocky intertidal.

This does not mean that the study of sandy beaches is unnecessary, or that it should be substituted by further studies on rock shores. On the contrary, a study of the ecology of sandy shores is of particular interest since the habitats present a different set of conditions to which the colonizing species have adapted in a variety of ways.

The South African west coast is chiefly influenced by the cold-water Benguela current which flows in a northerly direction parallel to the coastline carrying cold water as far north as central Angola (Hart and Currie, 1960). This current, consisting of both south Atlantic gyre water and cold upwelled water, makes these waters "the coldest in all Africa" (Brown and Jarman, 1978). This upwelling has resulted in one of the world's greatest fishing grounds.

Biogeographically, the west coast has been classified as cold-temperate (Stephenson and Stephenson, 1972; Brown and Jarman, 1978) although Ekman (1953) and Briggs (1974a) considered it to be warm-temperate. For the purposes of this study the west coast will be considered to consist of the area lying between Cape Town and the Orange River (Fig. 1.1).

Some 80 to 90% of the shores in the area designated are sandy and rocky headlands along this coastline are far and few between. The majority of the beaches are long and very exposed to wave action, the fetch of

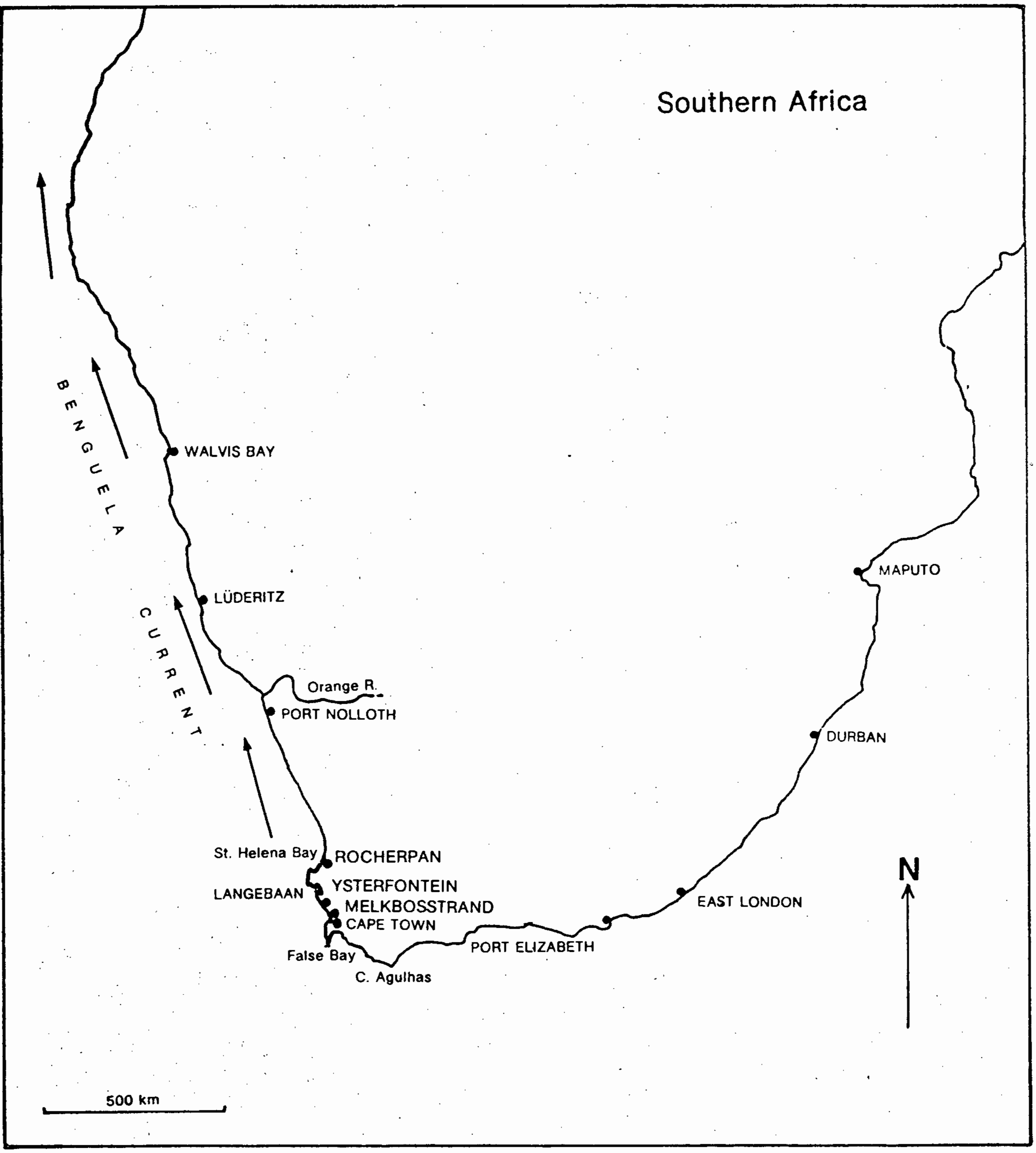


Figure 1.1 The locations of the beaches sampled.

incoming waves being several hundred kilometers across the south Atlantic (Shillington, 1978). Most of the beaches are backed by dunes and are thus permanent features of the coastline, unlike some west coast Cape Peninsula beaches which may be washed away completely during the winter (Brown, 1971a).

As noted earlier, sandy beaches in South Africa, as in the rest of the world, have received much less attention from biologists than have rocky shores. This is in spite of the fact that soft shores dominate the South African coastline. Summers *et al.* (1976) and Underhill *et al.* (1980) estimate that of the 1829 kilometers of shoreline between the Olifants River mouth on the west coast and the Kei River mouth on the east coast, 48 percent consists of sandy beaches and 20% of mixed sandy and rocky shores.

For the Natal coast, the only published reports are those of Oliff *et al.* (1967, 1970) which give the results of a baseline study of meiofaunal numbers and of the chemistry of interstitial beach water, and Dye *et al.* (1980) who carried out brief surveys of four Natal beaches. Unfortunately much of Oliff's work remains unpublished. The only report on Transkeian beaches is that of Wooldridge *et al.* (1980) in which three beaches are briefly surveyed.

A considerable amount of work has been carried out on south coast beaches in recent years. This area, lying between the Kei River and Cape Agulhas, has been particularly intensively studied in the vicinity of Port Elizabeth by Dr A. McLachlan and his co-workers. McLachlan (1977a, b, c, d, 1978) and McLachlan and Furstenberg (1977) have carried out surveys on both macrofauna and meiofauna as preliminary studies. Migration of meiofauna and macrofauna is reported by McLachlan *et al.* (1977) and (1979) respectively, while McLachlan (1977e) has studied the effects of iron ore dust pollution on beaches in Algoa Bay. In addition, McLachlan (1980a) reports on the zonation of both macrofauna and meiofauna.

The energetics of sandy beaches in the eastern Cape has been discussed by McLachlan *et al.* (in press) and McLachlan (1981). McLachlan proposes a partially closed cellular system whereby dissolved and particulate organics from the surf zone provide the food for intertidal fauna. Nutrients regenerated by the intertidal fauna would then have sufficient residence times in the surf zone to cause phytoplankton blooms, which would, in turn, be the food source of the intertidal fauna.

Individual species studied include the white mussel *Donax serra* of which Hanekom (1975) has studied the general biology, Dye (1979a) the respiratory physiology and McLachlan and Hanekom (1979) the biology, ecology and seasonal fluctuations in biochemical composition. The growth and reproduction of *Donax sordidus* discussed in both McLachlan (1979a) and McLachlan and Van der Horst (1979). The latter paper also deals with growth and reproduction of the whelk *Bullia rhodostoma*, while McLachlan, Cooper and van der Horst (1979 discuss the growth and production of that species. Dye and McGwynne (1980) discuss the effects of temperature and season on the respiratory rates of *B. rhodostoma*, *B. digitalis* and *B. pura*, while Dye (1980a) reports on the respiratory physiology of the mysid *Gastrosaccus psammodytes* and Wooldridge (1981) has carried out an exhaustive study of the population structure and dynamics of this species. McLachlan (1980b) refers to the occurrence of *Ocypode* in this region. Dye (1979b) has also estimated the distribution and abundance of protozoa on two beaches, and tidal variations in biological oxygen demand (Dye, 1980b), while McLachlan, Wooldridge, Schramm and Kunh (1980) make estimates of the shore birds of the eastern Cape, and the impact their feeding has on the macrofauna.

Finally, on a more physical basis, McLachlan, Dye and Van der Ryst (1979) investigated vertical gradients in the fauna and oxidation in two beaches, McLachlan (1979b) has calculated the quantities of sea water filtered through local beaches and McLachlan (1980c) proposes an exposure rating system for beaches.

The south coast-west coast overlap area lying between Cape Agulhas and Kommetjie on the Cape Peninsula (Brown and Jarman, 1978) has been investigated at Muizenberg and around the Cape Peninsula (Brown, 1964, 1971a; Brown and Jarman, 1978) while Boland (1974) worked on the macrofauna at Kommetjie. Winterbottom (1967) sampled from the surf zone at Muizenberg, while Brown (1971b, 1973), Brown and Talbot (1972), Kensley (1972, 1974) and Muir (1977) have examined several of the more important species inhabiting these beaches.

Brown (1971b) reviews the considerable amount of work carried out on the prosobranch whelk *Bullia* to that date. Subsequent studies include Brown and Currie (1973), Brown *et al.* (1974), Banks (1975) and Cuthberg *et al.* (1976a, b) all of which investigate the effects of various pollutants on the snail. Brown (1978, 1979a, b), Brown and Da Silva (1978) and Brown *et al.* (1978) examine various aspects of oxygen consumption in *B. digitalis* and *B. melanoides*. In addition, Newell and Brown (1977) describe the structure of the whelk's osphradium, while Trueman and Brown (1976) analyse *Bullia's* locomotion. Most recently, Brown (in press) reviews existing knowledge on the biology of this genus.

Brown and Talbot (1972) have made a study of the psammophilous mysid *Gastrosaccus psammodytes* and the oniscoid isopods *Tylos granulatus* and *T. capensis* have had aspects of their biology, ecology and behaviour studied by Kensley (1972, 1974). More recently, Marsh and Branch (1979) found marked circadian and circatidal rhythms of oxygen consumption in *T. granulatus*. In addition Muir (1977) has calculated the energy budget of the supralittoral amphipod *Talorchestia capensis*, while Stenton-Dozey and Griffiths (1980) and Griffiths and Stenton-Dozey (in press) have investigated the biology of the kelp fly *Fucellia capensis*, and its role in the degradation of kelp stranded on sandy beaches.

Pollution studies on the beaches of the Peninsula include a survey of Camps Bay beach by Eagle *et al.* (1977) while King (1974) investigated the effects of oil pollution on *Talorchestia* following reports of mass mortalities in this genus associated with oil on beaches (Stander, 1968). On the physical side, Colvin (1969) measured the oxygen content of the interstitial waters of some of these beaches. In addition Orren *et al.* (in press) and Fricke *et al.* (submitted for publication) have examined the physical conditions and meiofauna on ten beaches on the Peninsula and the south and west coasts. Finally Koop *et al.* (in press) and Koop and Griffiths (in prep.) have investigated the role of bacteria in the degradation of kelp in a sandy beach microcosm and the relative significance of macro-, meio- and microfauna on Noordhoek beach.

Thus the beaches of the Cape Peninsula have been among the most intensively studied in South Africa.

Along the west coast, as defined above, detailed studies have been carried out at Saldanha Bay and Langebaan Lagoon where the effects of varying degrees of exposure on the composition of beach faunas can be observed (Day, 1959; Carr, 1976). The beaches at Langebaan Lagoon were found to show many estuarine characteristics despite the absence of a salinity gradient (Day, 1959). Thus much of the work on South African estuaries (e.g. Day, 1967a; McLachlan and Grindley, 1974; Dye and Furstenberg, 1978; Dye *et al.*, 1978; Dye, 1978a, b, c; and see Day, 1981, for review) has considerable relevance to sheltered or low-energy beaches. This type of beach is, however, relatively uncommon along the South African littoral.

The only published studies of a west coast sandy beach species are those of De Villiers (1975a, b) which reports on the reproduction, distribution, growth and population dynamics of the mussel *Donax serra* with a view to controlling the commercial exploitation of that species, and Hodgson, in press, who has investigated autotomy and regeneration of siphons in that species.

Currie and Cook (1975) carried out baseline surveys including an intertidal sand beach on the future site of the Koeberg nuclear power station, just to the north of Melkbosstrand. Cuthbert *et al.* (1976b) investigated cadmium concentration levels in *Bullia* collected from Melkbosstrand, while Van As *et al.* (1975) looked at trace element concentrations in a variety of animals including *Donax*. Finally, Brown (1958) has reported on the results of a brief survey of the macrofauna of a beach at the mouth of the Orange River. Apart from these few articles, no other work has been published on the ecology or fauna of beaches on the west coast.

In South Africa, biomass studies on a seasonal basis have been carried out for meiofauna by McLachlan (1977c) and for *Donax serra, D. sordidus, Bullia rhodostoma* and *Gastrosaccus psammodytes* (McLachlan and Hanekom, 1979; McLachlan, 1979a; McLachlan, Cooper and Van der Horst, 1979; Wooldridge, 1981, respectively).

The above reviews the present state of biological knowledge concerning South Africa's sandy beaches. It also shows that there remains much to be examined and learnt about the ecology and biology of these beaches and their fauna. Apart from the paucity of published data on the beaches on the Natal and west coasts, there is a lack of information on the energetics of such beaches. Many aspects remain to be investigated. These include the relationship between the sedimentology of beaches and their constituent fauna, the energetic requirements of the fauna, variations in its biomass and turnover and its geographic distribution.

The answers to these questions will lead to a better understanding of the sort of environment beaches present to their infauna, and how that fauna adapts to this environment.

All the above studies, however, were carried out on the relatively warmer south coast, and this thesis represents the first such study for the colder west coast. In this thesis, a number of aspects of sandy beach ecology are examined. Since one of the major difficulties in the study of sandy beaches has been the absence of a truly representative sampling method, various methods are first discussed and a grid sampling technique is proposed. Most of the results in this thesis were obtained from sampling grids.

The sedimentology of the beaches was examined in detail on a seasonal basis, in order to obtain quantitative descriptions of the beach sediments. The zonation of macrofauna on the beaches is discussed next, and various proposed sandy beach zonation schemes are compared. The zonation proposed by Salvat (1964) is shown to be the most acceptable suggested to date.

From organisms collected seasonally from the above mentioned sampling grids, numbers, biomasses and calorific values were obtained. From this data, mean annual values of the species involved were calculated. In addition, an analysis of the patchiness of macrofauna in the intertidal zone is included.

Respirometry has been carried out on the three main isopod species found on west coast beaches and the effects of size, temperature and activity, together with an activity budget, are presented. These results are presented as response surfaces and described by equations. From these results and from seasonal biomass and number data, population respirations for the species have been obtained.

The biogeographic and zonational distributions of macrofaunal species are also examined, with a view to placing the above findings into context. Factors that might limit these distributions are also examined. The numbers and vertical distribution of meiofauna on west-coast beaches was also investigated for the first time. Meiofaunal data was collected chiefly for purposes of comparison both with the macrofaunal data and with other beaches, especially the South African ones investigated by McLachlan (see above).

Finally, the findings of this study are synthesized and presented together with recent ideas and concepts on the ecology of sandy beaches.

CHAPTER 2

SAMPLING METHODS

Introduction

There are limitations to any sampling method used on sandy beaches. The chief of these is that the macrofauna (and meiofauna) cannot be seen during low tide - which also happens to be the only time that it is practicable to collect from the intertidal zone. This applies particularly to exposed or high-energy beaches.

It is therefore impossible to locate concentrations of animals without first digging out many small sand samples and sieving out the animals from them. Since the distribution of sand-beach fauna is notoriously patchy (e.g. Hayes, 1977; Gerlach, 1977; Moran, 1972; Pichon, 1967; Ansell *et al.*, 1972), to carry out the above procedure would be excessively time-consuming for the limited time that is available for sampling.

The vast majority of workers have therefore sampled along a transect, often taking several replicates in order to correct for any patchiness (e.g. Penchaszadeh, 1971; Achuthankutty, 1976; Trevallion *et al.*, 1970; Dexter, 1972, 1974, 1976, 1979; Rees, 1939; De Villiers, 1975b; Platt, 1977; Gauld and Buchanan, 1956; Fincham, 1971, 1974, 1977; Pichon, 1967; McIntyre and Eleftheriou, 1968; Southward, 1953; Wood, 1968; McLusky *et al.*, 1975; and Dwivedi *et al.*, 1973).

Because of the heavy labour involved, single transects are usually taken, except where it appears likely that the beach fauna will differ along the beach, as, for example, on beaches in small bays (e.g. Wood, 1968; Fincham, 1971; McIntyre and Eleftheriou, 1968).

In this study, however, long and uniform beaches were chosen deliberately, in order to reduce the number of variables that might influence macrofaunal distribution and biomass.

The only long-shore studies of intertidal macrofauna are those of Dauer and Simon (1975), Moueza and Chessel (1976) and Moran (1972). Dauer and Simon (1975), however, draw their conclusions on the along-shore distribution of Polychaete worms from three transects irregularly spaced along the shore. Moueza and Chessel (1976) studied the along-shore distribution of a single species - the bivalve *Donax trunculus*. From data collected from a large number of stations, they were able to show considerable variation in the biomass of that species along the beach. Moran (1972) investigated the microdistribution of the mysid *Gastrosaccus mediterraneus* across and along a small section of beach on the Mediterranean coast of Israel. Finally, Corey (1970) employed a grid system on an irregularly-shaped pocket beach (Kames Bay, Scotland) in order to determine the intertidal distribution of the cumacean *Cumopsis goodsiri*.

The Sampling Grid

In order to sample successfully from all tidal levels while accounting for patchiness in faunal distribution along the beach, it was therefore necessary to combine the two strategies and sample from a grid.

The size and shape of this grid was dictated by a number of considerations. It was considered essential to carry out all the collecting during one period of low tide, since the density of animals at any one point may not be fixed. If, therefore, sampling were undertaken over two consecutive periods of low tide, it is conceivable that two different populations might be sampled. Or if there were two populations within the grid area, the same population might be sampled twice. Either possibility would produce erroneous results.

The necessity to sample during a single low tide restricted the number of samples that could be taken and eventually a grid of sixteen sampling points was decided upon. It was just possible for two workers to sample from this grid during one period of low tide, while three or four people could accomplish the sampling programme comfortably within three to four hours.

Each sample comprised a fairly large area (50 x 50 cm) so that replicates would not be necessary. Although many workers have been content to sample from the top 10 to 20 cm of sand (e.g. Stephen, 1929; Eleftheriou and Jones, 1976; Withers, 1977; Trevallion *et al.*, 1970; Jones, 1974; Ansell *et al.*, 1972; Schuster-Diedrichs, 1956; Seed and Lowry, 1973 and many others), a few (e.g. Dexter, 1969, 1974; Vohra, 1971) have limited sampling to the top 5 centimeters of sand. In this study, it was decided to sample to a depth of 35 cm, since some species burrow to a considerable depth at low tide. The giant isopod *Tylos granulatus* would have been missed completely had sampling not been carried out to this depth, thereby seriously affecting the biomass values.

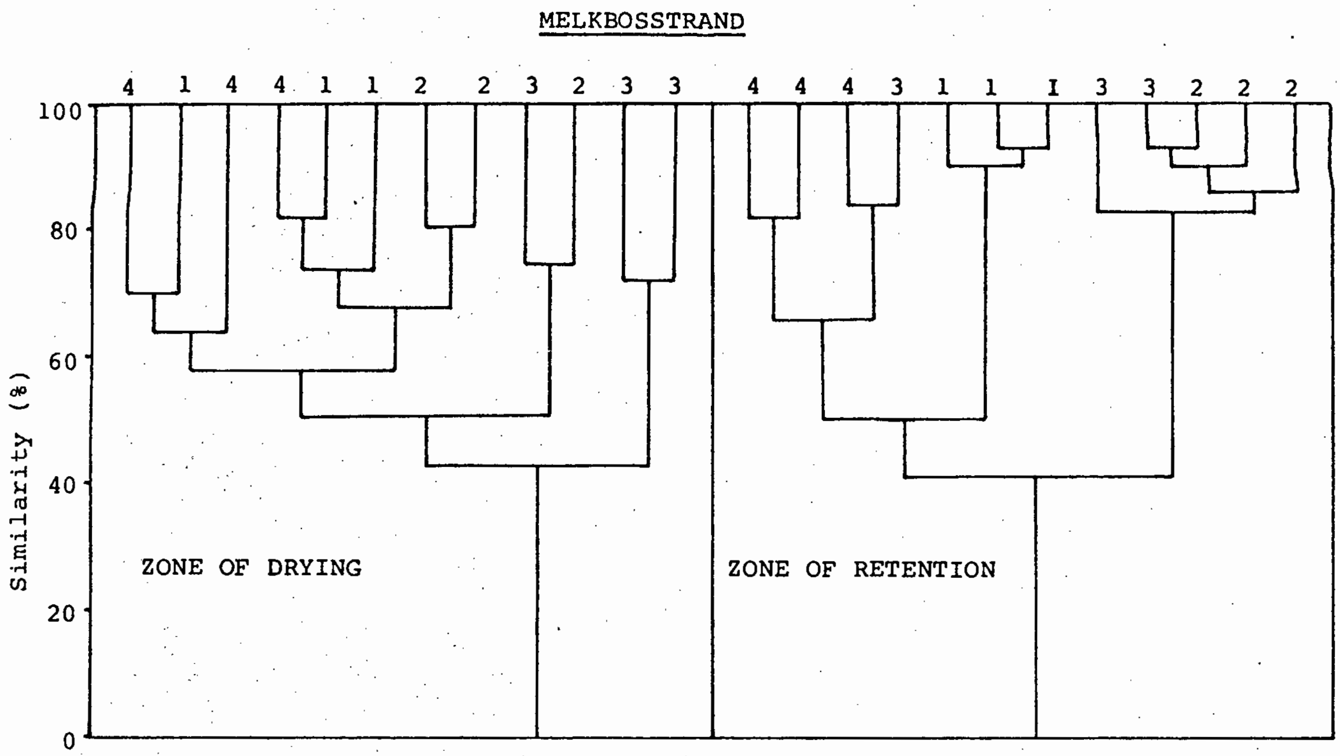
Thus one sampling session involved the sifting of a total of 1,40 m^3 of sand from various parts of the beach through 1 mm mesh sieves, and the removal of all the macrofauna therein. The area of beach sampled was 4,0 m^2.

In order to test the validity of the grid method as opposed to the replicate method, on one occasion at each beach three replicates of the above size were collected at each grid point. The results obtained indicate that the variation between grid points for any particular tidal level is greater than the variation of the replicates at any grid point (Figs 2.1a,b,c). The main exception is in the uppermost zone (the zone of drying), where there is considerable variability due to random distributions combined with low numbers.

The sampling grid consists of four transects of four sampling points each along the beach (Fig. 2.2). The positions of the stations in the various tidal levels were so chosen as to fit into Salvat (1964) and Pollock and Hummon's (1971) four zones of drying sand, retention, resurgence and saturation (see chapter 4). The positions of these zones can be determined by eye in the field with relative ease, although mistakes were occasionally made at the beginning of the study.

Although Ansell (1972), Kay and Knights (1975), Myren and Pella (1977), Warwick and Price (1975) and Hibbert (1977) have all used grid sampling techniques of variations thereof, all these studies have been either of subtidal regions or of mudflats. Other than Moran's (1972) study of the microdistribution of G. *mediterraneus* mentioned above, this study is the first using the grid sampling method on an intertidal sandy beach.

The results obtained from the present study show that macrofaunal distributional patches can be quite large in view of the size of the samples taken and the similarity of the replicates. Moran (1972) found *Gastrosaccus mediterraneus* to occur in patches measuring between a few meters and several tens of meters in width, as was found for G. *psammodytes* by Brown and Talbot (1972). Pichon (1967) notes that *Donax elegans* occurs in lens-shaped patches of between three and five meters in diameter. A grid sampling system is therefore superior to the traditional transect method provided that it is spread over a sufficiently large area. It is simpler to use than the stratified systematic sampling advocated by Scherba and



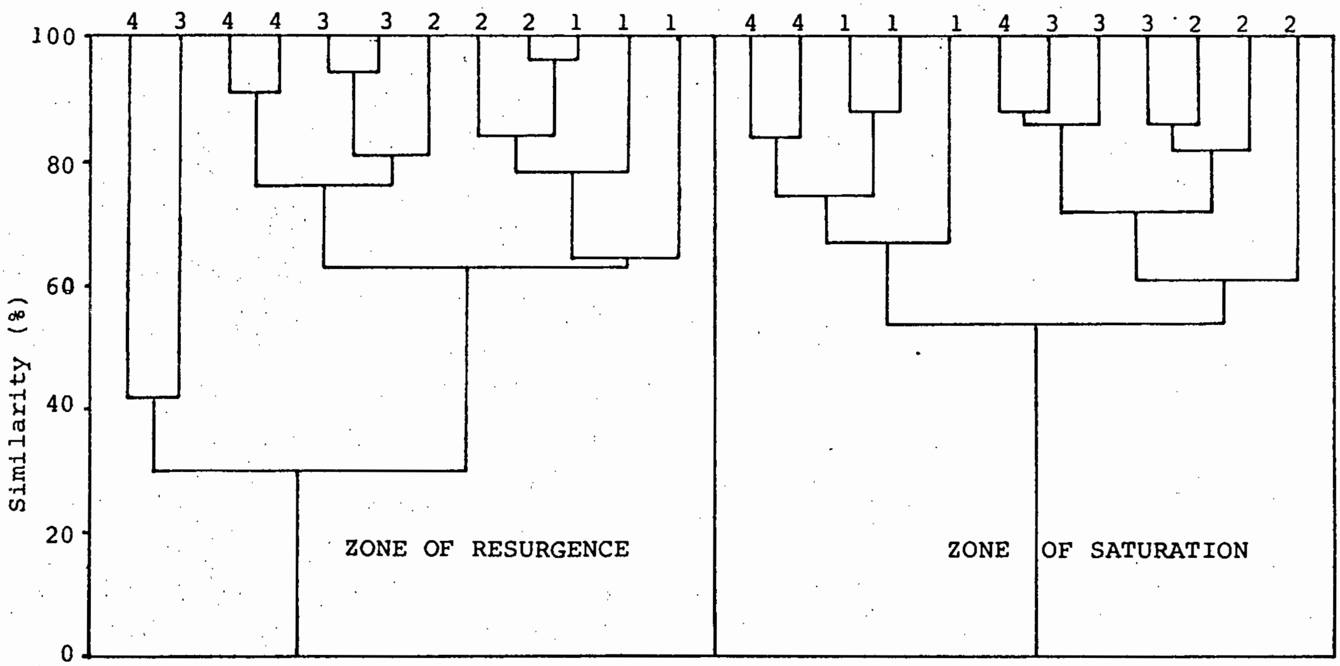


Figure 2.1a Dendrograms showing similarity between samples taken within the four intertidal zones at Melkbosstrand. Identical numbers (e.g. 4, 4, 4) represent replicate samples taken within that zone.

ROCHERPAN

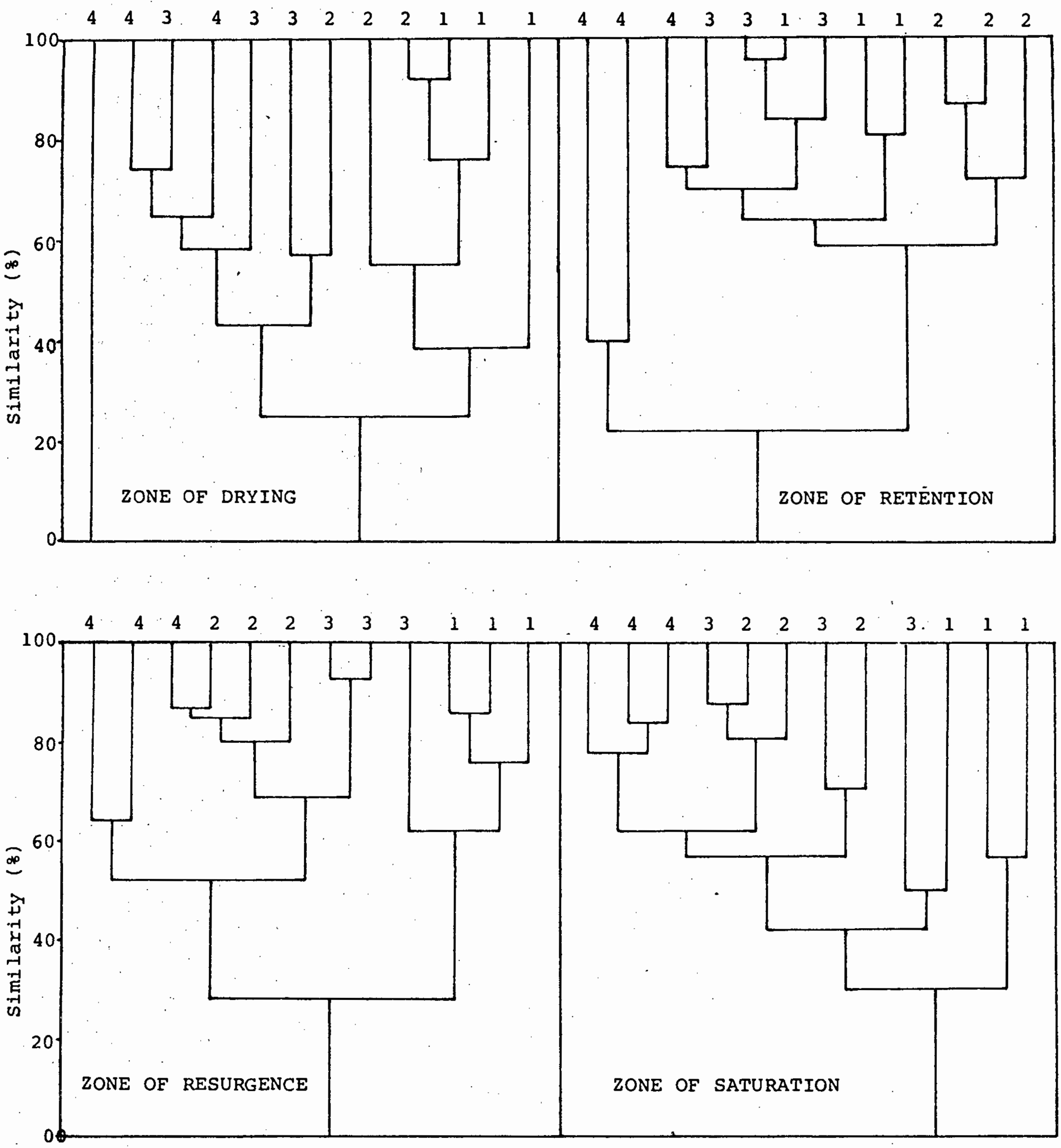
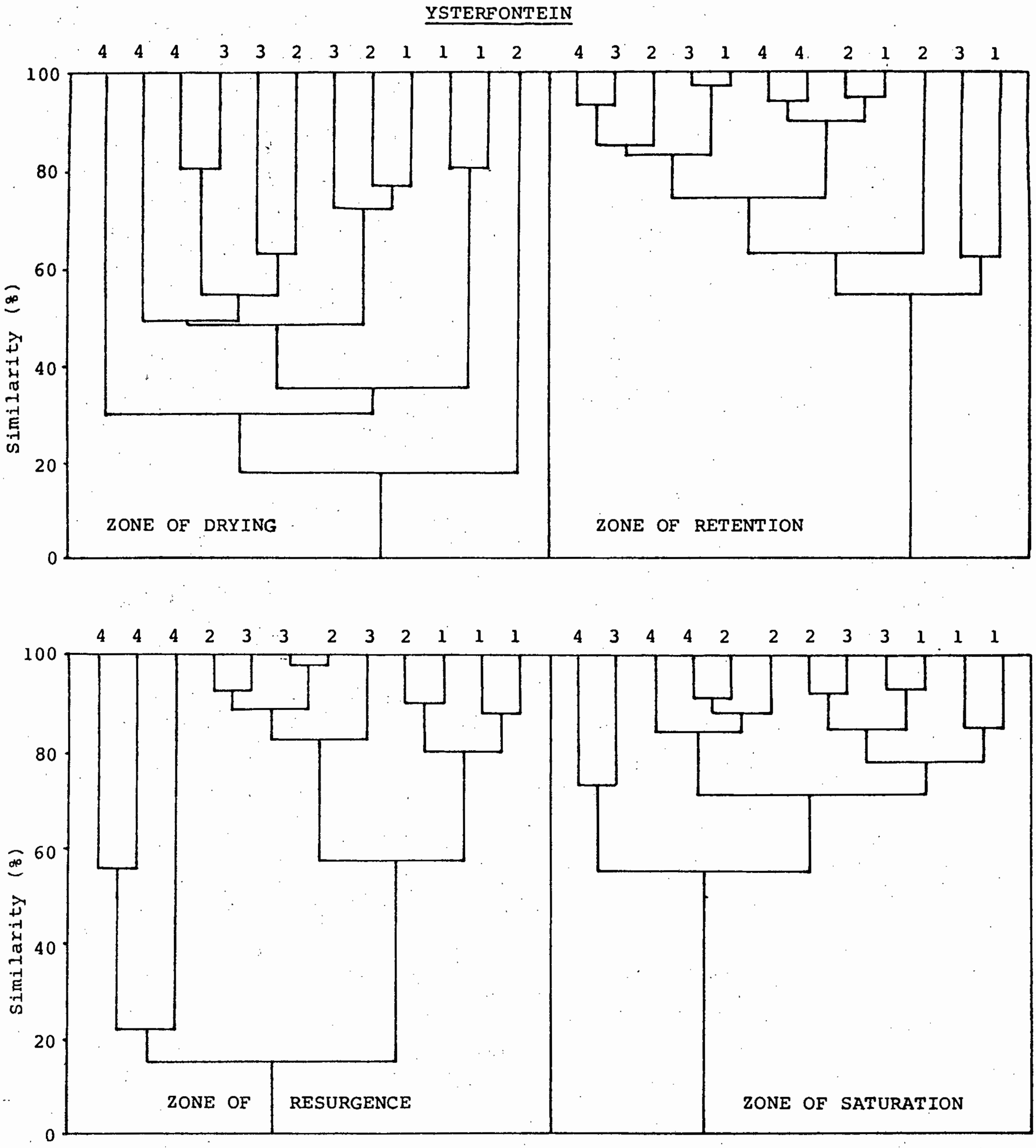


Figure 2.1b Similarity dendrograms for Rocherpan



YSTERFONTEIN

Figure 2.1c Similarity dendrograms for Ysterfontein

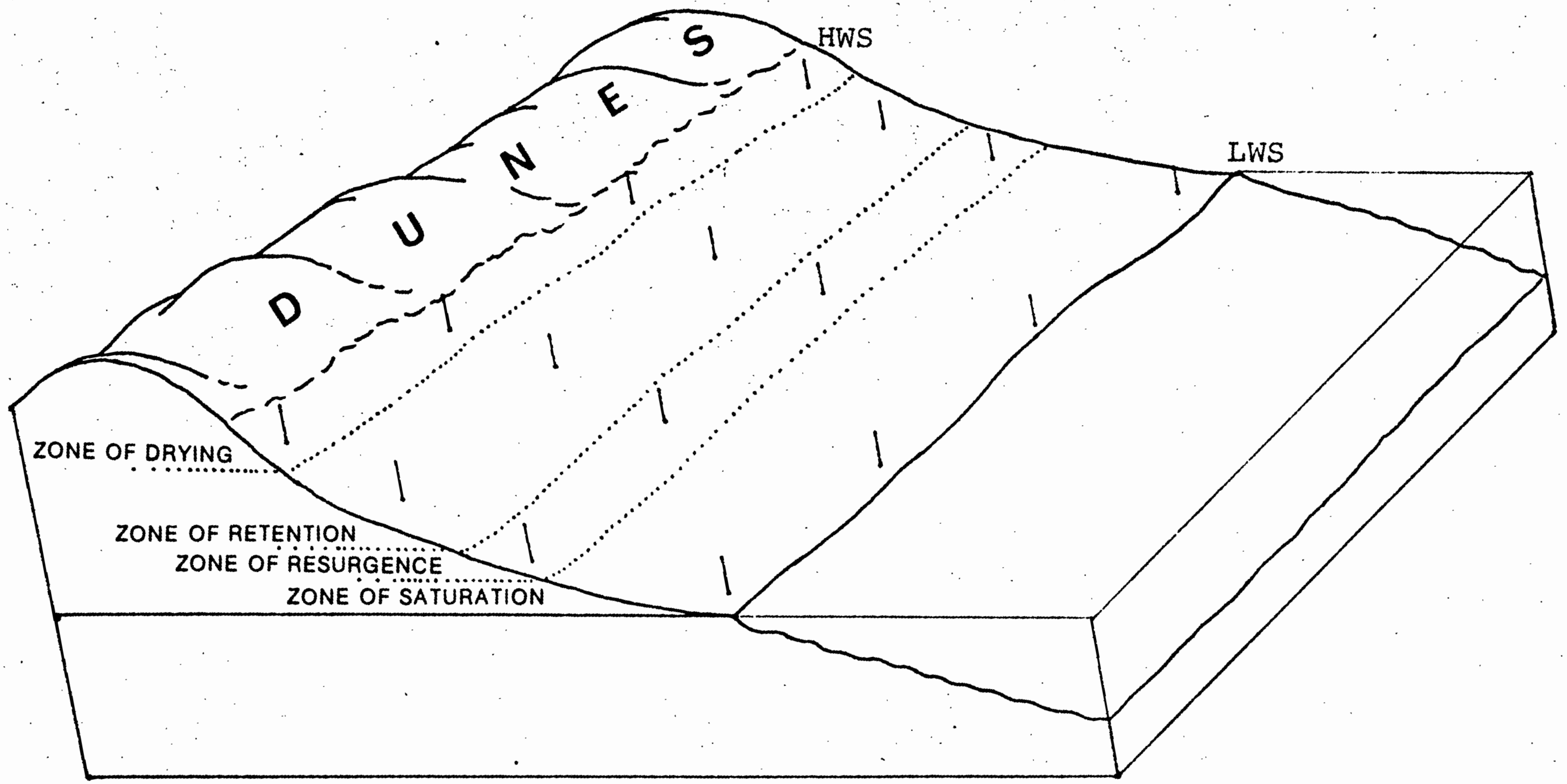


Figure 2.2 The sampling grid in relation to Salvat's four zones

Gallucci (1976). Although not necessarily preferable, it is probably also easier to use than stratified random sampling, where the correct positioning of the strata boundaries is important.

Locating the grid points within Salvat's four zones ensures that intertidally zoned animals are always sampled. The other alternative would be to employ fixed grid points. The zonational positions of these, however, are likely to vary depending on wave, weather and tidal conditions, as well as on seasonal changes in beach profiles. Since the majority of the intertidal fauna is mobile, it can be expected that species will select their zonational levels according to prevailing conditions.

Many species have been found to do just that (e.g. Loesch, 1957; Brown, 1961; Pichon, 1967; Wade, 1967; Ansell and Trevallion, 1969; Enright, 1963; Fish, 1970; Fish and Fish, 1972; Klapow, 1972a; Alheit and Naylor, 1976 and McLachlan, Wooldridge and Van der Horst, 1979), often using highly complex endogenous rhythms (Klapow, 1972b). This suggests that these species are selecting particular environmental conditions. As will be shown in chapter 3 (Sedimentology), the environment determines sediment particle size distributions as well, and therefore the grid system of sampling is equally suitable for the collection of sediment and meiofauna samples.

CHAPTER 3

SEDIMENTOLOGY

Introduction

In physical terms, a beach can be defined as "the zone of unconsolidated sediment that extends from the uppermost limit of wave action to the low-tide mark" (Davis, 1979, p.238). In any study of sandy beaches, it is desirable, therefore, to investigate the physical and chemical properties of the beach sediments. Examination of these properties in the case of ecological studies gives indications as to the environment experienced by the infauna of the beach, and additionally, the physical properties themselves can determine the nature of the fauna colonizing the beach.

Fine-grained beaches are deposited by relatively low-energy currents, which means that a relatively higher proportion of organic detritus can settle out. Small sand grains provide greater surface areas for colonization by bacteria (Meadows and Anderson, 1966; 1968) and thus the organic content of sand (i.e. organic detritus plus bacteria) from fine-grained beaches is generally higher than that of coarser-grained ones. Fine beaches are usually more gently sloping than coarse-grained beaches (Bascom, 1951) and thus offer wider intertidal areas for colonization by macrofauna. Large populations of species can therefore establish themselves in the various intertidal zones.

During low tide, fine-grained beaches drain slowly, thus imposing little desiccation stress to intertidal macrofauna. The depth of the black anoxic layers in low-energy beaches decreases with decreasing drainage ability of the sand (Webb, 1958) and oxygen levels are appreciably higher in well-drained coarse-grained beaches that in finer grained beaches where porosity is lower (Colvin, 1969).

Macrofaunal animals on fine-grained beaches also need to expend less energy in maintaining position (owing to relatively slower currents) and burrowing into the sand is considerably easier than on coarse-grained beaches.

Coarse-grained beaches are deposited in relatively high-energy environments and have a relatively lower organic content. The area available for colonization by macrofauna is also smaller, because the beach is steeper, and maintaining correct zonation on the consequently narrower beach becomes more critical. These beaches drain rapidly at low tide, producing greater desiccation stress to animals in the upper intertidal zone. On the other hand, because there is greater water movement on these beaches, greater amounts of both oxygenated water and air circulate through the sand and the beaches themselves are well-oxygenated as a consequence.

Thus a study of the sediments of a beach can reveal a number of features.

1. The calcium carbonate content of the sand reflects the sediment's derivation - whether it is partly or mostly composed of bioclastic sediment (e.g. derived from molluscan shells or other skeletal carbonates) or whether it consists mainly of terrigeneous sediments such as quartz and felspar (Davis, 1979).

2. The grain size variation of the sand can be analysed and a number of its aspects are reflections of the material that is available to build the beach and the energy that maintains the beach.

    a) The mean grain size gives the degree of fineness or coarseness of the beach. This is in part a function of the aspect of the beach and of the water currents that bear sediments to the beach, either in suspension or as bed-load (Komar, 1978) and deposit them there (Davis, 1979).

b) The degree of sorting gives the size range of the sand grains forming the beach. A poorly sorted beach (one with a large range of grain sizes and a high sorting value) would suggest that a wide range of depositional conditions occur there, or that a mixture of sediments of different origin is present in the sample. A well-sorted beach, on the other hand, would imply more constant depositional conditions, or that the beach is built up of previously well-sorted sediments.

c) Skewness measures departures from log-normal (Gaussian) distributions. Strongly skewed curves may indicate the presence of one or more additional sediment types in the sample.

d) Measures of kurtosis indicate the degree of peakedness of a normal curve. Leptokurtic distributions (i.e. those with a very narrow or pointed peak) may be composed of two normal distributions with the same mean but different variances, while platykurtic curves (with a wide or flattened peak) might be composed of two normal grain size distributions with similar variances but different means (Zar, 1974).

3. The beach slope for beaches of any given mean grain size depends on the energy reaching it. Thus beaches that are protected are steeper for any particular mean grain size than exposed ones (Bascom, 1951). The beach slope can therefore act as a useful indicator of exposure provided that the mean grain size is known.

The above characters can therefore serve to describe a beach, and thus the environment in which sandy beach macrofauna live.

Materials and Methods

Sand samples to a depth of 20 cm were collected during low spring tide from each sampling point in the sampling grid described in chapter 2 at Melkbosstrand, Ysterfontein and Rocherpan. This procedure was repeated on each collecting trip so that a record of sediment changes could be obtained simultaneously with the biological samples. Sand samples were transported to the laboratory and stored in labelled plastic bags.

Each sample was processed as follows:

1. The sample was mixed and split using a sand splitter, down to a volume of approximately 50 ml. This sand was then placed in dialysis tubing and kept in running water for 2 to 3 days in order to remove salts. After dialysis the sand was dried in a drying oven at 60°C for two days, and then further split to a volume of about 5 ml.

2. Half of this volume was placed in a predried crucible and weighed before being placed in a muffle furnace for 3 hours at 450°C (not higher to avoid decomposition of calcium carbonate). After cooling, the samples were reweighed to determine the amount of organic carbon lost by incineration.

3. Hydrochloric acid was then added to the muffled sand to dissolve the calcium carbonate. After washing and drying, the sample was again weighed to determine the decline in mass.

4. The other half of the sand sample was dropped down a settling column for particle size analysis. The design and operating procedure of this column are described by Flemming (1977). After processing data obtained from a cumulative settling curve with a psi-transformation computer program, the following parameters were obtained:

Deciles
Mean particle size of sample
Median particle size of sample
Sorting of sample
Skewness
Kurtosis

In addition a size-frequency histogram of 0,1 phi intervals and a cumulative curve on a log-normal scale are plotted by the program. The latter permits the differentiation of a sample into component normal distributions (Cassie, 1954; Harding, 1949).

The settling column was chosen for particle-size determination in preference to the more traditional sieving method for a number of reasons. Firstly, considerably more information could be extracted from data obtained from the settling column in a relatively short time, and these could be obtained from small sand samples.

Secondly, the results obtained are more precise, owing to the higher resolution of the method. Thirdly, it was felt that settling column data would be more meaningful to this study, than data obtained by sieving methods since, in sieving sediment samples, irregularly-shaped particles retained by a sieve of a particular mesh-size are assumed to be equivalent to spheres of a diameter greater than that mesh-size. Thus a plastic disc and a glass marble of the same diameter would be placed in the same category. Similarly a branched spicule and a spherical bead of the same overall diameter would be classed together. In both these examples however, the hydraulic properties of the two are very different indeed. In order to make sieved particle size results hydraulically meaningful it would be necessary to describe the sediment further with such parameters as specific gravity, sphericity, shape etc. all of which would involve making complicated and often vague approximations.

The hydraulic particle size or 'settling size' (Flemming, 1977) is much more relevant in characterising marine or even aeolian sediments. Dropping sediments down a water column immediately separates out the samples according to their Reynolds number which is a function of the density of the particle, the diameter of that particle, the velocity at which it travels through the water column and the viscosity of the water. It is these characteristics which determine the deposition of sediments in the natural environment.

Thus in trying to characterize marine sediments, it is more meaningful to employ settling size rather than directly measured particle size. As far as macrofauna is concerned, many species burrow by setting up a current of water which displaces the sand particles and enables the organism to penetrate the substrate (e.g. Brown and Talbot, 1972; Watkin, 1940) and for these species, settling size has the greater relevance. For species which burrow by physically displacing sand particles by applying mechanical force, there is no particular advantage in either method of obtaining particle size, since this data must be supplemented with particle shapes, packing characteristics, thixotropy, dilatancy etc, which it was not possible to determine in this study.

Beach slopes were measured using an Abni level for determining angles of depression and elevation, and a tape-measure for measuring horizontal distances. Knowing the angle of depression and the distance across the surface of the beach between two points, the elevation can be calculated using the formula:

$$\sin\theta \times \text{distance between points} = \text{elevation}$$

where θ is the angle of depression or elevation.

This method is considerably quicker and simpler in the field than that advocated by Day (1974) in that it does not require a horizon for sighting against, and can be undertaken singlehandedly.

Results

Distinguishing between the beaches

A visual inspection of the three beaches indicates that those at Melkbos and Ysterfontein are composed of fine sand and that at Rocherpan of medium grain sand Detailed analyses (Appendix 1), however, show both seasonal and positional differences within each beach.

Plots of percentage organic carbon versus percentage calcium carbonate show three distinct groupings which seldom overlap (Fig. 3.1). The sands from the beach at Rocherpan show the lowest proportions of both organic carbon and calcium carbonate, followed by sands from Melkbosstrand and Ysterfontein. The relationship between these two parameters is linear, with an average correlation coefficient of 0,95.

The ranges of percentage organic carbon and percentage calcium carbonate for samples from each beach are listed in Table 3.1. From this it can be seen that sands from the three beaches are separated easily on the basis of these two parameters.

Beaches	Range of % organic C	Range of % $CaCO_3$
Rocherpan	0,08 - 0,42	1 - 17
Melkbosstrand	0,24 - 0,87	21 - 38
Ysterfontein	0,40 - 1,30	30 - 59

Table 3.1: Ranges of percentages of organic carbon and calcium carbonate for the three beaches.

The size ranges covered by the deciles of each sample were plotted,

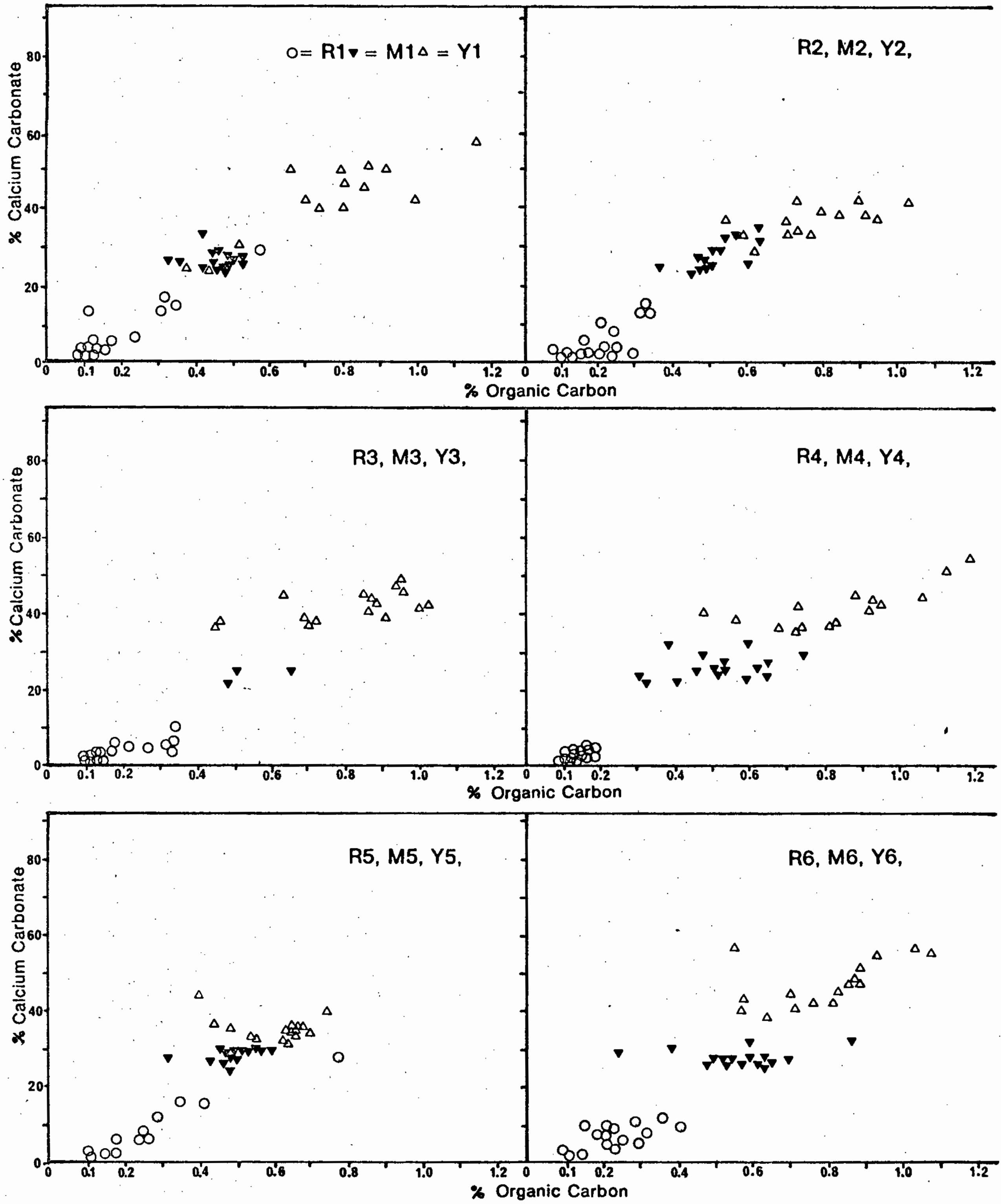


Figure 3.1 Showing the seasonal relationships between percentages of calcium carbonate and organic carbon in the sediment on all three beaches. R = Rocherpan, M = Melkbosstrand and Y = Ysterfontein. 1 and 5 represent July to September, 2 and 6 October to December, 3 January and February and 4 April and May.

giving some indication of sorting (the greater the range the poorer the sorting). Plotting all the sand samples resolved them into the same groups as the visual inspection had. There was little overlap in the decile ranges between these two groups.

A plot of median grain size versus sorting (the standard deviation of phi values) yields similar results to the decile plot, although occasionally the two fine-grained beaches separate out (Fig. 3.2). This is due to both differences in median grain size and differences in sorting. In general, however, the sorting of the three beaches is similar and it is the median grain size parameter that distinguishes the coarse beach from the two fine ones.

Mason and Folk (1958) plotted skewness (the asymmetry of a normal curve) against kurtosis (-the degree of peakedness of a normal curve) to distinguish between beach and dune sands. However these two parameters are of no use whatsoever in distinguishing between the sands from the three beaches (Fig. 3.3).

Mean and median grain size measures are usually fairly similar in value for any one sample. Both are measured on the phi scale (Table 3.2). Whereas the mean gives the average grain size of the sample, the median gives the middle measurement of a cumulative curve of percentages of grain sizes, and is always equal to the 5th decile or 50th percentile. If the mean is greater than the median, then the distribution curve is positively skewed, but if it is less, the curve is negatively skewed, assuming a normal distribution (Zar, 1974). Plotting mean against skewness can therefore give some idea of the coarseness or fineness of a sample, and how it conforms to a normal distribution.

When mean and skewness of samples from the three beaches are plotted against each other (Fig. 3.4), it can be seen that the main differentiating factor is the mean sand grain diameter. This always

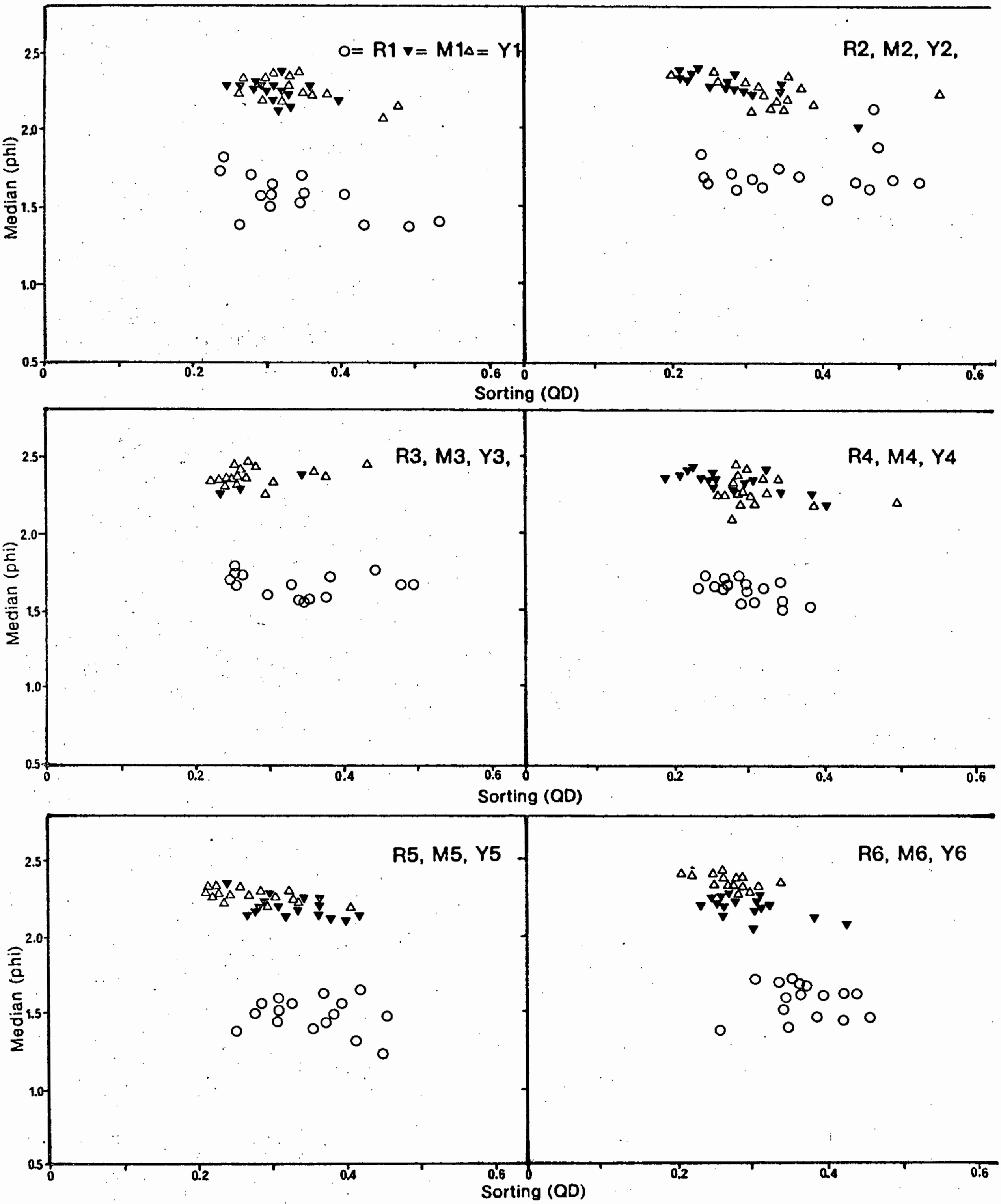


Figure 3.2 The relationship between median grain size and sorting of the sediments. Symbols are as in Figure 3.1

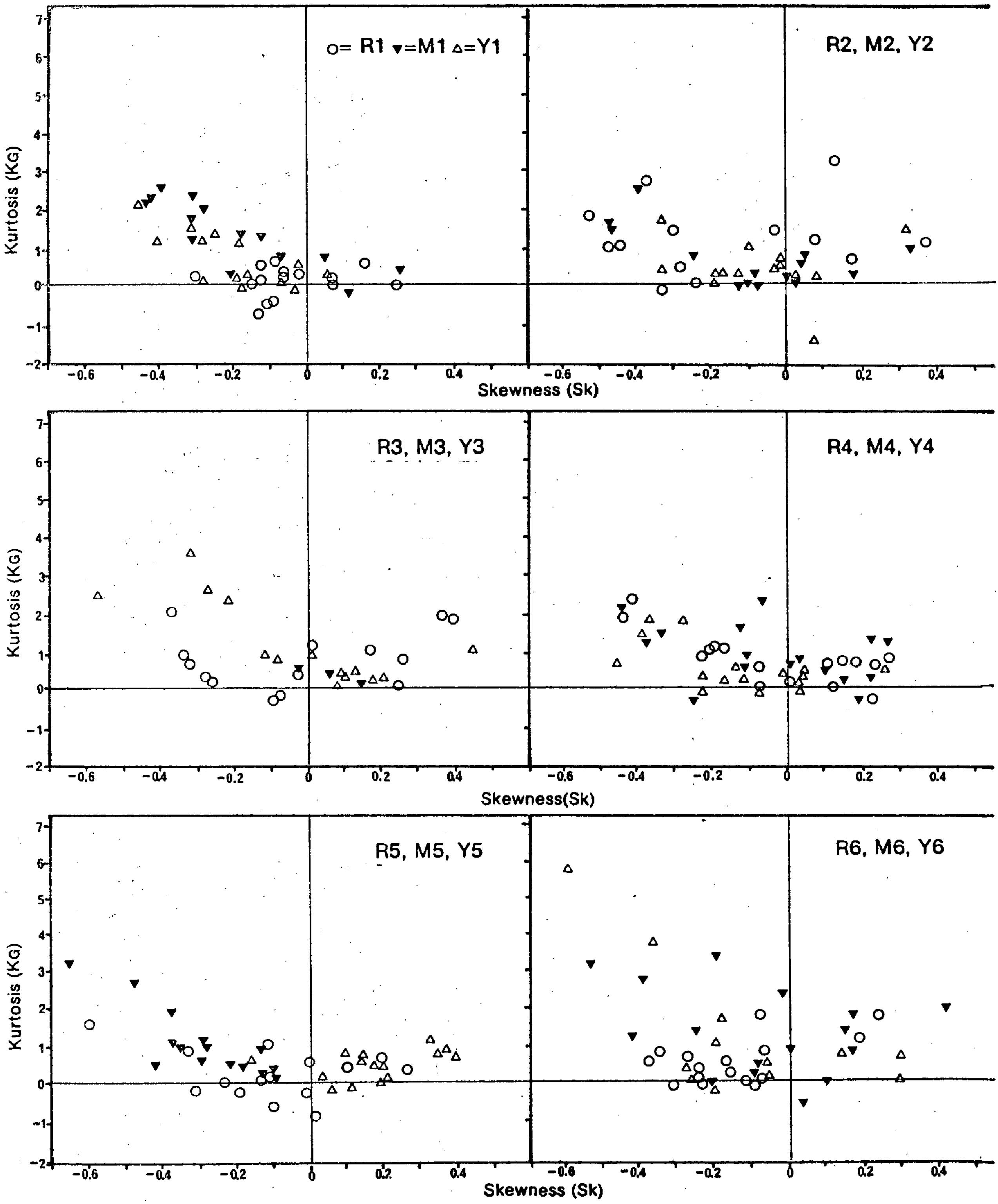


Figure 3.3 The relationship between the kurtosis (peakedness) and skewness of the sediments' grain size distribution

TABLE 3.2: Conversion from phi to millimeters (After Page, 1955)

Diameter (phi)	Diameter (mm)	Sand Size class	Diameter (phi)	Diameter (mm)	Sand Size class
-1,00	2,0000	V	1,00	0,5000	Coarse
-0,90	1,8861	E	1,10	0,4665	
-0,80	1,7411	R	1,20	0,4353	M
-0,70	1,6245	Y	1,30	0,4061	E
-0,60	1,5157		1,40	0,3789	D
-0,50	1,4142	C	1,50	0,3536	I
-0,40	1,3195	O	1,60	0,3299	U
-0,30	1,2311	A	1,70	0,3078	M
-0,20	1,1487	R	1,80	0,2872	
-0,10	1,0718	S	1,90	0,2679	
0,00	1,0000	E	2,00	0,2500	
0,10	0,9330		2,10	0,2333	
0,20	0,8705	C	2,20	0,2176	
0,30	0,8123	O	2,30	0,2031	
0,40	0,7579	A	2,40	0,1895	F
0,50	0,7071	R	2,50	0,1768	I
0,60	0,6598	S	2,60	0,1649	N
0,70	0,6156	E	2,70	0,1539	E
0,80	0,5743		2,80	0,1436	
0,90	0,5359		2,90	0,1340	
			3,00	0,1250	

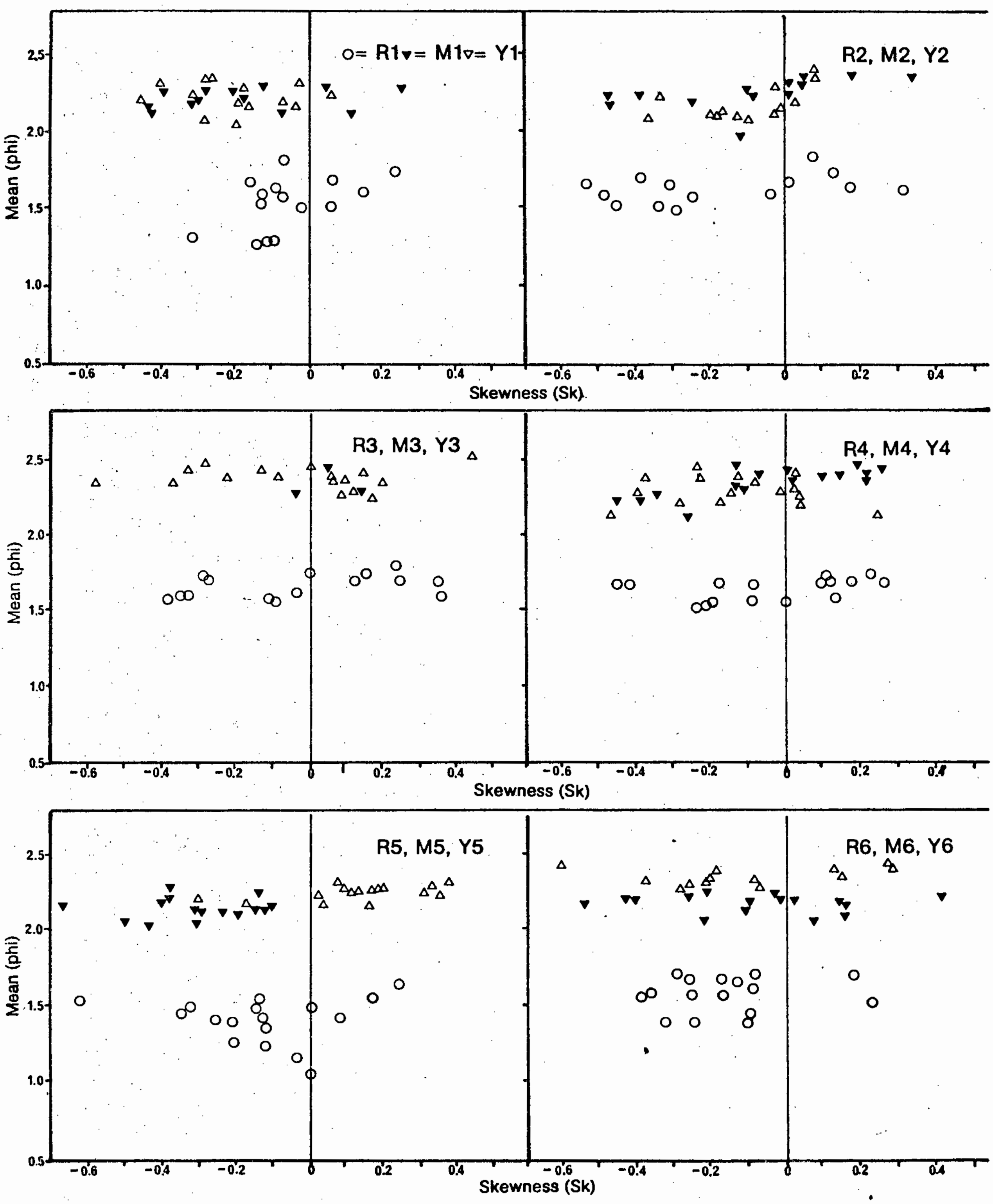


Figure 3.4 The relationships between the mean grain size of the sediments and the skewness of their distribution

separates the medium-sized Rocherpan grains from the finer Melkbosstrand and Ysterfontein sands, and occasionally also separates the sands from the latter two beaches (Fig. 3.4e, f). Skewness values usually do not separate the sands into their beaches of origin, and are therefore of no value for this purpose.

Plots of sorting against skewness (Fig. 3.5) show that in general the samples from Rocherpan are slightly more poorly sorted than those from the other two beaches. There is, nevertheless, considerable overlap between all three beaches and it is therefore not possible to use this method to determine the beach of origin of any single sample.

Plotting the differences between the 90th and 10th percentiles, 99th and 1st percentiles and last and first registers (i.e. coarsest and finest sand grains) against sorting all failed to resolve the sands into their beaches of origin. The above measures are essentially similar to sorting, but cover different spectra of grain size distribution.

In summary it can be said that of the parameters measured (percentage organic carbon, percentage calcium carbonate, deciles, median diameter, mean diameter, sorting, skewness, kurtosis, difference between 90th and 10th percentiles, difference between 99th and 1st percentiles and difference between coarsest and finest particles) only the first two were of any use in consistently distinguishing between sands from all three beaches.

Figure 3.6 shows the slopes of the three beaches. The beach at Rocherpan is distinctly the steepest one. The two finer beaches are less steep, the one at Melkbosstrand often being wider and with a gentler gradient that that at Ysterfontein. The profiles of all three beaches were usually concave with the exception of the Rocherpan beach which was occasionally convex between the high-water spring and high-water neap tide marks.

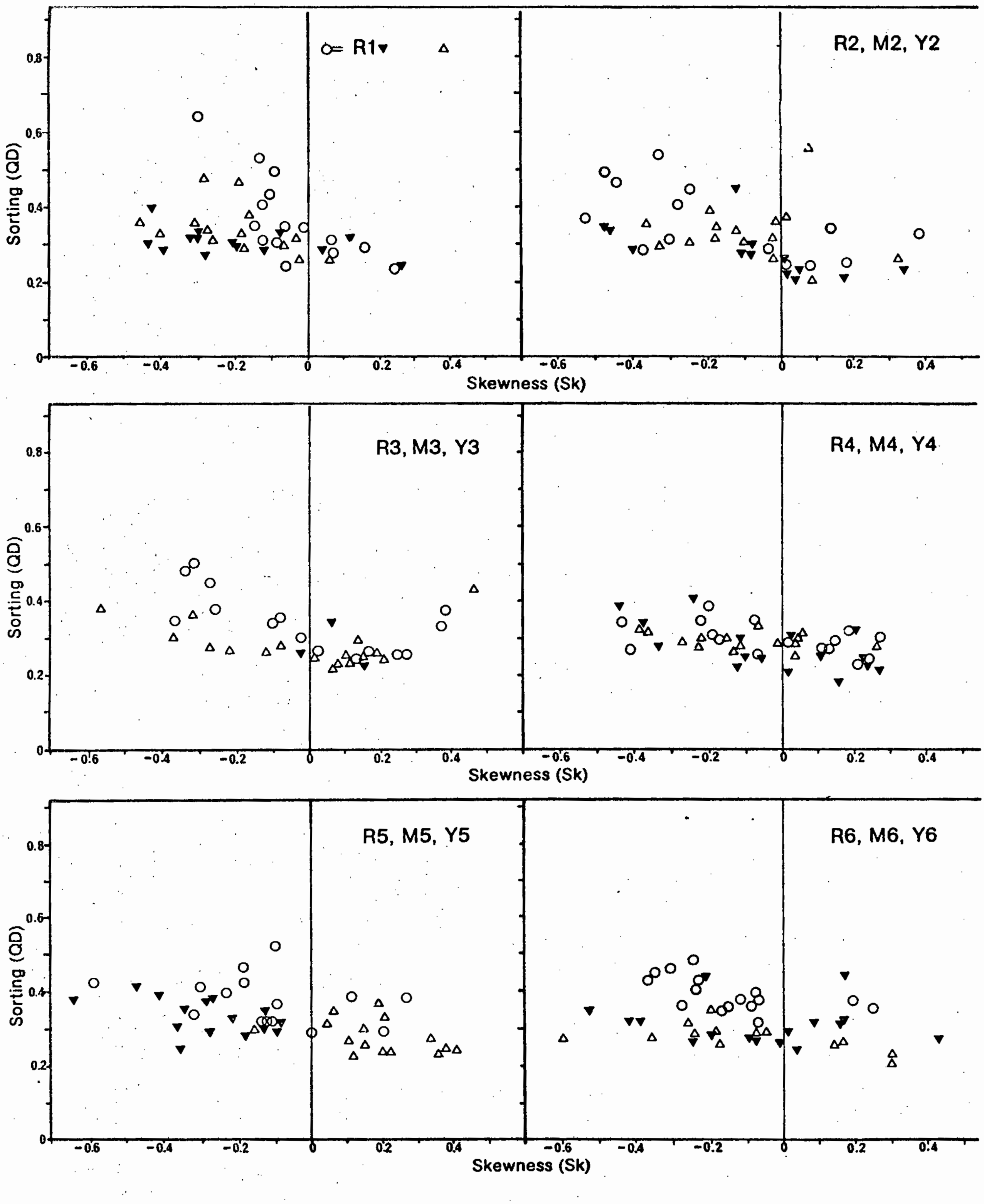


Figure 3.5 The relationship between the sorting and skewness of the sediments

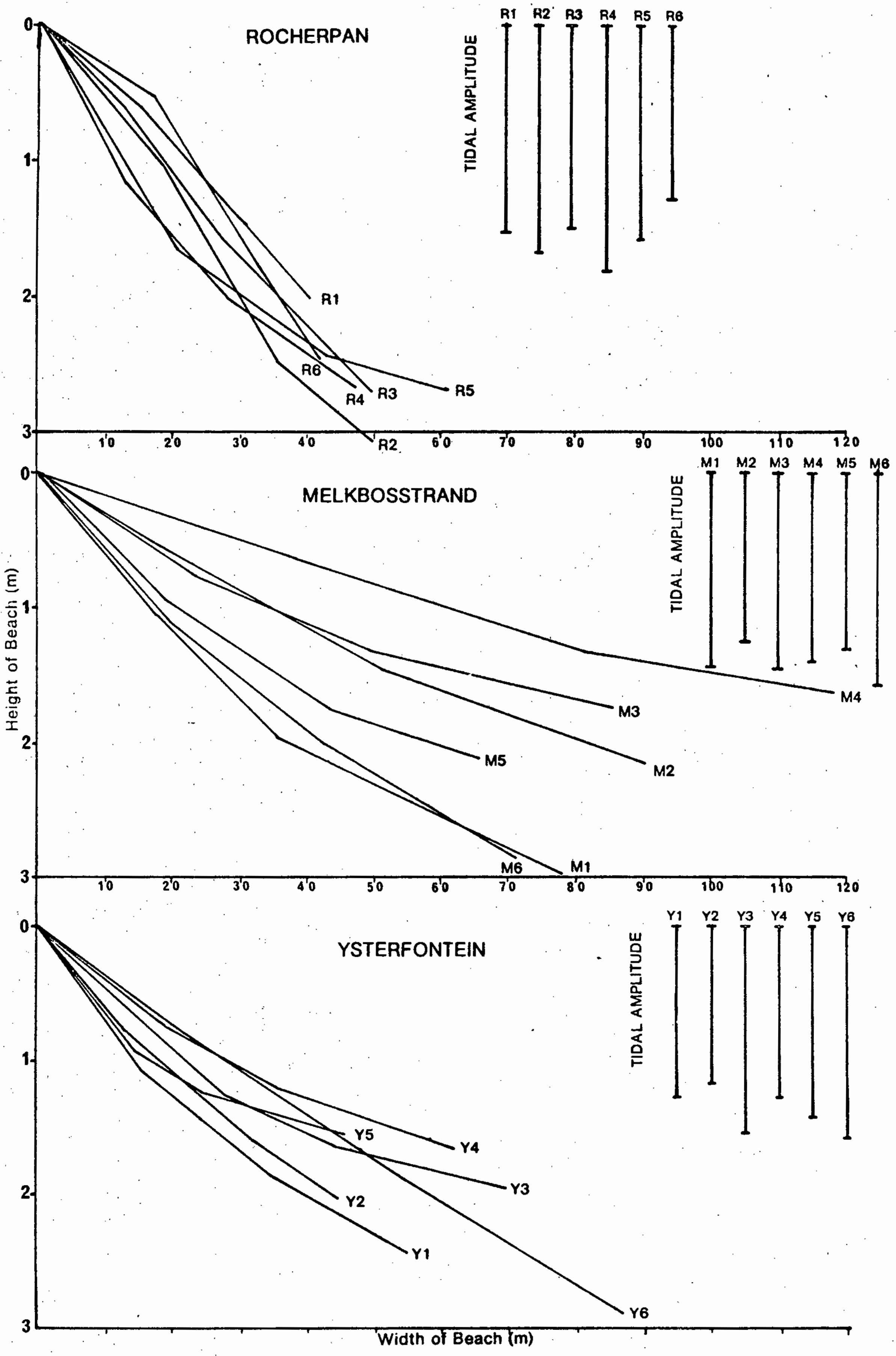


Figure 3.6 Some physical characteristics of the beaches studied. Symbols as in Figure 3.1

Distinguishing between sands within the beaches

Every sand sample possesses an unique combination of characteristics, so there is never any difficulty in distinguishing between individual samples. The purpose of this section is to determine whether sand collected from various intertidal zones differs in any consistent manner.

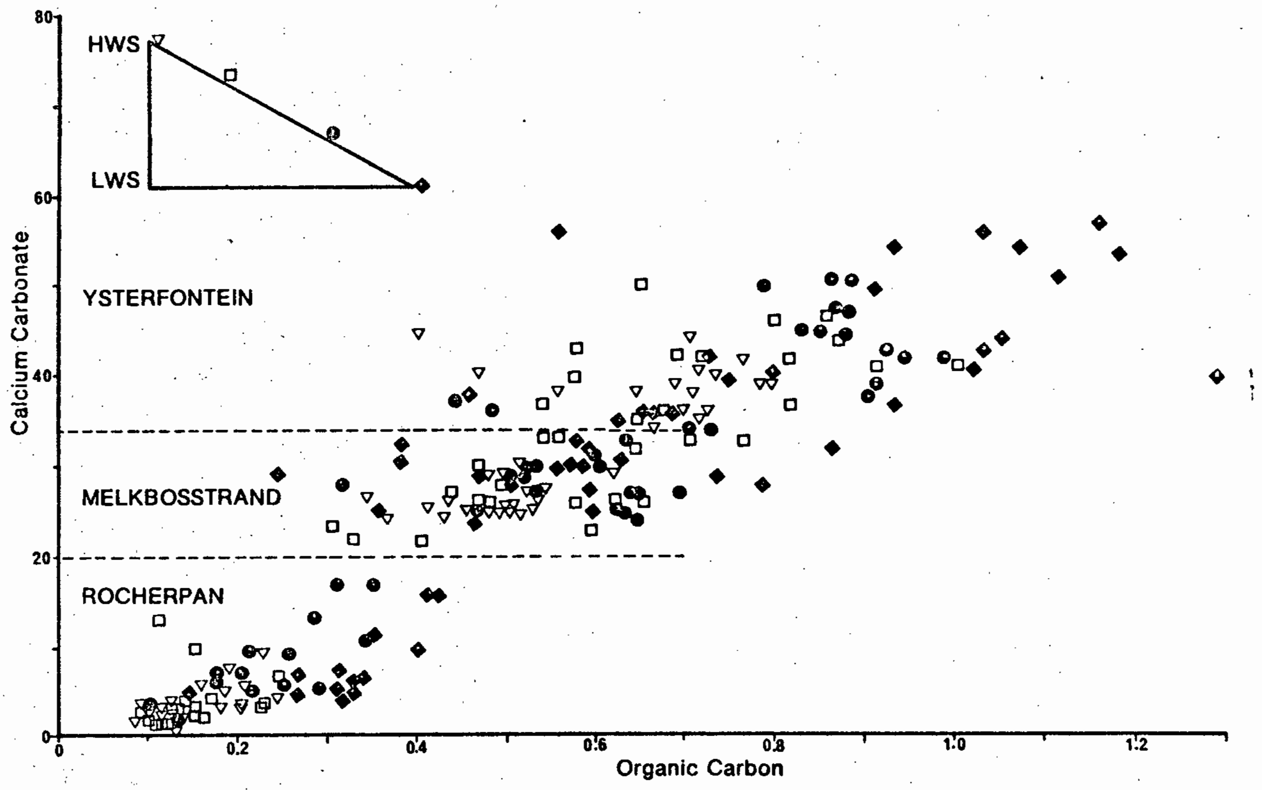
In order to determine this, the samples were again tested by plotting various combinations of parameters against each other, but this time the tidal level of origin was also noted.

Plotting the percentage organic carbon against percentage calcium carbonate shows that there is considerable overlap between sands from various intertidal levels (Fig. 3.7a). Nevertheless, a certain amount of segregation does occur, in that sands from lower tidal levels show both higher calcium carbonate and organic carbon levels than those from the upper intertidal (Fig. 3.7b).

A plot of mean grain size against skewness does not show any distinct trends for sands from different tidal levels. But if samples are sorted into their beaches of origin as well, it can be seen that in general sand samples from the upper beach are more positively skewed than those from the lower tidal levels. This agrees with the findings of Mason and Folk (1958) and Shepard and Young (1961), but the differences are too slight to permit reliable differentiation (Fig. 3.8). The mean grain size also does not vary consistently or markedly with tidal level (Fig. 3.8b) although it can be seen from this figure that the sands from Ysterfontein are slightly finer than those from Melkbosstrand.

The median grain size does not vary consistently with tidal level either, but in plots of median grain size against sorting (Fig. 3.9) and sorting against skewness (Fig. 3.10), the sorting of sediments from

3.7a



3.7b

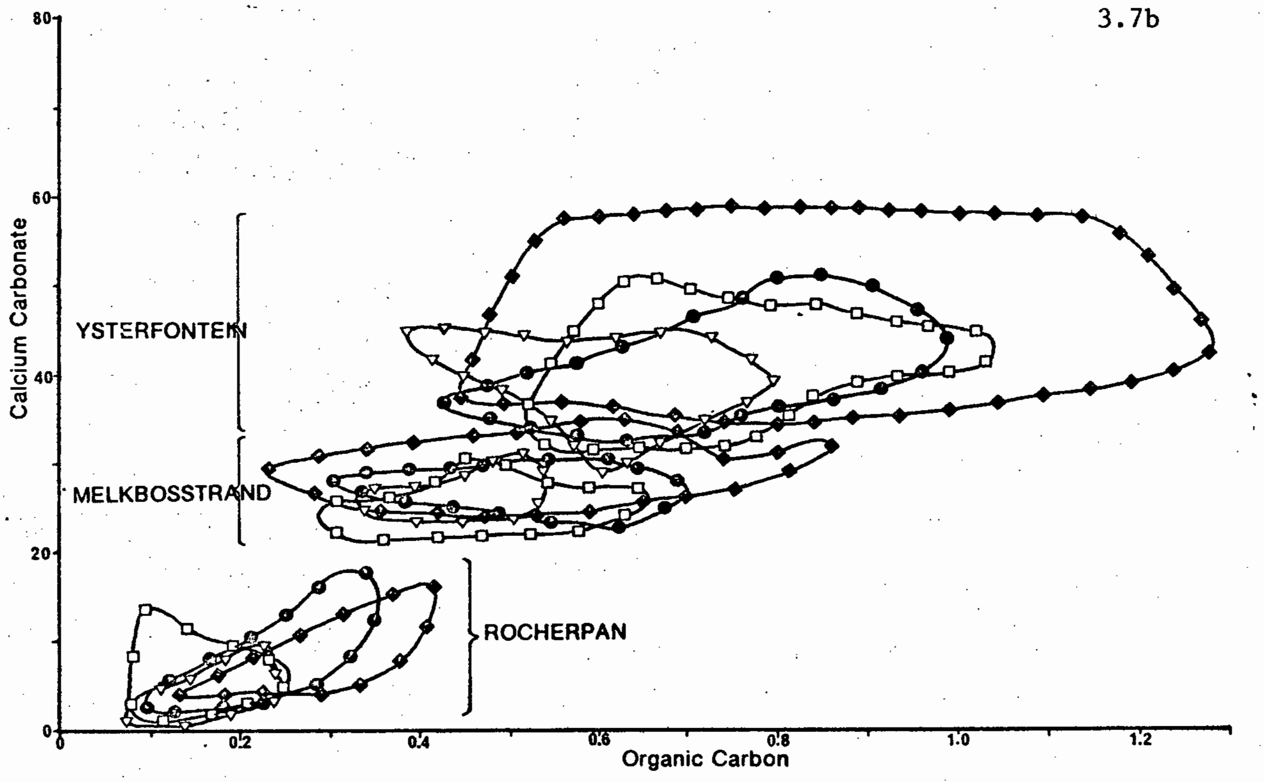
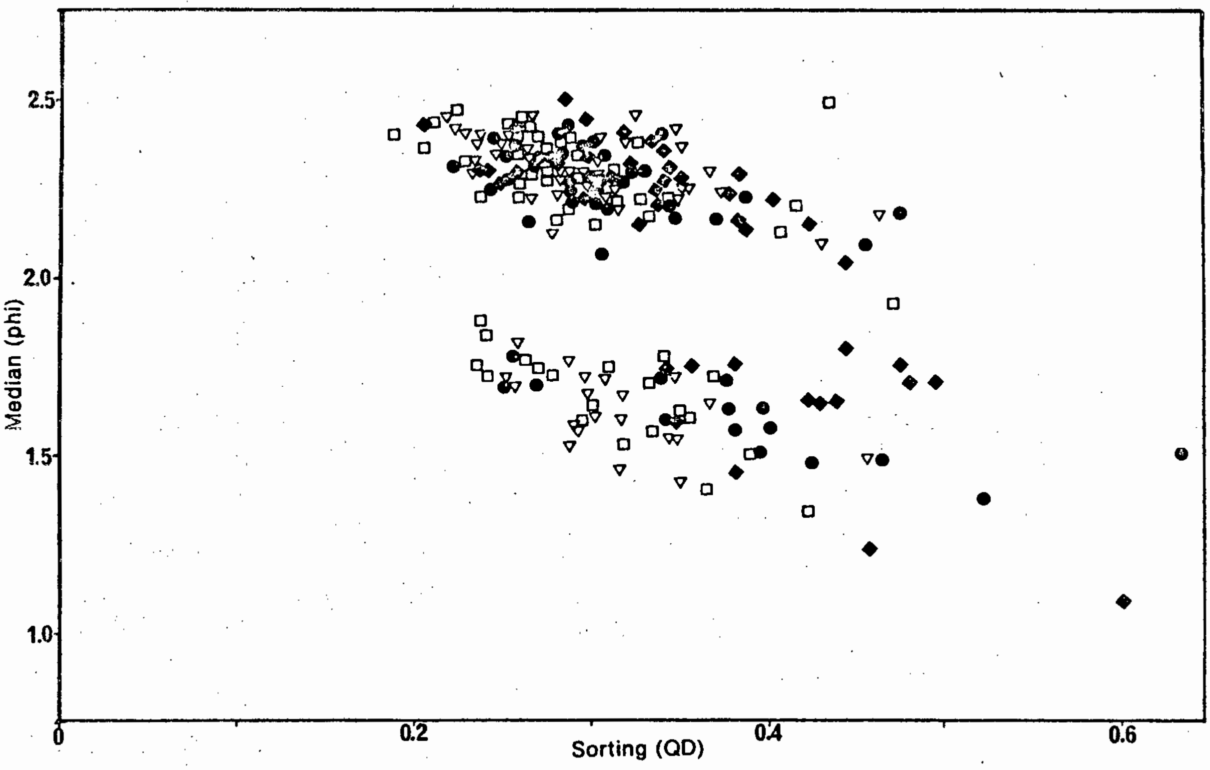


Figure 3.7 Showing the intertidal and between beach distributions of calcium carbonate and organic carbon percentages in sediments from the three beaches

3.8a



3.8b

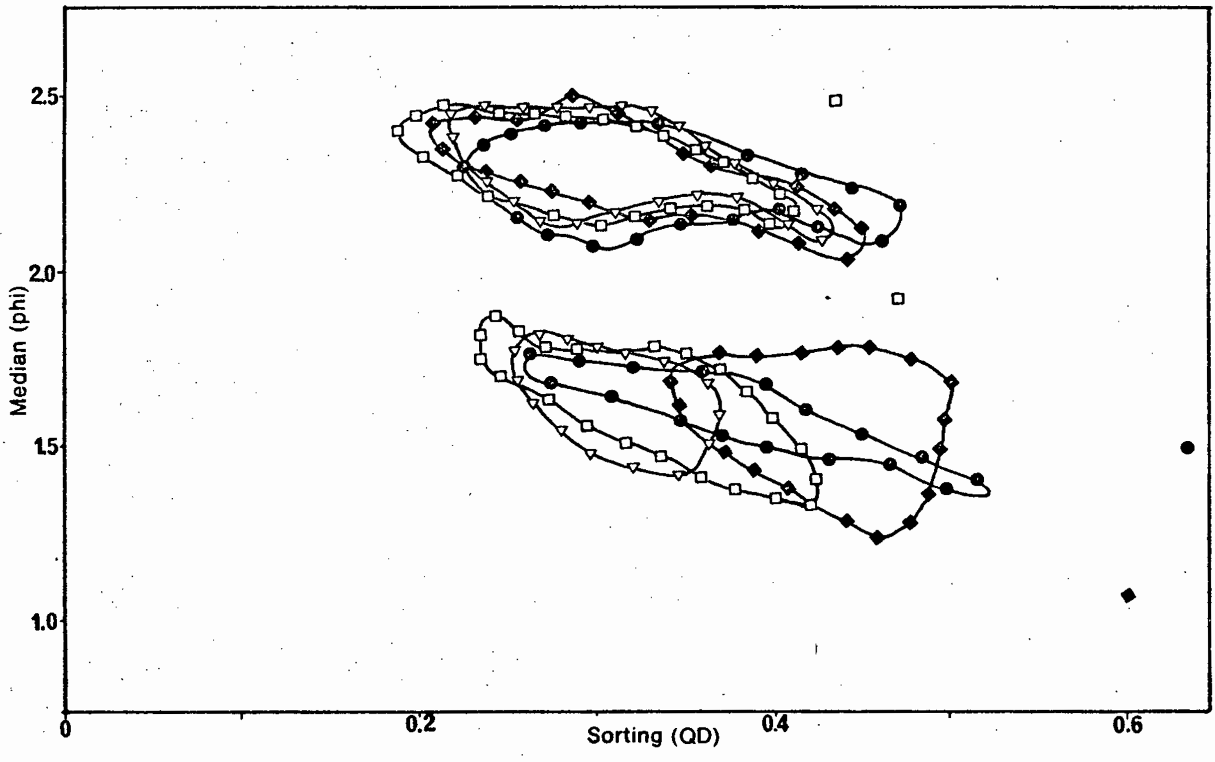


Figure 3.8 The relationship between median grain size and sorting on all three beaches. The lower cluster consists of samples from Rocherpan. The symbols show the zones of origin as in Fig. 3.7

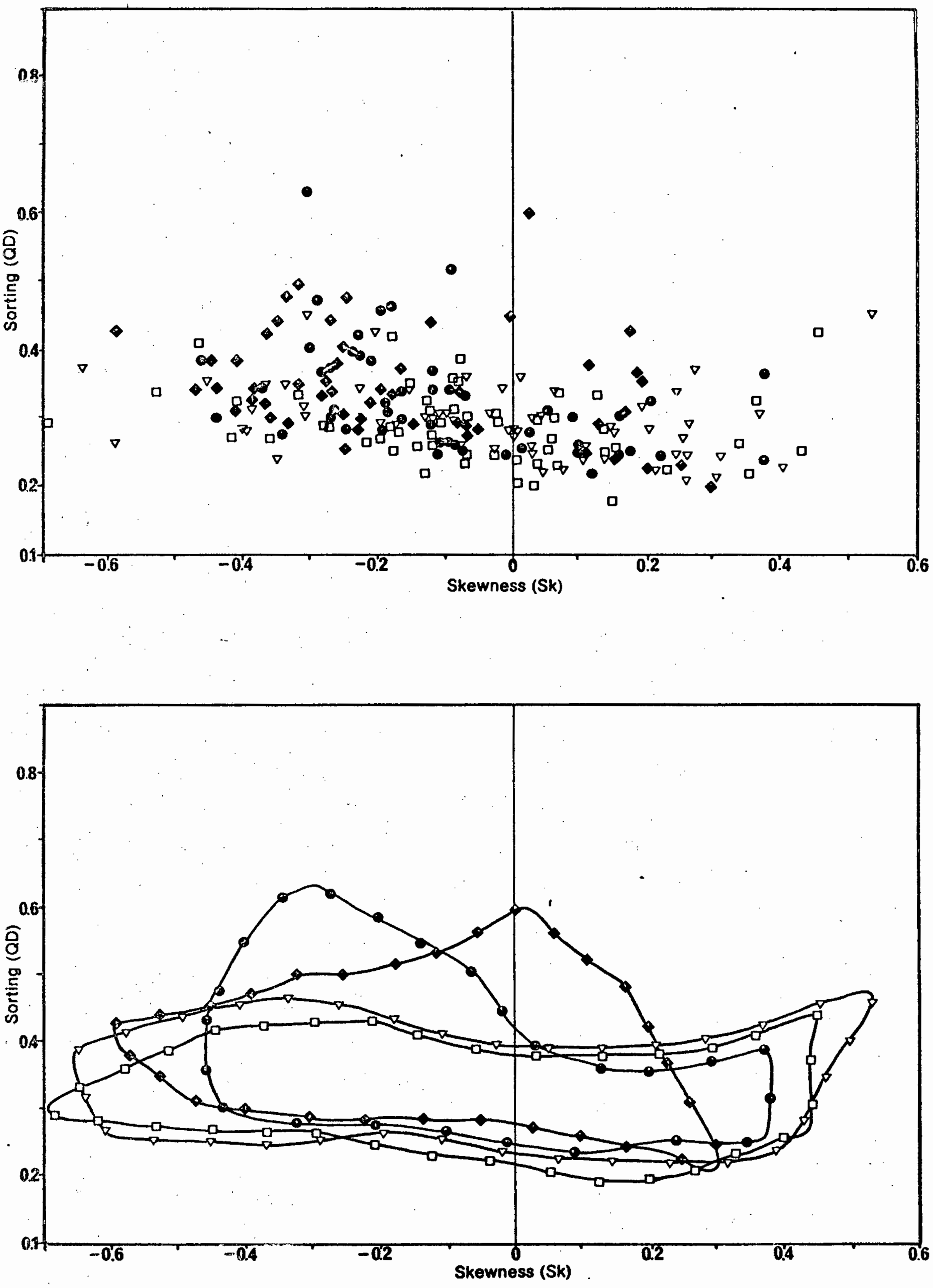


Figure 3.10 Plots of skewness against sorting on the three beaches. Symbols as in Fig. 3.7

the lower tidal zones is shown to be poorer. Finally, sands from the high-water mark show the widest range of kurtosis values, and this range decreases down towards the low-water mark (Fig. 3.11).

Seasonal variations

Table 3.3 shows the results of seasonal variations in the measured parameters for the whole beach. All of these, with the exception of the median grain size, are plotted in Figures 3.12 - 3.17. Slight seasonal trends can be detected and these will be discussed later.

Figures 3.18 to 3.24 show these seasonal variations broken down to include tidal levels of origin. Figure 3.18 shows that there is a consistent seasonal variation in the median sand grain size, as also occurs with the mean grain size (Fig. 3.19). In both cases there is a distinct coarsening of the beach in winter. The seasonal plots of sorting (Fig. 3.20) again show that usually sands from the lower intertidal are less well sorted than those from the upper intertidal. The sorting value tends to increase in winter. The skewness plots (Fig. 3.21) also show that sands from the lower intertidal tend to be more negatively skewed than those from the top of the beach. The seasonal variations in skewness are considerable, however, and do not vary consistently.

Kurtosis values (Fig. 3.22) for the three beaches also vary considerably. There does not seem to be any definite pattern to the seasonal variations of this parameter. The plots for percentage organic carbon and percentage calcium carbonate again reflect each other closely (Figs. 3.23 and 3.24 respectively). Again, samples from the lower beach are shown to have higher proportions of both organic carbon and calcium carbonate, almost throughout the year.

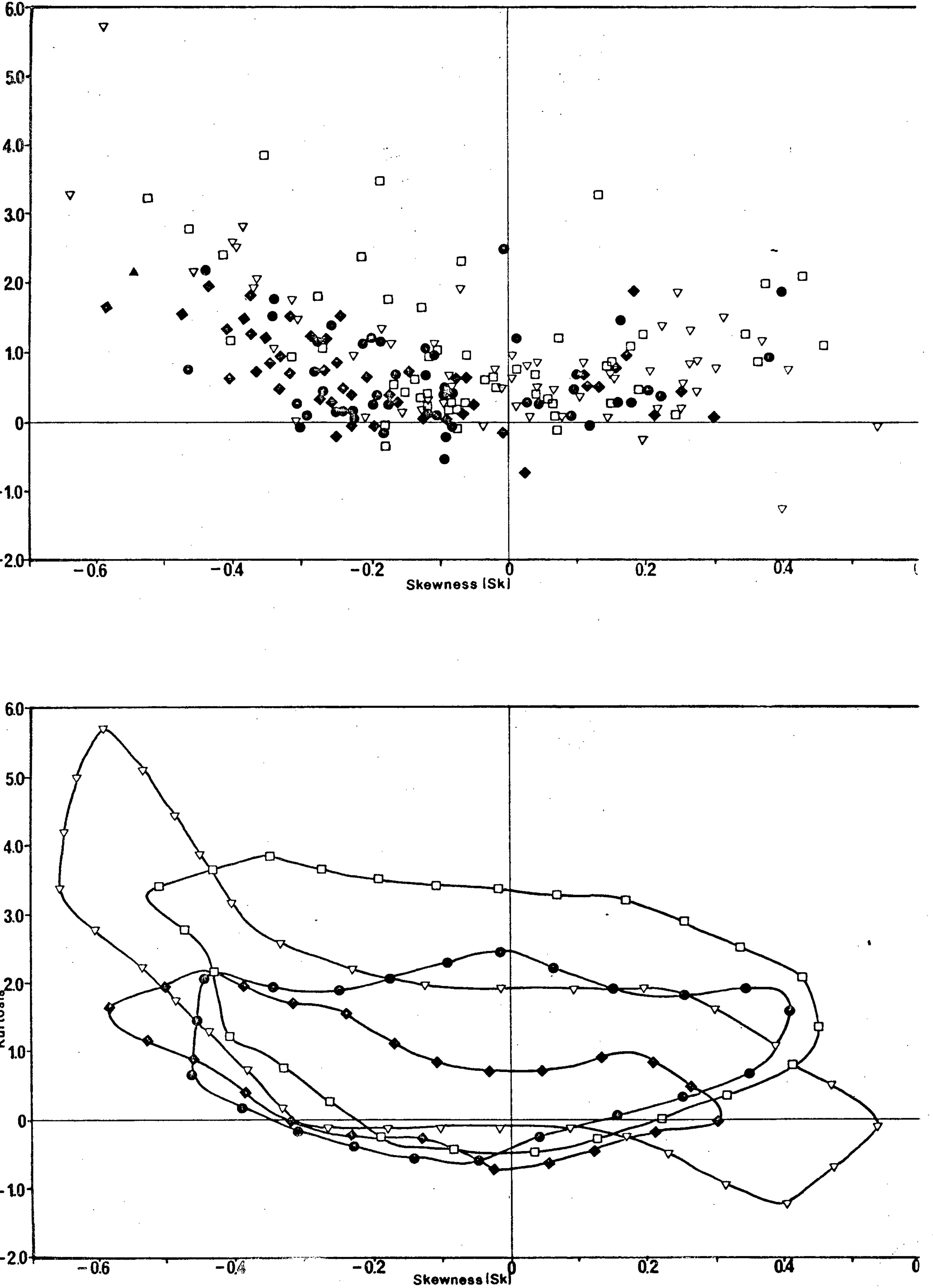


Figure 3.11 Plots of kurtosis against skewness - all samples.

TABLE 3.3 Seasonal variations in measured parameters for whole beaches

	Median		Mean		Sorting		Skewness		Kurtosis		% Organics		% $CaCO_3$	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
R1	1,58	0,14	1,56	0,17	0,37	0,11	-0,05	0,13	0,13	0,41	0,20	0,13	8,40	7,81
R2	1,74	0,14	1,73	0,20	0,37	0,10	-0,07	0,37	1,14	0,97	0,20	0,08	4,85	4,16
R3	1,69	0,07	1,68	0,08	0,34	0,08	-0,01	0,26	0,76	0,74	0,20	0,09	4,23	2,47
R4	1,65	0.07	1,66	0,07	0,30	0,04	-0,03	0,23	0,82	0,68	0,14	0,03	3,25	1,23
R5	1,45	0,14	1,42	0,15	0,39	0,09	-0,12	0,19	0,27	0,64	0,29	0,19	10,17	8,65
R6	1,61	0,11	1,59	0,12	0,39	0,05	-0,14	0,17	0,64	0,60	0,23	0,09	6,88	2,92
M1	2,25	0,05	2,24	0,06	0,31	0,04	-0,24	0,29	1,71	1,55	0,45	0,06	27,07	2,26
M2	2,30	0,09	2,31	0,10	0,28	0,06	-0,16	0,33	1,30	2,24	0,52	0,07	28,05	3,83
M3	2,34	0,07	2,35	0,08	0,28	0,06	0,07	0,08	0,37	0,19	0,55	0,09	24,23	1,21
M4	2,37	0,07	2,37	0,10	0,28	0,06	-0,03	0,24	0,97	0,76	0,52	0,12	26,24	3,11
M5	2,20	0,06	2,17	0,07	0,34	0,05	-0,31	0,20	1,26	1,34	0,50	0,07	28,65	1,89
M6	2,20	0,07	2,20	0,06	0,30	0,06	-0,07	0,25	1,42	1,17	0,57	0,14	27,77	2,10
Y1	2,26	0,09	2,25	0,09	0,34	0,06	-0,20	0,15	0,72	0,70	0,80	0,27	42,50	9,70
Y2	2,26	0,09	2,27	0,11	0,33	0,08	-0,13	0,28	1,01	2,07	0,77	0,13	37,04	3,61
Y3	2,40	0,05	2,41	0,06	0,29	0,06	-0,-2	0,26	1,11	1,05	0,81	0,18	42,25	3,55
Y4	2,31	0,09	2,29	0,09	0,31	0,06	-0,17	0,24	0,78	0,91	0,84	0,20	41,74	5,33
Y5	2,27	0,04	2,28	0,05	0,28	0,05	0,16	0,18	0,57	0,40	0,61	0,10	35,86	3,01
Y6	2,38	0,05	2,41	0,17	0,32	0,18	-0,15	0,36	1,73	2,52	0,79	0,15	47,19	5,72

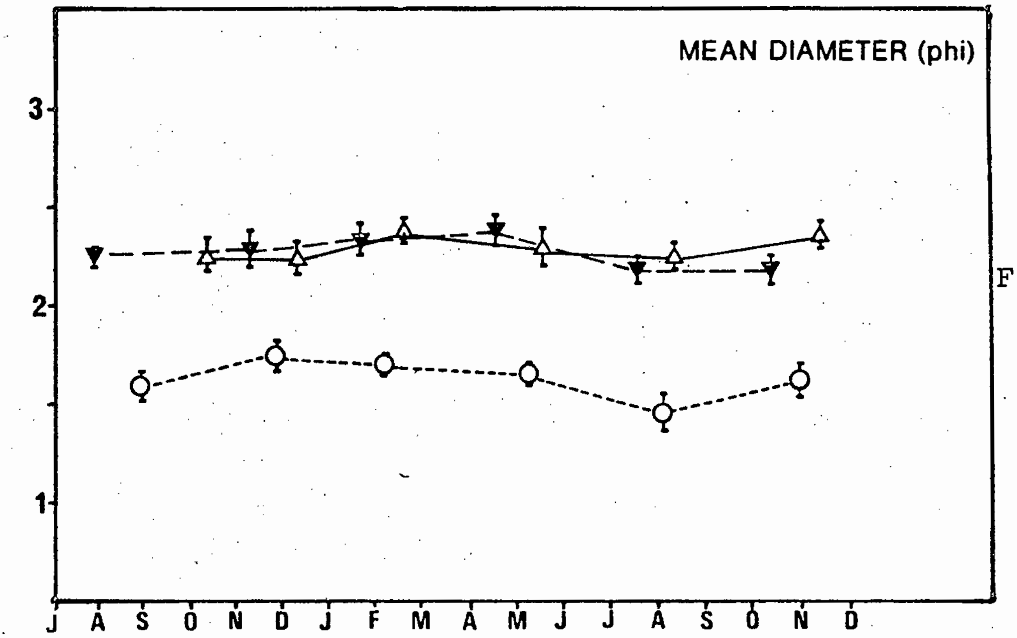


Figure 3.12

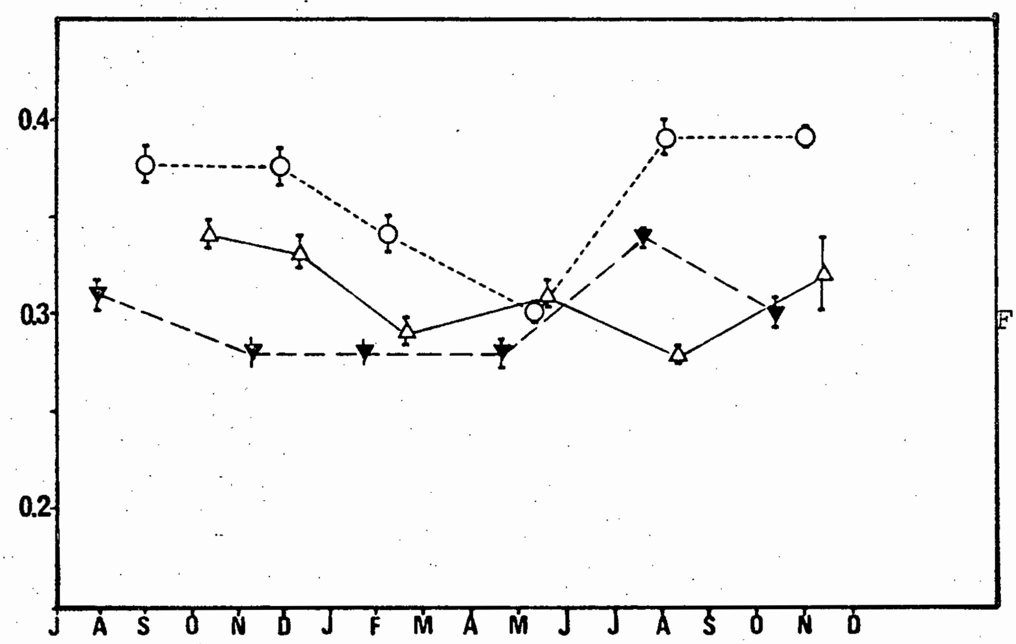


Figure 3.13

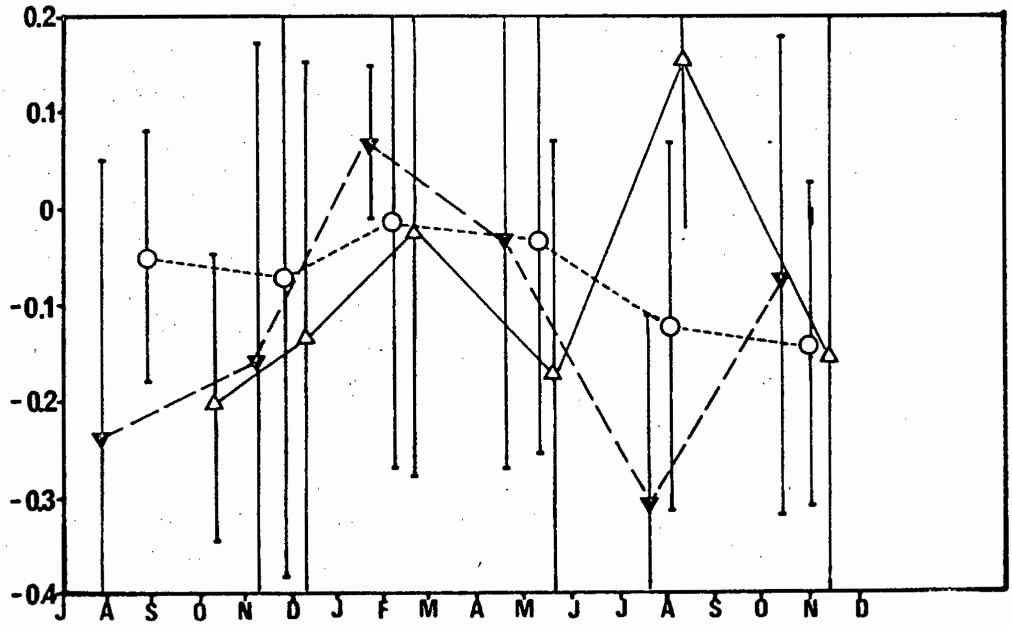


Figure 3.14

Figures 3.12-3.17. Seasonal fluctuations in sedimentary characters.

○= Rocherpan △Ysterfontein ▼Melkbosstrand

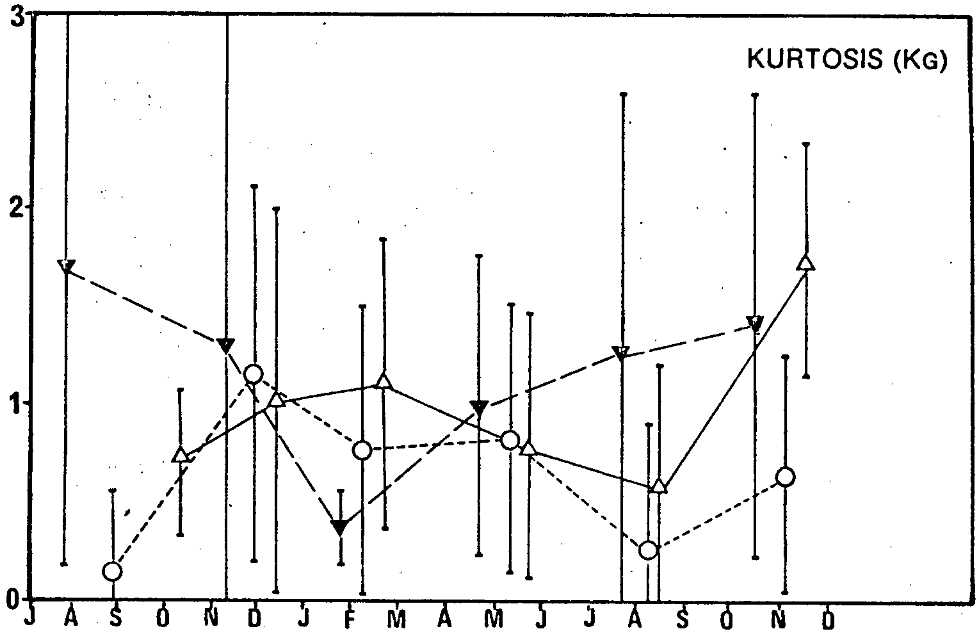


Figure 3.15

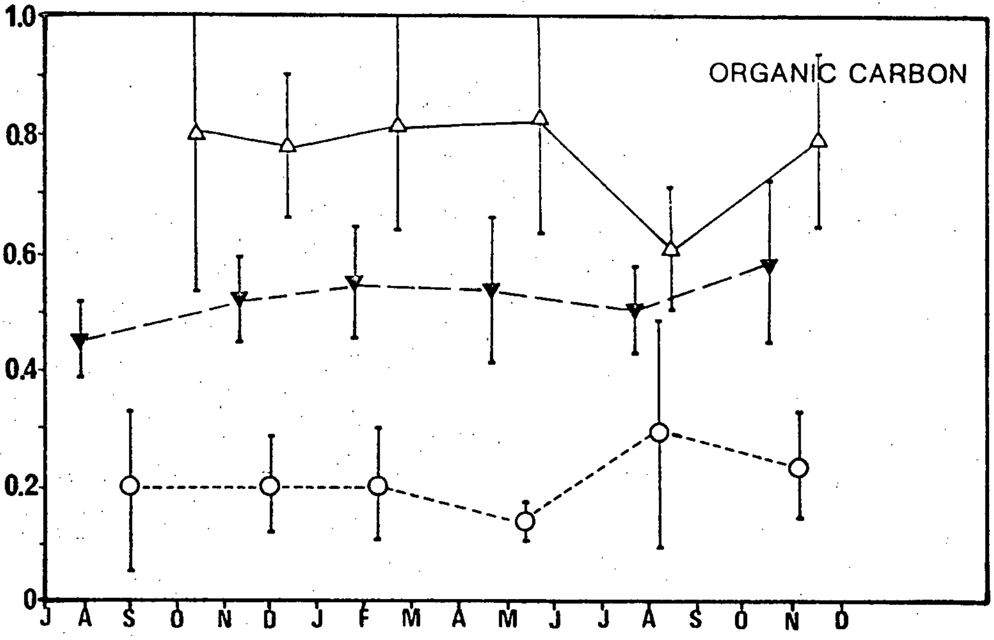


Figure 3.16

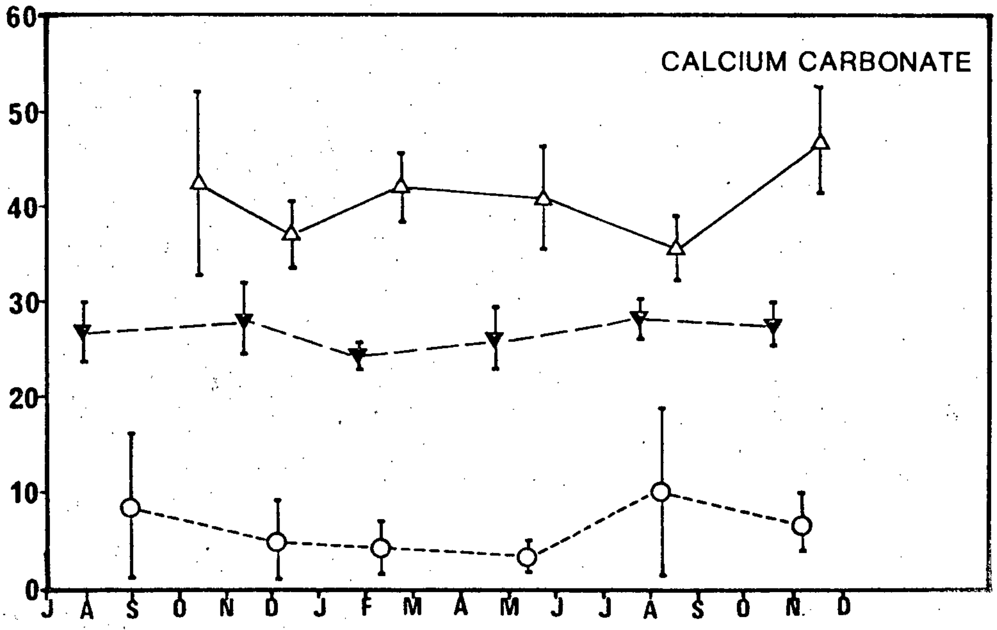


Figure 3.17

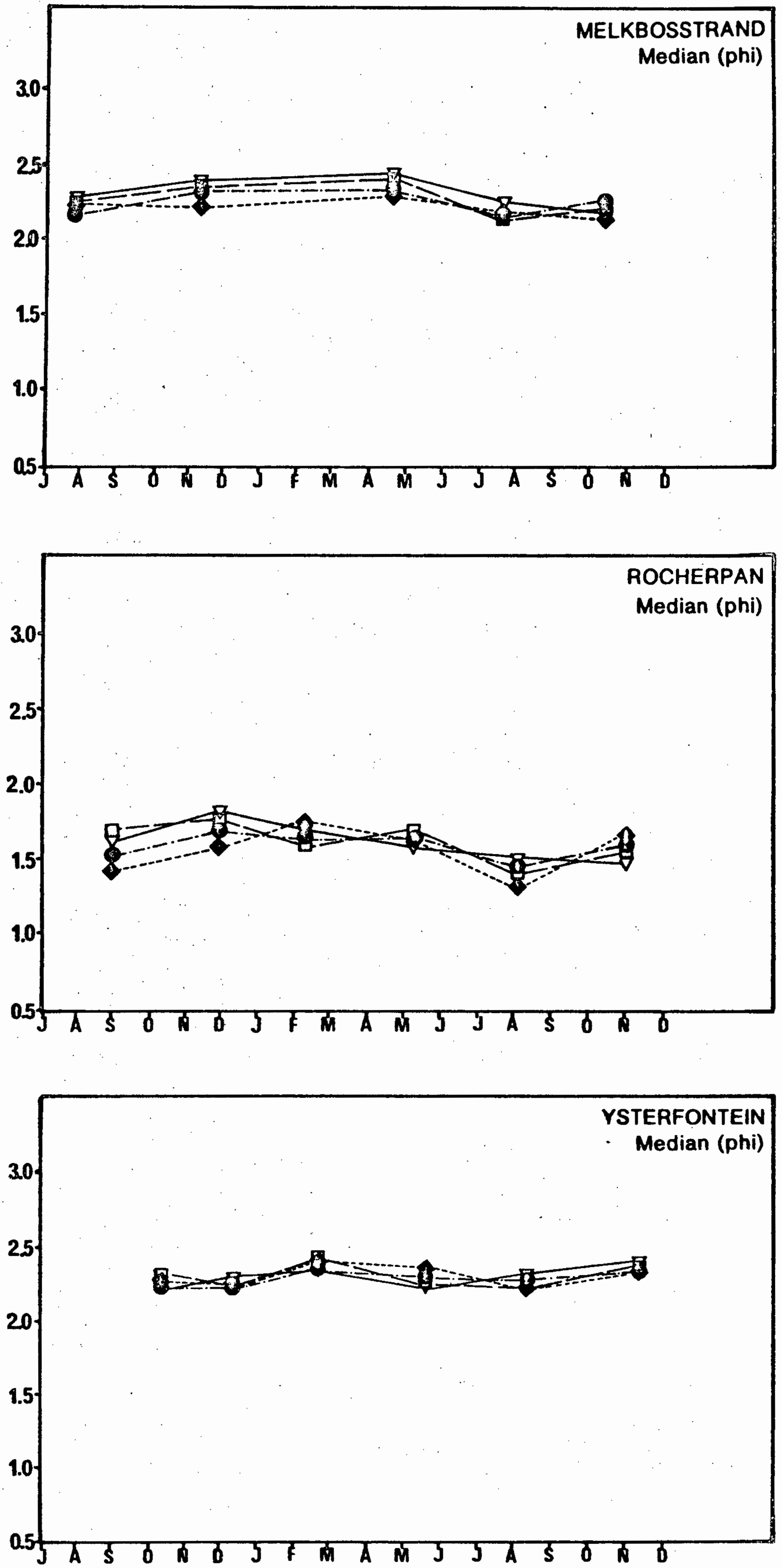


Figure 3.18 Seasonal fluctuations in median grain size. Symbols as in Fig. 3.7.

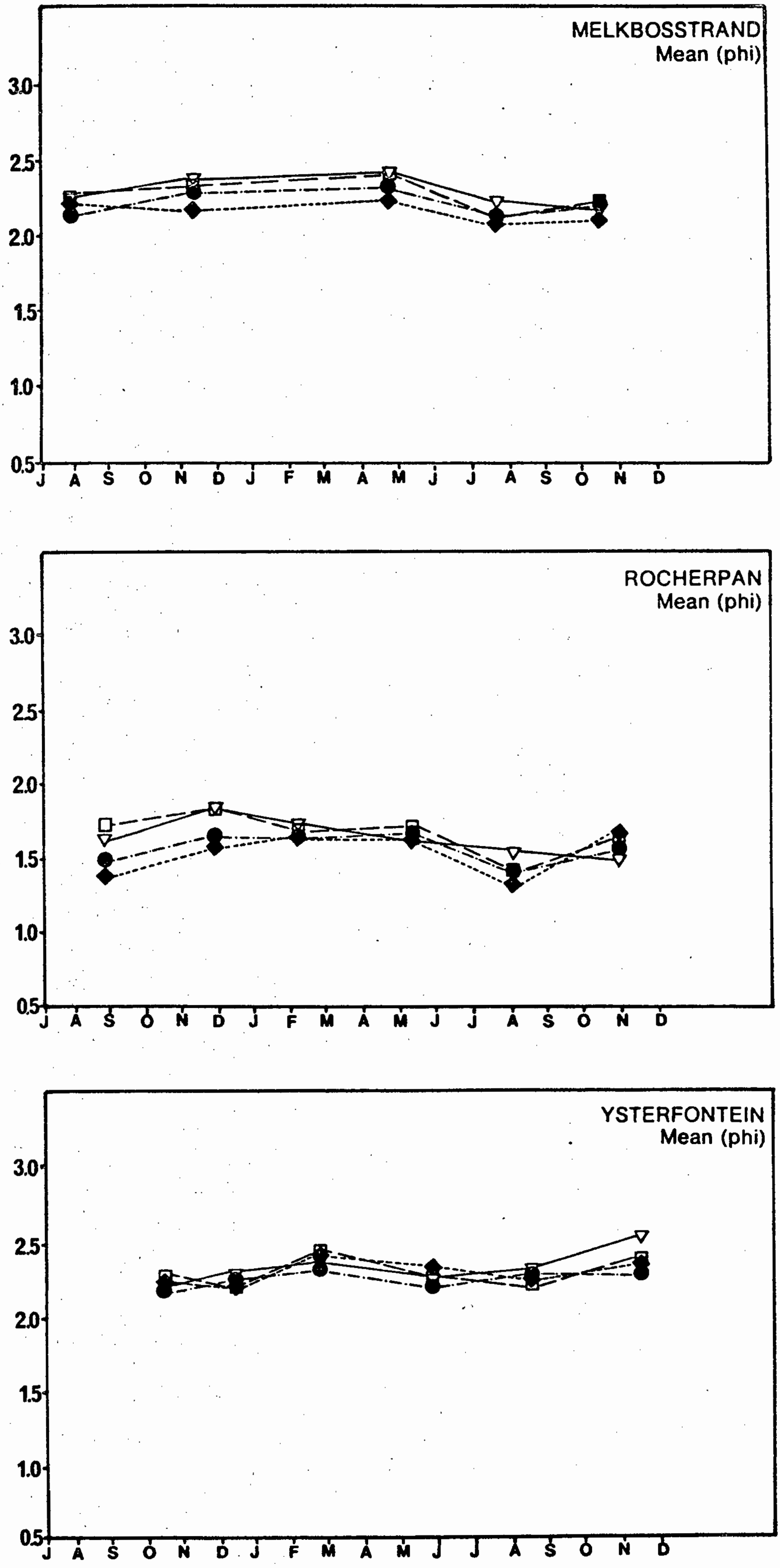


Figure 3.19 Seasonal fluctuations in mean grain size.

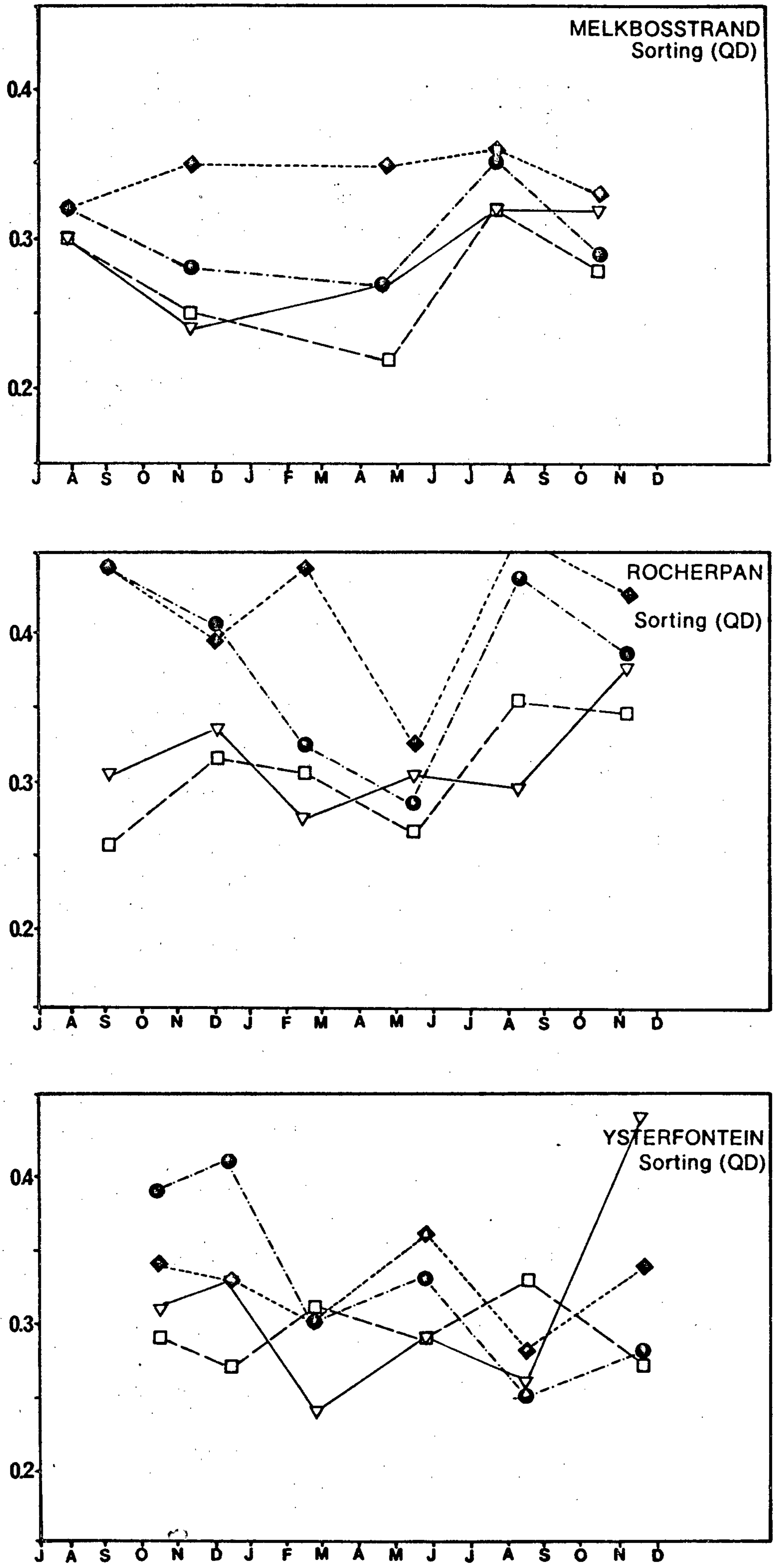
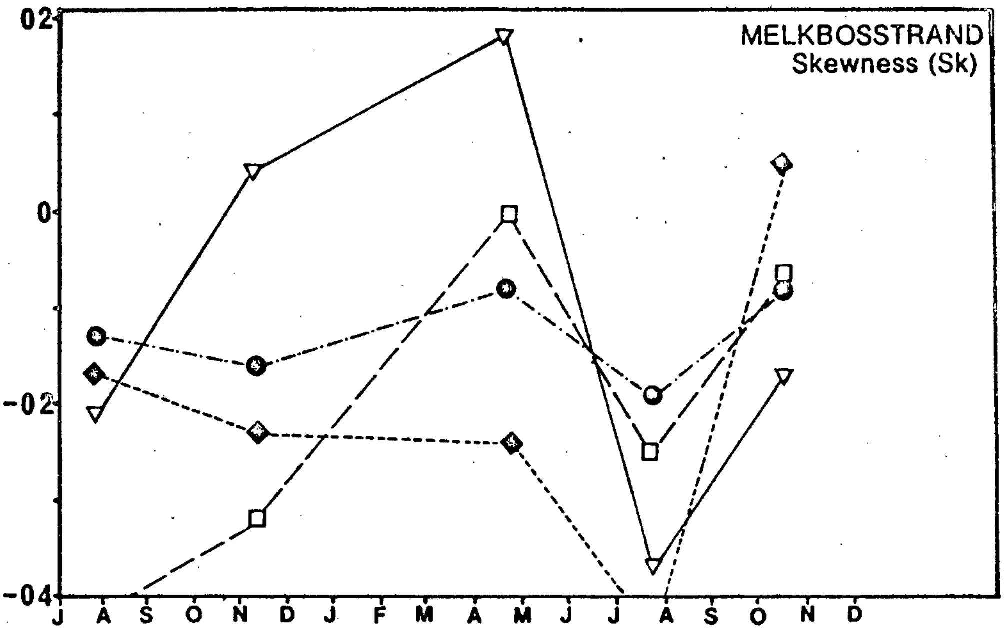
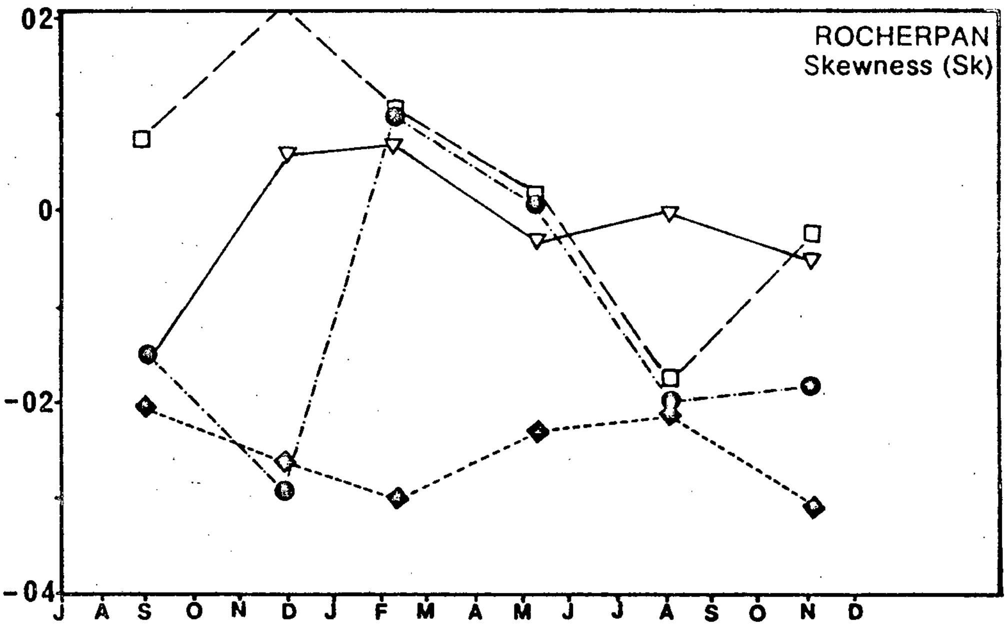


Figure 3.20 Seasonal fluctuations in sorting values.





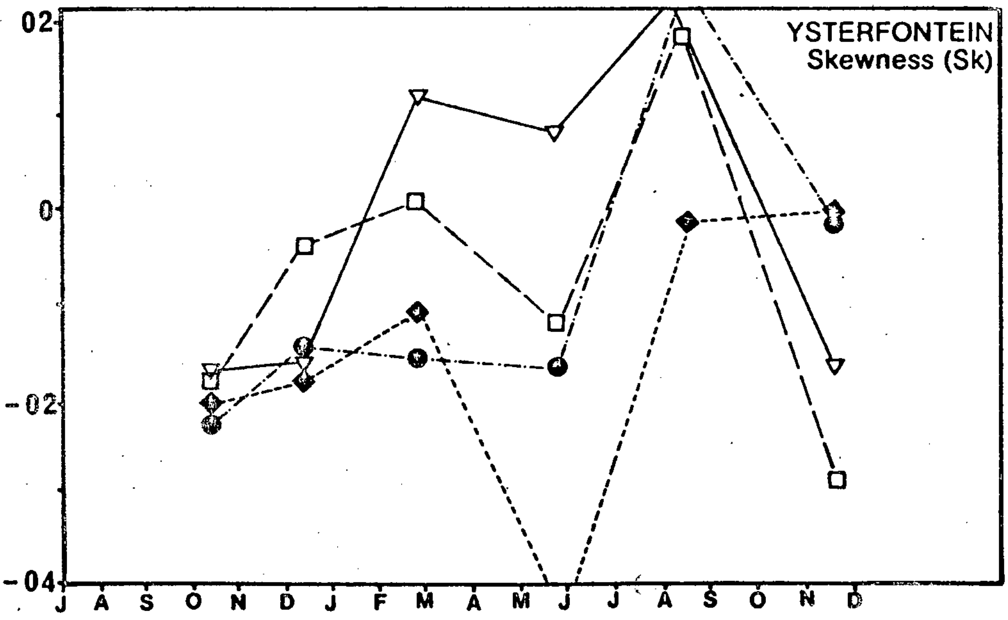


Figure 3.21 Seasonol fluctuations in skewness values.

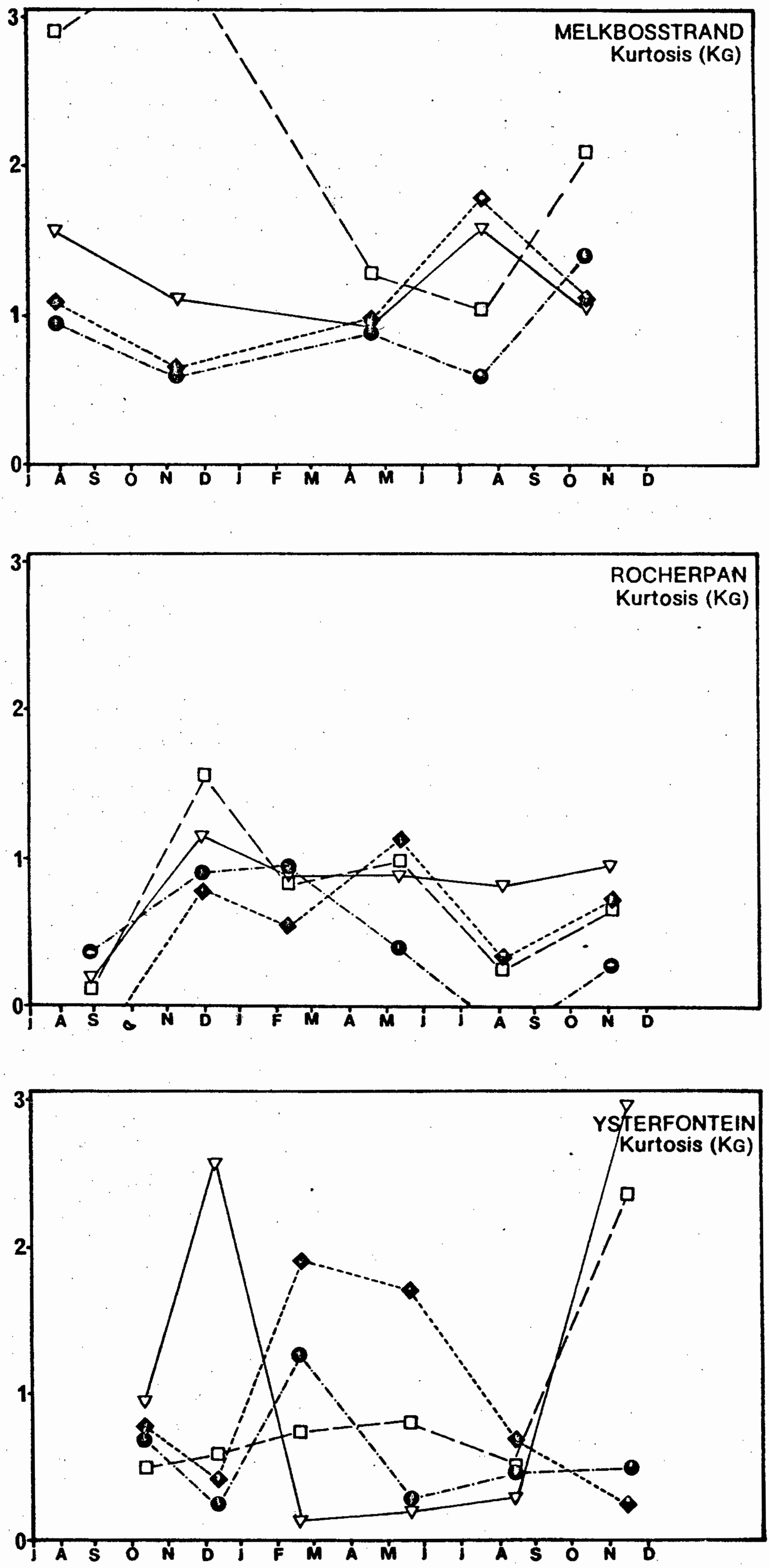


Figure 3.22 Seasonal fluctuations in kurtosis values.

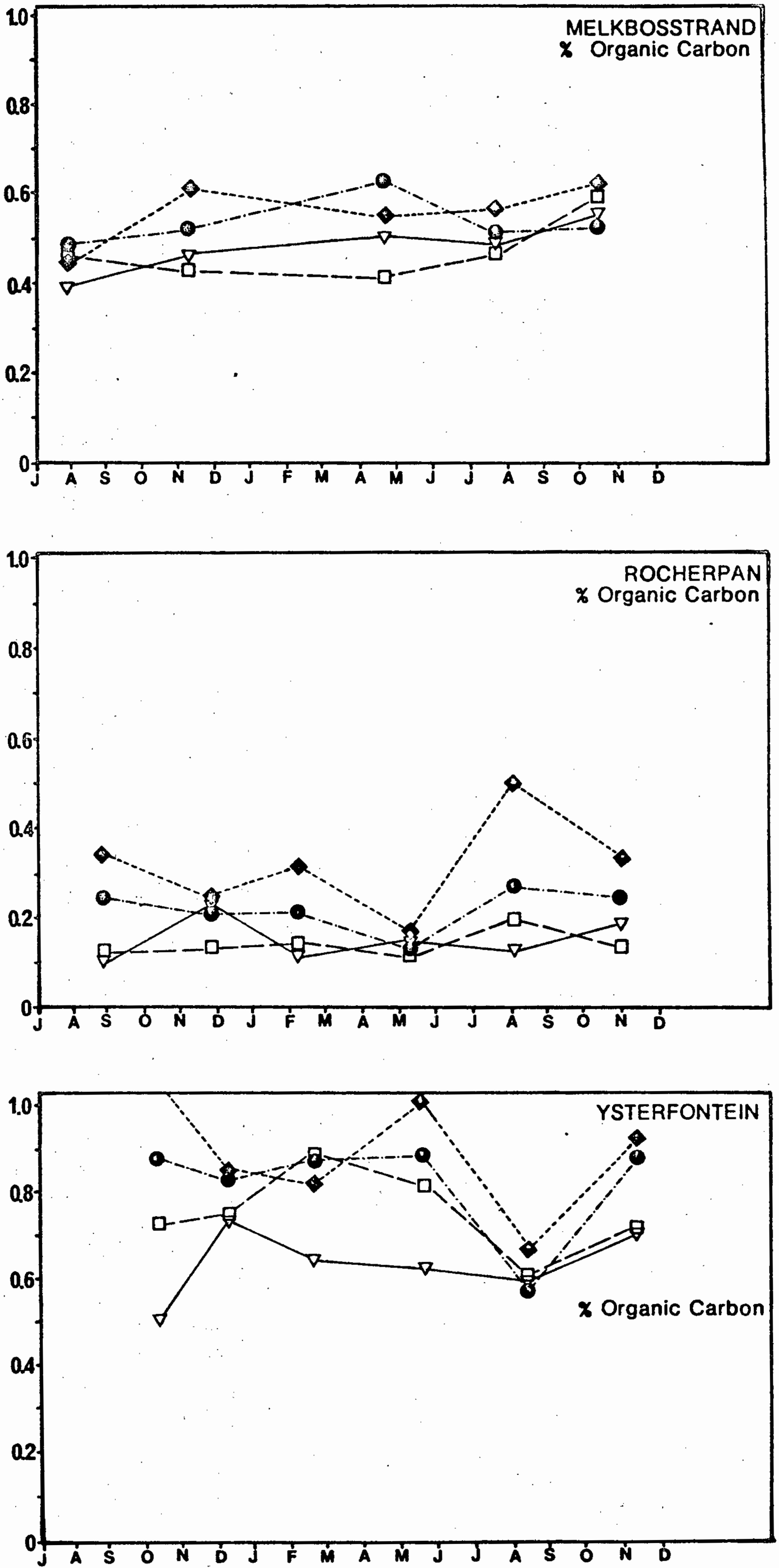


Figure 3.23 Seasonal fluctuations in percent organic carbon.

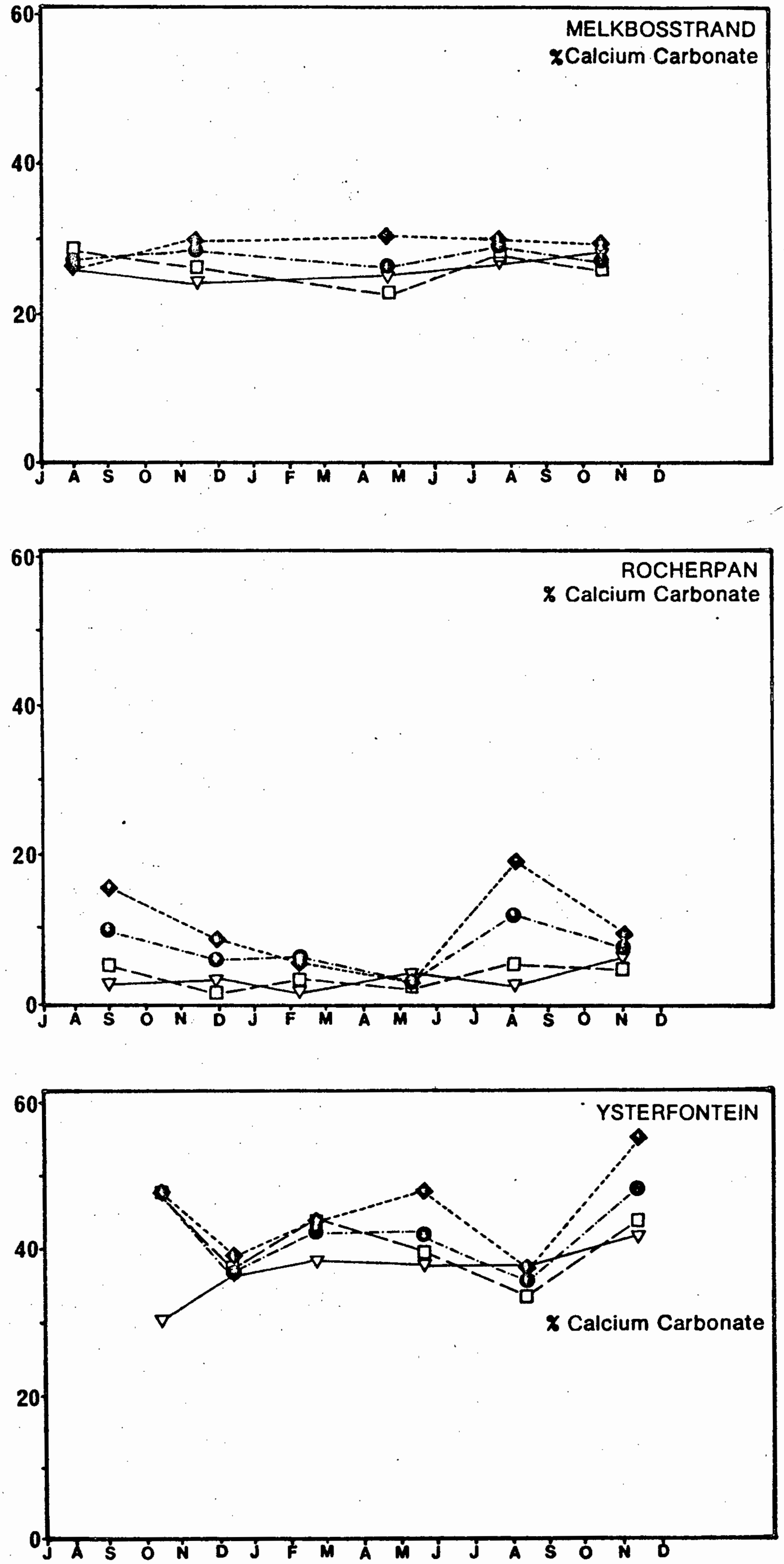


Figure 3.24 Seasonal fluctuations in percent calcium carbonate.

The results of regression analyses between various characteristics are listed in Table 3.4.

TABLE 3.4 Regression analyses between various related parameters

Parameters compared		Regression	Slope
x	y	r^2	$y = a_o + a_1 x$
% Organic C	% $CaCO_3$	0,9951	$y = -6,79 + 63,49x$
% Organic C	Mean diameter	0,8463	$y = 1,405 + 1,30x$
% Organic C	Median diameter	0,7347	$7= -0,97 + 3,76x$
% $CaCO_3$	Mean diameter	0,8933	$y = 1,53 + 0,02x$
% $CaCO_3$	Median diameter	0,8772	$y = 1,55 + 0,02x$
Sorting	Mean diameter	0,9989	$y = 5,57 + -11,269x$
Sorting	Median diameter	0,9999	$y = 0,51 + -0,09x$

Man-made sediments

Since a fairly large number of plastic pellets or beads are found on the beach occasionally, especially near the drift-line, it was decided to identify these using the flame and smell tests of Carpenter (1976). The results of these tests showed 96,8% of the pellets by weight were of high density polythene, 1,7% of cellulose acetate and 1,5% of polypropylene.

On no occasion during the sampling period were concentrations of the extent described by Gregory (1977) for New Zealand beaches encountered, other than his value for Ninety Mile beach. The only glass material found, consisted of well abraded pieces measuring up to 25 mm in diameter. Fortunately, west coast beaches are generally free of tar balls (Orren and Eagle, 1979). Thus, the only man-made contributions to the sedimentology of west coast beaches are happily of an inert and harmless nature and in sufficiently small quantities to be of no ecological significance.

Discussion

The sands of the three beaches can be differentiated on the basis of a number of parameters, although these differences are not all immediately obvious. After separating the sands visually into medium and fine sand categories, they can be separated further into medium sands with an overall mean grain size of 1,60 phi for Rocherpan and fine sands of overall mean grain sizes of 2,25 phi for Melkbosstrand and 2,31 phi for Ysterfontein. The latter two values are so close together, however, that it is not possible to determine which beach a sand sample came from on the basis of mean grain size or diameter alone. Overall median grain size for Rocherpan was 1,61 phi, for Melkbosstrand 2,27 phi and 2,31 phi for Ysterfontein. Again, the median grain size values for Melkbosstrand and Ysterfontein are too similar to be distinctive.

The sorting values for the three beaches tended to be similar with an overall mean value of 0,362σ for Rocherpan which was more poorly sorted than Melkbosstrand and Ysterfontein (0,303σ and 0,300σ respectively). Sands from Melkbosstrand tend to be more negatively skewed (mean skewness -0,130) than those from Rocherpan (-0,103) and Ysterfontein (-0,048).

The distribution curves of sand samples from Rocherpan and Ysterfontein were platykurtic (K_G = 0,65 and 0,68 respectively), while those of Melkbosstrand were more leptokurtic (K_G = 1,15).

The percentage of calcium carbonate in the sand differs markedly in the three beaches. At Rocherpan the overall mean percentage was 6,175%, at Melkbosstrand 27,218% and at Ysterfontein 41,330%. Finally, overall mean percentages of organic carbon in the sand were 0,213% at Rocherpan, 0,513% at Melkbosstrand and 0,770% at Ysterfontein.

TABLE 3.5 Mean values for organic percentage of calcium carbonate in the three beaches.

Beach	% Organic C	% $CaCO_3$	Organic % of $CaCO_3$	Mean grain size
Rocherpan	0,213	6,075	3,514	1,60 phi
Melkbosstrand	0,513	27,218	1,895	2,25 phi
Ysterfontein	0,770	41,330	1,877	2,31 phi

As mentioned before, there is a linear relationship between these last two parameters. There are two possible reasons for this. Since the sands with higher proportions of calcium carbonate also tend to have a smaller mean grain size (see Table 3.5), it could follow that they simply support greater numbers of bacteria and other microorganisms (Meadows and Anderson, 1966, 1968; Anderson and Meadows, 1978) owing to the greater surface area available. This does happen, as has been shown by Dale (1974), although not invariably (Meyer-Riel *et al.*, 1978).

Since most calcium carbonates are of organic origin (Blatt *et al.*, 1972), however, there is a good possibility that the organic carbon detected in the sand samples is of the same origin as the calcium carbonate. Gehman (1962) showed that ancient (i.e. pre-Holocene) limestones had a mean organic content of 0,24%, which originated from organisms in the environment at the time of deposition (Blatt *et al.*, 1972).

Price *et al.* (1976) have shown that organic contents of estuarine bivalve and gastropod shells averaged 4,6% and 3,0% respectively, a large proportion of which was present even after many years of exposure.

In addition, Wiener *et al.* (1976) were able to elucidate shell protein structure from 80 million year old bivalve shells. Gaudette *et al.* (1974) have suggested a possible influence of calcium carbonate contents on organic carbon values, and most recently Cameron *et al.* (1979) have found similar values in freshwater bivalves (2,26 to 3,82%) to those found by Price *et al.* (1976).

The literature cited above thus suggests that there is a considerable amount of organic carbon trapped in calcium carbonate laid down by organisms, which is only lost as the shells or skeletons are broken down. This is supported by calculations made to determine the percentage organic content of the calcium carbonate from the beaches studied. The results are listed in Table 3.6.

The median diameter is included to show that the possible effect of surface area on bacterial settlement and hence on measured organic carbon cannot be excluded. This is because the high ratio of organic carbon to calcium carbonate for the Rocherpan beach may merely be a function of the relatively small percentage of calcium carbonate in those sands.

From the results given by Dale (1974), however, it can be calculated that for fine intertidal sands of 2,24 to 2,90 phi, the bacterial biomass made up an average of 0,0026% of the weight of the sediment. There is no reason to expect bacterial biomass of vastly larger magnitude in west coast sediments.

The organic carbon must therefore be derived mostly from the calcium carbonate. A visual inspection of sands from the three beaches shows a substantial number of recognizable shell fragments, which probably constitute the major part of the calcium carbonate. Given this, the explanation for the high ratio of organic carbon to calcium carbonate at Rocherpan is easy to find. Driscoll (1967) has shown that shells abraded by coarse sands developed rougher and more irregular surfaces

TABLE 3.6 Mean parameter values for sediments from four tidal levels

		High Water Springs		High Water Neaps		Low Water Neaps		Low Water Springs	
Parameter		0001		0002		0003		0004	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Mean	R	1,62	0,10	1,64	0,15	1,56	0,15	1,57	0,05
	M	2,30	0,12	2,27	0,13	2,23	0,10	2,21	0,10
	Y	2,32	0,08	2,32	0,11	2,27	0,10	2,31	0,08
Median	R	1,61	0,10	1,64	0,14	1,59	0,12	1,60	0,21
	M	2,33	0,08	2,27	0,11	2,26	0,08	2,23	0,09
	Y	2,30	0,08	2,31	0,09	2,29	0,09	2,32	0,08
Sorting	R	0,32	0,05	0,31	0,05	0,38	0,10	0,44	0.07
	M	0,30	0,05	0,27	0,06	0,30	0,04	0,34	0,06
	Y	0,28	0,04	0,29	0,05	0,32	0,06	0,31	0,04
Skewness	R	-0,02	0,22	-0,03	0,18	-0,12	0,19	-0,24	0,19
	M	-0,13	0,25	-0,10	0,25	-0,10	0,18	-0,19	0,25
	Y	0,05	0,25	-0,03	0,24	-0,08	0,22	-0,13	0,05

continued -

Table 3.6 (continued)

Parameter		High Water Springs		High Water Neaps		Low Water Neaps		Low Water Springs	
		0001		0002		0003		0004	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Kurtosis	R	0,87	0,32	0,77	0,91	0,34	0,63	0,61	0,64
	M	1,32	1,06	1,42	1,25	0,91	0,72	0,93	0,68
	Y	0,62	0,55	0,97	0,92	0,52	0,53	0,62	0,58
% $CaCO_3$	R	3,36	2,02	4,21	3,90	7,98	4,71	8,75	4,16
	M	26,11	1,81	25,42	2,32	27,40	1,92	29,94	2,76
	Y	37,74	4,00	39,63	5,21	41,92	5,87	46,03	8,18
% Organic Carbon	R	0,15	0,05	0,15	0,06	0,23	0,08	0,32	0,08
	M	0,48	0,06	0,48	0,11	0,56	0,10	0,53	0,14
	Y	0,67	0,10	0,72	0,15	0,81	0,15	0,88	0,22

than those abraded by finer sands, suggesting that the resultant particles were also coarser for coarse sands and finer for fine sands. Again, this is evident when the sands from the three beaches are inspected.

Since the breakdown of shells leads to the loss of organic carbon trapped in those shells, it follows that shell-derived calcium carbonate from fine-grained beaches must have a lower proportion of organic carbon than that from coarse beaches.

The study area also has many carbonate deposits (Tankard, 1976) which may contribute to the total calcium carbonate content of the sand.

The differences in grain size between the Rocherpan beach and the other two beaches studied may be explained by the presence of the Cape submarine canyon, lying 28 km west of Cape Columbine (see Fig. 3.25). Tankard (1976) suggests that this has affected sedimentation along the St Helena Bay coastline by acting as a sediment drain, as occurs off southern California (Reed *et al.*, 1975). Thus, finer sediments may not be available for deposition in this area, explaining the coarseness of the sand at Rocherpan.

Finally, there is a good correlation between sorting and the mean and median grain sizes of the three beaches (Table 3.4). It should be noted that sorting values of 0,360 to 0,300 are indicative of well-sorted to very well-sorted sands on the standard sorting scale (Flemming, 1977). Walger (1962) showed that the mean grain size has a strong effect on the degree of sorting; fine sands of mean grain sizes of 2,5 to 3,1 phi are the best sorted, with sorting becoming progressively poorer on either side of this size range. The results obtained here fit Walger's findings.

One might expect to find differences in the sands obtained from different levels of the beach. At the top of the beach, in the zone reached only by waves of the high-water spring tides, one would expect to find

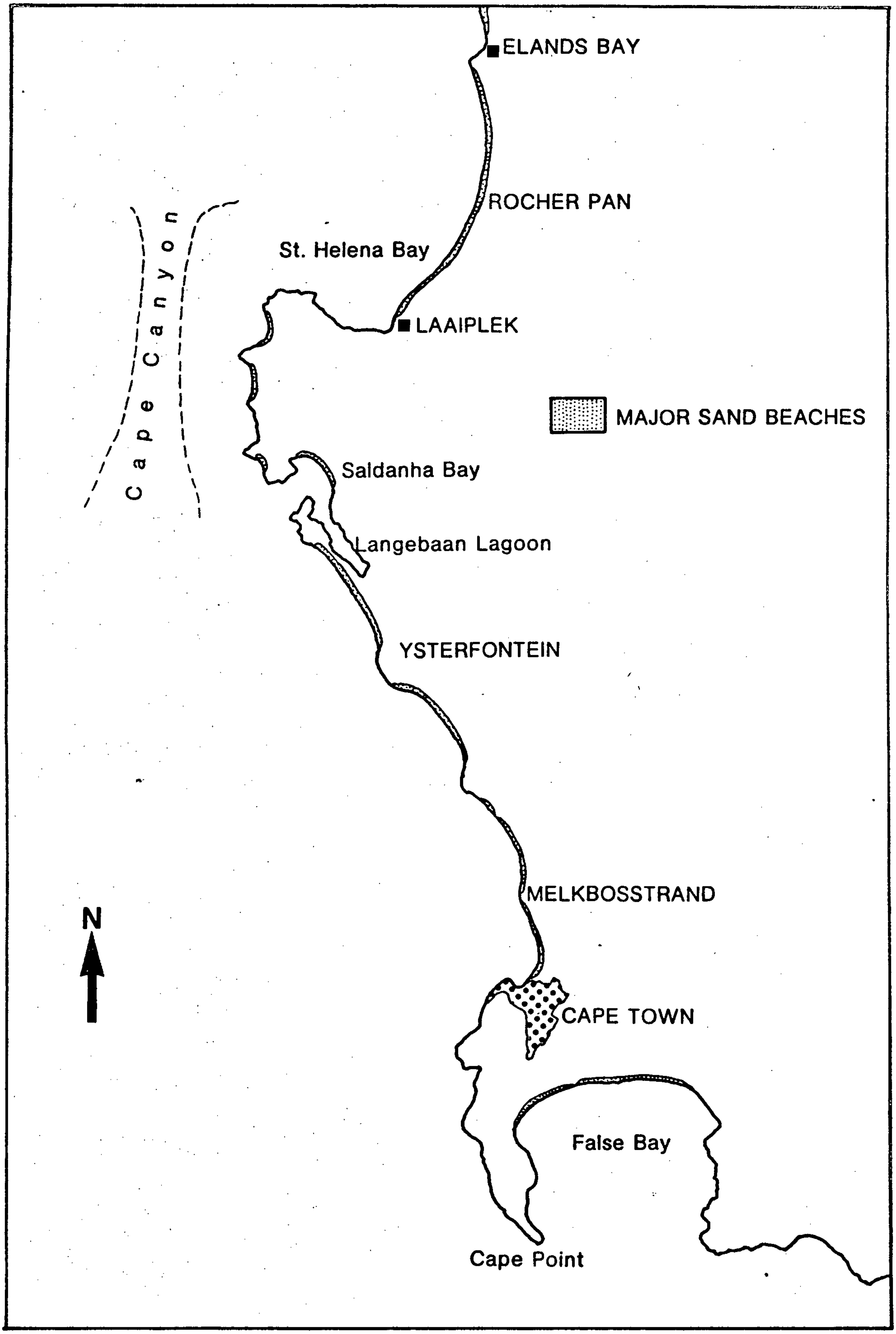


Figure 3.25 Map showing positions of sampling and other beaches in relation to the Cape Canyon.

a large proportion of dune sand, which has been transported and sorted by aeolian action. This sand would also be subject to thermal and chemical weathering. The occasional wave of cold seawater running over hot sand would add to this weathering. Only a small proportion of hydraulically transported and sorted sand would be found at this level.

At lower levels, the proportion of marine transported and sorted sand would become progressively more important, while the proportion of dune sand would decrease. Even if most of the sand on the beach were of dune origin, the influence of hydraulic sorting processes would increase towards the low-water spring tide mark. Differences in mean sand grain size, median sand grain size, sorting, skewness, kurtosis, percentage calcium carbonate and percentage organic carbon for four intertidal levels are listed in Table 3.6.

As can be seen there is a general tendency for the mean diameter to increase towards the low-water springs level. The median diameter increases in the same way.

The sands towards the top of the beach are better sorted than those lower down. This is consistent with the trend observed by Schiffman (1965) for coarser sand to be found in the transition zone lying in between the swash and surf zones (Fig. 3.26). It was from this zone that the lowest samples were collected in the present study. The transition zone corresponds to the area where the backwash reaches its maximum velocity (Fig. 3.26). In this region there is a broad velocity spectrum (Schiffman, 1965) and consequently poorer sorting of the sediments. It is important to realize that the position of this zone varies both daily and with the lunar tide cycle (Clifton *et al.*, 1971). Thus traces of this zone, in the form of coarser sand, can be found over a large proportion of the intertidal area, mixed in with or overlain by finer sand.

The sands of the Rocherpan and Ysterfontein beaches become progressively

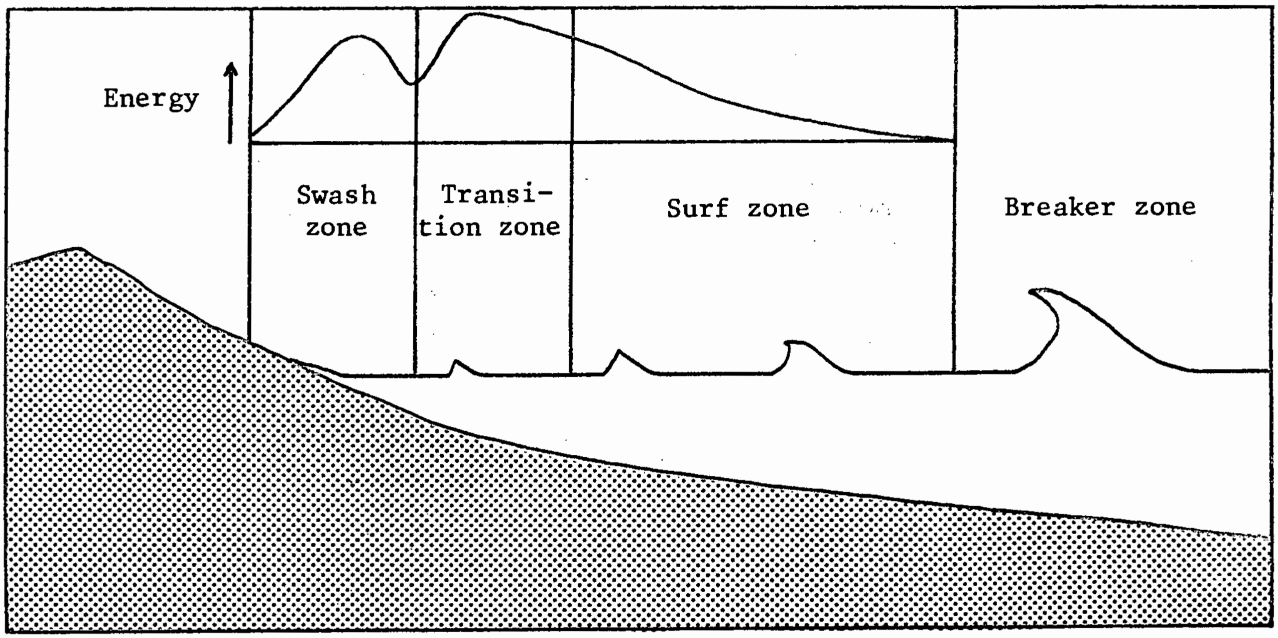


Figure 3.26 Generalized bottom energy profile (after Schiffman, 1965).

more negatively skewed towards the low water mark. This trend is also found in the Melkbosstrand samples but is less obvious. This finding is in agreement with those of Mason and Folk (1958) and Shepard and Young (1961), who found that dune sands tended to be more positively skewed than beach sands. As mentioned before, on a beach the samples from near the high-water mark would be expected to have a higher proportion of dune sands than those from lower down, and this expectation now seems confirmed.

Kurtosis values seem to vary almost randomly (Table 3.6) for the three beaches. They appear to be slightly higher in the upper beach than in the lower beach, but in no consistent manner.

There is a very definite trend on all three beaches for the proportion of calcium carbonate to increase down the beach. This suggests two possibilities. The first is that the calcium carbonate is derived somehow from the marine environment - either from broken-up shells or from carbonate deposits being eroded subtidally. Since beach deposition in the intertidal zone is almost always followed by erosion (Duncan, 1964), the calcium carbonate levels in sand on the upper beach would never be as great as in the lower beach. Only when berms are deposited at the top of a beach as the result of a storm (Bascom, 1951), are lower beach sediments deposited in quantity at the top of the beach. Because these displaced sediments are out of the reach of most tides, they are slow to erode, and consequently high calcium carbonate levels may be found at the top of a beach for a while.

The second possibility is that calcium carbonate in the sand at upper levels and in dune sand is leached out by atmospheric weathering. This probably does occur, but to a lesser degree than the first process.

Driscoll (1967) has shown that for a given beach, shell abrasion is strongest in the swash zone and least in the sublittoral zone.

Abrasion of shell material on a beach will continue until such a time as it becomes fine enough to be removed by hydraulic transport. Therefore the rate of abrasion determines the "survival time" of shell material or other calcium carbonate on the beach. At levels that are submerged most of the time (in the intertidal zone between low-water springs and low-water neaps), this "survival time" is longer than in those areas subjected to wave action most of the time (between low-water neaps and high-water neaps). Calcium carbonate in the zone between high water neaps and high water springs will have travelled through the previous zone, while the effects of erosion and atmospheric weathering would further reduce the proportion of calcium carbonate in the sand.

The percentage of organic carbon also increases towards the lower tidal levels. The relationship between organic carbon levels and those of calcium carbonate has been discussed already, although the tidal level may affect bacterial biomass and hence, to a very slight degree, organic carbon. Meadows and Anderson (1966) found greater concentrations of microfauna and microflora on sand grains from mid- and low-tide levels, while Meyer-Riel *et al.* (1978) showed a weak correlation between water content and bacterial biomass. Such effects would influence the organic carbon percentages only very slightly, however.

Correlations between the various parameters and tidal level are shown in Table 3.7.

The beaches studied showed profiles that were mostly concave. Thus the slope at upper tidal levels is generally steeper than at lower levels (Fig. 3.6). This is due to differences in relative exposure from the low-water mark to the high-water mark. Bascom (1951) found that for any given sand-grain size, the slope of a beach increases with increasing protection, and flattens with increasing exposure. The slope at any given point on the beach is determined therefore by the amount of wave-energy reaching that point.

TABLE 3.7 Regression analysis between parameters and tidal levels

Tidal levels vs. x	Parameter y	Beach	Regression r^2	Slope $y = a_o + a_1x$
Tidal levels	Mean	R	0,63	y = 1,56 + 0,00x
" "	"	M	0,99	y = 2,21 + 0,00x
" "	"	Y	0,23	y = 2,29 + 0,00x
Tidal levels	Median	R	0,25	y = 1,60 + 0,00x
" "	"	M	0,92	y = 2,23 + 0,00x
" "	"	Y	0,12	7 = 2,31 + -0,00x
Tidal levels	Sorting	R	0,83	y = 0,42 + -0,00x
" "	"	M	0,40	y = 0,32 + -0,00x
" "	"	Y	0,77	y = 0,32 + -0,00x
Tidal levels	Skewness	R	0,85	y = -0,21 + 0,00x
" "	"	M	0,24	y = -0,15 + 0,00x
" "	"	Y	1,00	y = -0,13 + 0,00x
Tidal levels	Kurtosis	R	0,53	y = 0,46 + 0,00x
" "	"	M	0,69	y = 0,91 + 0,01x
" "	"	Y	0,05	y = 0,64 + 0,00x
Tidal levels	% $CaCO_3$	R	0,94	y = 8,91 + -0,06x
" "	"	M	0,71	y = 29,05 + -0,04x
" "	"	Y	0,90	y = 44,84 + -0,08x
Tidal levels	% Organic C	R	0,85	y = 0,29 + -0,00x
" "	"	M	0,61	y = 0,55 + -0,00x
" "	"	Y	0.95	y = 0,86 + -0,00x

Since, at any given moment, the greatest amount of wave energy is found at the base of the swash zone and this progressively decreases higher up the beach (Schiffman, 1965), it follows that the slope at the higher levels is greater than at the lower levels. This produces the concave profile of beaches.

The above may appear to be a contradiction of previous statements that coarser sand grains are deposited in more exposed environments than fine sand grains, and that coarse-grained beaches are steeper than fine-grained ones. This is only an apparent contradiction, however. Bascom (1951) found that for any given grain size, the slope increases with increased protection, within limits that are dictated by that grain size. This means that there are two opposing factors influencing the beach slope and making it possible for exposed beaches to be found with gentler slopes than more sheltered ones, as was observed by Brown (1971a) and McLachlan (1977a).

The grain size of a beach may also depend to a large extent on the material available. Thus, where fine sand is removed from the system, as appears to be the case at Rocherpan, unusually coarse sediment may be deposited at sites that may not be especially exposed.

Seasonal changes for the three beaches do not appear to be very great. Figures 3.18 to 3.24 show the fluctuations observed over the study period. For all three beaches there is an increase in the mean and median grain size during July and August, probably due to the effects of winter storms. This is followed by a gradual decrease in grain size until the following winter.

In parallel with this cycle is a fluctuation in the sorting of the beach sediments. All three beaches show a gradual decrease of sorting values until July and August. Then two of them show a sudden increase, reflecting poorer sorting and a wider range of sand grain sizes. Again, this is due to the effects of greater wave energy depositing coarser material on the beaches during winter.

The overall values for skewness and kurtosis varied randomly throughout the year. The percentages of calcium carbonate and organic carbon paralleled each other closely, as might be expected. At Rocherpan and Melkbosstrand calcium carbonate levels increased in winter, suggesting a recruitment of shell particles to the beaches, probably due to mortalities and washing up caused by the winter storms. At Ysterfontein this trend is not as clear.

Some information is gained when seasonal variations of the parameters are plotted for each tidal level (Figs. 3.18 to 3.24). For instance, it can be seen that at Rocherpan the greatest seasonal fluctuations in median and mean grain sizes occur at the low-water mark, while higher up these variations become less pronounced. Furthermore, when calcium carbonate levels increase in winter, it is the samples from the low-water mark that show the greatest increases.

Conclusion

The overall picture of the sedimentology of the three beaches is one of exposed sand beaches, that encounter high-energy waves throughout the year, with a slight increase in winter. All three beaches are backed by coastal dunes and the intertidal zone forms a definite transition zone between aeolian and hydraulically-sorted sands. The influence of this transition on the sedimentology of the beaches is described in detail, and an attempt will be made in a subsequent chapter to discuss the effects of these characteristics on the fauna that inhabits these sands.

CHAPTER 4

ZONATION

Introduction

Zonation patterns occur in all marine animals and most terrestrial ones inhabiting the intertidal zone during part or the whole of their life cycles. The reason for this zonation is that there is a whole range of conditions across the intertidal zone, imposed by varying degrees of daily immersion and emersion. Thus organisms select the zone in which they are able to find food, survive, compete and reproduce most effectively. This basic pattern of intertidal zonation is further complicated by the lunar tide cycle in which tidal amplitudes vary between the extremes of spring and neap tides. The latter distinction mainly affects slow-moving or sedentary animals between the high-water neap and spring tide levels.

Zonation occurs on both rocky and sandy shores and has been extensively reviewed for the former by Lewis (1964), Stephenson and Stephenson (1972) and Newell (1976, 1979).

Newell (1976, 1979) has pointed out that zonation of sandy shore animals is dictated by lunar and daily tidal cycles in a similar manner to the zonation of rocky shore species. Because of the burrowing habits of the inhabitants of sandy shores, their zonation patterns have been much more difficult to determine than those of rocky shore organisms. Stephen (1929, 1930) was among the first to recognize that zonation existed on sand beaches and subsequent to his work a number of studies observed this on other beaches (e.g. Newcombe, 1935; Watkin, 1942; Brady, 1943 and Southward, 1953).

Dahl (1952) was the first to propose a universal zonation scheme for exposed sand beaches. He suggested three intertidal zones defined in terms of the fauna living in each zone. The supralittoral zone is characterized by the presence of air-breathing crustaceans with either talitrid amphipods or ocypodid decapods being the dominant types.

The midlittoral zone is characterized by cirolanid isopods (e.g. *Cirolana*, *Eurydice*), although haustoriid amphipods may also be found. The lowest zone is the sublittoral zone, 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, as well as a diversity of molluscs and polychaetes on all beaches (Dahl, 1952).

Dahl's intertidal zone classification for sandy beaches has been widely accepted, with reservations and modifications. Pichon (1967), for example, found talitrids and ocypodids coexisting in Madagascar, as did Macnae and Kalk (1962) in Mozambique and Wade (1967) on West Indian beaches. Pichon (1967) and Wade (1967) also found cirolanid isopods mixed with these air-breathing crustaceans, as did Gauld and Buchanan (1956) in Ghana.

Jones (1971, 1974) and Eleftheriou and Jones (1976) found that Kenyan, Saudi Arabian and Indian cirolanid isopods (genus *Eurydice*) varied their zonation both according to species and to locality within a single species (Eleftheriou and Jones, 1976). Thus, cirolanid isopods tend to be found not only in the zone classified by Dahl

(1952) as midlittoral, but in parts of the supralittoral and sublittoral as well.

Again, Dexter (1972) found "*Cirolana mayana*" (*Excirolana braziliensis* - Glynn *et al.*, 1976) from the high-water spring tide mark almost down to the low-water mark on Panamanian beaches, while Schuster-Diedrichs (1956) found *Ocypode*, talitrids and "*Cirolana salvadorensis*" (also *Excirolana braziliensis*) occupying the zone around the high-water mark on surf beaches in El Salvador.

In general, cirolanid isopods are found in Dahl's midlittoral zone (Trevallion *et al.*, 1970) at least on high-energy beaches. 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 other New Zealand beaches (Morton and Miller, 1968; Fincham, 1974, 1977).

Dahl's sublittoral is characterized by a diverse fauna, as well as by certain characteristic crustaceans. This appears to be the case generally (e.g. Pichon, 1967) but both Gauld and Buchanan (1956) and Philip (1974) found higher diversities in the midlittoral than in the sublittoral. In addition, phoxocephalids occur not only in the southern hemisphere, but have also been reported from the sublittoral of beaches in the northern hemisphere in Ghana (Gauld and Buchanan, 1956), North Carolina (Pearse *et al.*, 1942; Dexter, 1969) and the Atlantic and Pacific coasts of Colombia, Costa Rica (Dexter, 1974), Panama (Dexter, 1972, 1979) and Mexico (Dexter, 1976). Dahl's classificatory system therefore appears to hold in the majority of exposed beaches, with local exceptions to some of his rules.

It does not always hold 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 polycheates. Brown (1973) found a sphaeromatid isopod replacing a cirolanid species on sheltered, fine-grained beaches of the Cape Peninsula.

Pichon (1967) re-states Dahl's tropical zonation scheme as follows:

> "- a superior zone with talitrids and ocypodids (the one not excluding the other as suggested by Dahl, to whom the ocypodids would be the tropical equivalents of the talitrids);
>
> - a middle zone containing an isopod, an amphipod, a species of midlittoral *Donax* and a species of *Nerine;*
>
> - the lowest zone remains poorly characterized except by the presence of *Callianassa.*" (Translated from Pichon (1967) p.90.)

Whereas Dahl (1952) 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, 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 are still recognizable by the species found in them and Dahl's zonation can be superimposed easily on Salvat's scheme. The latter, however, is more universally applicable than the former.

Salvat divided the beach into four levels based on the degree of moisture in the sediment. The uppermost zone is of dry sand, only reached by large waves at high-water springs, or by spray.

Below that is the zone of retention which is reached by all tides. Gravitational water on the beach is lost at emersion, but water of retention is conserved. Considerable fluctuations in temperature may occur here during low tide and the sand is well-drained and oxygenated.

The next zone, the zone of resurgence, is subject to considerable water movement both on the incoming tide and on the outgoing tide. As the tide ebbs, gravitational water being lost from the zone of retention flows through the sand of this zone and appears at the surface of the of the beach as streams, similar to the freshwater rivulets caused by rainstorms reported by Brown (1971a). Salvat defined this zone as extending shorewards as far as the water table lies within 20 cm of the surface, since the macrofauna in this area will still encounter the same hydrodynamic conditions as lower down in the same zone.

The zone of saturation is permanently saturated with water, but in this level interstitial water circulation is reduced considerably. This results in poorer oxygenation of the sand and may lead to the formation of a black sulphide (i.e. anoxic) layer on sheltered beaches.

The work of Pollock and Hummon (1971) on cyclic changes in interstitial water content in a semiprotected beach in Massachusetts has confirmed the existence of Salvat's four levels. Pollock and Hummon did, however, subdivide the uppermost zone into a zone of dry sand and a zone of drying sand. The zone of dry sand is almost completely terrestrial and only receives seawater rarely, while the zone of drying receives seawater more frequently and loses capillary water by evaporation. The latter zone conforms to the region 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.

Methods and Materials

In order to determine the distribution of species across the intertidal area of the three beaches studied, samples were taken from the grid described in chapter 2. From these and other, less intensive, collections, a picture of the intertidal zonation of soft-shore macrofauna was developed.

To test the association of species into zones, dendrograms were generated by a computer program that used a Bray-Curtis similarity matrix and log-transformed data of species numbers. From the similarity matrix, a further program constructed two-dimensional ordination diagrams using multidimensional scaling and calculating the stress produced by reducing the multidimensional scaling to two dimensions.

An information statistic program then compared the species' presence, absence and numbers for each grouping derived from the ordination diagrams and showed at 90 and 95% confidence levels which species are characteristic for each zone, and at what densities. The results obtained from the information statistic program 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 95% 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 and Discussion

In the present study, little was found that was at variance with the literature on zonation in sandy beaches. Figures 4.1 and 4.2 show the zonation of species on the three beaches of the west coast of South Africa studied here.

At the high-water mark (Dahl's supralittoral and Pollock and Hummon's zone of drying), a mixture of terrestrial and marine adapted animals is evident. 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. On one of the beaches (Melkbosstrand), lumbricid oligochaetes are also found, especially after rain.

The marine derived macrofauna in this zone consists of the giant isopod *Tylos granulatus*, the talitrid amphipods *Talorchestia capensis* and *T. quadrispinosa*, *Excirolana natalensis*, a cirolanid isopod, as well as, on occasion, the cirolanid *Pontogeloides latipes*. The first three species are air-breathing (the herbivorous and scavenging *Tylos* are often found around washed-up 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 these 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) actually supports a lower diversity of species than the zone of drying. The reason for this is that 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. 4.3).

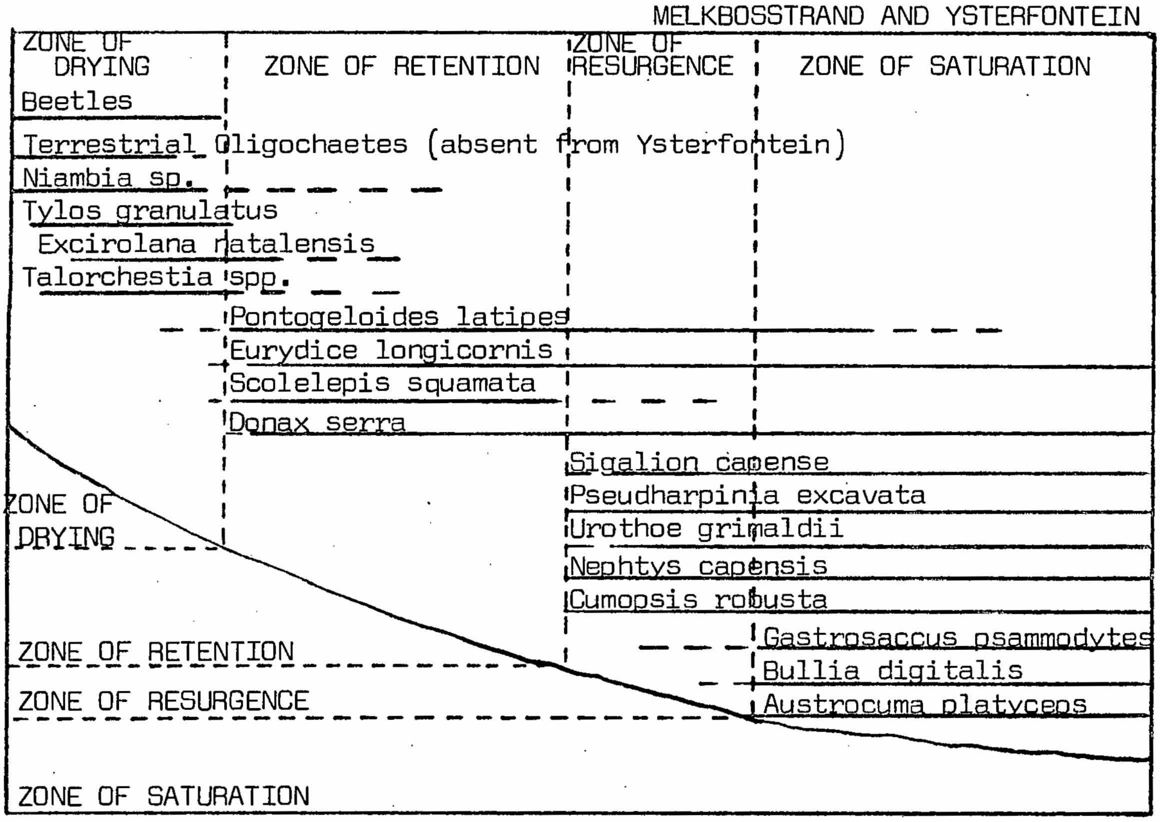


Fig 4.1: Zonation of species on fine-grained beaches of the west coast

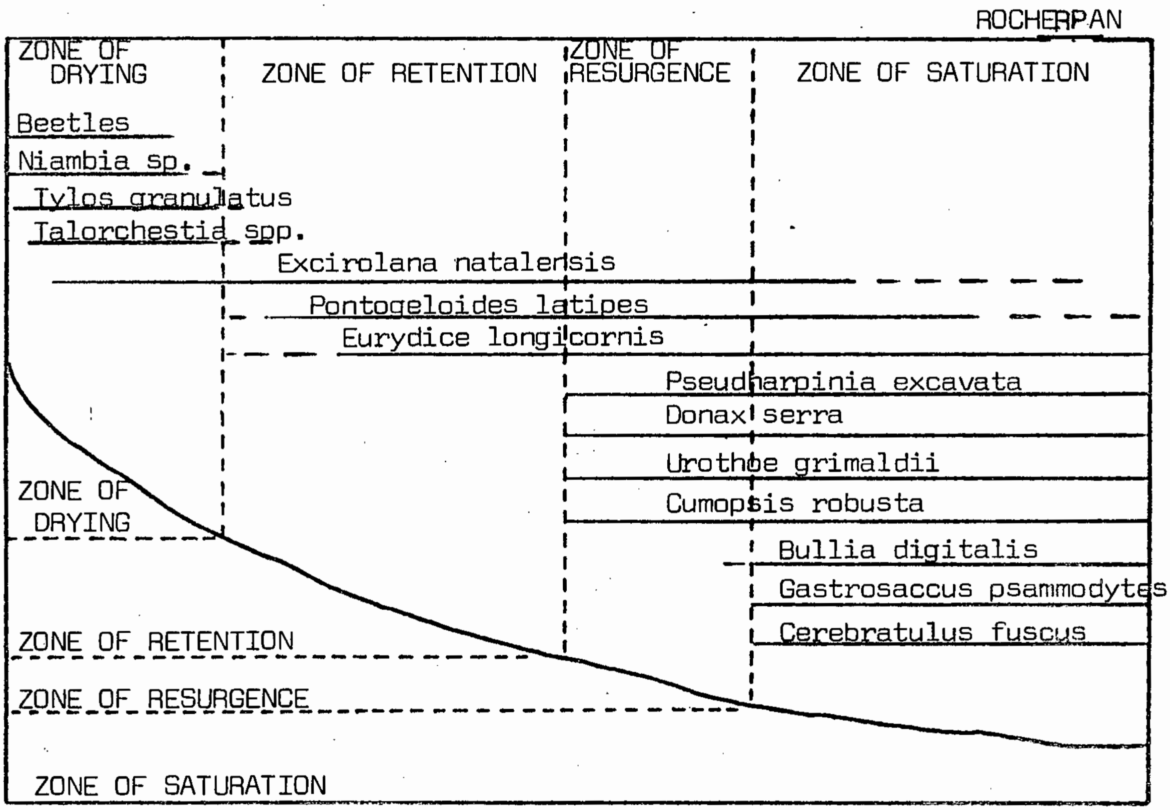


Fig. 4.2: Zonation of species on coarse-grained beaches of the west coast

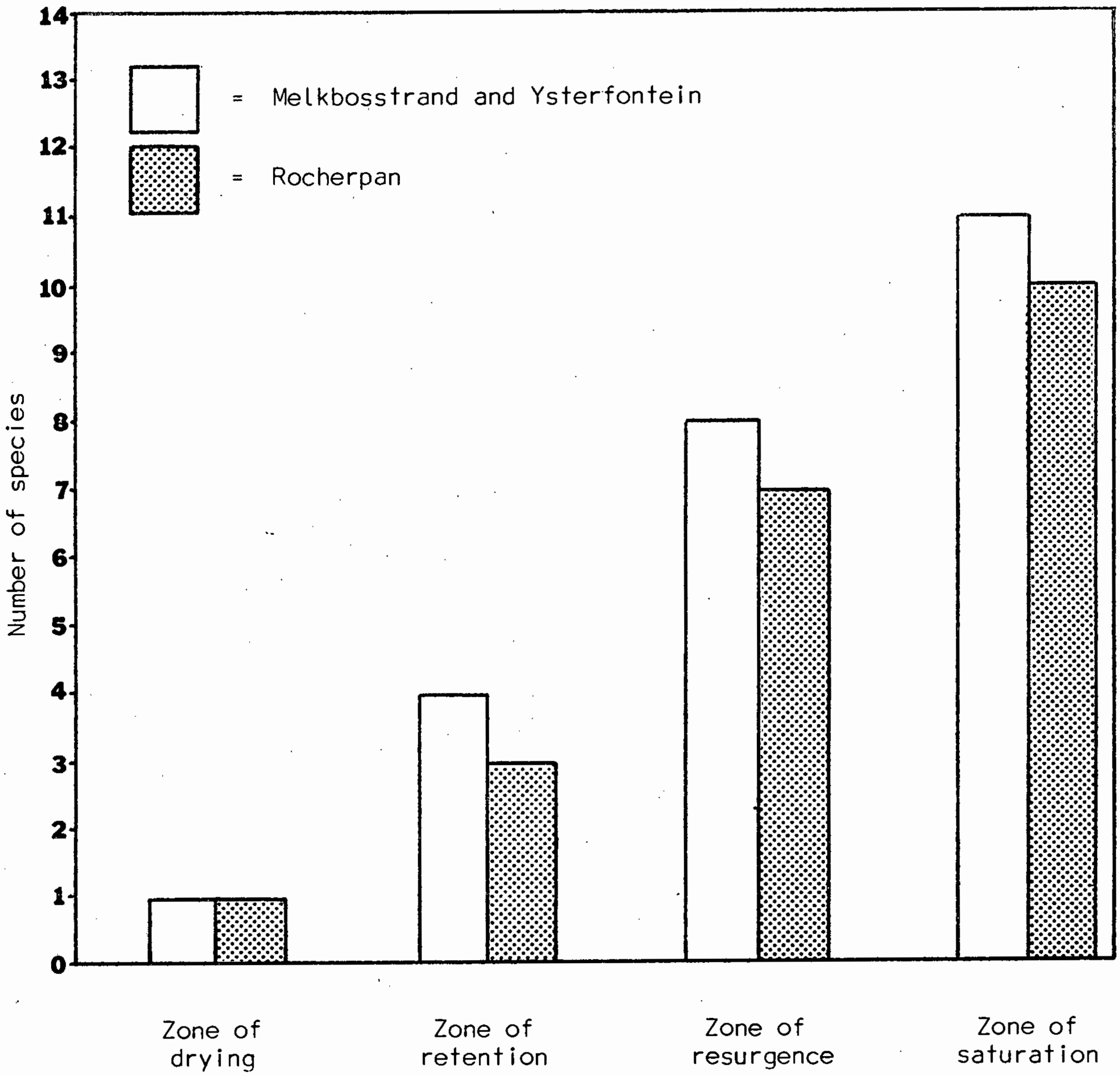


Figure 4.3 Diversity of marine species across the intertidal zone of west coast sand beaches.

This zone is characterized by great densities of the spionid sedentary polychaete *Scolelepis squamata* on two of the beaches (Melkbosstrand and Ysterfontein). *Scolelepis* is 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, 1975b). 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 numbers (up to 8 000 per m²) associated with *Scolelepis*. At Rocherpan, *Eurydice* is largely replaced in importance by *Excirolana natalensis*, which becomes the dominant species.

During low tide, some terrestrial species may extend down to the zone of retention. Thus *Talorchestia* and *Niambia* are occasionally found here. Muir (1977) has shown that zonation between adults and juveniles of *T. capensis* occurs, but densities of that species are several orders of magnitude lower on the west coast beaches than at Muir's study site at Kommetjie and therefore insufficient data was collected to confirm his findings quantitatively.

The zone of resurgence (part of Dahl's sublittoral) supports a greater diversity of species than the previous zones, although numbers and biomass per unit area may be lower than the zone of retention. Species also found in higher zones are *Scolelepis* (rarely), *Donax*, *Eurydice*, *Pontogeloides* and, at Rocherpan, *Excirolana*. *Scolelepis* is again absent at Rocherpan. 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 occasionally the psammophilous mysid *Gastrosaccus psammodytes* are also found in this zone.

---

* It should be noted at this point that the distinction between the genus *Scolelepis* and *Nerine*, which Pichon (1967) mentioned as characteristic of the "middle zone", is indistinct and subject to debate among taxonomists (Hartman, 1959).

The zone of saturation 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*, although it is rare at Rocherpan, and the nemertean *Cerebratulus fuscus*. At Rocherpan, small nematodes (unidentified) were also found, while at Melkbosstrand *Sigalion* and *Nephtys* occurred, as well as the occasional *Austrocuma platyceps*, a cumacean.

Species lists for the three beaches are shown in Tables 4.1 and 4.2.

Using part of the data obtained from the biomass collections, similarity analysis using the abundance-weighted Bray-Curtis similarity measure was employed. Selected dendrograms and two-dimensional ordination diagrams clearly separate species numbers and distributions into the four zones mentioned above (Figs 4.4, 4.5 and 4.6). Indicator species derived from the information statistic program are listed in Tables 4.3, 4.4 and 4.5.

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.

Only one specific account on the zonation of South African sandy beaches (that of McLachlan, 1980a) has been published at the time of writing. Brown (1964, 1971a) and McLachlan (1977c) present generalized descriptions of where some of the macrofaunal species are to be found, and Trevallion *et al.* (1970) have drawn up a rough zonation table from information in Brown (1964). Brown and Jarman (1978) reproduce a zonational diagram of Muizenberg beach in False Bay from unpublished work by Brown without comment. McLachlan (1977b) presents a zonation table for the macrofauna of a sheltered and an exposed beach near Port Elizabeth. McLachlan (1980a) does the same for six beaches in the same area, but concentrates on meiofaunal zonation.

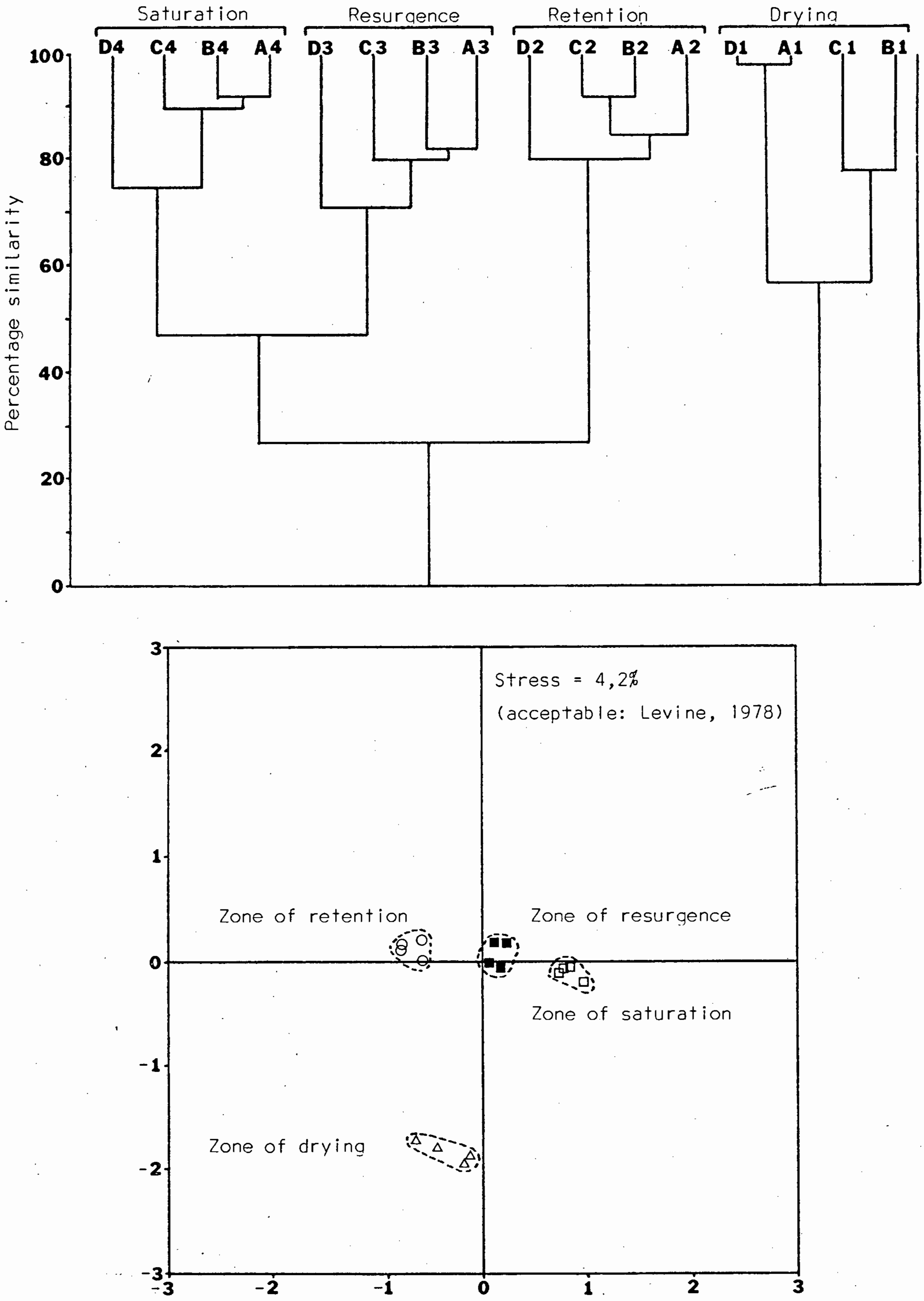
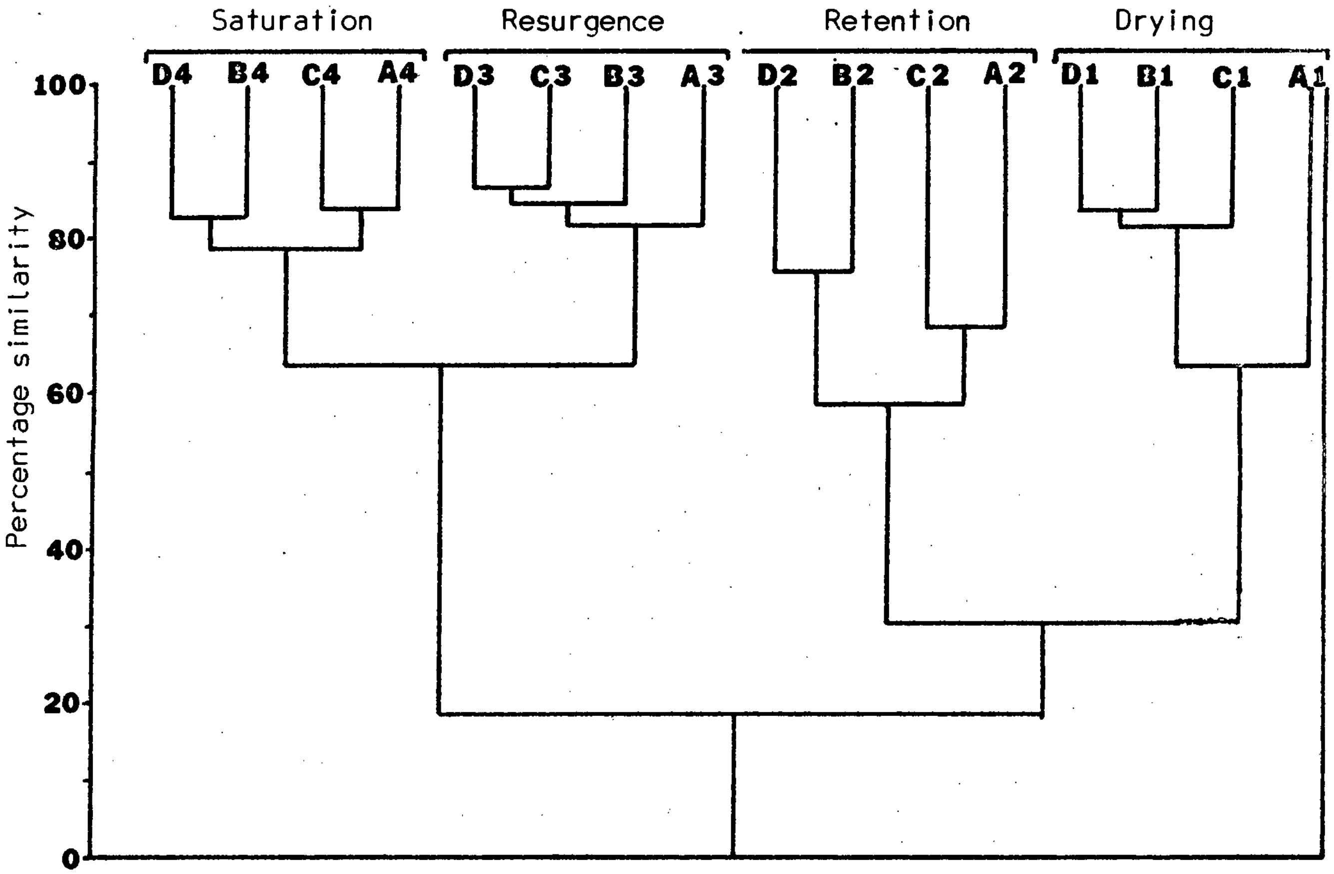


Figure 4.4 Dendrogram and ordination diagram showing zones at Melkbosstrand 22.1.77.



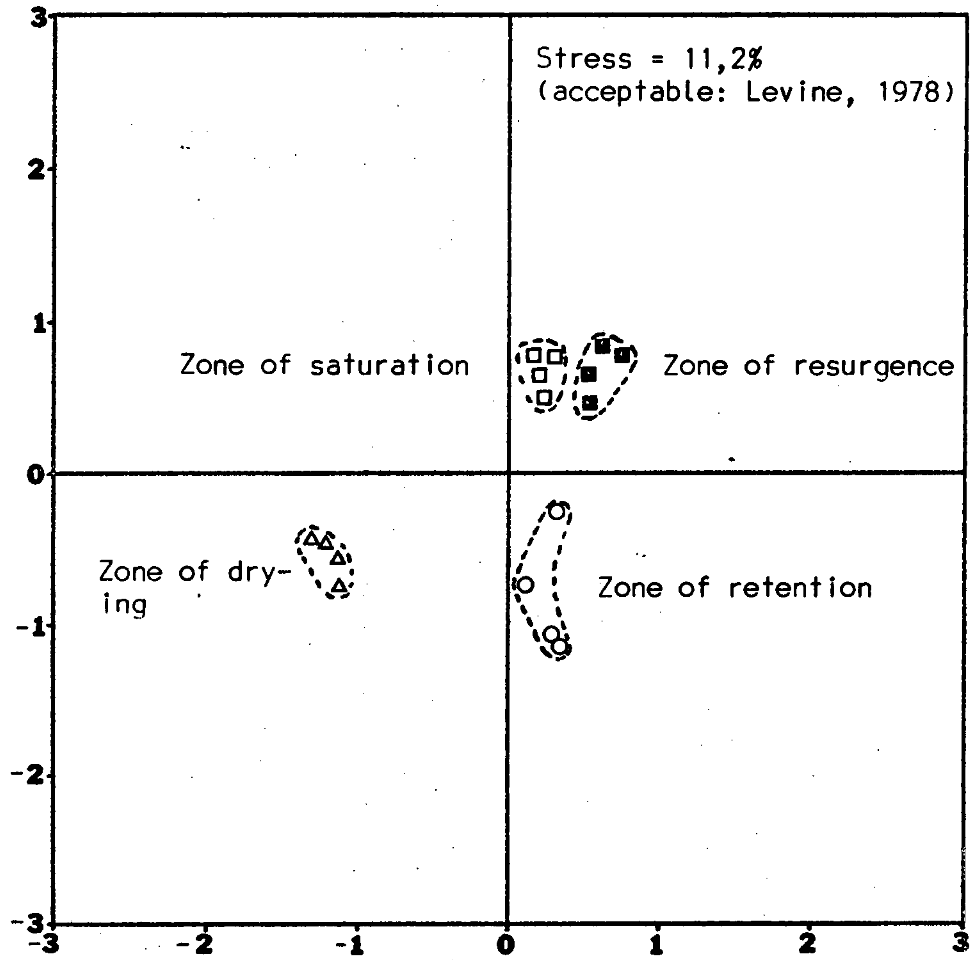


Figure 4.5 Dendrogram and ordination diagram showing zones at Rocherpan 4.5.77.

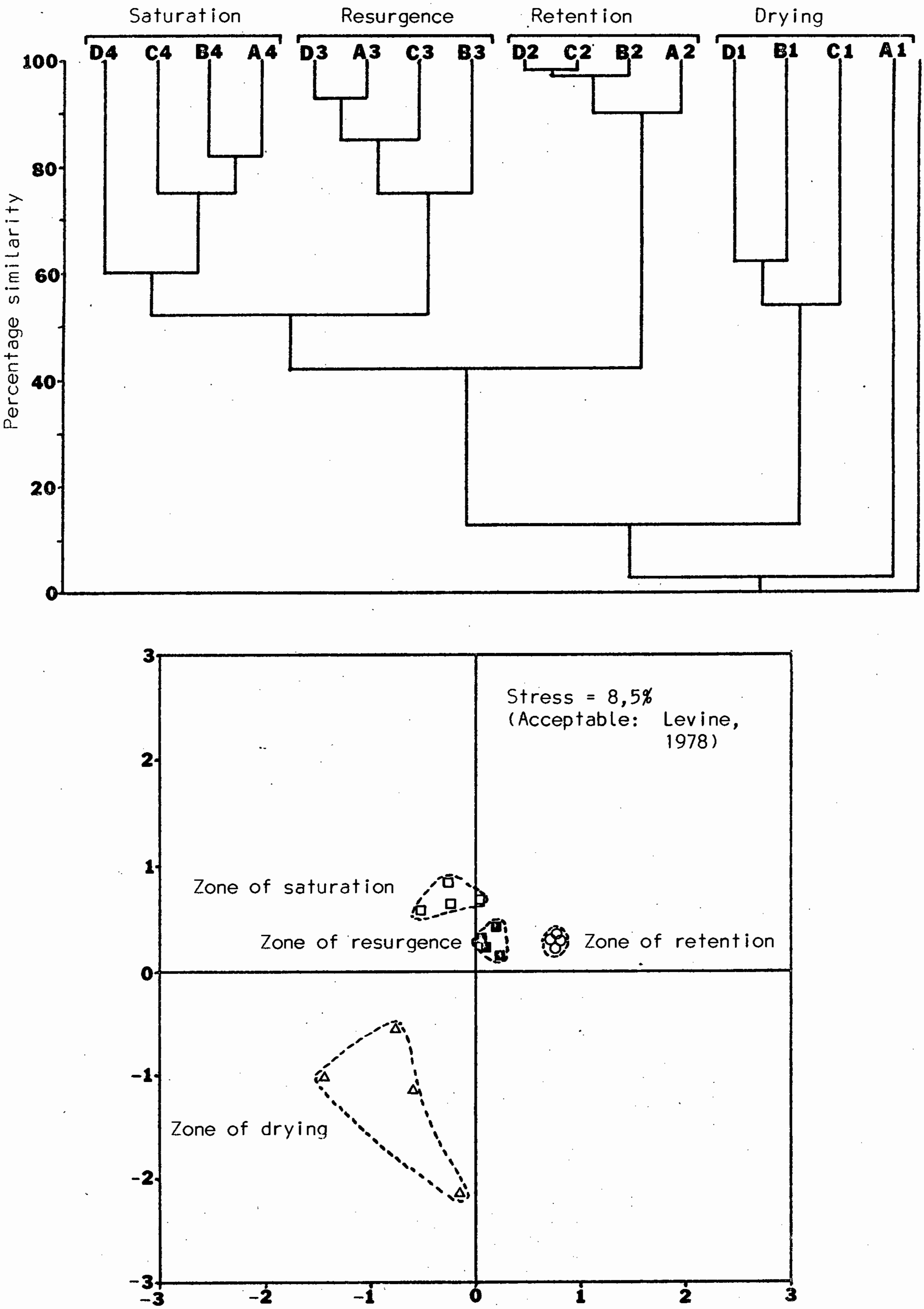


Figure 4.6 Dendrogram and ordination diagram showing zones at Ysterfontein 19.2.77.

TABLE 4.1 Common species of the exposed beaches of the west coast

Species	Rocherpan	Melkbosstrand	Ysterfontein
Oligochaetes		+	
Pachyphaleria capensis	+	+	+
Acanthoscelis ruficornis	+	+	+
Insect larvae	+	+	+
Niambia sp.	+	+	+
Talorchestia quadrispinosa	+	+	+
Talorchestia capensis	+	+	+
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

TABLE 4.2 Species found on beaches on rare occasions

Species	Rocherpan	Melkbosstrand	Ysterfontein
Trichodactylus sp.		+	
Perioculodes longimanus	+		
Choromytilus meridionalis	+		
Burnupena delalandii	+	+	
Exosphaeroma truncatitelson			+
Sipunculid			+
Bullia laevissima			+
Calanoides carinatus			+
Maera inaequipes			+
Paramoera capensis			+
Corophium ascheruscium			+
Chevalia aviculae			+

TABLE 4.3 Information Statistic Tests - MELKBOSSTRAND
(++ = 95% significance, + = 90% significance)

Species	Significance	Subset 1	Subset 2
		Zone of Drying	Zone of Retention
Tylos granulatus	++	28	0
Excirolana natalensis		2	0
Oligachaete	+	3	0
Insect larva		1	0
Scolelepis squamata	++	0	1491
Eurydice longicornis	++	0	132
Pontogeloides latipes	++	0	12
Donax serra	+	0	4
		Zone of Retention	Zone of Resurgence
Scolelepis squamata	++	1491	0
Eurydice longicornis	++	132	320
Pontogeloides latipes	++	12	1
Donax serra	++	4	111
Gastrosaccus psammodytes	++	0	13
Cumopsis robusta	++	0	0
Sigalon capense	+	0	3
Pseudharpinia excavata	+	0	3
		Zone of Resurgence	Zone of Saturation
Eurydice longicornis	++	320	24
Pontogeloides latipes		1	0
Gastrosaccus psammodytes	++	13	298
Donax serra	++	111	33
Sigalon capense		3	4
Pseudharpinia excavata	++	3	15
Urothoe grimaldii	++	0	18
Bullia digitalis	++	0	11

TABLE 4.4 Information Statistic Tests - ROCHERPAN

Species	Significance	Frequency	
		Subset 1	Subset 2
		Zone of Drying	Zone of Retention
Tylos granulatus	++	14	0
Excirolana natalensis	++	18	59
Talorchestia spp.	++	41	0
Niambia sp.	++	35	3
Eurydice longicornis	++	0	19
Pontogeloides latipes	++	0	5
Donax serra		0	1
Pdeudharpinia excavata	+	0	4
		Zone of Retention	Zone of Resurgence
Exciolana natalensis	++	59	15
Niambia sp.	+	3	0
Eurydice longicornis	++	19	114
Pontogeloides latipes		5	4
Gastrosaccus psammodytes	++	0	49
Donax serra	++	1	723
Cumopsis robusta	+	0	3
Pseudharpinia excavata	++	4	167
		Zone of Resurgence	Zone of Saturation
Excirolana natalensis		15	8
Eurydice longicornis	++	114	15
Pontogeloides latipes		4	1
Gastrosaccus psammodytes	++	49	12
Donax serra	++	723	53
Cumopsis robusta	+	3	0
Pseudharpinia excavata	++	167	42
Cerebratulus fuscus	++	0	6

the time of sampling. This should be borne in mind since Prus (1970) and others have shown that intraspecific variations of calorific values can depend on size, season and developmental stage.

Seasonal collections were made from each beach over a period of 18 months. Thus, seasonal variations in numbers, biomass, ash and calorific values were obtained. On one occasion on each beach a further 16 samples were taken at random from within the sampling grid. These results, in combination with the data from the grid, permitted a detailed analysis of the three-dimensional distribution of sandy beach macrofaunal species and the results of that study are discussed in chapter 7.

For comparative purposes, meiofauna was collected from the sampling grid to a depth of 30 cm at the same time as the additional 16 macrofaunal samples were collected. Subsequently, meiofauna was sampled on all three beaches to 30 cm below the water table, for which standard 10 cm^2 area stainless steel corers were used as recommended by A. McLachlan (pers. comm.). The meiofauna were relaxed in magnesium chloride, preserved in formalin and then elutriated from the sand using a modified Oostenbrink extractor (Fricke, 1980). After staining, the meiofauna were counted and identified under a binocular dissecting microscope.

Results and discussion

One of the commonest methods used to present biomass values in the literature, is to convert all results to a value per square metre of beach (e.g. Eleftheriou and Nicholson, 1975; McIntyre, 1970; Seed and Lowry, 1973; Dexter, 1972; Withers, 1977; Edwards, 1973a, b; Croker *et al.*, 1975). The other way of reporting biomass is to give figures per metre strip of beach (e.g. McLachlan, 1977a, b), although this method has been used less frequently until now.

From the diagram in Brown and Jarman (1978), the most notable difference is that the marine component of the fauna seems compressed seawards and therefore concentrated into the lower half of the beach. This could be because Muizenberg is a less exposed beach than those of the west coast and hence the swash does not run as high up the beach. The presence of *Exosphaeroma truncatitelson* (Brown, 1973) and *Callianassa* at Muizenberg confirms this impression.

The fauna listed by McLachlan (1977b and 1980a) is similar to that found on the beaches of the Cape Peninsula (Brown, 1971a) and the west coast beaches of this study, with a few exceptions. *Eurydice longicornis* extends to the high-water mark, while *Excirolana natalensis* is absent, even though Port Elizabeth lies well within the latter's geographical range. Also absent from this level are *Tylos* and *Talorchestia*. In the midlittoral zone (zone of retention), the polychaete *Glycera convoluta* is found, while *Nephtys* sp. and *Arabella iricolor* are also found in this zone on the sheltered beach. On the exposed beach, McLachlan found *Donax sordidus* together with *D. serra*, although the latter species occupies a lower intertidal position than the former (McLachlan, 1980a).

At the low-water mark, *Donax sordidus*, *Gastrosaccus psammodytes*, *Bullia rhodostoma* and *B. digitalis* were found, as well as the mole-crab *Emerita austroafricana*. *Eurydice* is not replaced by *Exosphaeroma* on the sheltered beach as occurs on some Cape Peninsula beaches (Brown, 1973).

On these east coast beaches, 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 the 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 west coast beaches is probably due to low ambient temperatures.

It is interesting to speculate on the gaps left 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 (e.g. Trevallion *et al.*, 1970; MacNae and Kalk, 1962). Kensley (1974) notes that the northernmost 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 *Ocypode quadrata* is mainly a predator, only 10% of its dietary intake being from scavenged material. On the other hand, Kensley (1974) has shown that *Tylos* is mainly a scavenger.

Tylos granulatus and *Tylos capensis* are the largest intertidal isopods in the world and one reason for their large size may 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 as 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 (Kuhn, 1978; McLachlan, Wooldridge, Schramm and Kuhn, 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 to feed 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 has observed that there seems to be a reduction in numbers of gulls in the inter-tidal zones of tropical areas in comparison to the beaches of the west coast of South Africa (pers. comm.) and this may be due to competition in both scavenging and predation by 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. *Eurydice longicornis* is the most pelagic of the three species, often being found in large numbers at the surface up to one kilometer offshore above sandy bottoms (C. Brownell, pers. comm.). *Eurydice* occurs intertidally in all the zones except the zone of drying, in densities of up to 8 000 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 there is some competitive exclusion between these three carnivorous and scavenging species, especially on fine beaches between *Eurydice* and *Excirolana*.

Intertidal zonation of a particular species on the basis of size or age has been found in many sandy beach species. Stephen (1930) had 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, 1975b; 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 was most noticeable in *Donax serra*. De Villiers (1975b) 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 - if anything, the smallest size class occurred lower down the beaches than did the larger ones. McLachlan and Hanekom (1979) note that the intertidal size-class distribution of *Donax serra* on east coast beaches is the reverse of that observed by De Villiers on the west coast.

On a few occasions in this study, it was found that the lower beach had both large and very small individuals of *Donax* (1,9 to 5,0 mm in length). Those higher up the shore measured from 4,5 to 29,0 mm in length (Fig. 4.7). On these occasions, 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). 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. After reaching a size in the zone of retention 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, the mussels move down the beach to the zone of saturation or to the subtidal fringe. De Villiers (1975a) found that individuals of *Donax serra* reach maturity when they attain 37,0 to 54,0 mm 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.

Edwards (1969) lists differences in osmotic, temperature and desiccation tolerances as the reasons for segregation by size of individuals of *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.

I suggest that small individuals are highly susceptible to predation by fish. Therefore, as soon as the mussels are sufficiently large to maintain a zonational position, they migrate up into the zone of

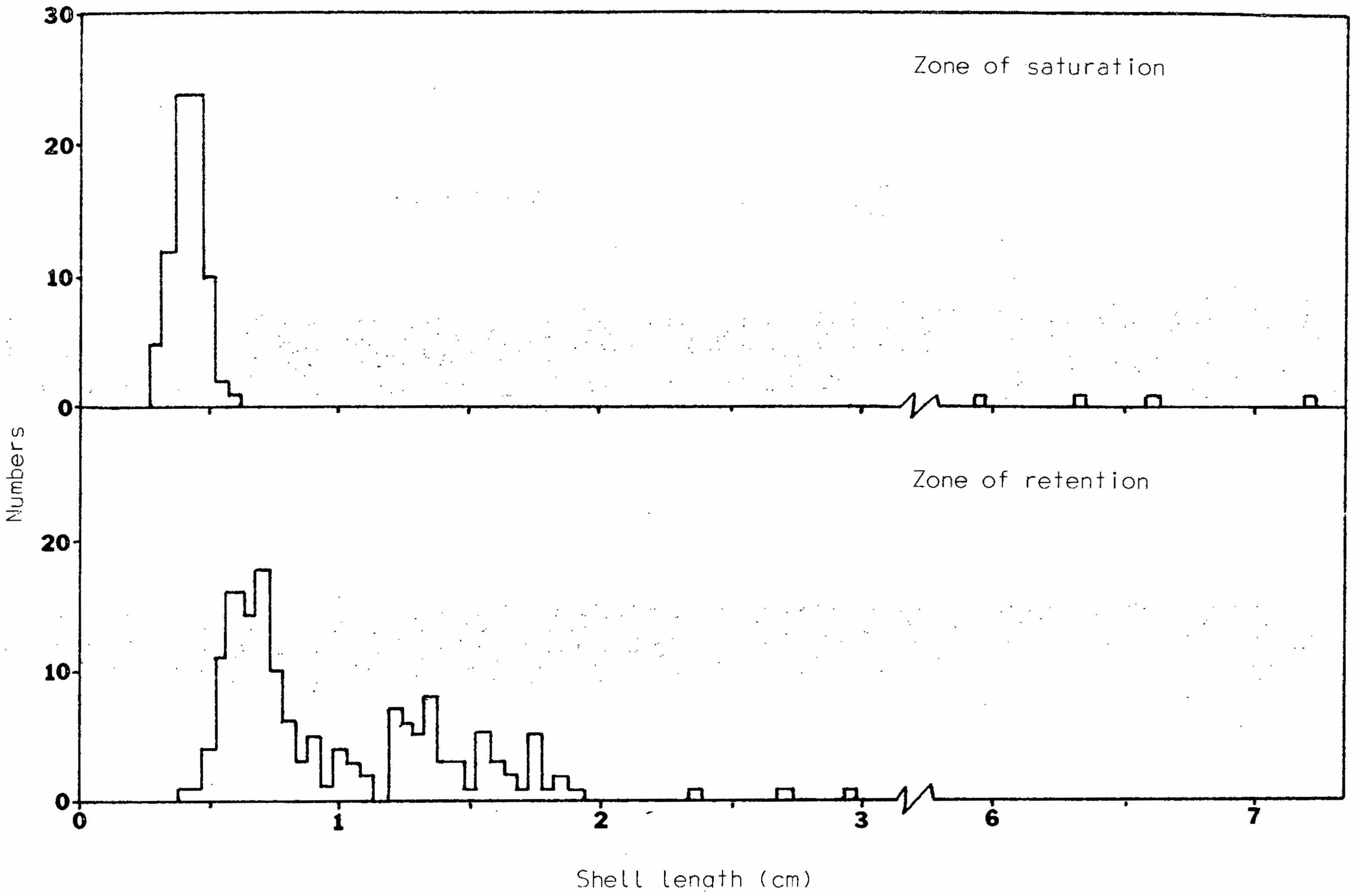


Figure 4.7. Size frequency distributions of *Donax serra* in two intertidal zones

retention, where the time during which they are vulnerable to these predators is much reduced.

A size may be reached when the *Donax* become too large to be taken by the majority of predatory fish, or sufficiently large to become a worthwhile prey item for the black-backed gull, or both. At this stage the mussels move downshore again, into the zone of saturation or into the subtidal fringe. Once in these permanently water-covered zones, the animals attain sexual maturity. It is probably energetically advantageous to delay sexual maturity until this stage, since spawning can then occur at any time, whereas in the zone of retention, spawn release would have to coincide with periods of high tide. The amount of time available for feeding in the lower zones is also greater, and this constitutes a further selective advantage to large individuals occupying these areas. The increased quantity of food available could also be a prerequisite for reproduction.

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).

The zonation exhibited on sandy beaches on the west coast of South Africa therefore follows 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.

CHAPTER 5

BIOMASS AND NUMBERS

Introduction

The numbers and biomass of organisms on sandy beaches reflect a number of features about these beaches. Numbers are an indication of the concentrations of organisms present on a beach while biomasses may reflect the degree of permanence of these numbers. While high numbers may simply be due to a large settlement of juveniles, there is no indication that these juveniles have settled in the correct environment, and their presence on a beach may be purely accidental. This is seen on rocky shores in particular, where heavy settlements of mussels or barnacles can occur in zones from which they are soon eliminated by more successfully competing species (Newell, 1979).

Although settlement in the wrong zone seldom occurs on sandy shores, because most species remain mobile, it does happen that large numbers of a species may settle on beaches of unsuitable degrees of exposure. The presence of such incorrectly settled juveniles would also be temporary. Biomass figures can, therefore, show the relative permanence of these numbers since it is highly unlikely that large numbers of adult organisms would settle on an unsuitable beach, and since it is improbable that juveniles would reach maturity in an unfavourable environment. Finally, biomass and density values are indicators of the richness of beaches and show their importance both as habitats for the species constituting the beach fauna and as feeding grounds for predators such as birds and fishes.

Methods and materials

Samples were collected from three sandy beaches on the west coast of South Africa (at Melkbosstrand, Ysterfontein and Rocherpan) using the grid sampling method of which a detailed description is given in chapter 2. Animals were removed from the sand by means of 1 mm mesh sieves and after collection were preserved in formalin until they could be processed. In the laboratory, the collected organisms were sorted into species and then counted, weighed, acidised, dried and reweighed. The animals were then ground into a fine powder and incinerated in a Phillipson microbomb calorimeter in order to obtain calorific values.

The procedure for obtaining calorific values was as follows: animals were acidised in hydrochloric acid in order to remove calcium carbonate - a major source of endothermy in bomb calorimetry (see Paine, 1966). Once all effervescence had ceased for approximately 10 minutes, the samples were washed in fresh water and oven-dried at 60°C for two days. The dry samples were then ground up in a dental mill until finely powdered. These were then made into pellets for combustion in the microbomb calorimeter.

It should be noted that all the individuals collected from each sampling session were ground up and mixed together before subsamples were taken for calorific analysis. The results obtained, therefore, reflect the energy value of a mixed population for each species at the time of sampling. This should be borne in mind since Prus (1970) and others have shown that intraspecific variations of calorific values can depend on size, season and developmental stage.

Seasonal collections were made from each beach over a period of 18 months. Thus, seasonal variations in numbers, biomass, ash and calorific values were obtained. On one occasion on each beach a further 16 samples were taken at random from within the sampling grid. These results, in combination with the data from the grid, permitted a detailed analysis of the three-dimensional distribution of sandy beach macrofaunal species and the results of that study are discussed in chapter 7.

For comparative purposes, meiofauna was collected from the sampling grid to a depth of 30 cm at the same time as the additional 16 macrofaunal samples were collected. Subsequently, meiofauna was sampled on all three beaches to 30 cm below the water table, for which standard 10 cm^2 area stainless steel corers were used as recommended by A. McLachlan (pers. comm.). The meiofauna were relaxed in magnesium chloride, preserved in formalin and then elutriated from the sand using a modified Oostenbrink extractor (Fricke, 1980). After staining, the meiofauna were counted and identified under a binocular dissecting microscope.

Results and discussion

One of the commonest methods used to present biomass values in the literature, is to convert all results to a value per square metre of beach (e.g. Eleftheriou and Nicholson, 1975; McIntyre, 1970; Seed and Lowry, 1973; Dexter, 1972; Withers, 1977; Edwards, 1973a, b; Croker *et al.*, 1975). The other way of reporting biomass is to give figures per metre strip of beach (e.g. McLachlan, 1977a, b), although this method has been used less frequently until now.

Neither method gives the reader complete information on its own; the first gives an indication of the mean "density" of the biomass, while the other gives one an idea of the carrying capacity of the beach. Figures expressed in the former way tend to be given the same weighting as if they had been expressed in the latter manner, i.e. they take the place of total biomass values, in the minds of both authors and readers. Although obviously an erroneous interpretation, this nevertheless occurs because of the associative and collocative meanings (Leech, 1974) of the term "biomass per metre squared".

Furthermore, this average per square metre gives the impression that such densities might be found anywhere across the beach, whereas in reality the effects of intertidal zonation impose a completely different distribution pattern. Chapter 7 shows that distribution patterns also vary along the beach. Thus the terms "numbers or biomass per metre squared" are really more indices of beach "richness" than conveyors of real values if used on their own.

Tables 5.1 and 5.2 show the maximum densities and biomass values obtained for all the macrofaunal species during the course of this study. While these values reflect extreme concentrations, they show the possible ranges that may be encountered on west coast sandy beaches. As can be seen, both very high densities and biomass values occur on occasion. It is interesting to note that the highest densities of all the most important intertidal species (i.e. *Tylos, Pontogeloides, Eurydice, Scolelepis* and *Donax*) were found at Ysterfontein, as was the greatest overall density of organisms. The lowest densities tended to be found at Rocherpan. There was a similar difference between the beaches for maximum biomass values.

Although of interest, the above results only represent extreme values. Of greater significance are the mean annual values found on these beaches. Total biomass values per metre strip of beach, per square metre of beach and the mean annual widths of the beaches are listed in Table 5.3 These results too, show that Ysterfontein is the richest beach in terms of faunal numbers and biomass, while

TABLE 5.1 Maximum densities (m^{-2}) of all species of macrofauna. Underlined values indicate greatest densities encountered for that species.

Species	Density (No. m^{-2})		
	Melkbosstrand	Rocherpan	Ysterfontein
Tylos granulatus	68	32	100
Talorchestia capensis	28	360	32
Oligochaetes	48	-	-
Excirolana natalensis	48	584	72
Niambia sp.	4	56	40
Pontogeloides latipes	184	44	584
Eurydice longicornis	2400	188	8956
Scolelepis squamata	4636	-	7216
Donax serra	1700	1316	1748
Gastrosaccus psammodytes	1340	336	936
Sigalion capense	12	-	12
Pseudharpinia excavata	116	396	16
Urothoe grimaldii	132	8	24
Cumopsis robusta	280	8	112
Cerebratulus fuscus	12	20	8
Bullia digitalis	204	1	76
Nephtys capensis	32	-	8
All species	5794	1680	11 608

TABLE 5.2 Maximum biomass values (grams acidised dry weight.m^{-2}) of macrofaunal species from three beaches on the west coast of South Africa.

Species	Biomass ($g.m^{-2}$)		
	Melkbosstrand	Rocherpan	Ysterfontein
Tylos granulatus	13,7884	0,5492	0,3592
Eurydice longicornis	0,6592	0,1196	2,7280
Talorchestia capensis	0,0884	0,4356	0,0360
Scolelepis squamata	10,7920	-	32,7892
Oligochaetes	2,1624	-	-
Pontogeloides latipes	1,7244	0,9200	4,9676
Donax serra	68,4444	19,9532	65,5224
Gastrosaccus psammodytes	1,0972	1,4712	1,9198
Sigalion capense	3,3152	-	2,0704
Pseudharpinia excavata	0,0500	0,2100	0,0104
Excirolana natalensis	0,1640	2,9004	0,3428
Bullia digitalis	3,3528	0,2846	9,7260
Urothoe grimaldii	0,0136	0,0008	0,0068
Cumopsis robusta	0,0264	0,0008	0,0012
Cerebratulus fuscus	0,3256	0,1572	0,2448
Niambia sp.	0,0024	0,0124	0,0052
Nephtys capensis	0,0480	-	0,0264
All species	68,5144	23,7220	70,3700

TABLE 5.3 Mean annual values for Melkbosstrand, Ysterfontein and Rocherpan of biomass per metre strip of beach, biomass per metre squared of beach and widths of beaches.

Mean annual values	Melkbosstrand	Rocherpan	Ysterfontein
Biomass ($g.m^{-1}$ of beach)	324,3009	92,4819	682,5707
Biomass ($g.m^{-2}$ of beach)	3,6033	1,8874	11,4333
Width of beach (m)	90,0	49,0	59,7

Rocherpan is the poorest, despite the fact that the beach at Melkbosstrand is, on average, some 60% wider than at Ysterfontein. It must be concluded, therefore, that differences in mean sediment size and possibly shelter account for the differences in biomass and numbers supported by these beaches.

Table 5.4 gives a breakdown of the mean annual biomass per metre strip of beach into the constituent species, while Table 5.5 shows the percentage of the total biomass made up by these species. It can be seen from the latter table that the five most important species constitute 90% of the total biomass at Melkbosstrand, 96% at Rocherpan and 98% at Ysterfontein. These species are *Donax serra* (all three beaches), *Scolelepis squamata* (Melkbosstrand and Ysterfontein), *Excirolana natalensis* (Rocherpan), *Eurydice longicornis* (Melkbosstrand and Ysterfontein), *Pontogeloides latipes* (Rocherpan), *Bullia digitalis* (Melkbosstrand and Rocherpan), *Sigalion capense* (Ysterfontein) and *Gastrosaccus psammodytes* (Rocherpan).

The relative importance of these species is not constant throughout the year as is apparent from Table 5.6 It can also be seen that fluctuations in the total biomass value are mainly caused by changes in the relative importance of *Donax* to the total value. These changes can be ascribed to several factors: seasonal fluctuations, longer term fluctuations of the type described by De Villiers (1975b) and fluctuations caused by patchiness (see chapter 7).

The effects of patchiness have been minimized to a certain extent by the use of a sampling grid stretching a considerable distance (up to 150 m) along the beach (see chapter 2). It is not known what the larger-scale distribution patterns are, however, nor is it known if these patterns are repeated or not. In other words, it is quite possible that patches may be missed even when sampling 150 metre wide strips of beach.

Since the great majority of studies on beaches have been carried out using only one or two transects, however, the results of this

TABLE 5.4 Mean annual biomass per metre strip of beach for each species of macrofauna and total mean annual macrofaunal biomass.

Species	Biomass ($g.m^{-1}$ of beach)		
	Melkbosstrand	Rocherpan	Ysterfontein
Tylos granulatus	16,3330	1,2235	0,3373
Eurydice longicornis	10,3946	0,9238	22,3827
Talorchestia capensis	0,0632	0,4908	0,1219
Scolelepis squamata	76,4707	-	244,4799
Oligochaetes	3,8292	-	-
Pontogeloides latipes	7,2436	2,4537	10,7833
Donax serra	170,5344	76,3281	370,9755
Gastrosaccus psammodytes	2,8697	2,2702	3,5728
Sigalion capense	10,0378	-	11,3975
Pseudharpinia excavata	0,3398	0,6563	0,0379
Excirolana natalensis	0,3733	6,3200	0,7595
Bullia digitalis	18,3323	0,7471	16,4121
Urothoe grimaldii	0,0495	0,0001	0,0071
Cumopsis robusta	0,1622	0,0025	0,0420
Cerebratulus fuscus	0,2100	0,1907	0,1025
Niambia sp.	0,0005	0,0269	0,0034
Nephtys capensis	0,2834	-	0,0688
Total	324,3009	92,4819	682,5707

TABLE 5.5 Percentages of mean annual total biomass for each species. Figures in brackets indicate the five most important species in terms of biomass on each beach.

Species	Percentage of mean annual total biomass		
	Melkbosstrand	Rocherpan	Ysterfontein
Tylos granulatus	5,0364 (4)	1,2967 (5)	0,0494
Eurydice longicornis	3,2052 (5)	0,9989	3,2792 (3)
Talorchestia capensis	0,0195	0,5307	0,0179
Scolelepis squamata	23,5802 (2)	-	35,8175 (2)
Oligochaetes	1,1808	-	-
Pontogeloides latipes	2,2336	2,5970 (3)	1,5798
Donax serra	52,5852 (1)	82,5330 (1)	54,3498 (1)
Gastrosaccus psammodytes	0,8849	2,4548 (4)	0,5234
Sigalion capense	3,0952	-	1,6698 (5)
Pseudharpinia excavata	0,1048	0,7097	0,0055
Excirolana natalensis	0,1151	6,8338 (2)	0,1113
Bullia digitalis	5,6547 (3)	0,8078	2,4045 (4)
Urothoe grimaldii	0,0153	0,0001	0,0010
Cumopsis robusta	0,0500	0,0027	0,0062
Cerebratulus fuscus	0,0651	0,2062	0,0150
Niambia sp	0,0001	0,0291	0,0005
Nephtys capensis	0,0874	-	0,0101
Others	2,0865	0,9995	0,1592
Top 5 species	90,0617	95,7183	97,5208

SPECIES (% OF TOTAL BIOMASS)	MELKBOSSTRAND JUL	NOV	JAN	APR	JUL	OCT	ROCHERPAN AUG	NOV	FEB	MAY	JUL	OCT	YSTERFONTEIN OCT	DEC	FEB	MAY	AUG	NOV
Donax serra	32	57	47	33	85	46	65	40	84	93	74	86	38	14	32	57	82	8
Scolelepis squamata	50	8	34	27	3	17	0	0	0	0	0	0	16	18	60	36	8	67
Bullia digitalis	1	11	6	16	0	2	0	10	0	0	0	0	23	0	2	2	1	2
Tylos granulatus	4	1	7	1	3	20	0	1	7	1	0	1	0	1	1	1	1	1
Eurydice longicornis	3	4	1	9	2	5	1	2	1	1	1	1	13	22	3	2	5	5
Pontogeloides latipes	4	1	1	1	5	2	8	6	2	1	6	2	2	38	1	1	3	2
Excirolana natalensis	1	1	1	1	1	1	16	39	5	3	2	8	1	1	0	1	1	1
Gastrosaccus psammodytes	4	1	1	1	1	1	2	1	1	1	12	1	1	1	1	1	1	1
Sigalion capense	2	5	5	1	1	7	0	0	0	0	0	0	5	7	3	1	1	15
Other species	1	13	1	13	1	1	8	2	1	1	6	2	2	1	1	1	1	1
Total (g)	574	265	362	185	439	268	62	45	52	199	82	40	210	67	671	1339	841	135

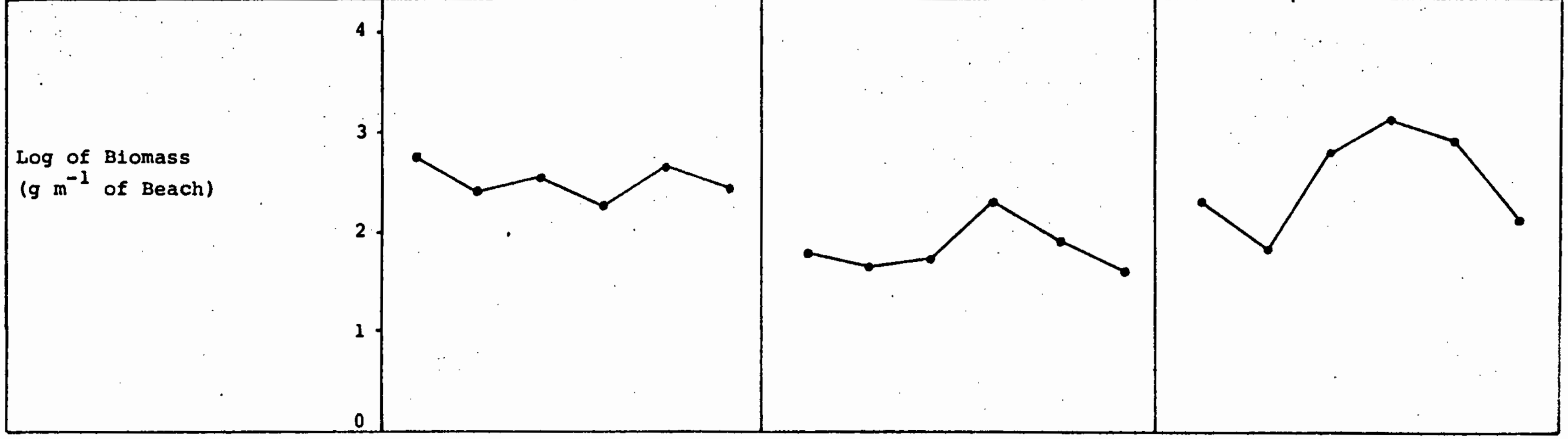


Table 5.6 Seasonal fluctuations in percentage composition of macrofauna and in total biomass (gm^{-1} beach). Percentage values have been rounded off.

study are still comparable with those of other studies. Table 5.7 lists the results obtained both by other workers and from this study for a total of 105 beaches. Although many other beaches have been studied, those investigations were all either of a qualitative nature, or else only single species or groups were studied. It will be seen that the results obtained from the west coast of South Africa fall well within the ranges obtained from other beaches, both in terms of animal densities and biomass.

Tables 5.7 and 5.8 show that there is a fairly general trend in sandy beaches as determined by their degrees of exposure. Although there is considerable variation in all the parameters listed, it should be remembered that nearly all exposure ratings given tend to be subjective. It is quite probable that assessment of exposure differs from one author to another. Secondly, the exposure categories are very broad, covering a wide range of exposures and thirdly, no account is taken of latitudinal variations. For these reasons, the results given in Table 5.8 can only be called trends.

To obtain more definite results, considerably more information is needed. The use of McLachlan's (1980c) scheme for rating exposure would probably give excellent results, given the required data. Even with the information presently available, however, two trends are clearly apparent, these being the increasing diversity of sandy beach species and the increasing fineness of sand associated with increasing shelter. This is to be expected, since sheltered beaches offer more stable environments than do high energy ones. Although these two trends are especially clear, they do not preclude considerable ranges of results within these categories.

The major result of interest in Table 5.8 is the unexpectedly low biomass found on beaches rated as moderately exposed (medium energy). In fact, it seems that high energy beaches generally support higher biomasses than do medium energy ones. One possible reason for this is that high energy beaches have a higher food input than do medium energy ones, while the cost of zonation

TABLE 5.7 Mean grain size, density, biomass, exposure and species diversity values for macrofauna reported in the literature.

Location	Mean Grain size (Ø)	Density		Biomass		Exposure	No. of species	Reference
		m^{-2}	m^{-1} of beach	m^{-2}	m^{-1}			
Dunnet Bay, Scotland	2,15	562		1,171		High energy	11	Eleftheriou & Nicholson, 1975
Sandside, Scotland	1,35	470		0,200		High energy	17	Eleftheriou & Nicholson, 1975
Strathy, Scotland	1,41	192		0,378		High energy	9	Eleftheriou & Nicholson, 1975
North Mist, Scotland	2,15	186		0,100		High energy	12	Eleftheriou & Nicholson, 1975
Barra 1, Scotland	1,80	813		0,453		High energy	15	Eleftheriou & Nicholson, 1975
Loch Ewe, Scotland	2,30	815		1,412		Medium energy	21	Eleftheriou & Nicholson, 1975
Firemore Bay S, Scotland	2,10	584		1,060		Medium energy	18	Eleftheriou & Nicholson, 1975
Firemore Bay N, Scotland	2,29	763		2,287		Medium energy	29	Eleftheriou & Nicholson, 1975
Gairloch 1, Scot	1,80	1232		2,257		Medium energy	26	Eleftheriou & Nicholson, 1975
Gairloch 2, Scotland	2,02	906		1,219		Medium energy	21	Eleftheriou & Nicholson, 1975
Turnberry, Scotland	1,00	2666		3,798		Medium energy	22	Eleftheriou & Nicholson, 1975
Lendalfoot, Scotland	2,51	2069		1,887		Medium energy	30	Eleftheriou & Nicholson, 1975
Port Logan, Scotland	2,51	1612		1,099		Medium energy	20	Eleftheriou & Nicholson, 1975
Barra 2, Scotland	1,00	4292		3,172		Low energy	45	Eleftheriou & Nicholson, 1975
Gruinard, Scotland	2,20	3002		5,906		Low energy	34	Eleftheriou & Nicholson, 1975
Barassie, Scotland	2,75	3081		16,975		Low energy	33	Eleftheriou & Nicholson, 1975
Prestwick, Scotland	2,49	1689		11,135		Low energy	28	Eleftheriou & Nicholson, 1975
Luce Bay, Scotland	2,71	1066		4,369		Low energy	32	Eleftheriou & Nicholson, 1975
Sardinia A, Port Elizabeth, S.A.	1,75			1,778	98,49	Low energy	4	McLachlan, 1977b
Sardinia B, Port Elizabeth, S.A.	1,88			0,158	7,04	High energy	3	McLachlan, 1977b
St Georges Strand, Port Elizabeth, S.A.	1,83			1,769	108,28	High energy	6	McLachlan, 1977b
Maitland River, Port Elizabeth	1,74			118,662	6621,33	High energy	10	McLachlan, 1977b
South Carolina, U.S.A.	2,00	1423				Low energy	56	Holland & Polgar, 1976
St Kilda, Scotland		1300		0,58		High energy	5	McIntyre, 1970
Isla San Andrès, Colombia (Atlantic)	1,45	7,5	45			High energy	3	Dexter, 1974
Playa Bonita, Costa Rica (Atlantic)	1,90	114,1	1597			High energy	7	Dexter, 1974
Limòn, Costa Rica (Atlantic)	2,29	212,9	2981			High energy	7	Dexter, 1974
Cahuita North, Costa Rica (Atlantic)	2,35	28,3	708			High energy	8	Dexter, 1974
Cahuita South, Costa Rica (Atlantic)	1,40	194	2328			High energy	12	Dexter, 1974
Puerto Viejo, Costa Rica (Atlantic)	1,40	56,7	1418			High energy	9	Dexter, 1974
Puerto Colombia, Colombia (Atlantic)	2,09	60,2	361			High energy	8	Dexter, 1974
Santa Marta, Colombia (Atlantic)	1,62	148,4	742			High energy	15	Dexter, 1974
Cartagena, Colombia (Atlantic)	2,60	132,6	2387			High energy	12	Dexter, 1974

Location	Mean Grain size (Ø)	Density		Biomass		Exposure	No. of Species	Reference
		m^{-2}	m^{-1} of beach	m^{-2}	m^{-1}			
Coco, Costa Rica (Pacific)	1,87	1960	58800			Medium Energy	12	Dexter, 1974
Tamarindo, Costa Rica (Pacific)	2,89	847	76230			Medium energy	11	Dexter, 1974
Samata, Costa Rica (Pacific)	2,75	450	58500			Medium energy	7	Dexter, 1974
Puntarenas, Costa Rica (Pacific)	2,10	1218	73080			Medium energy	8	Dexter, 1974
Boca de Barranca, Costa Rica (Pacific)	2,21	203	16240			Medium energy	13	Dexter, 1974
Jaco, Costa Rica (Pacific)	2,43	458	82,440			Medium energy	16	Dexter, 1974
Playa Cocal, Quespos, Costa Rica (pacific)	2,29	215	23650			Medium energy	11	Dexter, 1974
Playa Espadilla, Costa Rica (Pacific)	2,30	1231	110790			Medium energy	9	Dexter, 1974
Juan Chaco, Colombia (Pacific)	2,31	1137	85275			Medium energy	11	Dexter, 1974
Newcastle, Northern Ireland	1,28	805		977 (wet)		High energy	13	Seed & Lowry, 1973
Cloghy, Northern Ireland	1,67	175		789 (wet)		Medium energy	15	Seed & Lowry, 1973
Ballyholme, Northern Ireland	1,80	437		83,72 (wet)		Medium energy	12	Seed & Lowry, 1973
Greyabbey, Northern Ireland	1,95	1256		18,35 (wet)		Medium energy	17	Seed & Lowry, 1973
Kircubbin, Northern Ireland	1,40	387		40,80 (wet)		Medium energy	15	Seed & Lowry, 1973
Dundrum, Northern Ireland	2,63	1447		33,03 (wet)		Low energy	17	Seed & Lowry, 1973
Island Hill, Northern Ireland	2,50	659		721,25 (wet)		Low energy	17	Seed & Lowry, 1973
Panama (Pacific)	2,17	1434	114720	9,132	730,56	High energy	41	Dexter, 1972
Panama (Atlantic)	2,18	228	3192	1,047	14,658	Medium energy	15	Dexter, 1972
Sancoale, Goa, India	2,10			71,448(wet)	2072 (wet)	High energy	11	Achuthankutty, 1976
Whidbey Island, Washington, U.S.A.	1,72-2,31	52	2045	0,265	10,42	Medium energy	58	Webber, 1979
Lindsway Bay, Wales	1,60,			1,01		Medium energy	9	Withers, 1977
Sandy Haven, Wales	2,11			2,50		Medium energy	27	Withors, 1977
Angle Bay, Wales	1,98			9,18		Low energy	15	Withers, 1977
West Angle Bay, Wales	1,94			3,49		Low energy	14	Withers, 1977
Freshwater West, Wales	1,95			0,25		High energy	9	Withers, 1977
Freshwater East, Wales	1,10			0,72		Medium energy	10	Withers, 1977
Tenby, Wales	1,40			0,37		Medium energy	13	Withers, 1977
Saundersfoot, Wales	2,20			3,27		Low energy	24	Withers, 1977
Pendine, Wales	2,43			7,71		Medium energy	36	Withers, 1977
Whitford, Wales	2,00			11,65		Low energy	22	Withers, 1977
Llagennith, Wales	1,35			1,51		High energy	19	Withers, 1977
Rhossil, Wales	2,18			2,48		High energy	32	Withers, 1977
Porteynors, Wales	2,20			1,52		Medium energy	25	Withers, 1977

Location	Mean Grain size (Ø)	Density		Biomass		Exposure	No. of Species	Reference
		m^{-2}	m^{-1} of beach	m^{-2}	m^{-1}			
Oxwich T_1, Wales	2,00			5,92		Low energy	74	Withers, 1977
Oxwich T_2, Wales	2,13			3,75		Low energy	72	Withers, 1977
Oxwich T_3, Wales	1,53			1,36		Medium energy	42	Withers, 1977
Caswell Bay, Wales	1,57			0,38		High energy	12	Withers, 1977
Swansea Bay, Wales	1,45			13,70		Low energy	32	Withers, 1977
Cohin, India	1,87			0,85	11,50	High energy	10	Trevallion et al, 1970
Shertallai, India	2,51			0,73	29,20	High energy	12	Trevallion et al, 1970
King's Beach, Port Elizabeth, S.A.	2,28	13		1,11		Low energy	8	McLachlan, 1977a
Sunday's River, Port Elizabeth, S.A.	?	44		6,39		High energy	11	McLachlan, 1977a
Las Maritas, Venezuela	1,58			1,079	14,70	Medium energy	-	Edwards, 1973a
San Luis, Venezuela	2,18			2,894	20,29	Low energy	-	Edwards, 1973a
Tampico, Mexico (Atlantic)	2,59	27	864			Medium energy	9	Dexter, 1976
Veracruz, Mexico (Atlantic)	2,56	446	8920			Medium energy	3	Dexter, 1976
Champoton, Mexico (Atlantic)	1,21	751	3004			High energy	5	Dexter, 1976
Salina Crus, Mexico (Pacific)	1,13	57	2850			High energy	1	Dexter, 1976
Acapulco, Mexico (Pacific)	0,88	0	0			High energy	0	Dexter, 1976
Santiago Bay, Mexico (Pacific)	1,30	92	3680			High energy	9	Dexter, 1976
Puerto Vallerta, Mexico (Pacific)	1,25	39	468			High energy	1	Dexter, 1976
Mazatlan, Mexico (Pacific)	2,28	103	3296			Medium energy	18	Dexter, 1976
Topolobampa, Mexico (Pacific)	2,20	142	2130			Medium energy	8	Dexter, 1976
Kino Bay, Mexico (Pacific)	1,45	125	6250			High energy	8	Dexter, 1976
Puerto Penasco, Mexico (Pacific)	2,04	149	33525			High energy	16	Dexter, 1976
Chilca, Peru	-			467,9	25734,5	High energy	9	Penchaszadeh, 1971
Singapore	1,50	3823	839231			Low energy	82	Vohra, 1971
Wallis Sands, New Hampshire, U.S.A.	2,25			0,95	110,20	Medium energy	7	Crocker et al, 1975
Long Sands, New Hampshire, U.S.A.	2,25			4,25	70,125	Medium energy	8	Crocker et al, 1975
Foss Beach, New Hampshire, U.S.A.	2,25			0,50	29,50	Low energy	8	Crocker et al, 1975
Frost Point, New Hampshire, U.S.A.	2,25			2,70	140,40	Low energy	20	Crocker et al, 1975
Telok Aling, Penang, Malaysia	0,40	175	4724			High energy	4	Jones, 1979
Telok Bahang, Penang, Malaysia	-0,2	96	3332			High energy	3	Jones, 1979
Telok Kumbar, Penang, Malaysia	0,69	304	8210			Medium energy	4	Jones, 1979
Bagan Jermal, Penang, Malaysia	2,07	1	210			Low energy	2	Jones, 1979

Location	Mean Grain size (Ø)	m^{-2}	m^{-1} of beach	m^{-2}	m^{-1}	Exposure	No. of Species	Reference
Karfas, Chios, Greece	1,32	15	160			Low energy	3	Jones, 1969
Komi, Chios, Greece	0,00	25	352			Medium energy	4	Jones, 1969
Volissos, Chios, Greece	1,09	2	32			High energy	1	Jones, 1969
Villa Gesell, Argentina	-	621	13660			High-med. energy	13	Penchaszadeh & Olivier, 1975
Melkbosstrand, S.A.	2,25	1056	95066	3,6033	324,3009	High energy	17	This study
Rocherpan, S.A.	1,60	149	7283	1,8874	92,4819	High energy	13	This study
Ysterfontein, S.A.	2,31	2579	153945	11,4333	682,5707	High energy	16	This study

TABLE 5.8 Mean values of macrofaunal densities, biomass values, species diversities and mean grain size obtained for beaches of various degrees of exposure.

	High Energy			Medium Energy			Low Energy		
	n	$\overline{x}$	SD	n	$\overline{x}$	SD	n	$\overline{x}$	SD
Density.m^{-2}	30	400	570	30	752	669	12	1 710	1 508
Density.m^{-1}	22	20 045	42 664	18	34 571	37 565	3	2 797 867	4 845 720
Biomass.m^{-2} (g)	20	2,26	3,14	19	1,97	1,71	16	6,23	4,48
Biomass.m^{-1} (g)	10	870,6	2038	5	170,2	300	3	63,4	67
Mean diameter (phi)	39	1,69	0,56	36	1,96	0,60	30	2,07	0,46
No. of species	41	10,8	7,5	39	16,7	11,2	21	30,4	23,3

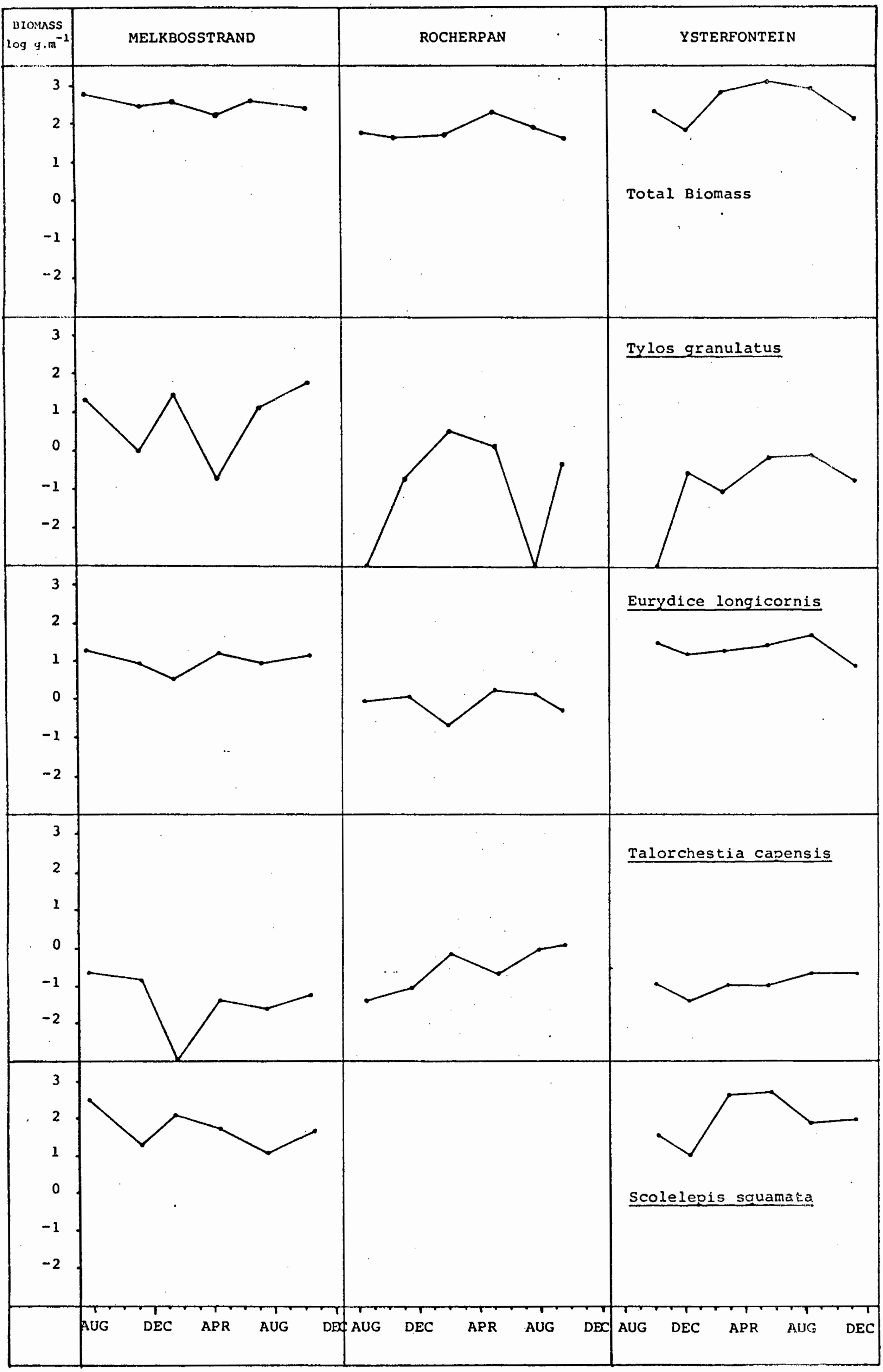
maintenance might not increase to the same degree. High energy beaches also have wider intertidal zones than do moderately exposed ones given the same slope - and this is probably also a factor of importance.

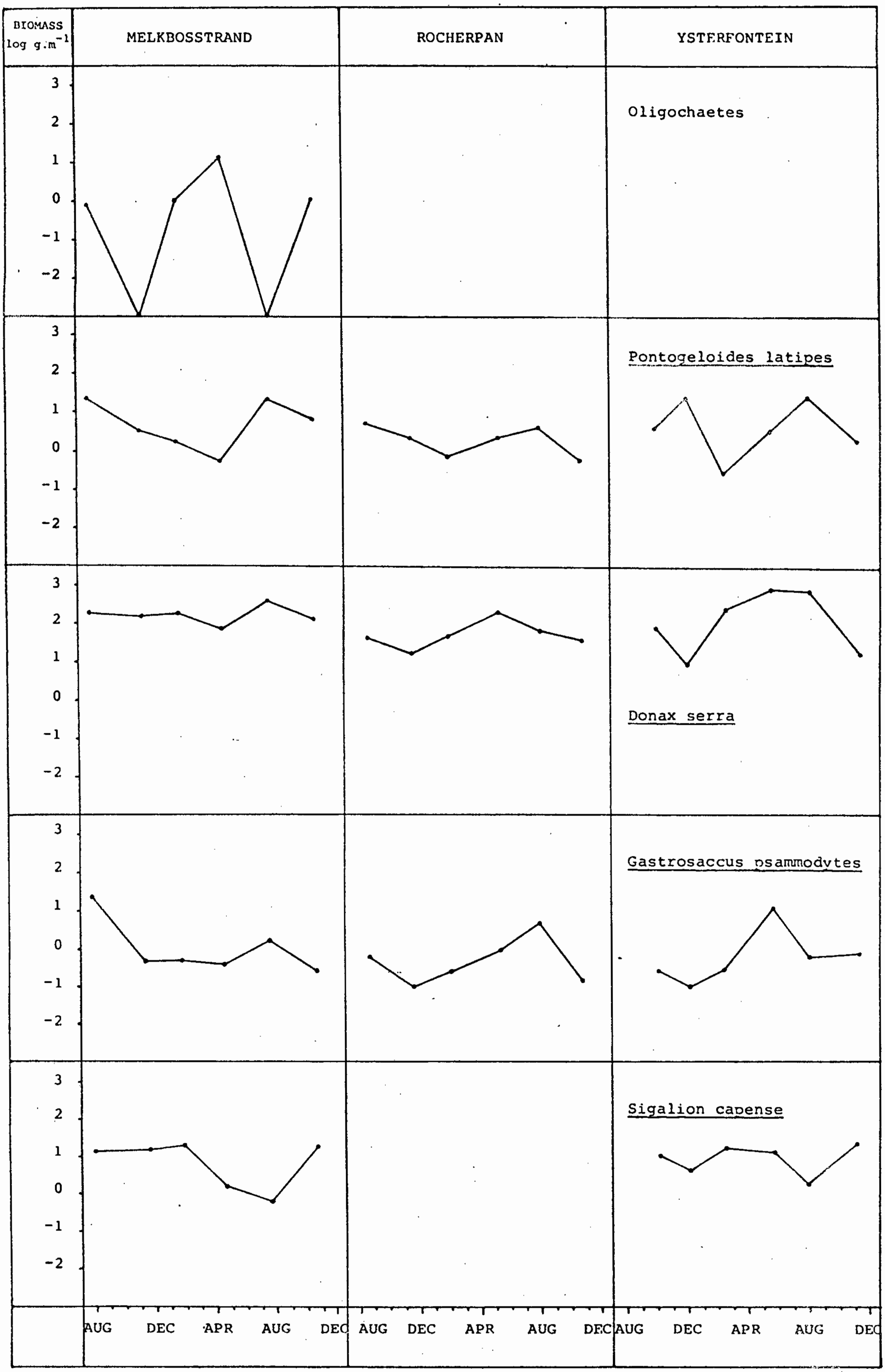
Although the biomass is higher on exposed beaches, densities are lower, implying that larger organisms tend to occupy higher energy beaches than medium energy ones. (Mean masses of organisms are 5,56 x 10^{-3} g on the former type and 2,26 x 10^{-3} g on the latter). Evidence supporting this can be found in chapter 4, where it is shown that juveniles of the bivalve *Donax serra* are only able to occupy the intertidal zone itself once they have reached a certain size. Lack of suitable biomass and density data for sheltered beaches does not permit the calculation of valid estimates.

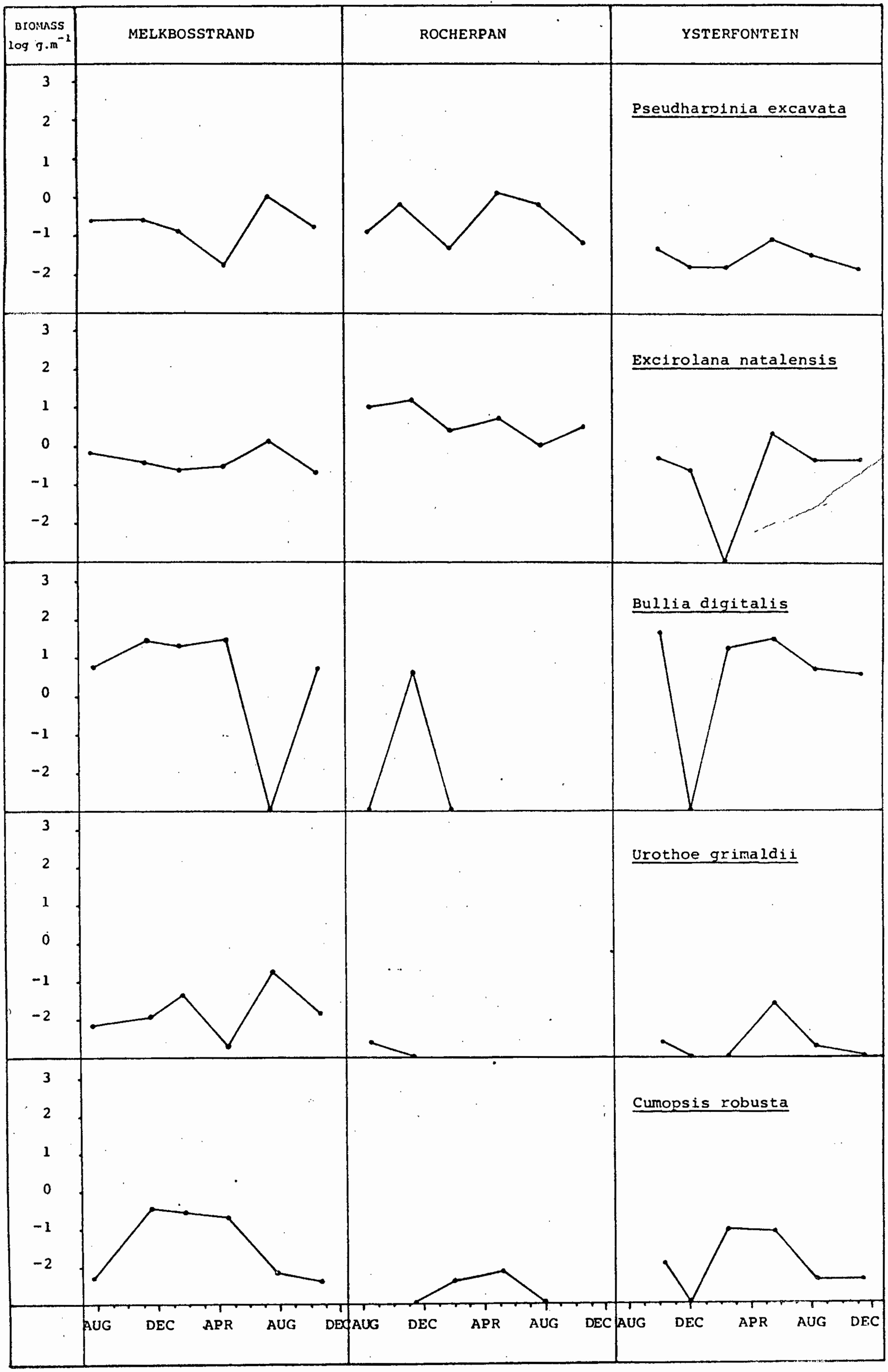
One can conclude from the above, that high energy beaches tend to support larger organisms than medium energy ones. In the main, large animals have a slower turnover than small ones and it seems, therefore, that although moderately exposed beaches support lower biomasses than exposed ones, the annual production of animals on the former type is probably higher.

Figure 5.1 shows the fluctuations of the total biomass during the study period and the biomass fluctuations of the individual species on all three beaches. All species show fluctuations, some of them quite considerable, although no seasonal pattern of fluctuation could be detected in *Tylos*, *Talorchestia*, *Sigalion*, *Excirolana*, *Bullia*, *Urothoe* or *Cumopsis*. A summer biomass peak was found in oligochaetes at Melkbosstrand, while autumnal or early winter peaks were found in *Niambia* and *Nephtys*. The species showing peaks in winter were *Eurydice*, *Scolelepis*, *Pontogeloides*, *Donax*, *Gastrosaccus*, *Pseudharpinia* and *Cerebratulus*. It is very likely that longer term fluctuations are superimposed on these patterns.

Natural populations often show substantial variations in numbers and biomass both seasonally and from year to year. On the west coast,


BIOMASS log g.m^{-1}
MELKBOSSTRAND
ROCHERPAN
YSTERFONTEIN
3
2
1
0
-1
-2
Total Biomass
Tylos granulatus
Eurydice longicornis
Talorchestia capensis
Scolelepis squamata
AUG
DEC
APR
AUG
DEC


BIOMASS log g.m^{-1}
MELKBOSSTRAND
ROCHERPAN
YSTERFONTEIN
Oligochaetes
Pontogeloides latipes
Donax serra
Gastrosaccus psammodytes
Sigalion capense
3
2
1
0
-1
-2
AUG
DEC
APR
AUG
DEC


BIOMASS log g.m^{-1}
MELKBOSSTRAND
ROCHERPAN
YSTERFONTEIN
Pseudharpinia excavata
Excirolana natalensis
Bullia digitalis
Urothoe grimaldii
Cumopsis robusta
3
2
1
0
-1
-2
AUG
DEC
APR
AUG
DEC

Koop (1979) and Koop and Field (1980) found considerable seasonal variations in the rocky-shore isopod *Ligia dilatata*, while Muir (1977) found that both numbers and biomass of the amphipod *Talorchestia capensis* varied not only seasonally, but also according to a longer-term cycle. Such long-term variations have been observed in many organisms including noctuid moths (Swerdfeger in Solomon, 1976), the bivalve *Tellina tenuis* (McIntyre, 1970), the gastropods *Oxystele variegata* and *Littorina africana knysnaensis* and the alga *Gigartina radula* (McQuaid, 1980) to cite only a few examples.

Other studies such as those of Coe (1955), Loesch (1957) and Edgren (1959) have shown large number and biomass fluctuations in various species of *Donax*. Thus it seems likely that sandy beach organisms other than *Talorchestia* and *Donax* are also affected by these longer-term fluctuations.

It is well known that most sandy beach species are highly mobile, a matter of necessity if they are to maintain zonation. Of the species collected on the west coast beaches, only one, *Scolelepis squamata*, is sedentary, but even this species is not obliged to be sessile, and Behrends and Michaelis (1977) have described the tracks left by this polychaete when it moves across sandy surfaces.

Since long-shore distribution has been shown to be patchy (chapter 7), there is a possibility that different populations are being sampled from one season to another. The answer is not known, but it seems most unlikely that, given the fact that long shore transportation of sediments takes place along all beaches, organisms should maintain their positions along the beach as well as in their preferred intertidal zones. The assumption must be made, therefore, that the samples collected are representative of the whole beach and that similar results would be obtained if the same sized samples were collected from other sites along the beach.

The vertical distribution of the macrofauna in the sandy beaches studied are shown in Figure 5.2. This shows that, in the top 30 cm of sand on the beaches, between 47 and 67% of the macrofauna in terms of numbers is concentrated in the top 10 cm of beach sand. The lowest percentage for the top 10 cm (47%) was recorded at Rocherpan, where the coarseness of the sand would be expected to result in more rapid percolation of water through the beach resulting in less water being retained and consequently lower humidity in the top few centimetres. It appears, therefore, as if organisms avoid unfavourable conditions in the uppermost levels of sand at Rocherpan by burrowing deeper. It is also interesting to note that the beach with the finest sediment (Ysterfontein) had the highest proportion of animals in the top 10 cm of sand. On all three beaches, a general decrease in numbers was noted with increasing depth, however.

This contrasts with the vertical distribution of the meiofauna (Figure 5.3), where the distribution continued well below the top 30 cm of sediment, and only some 67% of the meiofauna actually occur in the top 30 cm of the three beaches studied. Similar results have been found by McLachlan and Furstenberg (1977) and Koop and Griffiths (in prep.). Figure 5.4 shows the distribution of meiofaunal biomass over the top 30 cm within the sampling grid for each beach. These results show some of the variations that may occur between samples. One hesitates to compare these results with the studies on macrofaunal patchiness, however, since only 16 samples of meiofauna were taken on each beach as opposed to 32 macrofaunal samples. Nevertheless, it appears that patchiness in distributions of meiofauna are just as prevalent as among macrofauna (see chapter 7).

The results in Figure 5.4 are also of interest in that they show a finer resolution of the vertical distribution, since values are given for every 10 cm instead of every 30 cm in Figure 5.5 and Table 5.9. One final feature apparent in Figure 5.4 is the very low biomass of meiofauna in the top 20 cm of sediment at the low water mark at Rocherpan. This region was subject to wave action

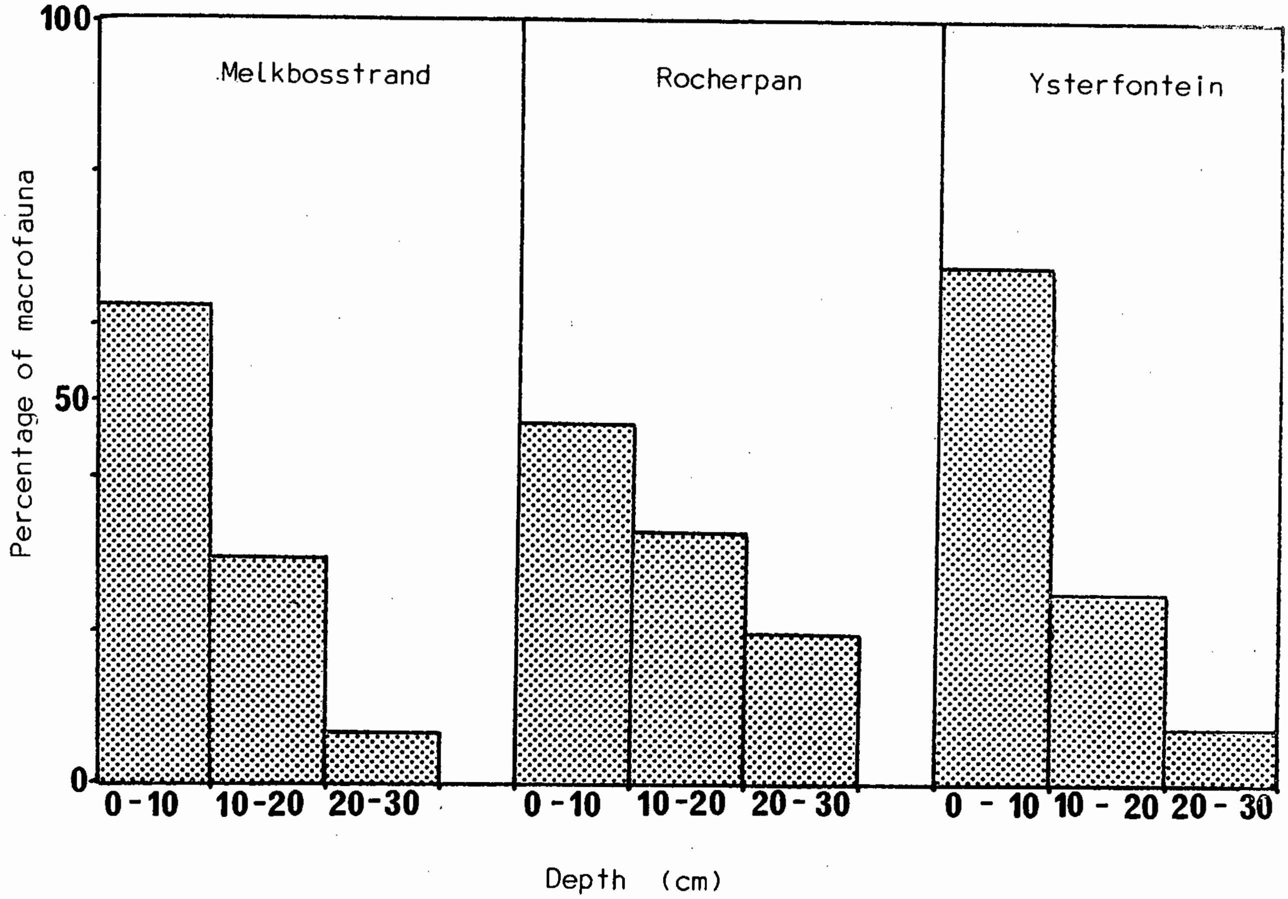


Figure 5.2 Depth distribution of macrofauna in the top 30 cm of sediment.

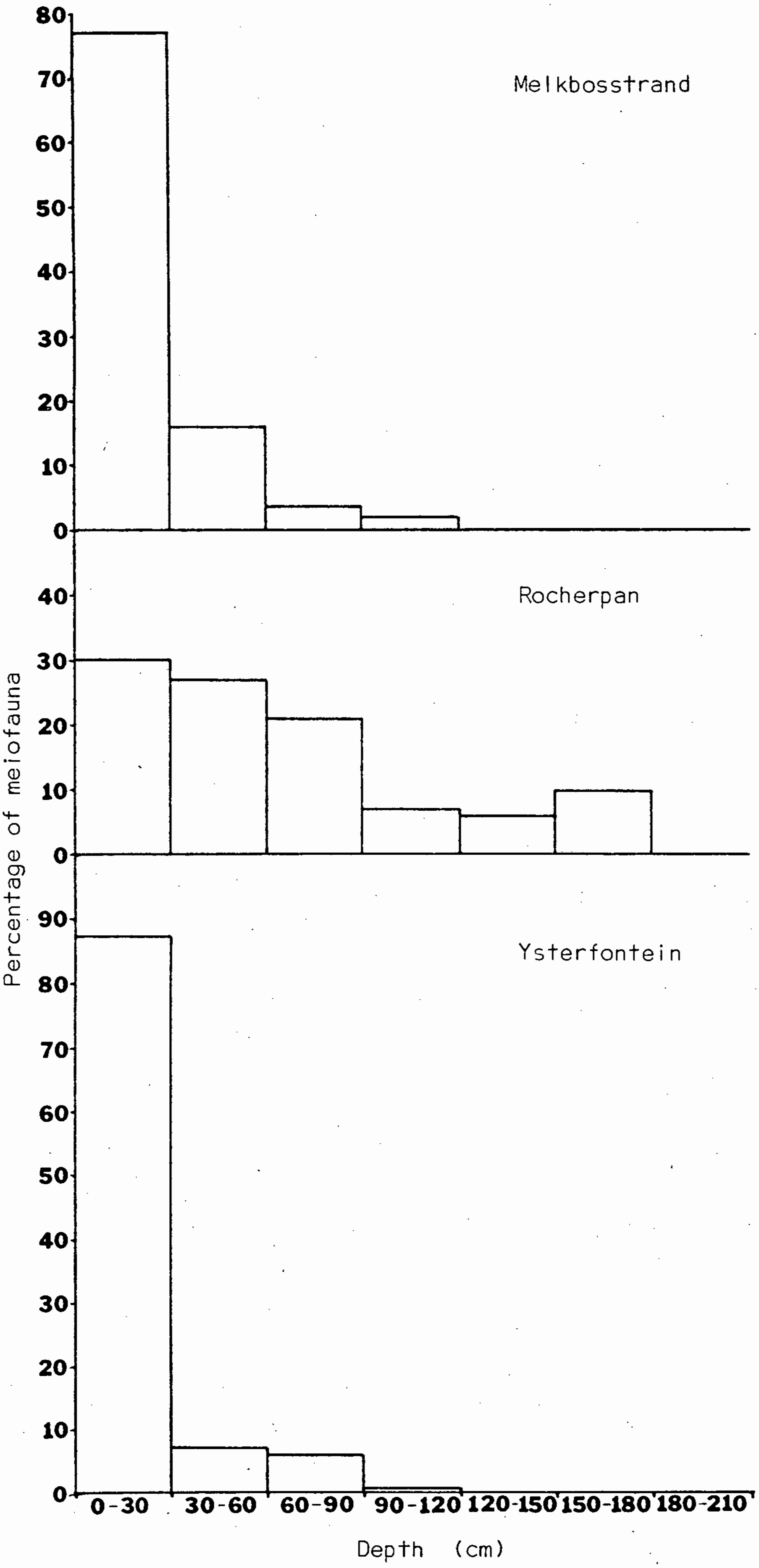


Figure 5.3 Depth distribution of meiofauna on the three beaches.

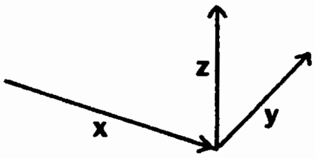
Figure 5.4 Distribution of meiofaunal biomass at the three beaches in the top 30 cm of sediment.

Axes are as follows:

x = distance along the beach

y = distance across the beach

z = biomass of meiofauna (x 5000) in g.m^{-2}.



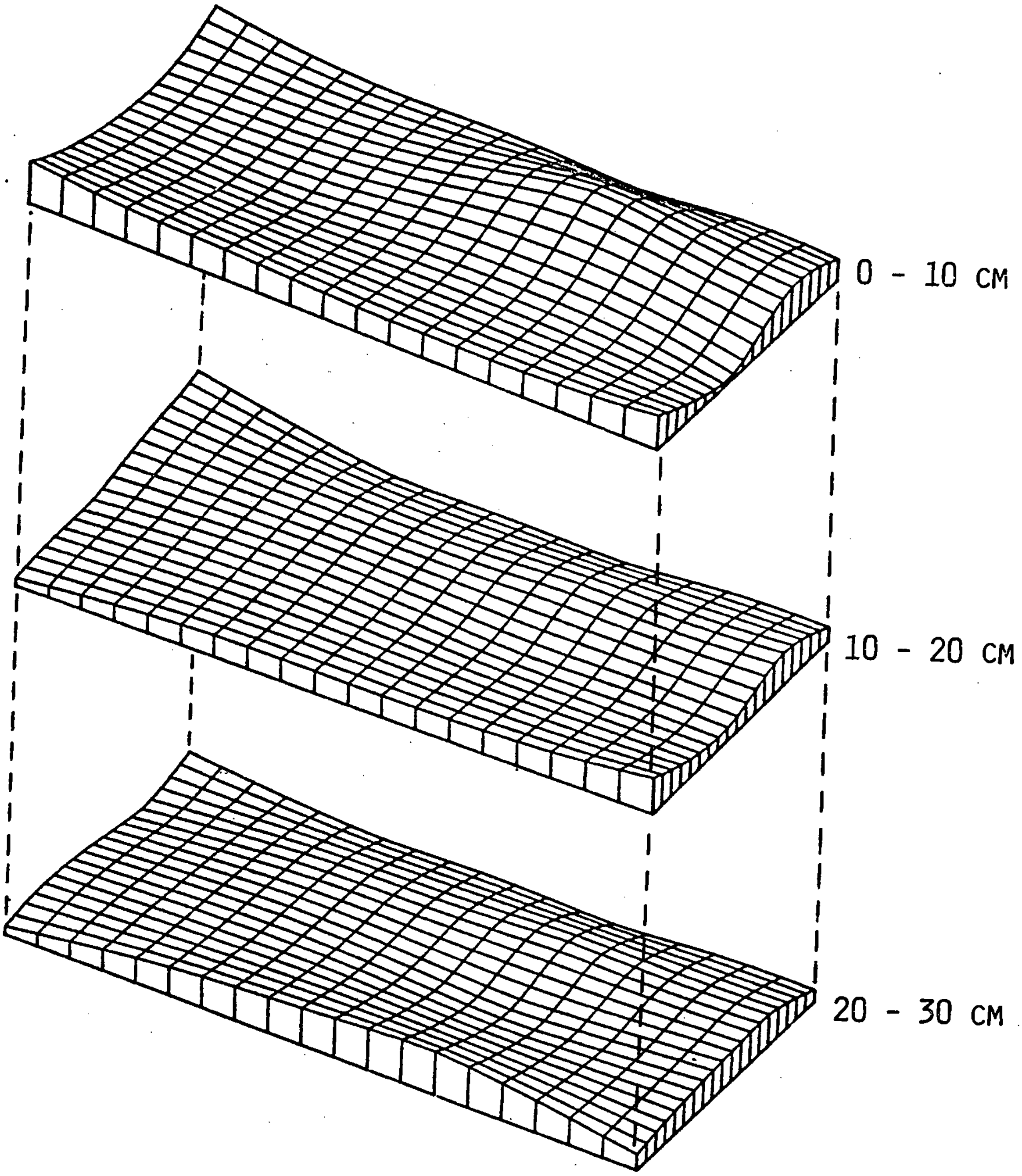


Figure 5.4 Melkbosstrand

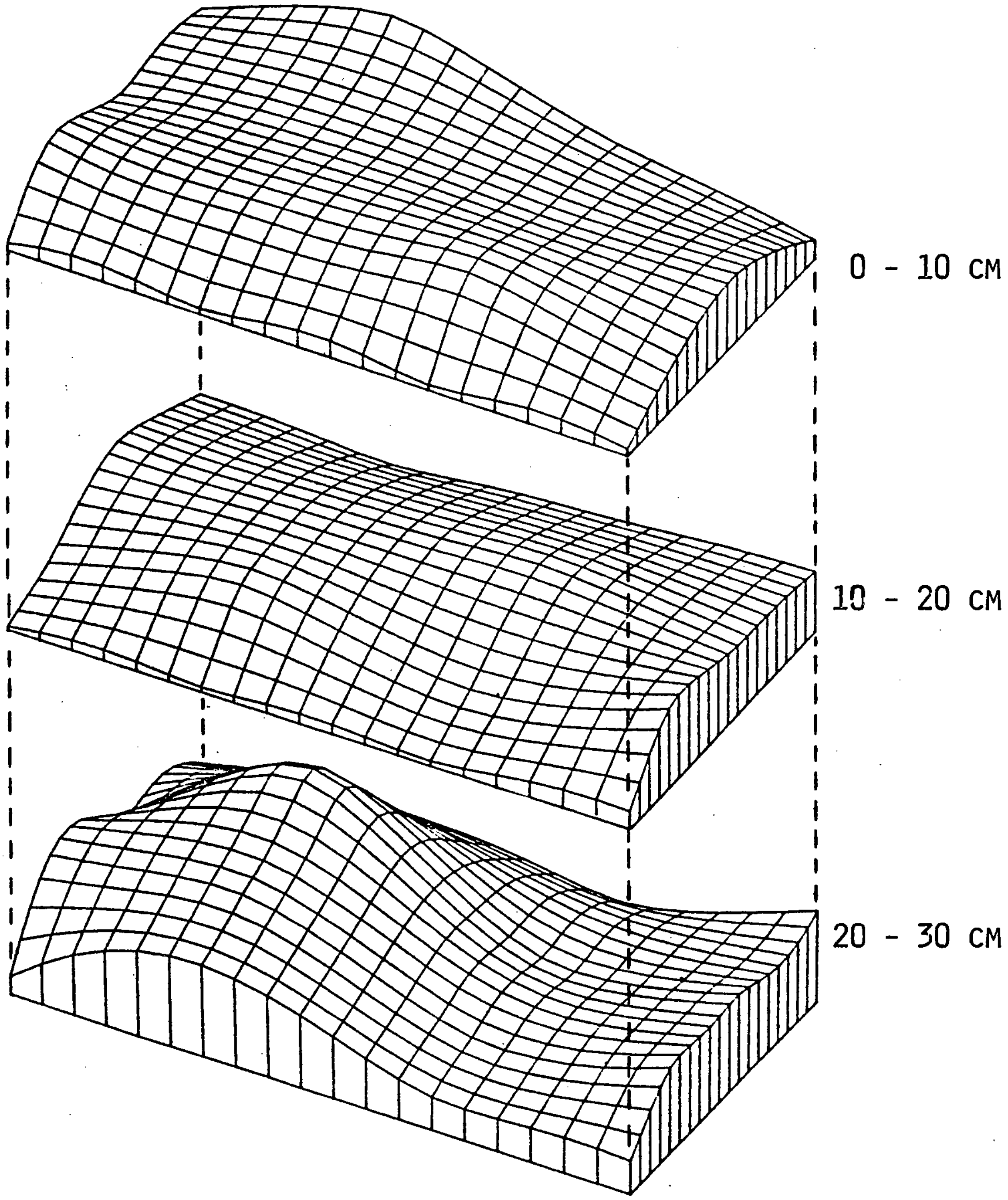


Figure 5.4 (contd) Rocherpan

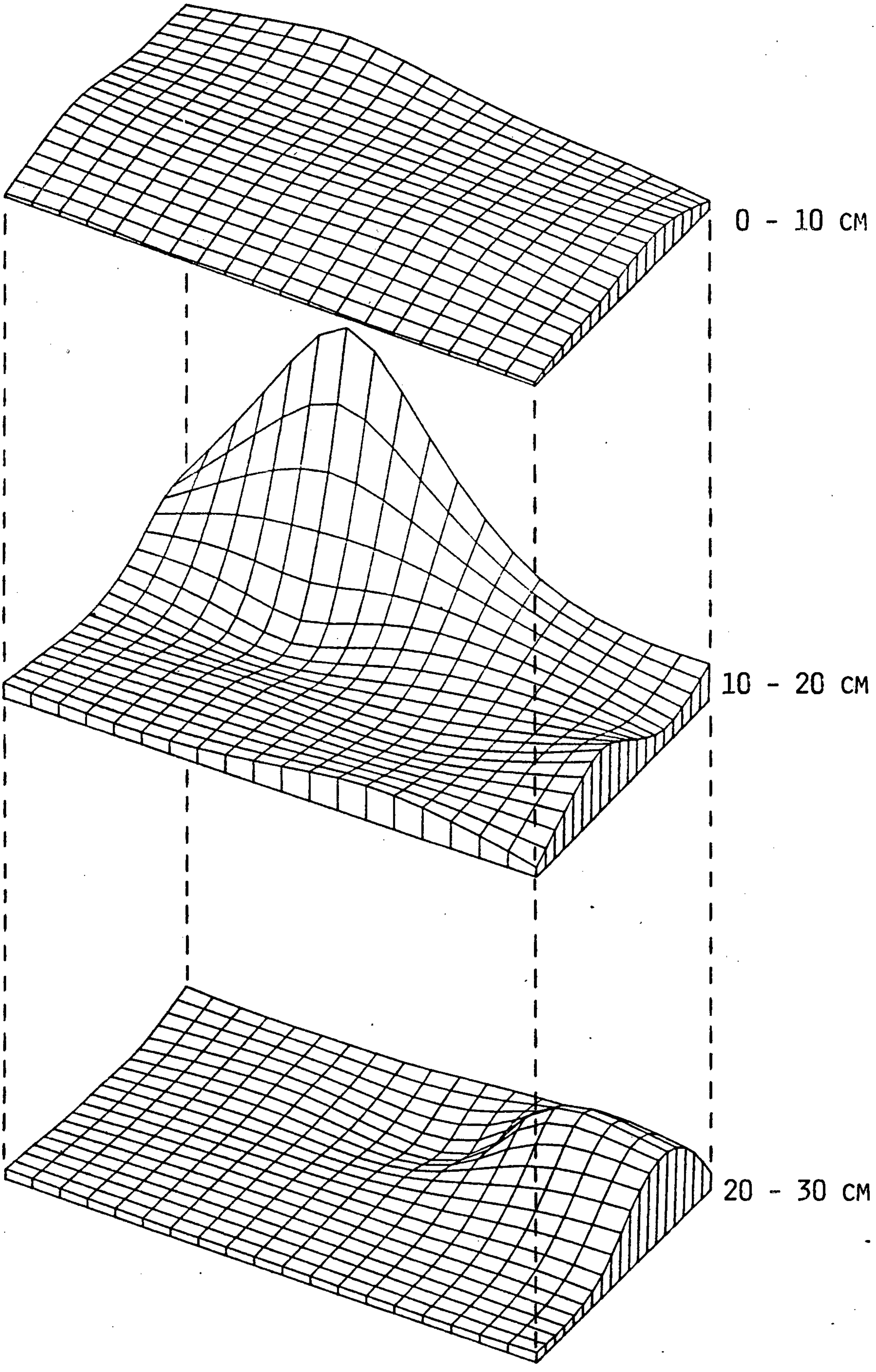


Figure 5.4 (contd) Ysterfontein

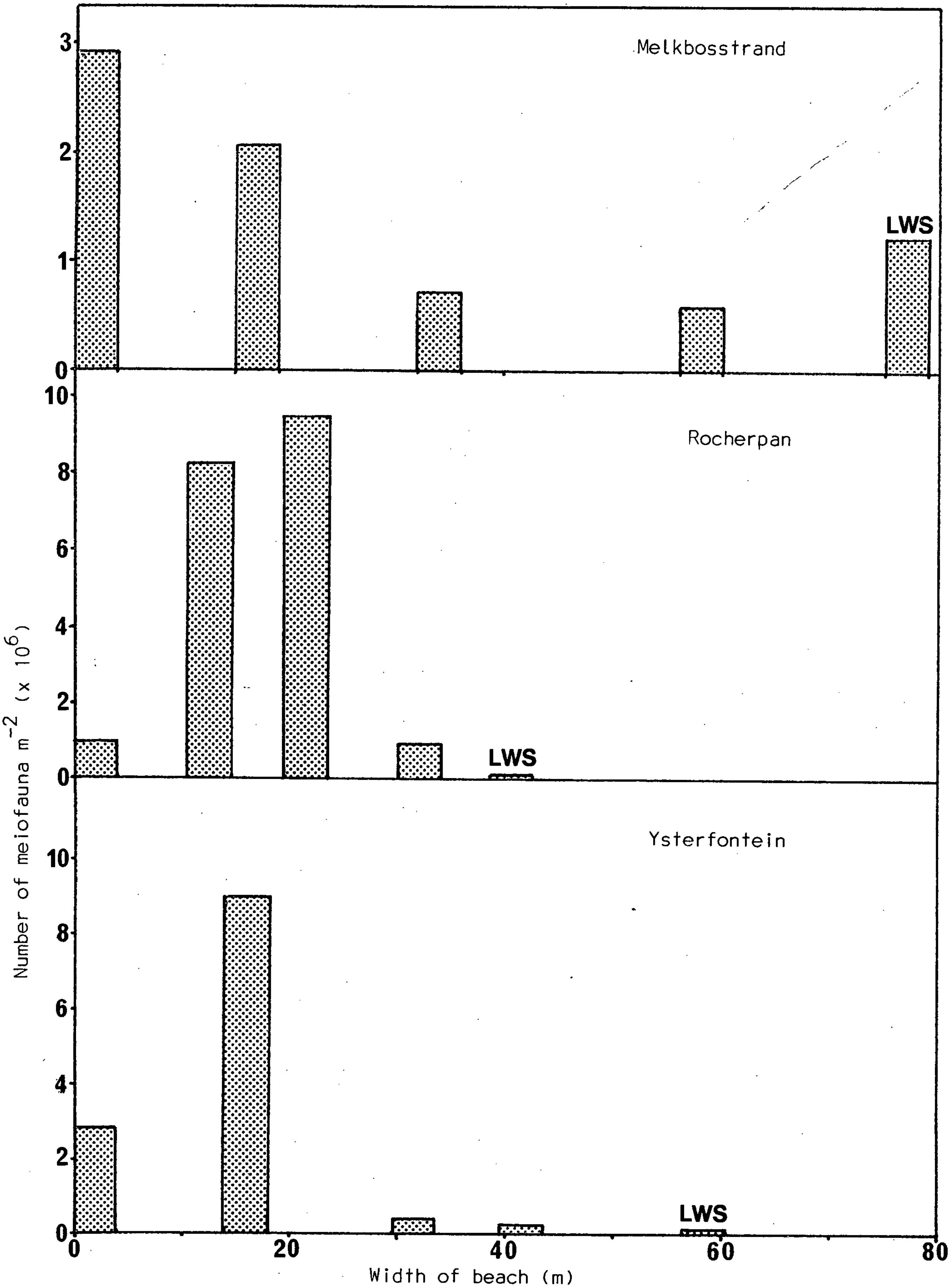


Figure 5.5 Meiofaunal numbers in the top 30 cm of sand across the three sandy beaches. LWS = low water spring tide mark.

TABLE 5.9 Numbers of meiofauna per 100 cm^3 from the three beaches. Values in brackets indicate results from samples below the black, anoxic layer.

Depth of sample (cm)	1 (high water mark)	2	3	4	5 (low water mark)
MELKBOSSTRAND					
0 - 30	757	652	162	196	406
30 - 60	157	39	81		
60 - 90	43	2			
90 - 120	18				
ROCHERPAN					
0 - 30	92	1071	2347	291	22
30 - 60	83	919	812		
60 - 90	63	430			
80 - 110	-	323			
90 - 120	20				
120 - 150	17				
140 - 170	30				
YSTERFONTEIN					
0 - 30	817	1255	59	75	53
15 - 45	-	-	52		
30 - 60	67	1707(12)			
60 - 90	56	(13)			
90 - 120	2				
120 - 150	(0)				

at the time of sampling, and this fact, combined with the coarseness of the sediment, has resulted in the meiofauna either being washed out of the sediment or migrating to deeper levels. This type of migration has been described by McLachlan *et al.* (1977) and Boaden (1968).

In the majority of cases where meiofaunal densities were determined down to the water table (see Table 5.9 for results), the highest densities were found in the top 30 cm of sediment, followed by a steady decrease in numbers until either the water table or (as at Ysterfontein) an impermeable layer of clay was reached that resulted in anoxic conditions. Occasionally, however, these trends were reversed, although no consistent factors could be found to account for such reversals.

When total numbers in the sediment lying between the surface and 30 cm below the water table are plotted (see Figure 5.5), the beaches at Rocherpan and Ysterfontein show low densities at the high and low water marks and high densities in between. At Melkbosstrand, however, the highest values were found at the high water mark and there was a general decrease in densities towards low water (except at low water itself). This distribution is in accordance with the findings of Koop and Griffiths (in prep.) for beaches with high kelp input, and suggests possible similarities with such beaches. The absolute values, however, suggest an impoverishment of meiofaunal densities in the area between the tide marks.

The results for meiofaunal biomass at Melkbosstrand in Figure 5.4 show no such trends, however. The anomalous results may, therefore, be the consequence of unusual circumstances such as the attraction of the mid-beach meiofauna away from the transect line to an adjacent area by decomposing matter in the manner reported by Gerlach (1977) on beaches in Bermuda.

The meiofauna consisted primarily of nematodes, which constituted over 80% of the total numbers. Other groups (in order of decreasing importance) were the harpacticoid copepods (15%), oligochaetes (2%), flatworms, gastrotrichs, polychaetes and amphipods. In addition, several species of diatoms were observed, although it was not known whether these were indigenous to the intertidal area. These included pennate diatoms (similar in appearance to *Synedra*) and triangular centric ones similar to *Entogonia*. The centric species occurred mainly in samples from Rocherpan, while the others occurred on all three beaches.

It is interesting to note the correlation between numbers of harpacticoids and the mean grain sizes of the beaches. In these studies, the greatest densities of harpacticoid copepods were found at Rocherpan (also the coarsest beach) while numbers were substantially lower at Melkbosstrand and Ysterfontein. This is in agreement with other studies, such as those of Bally *et al.* (1980), McLachlan and Furstenberg (1977) and McLachlan (1978). It appears from these studies that intertidal sands finer than 2,6 phi are virtually devoid of harpacticoids.

Figure 5.6 illustrates the increasing proportion of nematodes in sands of increasing fineness, and the corresponding decrease in importance of harpacticoids. Although the data from the Strand (see Bally *et al.*, 1980) is from a beach in False Bay to the east of the Cape of Good Hope, it nevertheless serves to illustrate the point. The proportions of oligochaetes and flatworms remain relatively constant throughout the spectrum of sediment fineness, as does the proportion of other groups, although the actual composition of this category may vary with the sediment.

The results from the Strand are from sediments near the limit of being capable of supporting meiofauna in terms of fineness (Hulings and Gray, 1976). There was, nevertheless, a substantial meiofauna in most of these sands, with densities of 600 individuals, 100 cm^{-3} being encountered in some sediments. It should be noted that Fricke *et al.* (submitted for publication) found on average a 1:1

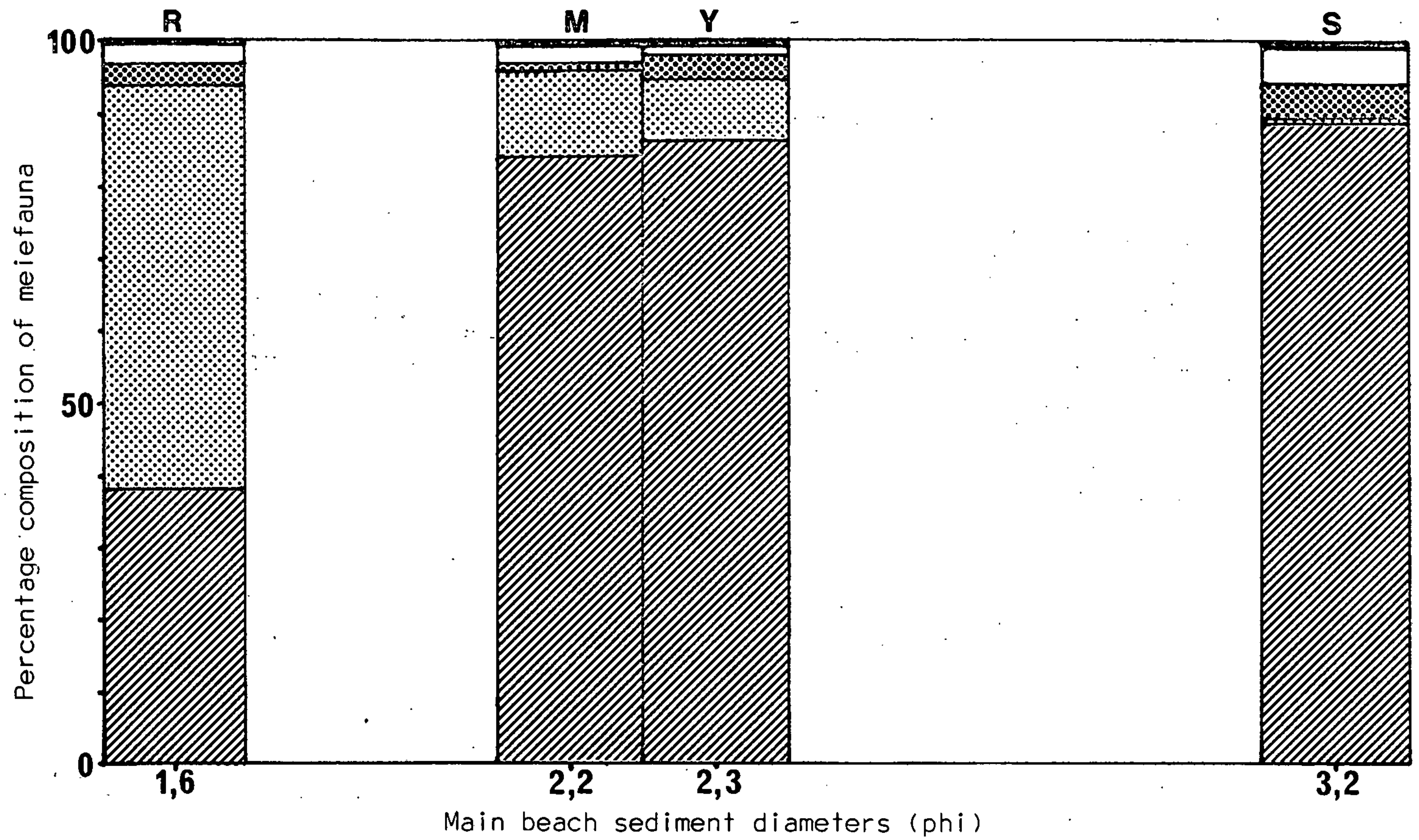


Figure 5.6. Percentage composition of meiofauna. R = Rocherpan, M = Melkbosstrand, Y = Ysterfontein, S = Strand.

▨ = Nematodes ░ = Harpacticoids ▩ = Oligochaetes ☐ = Flatworms

■ = Other groups

ratio of nematodes to harpacticoids (regardless of sediment size) in their study of 10 unpolluted beaches on the south and west coasts of South Africa. Orren *et al.* (in press) note, however, that these beaches were all characterised by a paucity of macrofauna "such as bivalves, polychaete worms and crustaceans", a feature definitely not characteristic of the beaches studied here. The environmental conditions permitting the substantial macrofaunal populations to settle and survive on the beaches described in this thesis may, therefore, also account for the discrepancies between the results obtained in this study and those of Fricke *et al.*

Many workers have referred to a meiofaunal "thiobios" limited to anaerobic conditions (see Wieser, 1975 for a review). One of the major groups in this would be the nematodes, while Wieser (1975) states that harpacticoid copepods appear to be one of the least resistant groups to anoxic conditions. The concept of a meiofaunal "thiobios" limited to the anaerobic sulphide system found in marine sands has recently been rejected by Riese and Ax (1979) and is still being debated (see Boaden, 1980 and Riese and Ax, 1980), but this does not preclude differential resistance to anaerobic conditions between various taxa, and this has been described by Lasserre and Renaud-Mornant (1973). Since fine grained sands have a lower porosity than coarse grained ones (Webb, 1958), the circulation of water through fine sands is consequently slower, resulting in poor oxygenation of these sands. The decrease in harpacticoid numbers with increasing sediment fineness may, therefore, also be a consequence of reduced oxygen availability. Thus physiological as well as the physical limitations discussed by McLachlan (1978) probably affect the composition of meiofaunal populations.

One further possibility concerning harpacticoid-sediment interrelationships is that copepods may prefer particular sediment grades because of the microbes attached to these sediments. This was found by Ravenel and Thistle (1981) in a study on two subtidal species, although the field distribution of one of the species also appeared to be influenced by predation and hydrographic conditions.

The biomass values obtained show that the standing stock of the meiofauna on the three beaches was at least some 2,3 times that of the macrofauna at the time of collection and twice the mean annual macrofaunal biomass. The macro- and meiofauna values are compared in greater detail in Table 5.10, which shows that the relative importance of the meiofauna appears to increase with mean beach sediment diameter. These values only reflect part of the meiofauna's importance, since Gerlach (1971) estimates that meiofauna has approximately three times the turnover rate of macrofauna.

The importance of the meiofauna in terms of biomass and turnover naturally gives rise to the question of whether there is any interaction between it and the macrofauna. McLachlan *et al.* (in press) state that these constitute two systems that are independent of each other. In this view there would be no significant predation of meiofauna by macrofauna, although meiofaunal scavengers would presumably feed on dead and decomposing macrofauna under suitable circumstances.

There is, however, a certain amount of evidence that refutes this view. Warwick and Price (1975) were unable to account for the high biomass and production of *Nephtys hombergi* on the basis of predation on macrofauna alone, and concluded that meiofauna must also form an important part of the diet of that species. Bell and Coull (1978) found that the grass shrimp *Palaemonetes pugio* both preyed on and regulated meiofaunal populations. Riese (1979) found moderate predation by macrobenthic juvenile crabs, hermit crabs, colonial hydrozoans and a polychaete in the Wadden Sea. Hummon *et al.* (1976) found that differential aggregations of meiofauna on a beach in Delaware were associated with the presence of maturing eggs of the horseshoe crab *Limulus*.

Fish are also known to feed on meiofauna and occasionally seem to exert considerable influence on individual species. Thus Sibert (1979) found a close relationship between prey and predator in the case of the copepod *Harpacticus uniremis* and juvenile chum salmon

TABLE 5.10 Meiofaunal biomass values compared with those for macrofauna. Macrofaunal biomass 1 values indicate values at the time the meiofauna was sampled. Macrofaunal biomass 2 values are mean annual values.

Beach	Mean Sediment diameter (Ø)	Meiofaunal biomass		Macrofaunal biomass 1		Macrofaunal biomass 2	
		$g.m^{-1}$ of beach	$g.m^{-2}$	$g.m^{-1}$ of beach	$g.m^{-2}$	$g.m^{-1}$ of beach	$g.m^{-2}$
Melkbosstrand	2,25	625,8143	8,4455	268,3142	3,6280	324,3009	3,6033
Rocherpan	1,60	571,6175	13,5134	40,1190	0,7745	92,4819	1,8874
Ysterfontein	2,31	1277,6031	14,8386	135,2200	1,5705	682,5707	11,4333

(*Oncorhynchus keta*) in a west Canadian estuary. It also appears likely that the mullet ***Liza richardsoni*****,** found on South African coasts, feeds on meiofauna since Masson and Marais (1975) found nematodes, foraminifera and "crustacean remains" in addition to diatoms in the stomach contents of that species, while Blaber (1976) found *Mugil cephalus* feeding on diatoms and some harpacticoids.

The above references show clearly that meiofauna-macrofauna interactions do occur, although they have only rarely been quantified. A considerable amount of study still needs to be undertaken to quantify these relationships, both on sandy beaches and in other environments. The role of the microbial fauna and flora of sandy beaches also needs considerably more investigation, although initial studies have now been carried out. Tietjen (1980) has reviewed the existing knowledge on microbial-meiofaunal interrelationships, but he shows that very little is known on this subject. Tietjen suggests that a substantial proportion of the meiofauna may feed directly on microorganisms, while Meyer-Riel and Faubel (1980) found that high meiofaunal biomasses correlated with low bacterial masses, and vice versa, in agreement with Tietjen's views. Tietjen also proposes secondary interrelationships and it would appear, therefore, that there is a direct link between the meiofauna and the microfauna of sandy beaches. The interrelationships between the three categories of beach fauna, however, remain virtually virgin fields, for the time being.

The range of calorific values in animals is 3,3 to 9,4 kcal.g^{-1} ash-free dry weight (13,81 to 39,35 kJ.g^{-1} ash-free dry weight) according to Cummins and Wuycheck (1971). The results obtained from the sandy beaches on the west coast are presented in Figure 5.7 and all results fall well within this range. Cummins and Wuycheck found the average value to be 5,6 kcal (23,41 kJ) which is slightly lower than the average of 23,94 kJ.g^{-1} found for the species investigated here.

D. Griffiths (1977) mentions that calorific values may depend on

Figure 5.7 Seasonal variations in calorific values (kJ. g^{-1}) and percentage ash (excluding shell weights of molluscs) for the macrofaunal species encountered on the three study beaches.

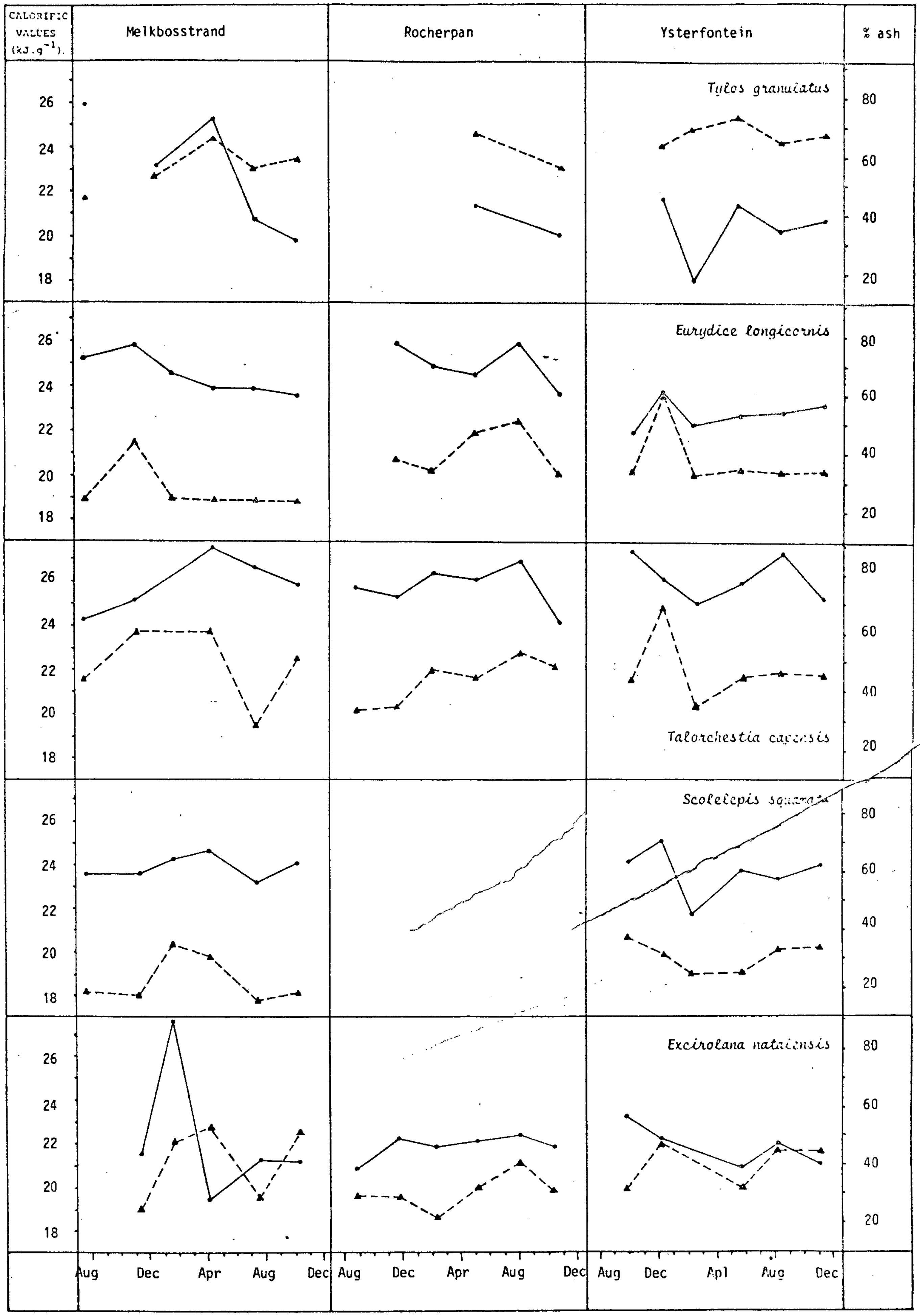

CALORIFIC VALUES (kJ.g^{-1}).
Melkbosstrand
Rocherpan
Ysterfontein
% ash
Tylos granulatus
Eurydice longicornis
Talorchestia capensis
Scolelepis squamata
Excirolana natalensis
26
24
22
20
18
80
60
40
20
Aug
Dec
Apr
Aug
Dec
Aug
Dec
Apr
Aug
Dec
Aug
Dec
Apl
Aug
Dec

Figure 5.7

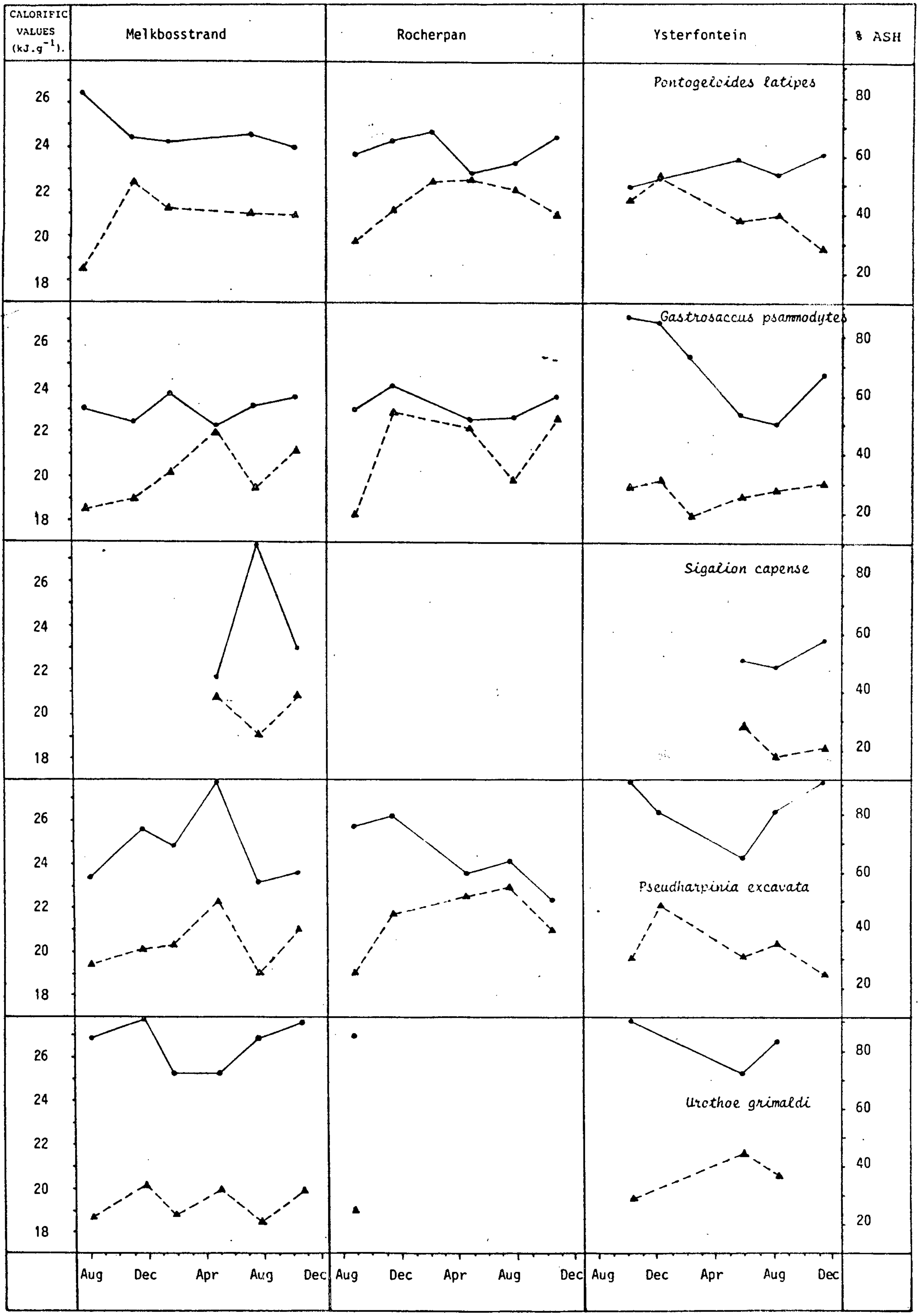

CALORIFIC VALUES (kJ.g^{-1}).
Melkbosstrand
Rocherpan
Ysterfontein
% ASH
Pontogeloides latipes
Gastrosaccus psammodytes
Sigalion capense
Pseudharpinia excavata
Urothoe grimaldi
26
24
22
20
18
80
60
40
20
Aug
Dec
Apr
Aug
Dec

Figure 5.7

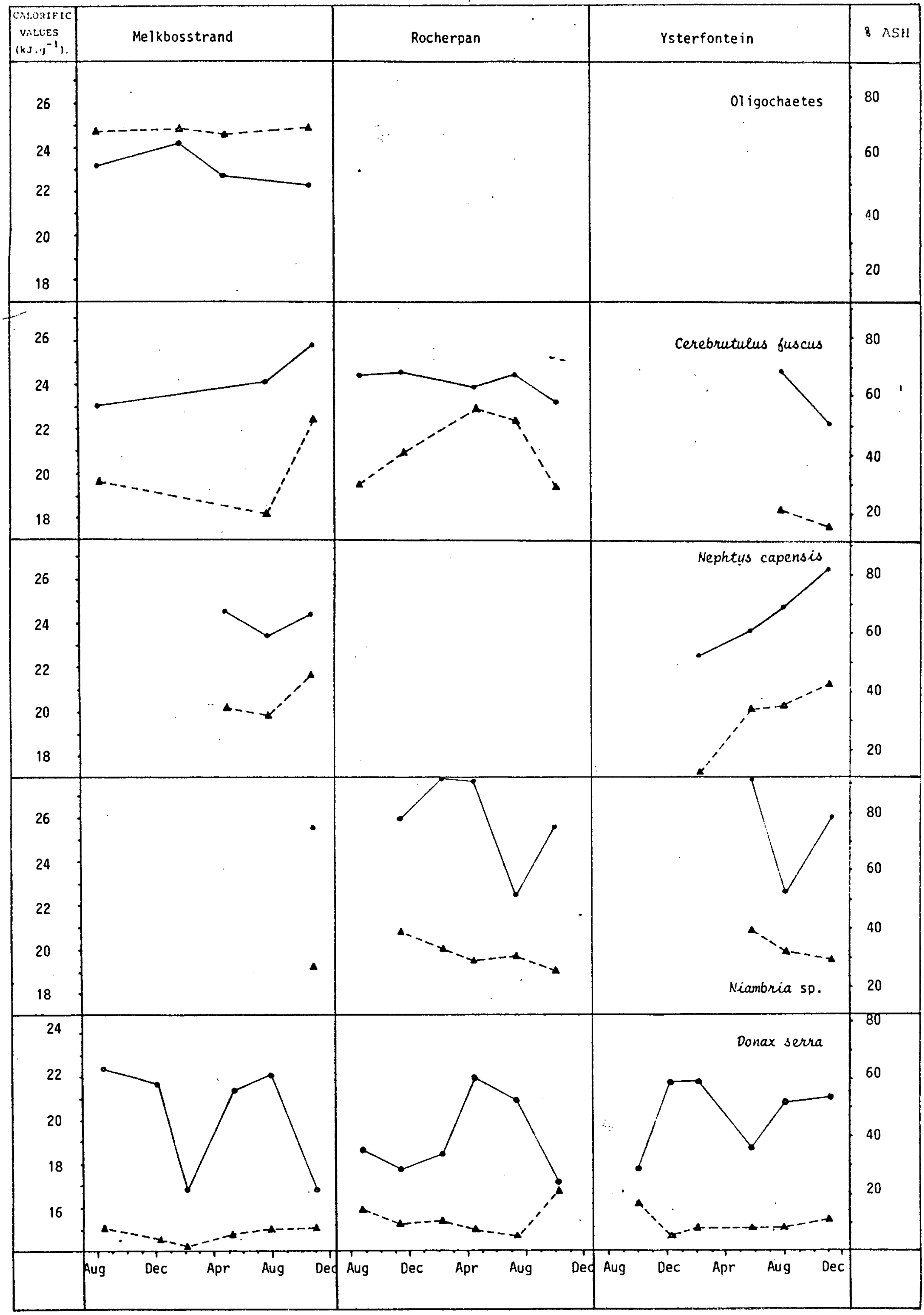

CALORIFIC VALUES (kJ.g-1).
Melkbosstrand
Rocherpan
Ysterfontein
% ASH
Oligochaetes
Cerebrutulus fuscus
Nephtys capensis
Niambria sp.
Donax serra
26
24
22
20
18
16
80
60
40
20
Aug
Dec
Apr
Aug
Dec

Figure 5.7

the size or mass of the animals involved. Figure 5.8 shows the effect of plotting the log of the mean mass of individuals of the various species encountered in this study against their calorific value in $\mathrm{kJ.g^{-1}}$. The results show a correlation between these two parameters which follows the equation:

$$y = 20{,}61 - 1{,}33x$$

where:

x = log of mean individual mass in grams;
y = calorific value in $\mathrm{kJ.g^{-1}}$

The regression coefficient r was 0,69 and was significant (P 0,005).

It appears, therefore, that the calorific value per unit weight of sandy beach organisms is a function of their size, at least within the environmental conditions and size range measured.

One general feature in the results obtained should be noted. This is that the highest calorific values were usually obtained from very small samples - samples so small, in fact, that replicates could not normally be taken to check for possible error. The high values obtained occasionally may, therefore, be a function of the small samples used. There is, however, an alternative explanation: species that show substantial variations in population densities on beaches may not enjoy continuous recruitment and, therefore, as each cohort approaches maturity, the numbers in the cohort decline through natural mortality, while, at the same time, energy is stored in individuals in anticipation of reproduction. This would account for both the high energy values obtained and the small size of the samples collected. Variation in calorific values of this sort has been noted by Prus (1970) for many aquatic animals.

D. Griffiths (1977) found certain differences in calorific values in crustacea that depended on the predictability of their environments and of their food supplies. According to D. Griffiths,

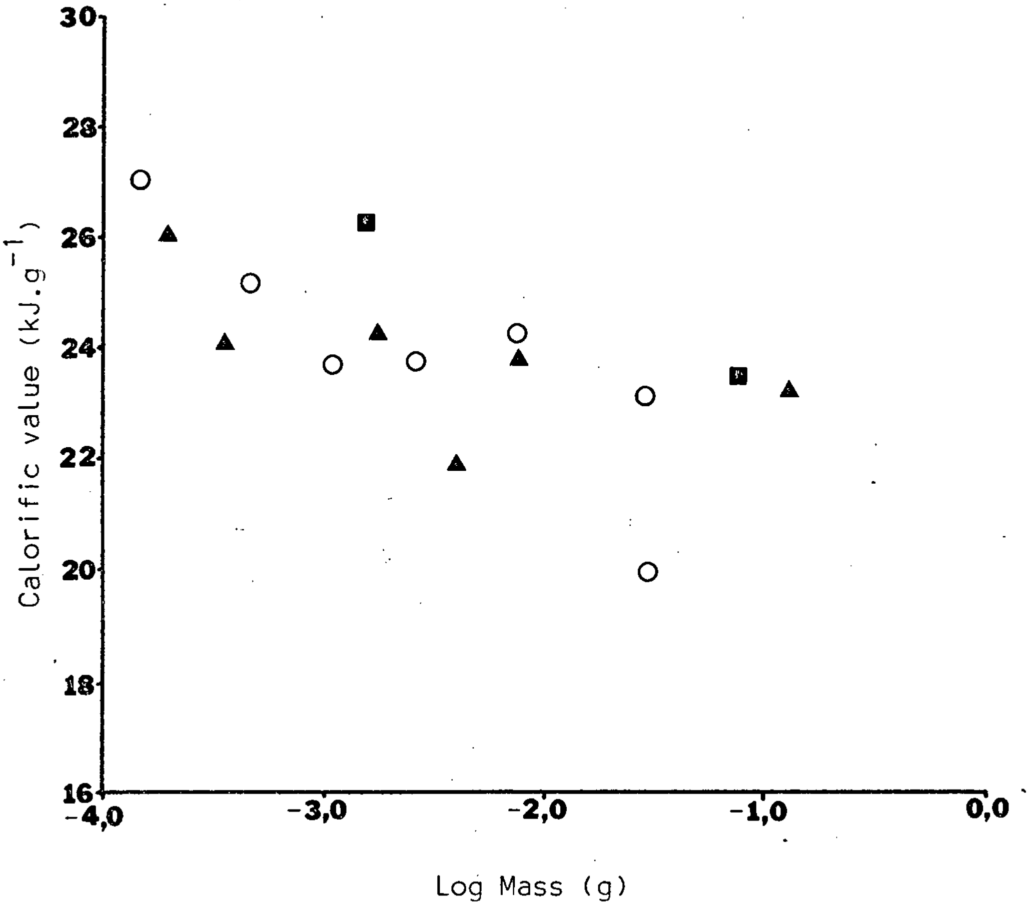


Figure 5.8 Plot of mean individual mass of species against mean calorific value

▲ carnivores and scavengers
○ filter and deposit feeders
■ herbivores

organisms living in environments where food supply was unpredictable would be expected to show a greater variation in calorific values than those enjoying predictable food supplies, and at the same time to have the capacity to develop much higher calorific values. Those animals living in unpredictable environments would be opportunists. From the evidence to hand, Griffiths concluded that this was, indeed, the case.

While no calorific values for the meiofauna were obtained, Sikora *et al.* (1977) obtained a mean value of 6,1174 kcal.g^{-1} ash-free dry weight or 25,44 kJ.g^{-1} AFDW for meiobenthic nematodes. Since nematodes account for over 75% of the meiofauna on west coast sandy beaches, this value is probably a reasonable measure for the whole meiofauna as well.

The food available to organisms on west coast sandy beaches is a relatively unknown factor, at present. Koop (1980) showed a seasonal pattern in the deposition of kelp at Kommetjie, a beach immediately adjacent to large kelp-beds. Although a similar seasonal stranding pattern can be expected on the beaches studied here (since they all face roughly the same direction as Kommetjie), the quantities of kelp deposited would be substantially lower, and the fauna of the beaches is not, in fact, dominated by the deposition of kelp.

One notable feature of west coast beaches, however, is the regular deposition of thick banks of marine foam, especially during the winter months. The origin of this foam is not known, although it is highly probable that it is generated either from kelp beds or phytoplankton blooms. Velimirov (1980) has reported on the formation and chemical composition of kelp-derived foam and found it to be stable for up to two days in nearshore waters after the cessation of onshore winds. This long period of stability means that the foam can be transported over considerable distances by suitable winds and waves before being stranded.

Although no measurements of the foam deposited on the three study beaches were made, substantial quantities were observed to be washed ashore and large banks, up to 40 cm thick, were frequently seen, and on occasion the whole beach was covered with such deposits. Velimirov found bacterial densities of 3,45 x 10^9 cells. ml^{-1} of foam suspension, calorific values of up to 15,39 $kJ.g^{-1}$ ash-free dry weight and biochemical compositions averaging 22,05% protein, 10,76% lipids and 3,07% carbohydrates.

Foam formed in the presence of phytoplankton (Maynard, 1968) following upwelling is probably also deposited on west coast shore when wind directions are suitable. Thus foam is likely to represent a substantial seasonal input into the intertidal sandy beaches on the west coast. This may also be reflected in the generally higher nutrient concentrations found on these beaches (as opposed to those of the south coast) by Orren *et al.* (in press).

The overall results of the studies outlined in this chapter have shown that the beaches of the west coast of South Africa fall within the range of densities and biomasses previously reported for macro- and meiofauna on sandy beaches elsewhere in the world. The beaches studied here, however, rank among the richest, both in terms of density and biomass. This richness may be due to several factors, including their location along a coastline where upwelling occurs regularly enhancing production in nearshore waters, while at the same time being relatively free of deleterious pollution.

CHAPTER 6

RESPIRATORY METABOLISM OF THE DOMINANT ISOPOD SPECIES

Introduction

Respiration can be considered as the process of taking oxygen from the environment and returning carbon dioxide to it (Abercrombie *et al.*, 1973). Most larger marine animals do this through respiratory organs - the gills. Since respiration is an oxidative process in which energy is released by the organism to carry out its life functions, respiration rate is an indirect measure of the energy consumption of life. Respiration has therefore been called "energy expenditure" by Newell *et al.* (1977) and "respiratory metabolism" by Phillipson (1966).

Cirolanid isopods are among the most successful colonizers of the intertidal zones of sandy beaches all over the world (Dahl, 1952). On exposed beaches of the west coast of South Africa, three species are found, these being *Eurydice longicornis*, *Pontogeloides latipes* and *Excirolana natalensis*. These species have wide geographical ranges, *Eurydice* occurring from Lüderitz (Day, 1974) to the Transkei (Branch and Grindley, 1979), *Pontogeloides* from Mauritania (Brian and Darteville,

(1949) to Natal (Day, 1974) and *Excirolana* from the west coast (this study) to Madagascar (Pichon, 1967).

Brown (1971a) has remarked that the isopod *Exosphaeroma truncatitelson* is replaced by *Eurydice* on exposed beaches, while *Pontogeloides*, although present on most beaches in small numbers, seems to be most abundant near rocks. *Pontogeloides* also occurs at the Congo River mouth (Brian and Darteville, 1949) where it adopts a tubiculous habit, in Lake Sibayi (Allanson *et.al.*, 1974) and at the mouths of small estuaries between Cape Agulhas and False Bay. This study has shown that *Excirolana natalensis* partly replaces *Eurydice* on coarser, better-drained beaches (see chapters 4 and 8).

The three species are present on all three beaches studied, although in varying numbers and at different intertidal levels. The most pelagic species is *Eurydice longicornis*, which occupies the zones of saturation, resurgence and retention, particularly at Melkbosstrand and Ysterfontein. *Eurydice* is also found off-shore in large numbers (C. Brownell, pers. comm.). *Pontogeloides latipes* occupies the zones of resurgence and retention at Melkbosstrand and Ysterfontein, and the zone of resurgence and the lower part of the zone of retention at Rocherpan. Finally, *Excirolana natalensis* mainly occupies the zone of drying and retention at Rocherpan, with only a few individuals being found in the lower zones. On the other two beaches, *Excirolana* is only found in very small numbers in the zone of drying.

The three species thus occupy a gradient from the subtidal almost into the terrestrial environment. All are carnivorous and water breathing, but each species encounters different conditions and periods when activity and feeding can take place. A study of the respiratory metabolism of these animals might, therefore, reflect the above-mentioned zonation.

Studies on the respiration of intertidal animals have been numerous, the majority being concerned with rocky shore animals (see Newell, 1976 and

1979 for reviews). Although rocky shore intertidal macrofauna encounter stress periods of similar length to those experienced by sandy beach animals, the nature of the stresses are different and intensities probably much greater.

Respiration studies of sand-beach animals have concentrated on molluscs (e.g. Trevallion, 1971; Ansell, 1973; McLusky *et al.*, 1975; Hanekom, 1975; Edwards, 1973b; Ansell *et al.*, 1978; Brown, 1979; Brown and da Silva, 1979; McLachlan, 1979a; Brown *et al.*, 1978 and Dye, 1979a) and crustaceans (e.g. Edwards and Irving, 1943; Edwards, 1973a; Johnson, 1976b; Ansell *et al.*, 1978; Dame and Vernberg, 1978 and Dye, 1980a). Edwards (1973a) and Shumway (1979) have carried out some of the few studies on soft-shore intertidal polychaete respiration.

The only measurements of respiratory metabolism in cirolanid isopods to date have been those of Johnson (1976b) on *Cirolana harfordi*, an intertidal species; Skjoldal and Bakke (1978a, b) and deZwaan and Skjoldal (1979) on the anaerobic energy metabolism of *Cirolana borealis*, and Shafir (1978) on the respiration of *Cirolana imposita*, a subtital species living in kelp holdfasts.

Methods and Materials

Animals collected from the field were placed in a Gilson Differential Respirometer as soon as possible. Animals were collected from those beaches on which they were most abundant. Thus *Eurydice* and *Pontogeloides* were taken from Melkbosstrand and Ysterfontein, and *Excirolana* from Rocherpan.

After equilibration, respiration readings were taken for periods of six to thirty-six hours. Initially, measurements on each species were recorded for at least 24 hours to determine any activity or respiratory rhythms, as were found by Shafir (1978). Since no consistent rhythms were observed, shorter runs were then carried out.

It was not deemed necessary to acclimatize animals to particular temperatures prior to respirometry, since it was felt that in the field, intertidal animals are never subjected to constant temperatures for longer than a few hours. Dame and Vernberg (1978) have provided quantitative confirmation of this view. Using two species of intertidal crab, they found significant differences in respiration rates between animals that had been acclimatized to constant temperatures and those kept under cyclic temperature regimes prior to the experiments. They concluded that "any previous estimates of the role of oxygen consumption in energy budgets of a species and/or a community might be in error, unless the influence of cyclic temperature on respiration has been determined" (Dame and Vernberg, 1978, p.195).

The problem of monitoring activity levels during the experiment could not be resolved. In an attempt to constrain animals' movements, some runs were made with sand in the flasks into which the isopods could burrow. Runs were made both with and without supernatant water, the latter to simulate conditions at low tide. These runs were made with blanks containing sand only as controls.

After the experiment, animals were killed, measured, dried, acidised, washed, dried again and weighed, in order to determine oxygen consumption against mass. Respiration runs were repeated over a range of temperatures.

Gilson respirometer results must be converted to standard temperature and pressure (273° K and 760 mm Hg) for comparative purposes. The following formula is used:

$$\text{microliters gas exchanged at STP} = \frac{273\ (P - P_w)\ V_g}{760\ T} \quad ....(1)^*$$

where P = barometric pressure in mm Hg,
P_w = vapour pressure of water at temperature T,
T = temperature in K° at micrometer,
V_g = microliters gas change measured with micrometer.

The value for P_w must be looked up in a table. If the water is in contact with the atmosphere (as it was in these experiments), the corresponding vapour pressure is slightly higher. The new value can be obtained by adding a small increment ΔP_w to the value given in the table. ΔP_w is calculated as follows for temperatures between 0 and 40° C:

$$100\ \frac{\Delta P_w}{P_w} = 0{,}0775 - 3{,}13 \times 10^{-4} t \quad ....(2)$$

where t = temperature in °C,

(Washburn, 1928).

A correction is also necessary for T in equation (1). The temperature at the manometer does not necessarily equal the experimental temperature in the water bath. Indeed, the difference between these two

---

* From: Directions for operation, Gilson Differential Respirometer. Gilson Medical Electronics, Inc. Middleton, Wi.

temperatures increases the lower the experimental temperature. For example, if the experimental temperature is 5°C, the temperature at the manometer can range from 25 to 30°C or more due to heat given off by lights and the cooling apparatus. Correcting volumes of gas exchanged to S.T.P. using a T value of 30°C (303° K), therefore, bears very little relation to volume changes in the flask at 5°C (278° K).

It is not realistic either, to use the experimental temperature value for T since the effects of high temperatures on air at the manometer and in the connective Tygon tubing of the apparatus cannot be ignored. The answer obviously lies somewhere between these two extremes.

To obtain a realistic and workable value for T it is necessary to know the volume of air in the flask that is in the water bath at the experimental temperature. This air will have the same temperature as the water bath. The volume of air in the Tygon tubing and below the manometer fluid must also be known, and will have the manometer temperature.

The ratio of volume of air in the flask to total volume of air on the reactive side of the manometer can then be calculated.

$$\frac{V_{\text{manometer}}}{V_{\text{total}}} = a \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots(3)$$

where $V_{\text{manometer}}$ = volume of air in Tygon tubing and manometer,

V_{total} = Volume of air in flask, tubing and manometer,

a = constant for one flask.

T can then be calculated as follows:

$$T = (T_{\text{manometer}} - T_{\text{exp.}})\ a + T_{\text{exp.}} \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots(4)$$

where $T_{exp.}$ = experimental temperature in °K,

$T_{manometer}$ = temperature at manometer in °K.

This new definition of T can be substituted for the one given in equation (1). The importance of this correction is shown in the following hypothetical examples:

Using an experimentally obtained respiration rate of 1000 l 0_2/g/hr at an experimental temperature of 5°C, manometer temperature of 30°C and pressure of 754,00 mm Hg.

a) When T = temperature at manometer in °K.

$$\text{microliters gas exchanged at S.T.P.} = \frac{273\ (P - P_w)\ V_g}{760\ T}$$

$$= \frac{273\ (754{,}00 - 31{,}82)\ 1000}{760 \times 303}$$

$$= 856{,}15 \text{ l } 0_2\text{/g/hr}$$

b) When T = experimental temperature in °K.

$$\text{microliters gas exchanged at S.T.P.} = \frac{273\ (754{,}00 - 6{,}545) \times 1000}{760 \times 278}$$

$$= 965{,}80 \text{ l } 0_2\text{/g/hr}$$

c) When $T = (T_{manometer} - T_{exp.})\ a + T_{exp.}$ as in equation (4).

where a = 0,3.

$$\text{microliters gas exchanged at S.T.P.} = \frac{273\ (754{,}00 - 10{,}87) \times 1000}{760 \times 285{,}5}$$

$$= 935{,}00 \text{ l } 0_2\text{/g/hr.}$$

The value obtained in example a) is 8,4% lower than that in c). The value from b) is 3,3% higher than that from example c), while b) is 12,8% higher than the value from a).

These differences are all important, especially when results are compared with those obtained by other methods. It should be noted that for a given flask size, differences will be greatest at low temperatures and will decrease as experimental temperature approaches that of the manometer. At any given temperature, the differences will increase the smaller the ratio of volume of tubing and manometer to total volume (i.e. a) becomes.

The results obtained were converted to mass-specific respiration rates. An immediate problem was that there were no regular periods of high or low activity. Each hourly reading consisted of oxygen consumptions from animals that were active or inactive to varying degrees. Mean rates showed wide scatters and it was often not possible to obtain satisfactory mass-specific respiration rate to mass relationships. In order to circumvent this problem, therefore, it was decided to use only the lowest readings obtained from the Gilson as indicative of a low rate that approaches the animal's basal metabolic rate. The degree to which this rate does approach the basal metabolic rate (BMR) is not known, but, as will be explained later the minimum rate is probably a conservative estimate of BMR.

Active rates were obtained as follows: the animals were placed in Gilson flasks and, after equilibration, readings were taken at 10 minute intervals for an hour, after which the flask shaker was speeded up to its maximum rate. This ensured that the animals were agitated to a degree resembling natural conditions as the swash washes across exposed beaches. Readings obtained in this way were consistently high. On occasion, high readings were also obtained prior to shaking, showing that these were not a result of improved gas-exchange brought about by increased shaking.

Regressions of mass-specific respiration rates against mass were obtained separately for active and inactive animals by means of a computer program. Response surfaces for each species and for active and inactive animals were then plotted by the SACLANT contouring and three-dimensional graphics package. Equations for the three-dimensional surfaces and also for the effect of activity (using arbitrary activity values of 0,1 and 100) were obtained with a step-wise regression computer program from the Madison Academic Computing Center.

Results

Figure 6.1 shows the relationships between mass and respiration rate, and between mass and mass-specific respiration rate for a given temperature and level of activity. These relationships may be expressed by equations in the form:

$$R = a\ W^{b} \qquad \text{.........} \ (5)$$

where R = respiration rate (ml O_2/hr),

a = intercept on the y axis,

W = ash-free dry mass of animal (g),

b = exponent,

in the case of respiration against mass, and

$$\frac{R}{W} = a\ W^{b-1} \qquad \text{.........} \ (6)$$

where R/W = mass-specific respiration rate (ml O_2/g/hr).

These can be rewritten as:

$$\log_{10}R = \log_{10}a + b.\log_{10}W \qquad \text{.........} \ (7)$$

and $$\log_{10}\frac{R}{W} = \log_{10}a + (b-1)\ \log_{10}W \qquad \text{.........} \ (8)$$

for equations (5) and (6) respectively.

Table 6.1 shows the equations obtained for all the temperatures and activity levels measured in the three isopod species. The effects of temperature, size and activity on mass-specific respiration rates are shown in Figures 6.2 to 6.7. These figures represent the effects of

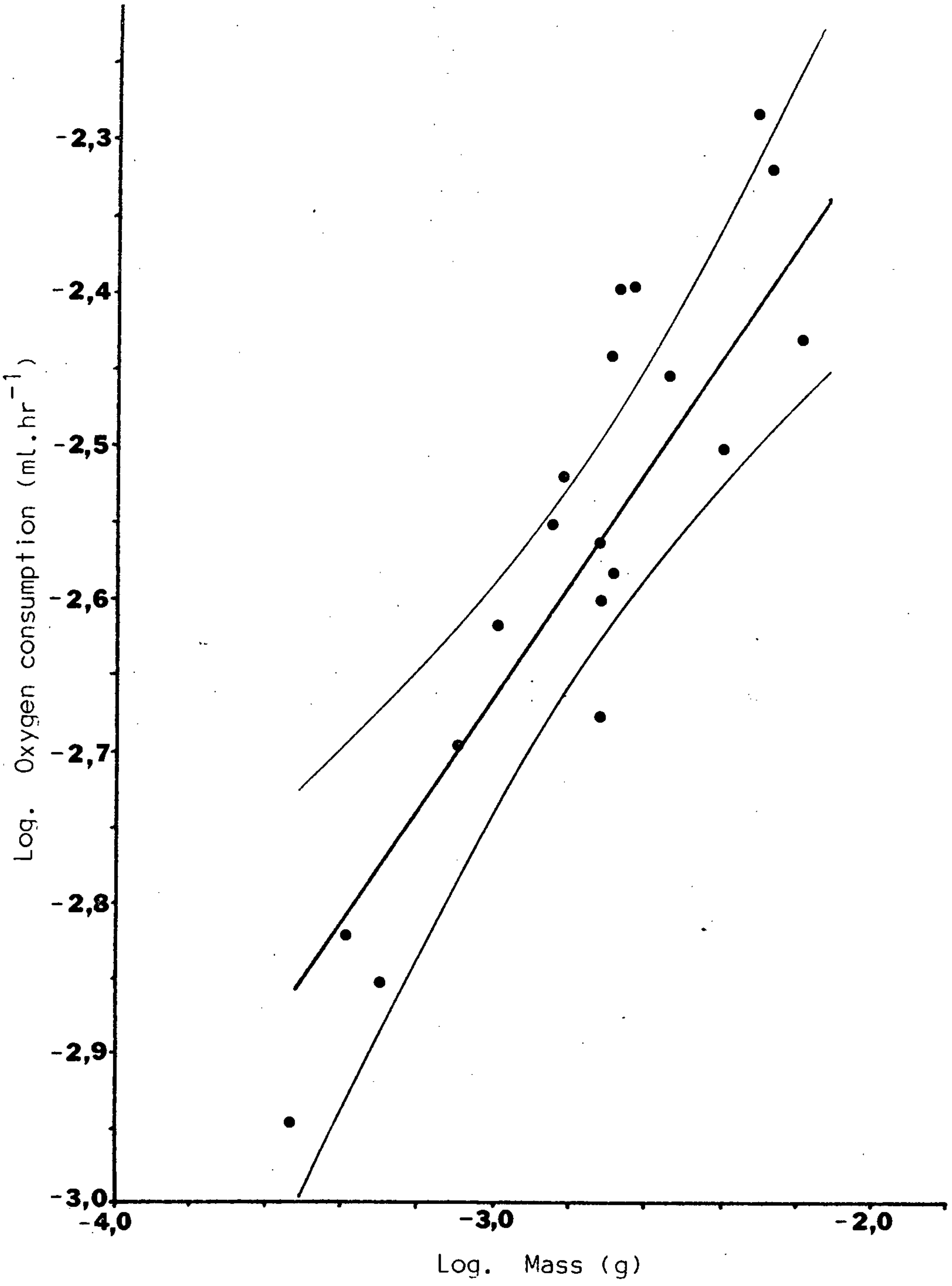


Figure 6.1a: Respiration rate of *Eurydice longicornis* at 10°C. Regression line with 95% confidence limits.

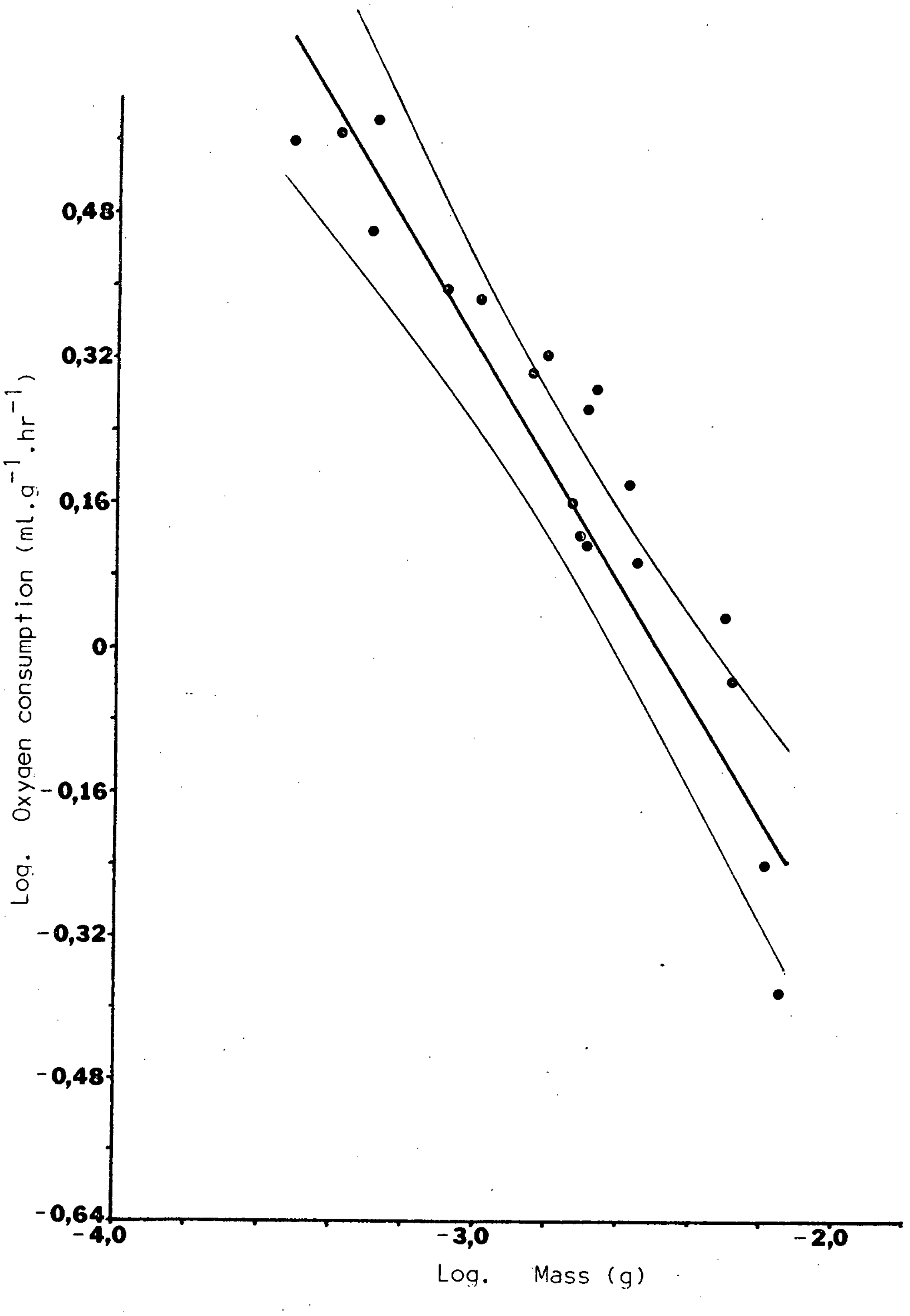


Figure 6.1b: Weight specific respiration rate of *Eurydice longicornis* at 10°C. Regression line with 95% confidence limits.

TABLE 6.1 Equations for mass-specific respiration regression lines in the three species of isopod studied

Species	Temperature (°C)	Activity	Mass specific respiration	r^2
Eurydice longicornis	8,0	0,1	$R/W = 0{,}0092W^{-0{,}75}$	0,950
	10,0	0,1	$R/W = 0{,}0240W^{-0{,}65}$	0,810
	12,5	0,1	$R/W = 0{,}0138W^{-0{,}69}$	0,960
	14,0	0,1	$R/W = 0{,}0316W^{-0{,}60}$	0,895
	16,0	0,1	$R/W = 0{,}0288W^{-0{,}64}$	0,923
	18,0	0,1	$R/W = 0{,}0501W^{-0{,}62}$	0,929
	20,0	0,1	$R/W = 0{,}2218W^{-0{,}45}$	0,768
	6,0	100	$R/W = 0{,}0295W^{-0{,}65}$	0,966
	10,0	100	$R/W = 0{,}2089W^{-0{,}45}$	0,918
	14,0	100	$R/W = 0{,}2388W^{-0{,}43}$	0,955
	16,0	100	$R/W = 0{,}2163W^{-0{,}44}$	0,963
	18,0	100	$R/W = 0{,}1445W^{-0{,}54}$	0,962
	20,0	100	$R/W = 0{,}2761W^{-0{,}51}$	0,924
Pontogeloides latipes	22,0	0,1	$R/W = 0{,}0537W^{-0{,}59}$	0,967
	10,0	0,1	$R/W = 0{,}0092W^{-0{,}49}$	0,986
	12,5	0,1	$R/W = 0{,}0501W^{-0{,}316}$	0,852
	14,0	0,1	$R/W = 0{,}0977W^{-0{,}50}$	0,993
	17,5	0,1	$R/W = 0{,}1107W^{-0{,}55}$	0,975
	20,0	0,1	$R/W = 0{,}0324W^{-0{,}70}$	0,968

continued -

TABLE 6.1 (continued)

Species	Temperature (°C)	Activity	Mass specific respiration	r^2
Pontogeloides latipes (continued)	12,5	100	$R/W = 0{,}5105W^{-0{,}63}$	0,984
	14,0	100	$R/W = 0{,}5420W^{-0{,}63}$	0,987
	15,0	100	$R/W = 0{,}4688W^{-0{,}60}$	0,985
	17,5	100	$R/W = 0{,}6918W^{-0{,}53}$	0,989
	20,0	100	$R/W = 0{,}3105W^{-0{,}66}$	0,992
	22,0	100	$R/W = 0{,}1734W^{-0{,}72}$	0,993
Excirolana natalensis	12,5	0,1	$R/W = 0{,}0076W^{-0{,}76}$	0,988
	14,0	0,1	$R/W = 0{,}0105W^{-0{,}70}$	0,990
	15,0	0,1	$R/W = 0{,}0178W^{-0{,}61}$	0,995
	17,5	0,1	$R/W = 0{,}0110W^{-0{,}81}$	0,967
	20,0	0,1	$R/W = 0{,}0966W^{-0{,}28}$	0,945
	22,5	0,1	$R/W = 0{,}0331W^{-0{,}43}$	0,886
	12,5	100	$R/W = 0{,}1722W^{-0{,}78}$	0,925
	14,0	100	$R/W = 0{,}1330W^{-0{,}86}$	0,953
	17,5	100	$R/W = 0{,}2323W^{-0{,}81}$	0,986
	19,3	100	$R/W = 0{,}1837W^{-0{,}78}$	0,988
	20,2	100	$R/W = 0{,}1578W^{-0{,}53}$	0,879
	22,5	100	$R/W = 0{,}2636W^{-0{,}65}$	0,949

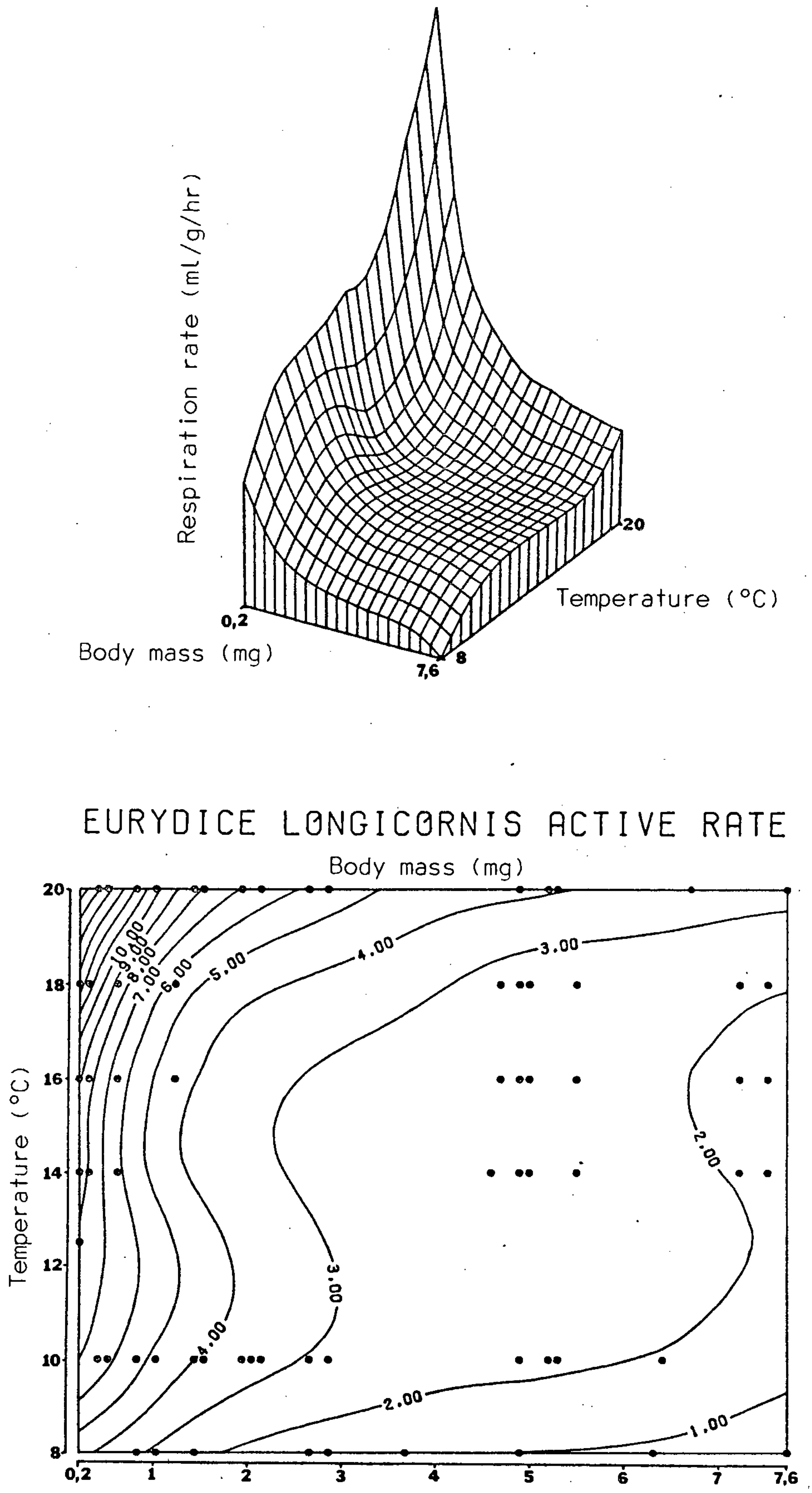


Figure 6.2 Active weight-specific respiration rate of *Eurydice longicornis*. Vertical axis and contour values show weight-specific respiration rate in ml.g^{-1}.hr^{-1}.

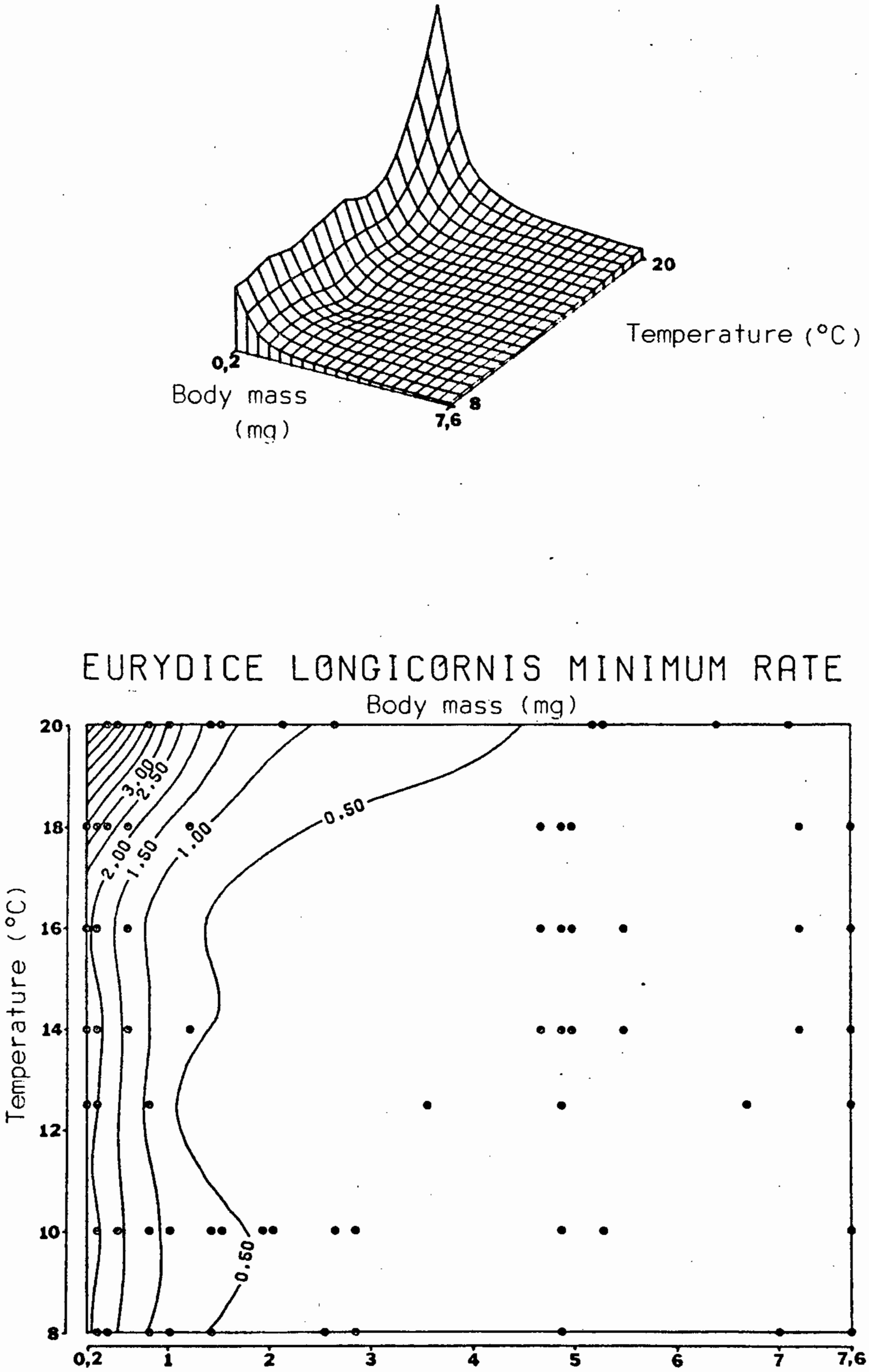


Figure 6.3 Minimum weight-specific respiration rate of *Eurydice longicornis*. Vertical axis and contour values show weight-specific respiration rate in $ml.g^{-1}.hr^{-1}$.

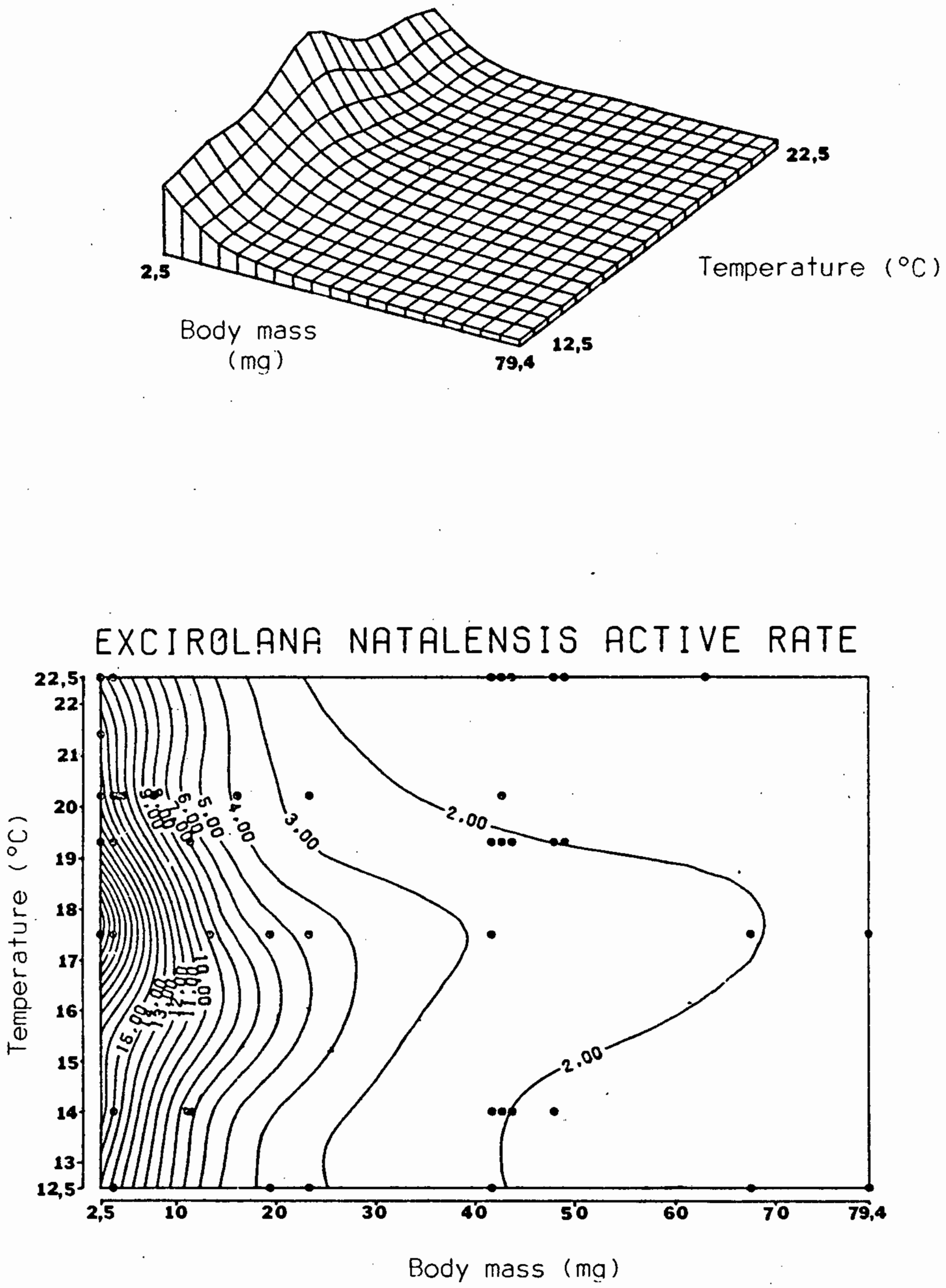


Figure 6.4 Active weight-specific respiration rate of *Excirolana natalensis*. Vertical axis and contour values as for Fig. 6.2

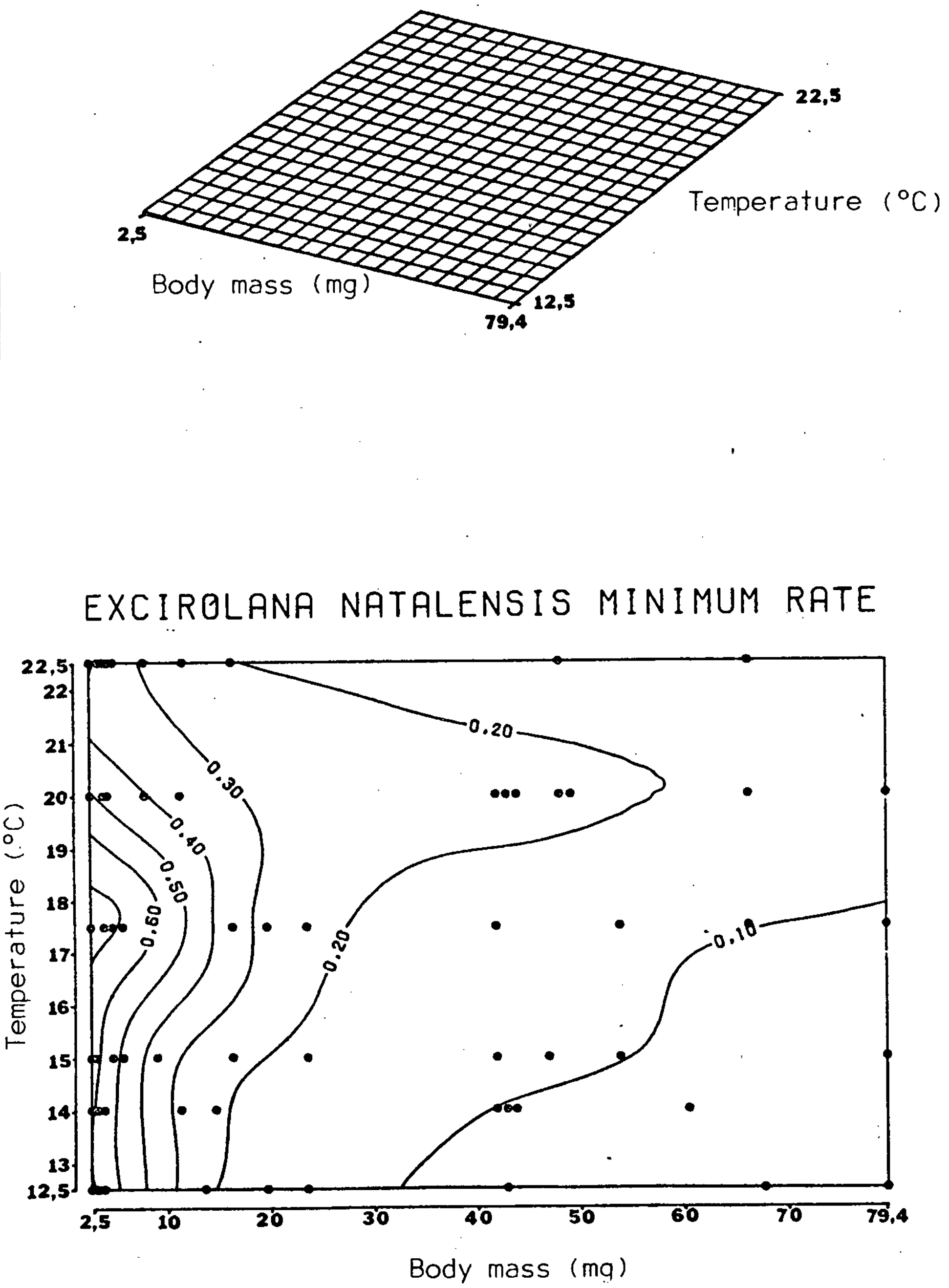


Figure 6.5 Minimum weight-specific respiration rate of *Excirolana natalensis*. Vertical axis and contour values as for Fig. 6.2

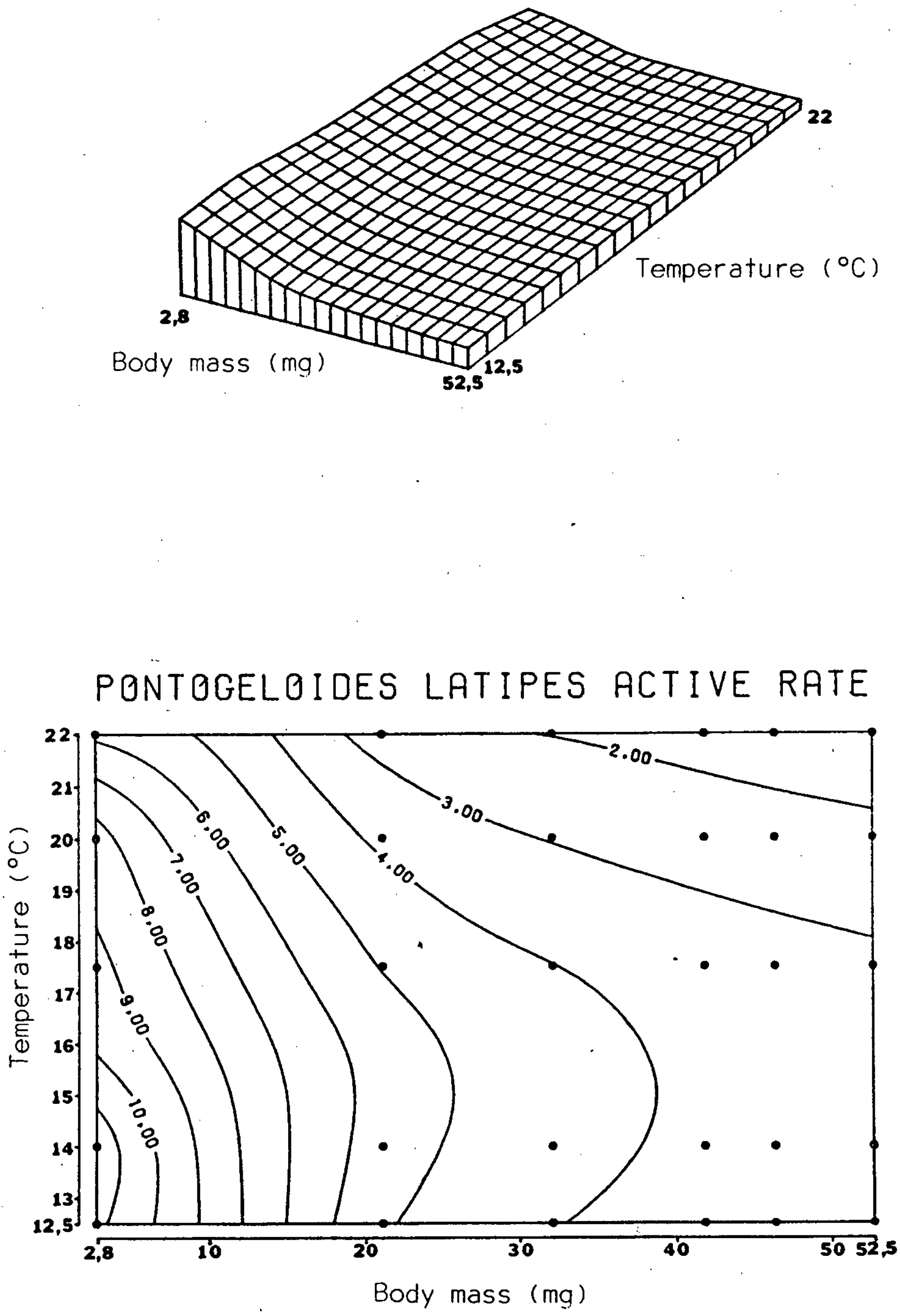


Figure 6.6 Active weight-specific respiration rate of *Pontogeloides latipes*. Vertical axis and contour values as for Fig. 6.2.

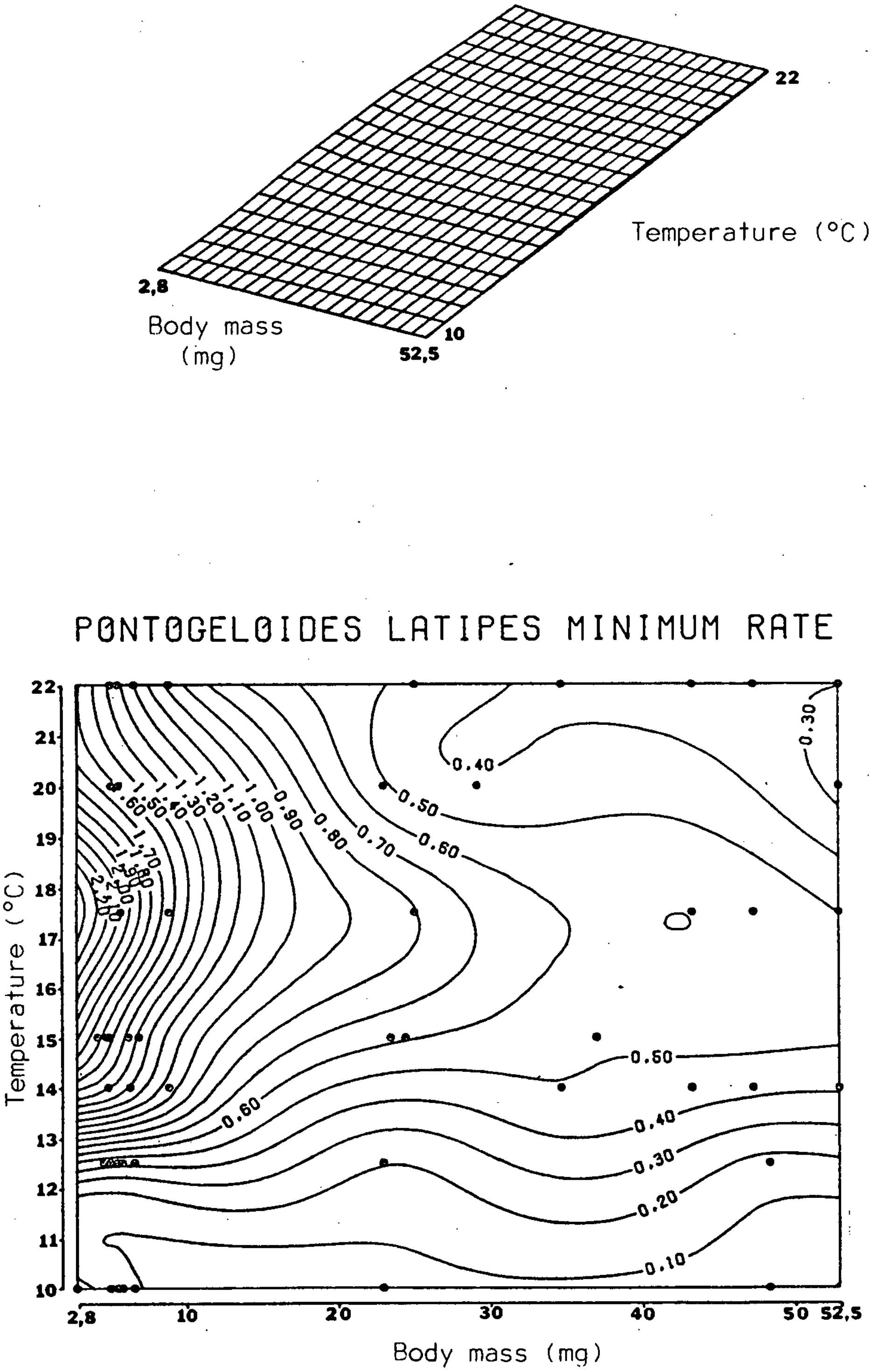


Figure 6.7 Minimum weight-specific respiration rate of *Pontogeloides latipes*. Vertical axis and contour values as for Fig. 6.2

size and temperature in animals with minimal activity (Figs 6.3, 6.5 and 6.7) and in active animals (Figs 6.2, 6.4 and 6.6). As can be seen from these figures, there is a general decrease in mass-specific respiration rates with increasing size in the classical manner discussed by Schmidt-Nielsen (1975). The effects of temperature vary with species.

Using a stepwise regression program, the following equations were obtained for the response surfaces in Figures 6.2 to 6.7.

For active rates of *Eurydice longicornis*:

Log_{10} mass-specific oxygen consumption (ml/mg/hr)

$$\begin{aligned} = &- 15{,}4735 \\ &+ 30{,}0942 \log \text{temp. } (^\circ\text{C}) \\ &- 1{,}8470 \text{ temp. } (^\circ\text{C}) \\ &- 0{,}9506 \log \text{dry mass (mg)} \\ &+ 3{,}7862 \times 10^{-2} \text{ temp.}^2 \\ &+ 3{,}6084 \times 10^{-2} \text{ dry mass} \\ &- 1{,}5590 \times 10^{-4} \text{ temp.}^3 \qquad \text{............(9)} \end{aligned}$$

The multiple correlation coefficient for this equation was 0,9881. This means that the equation accounts for 99% of the variation of the log mass-specific oxygen consumption in the data on which the formula is based.

For inactive rates of *Eurydice longicornis*:

Log mass-specific respiration rate

$$\begin{aligned} = &-3{,}4796 \\ &+8{,}2382 \log \text{temp.} \\ &-4{,}9684 \log \text{dry mass} \end{aligned}$$

continued -

$$\begin{aligned}
&+ 1{,}1392 \text{ dry mass} \\
&- 0{,}5491 \text{ temp.} \\
&- 0{,}1363 \text{ dry mass}^2 \\
&+ 1{,}1195 \times 10^{-2} \text{ temp.}^2 \\
&+ 7{,}2650 \times 10^{-3} \text{ dry mass}^3 \text{ ....} (10)
\end{aligned}$$

(Multiple correlation coefficient for equation (10) = 0,9504.)

For active rates of *Excirolana natalensis*:

Log mass-specific respiration rate

$$\begin{aligned}
= &+ 327{,}5374 \\
&- 635{,}1482 \log \text{ temp.} \\
&+ 44{,}9607 \text{ temp.} \\
&- 1{,}2946 \text{ temp.}^2 \\
&- 0{,}2751 \log \text{ dry mass}^3 \\
&+ 1{,}6570 \times 10^{-2} \text{ temp.}^3 \\
&+ 2{,}8740 \times 10^{-3} \text{ dry mass} \text{ ....} (11)
\end{aligned}$$

Multiple correlation coefficient for equation (11) = 0,9947.

For inactive rates of *Excirolana natalensis*:

Log mass-specific respiration rate

$$\begin{aligned}
= &+ 7{,}4829 \\
&- 11{,}5587 \log \text{ temp.} \\
&+ 0{,}5587 \text{ temp.} \\
&- 0{,}3812 \log \text{ dry mass} \\
&- 0{,}9144 \times 10^{-4} \text{ temp.}^2 \\
&+ 0{,}7652 \times 10^{-4} \log \text{ dry mass} \times \text{temp.} \\
&- 0{,}1208 \times 10^{-4} \text{ dry mass} \text{ ....} (12)
\end{aligned}$$

(Multiple correlation coefficient for equation (12) = 0,9512.)

For active rates of *Pontogeloides latipes*:

Log mass-specific respiration rate

$$\begin{aligned} = &+ 0{,}2913 \times 10^{-4} \\ &+ 1{,}9788 \log \text{temp.} \\ &- 0{,}7145 \log \text{dry mass} \\ &- 0{,}0339 \text{ temp.} \\ &- 0{,}3045 \times 10^{-2} \text{ dry mass} \\ &- 0{,}4367 \times 10^{-4} \text{ temp.}^3 \qquad \ldots\ldots\ldots\ldots\ldots (13) \end{aligned}$$

(Multiple correlation coefficient for equation (13) = 0,9977.)

For inactive rates of *Pontogeloides latipes*:

Log mass-specific respiration rate

$$\begin{aligned} = &+ 1202{,}6000 \\ &- 2{,}5193 \times 10^{3} \log \text{temp.} \\ &+ 1{,}9358 \times 10^{2} \text{ temp.} \\ &- 33{,}9840 \log \text{dry mass} \times \log \text{temp.} \\ &+ 28{,}0870 \log \text{dry mass} \\ &- 5{,}9372 \text{ temp.}^2 \\ &+ 0{,}6737 \log \text{dry mass} \times \text{temp.} \\ &+ 0{,}7973 \times 10^{-2} \text{ temp.}^3 \qquad \ldots\ldots\ldots\ldots\ldots (14) \end{aligned}$$

(Multiple correlation coefficient for equation (14) = 0,9770.)

Although the temperature ranges studied are not quite the same for all three species (see Figs 6.2 to 6.7), it is evident that the species respond differently to temperature. Thus the minimum respiration rate of *Eurydice longicornis* increases slightly between 8 and 10°C followed by a constant rate which is maintained until 16°C. Above that temperature, the respiration rate increases exponentially, to 20°C. The active respiration rate increases steadily between 8 and 20°C.

Both minimum and active respiration rates of *Excirolana natalensis* show a peak at 17,5°C, with a steady decline on either side. Similarly, the respiration rates of *Pontogeloides latipes* show peaks at 15 and 17,5°C for the active and inactive rates respectively.

When arbitrary activity values of 0,1 for the inactive rates and 100 for the active rates are included in the data handled by the stepwise regression program, the following equations are obtained:

For *Eurydice longicornis:*

Log mass-specific respiration rate

$$
\begin{aligned}
&= -\ 72{,}6980 \\
&\quad +\ 1{,}2569 \times 10^{2} \text{ log temp.} \\
&\quad -\ 10{,}8380 \text{ log dry mass} \\
&\quad -\ 5{,}1025 \text{ temp.} \\
&\quad -\ 0{,}7877 \text{ log temp. } \times \text{ activity} \\
&\quad +\ 0{,}6025 \text{ dry mass} \\
&\quad +\ 0{,}1241 \times 10^{-4} \text{ temp.}^{4} \\
&\quad +\ \text{o}{,}6599 \times 10^{-5} \text{ log temp. } \times \text{ activity} \\
&\quad +\ 0{,}2032 \times 10^{-8} \text{ activity}^{2} \\
&\quad -\ 0{,}8108 \times 10^{-13} \text{ activity}^{3} \qquad \ldots\ldots\ldots\ldots(15)
\end{aligned}
$$

(Multiple correlation coefficient for equation (15) = 0,9002.)

For *Excirolana natalensis:*

Log mass-specific respiration rate

$$
\begin{aligned}
&= -\ 3{,}8902 \\
&\quad -\ 2{,}0879 \text{ log dry mass } \times \text{ log temp.} \\
&\quad +\ 1{,}6591 \text{ dry mass} \\
&\quad +\ 0{,}7447 \times 10^{-2} \text{ temp.}^{2} \\
&\quad -\ 0{,}2752 \times 10^{-3} \text{ temp.}^{3} \\
&\quad -\ 0{,}1940 \times 10^{-3} \text{ activity/temp.} \\
&\quad -\ 0{,}3746 \times 10^{-4} \text{ activity } \times \text{ log temp.} \\
&\quad +\ 0{,}2634 \times 10^{-4} \text{ activity/dry mass} \\
&\quad +\ 0{,}6949 \times 10^{-8} \text{ activity}^{2} \\
&\quad +\ 0{,}5793 \times 10^{-8} \text{ dry mass}^{4} \qquad \ldots\ldots\ldots\ldots(16)
\end{aligned}
$$

(Multiple correlation coefficient for equation (16) = 0,9377.)

For *Pontogeloides latipes*:

Log mass-specific respiration rate

$$
\begin{aligned}
= &- 6{,}2303 \\
&- 6{,}9325 \text{ log activity} \times \text{log temp.} \\
&+ 5{,}2415 \text{ log activity} \\
&+ 2{,}268 \text{ log activity} \times \text{log dry mass} \\
&- 0{,}6881 \text{ dry mass} \times \text{log temp.} \\
&+ 0{,}1644 \text{ temp.}^{2} \\
&+ 0{,}1854 \times 10^{-2} \text{ dry mass} \times \text{temp.} \\
&+ 0{,}5779 \times 10^{-3} \text{ dry mass}^{2} \\
&- 0{,}5566 \times 10^{-3} \text{ temp.}^{3} \\
&- 0{,}8578 \times 10^{-5} \text{ log dry mass} \times \text{activity} \\
&+ 0{,}4132 \times 10^{-8} \text{ activity}^{2} \qquad \ldots\ldots\ldots\ldots(17)
\end{aligned}
$$

(Multiple correlation coefficient for equation (17) = 0,8960.)

Discussion

Figure 6.1 shows that the isopods studied show the usual effect of body size on respiration rate, i.e. metabolism increases with increasing body size, while mass-specific metabolism decreases.

The slopes for the regression line equations (exponent b) listed in Table 6.1 differ considerably from the average value of 0,75 found by Hemmingsen (1960) for metabolic rate against body mass, or - 0,25 for mass-specific metabolism against mass. In theory, the value of b varies depending on the relationship between metabolism, mass and surface area (Newell, 1979). Where mass-specific metabolism varies proportionally with body mass, the value of b approaches - 0,01, while where it depends on surface area, it is - 0,33.

Most of the slopes given in Table 6.1 fall below the latter value, but lie within the range found in such intertidal animals as *Littorina littorea* (Newell and Roy, 1973), *Ligia oceanica* (Newell *et al.*, 1976), *Ligia dilatata* (Koop, 1979), *Bullia melanoides* and *B. digitalis* (Brown *et al.*, 1978) and *Donax serra* and *D. sordidus* (Dye, 1979a), as well as the subtital *Cirolana imposita* (Shafir, 1978).

The formulas obtained from the stepwise regression program and which describe the surfaces in Figures 6.2 to 6.7, all tend to show that temperature has a greater influence on respiratory rate than body mass. This is the reverse of the findings by Newell and Roy (1973) and Newell *et al.* (1976) in *Littorina* and *Ligia.*

If activity is considered in addition to the other two parameters (i.e. temperature and body mass) it becomes apparent from equations (14)-(17) that activity is the least important of the three parameters affecting metabolism in *Eurydice.* In *Pontogeloides*, on the other hand, activity has a greater effect on rate of respiration than either temperature or body mass, while in *Excirolana* the influence of activity is of intermediate importance. It is evident from the results obtained that the habitats of the three species have a profound effect on their respiration rates.

Eurydice longicornis shows a supression in the rate-temperature curve when it is inactive, which is remarkably similar to that obtained by Brown and da Silva (1978) for *Bullia digitalis.* Figure 6.8 compares rate-temperature curves for these two species. Suppression of the rate-temperature curve is an energy conservation mechanism which usually extends over the range of temperatures normally encountered by the animal. It is, in effect, a reduction in the animal's sensitivity to temperature, and has been shown to occur in many intertidal species (Newell, 1979).

The two isopod species from the higher shore, *Pontogeloides* and *Excirolana*,

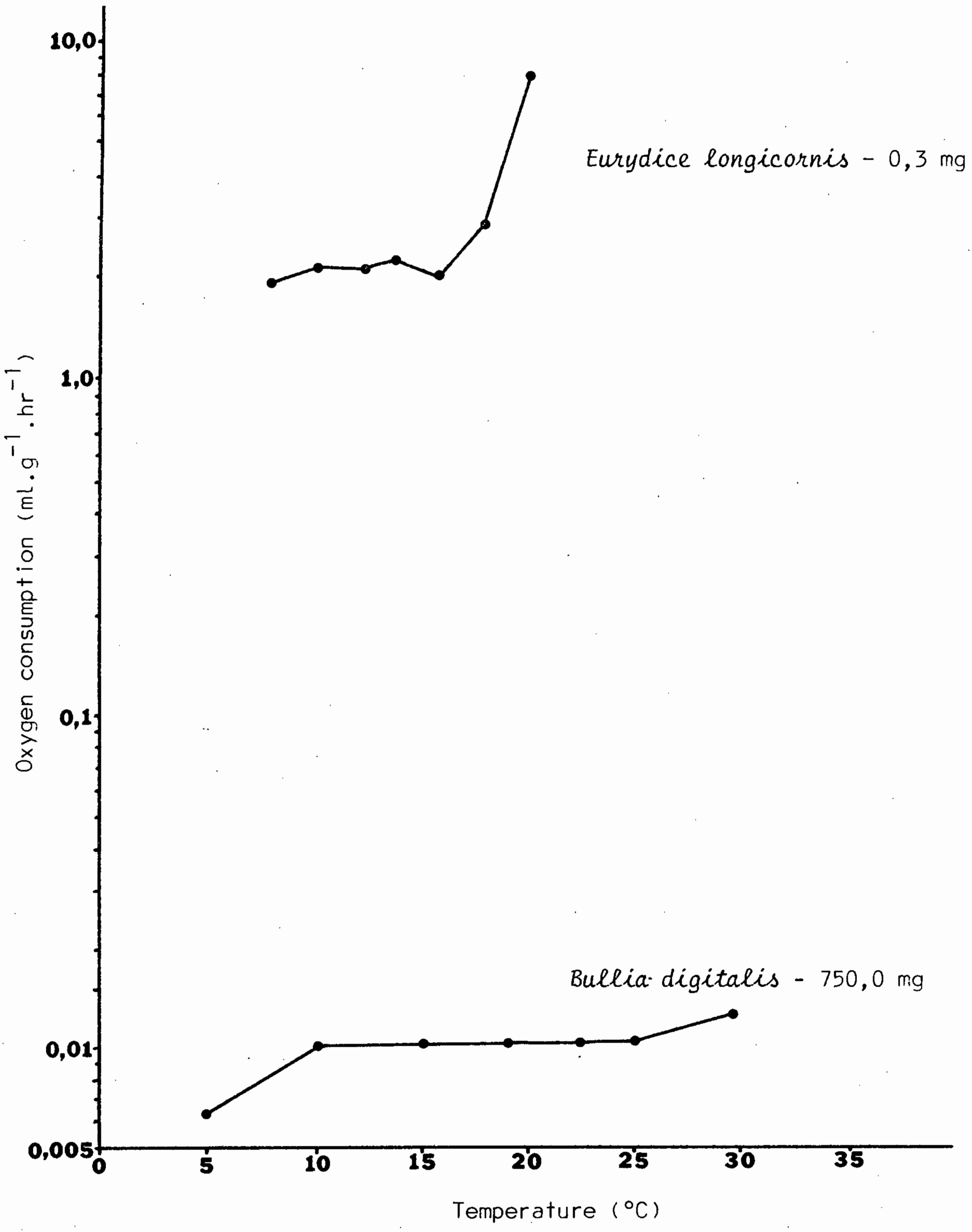


Figure 6.8: Comparison of weight specific respiration rates in *Eurydice longicornis* and *Bullia digitalis* over a range of temperatures. Data for *Bullia digitalis* from Brown and Da Silva (1978).

both show active metabolic peaks in the 15 - 18°C range. Above these temperatures, respiration is probably suppressed as an energy conservation measure. Unfortunately, the range of temperatures over which respiration of these two species was measured was not sufficient to determine whether an increase in respiration rate occurred above 22,5°C. There is a strong possibility that these species show suppression of respiration over a wider thermal range than do the lower-shore *Eurydice*. Such a difference has been shown by Griffiths (1977) in rocky-shore anemones.

Under normal conditions, however, sand is a very effective insulator against temperature fluctuations. Figure 6.9 shows temperature records taken over a low tide period at Rocherpan in the zone of drying occupied by *Excirolana*. The figure shows that temperature variations at the surface gradually disappear with increasing depth. Similar results have been obtained by Newcombe (1935), Johnson (1965) and Pollock and Hummon (1971). These results show that even in the most extreme intertidal zone, occupied by only one water-breathing species, the evaporative cooling of the sand insulated the infauna from high temperatures. It is thus very unlikely that sandy beach intertidal isopods encounter the high temperatures experienced by rocky shore animals.

Thus, while it is not possible to see what mechanisms control the shapes of the rate-temperature curves from the data obtained, the fact remains that within the temperature ranges measured (i.e. the normal range experienced by the isopods) respiration rates decline steadily from the peak values, in both active and inactive animals.

Halcrow and Boyd (1967) have shown that by plotting the routine rate of oxygen consumption for a range of temperatures against the standard rate, the scope for activity can be obtained. Newell (1979) has obtained a potential range of activity for the animals used by Halcrow and Boyd. He comments that the greatest scope for activity occurs at a temperature well within the range of tolerance of the organisms.

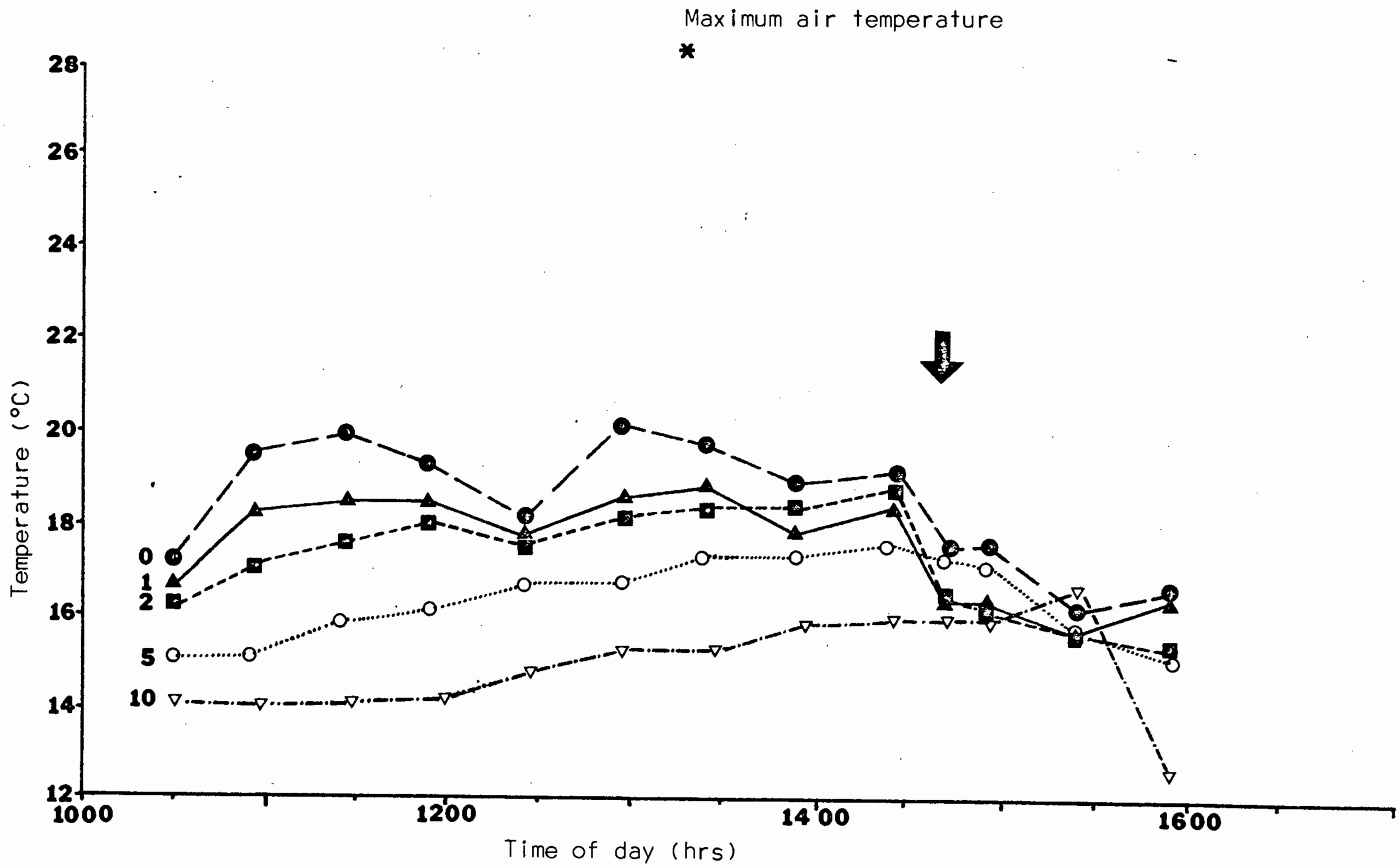


Figure 6.9: The effects of depth in sand on temperature at Rocherpan in the zone of drying. Numbers in the graph indicate depth at which temperatures were measured in cm. Arrow indicates the first wave of incoming tide to reach the study site.

The problem with applying this technique to sandy beach isopods lies in the definition of "routine" rates, and its measurement. The total amount of oxygen consumed over 24 or 48 hours might be considered a good measure of a routine rate. But the conditions inside a respirometer are not representative of nature. Since activity has a very great influence on oxygen consumption (see Newell (1979) for review, also this study), the activity of an animal in the respirometer should parallel that of an animal in its natural habitat during the measurement of a 24 or 48 hour routine rate. The studies of Shafir (1978) and Marsh and Branch (1979) show that this does occur under certain circumstances. In the three isopod species studied here, however, endogenous respiratory or activity rhythms were not expressed in the respirometer, as can be seen from Figure 6.10.

Nevertheless, there is a considerable body of literature showing the existence of circatidal and circumlunar rhythms in other species of the genera *Eurydice* and *Exicrolana* (Jones and Naylor, 1970; Fish and Fish, 1972; Enright, 1972; Klapow, 1972a,b; Alheit and Naylor, 1976; Macquart-Moulin, 1977).

What is the behaviour shown by isopods under natural conditions? Brown (1973) has described the activity rhythm of *Eurydice longicornis*, while an illustration of the probable lifestyle of *Excirolana natalensis* is given below. Similar activity rhythms are likely to occur in other species.

Excirolana buries itself in sand near the top of the beach (in the zone of drying) as the tide recedes. As Figure 6.9 shows, the temperature rises gradually throughout the period of exposure if this occurs in the daytime, even at 4 to 8 cm depth where the isopods are buried. Evaporative cooling keeps the temperature of the sand fairly low, but is possible that on hot, windless days, the temperature may rise to 20°C or more. Whatever happens, the isopods are virtually trapped in the sand during the period of exposure, since digging in moist sand requires considerable effort. It was found that captive isopods rarely dug to

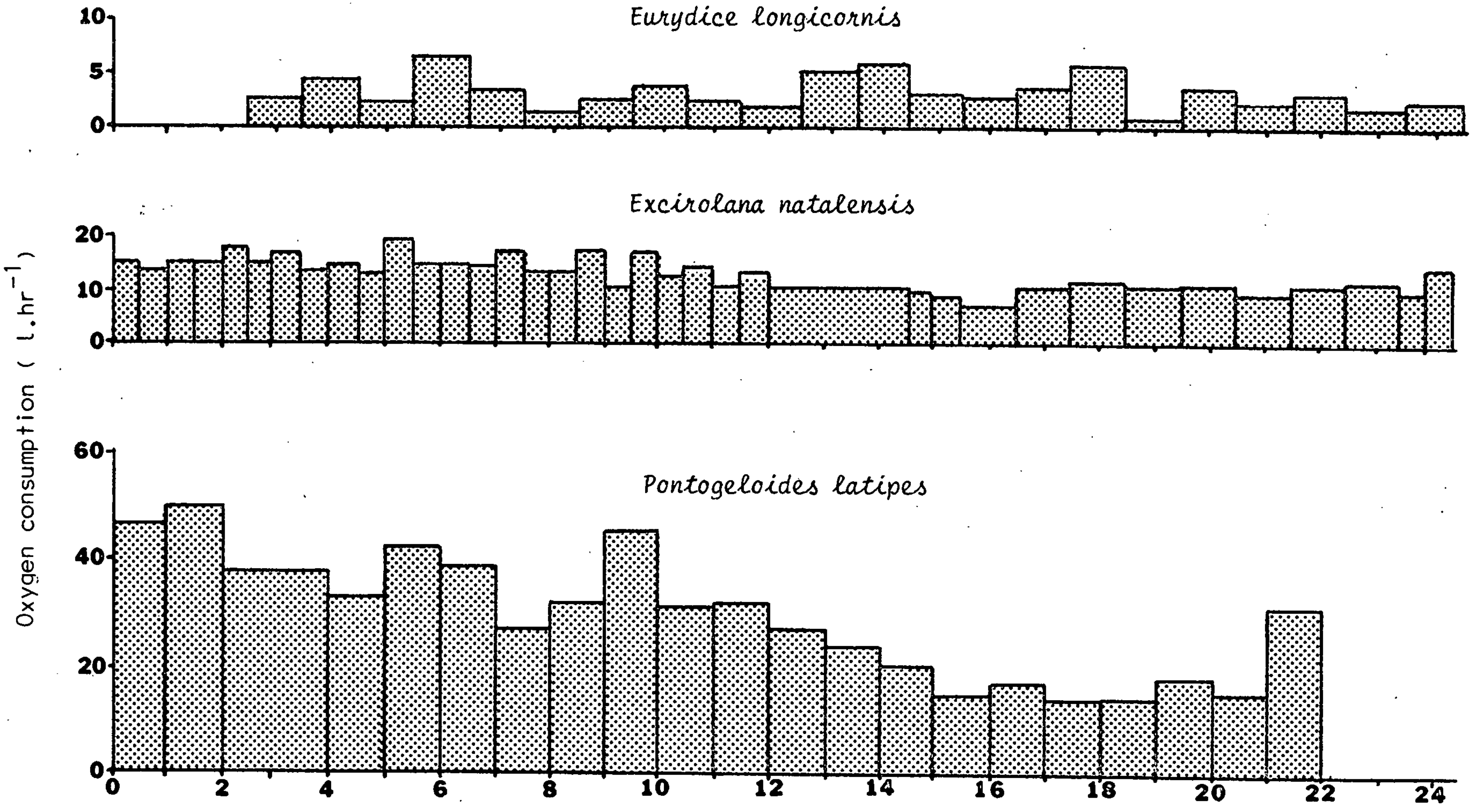


Figure 6.10: Hourly rates of oxygen consumption over 24 hrs showing absence of endogenous rhythms.

a depth greater than 1 cm below the surface if placed on damp sand.

The animals, therefore, are unlikely to move much during low tide, thereby saving considerable energy (Newell, 1979). Captive animals kept in moist sand were sometimes found to come to the surface at night and to wander about. This may act as a mechanism to avoid remaining stranded high up the shore during a period of decreasing tidal amplitude. Movements across the surface of an exposed section of the beach can only be undertaken at night when desiccation is reduced. Presumably such movement would take place at high tide, when the isopod stands a better chance of being caught by the swash. Naturally, the time for which water-breathing isopods can walk about in the air, even at night, is strictly limited.

With the incoming tide, the animals are either washed out of the sand or leave it deliberately. Alheit and Naylor (1976) and Macquart-Moulin (1977) both report that if captive *Eurydice* (*E. pulchra* and *E. affinis* respectively) were provided with sand, individuals could remain permanently buried. Thus an environmental stimulus of some sort is probably important in cueing the onset of swimming. Furthermore, King (1951) has shown that up to 4 cm of sand can be removed by a single swash-backwash cycle on exposed beaches, thereby increasing the likelihood of mobile infauna getting washed out of the sand.

Other environmental stimuli such as the sharp drop in temperature shown in Figure 6.9 may also trigger a swimming response. Enright (1965) has tried to trigger swimming responses in *Excirolana chiltoni* in a number of ways but, with the exception of mechanical stimulation, all failed. He does not mention trying thermal stimulation, however.

During high tide, the animals presumably forage for food, while maintaining their positions on the beach and making sure that they are not washed off the beach altogether. This is a period of high activity when the animals must expend considerable energy in swimming. Klapow (1972b) has suggested that *Excirolana* buries itself in sand on the receding tide to ensure that it will be washed out at the next high tide, even during a period of decreasing amplitude. This would imply that the animals migrate up and down the beach with the spring-neap-spring tidal cycle. Such migration has been observed in *Eurydice pulchra* (Fish, 1970), *Excirolana chiltoni* (Klapow, 1972a) and *Excirolana braziliensis* (Dexter, 1977). Figure 6.11 indicates that the same thing occurs in *Excirolana natalensis*.

Once the tide has receded from the upper half of the beach, the population lies buried and inactive until the following high tide. There are, however, a number of unknown factors complicating the picture. It was found that animals kept in captivity could survive long periods (2 to 3 months) without food, and Enright (1972) reports that an individual of *E. chiltoni* survived for 6 months without food. This may mean that for a considerable period after feeding, the animals remain inactive even on the beach, simply remaining buried in the sand.

In the absence of a complete activity budget in free-living animals it is therefore not possible to define, let alone obtain, a "routine" respiration rate for sandy beach isopods.

Newell (1979) shows the relationship between routine and standard rates and how this determines both the scope for routine activity and the potential range for activity. In the three species of isopod studied here, it was not possible to do the same thing. When active rates are plotted over the standard rates, however, a scope for maximum activity is obtained. This reflects the energy that is potentially available for escape, foraging, maintaining zonation etc. which may well be very important in intertidal animals subject to varied and considerable stresses.

The scopes for maximum activity in the three species are shown in Figure 6.12 for a standard animal of 2,5 mg. It is interesting to note that there is a gradation in scope for activity from *Eurydice*, the low tide species with the lowest scope for activity, through *Pontogeloides*, to *Excirolana*, the highwater form with the greatest scope for activity.

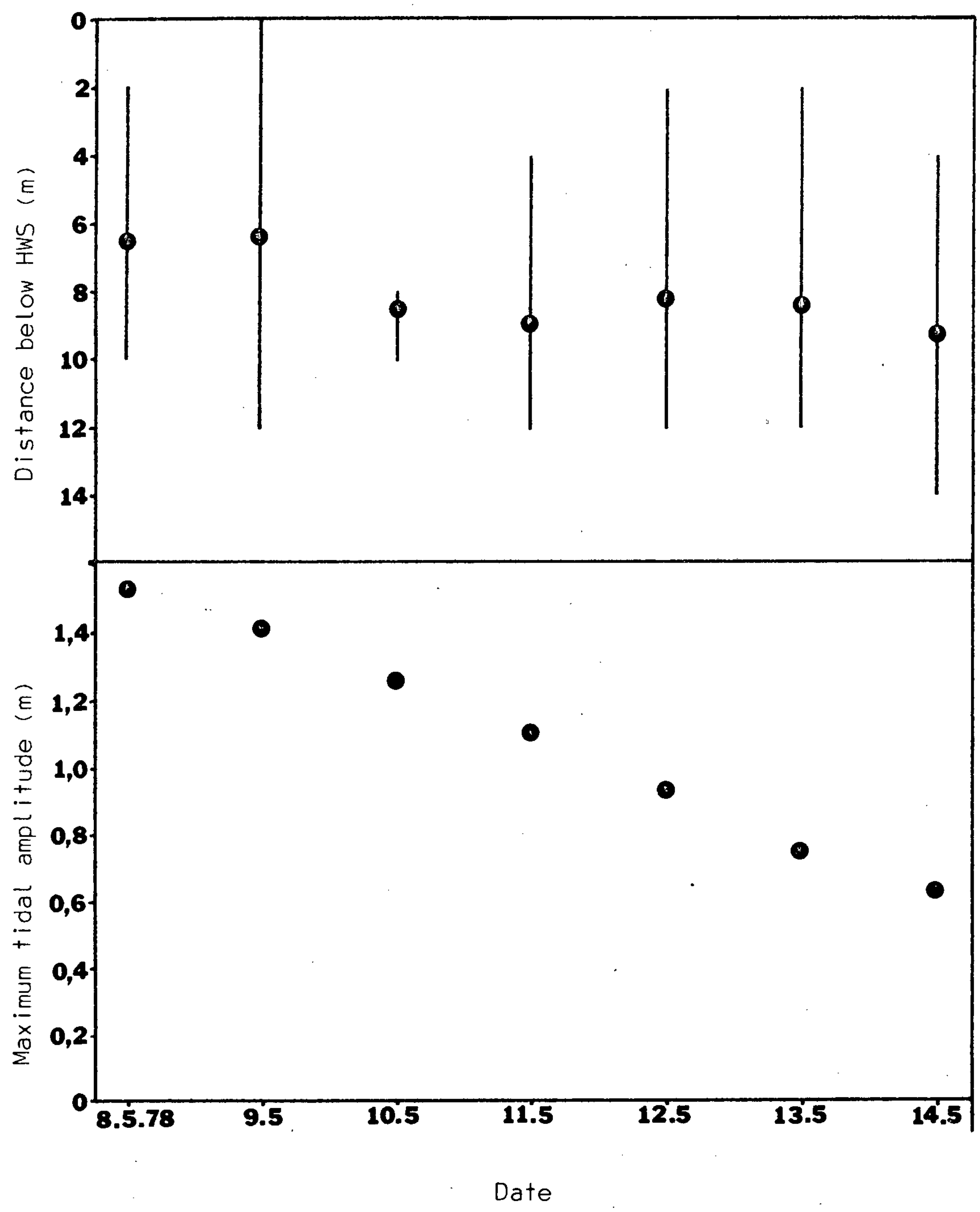


Figure 6.11 The intertidal position of *Excirolana natalensis* on successive days of decreasing tidal amplitude. Vertical bars indicate distribution range below the high-water spring tide mark (HWS) and loci indicate the means of the daily distributions.

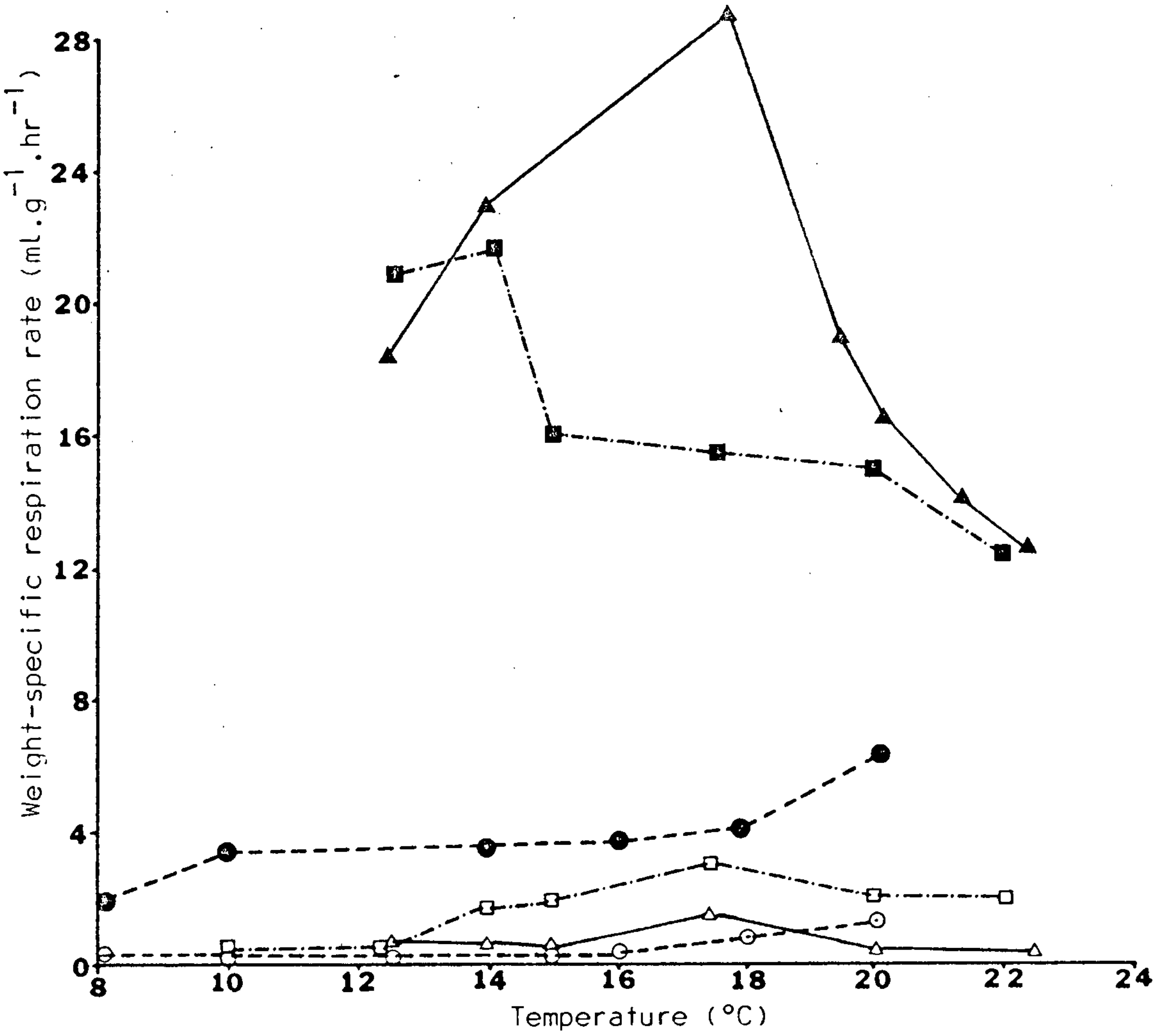


Figure 6.12: The effect of temperature on minimal (open sumbols) and active (solid symbols) weight-specific metabolic rates in *Eurydice longicornis* (circles), *Pontogeloides latipes* (squares) and *Excirolana natalensis* (triangles) for standard animals of 2,5 mg.

It would appear from this that scope for activity is proportional to the harshness of the environment occupied by the animals. One possible reason for the relatively low scope for activity in *Eurydice* may lie in the fact that *Eurydice* of 2,5 mg are adults whereas individuals of that mass in the other two species are juveniles.

A comparison with metabolic rates of a sub-tidal cirolanid species would be of interest but unfortunately, the only respiration study on such an animal is that of Shafir (1978) and the data is not presented in a format comparable with the one used here.

Branch and Newell (1978) have shown a similar zonation in metabolic activity in limpets of the genus *Patella*. They investigated three species occurring on the same shores but favouring different intertidal zones. In all cases, metabolic activity was optimized for the particular conditions prevailing in their zones. Branch (1979) found similar adaptations in a fourth species.

The inference is, therefore, that the metabolic capabilities of intertidal animals are modified according to the environment. Newell (in press) suggests that food availability also plays a considerable role in whether organisms adopt a "conservationist" or "exploitative" strategy in regulating metabolism at various temperatures. The data obtained here are not suitable for investigating how this happens in sandy beach isopods, although it was noticed that one or two individuals showed consistently high respiration rates, perhaps because they were adopting a different strategy to the norm.

Conclusions

Mass-specific metabolisms in the three isopod species studied show relationships to body size similar to those of a variety of intertidal animals as well as to a closely-related sub-tidal cirolanid species. The effects of temperature, body-size and activity on respiratory metabolism were investigated, and it was found that these parameters varied in relative importance according to species. In all cases, temperature had a greater influence than body mass, but the effect of activity varied from species to species. The effect of activity was least important in *Eurydice* and rather more important in *Excirolana,* while in *Pontogeloides* activity, activity-temperature and activity-body mass interactions were the most important factors influencing respiration.

These differences are postulated to be related to differences in the intertidal environments occupied by the three species. The scope for activity of the three species is shown to be greatest in those animals living near the top of the intertidal zone (i.e. in the zone experiencing the greatest environmental variability and the least predictability). The scope for activity probably represents a "reserve" to cope with unfavourable conditions or situations. Suppression of metabolism appears to occur in all three species, although it is most evident in the rate-temperature curve for *Eurydice.*

In conclusion, it can be said that both activity potentials and respiratory responses to temperature are modified according to the environmental factors which occur in the intertidal zones normally occupied by these sandy beach isopods.

CHAPTER 7

THE PATCHY DISTRIBUTION OF SANDY BEACH ORGANISMS

Introduction

The fauna of sandy beaches has long been regarded as notoriously patchy. Patchiness has been found both in meiofauna (e.g. Gerlach, 1977; Platt, 1977; Giere, 1979; Gray and Rieger, 1971) and in macrofauna (e.g. Moran, 1972; Gray, 1971; Pichon, 1967) and appears to present a universal problem to researchers working on sandy beaches. To date, no studies have been carried out on the problem, other than Moran's (1972) study on the microdistribution of *Gastrosaccus mediterraneus*.

In an attempt to provide more information, this problem was investigated on the three beaches along the west coast of South Africa described in previous chapters. The aims of the study were, firstly, to see whether patchiness does occur to any significant degree and, secondly, to attempt to quantify the degree of patchiness.

Methods and Materials

Sixteen random samples were collected from within the sampling grid on each beach in addition to the usual sixteen grid samples (see chapter 2). Each sample comprised a 0,25 m^2 quadrat excavated to a depth of 30 cm. The sand was washed through a 1 mm mesh sieve that retained the macrofauna. The positions of the randomly chosen sampling sites were mapped out and grid references were calculated for all 32 sampling sites.

After sorting (see chapter 5) had been completed, the results were fed into the SACLANT graphics display package programme together with the associated grid references. The SACLANT programme produces both three-dimensional displays and contour diagrams for each set of inputted data. The resultant diagrams were then compared with each other.

For the first section of this chapter, patches were determined by eye. In the second half, however, the mean number of individuals per square metre was calculated for the zone in which a particular species was present. Areas with densities above this mean value were then designated patches. Although this method failed to resolve all the patches it was adopted in order to treat all species in an identical manner when considering interspecific relationships.

Note on the interpretation of figures:

Figure 7.1 shows a sample of the figures appearing in the remainder of this chapter and chapter 8. It should be noted that for reasons of clarity, all three beaches have been plotted to an approximately equal size, although the areas sampled in fact measured 150 x 71,4 m at Melkbosstrand, 150 x 86,1 m at Ysterfontein and 78 x 42,3 m at Rocherpan. Thus, while the contour diagrams for Melkbosstrand and Ysterfontein are to the same scale, those for Rocherpan are to a larger scale. These contour diagrams have all been plotted as they would appear from the air directly above the sample area. The horizontal or x axis runs parallel to the shore, while the vertical or y axis runs across the beach at right angles to the shore. The upper margin of the contour diagram lies along the high water spring tide level and the lower margin at low water springs.

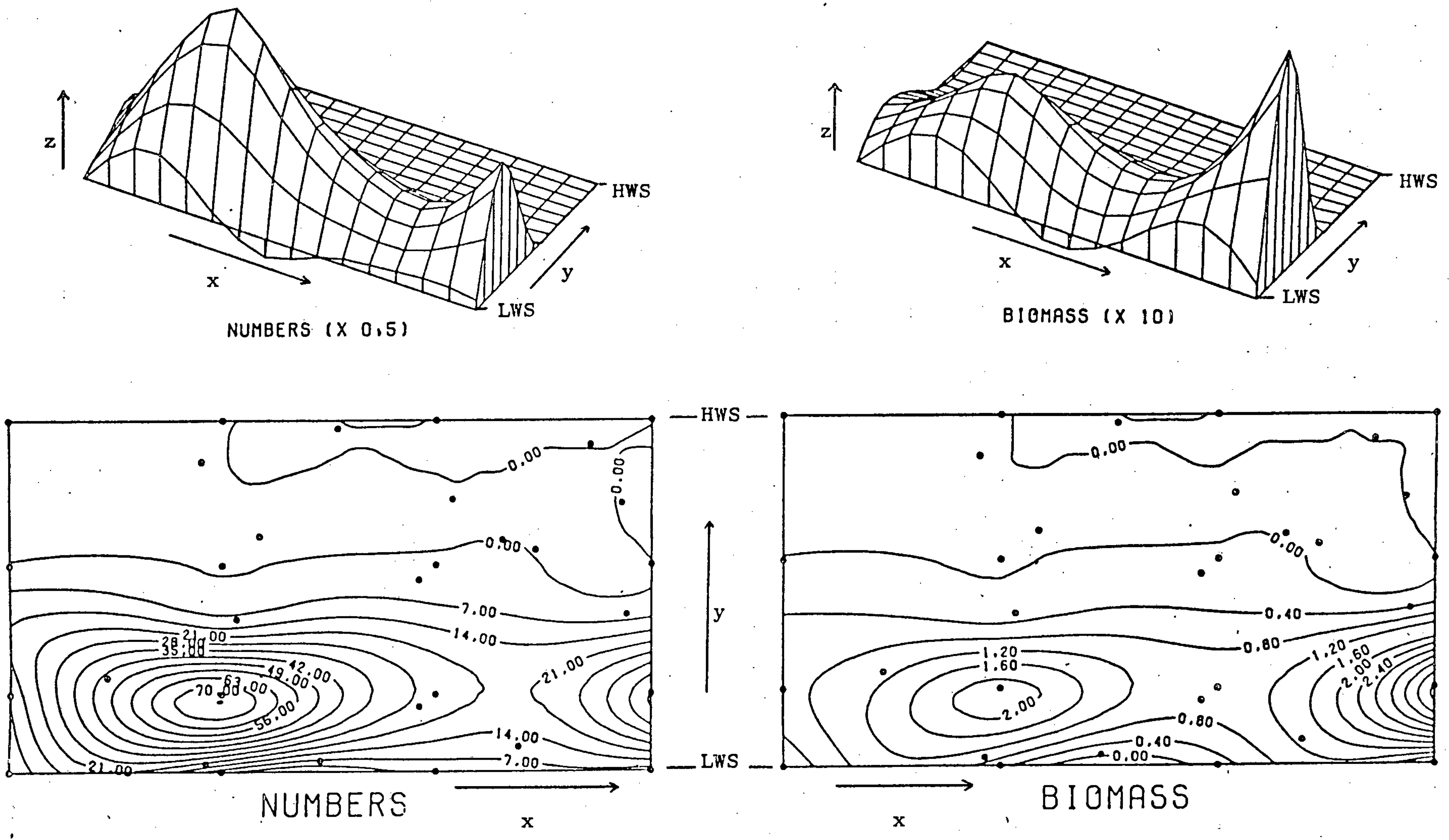


Figure 7.1 Illustrating the interpretation of 3D diagrams. x = distance along beach; y = distance across beach; z = numbers or biomass values.

On some of the contour maps, isometric lines representing negative values will occasionally be seen. These "depressions", which are also visible in some three-dimensional figures, are artefacts of the computer programme, caused by a steep decline in values.

The three dimensional diagrams are all viewed from a point offshore 30 degrees to the right of the crossbeach axis and 35 degrees above the horizontal. The vertical "mountains and valleys" in these figures are an expression of the contour values in the contour maps. In this chapter, they represent numbers of individuals per square metre and biomass per square metre, but in chapter 8 they have also been used to show the distribution of some sedimentary characteristics.

In order to emphasize features, the vertical scale of the three-dimensional diagrams has occasionally been multiplied by a factor: less than 1 in order to reduce the scale; greater than 1 to magnify it. When used, the value of this factor is given in brackets in the legend below the 3-D figure.

A comparison of the number and biomass figures in this chapter will give some indication of the relative size compositions of the populations studied. In figure 7.1, for example, the "mountain" in the right half of the figure is roughly to the same scale in both the number and biomass representations, whereas the "mountain" to the left is much higher in the number diagram. This means that although there are high numbers in this area, the biomass is not correspondingly high, implying a large number of individuals of low mass. In this chapter these are referred to as 'juveniles' for convenience, but it should be remembered that they might simply be adults of a smaller size class.

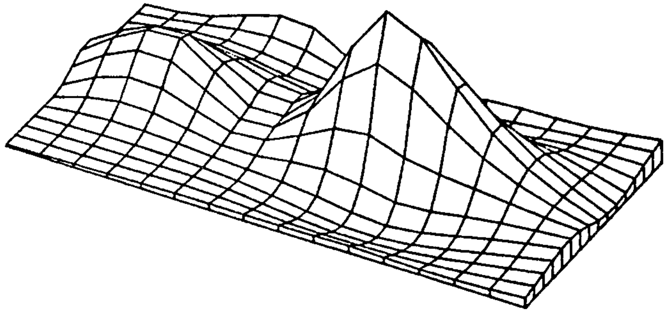
Results and Discussion

Inspection of figures 7.2 to 7.4 shows that the fauna of the various beaches is not evenly distributed. At Melkbosstrand (fig. 7.2) the bulk of the biomass is concentrated in the mid-tidal region - mainly in the lower portion of the zone of retention (see chapter 4). Even within this zone, however, distribution is discontinuous, two patches being apparent, each one measuring between 50 and 70 metres in length. A smaller patch of relatively high biomass lies at the high-water mark but the rest of the intertidal region is distinguished by low biomass values of under $2g.m^{-2}$.

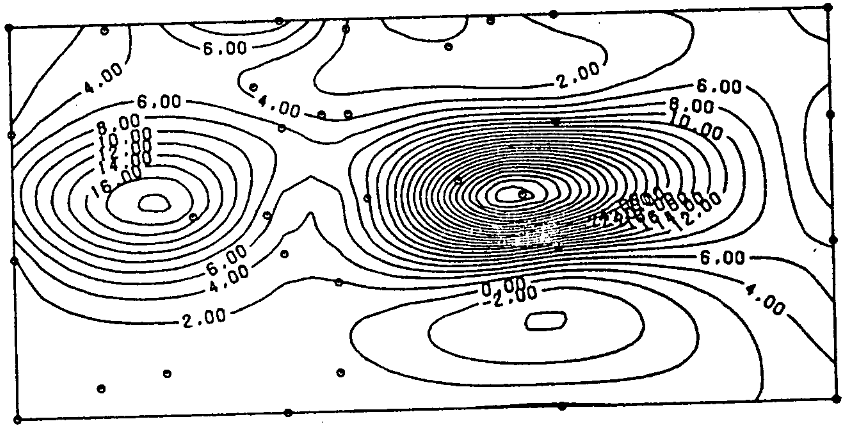
Figure 7.3 shows the total biomass at Ysterfontein. A single patch, some 100 metres long is shown, occupying the same zone as the patches at Melkbosstrand. Finally, in figure 7.4, the biomass at Rocherpan is magnified five-fold to emphasize the patchiness. Here there are two patches, both in the zone of resurgence and the one that falls entirely within the area studied measures 31 metres in length. The second patch, the entire extent of which is not known, is at least 34 metres long. The reason for the presence of these patches in the zone of resurgence at Rocherpan rather than in the zone of retention is discussed in chapter 8.

A single glance at any one of these figures is sufficient to show the complete inadequacy of the single-transect method of sampling discussed in chapter 2. It is obvious from the figures that a single transect can either hit a patch or miss it; it can either cut across the peak or across a lower slope. In each case different values are obtained and the dangers of extrapolating results obtained in this way to apply to entire beaches are clear. There is no substitute for intensive sampling in sandy beach ecology.

In the following section, the patchiness found in individual species on each beach will be described.

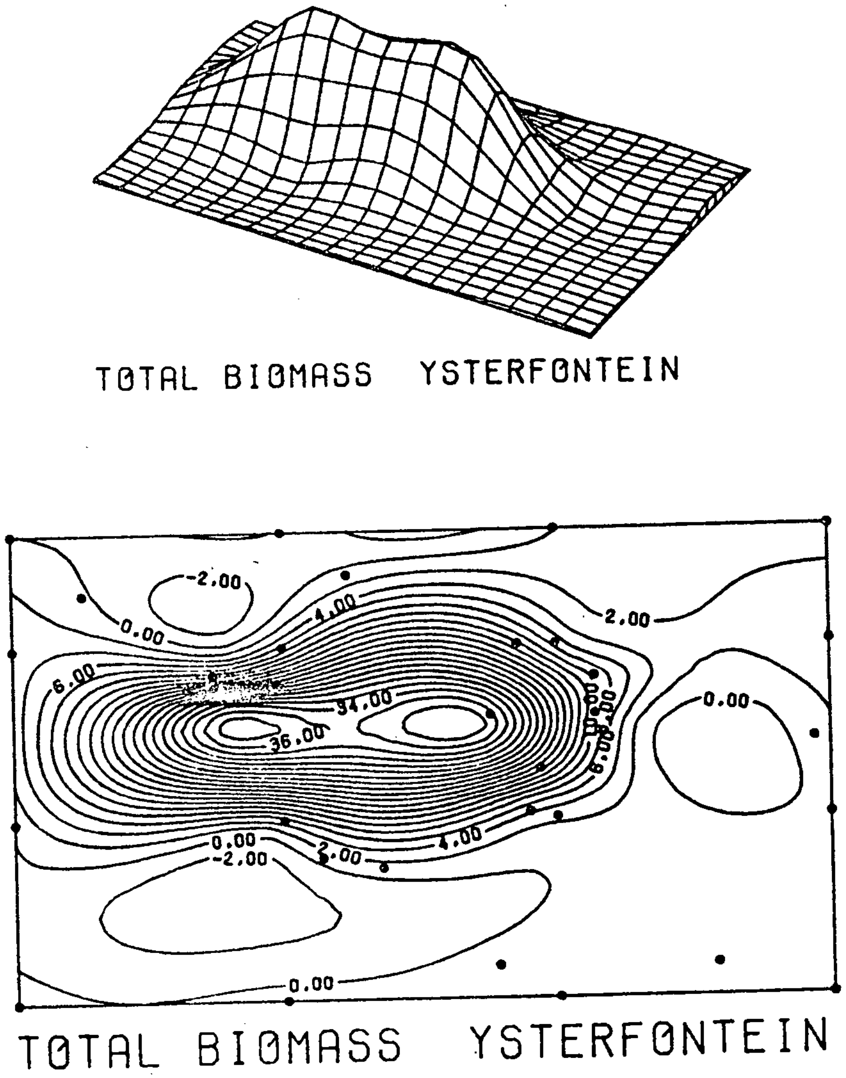


TOTAL BIOMASS MELKBOSSTRAND



TOTAL BIOMASS MELKBOSSTRAND

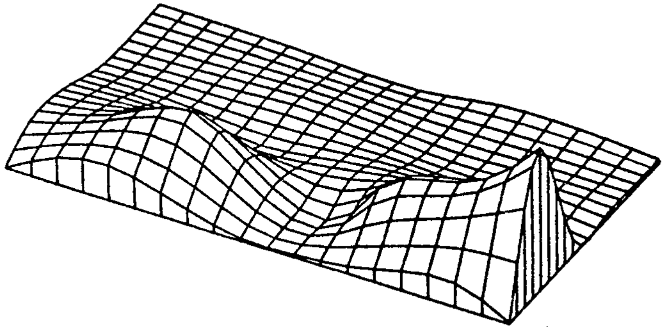
Figure 7.2. Distribution of total biomass at Melkbosstrand



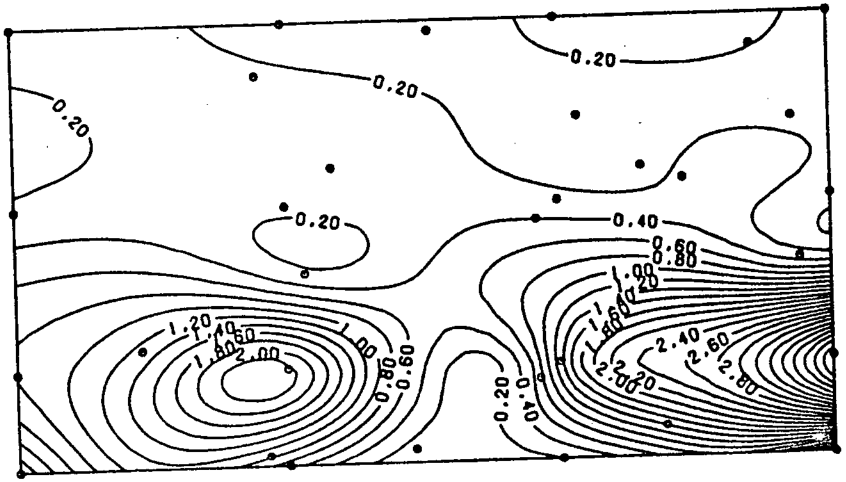
TOTAL BIOMASS YSTERFONTEIN

TOTAL BIOMASS YSTERFONTEIN

Figure 7.3. Distribution of total biomass at Ysterfontein



TOTAL BIOMASS (X 5) ROCHERPAN



TOTAL BIOMASS ROCHERPAN

Figure 7.4. Distribution of total biomass at Rocherpan

Tylos granulatus

At Melkbosstrand (fig. 7.5), parts of two patches were sampled, each portion measuring some 64 metres in length. The widths of these patches is not known, since only *Tylos* in the intertidal area were sampled. Brown (1971a) mentions that on the Cape Flats, *Tylos capensis* may wander several kilometres inland, although in general species of this genus are considered halophilous (Roman, 1977) as opposed to truly terrestrial. In this case, however, it is clear that only the seaward fringe of the distribution has been sampled. The left-hand patch in figure 7.5 consists of a greater proportion of juveniles than occurs in the rest of the distribution, as can be seen by comparing the number and biomass figures with each other.

At Ysterfontein (fig. 7.6), a relatively small patch in terms of numbers has been sampled, measuring some 78 metres in length. The beginnings of other patches are seen on the edges of the sampling area, including a numerically important one to the right. The size composition of the sampled population or populations appears to be fairly constant throughout the area sampled.

At Rocherpan (fig. 7.7) an intertidal patch of *Tylos* was sampled measuring some 45 metres along the beach and 20 metres across it. This patch consists mainly of juveniles, but the seaward edge of a second patch of adults was also sampled. The border of a third patch of juveniles appears at the right of the figures. Thus it would seem that on this occasion, juveniles were occupying a lower intertidal position than were the adults. *Tylos granulatus*, therefore, shows a patchy or discontinuous distribution on all three beaches studied. These results are similar to those obtained by Hayes (1977) for *Tylos punctatus* on the west coast of North America.

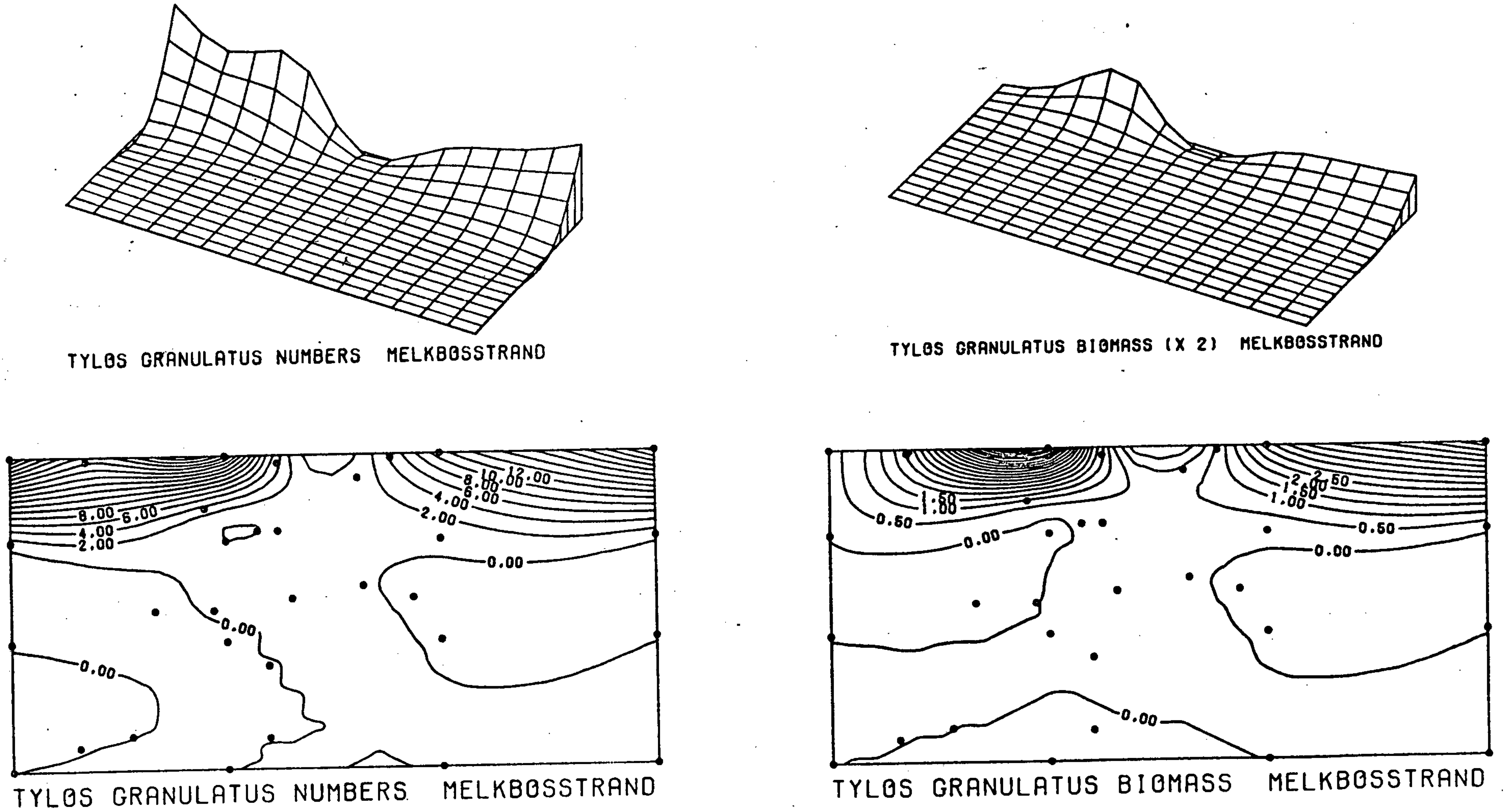
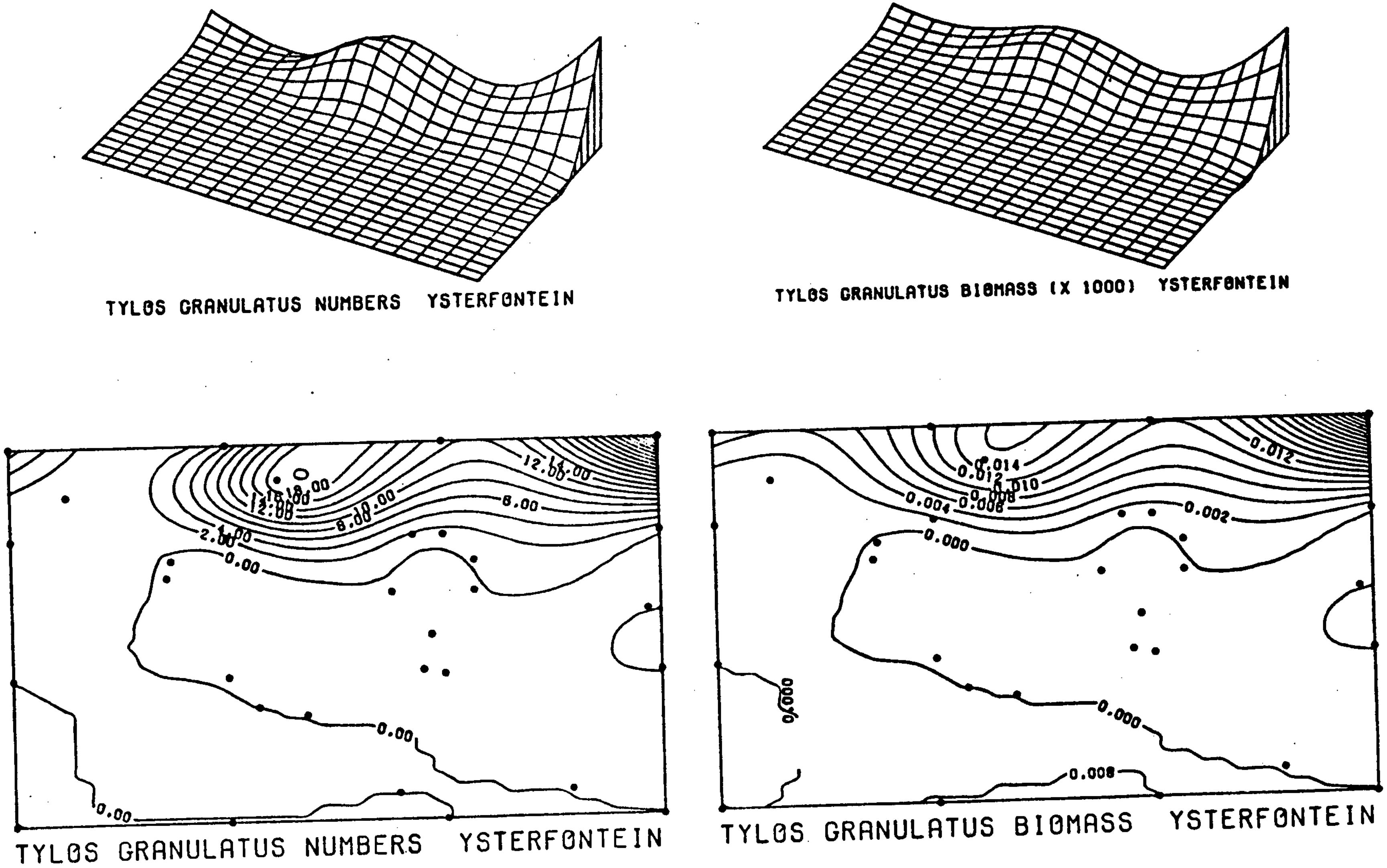


Figure 7.5. Distribution of *Tylos granulatus* at Melkbosstrand



TYLOS GRANULATUS NUMBERS YSTERFONTEIN

TYLOS GRANULATUS BIOMASS (X 1000) YSTERFONTEIN

TYLOS GRANULATUS NUMBERS YSTERFONTEIN

TYLOS GRANULATUS BIOMASS YSTERFONTEIN

Figure 7.6. Distribution of *Tylos granulatus* at Ysterfontein

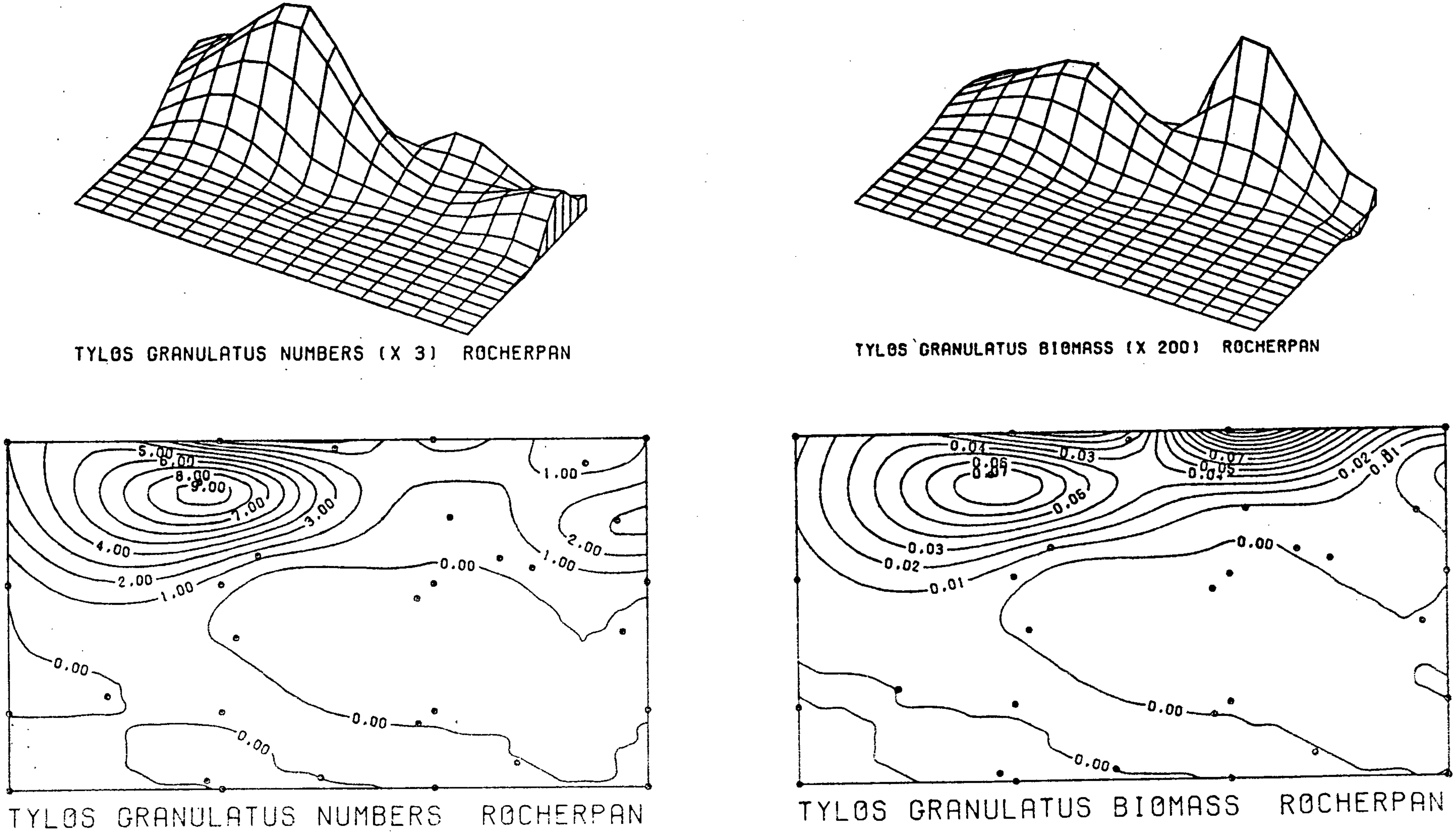


Figure 7.7. Distribution of *Tylos granulatus* at Rocherpan

Oligochaetes

Oligochaetes are only found at Melkbosstrand (fig. 7.8), where their distribution extends into the zone of drying. Two small patches each measuring some 40 metres in length are found, although these may simply represent the edges of a larger patch occurring further inland. It is apparent that the size distribution of oligochaetes is uneven, the right half of the figures apparently having a higher proportion of juveniles than the left half.

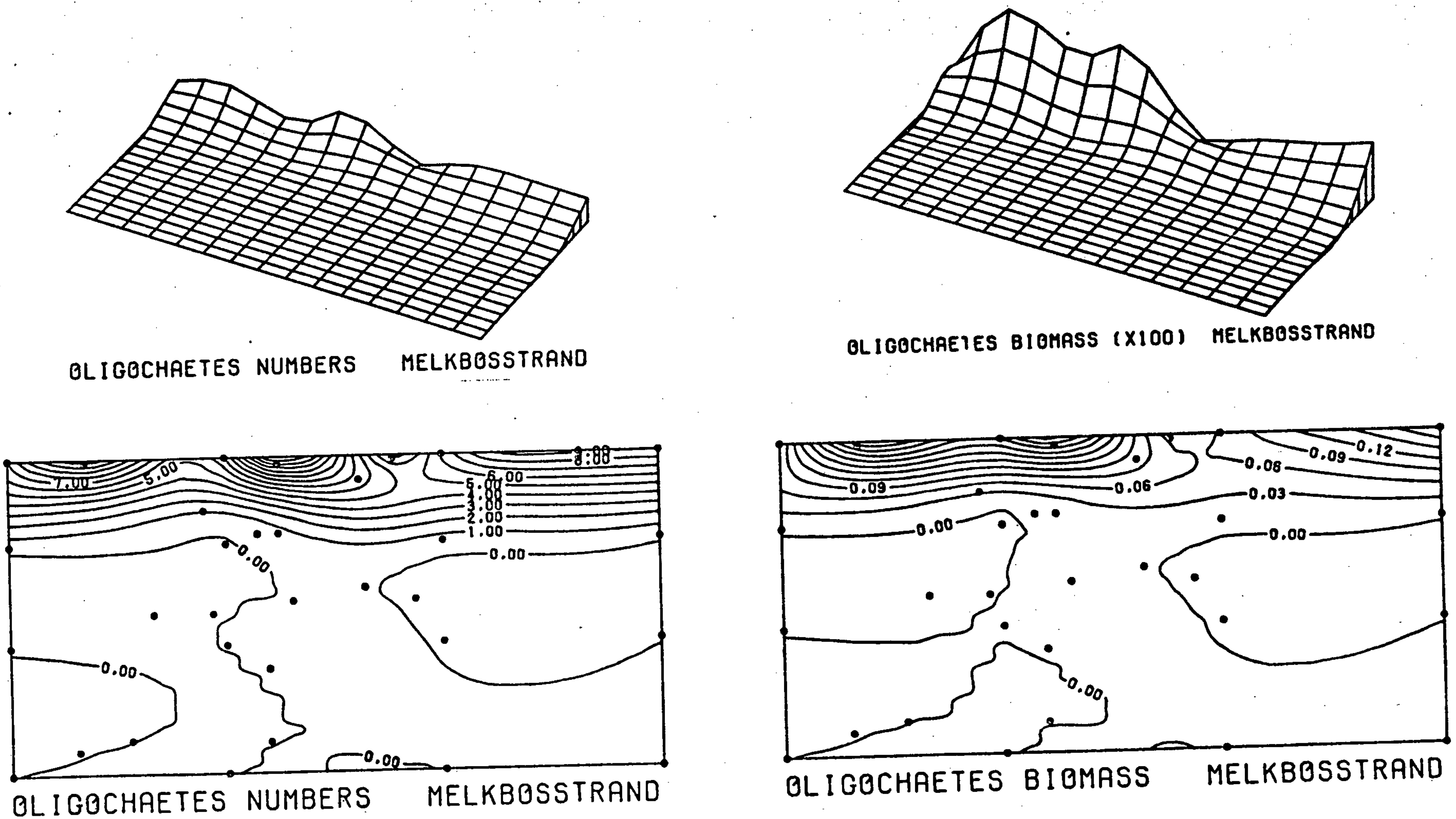
Niambia sp

Insufficient numbers of the terrestrial isopod were collected from Melkbosstrand to permit interpretation. But at Ysterfontein (fig. 7.9) and Rocherpan (fig. 7.10), distinct patchiness was observed. On the former beach, a part of one patch, measuring some 50 metres along the beach and 28 metres in width was sampled. In this case, the size composition of the population is uniform. At Rocherpan, however, one patch consists of juveniles, while the edge of another patch is composed of much larger animals. The patch of juveniles is 33 metres long.

As in the case of the two species already mentioned, the distribution of *Niambia* shown in these figures represents only the seaward fringe of the distribution.

Talorchestia capensis

Two relatively small patches, measuring some 45 and 57 metres in length



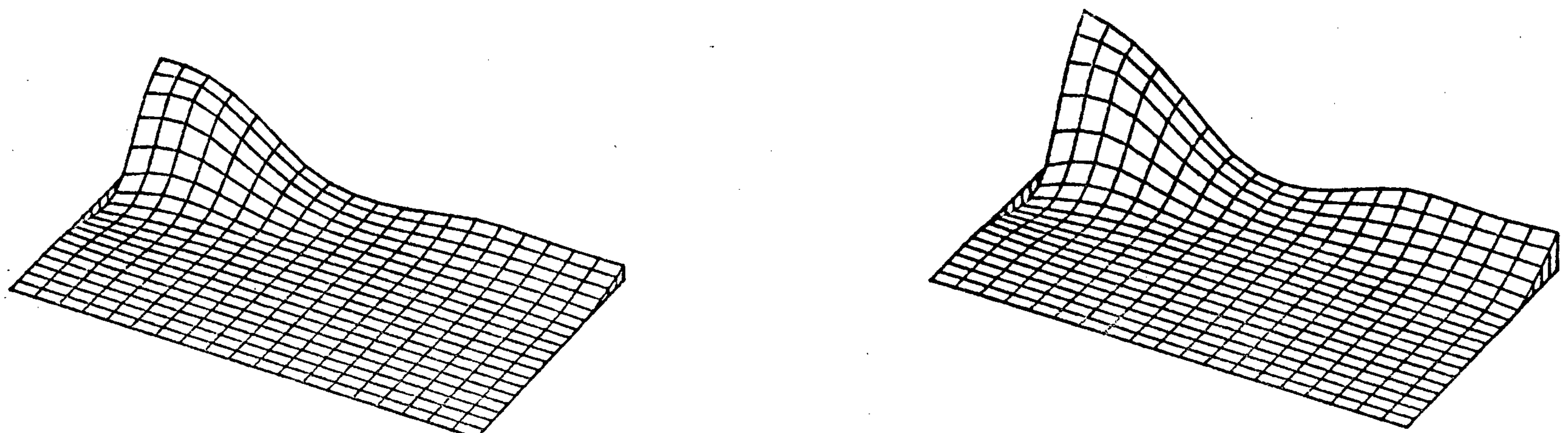
OLIGOCHAETES NUMBERS MELKBOSSTRAND

OLIGOCHAETES BIOMASS (X100) MELKBOSSTRAND

OLIGOCHAETES NUMBERS MELKBOSSTRAND

OLIGOCHAETES BIOMASS MELKBOSSTRAND

Figures 7.8. Distribution of *Oligochaetes* at Melkbosstrand



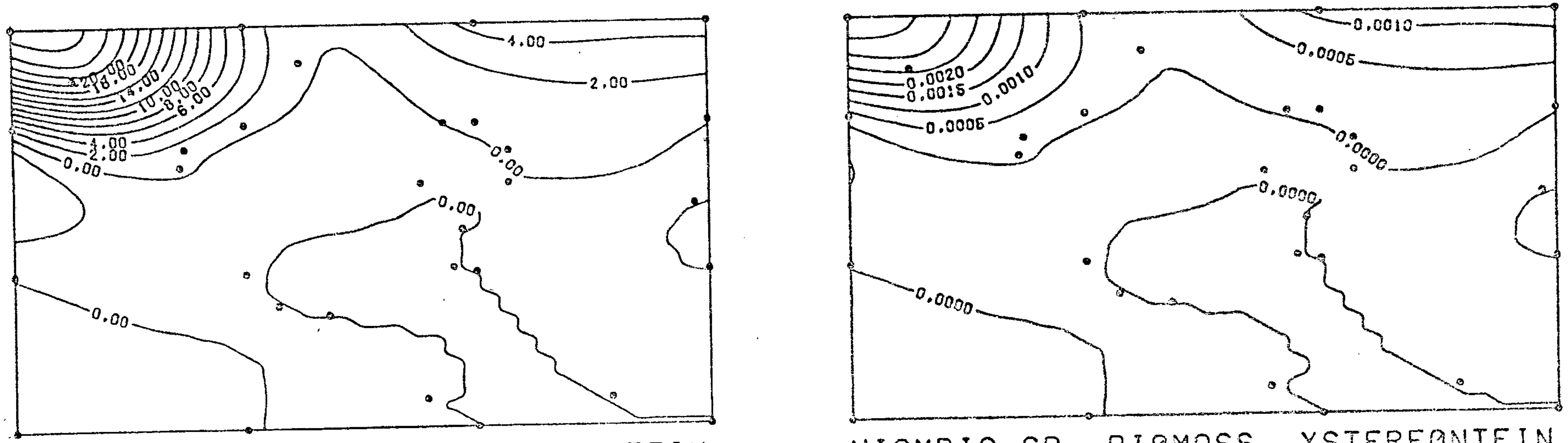
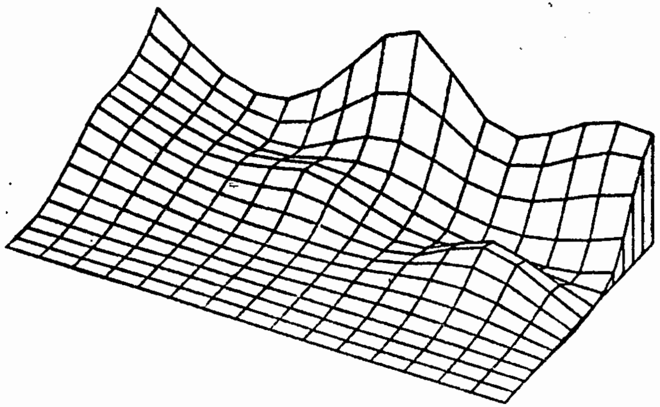
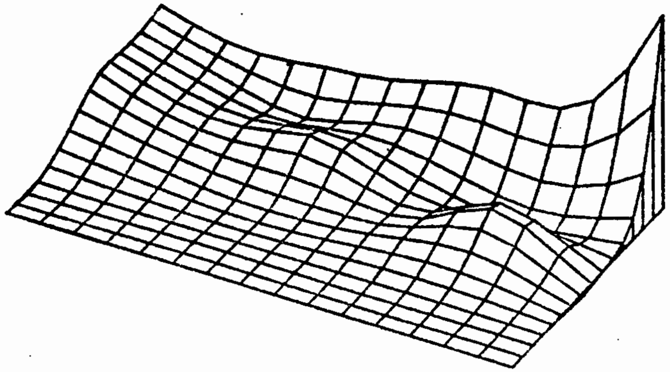


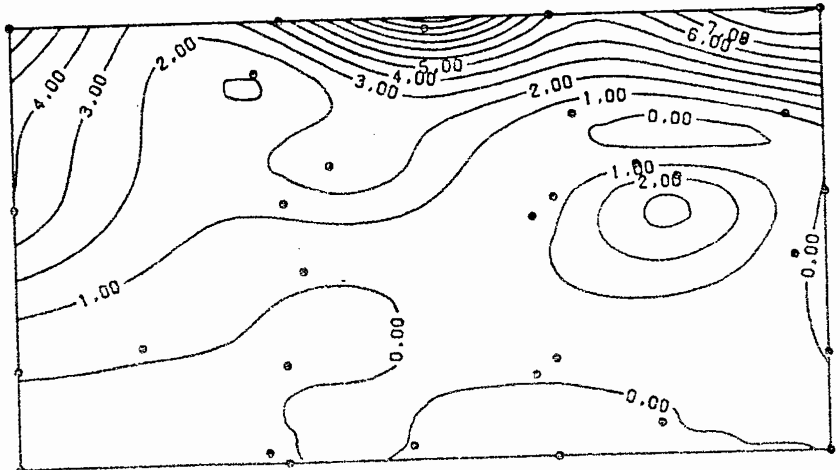
Figure 7.9. Distribution of *Niambia* sp. at Ysterfontein



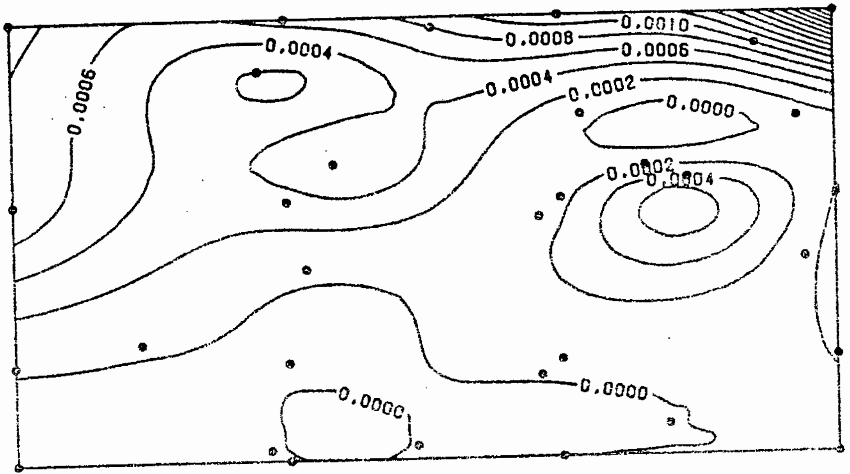
NIAMBIA SP. NUMBERS (X 2) ROCHERPAN



NIAMBIA SP. BIOMASS (X .10000) ROCHERPAN



NIAMBIA SP. NUMBERS ROCHERPAN



NIAMBIA SP. BIOMASS ROCHERPAN

Figure 7.10: Distribution of *Niambia* sp. at Rocherpan

were found in the distribution of this amphipod at Melkbosstrand (fig. 7.11). At Ysterfontein, a single larger patch 104 metres long was found, of which one section consisted of a greater proportion of juveniles than the rest (fig. 7.12). Finally, at Rocherpan (fig. 7.13), two patches, the one measuring approximately 25 metres and the other at least 40 metres, were found. Both patches have similar size compositions. On all three beaches these patches are centered on the high-water mark.

Muir (1977) found this species closely associated with stranded kelp, its main food source. At his study site at Kommetje, both occurred in large quantities, but stranded kelp is considerably rarer on west coast beaches. Generally, however, *Talorchestia* is found in greater concentrations in the vicinity of stranded plants. The relative paucity of this food is reflected in the small maximum size attained by individuals on these beaches (35 mg) when compared with the 50 mg adults at Kommetje (Muir, 1977).

Excirolana natalensis

At Melkbosstrand (fig. 7.14) and Ysterfontein (fig. 7.15), this species is found from the high water mark to about one third of the way across the intertidal zone (see chapter 4). At Melkbosstrand a single aggregation, 110 x 22 m occurred within the study area. At Ysterfontein a single patch was also found within the study area measuring 70 x 25 metres.

On both these beaches, numbers and biomass of *Excirolana* were low when compared with the values at Rocherpan (fig. 7.16), where it is the dominant isopod species. Here no discrete patches are evident, the distribution extending over most of the beach, although numbers are quite low near the low water mark. The long-shore distribution of numbers is relatively consistent and, although there are areas of increased density, these are not sufficiently conspicuous to merit the term 'patches'.

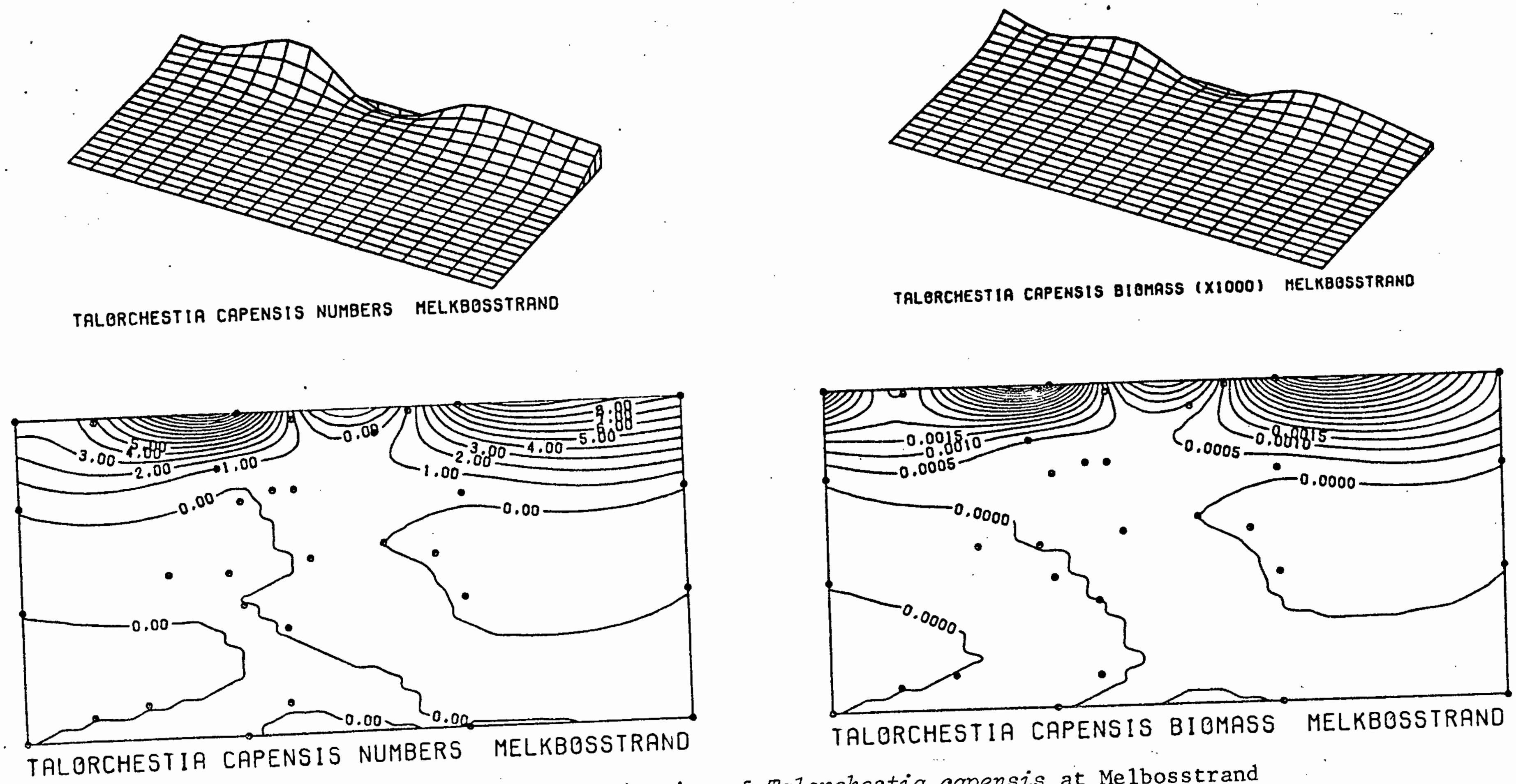
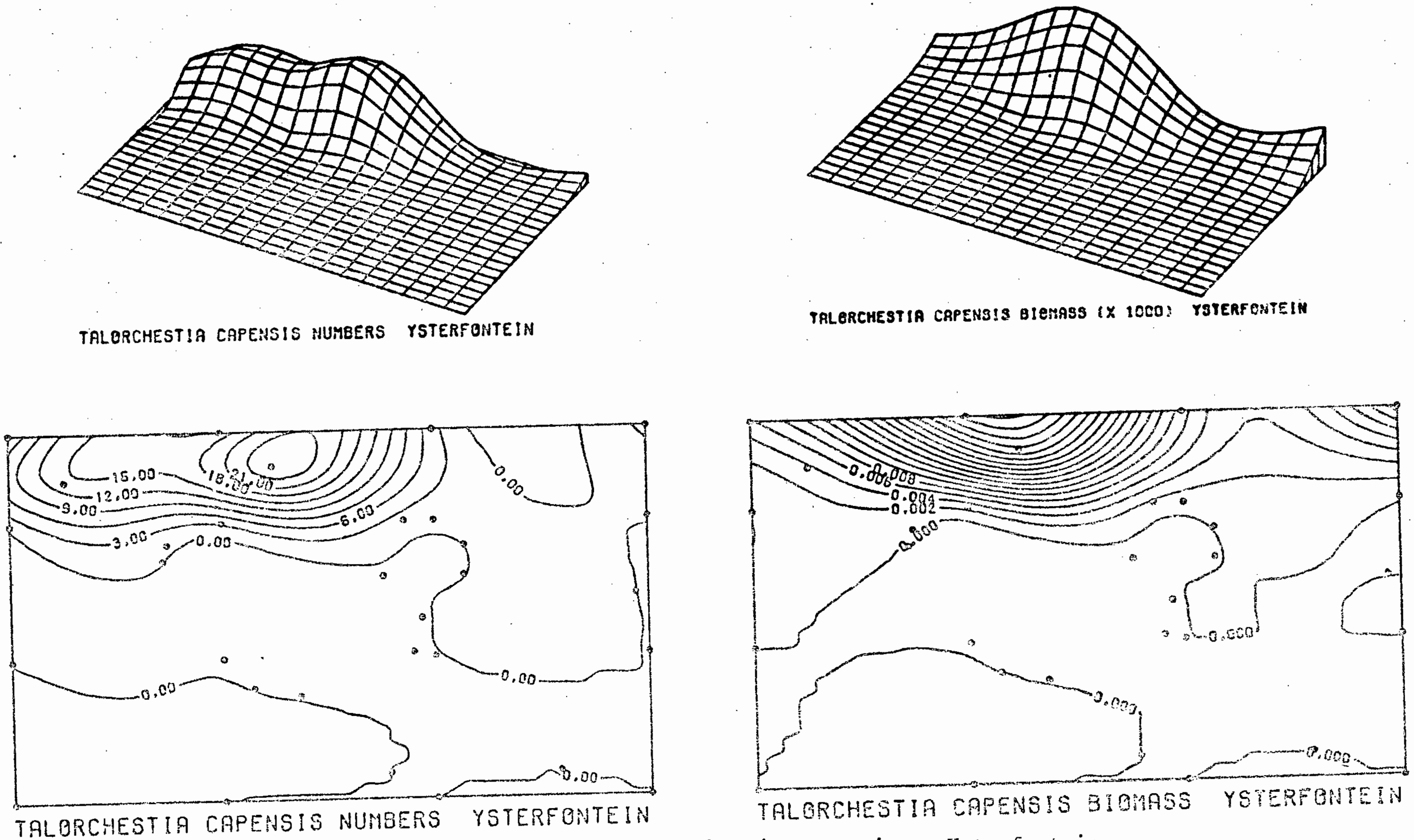


Figure 7.11: Distribution of *Talorchestia capensis* at Melbosstrand



TALORCHESTIA CAPENSIS NUMBERS YSTERFONTEIN

TALORCHESTIA CAPENSIS BIOMASS (X 1000) YSTERFONTEIN

TALORCHESTIA CAPENSIS NUMBERS YSTERFONTEIN

TALORCHESTIA CAPENSIS BIOMASS YSTERFONTEIN

Figure 7.12: Distribution of *Talorchestia capensis* at Ysterfontein

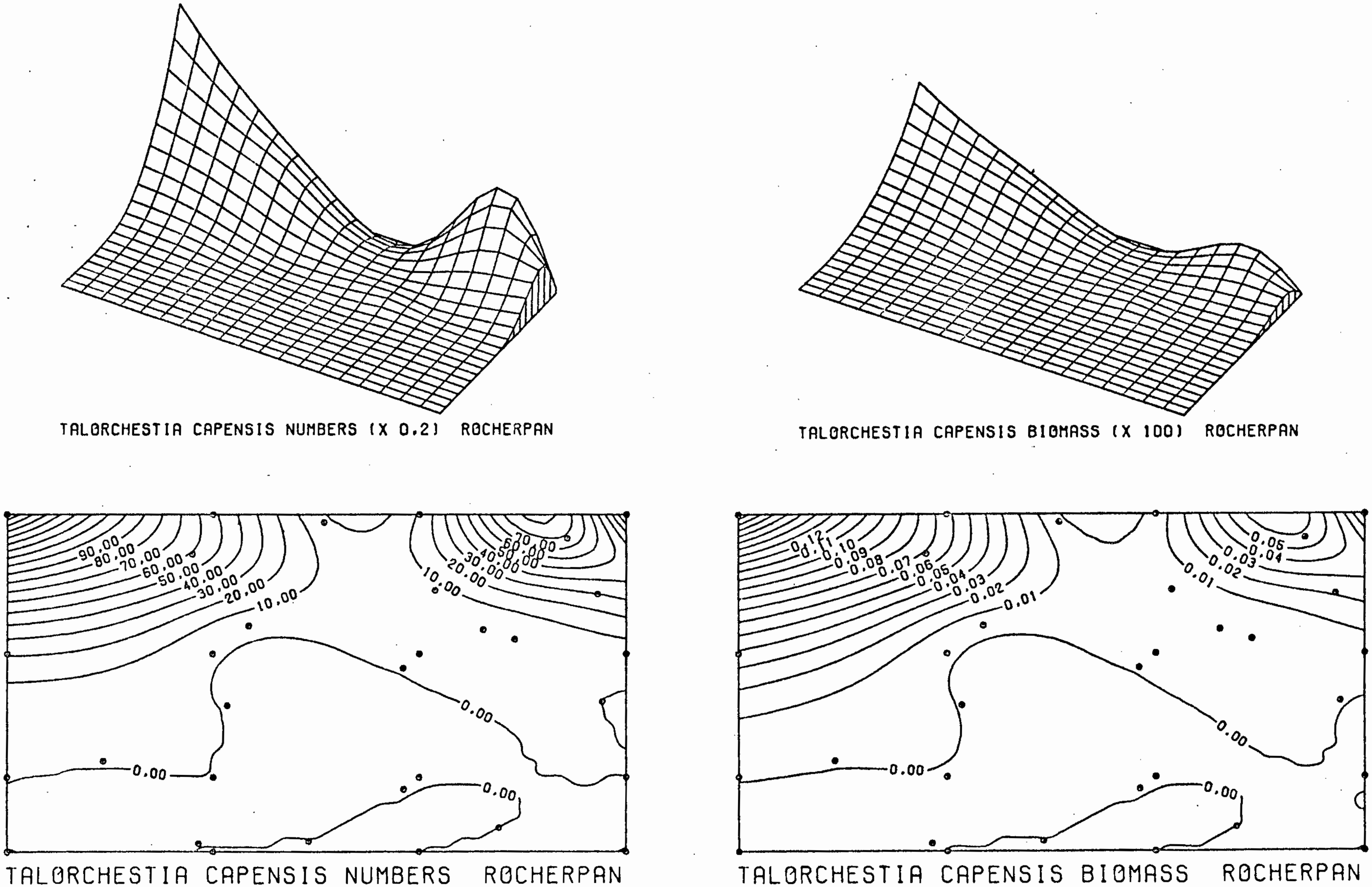


Figure 7.13: Distribution of *Talorchestia capensis* at Rocherpan

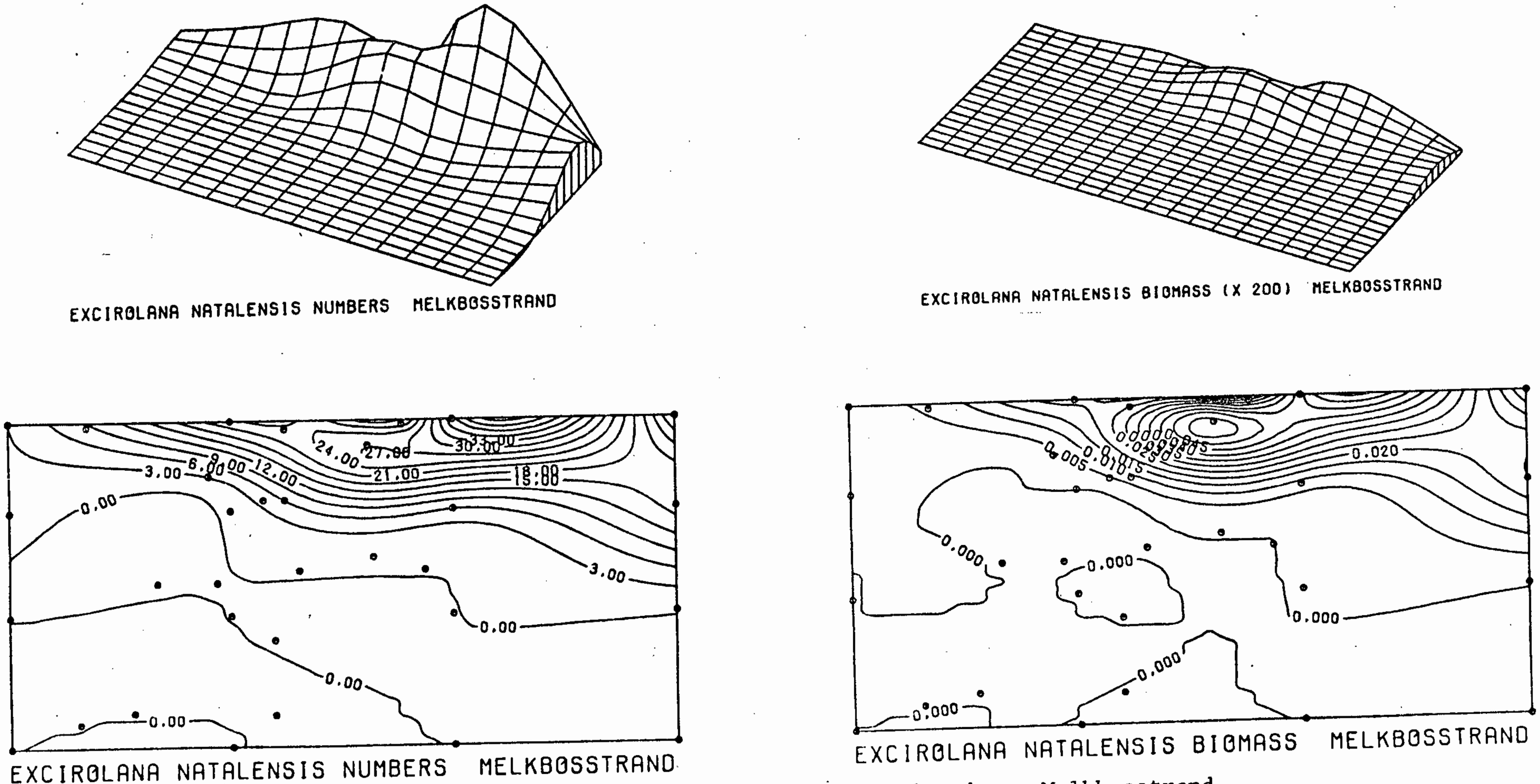
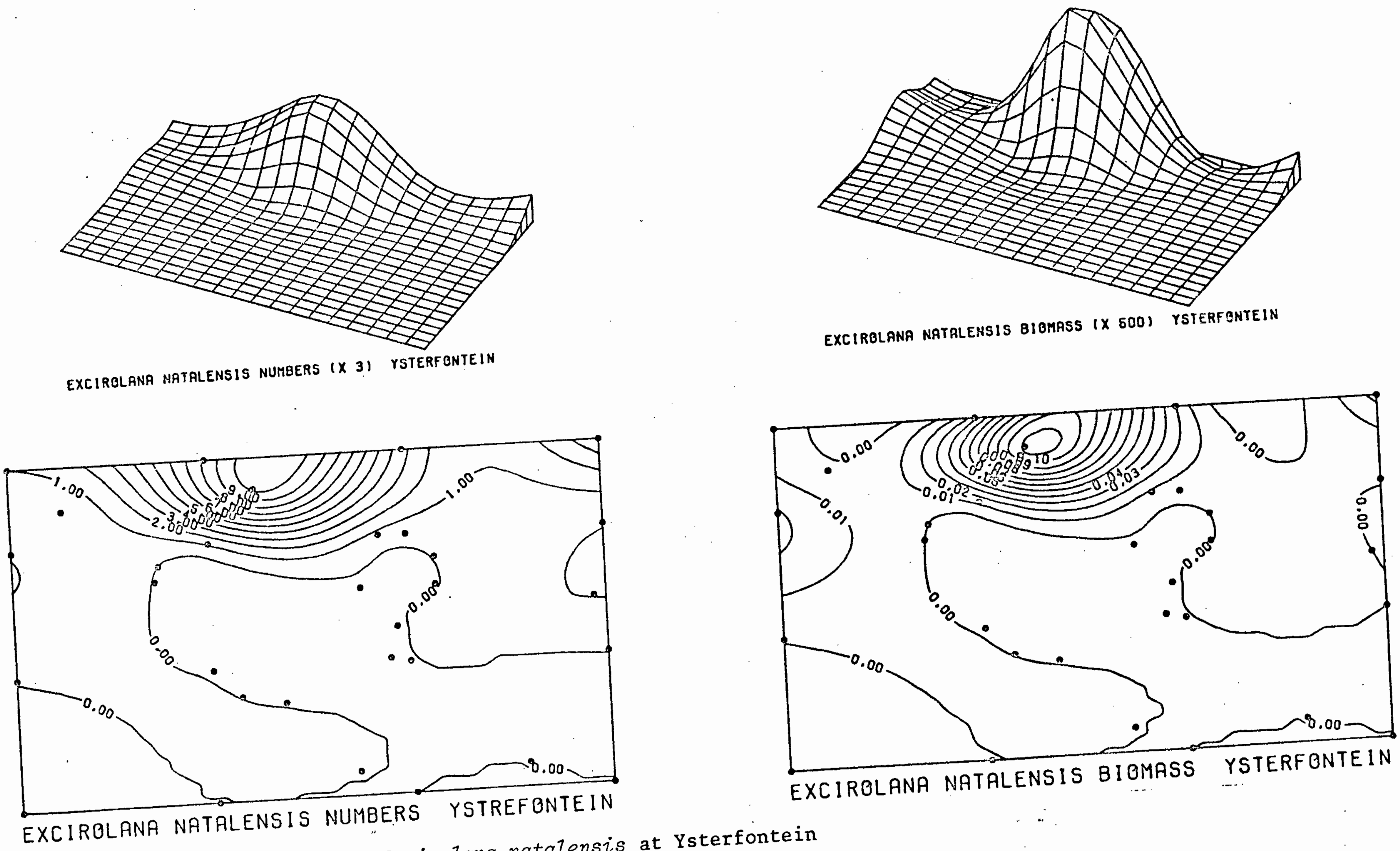


Figure 7.14: Distribution of *Excirolana natalensis* at Melkbosstrand



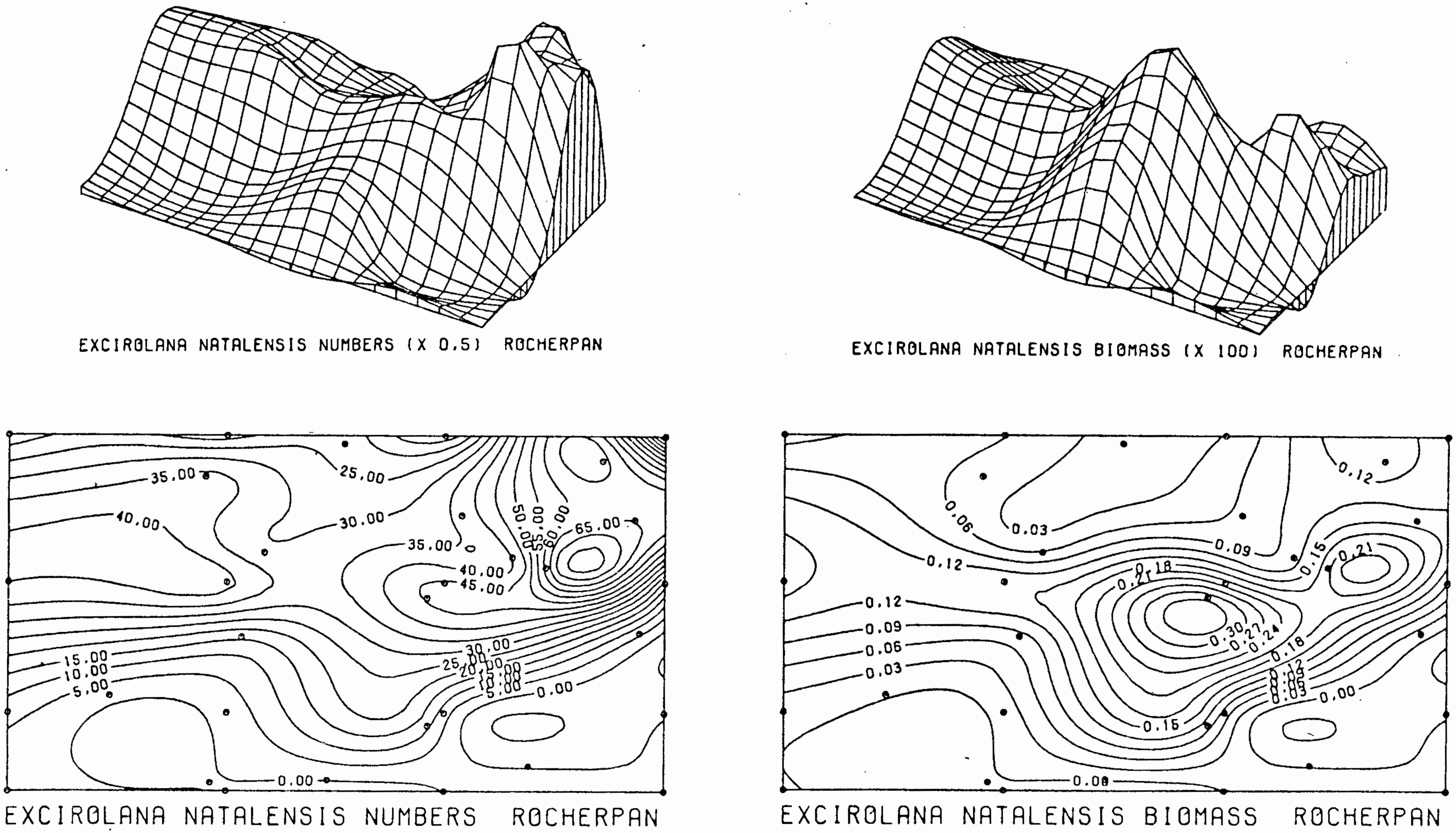
EXCIROLANA NATALENSIS NUMBERS (X 3) YSTERFONTEIN

EXCIROLANA NATALENSIS BIOMASS (X 500) YSTERFONTEIN

EXCIROLANA NATALENSIS NUMBERS YSTREFONTEIN

EXCIROLANA NATALENSIS BIOMASS YSTERFONTEIN

Figure 7.15. Distribution of *Excirolana natalensis* at Ysterfontein



EXCIROLANA NATALENSIS NUMBERS (X 0.5) ROCHERPAN

EXCIROLANA NATALENSIS BIOMASS (X 100) ROCHERPAN

EXCIROLANA NATALENSIS NUMBERS ROCHERPAN

EXCIROLANA NATALENSIS BIOMASS ROCHERPAN

Figure 7.16: Distribution of *Excirolana natalensis* at Rocherpan

Cohort distribution may be patchy, however, as suggested by the biomass plot. It would thus seem as if the size-class composition of the population varies considerably along the beach, although it is not possible to determine this more exactly. It is not possible, either, to assess the extent of these size-class aggregations since they blend with others.

Pontogeloides latipes

A single patch measuring 85 x 28 metres was found in the zone of retention at Melkbosstrand (fig. 7.17). This seems to consist of a larger proportion of juveniles than are present in the remainder of the distribution area. A similar situation occurred at Ysterfontein (fig. 7.18), where the patch measured 89 x 31 metres within the sampled area. If, however, the peak is assumed to be at the centre of the patch, it would measure 150 metres along the beach.

Figure 7.19 shows that at Rocherpan, *Pontogeloides* was distributed into two patches which were at different intertidal levels. These two patches showed different size-class compositions, the one from the zone of retention having a smaller proportion of large animals than the one from the zone of resurgence. The dimensions of these two patches were 35 x 25 metres and 17 x 9 metres respectively.

Scolelepis squamata

On both beaches where this deposit or detritus feeding polychaete was found, it showed a patchy distribution within the zone of retention. The patches measured 68 x 42 metres at Melkbosstrand (fig. 7.20) and

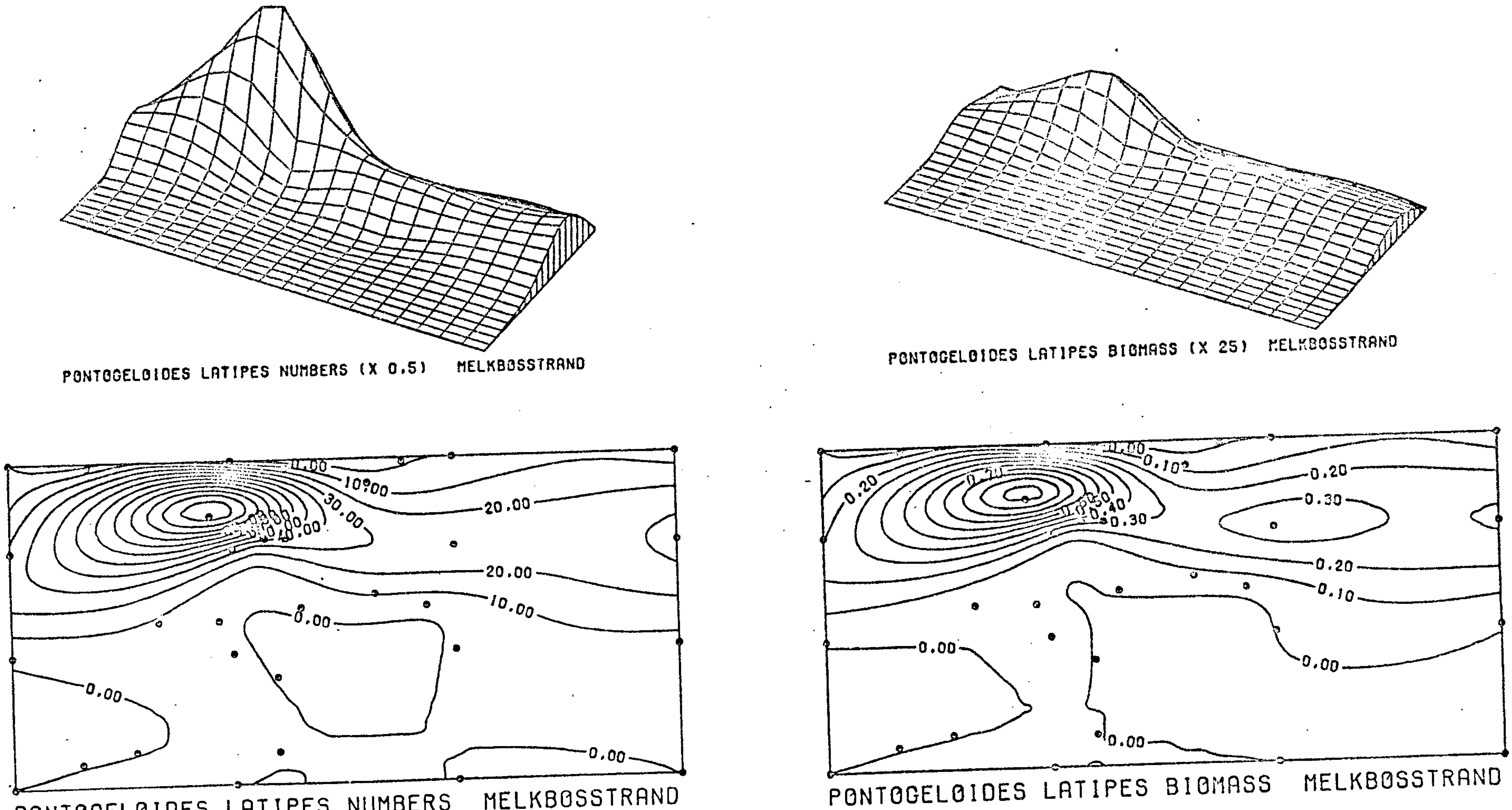


Figure 7.17: Distribution of *Pontogeloides latipes* at Melkbosstrand

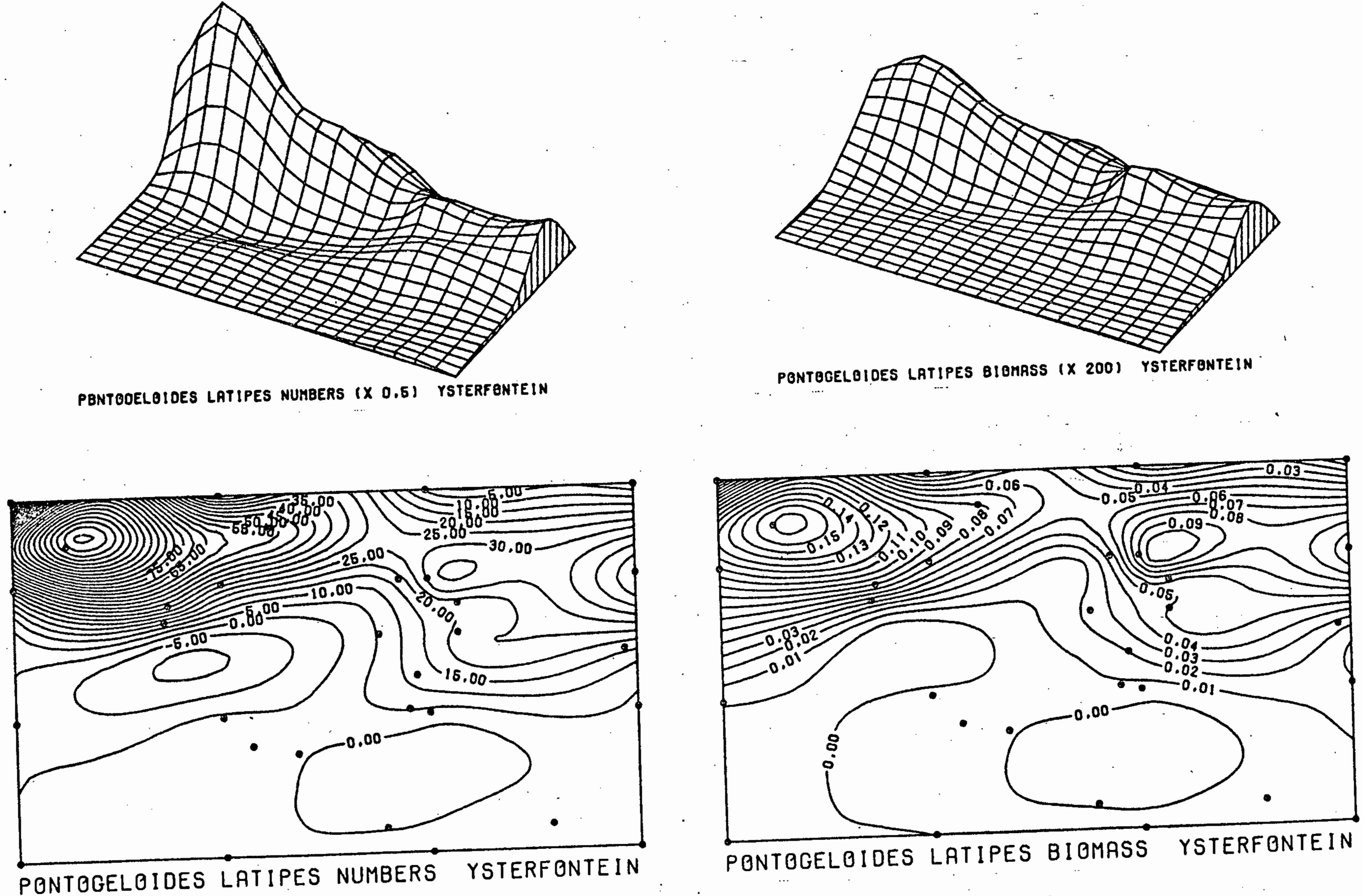
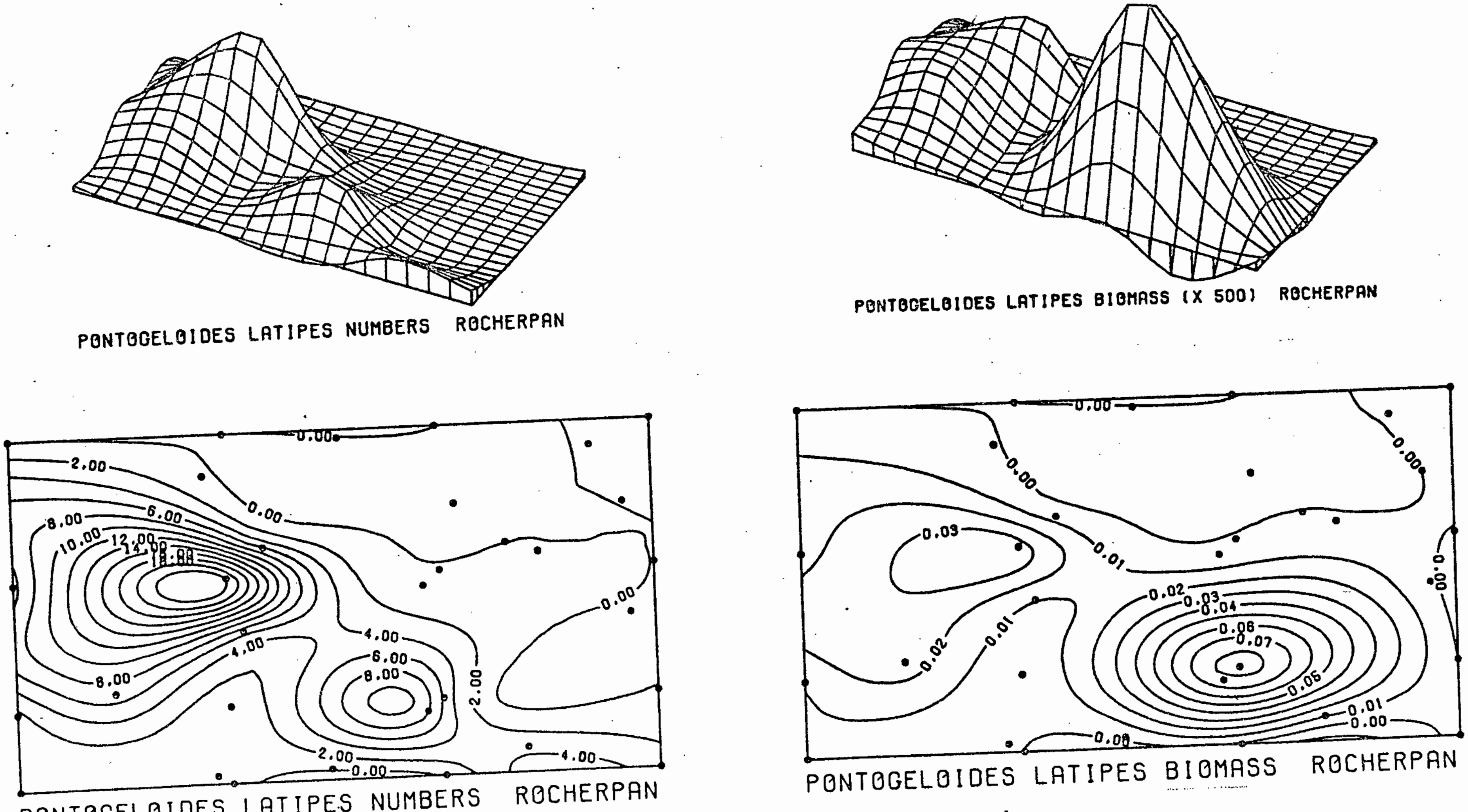


Figure 7.18: Distribution of *Pontogeloides latipes* at Ysterfontein



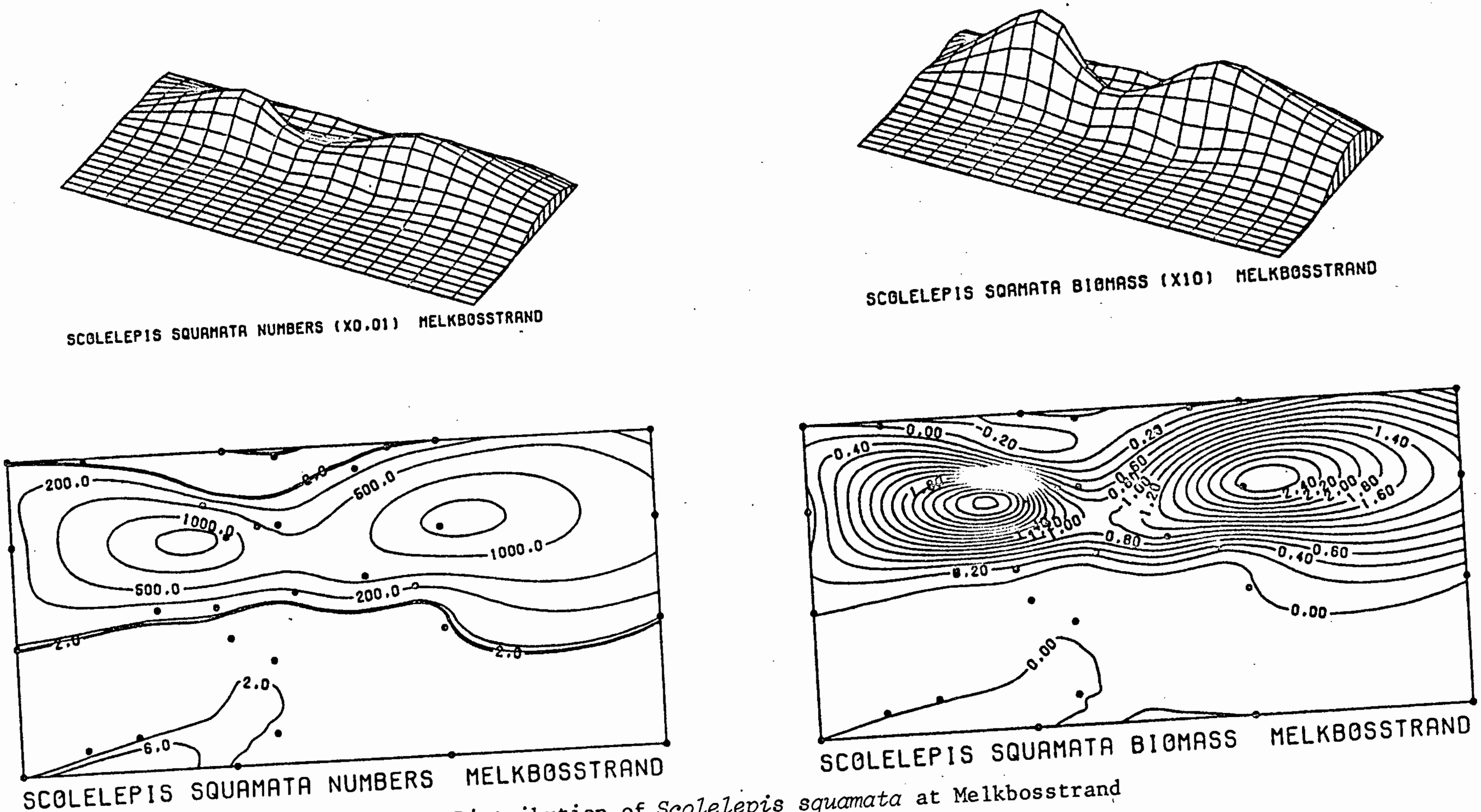
PONTOGELOIDES LATIPES NUMBERS ROCHERPAN

PONTOGELOIDES LATIPES BIOMASS (X 500) ROCHERPAN

PONTOGELOIDES LATIPES NUMBERS ROCHERPAN

PONTOGELOIDES LATIPES BIOMASS ROCHERPAN

Figure 7.19: Distribution of *Pontogeloides latipes* at Rocherpan



SCOLELEPIS SQUAMATA NUMBERS (X0.01) MELKBOSSTRAND

SCOLELEPIS SQAMATA BIOMASS (X10) MELKBOSSTRAND

SCOLELEPIS SQUAMATA NUMBERS MELKBOSSTRAND

SCOLELEPIS SQUAMATA BIOMASS MELKBOSSTRAND

Figure 7.20: Distribution of *Scolelepis squamata* at Melkbosstrand

60 x 36 metres at Ysterfontein (fig. 7.21). The size-class distribution seemed fairly uniform on both beaches. On west coast beaches this species is strictly intertidal although Edwards (1973a), Hartmann-Schröder (1971) and others have found it extending to depths of 45 m in other parts of the world.

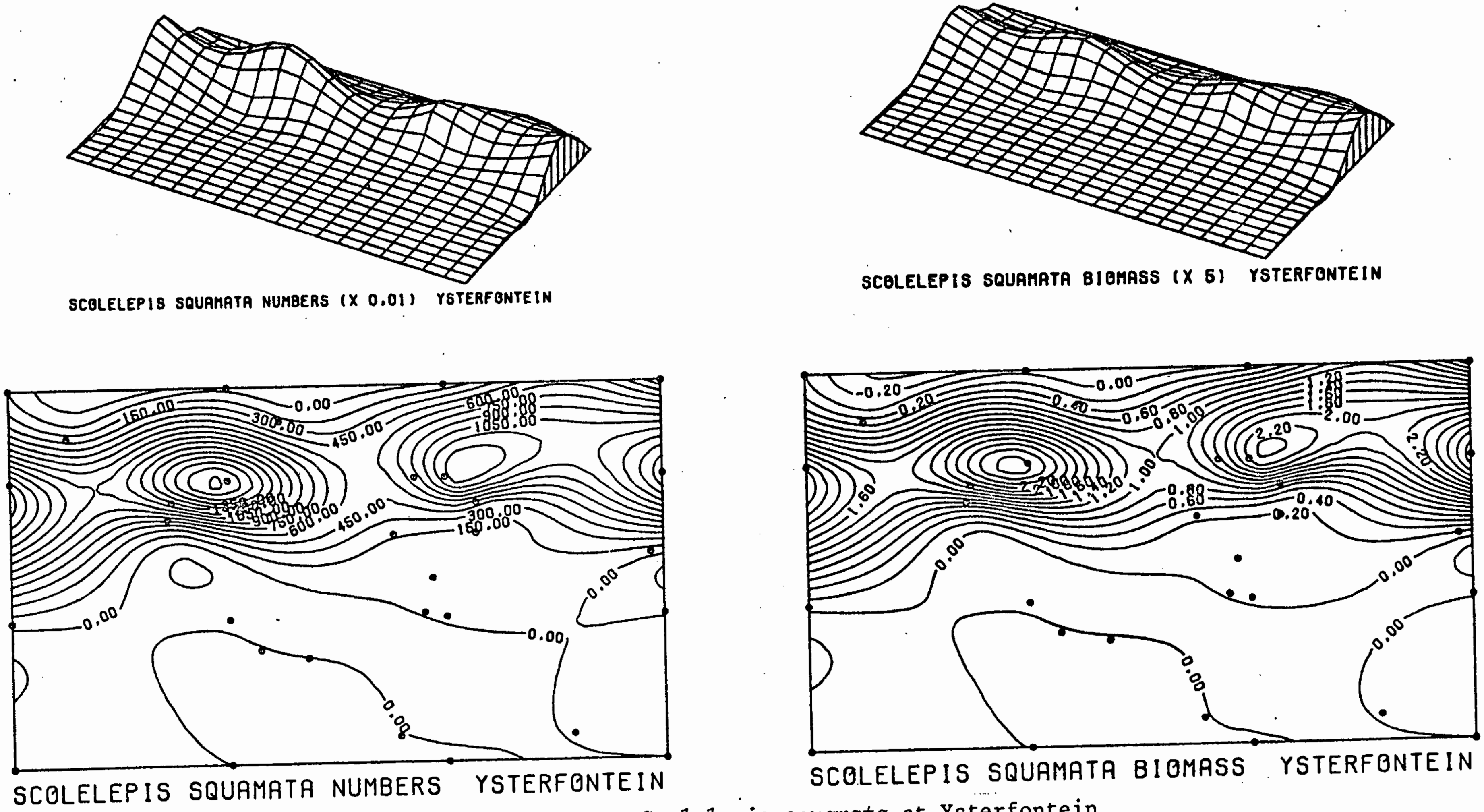
Donax serra

This bivalve is the most important species in terms of biomass on all three beaches, as well as one of the most important numerically (see chapter 5). Its size-class zonation has been described in chapter 4. At Melkbosstrand (fig. 7.22), two distinct patches were encountered in the study area, the denser one measuring 70 x 30 metres and the other 55 x 30 metres. The size-class composition of the patches does not appear to vary significantly along this beach, or the one at Ysterfontein (fig. 7.23). Here the single patch measured 135 x 47 metres and, as at Melkbosstrand, occupied the zone of retention.

Different zones were occupied by the patches at Rocherpan (fig. 7.24), however, where they were found in the zones of resurgence and saturation. On this beach a complete patch of mainly juvenile animals was sampled, measuring 58 x 18 m, as well as a portion of a second patch which also included some larger animals.

Eurydice longicornis

At both Melkbosstrand and Ysterfontein (figs 7.25 and 7.26 respectively) *Eurydice* occurred at nearly all intertidal levels. On these two beaches



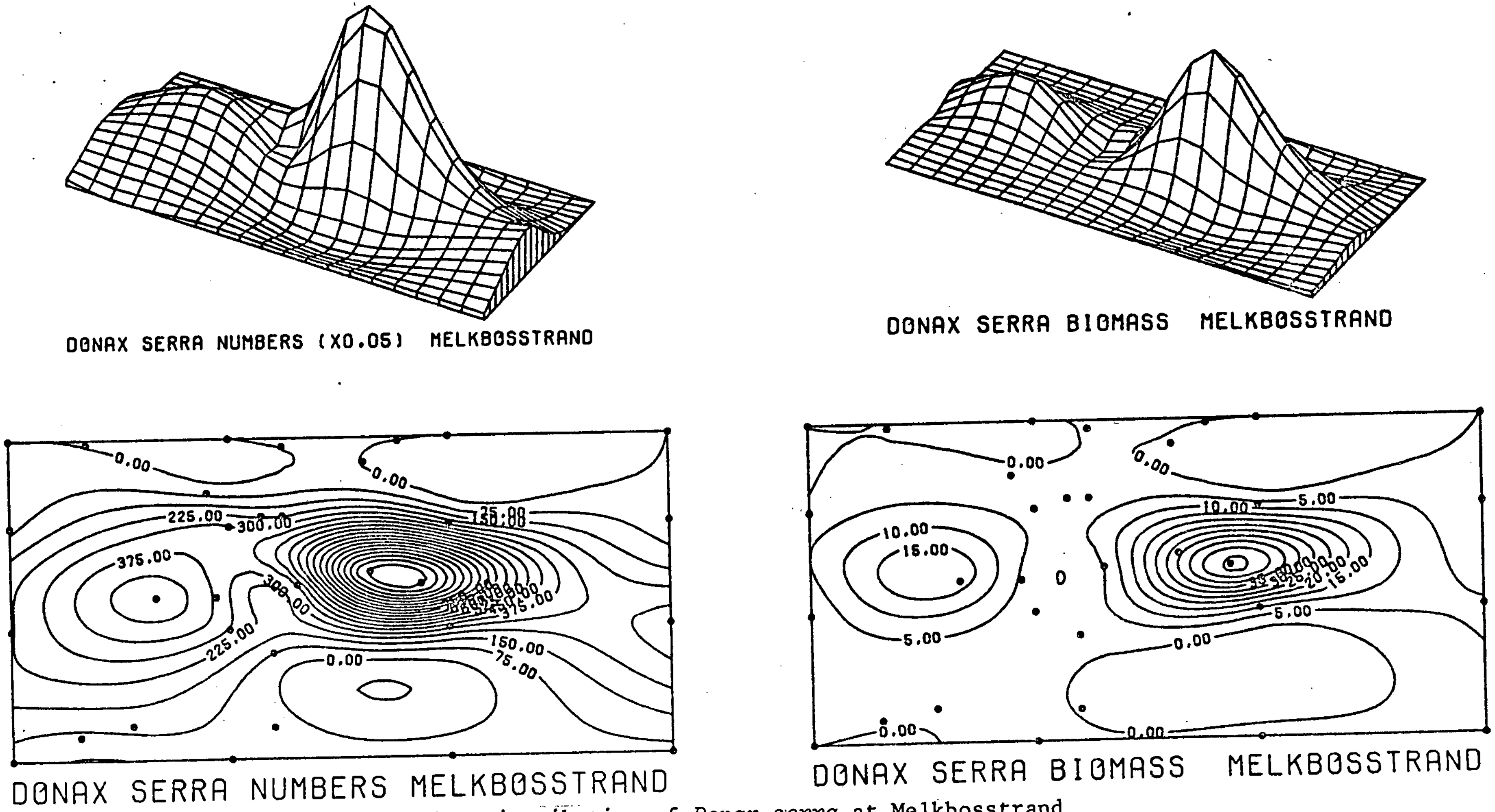
SCOLELEPIS SQUAMATA NUMBERS (X 0.01) YSTERFONTEIN

SCOLELEPIS SQUAMATA BIOMASS (X 5) YSTERFONTEIN

SCOLELEPIS SQUAMATA NUMBERS YSTERFONTEIN

SCOLELEPIS SQUAMATA BIOMASS YSTERFONTEIN

Figure 7.21: Distribution of *Scolelepis squamata* at Ysterfontein



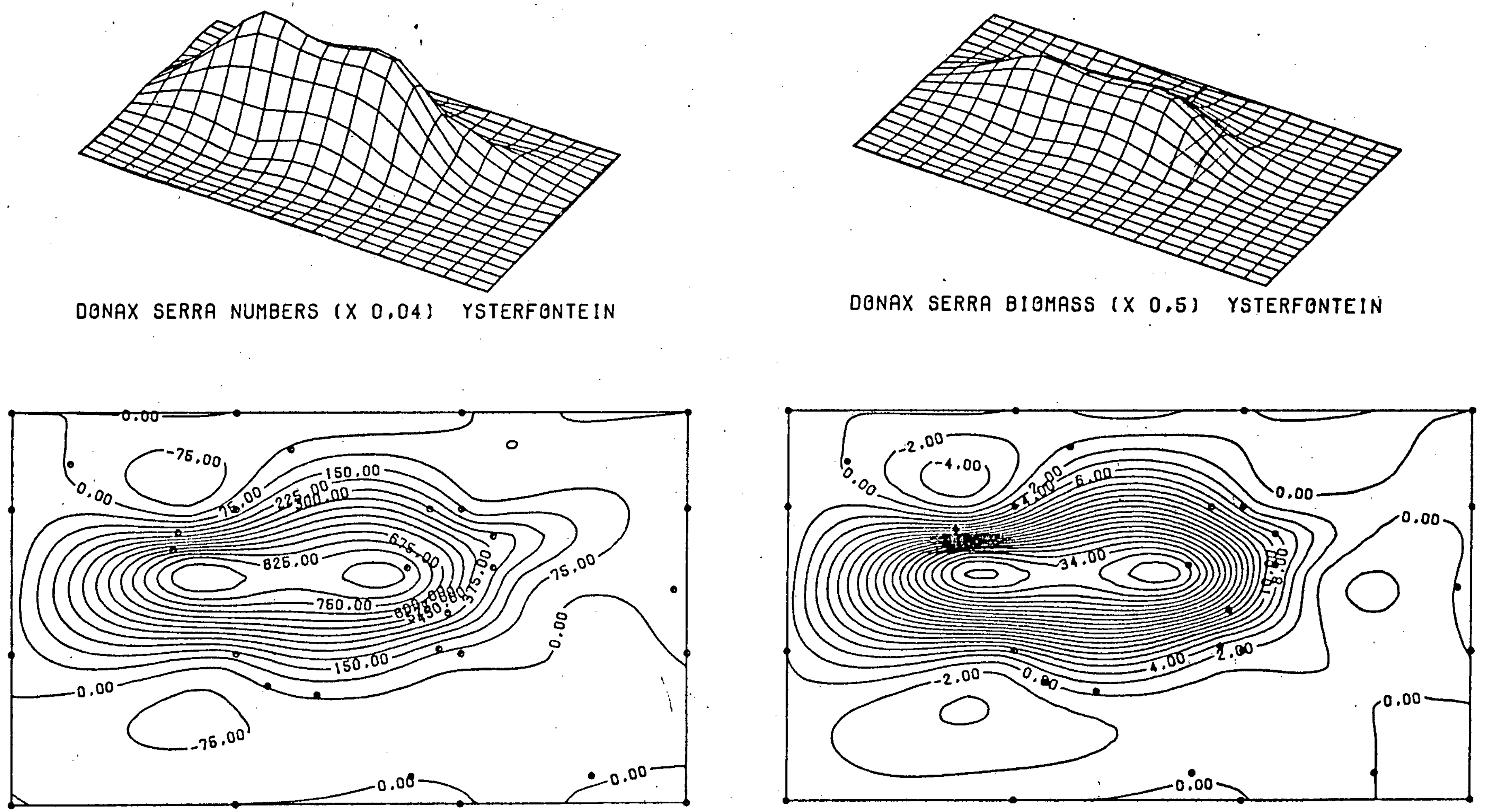
DONAX SERRA NUMBERS (X0.05) MELKBOSSTRAND

DONAX SERRA BIOMASS MELKBOSSTRAND

DONAX SERRA NUMBERS MELKBOSSTRAND

DONAX SERRA BIOMASS MELKBOSSTRAND

Figure 7.22: Distribution of *Donax serra* at Melkbosstrand



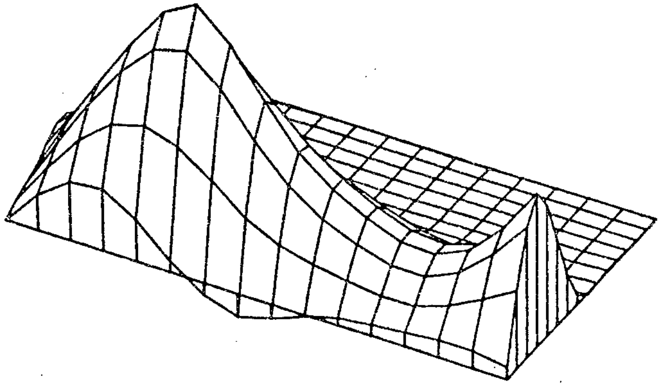
DONAX SERRA NUMBERS (X 0.04) YSTERFONTEIN

DONAX SERRA BIOMASS (X 0.5) YSTERFONTEIN

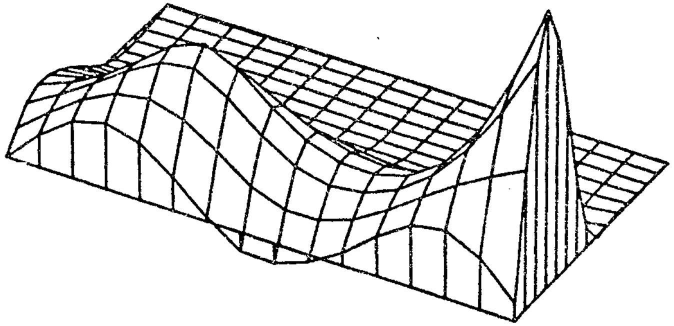
DONAX SERRA NUMBERS YSTERFONTEIN

DONAX SERRA BIOMASS YSTERFONTEIN

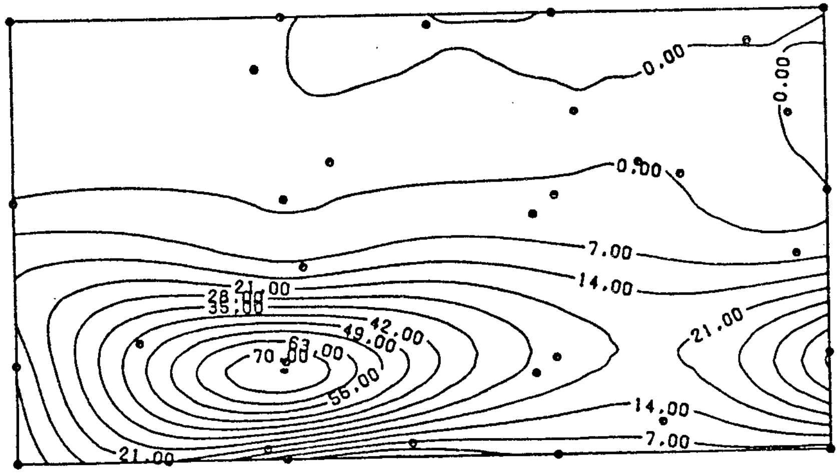
Figure 7.23: Distribution of *Donax serra* at Ysterfontein



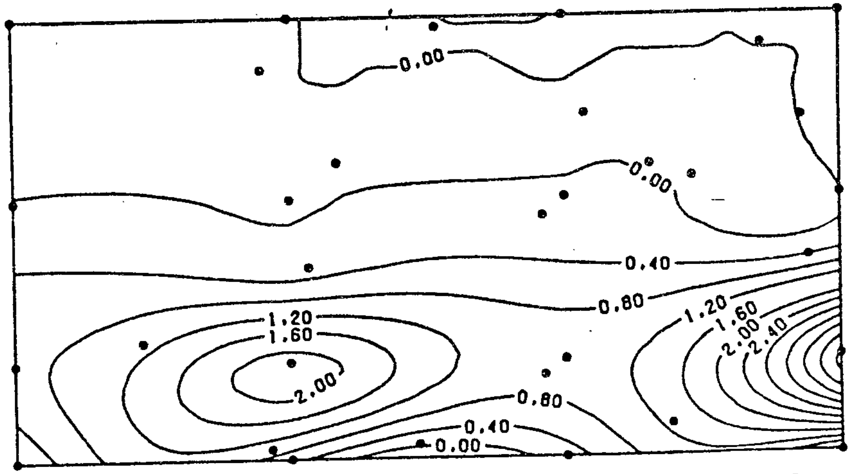
DONAX SERRA NUMBERS (X 0.5) ROCHERPAN



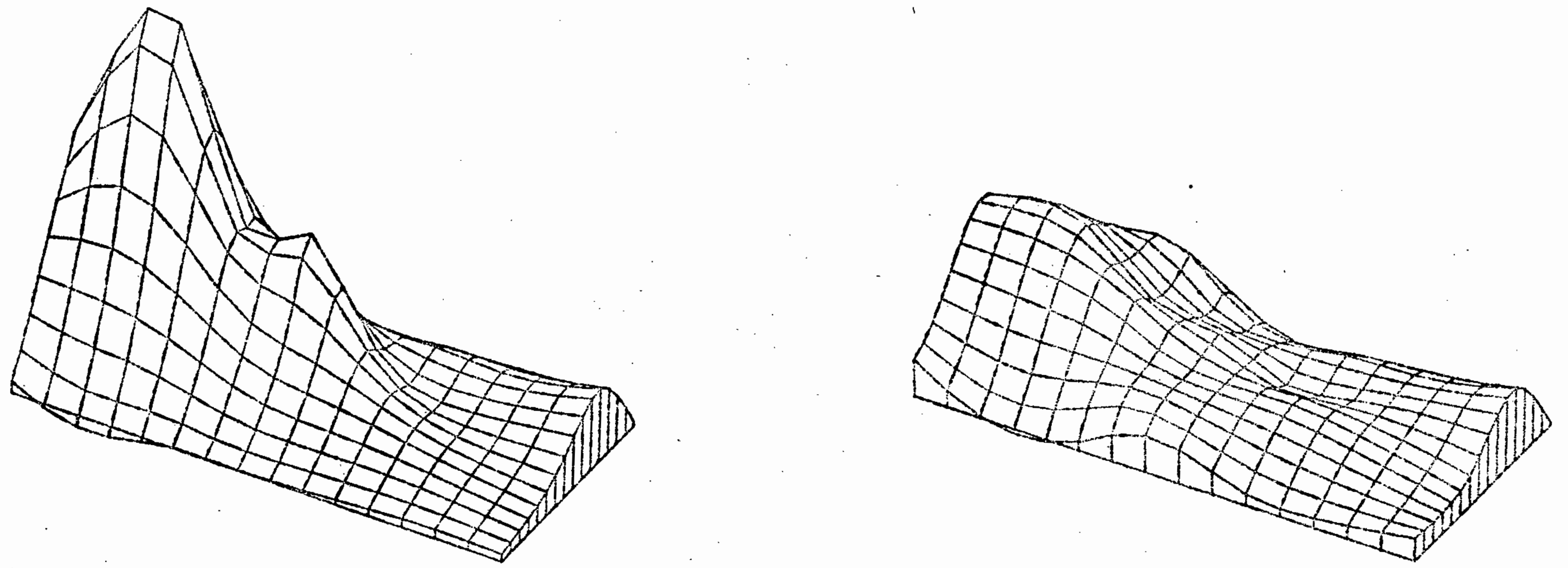
DONAX SERRA BIOMASS (X 10) ROCHERPAN



DONAX SERRA NUMBERS ROCHERPAN

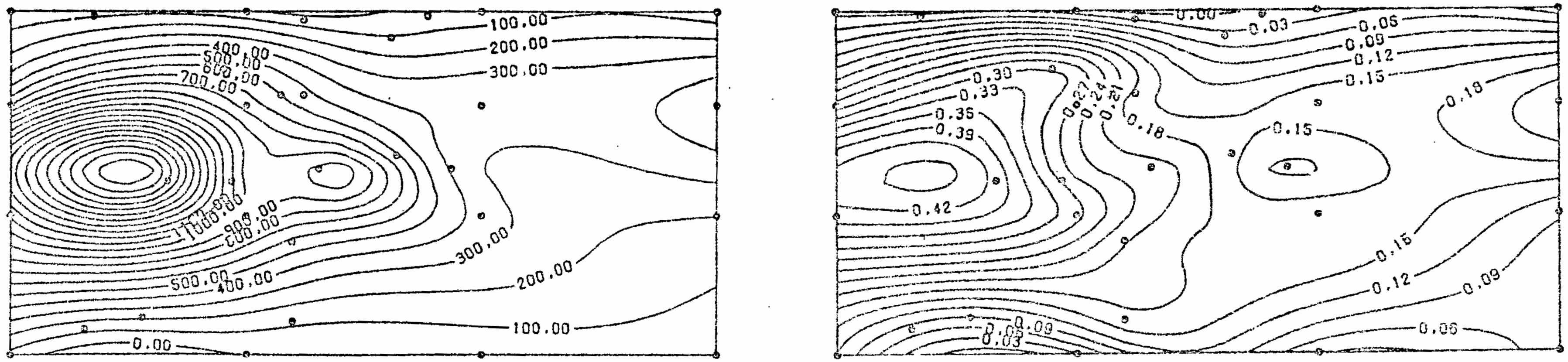


DONAX SERRA BIOMASS ROCHERPAN



EURYDICE LONGICORNIS NUMBERS (X0.05) MELKBOSSTRAND

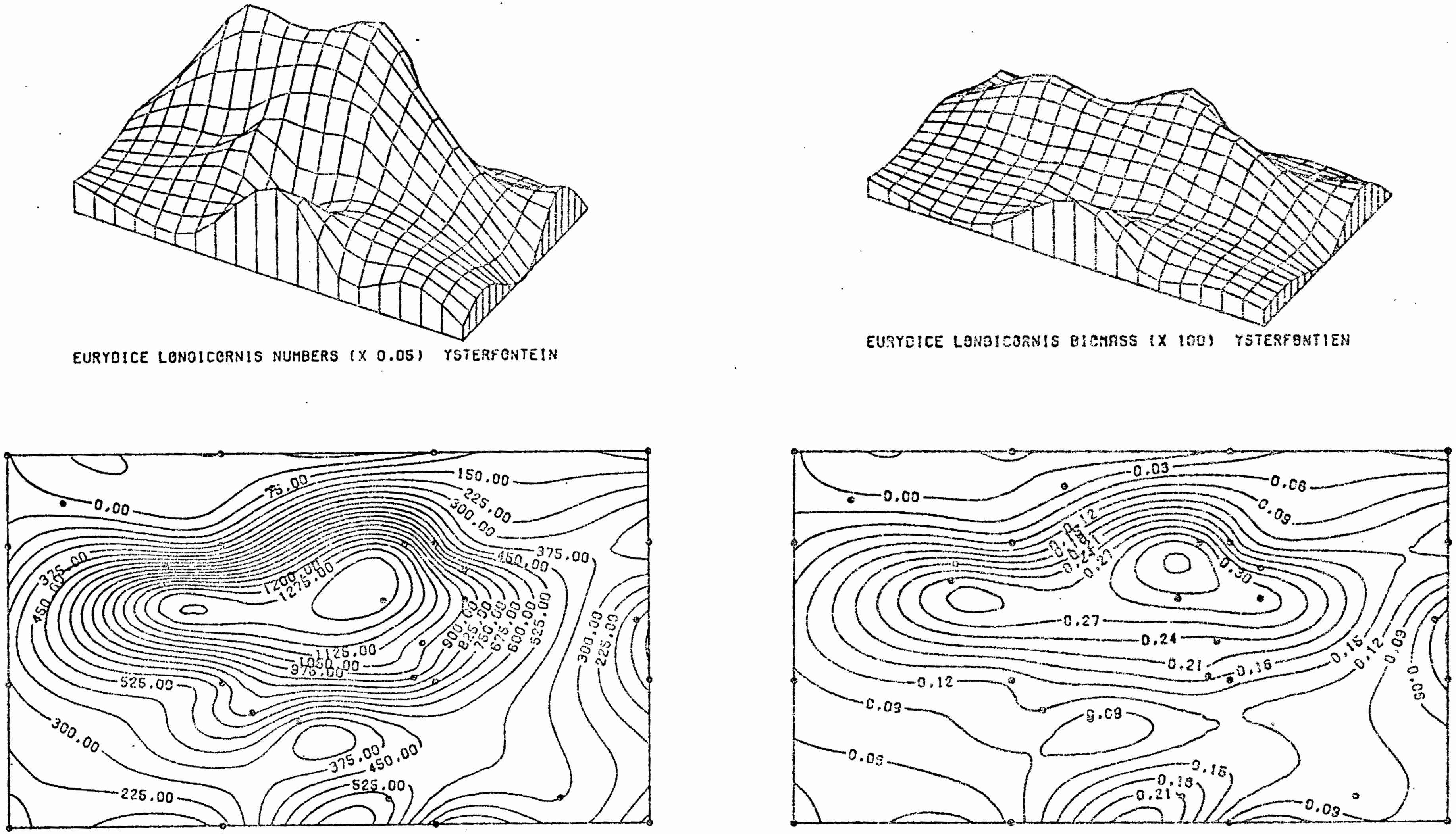
EURYDICE LONGICORNIS BIOMASS (X100) MELKBOSSTRAND



EURYDICE LONGICORNIS NUMBERS MELKBOSSTRAND

EURYDICE LONGICORNIS BIOMASS MELKBOSSTRAND

Figure 7.25: Distribution of *Eurydice longicornis* at Melkbosstrand


EURYDICE LONGICORNIS NUMBERS (X 0.05) YSTERFONTEIN

EURYDICE LONGICORNIS BIOMASS (X 100) YSTERFONTIEN

EURYDICE LONGICORNIS NUMBERS YSTERFONTEIN

EURYDICE LONGICORNIS BIOMASS YSTERFONTEIN

Figure 7.26. Distribution of *Eurydice longicornis* at Ysterfontein

it is the most important species numerically. At Melkbosstrand only a portion of the patch was sampled, one that probably measured some 100 x 50 m, assuming the peak to lie in the centre of the patch. Comparison of the number and biomass figures shows the patch to consist largely of juveniles. At Ysterfontein a single patch was sampled in the zone of retention, measuring 130 x 50 m, while in the zone of saturation part of a smaller patch was sampled, which appeared to have a lower proportion of juveniles than the large patch.

At Rocherpan (fig. 7.27) two patches were sampled, the smaller one measuring 25 x 20 m, while the larger one (of which only a portion was included in the study area) probably measured about 50 x 25 m. On this beach *Eurydice* is absent from the higher intertidal zones and the patches were centered on the zone of resurgence. As can be seen from figure 7.27, the size-class composition of the two patches differed, the smaller patch having relatively fewer juveniles.

Pseudharpinia excavata

This amphipod occupies the lower half of the intertidal zone on all three beaches. At Melkbosstrand (fig. 7.28) it appears as if the very edge of a patch has been sampled. The distribution is otherwise uniform along the beach in the study area. There is a clear increase in density from mid-tide low water, suggesting that the intertidal zone represents only the fringe of *Pseudharpinia's* distribution. An essentially similar pattern was found at Ysterfontein (fig. 7.29), although here a small patch of 50 x 21 m was also found. In both these beaches, the size-class composition of the population seemed fairly uniform. At Rocherpan (fig. 7.30), however, the segments of patches along the low-water mark seemed to consist of juveniles, while those in the zone of resurgence were made up of larger organisms. The only patch measured in its entirety measured 22 x 13 m.

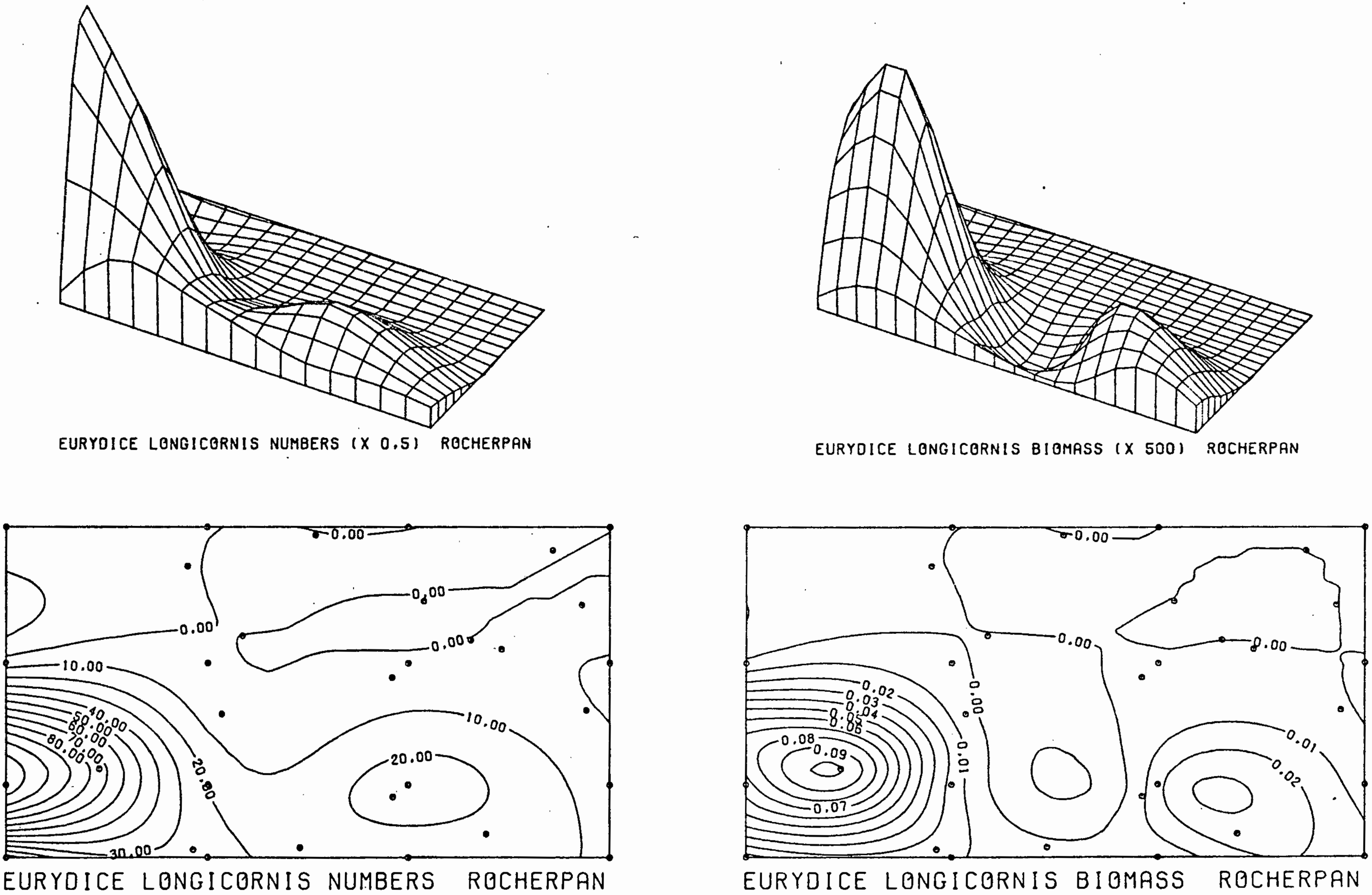
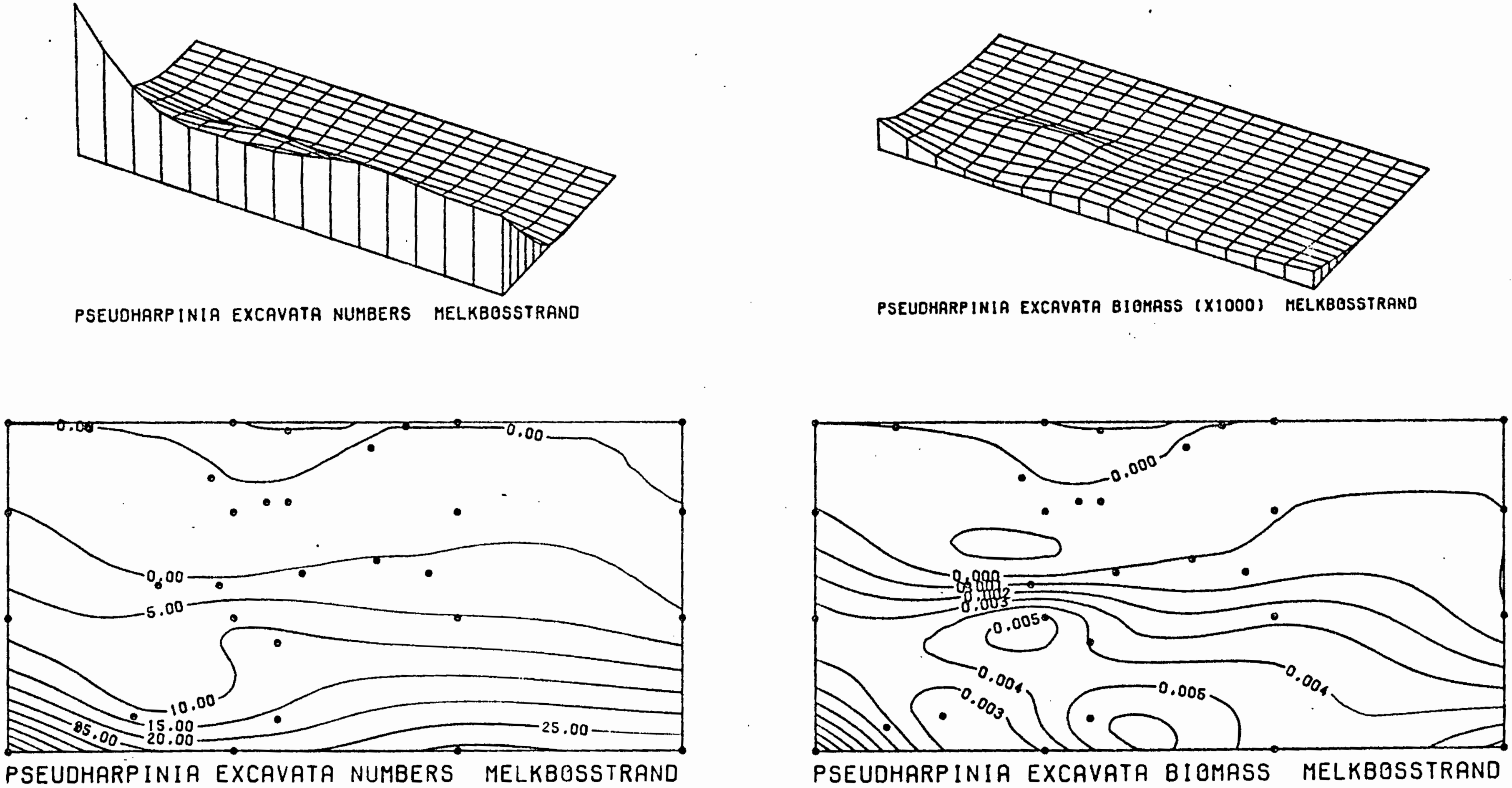


Figure 7.27. Distribution of *Eurydice longicornis* at Rocherpan


PSEUDHARPINIA EXCAVATA NUMBERS MELKBOSSTRAND

PSEUDHARPINIA EXCAVATA BIOMASS (X1000) MELKBOSSTRAND

PSEUDHARPINIA EXCAVATA NUMBERS MELKBOSSTRAND

PSEUDHARPINIA EXCAVATA BIOMASS MELKBOSSTRAND

Figure 7.28: Distribution of *Pseudharpinia excavata* at Melkbosstrand

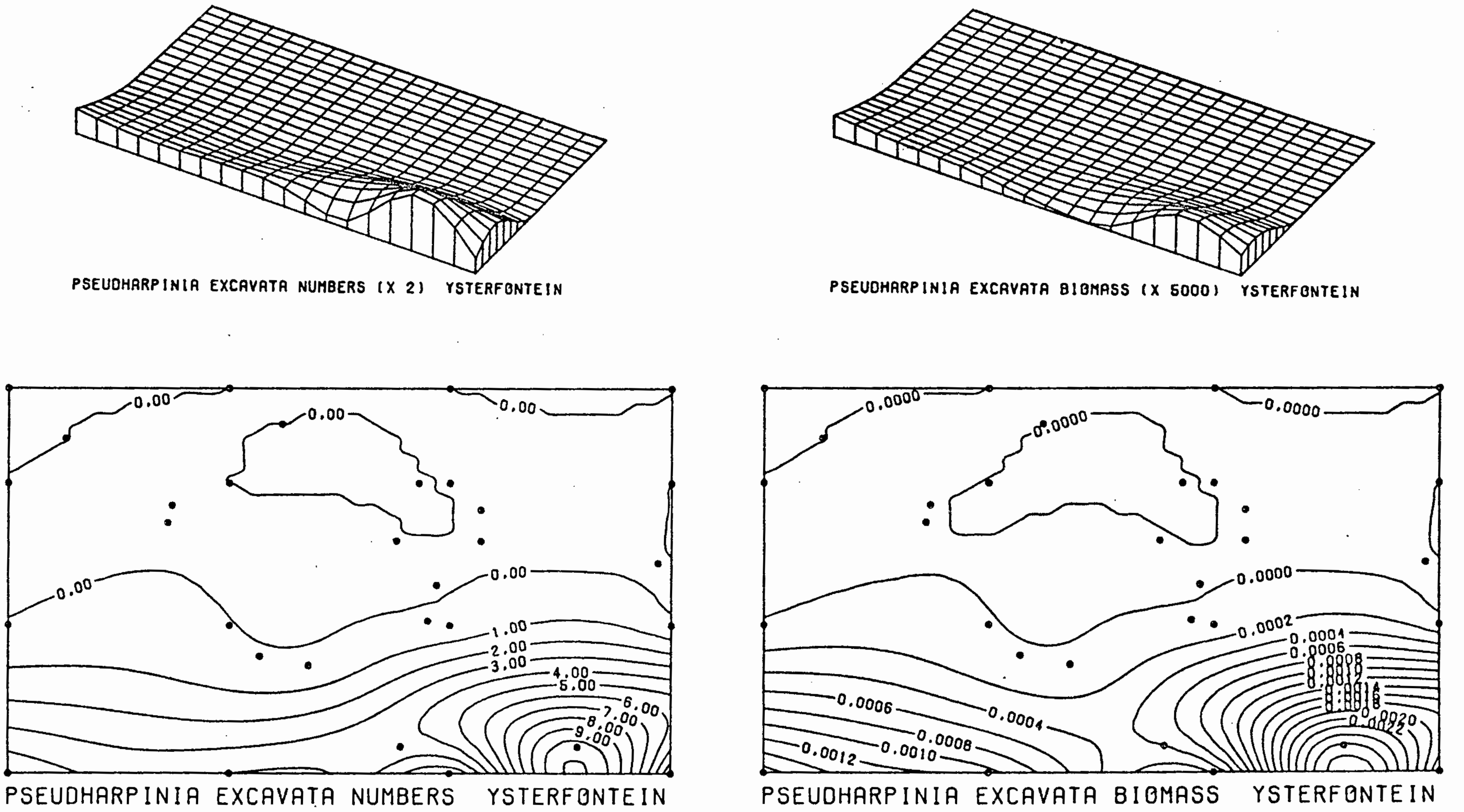
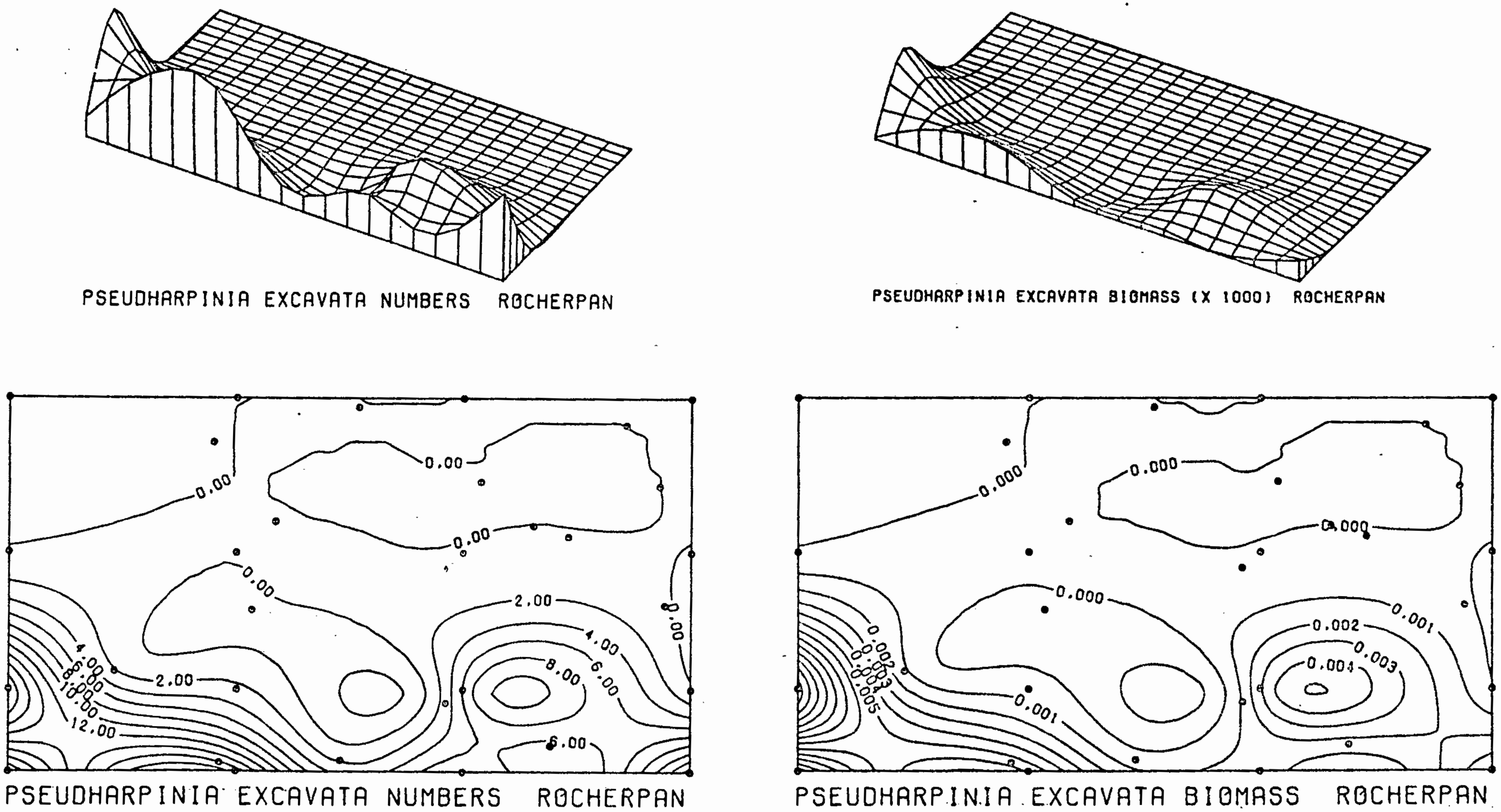


Figure 7.29. Distribution of *Pseudharpinia excavata* at Ysterfontein



PSEUDHARPINIA EXCAVATA NUMBERS ROCHERPAN

PSEUDHARPINIA EXCAVATA BIOMASS (X 1000) ROCHERPAN

PSEUDHARPINIA EXCAVATA NUMBERS ROCHERPAN

PSEUDHARPINIA EXCAVATA BIOMASS ROCHERPAN

Figure 7.30: Distribution of *Pseudharpinia excavata* at Rocherpan

Gastrosaccus psammodytes

This psammosphilous mysid did not show any marked patchiness in its distribution at Melkbosstrand (fig. 7.31), although there was some unevenness. As in the case of *Pseudharpinia*, the intertidal zone represents the fringe of its distribution. Wooldridge (1981) has shown that zonation occurs between various size-classes of *Gastrosaccus* but in this study insufficient data and no subtidal samples were obtained to show this. At Ysterfontein (fig. 7.32) a portion of a patch was encountered the dimensions of which were approximately 71 x 27 m. This consisted mainly of juveniles while a greater proportion of adults was present elsewhere. Insufficient animals were collected at Rocherpan to permit study.

Sigalion capense

This polychaete was relatively evenly distributed across the lower half of the beach both at Melkbosstrand and Ysterfontein (figs.7.33 and 7.34). At Melkbosstrand a single patch measuring 35 x 15 m was found at the upper edge of the zone of resurgence; this may have been caused by a decaying organism buried in the sand and attracting individuals to the area. The size-class composition of the population in both beaches was uniform. *Sigalion* too, is absent from Rocherpan.

Bullia digitalis

This gastropod is highly mobile and Brown (1971b) has described both its

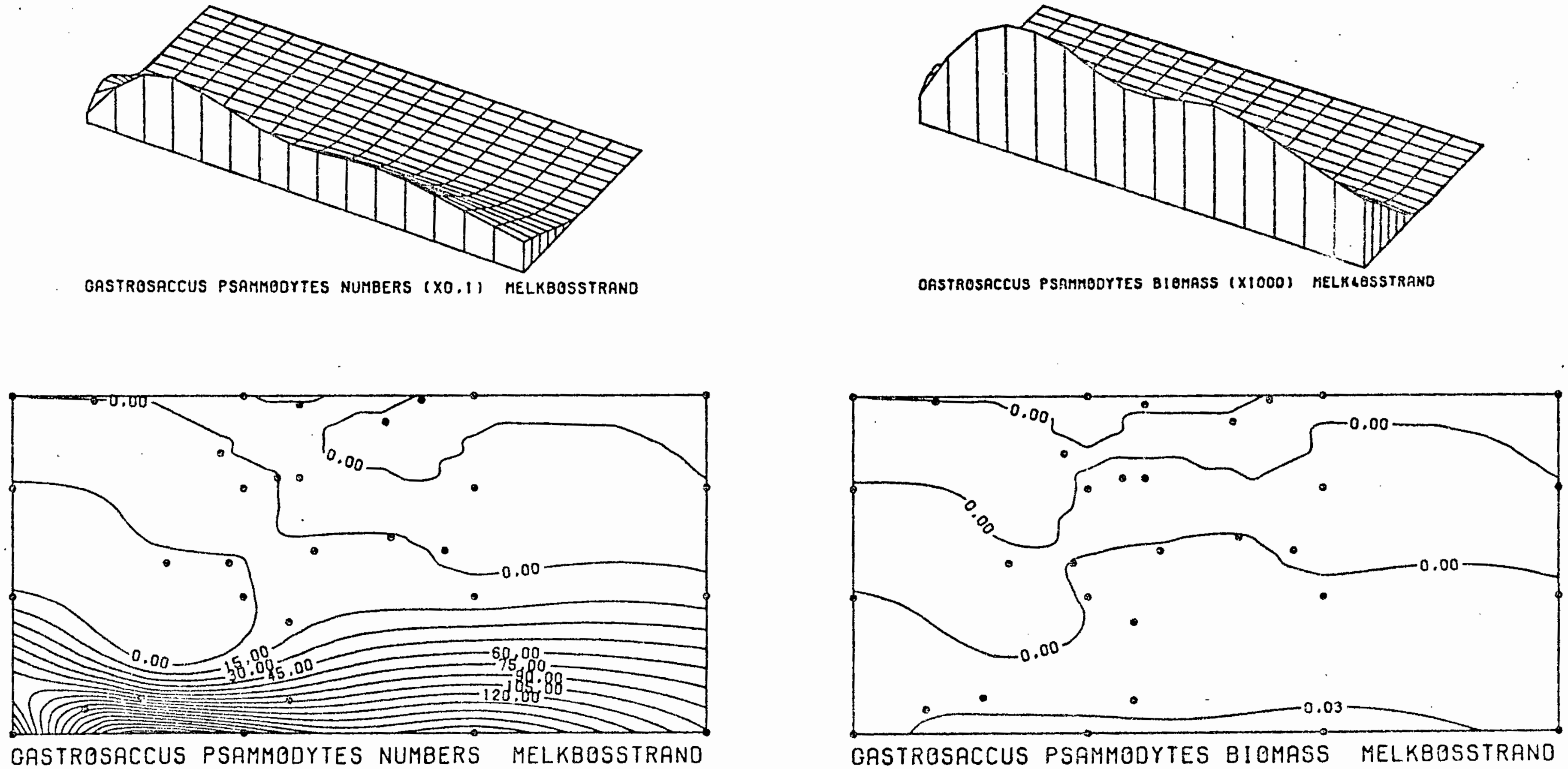
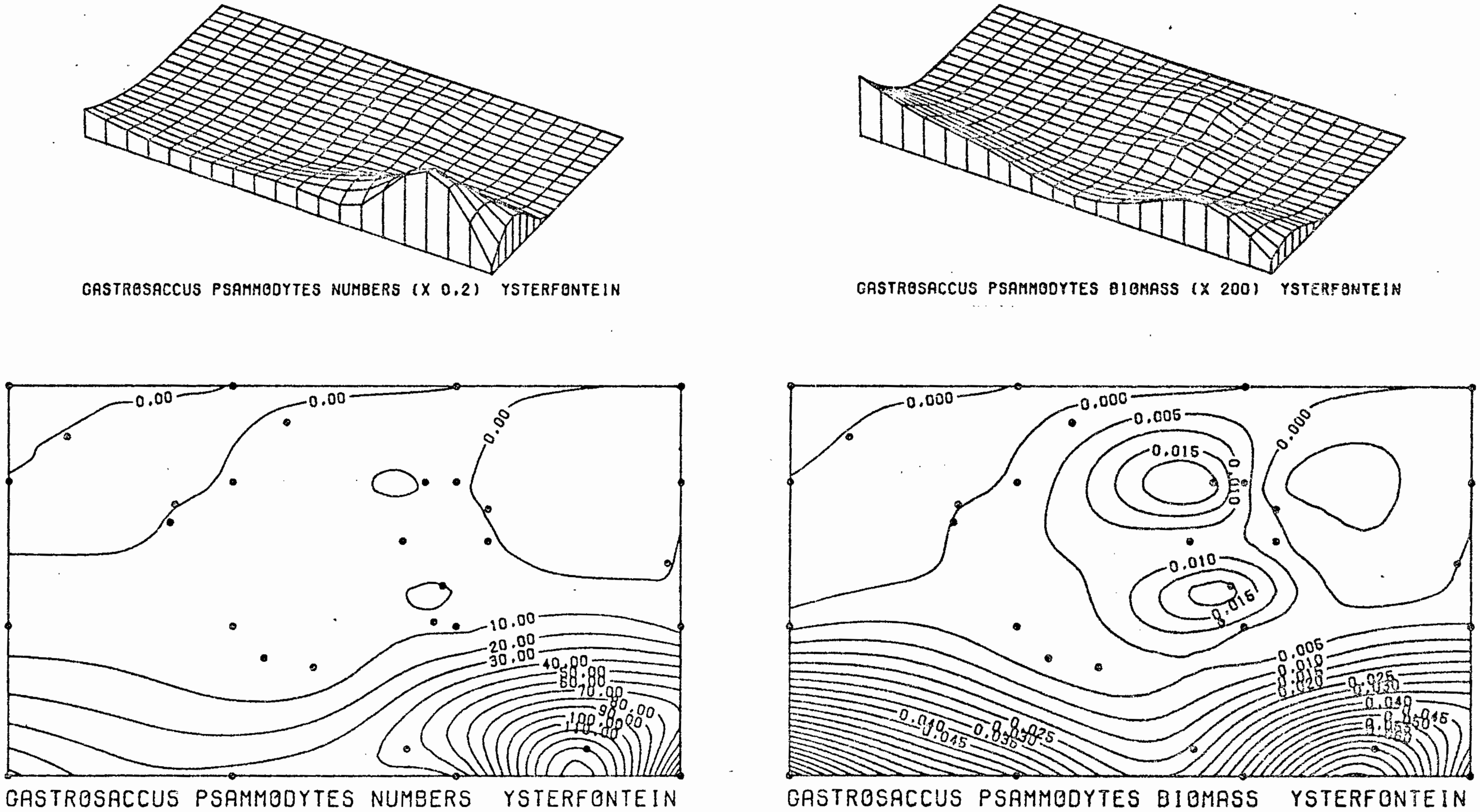


Figure 7.31: Distribution of *Gastrosaccus psammodytes* at Melkbosstrand



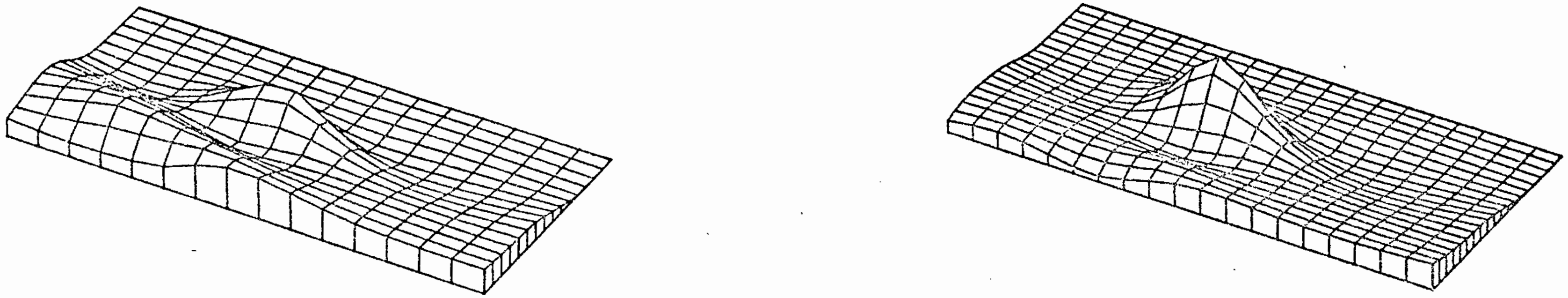
GASTROSACCUS PSAMMODYTES NUMBERS (X 0.2) YSTERFONTEIN

GASTROSACCUS PSAMMODYTES BIOMASS (X 200) YSTERFONTEIN

GASTROSACCUS PSAMMODYTES NUMBERS YSTERFONTEIN

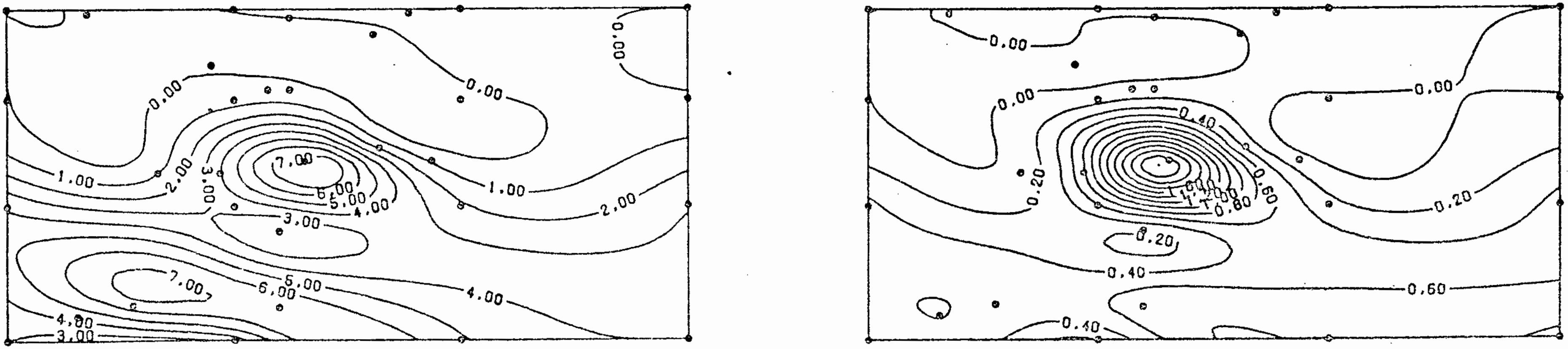
GASTROSACCUS PSAMMODYTES BIOMASS YSTERFONTEIN

Figure 7.32: Distribution of *Gastrosaccus psammodytes* at Ysterfontein



SIGALION CAPENSE NUMBERS (X 2) MELKBOSSTRAND

SIGALION CAPENSE BIOMASS (X10) MELKBOSSTRAND



SIGALION CAPENSE NUMBERS MELKBOSSTRAND

SIGALION CAPENSE BIOMASS MELKBOSSTRAND

Figure 7.33. Distribution of *Sigalion capense* at Melkbosstrand

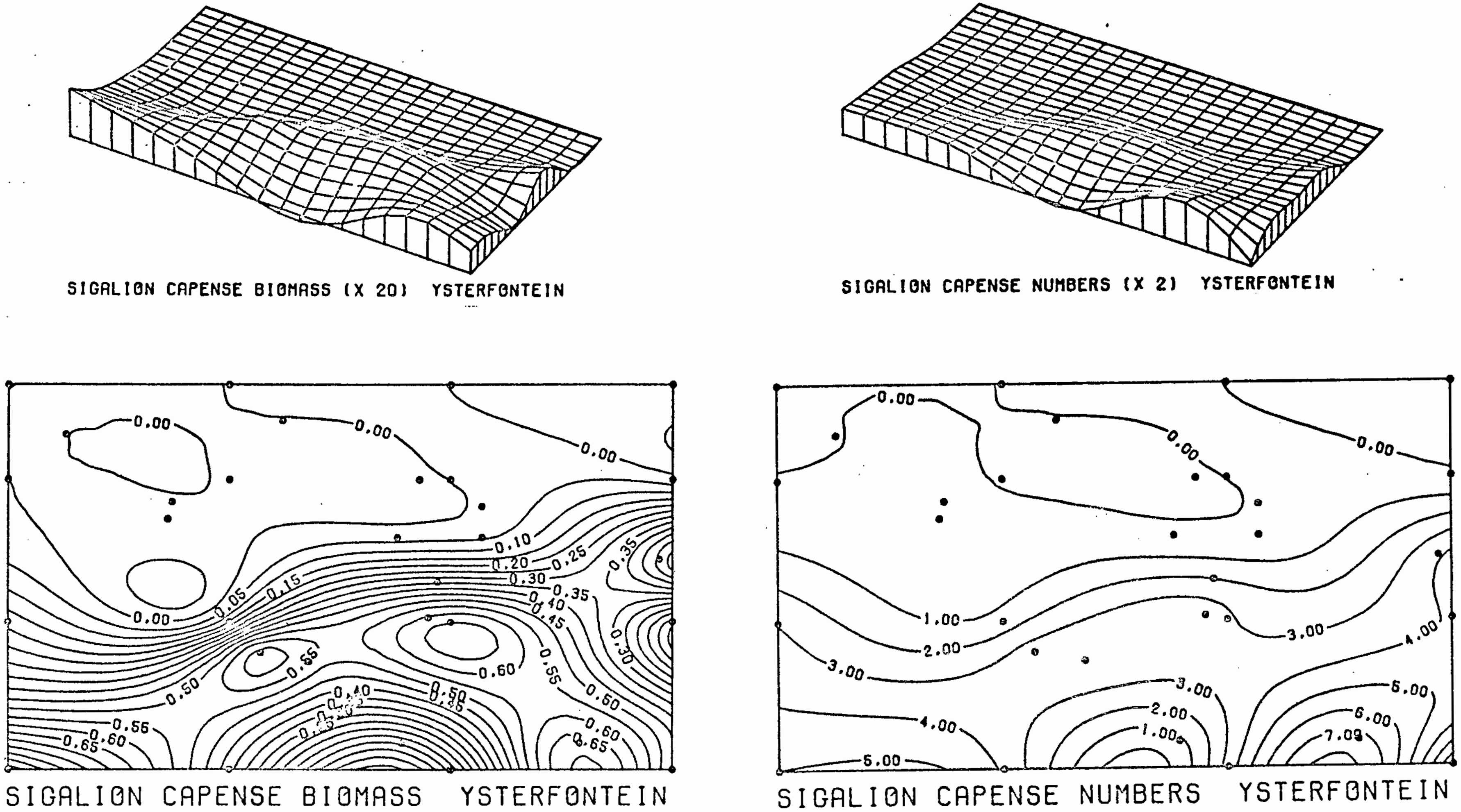


Figure 7.34: Distribution of *Sigalion capense* at Ysterfontein

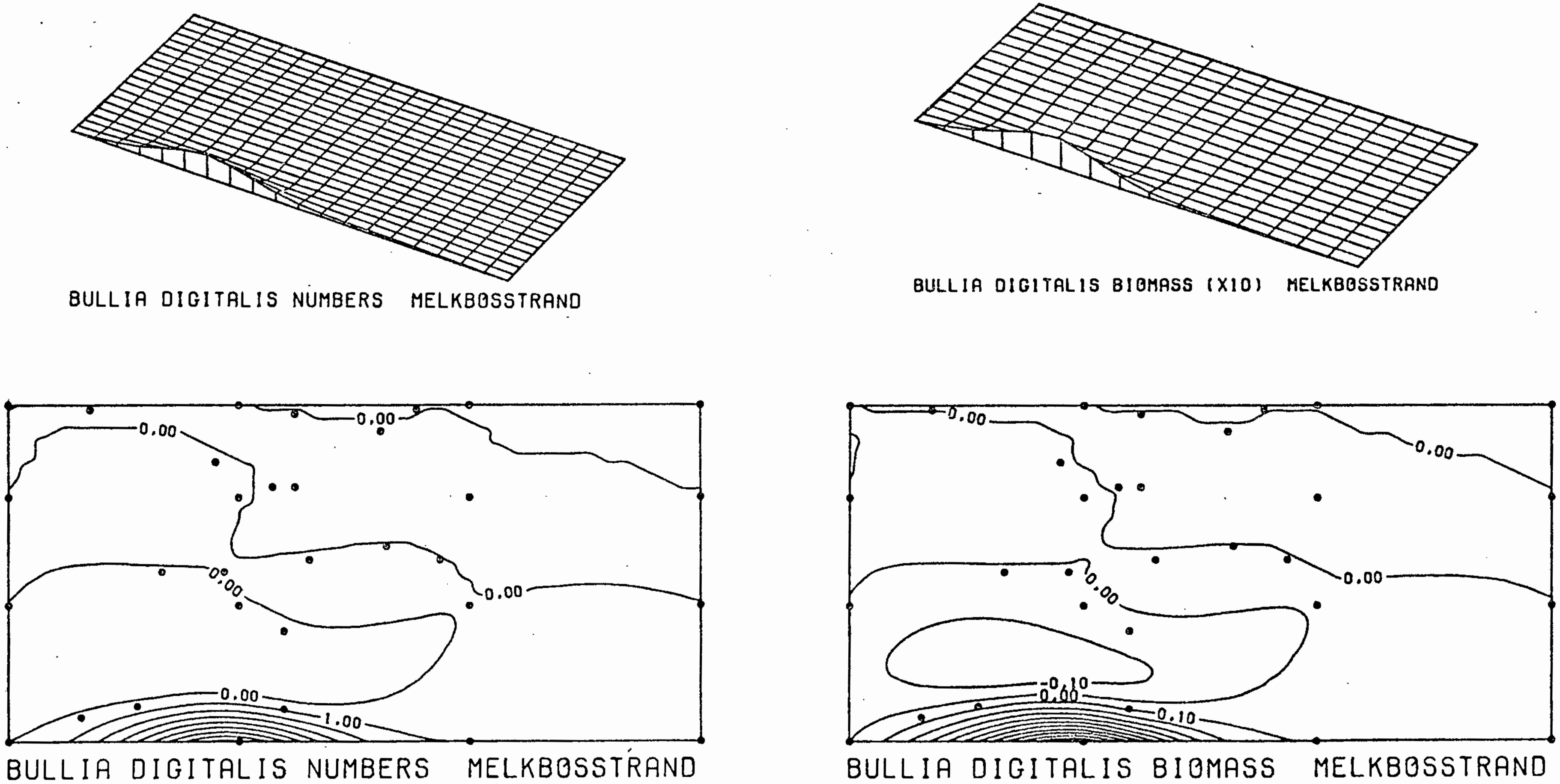
considerable sense of chemoreception and the aggregations that occur in the vicinity of food. Patchiness in this species therefore occurs continually, except when there is a complete absence of food or an evenly-distributed abundance of it. Both at Melkbosstrand (fig. 7.35) and Ysterfontein (fig. 7.36) patches measuring 50 metres in length occurred along the low-water mark. The size-composition was similar in both cases. *Bullia* is only found occasionally at Rocherpan.

Other Species

Low numbers of the amphipod *Urothoe grimaldii*, the cumacean *Cumopsis robusta*, the polychaete *Nephtys capensis* and the nemertean *Cerebratulus fuscus* prevented any conclusions from being drawn on the distribution of these species. With the exception of *Nephtys* (which does not occur at Rocherpan), these species occur on all three beaches. The data collected on the other, less intensive, sampling sessions, indicates that the distribution of these species is patchy as well.

A comparison of the distribution of the patches shows certain features of interest. Figures 7.37 to 7.39 show the distributions across the beach of patches of carnivores, deposit and filter feeders and terrestrial scavengers at Melkbosstrand, Ysterfontein and Rocherpan respectively. These figures should be "read" in the same way as the contour plots previously used in this chapter.

It will be seen that the patches of potentially competing species do overlap to a certain extent, particularly in the case of the carnivorous species. There is rarely a complete overlap of patches, however, suggesting that areas of high densities of one species are avoided by competing species. Where this does not appear to hold, as in the cases of the filter feeders *Gastrosaccus* and *Pseudharpinia*, or among the terrestrial organisms, it is probably because true competition does



BULLIA DIGITALIS NUMBERS MELKBOSSTRAND

BULLIA DIGITALIS BIOMASS (X10) MELKBOSSTRAND

BULLIA DIGITALIS NUMBERS MELKBOSSTRAND

BULLIA DIGITALIS BIOMASS MELKBOSSTRAND

Figure 7.35. Distribution of *Bullia digitalis* at Melkbosstrand

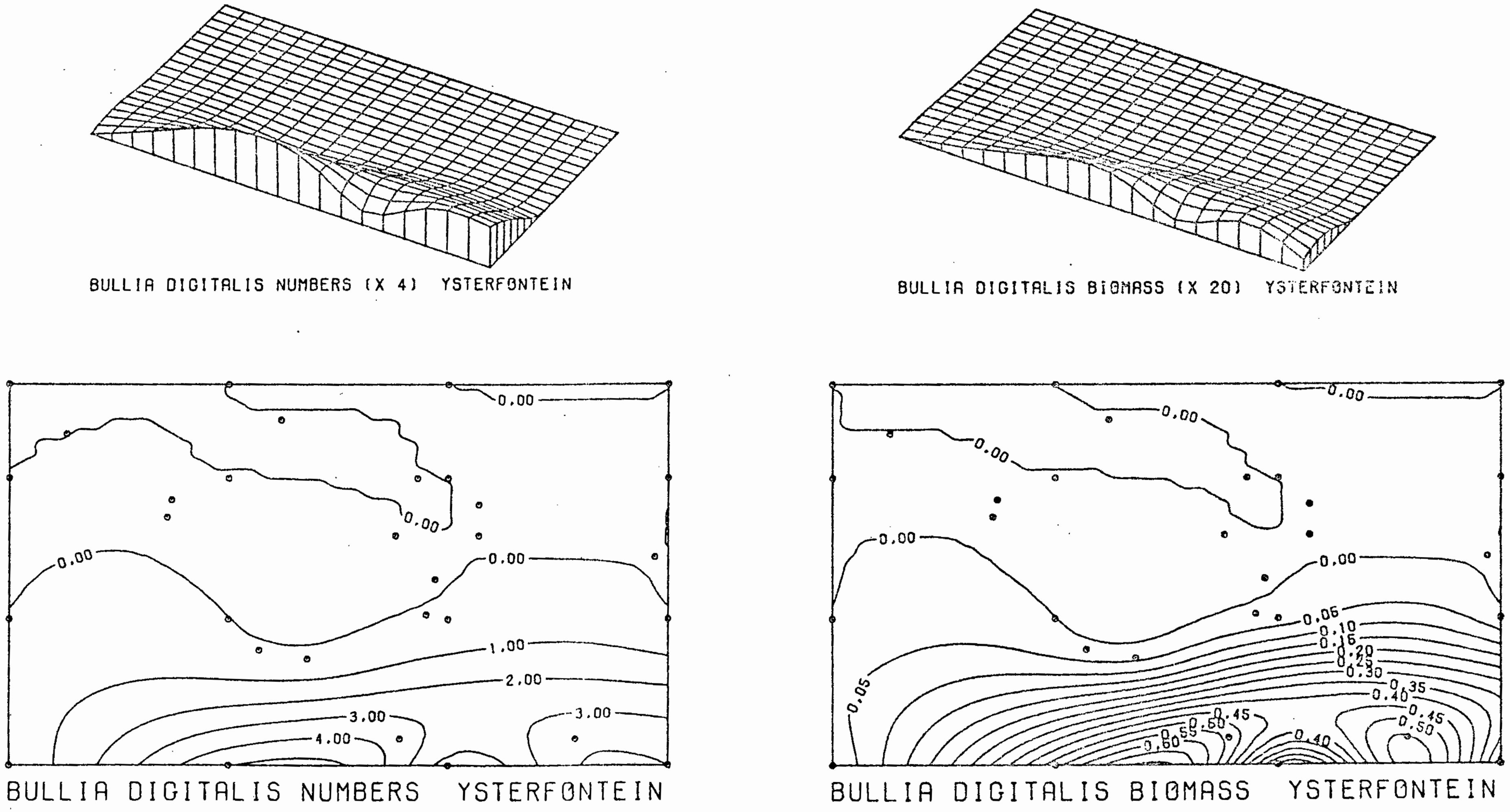


Figure 7.36. Distribution of *Bullia digitalis* at Ysterfontein

not take place since these animals probably feed on different categories of food. Alternatively, the densities of competing species may be too low for them to exert any influence on each other.

Thus lumbricid oligochaetes feed on organic remains in soil and sand (Dales, 1967) as well as diatoms and sediment-filtered plankton (Giere, 1975), while *Talorchestia* feed on washed-up kelp (Muir, 1977) and *Tylos* both on stranded kelp and other organic detritus (Kensley, 1974) There may also be different feeding preferences in the two crustaceans related to the decomposition state of the kelp.

The cirolanid carnivores, however, all feed on similar prey. Monod (1930) reports that *Pontogeloides* will even attack bathers, while the author has had the same experience with *Eurydice*. Both these species as well as *Excirolana* have been kept alive for several months in the laboratory on meat scraps. It is thus apparent that all three species are highly opportunistic feeders with catholic food preferences and therefore likely to be in competition with each other. On all three beaches it appears as if the concentrations of the cirolanid isopod species are separate to a certain degree.

At Melkbosstrand there is no overlap at all between *Excirolana* and *Eurydice* patches (although it must be remembered that the definition of "patches" as used in figures 7.37 - 7.39 is purely arbitrary), while the aggregation of *Pontogeloides* lies to one side of *Excirolana* although occupying the same zone.

It is evident that both zonation and competition affect the distribution of these species - chapter 8 will show how sediments can further influence it. Similar separations occur at Ysterfontein and Rocherpan.

The distribution of *Donax* relative to that of *Scolelepis* is harder to determine. Although patches of these species occupy slightly different zones on both beaches where they occur together, at Melkbosstrand it

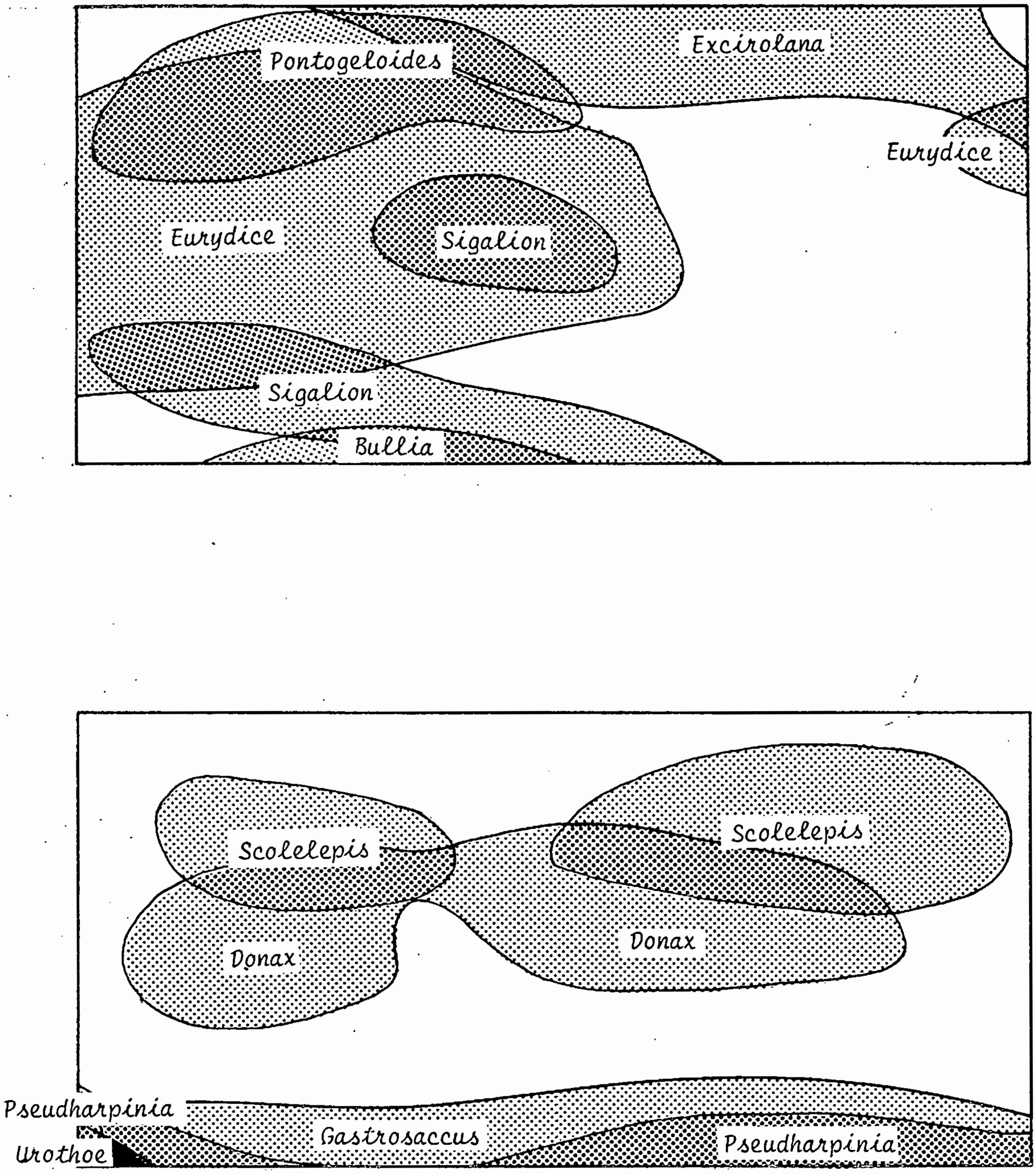


Figure 7.37 Distribution of patches of carnivores, filter and deposit feeders and air-breathing organisms (overleaf) at Melkbosstrand. Shading represents distribution of patches. Pale shading = 1 species; dark shading = overlap of 2 species; black shading = overlap of 3 species.

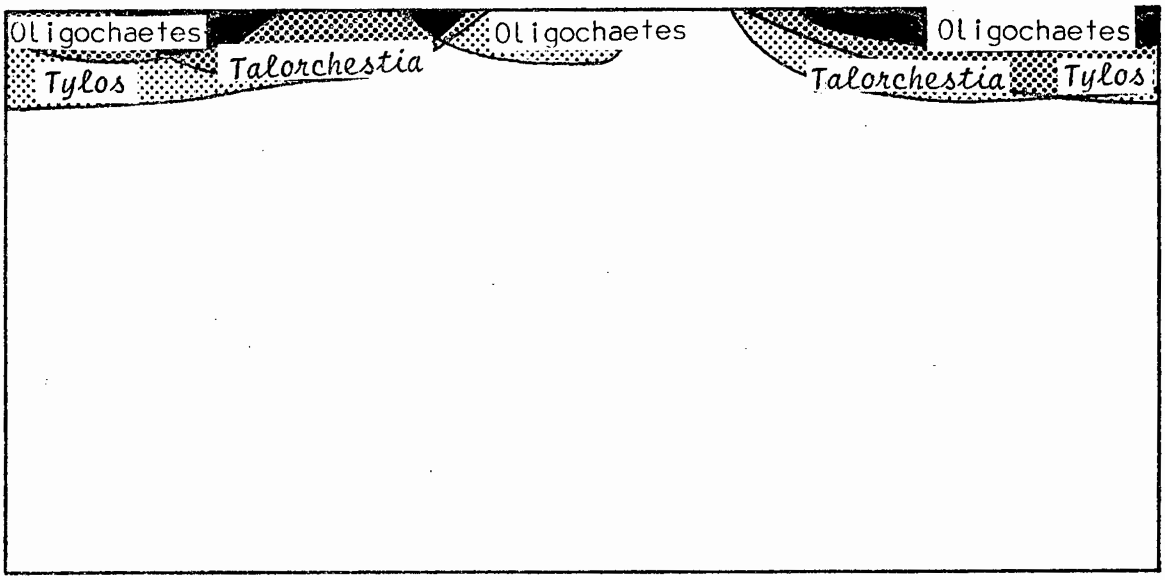
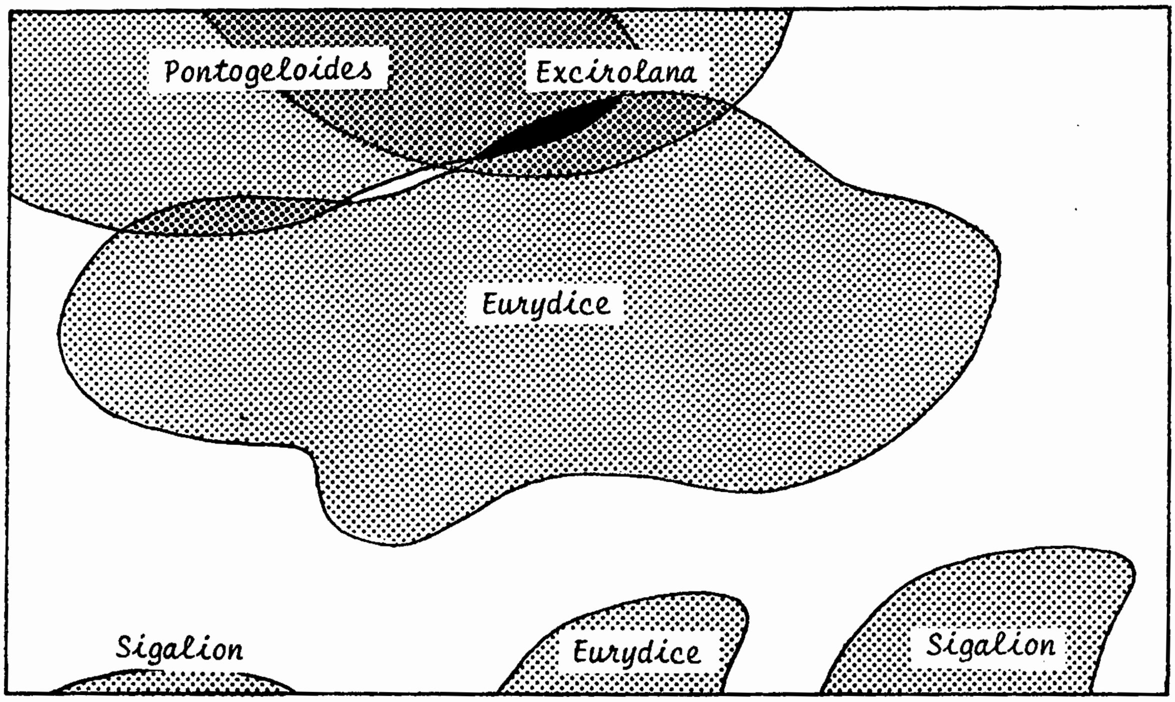


Figure 7.37 (contd) Distribution of patches of carnivores, filter and deposit feeders and air-breathing organisms at Melkbosstrand.



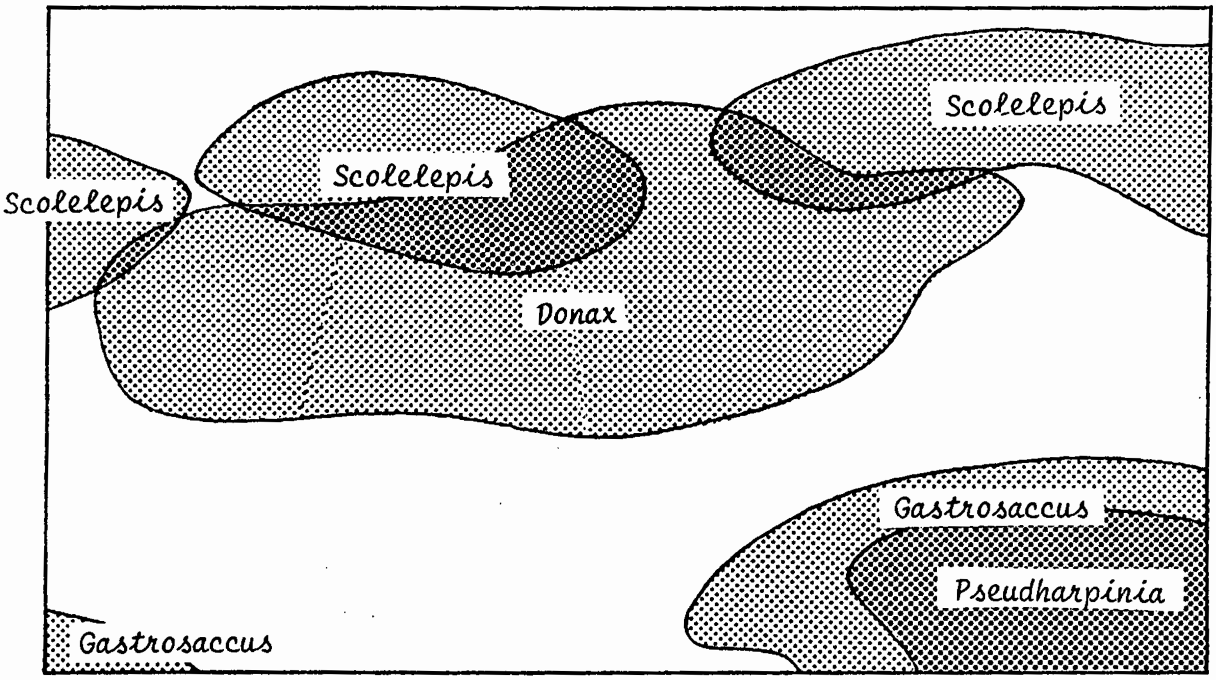


Figure 7.38 Distribution of patches of carnivores, filter and deposit feeders and air-breathing organisms (overleaf) at Ysterfontein.

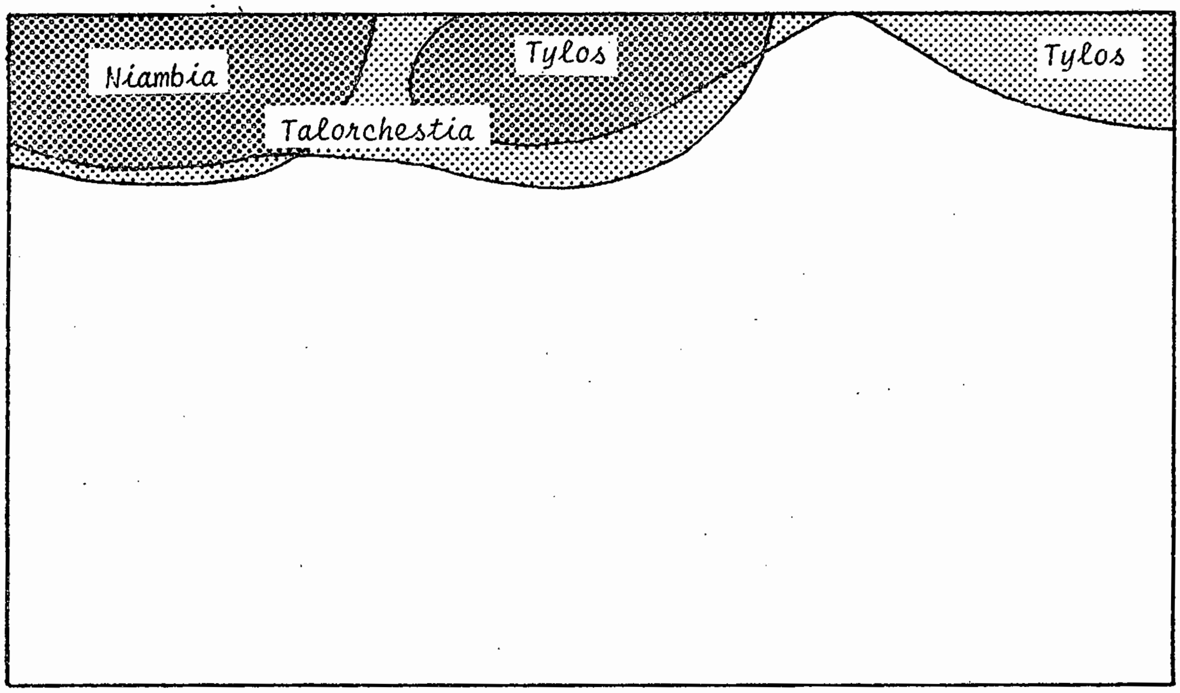
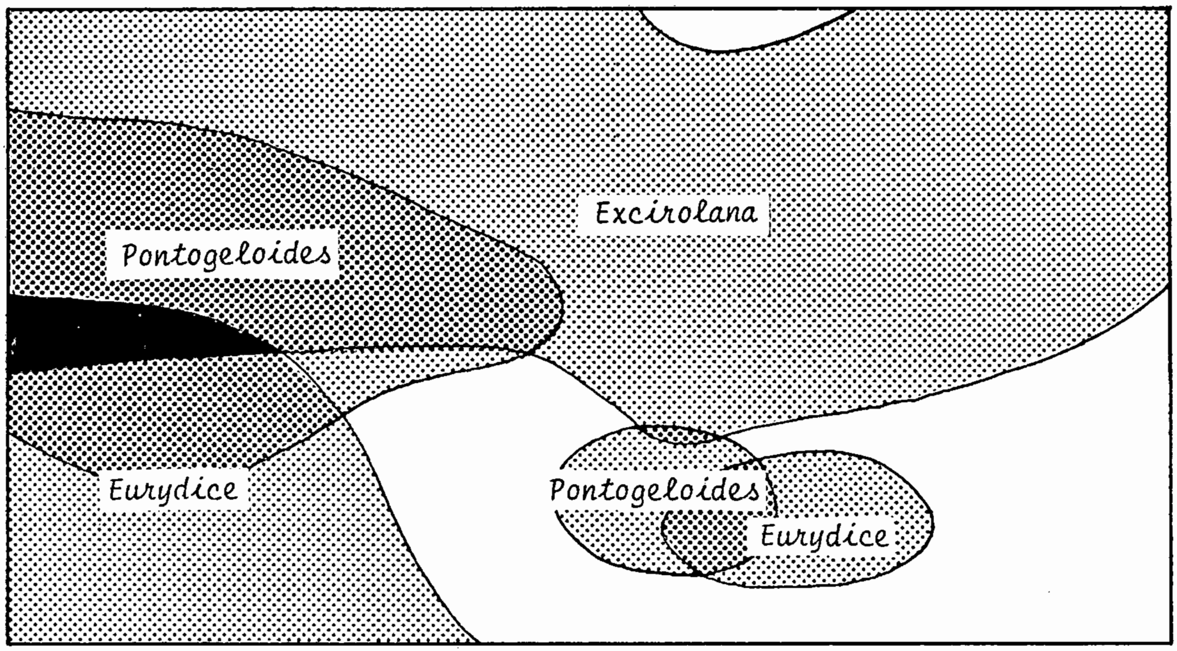


Figure 7.38 (contd)



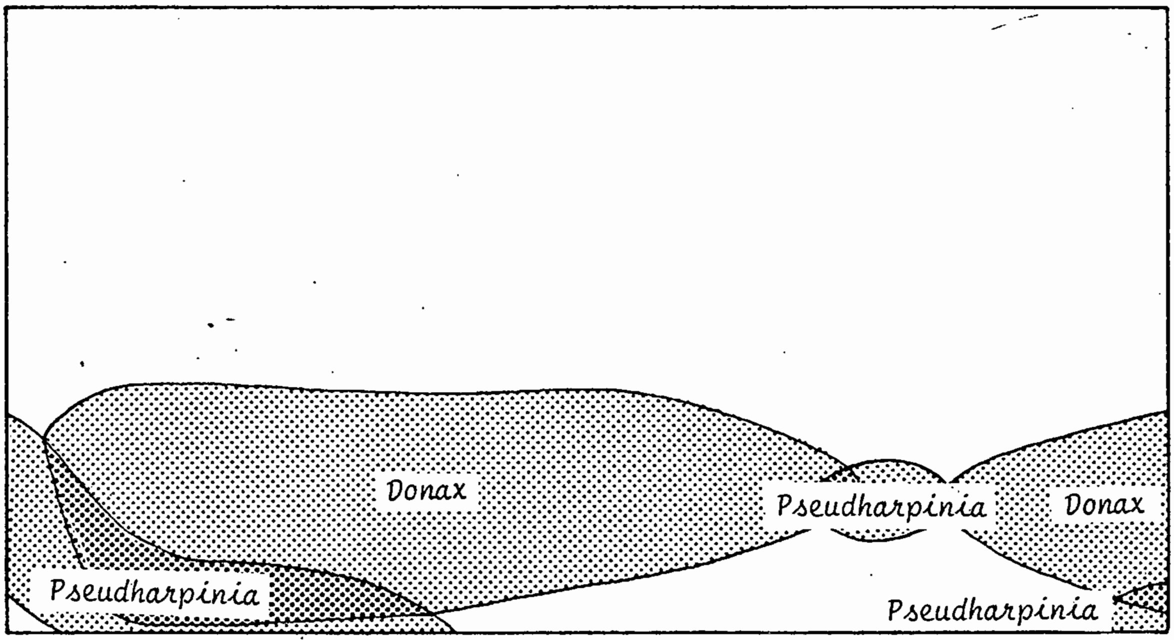


Figure 7.39 Distribution of patches of carnivores, filter and deposit feeders and air-breathing organisms (overleaf) at Rocherpan.

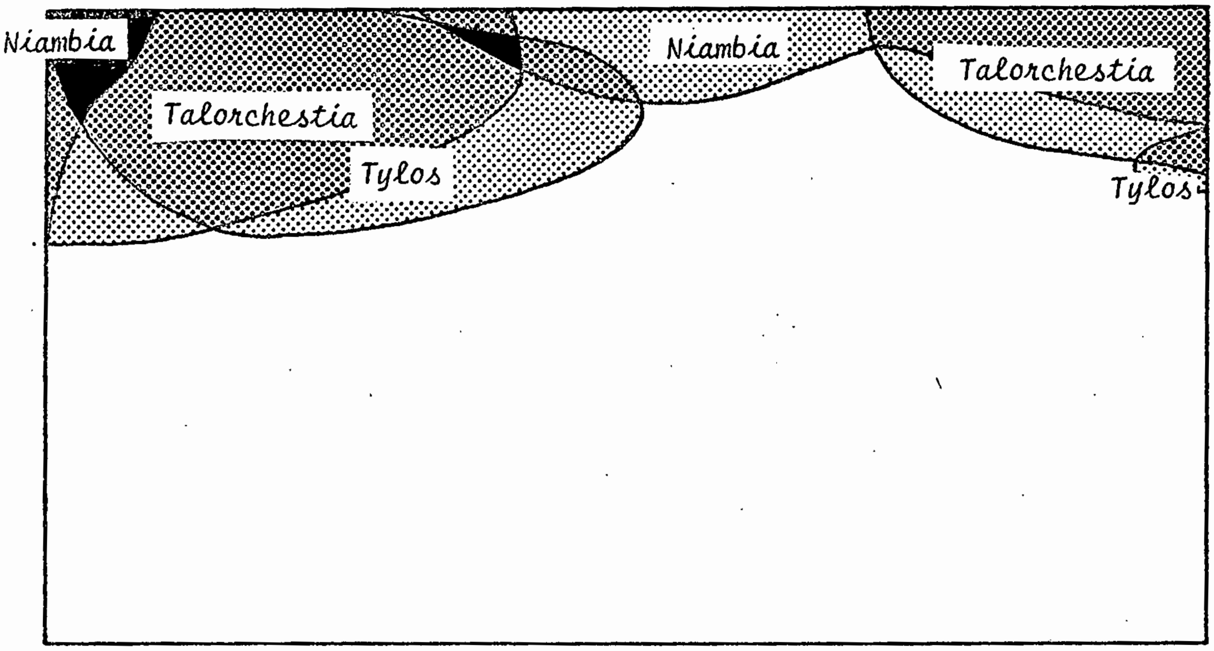


Figure 7.39 (contd)

appears as if the two species are associated with each other, while at Ysterfontein the reverse seems to be the case. Nevertheless, on both beaches there are areas where high densities of both species are to be found. It would therefore seem as if competition between these two species only occurs when both species are present in very high densities. High densities of *Donax* may then limit the colonizing space available to *Scolelepis*.

It should be noted that only *Eurydice*, *Scolelepis* and *Donax* occur in consistently high numbers on west coast beaches. At Rocherpan, *Excirolana* is at times also present in high densities. The other species, however, rarely approach these densities. Thus competition between *Gastrosaccus*, *Pseudharpinia* and *Urothoe* is not likely to occur since areas available to these species are probably reduced to a critical level only occasionally.

The distributional predator-prey relationships are also of interest. Figure 7.40 shows the distributions of *Eurydice* patches with respect to those of *Donax* and *Scolelepis* at Melkbosstrand and Ysterfontein. On the former beach, *Eurydice* were concentrated over one patch of *Scolelepis* and over one of *Donax* but not over the other patches of these two species. At Ysterfontein the concentration of *Eurydice* mainly followed that of *Donax* although there was some overlap with *Scolelepis* patches as well. At Rocherpan there was almost complete segregation between *Excirolana* and *Donax*, although this is probably mainly due to the different zones inhabited by these two species. *Eurydice* patches did occur where there were high concentrations of *Donax*, however.

In the case of the distributional relationship between *Eurydice* and *Scolelepis* another possibility in addition to a straightforward predator-prey relationship should be mentioned. It must be assumed that the polychaete is not totally immune to predation by carnivorous isopods, otherwise the patterns of association would not persist for very long. However, Thijssen *et al.* (1974) have shown that in the Wadden Sea, *Scolelepis squamata* forms the main prey item of the flatfish

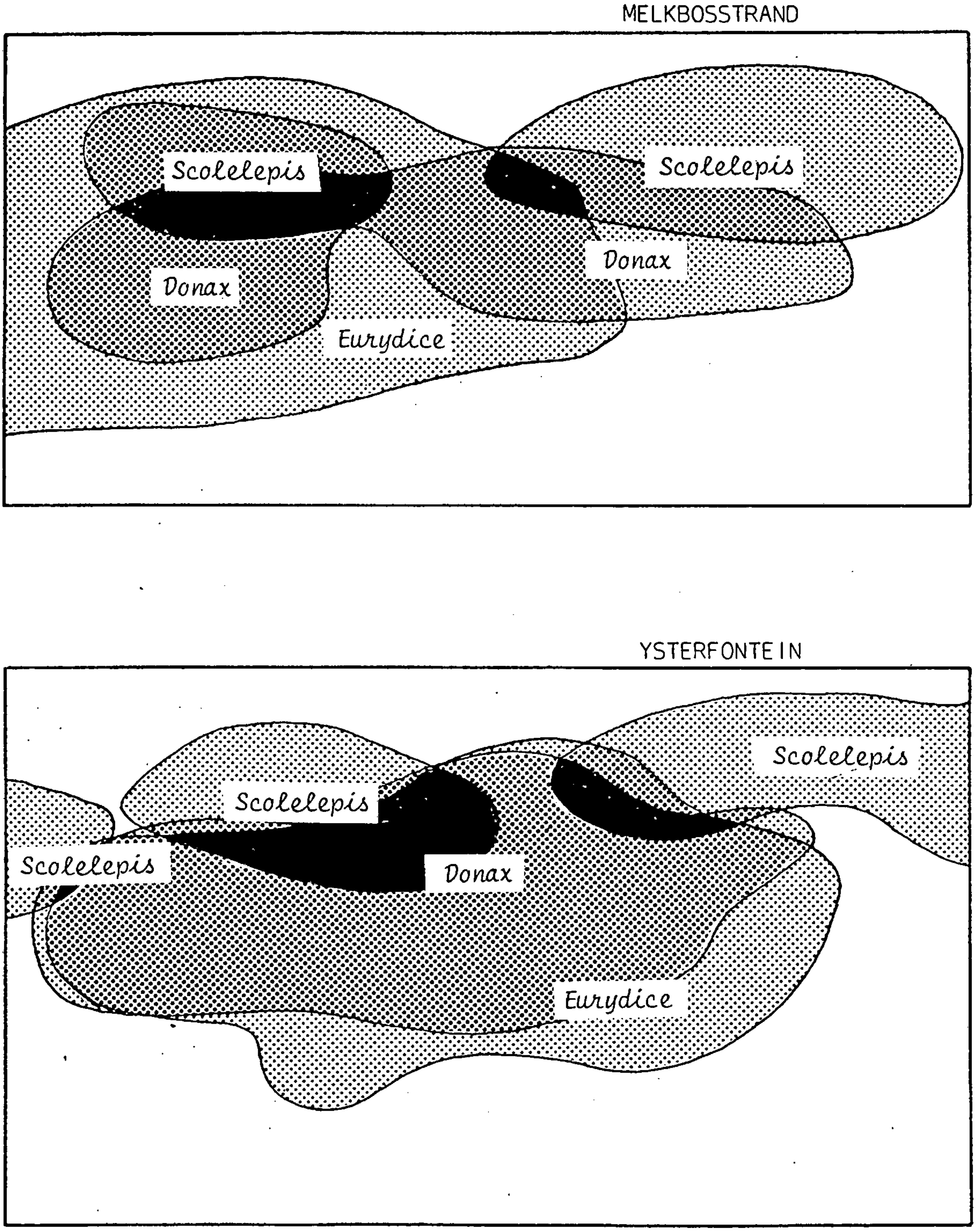


Figure 7.40 Relative distributions of patches of the most abundant carnivore and filter and deposit-feeding species at Melkbosstrand and Ysterfontein. Shading as in Fig. 7.37.

Pleuronectes platessa. Since *Scolelepis* lives in 15 - 30 cm long vertical tubes and is extremely fragile, it is very unlikely that predation by flatfish results in the removal of the entire animal. It is more probable that portions of the body and tail would remain in the burrow, since *Scolelepis* feeds by waving relatively short tentacles attached to the head in the water while submerged (Behrends and Michaelis, 1977). These headless remnants could well be a source of food for *Eurydice*. Birds are known to feed on *Scolelepis* at low tide (Croker, 1970) and this too could result in food items for scavenging isopods.

Although there is some overlap of distributions between *Excirolana* and the terrestrial species, this only occurs at low tide, when *Excirolana* are inactive and buried in the sand. No direct relationship thus exists between the distributions of air-breathing animals and those of water breathing ones.

While there may be certain other relationships between predator and prey, particularly in the zone of saturation, these are not detectable by the method used above. The reason is that *Eurydice* in particular occurs in densities of up to one order of magnitude greater than do the species characteristic of the zones of resurgence and saturation. Since the highest *Eurydice* densities are in the zone of retention, the distribution of this species in the lower zones is not reflected in figures 7.37 to 7.40. In order to determine the existence of predator-prey relationships in the zones occupied by *Gastrosaccus*, *Pseudharpinia* and *Urothoe* it is necessary to examine the distribution of *Eurydice* exclusively in these zones. For this, patchiness of *Eurydice* was determined in the same way as before, but only data from the zones of resurgence and saturation were used.

The results obtained by this method show higher concentrations of potential prey species in areas where *Eurydice* concentrations are comparatively low, except at Rocherpan (where concentrations were low in any case). Whereas it is possible to discuss predator-prey relationships in terms of relative distributions in the cases of *Eurydice*, *Donax* amd *Scolelepis*, however, it should be remembered that while *Eurydice* is highly mobile, the two prey species are considerably less mobile. *Gastrosaccus*, *Pseudharpinia* and *Urothoe*, on the other hand, are highly mobile. Thus, while it is reasonable to expect *Eurydice*, as the mobile predator, to be associated with its less mobile prey, no such expectations can be held when the potential prey is equally or more mobile.

The patterns of predator-prey concentrations in the zones of resurgence and saturation at Melkbosstrand and Ysterfontein suggest an active avoidance by the prey of its predators. This, however, must remain in the realms of pure speculation, since the relative mobilities of the species involved are not known. The other possibility, of course, is that where *Eurydice* occurs in high concentrations, the number of prey organisms is reduced by predation.

Conclusions

This chapter has shown clearly that the distributions of intertidal benthic macrofauna on sandy beaches is highly uneven. These irregularities of longshore distribution have been quantified where possible, and compared with the little information existing from other studies. Finally, the comparative distribution of patches of the various species represented has been investigated on the basis of competitive and predator-prey relationships. Both types of interspecific interactions seem to operate on sandy beaches, but these only become apparent when high densities of organisms are involved.

CHAPTER 8

ANIMAL-SEDIMENT INTERACTIONS

Introduction

It is very difficult to distinguish animal-sediment interactions in sandy beaches from those of zonation. This is because, in addition to the zonation exhibited by macrofauna (chapter 4),sediment characters show slight zonation effects (chapter 3). As far as intertidal sandy beaches are concerned, therefore, animal-sediment interaction studies must be restricted to comparisons between beaches that lie within the same biogeographical province, and to comparisons within particular zones.

There can be no doubt that animal distributions are affected by sediments, as shown by a considerable body of literature. Most of the evidence deals with subtidal benthic communities (e.g. James and Gibson, 1980; Sanders, 1958, 1960; McNulty *et al.*, 1962; Driscoll, 1975; Warwick and Davies, 1977; Biernbaum, 1979). Intertidal evidence is scantier and less direct. Carr (1976) showed some correlation between particle sizes and faunal distributions, although she noted that most of these effects were probably due to differences in amounts of shelter at the various sites she studied. A similar conclusion was reached by Eleftheriou and Nicholson (1975) to the effect that particle size is an indicator of exposure, but is not sufficient to characterize beaches and explain faunistic differences. This is in fact the difficulty with all sandy beach data. Although McLachlan (1980c) has proposed an exposure rating scheme for beaches, this is not always satisfactory (Bally *et al.*, 1980). It is the only system available at present, but its resolving power is unfortunately insufficient to allow distinctions to be made between the effects of exposure and those of sediments on beach organisms.

The purpose of this chapter is to consider the implications of changing sediment composition on faunal distribution, both within a single beach and between beaches.

Methods and Materials

Number and biomass data on the macrofauna from the three beaches (see chapter 5) were compared with the results obtained from sediment analysis (chapter 3). Only data obtained on the one occasion on each beach when sixteen random samples were collected as well as the usual grid samples were used. Using the SACLANT contouring and three-dimensional plotting programme, the distributions of sediment characteristics across the beach were plotted - to be compared later with the patchiness diagrams described in chapter 7. Comparison of these figures showed any correlations that might exist between mean sand-grain diameters, sorting of the sediments, percentage by mass of organics and percentage by mass of calcium carbonate present in the sand and the animal distributions in terms of numbers and biomass.

Results and Discussion

As is shown in chapter 3, mean grain sizes of the beaches at Melkbosstrand, Ysterfontein and Rocherpan are 2,25, 2,31 and 1,60 phi respectively. Of the species occurring on these beaches, only oligochaetes and the polychaetes *Scolelepis squamata, Sigalion capense* and *Nephtys capensis* are not found on all three beaches. The oligochaetes are terrestrial and are probably only present at Melkbosstrand because of favourable humidity conditions in the dunes behind the beach and the extension of these conditions to the edge of the intertidal area (oligochaetes are absent from the other two beaches).

The three polychaete species are absent from Rocherpan and seem to be excluded on the basis of the particle size of the beach. Thus, somewhere between 2,25 and 1,60 phi lies a cut-off point beyond which these polychaetes do not penetrate, although the limiting grain size probably varies from species to species. The reason for this cut-off point is likely to be the increased difficulty of burrowing in a coarser-grained sediment. On a purely subjective basis, it was evident during the meiofaunal studies that it is much easier to drive a meiofauna corer into fine sand than coarse sand. In addition, since coarse sand is usually better drained than fine sand, it follows that during periods of exposure, coarse sand will be relatively drier than fine sand and, as Chapman (1949) has shown, the dilatancy or "hardness" of unsaturated sands is higher than that of saturated ones.

Burrowing organisms would obviously also encounter these conditions. Thus the energetic cost of burrowing on coarse-grained beaches, together with the usual energetic requirements for feeding, reproduction and respiration, would simply outweigh the energy obtained from food. Although Trevor (1978) has determined the energy expenditure of *Nephtys cirrosa* during burrowing, he does not specify the grain size of the sediments used during the experiments. In any event, food is less available on coarse-grained beaches than on fine-grained ones. This applies both to the detritus-feeding *Scolelepis* and to the carnivorous or scavenging *Sigalion* and *Nephtys*.

The lack of food is in part a function of the increased wave action and higher porosity of coarse-grained beaches (resulting in less deposition and greater erosion and removal of detritus) and partly due to the increased slope usually associated with such beaches (see Bascom, 1951 and chapter 3 of this study). An increase in slope means a decrease in intertidal area and a consequent decrease in numbers of intertidal prey organisms. In the case of deposit or detritus feeders, an increase in slope also implies a faster backwash and removal of detritus. Conversely, the amount of backwash on coarse-grained beaches is reduced, since more swash water percolates into the sand, taking the finer detrital material with it. This further reduces the food available to deposit and detritus feeders.

Thus it can be seen that a number of factors combine to render coarse-grained beaches unsuitable for benthic polychaetes.

One further gross difference in the macrofauna attributable to animal-sediment interactions has been observed on west coast beaches. Already partly described in chapters 4 and 6, this is the change in dominance of the isopod *Eurydice longicornis* in the finer grained beaches by *Excirolana natalensis* (another isopod) in the coarser ones. A similar situation has been described by Brown (1973) for the replacement of *Eurydice* to *Exosphaeroma truncatitelson* on fine-grained sheltered beaches, although it is not known to what extent this is due to the effects of increased shelter rather than purely sedimentological differences.

The most likely reason for replacement of *Eurydice* by *Excirolana* on coarser beaches is sheer size. On the west coast,*Excirolana* grows to a very much larger size than does *Eurydice*. Even juveniles of the former species are as large as adults of the latter. Table 8.1 shows the average masses of individuals of both species on all three beaches

TABLE 8.1 Mean mass of *Eurydice* and *Excirolana* individuals on all three beaches

Sampling times	Melkbosstrand				Ysterfontein				Rocherpan			
	Eurydice		*Excirolana*		*Eurydice*		*Excirolana*		*Eurydice*		*Excirolana*	
	Mean weight	N	Mean weight	N	Mean weight	N	Mean weight	N	Mean weight	N	Mean weight	N
Winter 1976	0,0014	200	0,0085	3	0,0004	3712	0,0031	20	0,0016	39	0,0028	306
Spring 1976	0,0008	393	0,0017	2	0,0002	5038	0,0016	25	0,0007	114	0,0056	175
Summer 1977	0,0003	476	0,0021	2	0,0002	4327	-	-	0,0003	23	0,0104	17
Autumn 1977	0,0003	1154	0,0026	4	0,0004	2931	0,0069	35	0,0007	157	0,0046	100
Winter 1977	0,0007	573	0,0171	4	0,0004	8848	0,0035	36	0,0018	41	0,0039	16
Spring 1977	0,0005	2755	0,0012	73	0,0003	2531	0,0059	13	0,0006	218	0,0037	270

throughout the sampling period.

The increased size and consequent additional power of *Excirolana* are very necessary for burrowing between large sand grains. The larger size also confers an increased resistance to desiccation, since the surface to volume ratio is decreased. Desiccation resistance may be of considerable importance on coarse-grained beaches since these drain much more rapidly and completely than do fine-grained ones.

These are the gross, easily observed effects directly attributable to animal-sediment interactions.

A comparison between distribution patterns of sediment characteristics and animal numbers and biomass holds certain dangers. In particular, the danger exists that correlations will be made between distribution pattern similarities that are entirely due to intertidal zonational effects. Chapters 3 and 4 have shown that both animals and certain sedimentological characteristics exhibit zonational trends. In a comparison such as this one, therefore, it is long-shore similarities that must be looked for.

A further point to be borne in mind is that while animals may prefer sediment characteristics that have certain absolute values, two conditions apply to these preferences. The first is that, as has been shown in chapter 3, a beach is made up of those sediments that are available for beach construction, and its sedimentary characteristics are a function of the characteristics of the beach building material. Intertidal organisms must therefore colonize a beach regardless of its characteristics, within certain limits, and compromise with the sediments available to them.

Secondly, the preference of certain characteristic values may be modulated by other variables which have not been measured. For example, a particular grain size may be preferred because it is easily burrowed into and confers reasonable protection against thermal stress and desiccation. If the same animals were to colonize a beach of brown or black, volcanic sand, the beach would, however, absorb much more heat in the daytime, and temperature fluctuations and desiccation rates would be much higher. A finer-grained sand might then be preferred by those organisms and their tolerance limits would have been altered.

The above example shows that there is probably a very large number of variables affecting intertidal animal-sediment relationships. Many of these may only come into effect under conditions of competition for resources with other species, whose distribution in turn would also have been influenced by sediment characteristics, either directly or indirectly. In this study, I have only investigated four variables. A description of the animal-sediment relationships for all the species commonly occurring on west coast beaches follows.

Figures 8.1 to 8.3 show the sediment characteristics for Melkbosstrand, Ysterfontein and Rocherpan respectively. The interpretation of these figures has been discussed in chapter 7. At Melkbosstrand, the general trends of increasing fineness and better sorting of the sediment from low water to the high-water mark are obvious. In addition, the slight decrease in percentage organics and percentage calcium carbonate from low water to high water are also apparent, as is the correlation between these two factors. Certain localized differences are evident, however. There are noticeable along-shore variations in all four sediment characteristics. The characteristics at Ysterfontein show similar trends to those at Melkbosstrand, except for the percentage organics which only show a slight similarity in their distribution pattern with percentage calcium carbonate. Finally, at Rocherpan there is a considerable variation in sediment diameter both along and across the beach (Fig. 8.3). In general, however, the trend is similar to those of the other beaches, while the remaining characteristics also show trends comparable to those at Melkbosstrand and Ysterfontein.

On all three beaches, total biomass distributions are largely a function of the distribution of *Donax serra* (see chapter 5). As will be seen

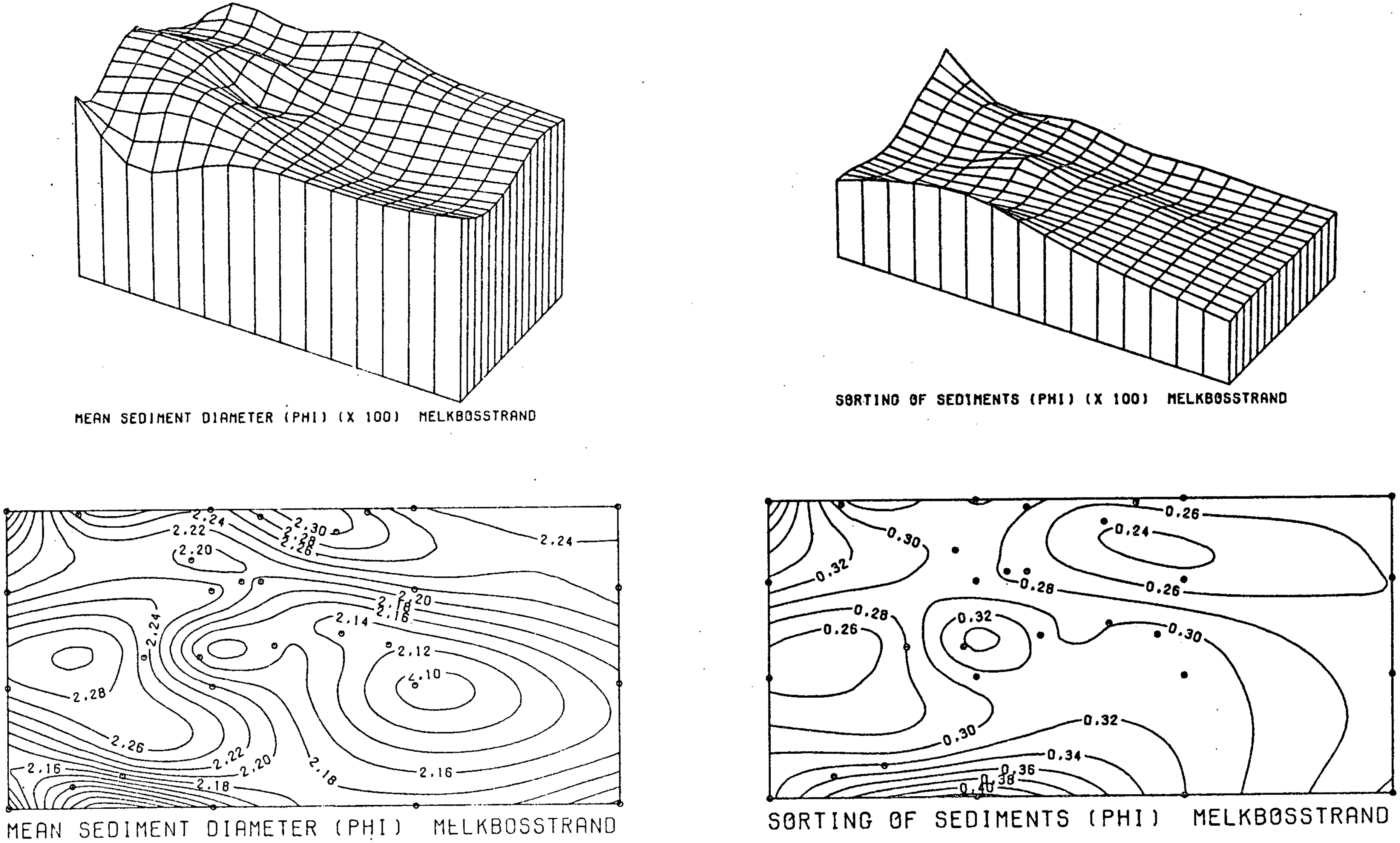
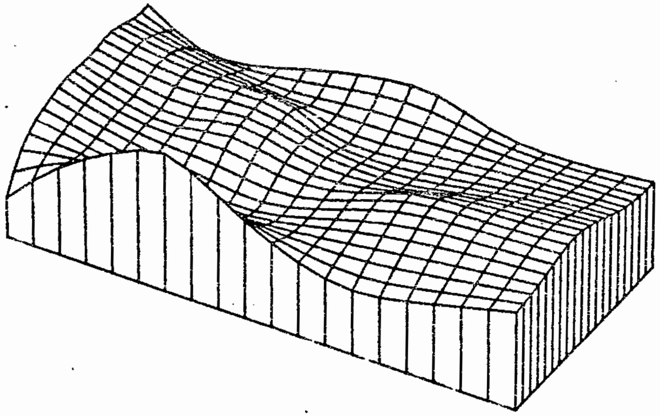
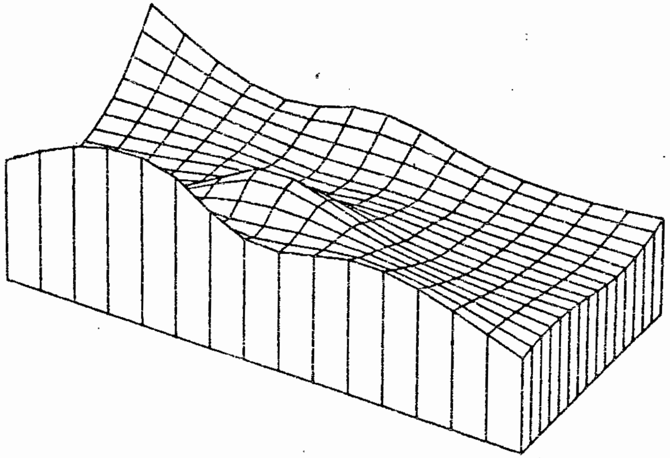


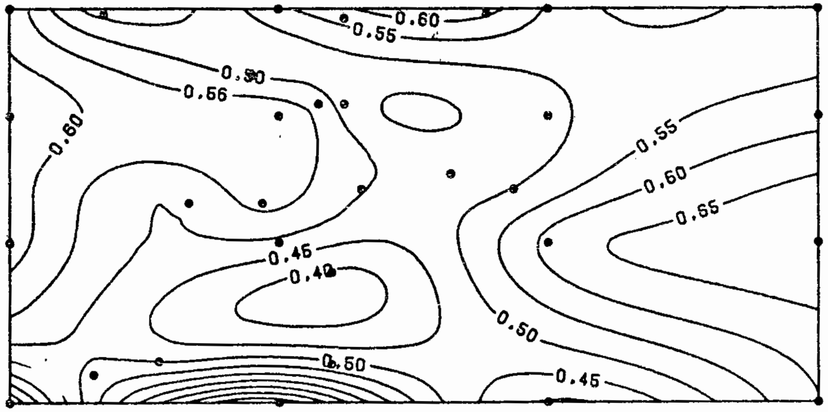
Figure 8.1. Sediment characteristics at Melkbosstrand



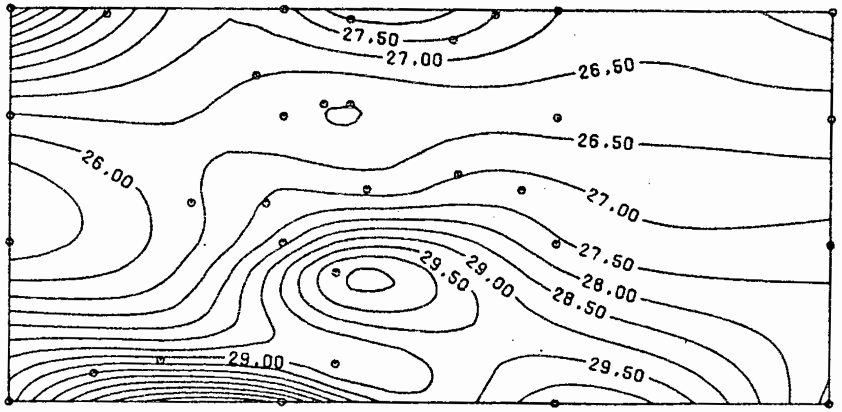
% ORGANICS (X 50) MELKBOSSTRAND



% CALCIUM CARBONATE (X 4) MELKBOSSTRAND

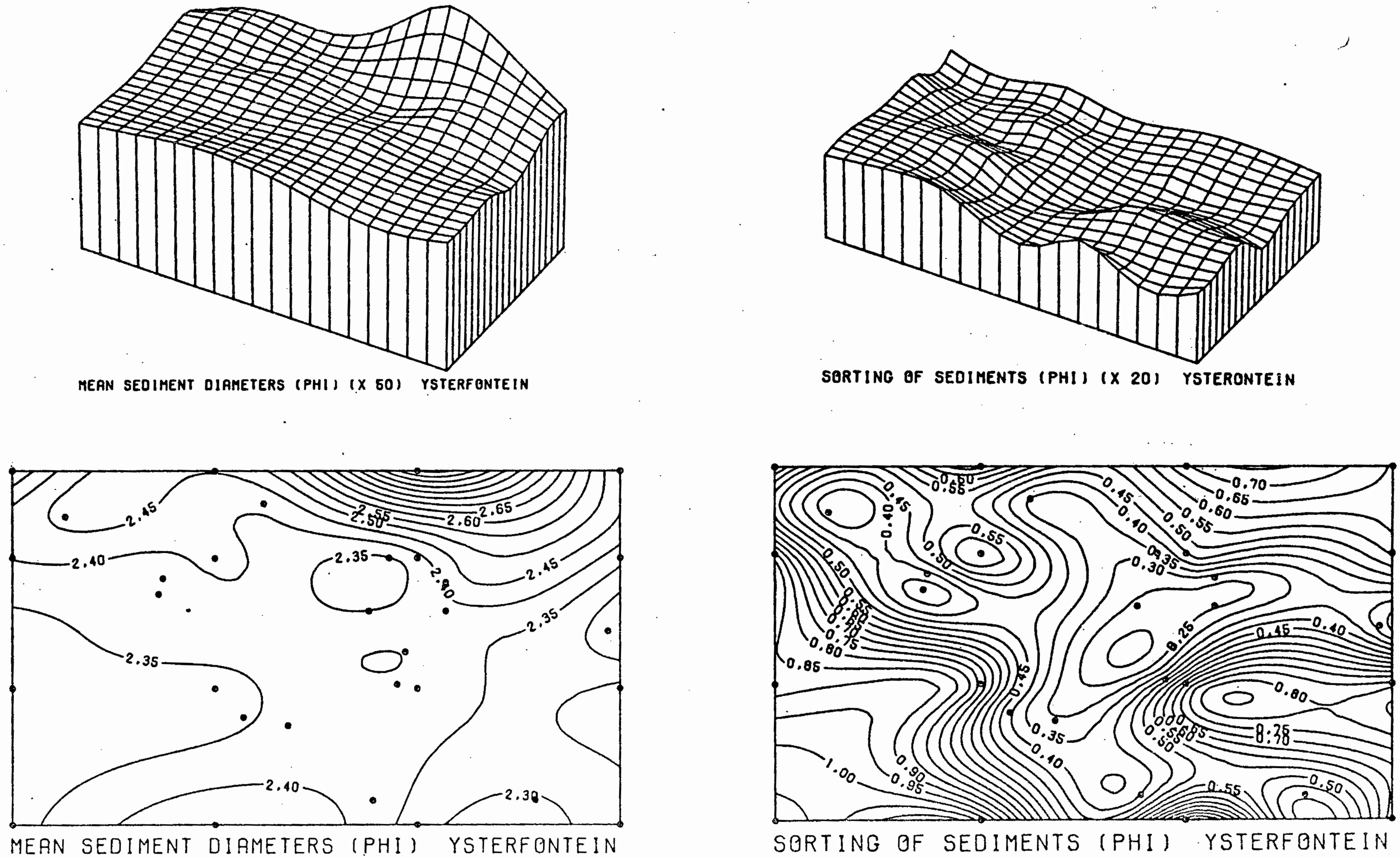


% ORGANICS MELKBOSSTRAND



% CALCIUM CARBONATE MELKBOSSTRAND

Figure 8.1. (contd.)



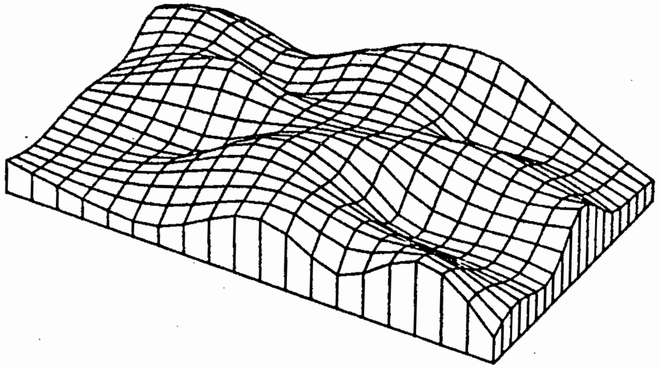
MEAN SEDIMENT DIAMETERS (PHI) (X 50) YSTERFONTEIN

SORTING OF SEDIMENTS (PHI) (X 20) YSTERONTEIN

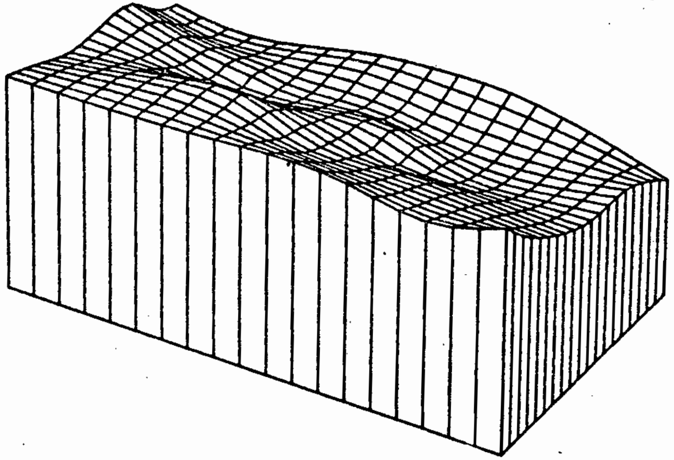
MEAN SEDIMENT DIAMETERS (PHI) YSTERFONTEIN

SORTING OF SEDIMENTS (PHI) YSTERFONTEIN

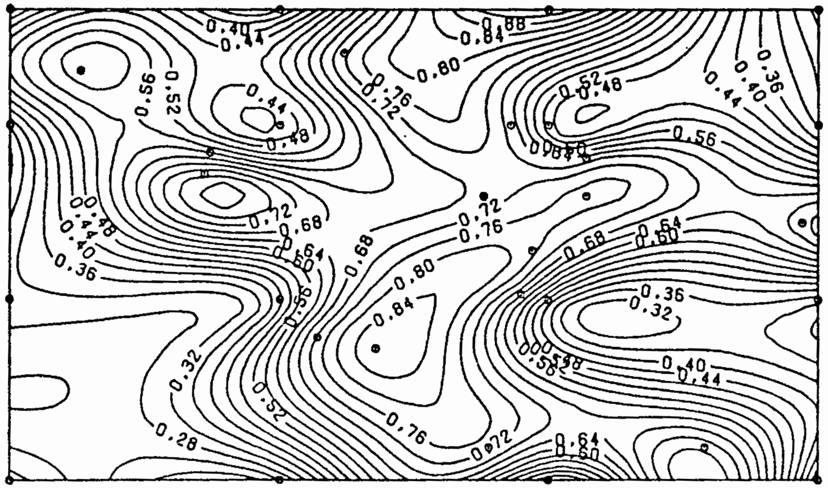
Figure 8.2. Sediment characteristics at Ysterfontein



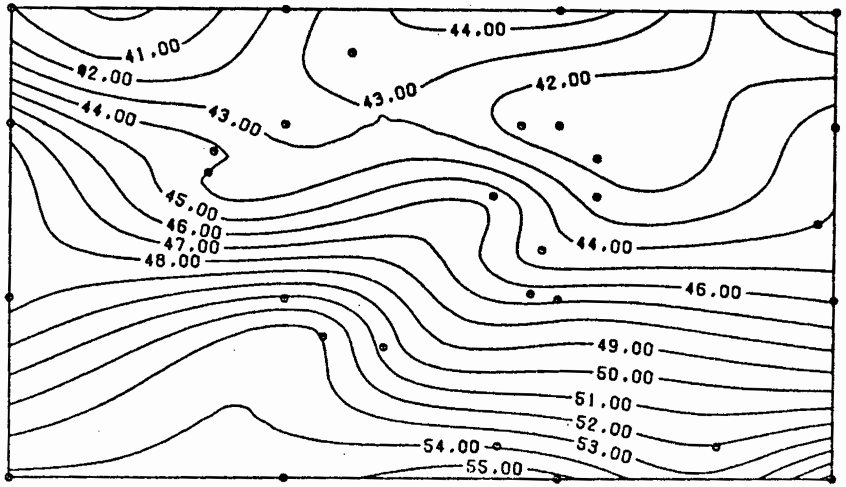
% ORGANICS (X 30) YSTERFONTEIN



% CALCIUM CARBONATE (X 2) YSTERFONTEIN

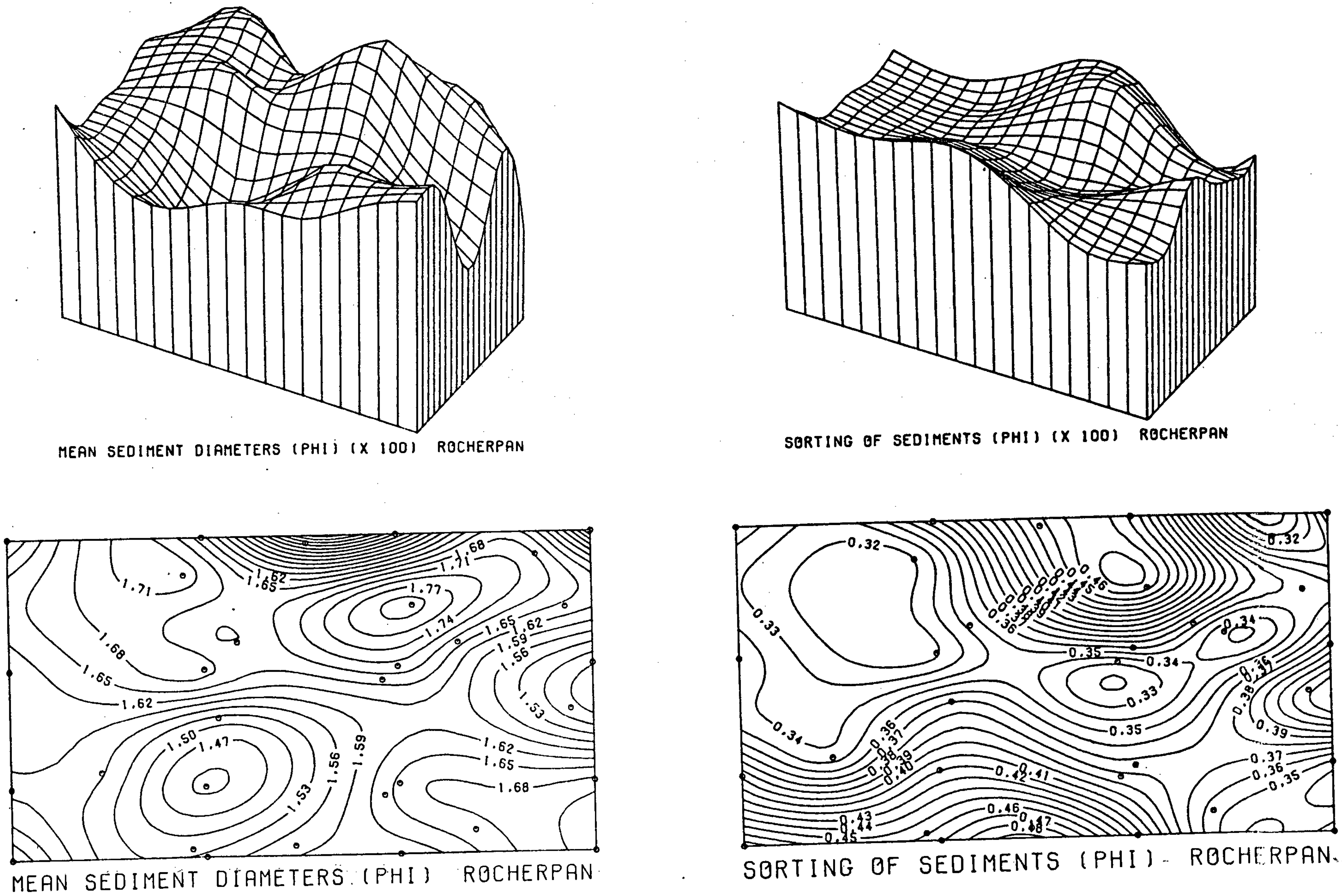


% ORGANICS YSTERFONTEIN



% CALCIUM CARBONATE YSTERFONTEIN

Figure 8.2. (contd.)



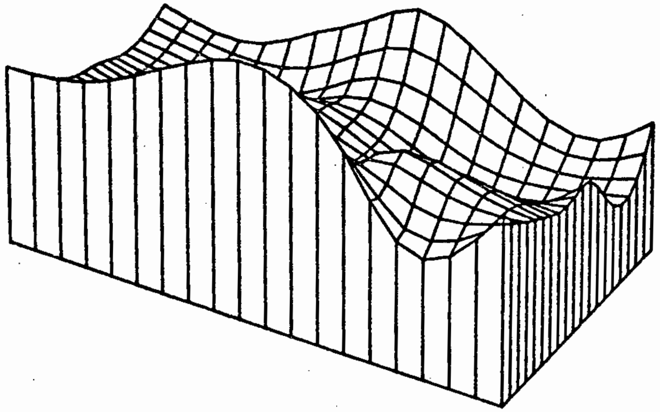
MEAN SEDIMENT DIAMETERS (PHI) (X 100) ROCHERPAN

SORTING OF SEDIMENTS (PHI) (X 100) ROCHERPAN

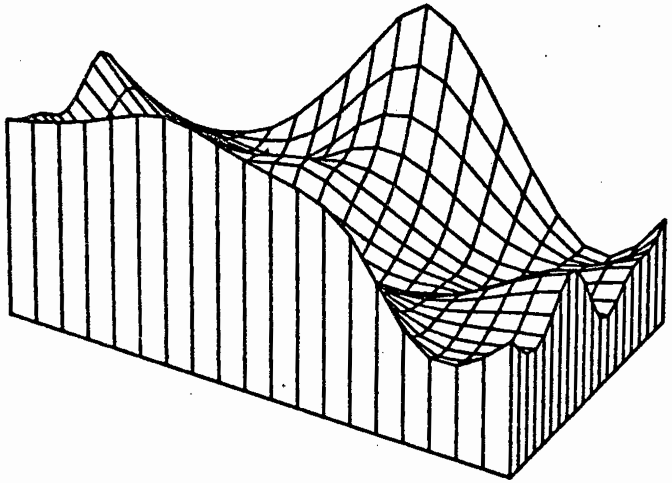
MEAN SEDIMENT DIAMETERS (PHI) ROCHERPAN

SORTING OF SEDIMENTS (PHI) ROCHERPAN

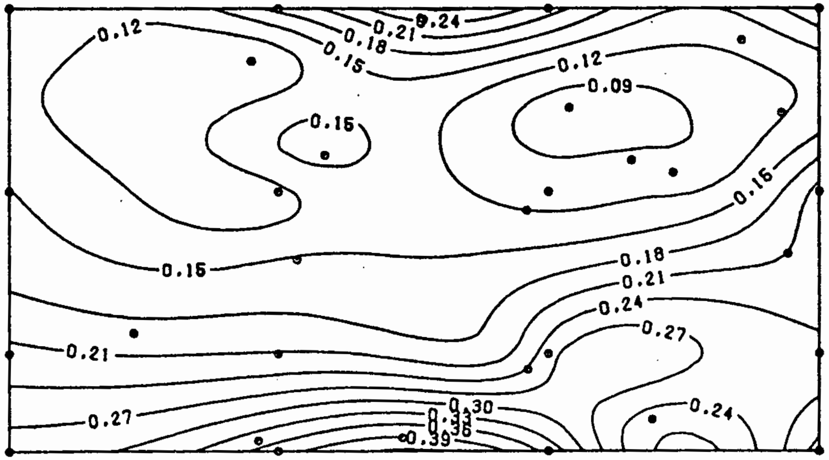
Figure 8.3. Sediment characteristics at Rocherpan



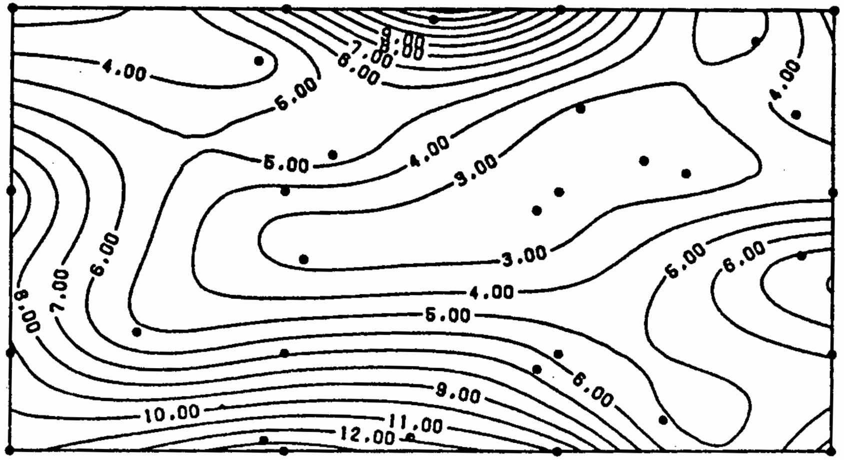
% ORGANICS (X 100) ROCHERPAN



% CALCIUM CARBONATE (X 3) ROCHERPAN



% ORGANICS ROCHERPAN



% CALCIUM CARBONATE ROCHERPAN

Figure 8.3. (contd.)

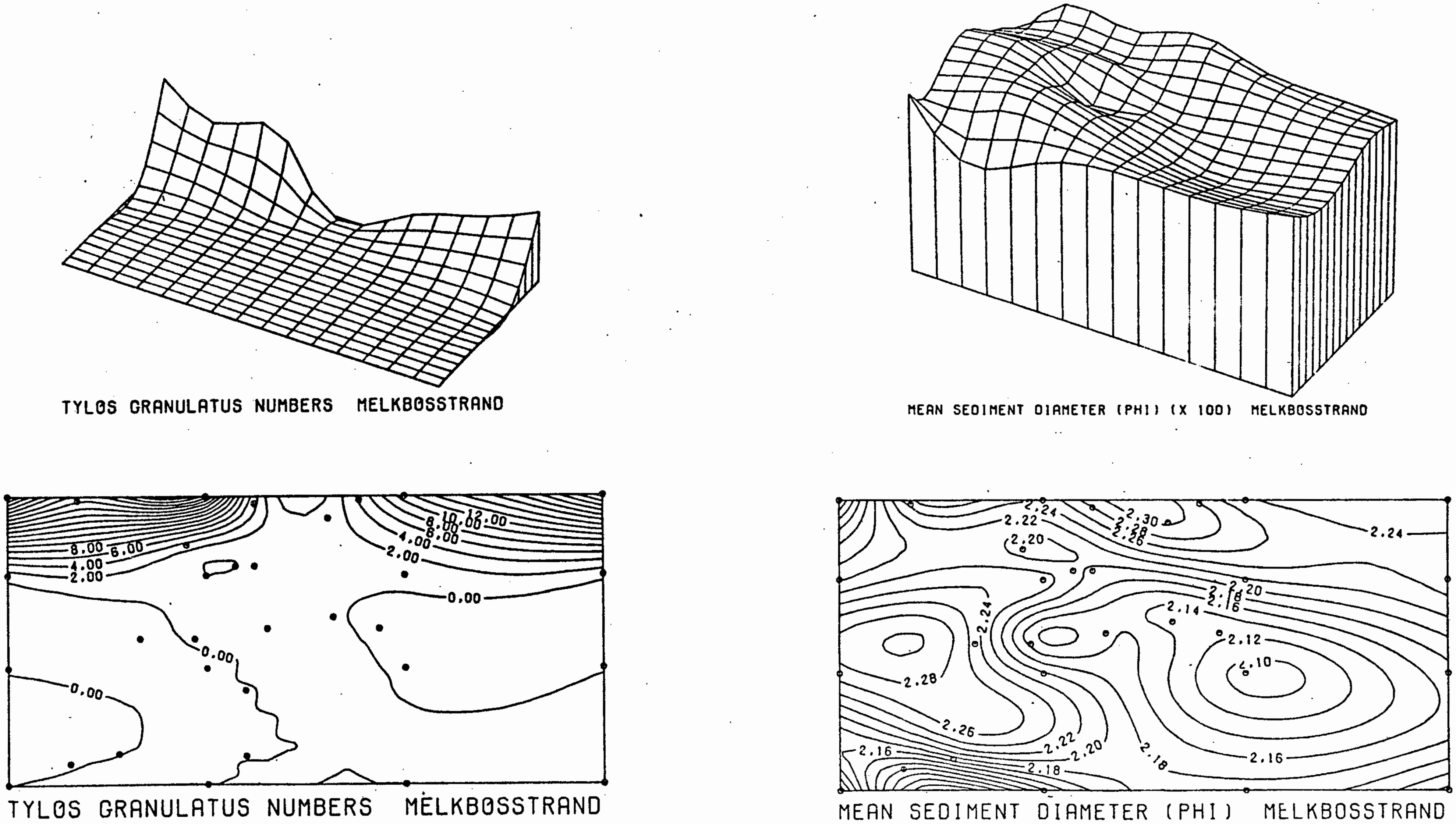
later, this species is not influenced by sediment characteristics within individual beaches and therefore no correlations between total macrofaunal biomass and sedimentary characteristics can be inferred. On the larger scale (i.e. differences between beaches), total biomass is considerably lower on the coarse-grained beach at Rocherpan than on the two finer beaches.

Tylos granulatus

On all three beaches, this air-breathing isopod seems to favour the coarser-grained sediments available to it. In each case (Figs. 8.4 to 8.6) the distribution peaks coincide with areas of coarser sand along the high-water mark. This is to be expected, since coarse-grained sands drain better than fine ones and, therefore, the chances of individuals being suffocated in moist or saturated sand at this level are reduced. Holanov and Hendrickson (1980) have shown that *Tylos granulatus* burrows down into sand to reach moisture contents of 1,0 to 2,5%. They have also shown that sands which are relatively dry on the surface may reach the above moisture contents within 5 - 10 cm depth. Kensley (1972) and this study have shown, however, that *Tylos granulatus* burrows to depths of 30 cm in order to avoid predation, environmental extremes and washing out to sea by the high tide (Kensley, 1972). Thus, coarser surface sands and, by implication drier ones, are actively selected for burrowing into, in order to avoid excessive moisture levels at the preferred depths.

Because the sand is drier as a result of its relative coarseness, it is also easier to burrow into than moister sand. Chapman (1949) has shown that moist sand is also more dilatant than saturated sand, and it is thus energetically advantageous to *Tylos granulatus* to inhabit drier sands.

The above-mentioned pattern of correlation was clearest at Ysterfontein



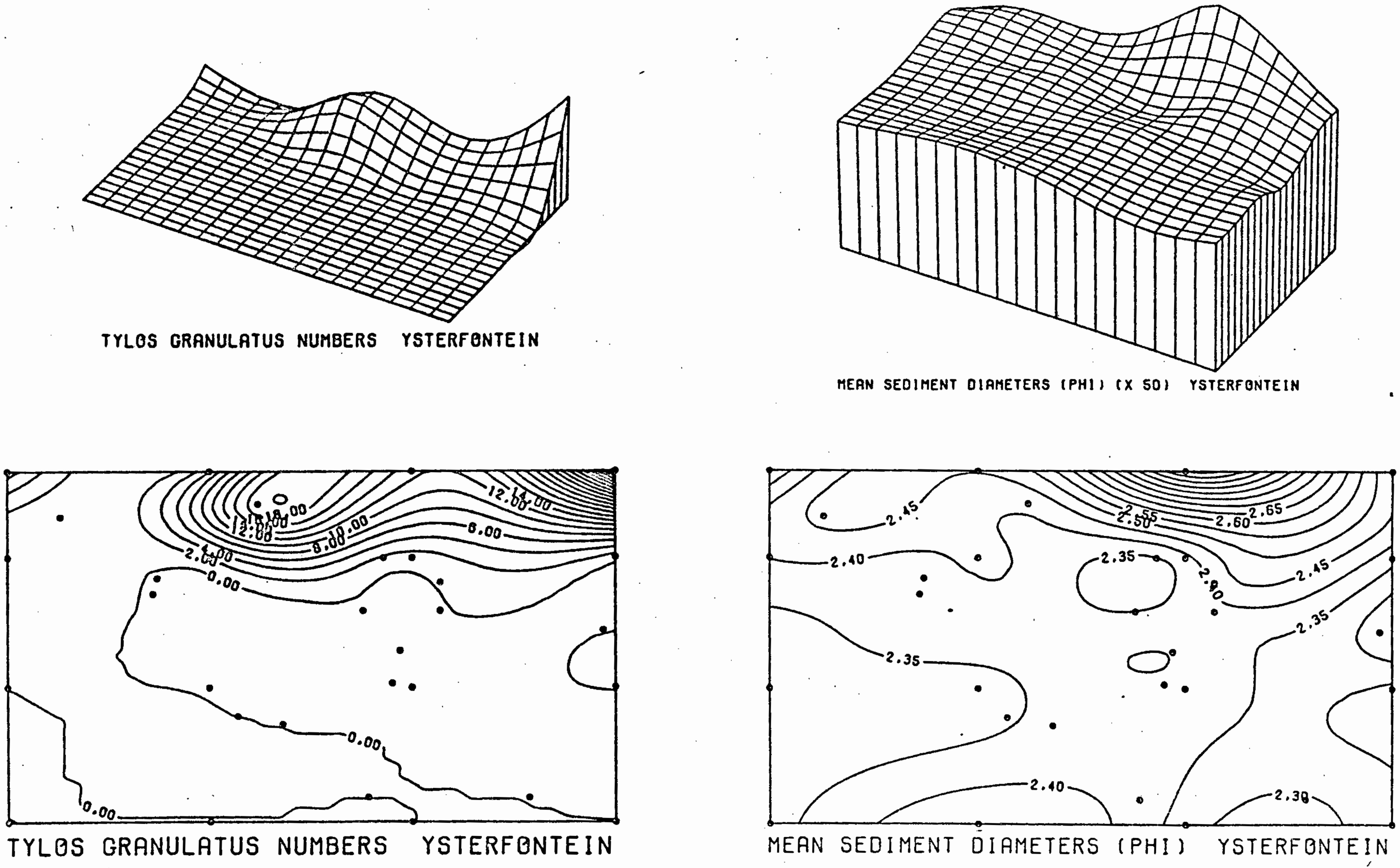
TYLOS GRANULATUS NUMBERS MELKBOSSTRAND

MEAN SEDIMENT DIAMETER (PHI) (X 100) MELKBOSSTRAND

TYLOS GRANULATUS NUMBERS MELKBOSSTRAND

MEAN SEDIMENT DIAMETER (PHI) MELKBOSSTRAND

Figure 8.4 The relationship between the distribution of *Tylos granulatus* and mean sediment diameters at Melkbosstrand



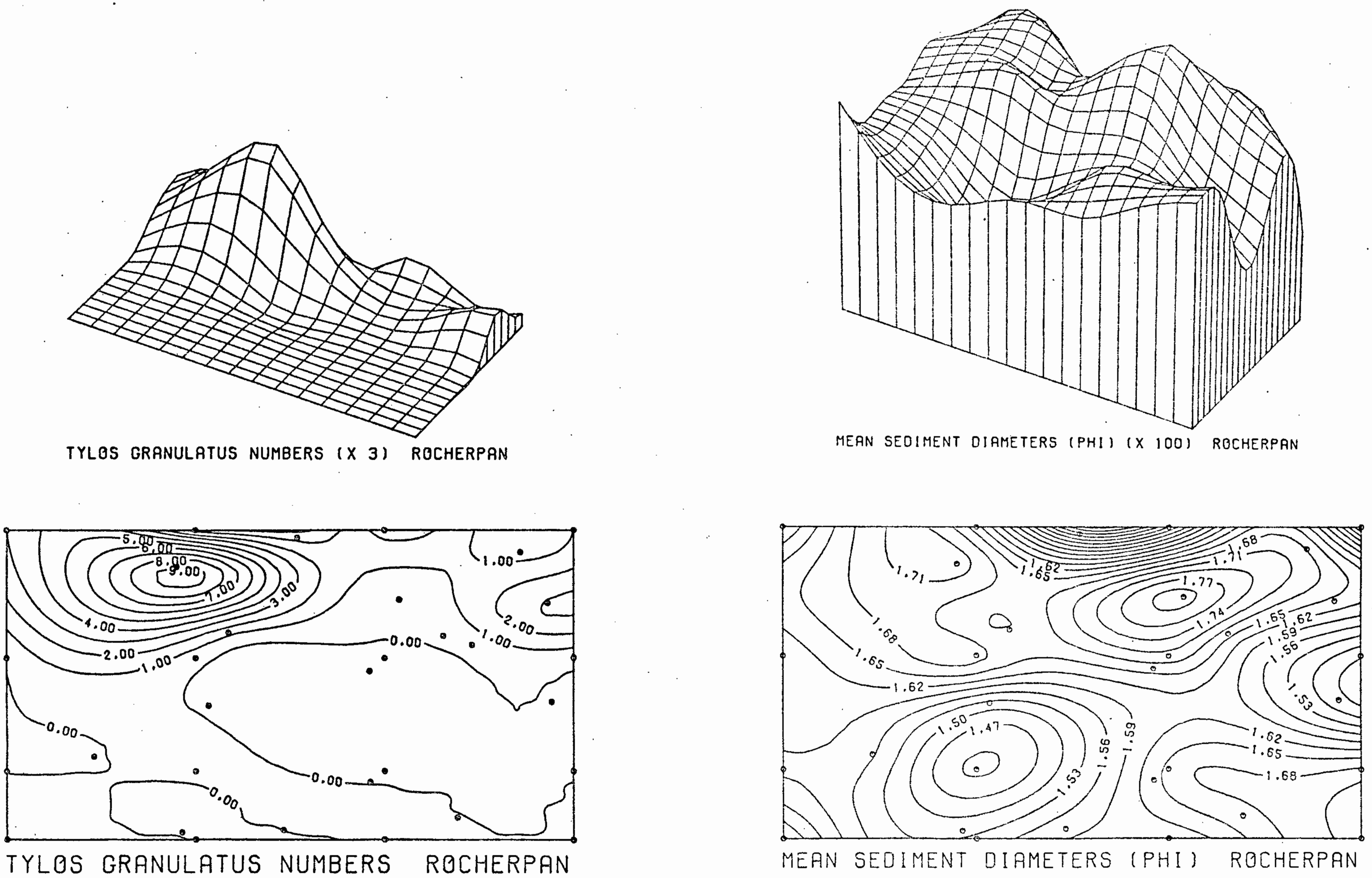
TYLOS GRANULATUS NUMBERS YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) (X 50) YSTERFONTEIN

TYLOS GRANULATUS NUMBERS YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) YSTERFONTEIN

Figure 8.5 The relationship between the distribution of *Tylos granulatus* and mean sediment diameters at Ysterfontein


TYLOS GRANULATUS NUMBERS (X 3) ROCHERPAN

MEAN SEDIMENT DIAMETERS (PHI) (X 100) ROCHERPAN

TYLOS GRANULATUS NUMBERS ROCHERPAN

MEAN SEDIMENT DIAMETERS (PHI) ROCHERPAN

Figure 8.6 The relationship between the distribution of *Tylos granulatus* and mean sediment diameters at Rocherpan

(Fig. 8.5) and Rocherpan (Fig. 8.6); it was present to a lesser degree at Melkbosstrand (Fig. 8.4). The ranges of sediment diameters apparently favoured were 2,08 - 2,61 phi at Melkbosstrand, 2,35 - 2,70 phi at Ysterfontein, and 1,32 - 1,71 phi at Rocherpan.

Oligochaetes

As mentioned previously, these terrestrial annelids were only found at Melkbosstrand, where they favoured fine sand (Fig. 8.7) of 2,26 phi diameter or smaller, although they are also present in coarser sediments. This correlation is to be expected, since fine sand has better water retention characteristics (Newcombe, 1935), thereby reducing the chances of desiccation. In addition, fine moist sand would be an easier burrowing medium than moist or dry coarse sand.

Niambia sp.

There is no correlation between the distribution of sediment characteristics and this terrestrial isopod at Ysterfontein (Fig. 8.8). At Rocherpan (Fig. 8.9), however, it appeared as if it favours areas of high organic content. Species of the genus *Niambia* are normally found in commensal relationships with ants (S. Taiti, pers. comm.) and seem to wander into the intertidal zone on the surface of the sand at low tide, possibly to scavenge. If this is so, *Niambia* would favour areas where organic detritus is available, i.e. along drift lines.

Although present at Melkbosstrand, only a single individual was collected during the intensive sampling session. At Rocherpan, *Niambia* is concentrated on areas where the percentage of organics in the sand exceeded 0,15% and that of calcium carbonate 5%. At Ysterfontein no such pattern was observed, however. These differences, therefore, are either due to the fact that organics are available at Ysterfontein in sufficiently high quantities throughout the zone of drying (0,30 - 0,88%) not to necessitate an active search for areas relatively

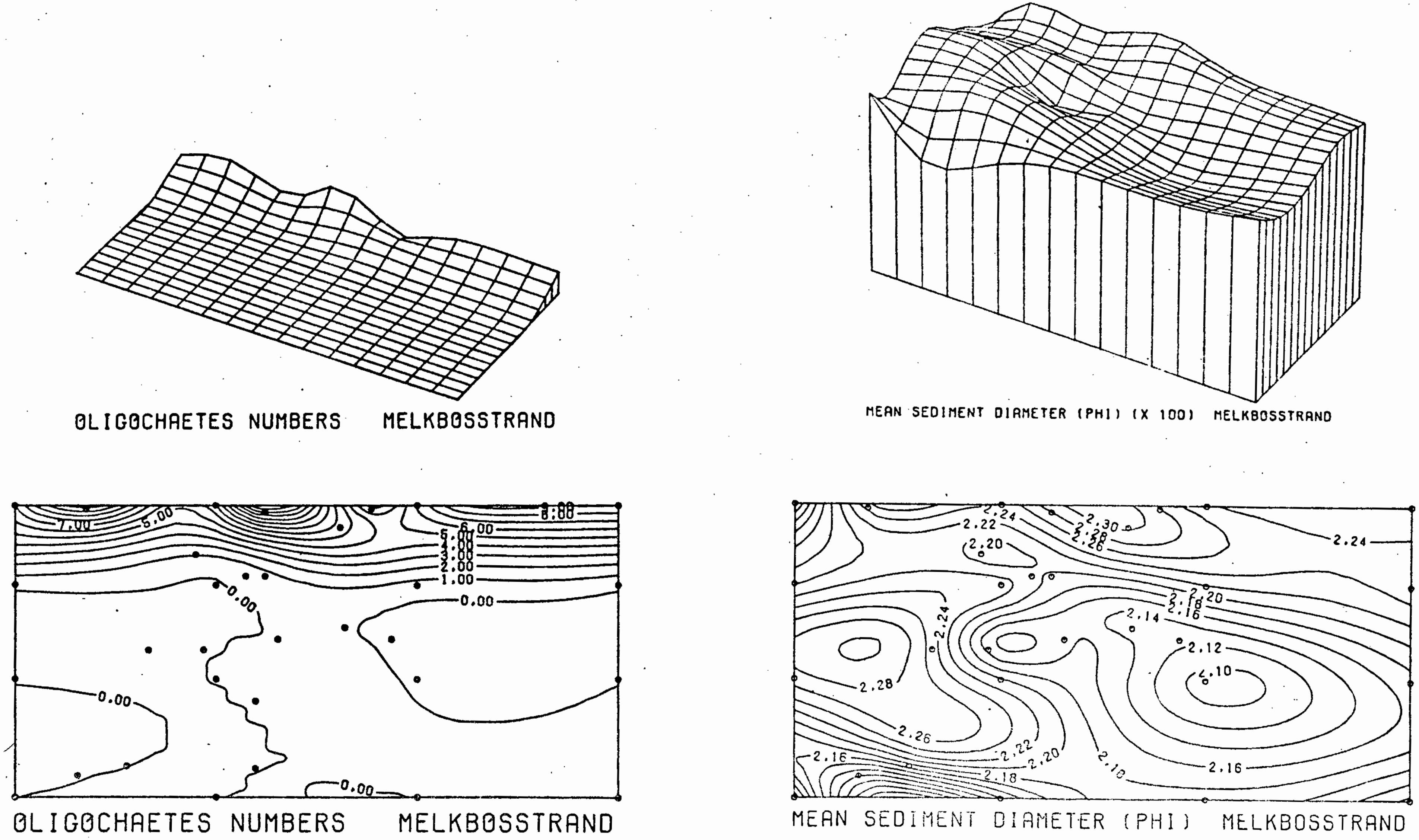
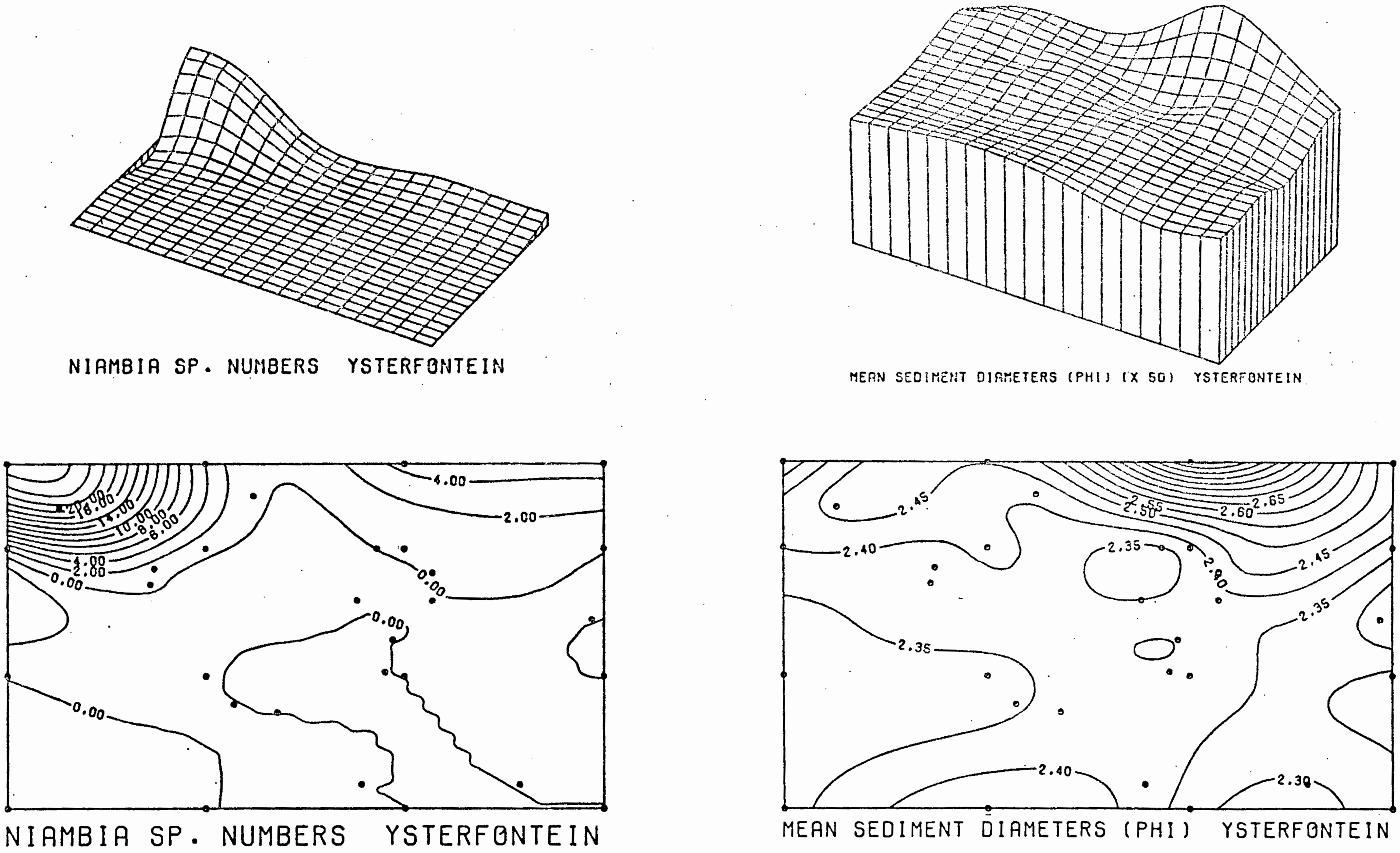


Figure 8.7 The relationship between the distribution of oligochaetes and mean sediment diameters at Melkbosstrand



NIAMBIA SP. NUMBERS YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) (X 50) YSTERFONTEIN

NIAMBIA SP. NUMBERS YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) YSTERFONTEIN

Figure 8.8 The relationship between the distribution of *Niambia* sp. and mean sediment diameters at Ysterfontein

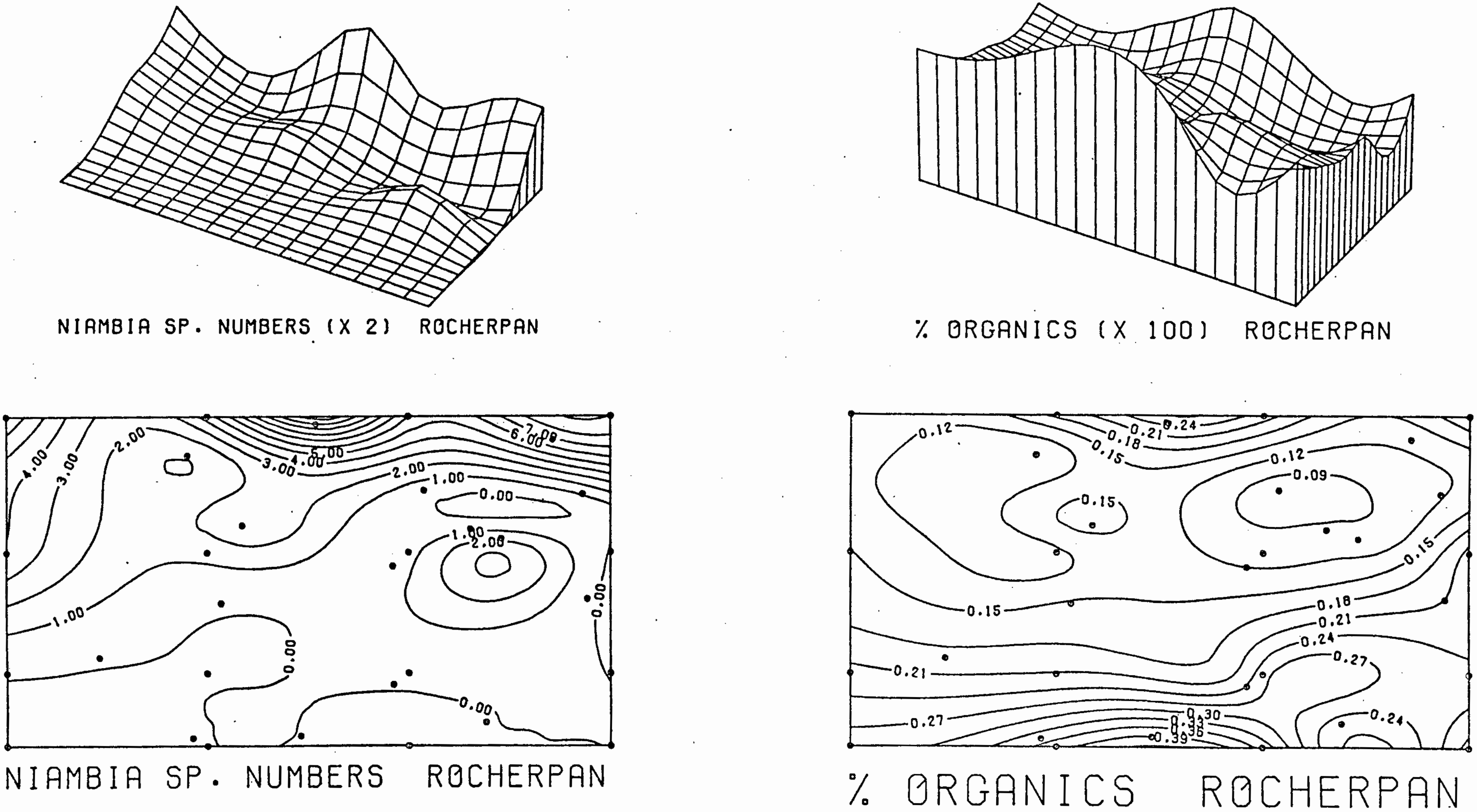


Figure 8.9 The relationship between the distribution of *Niambia* sp. and percentage organics of the sediment at Rocherpan

rich in organics, or the correlations at Rocherpan are coincidental.

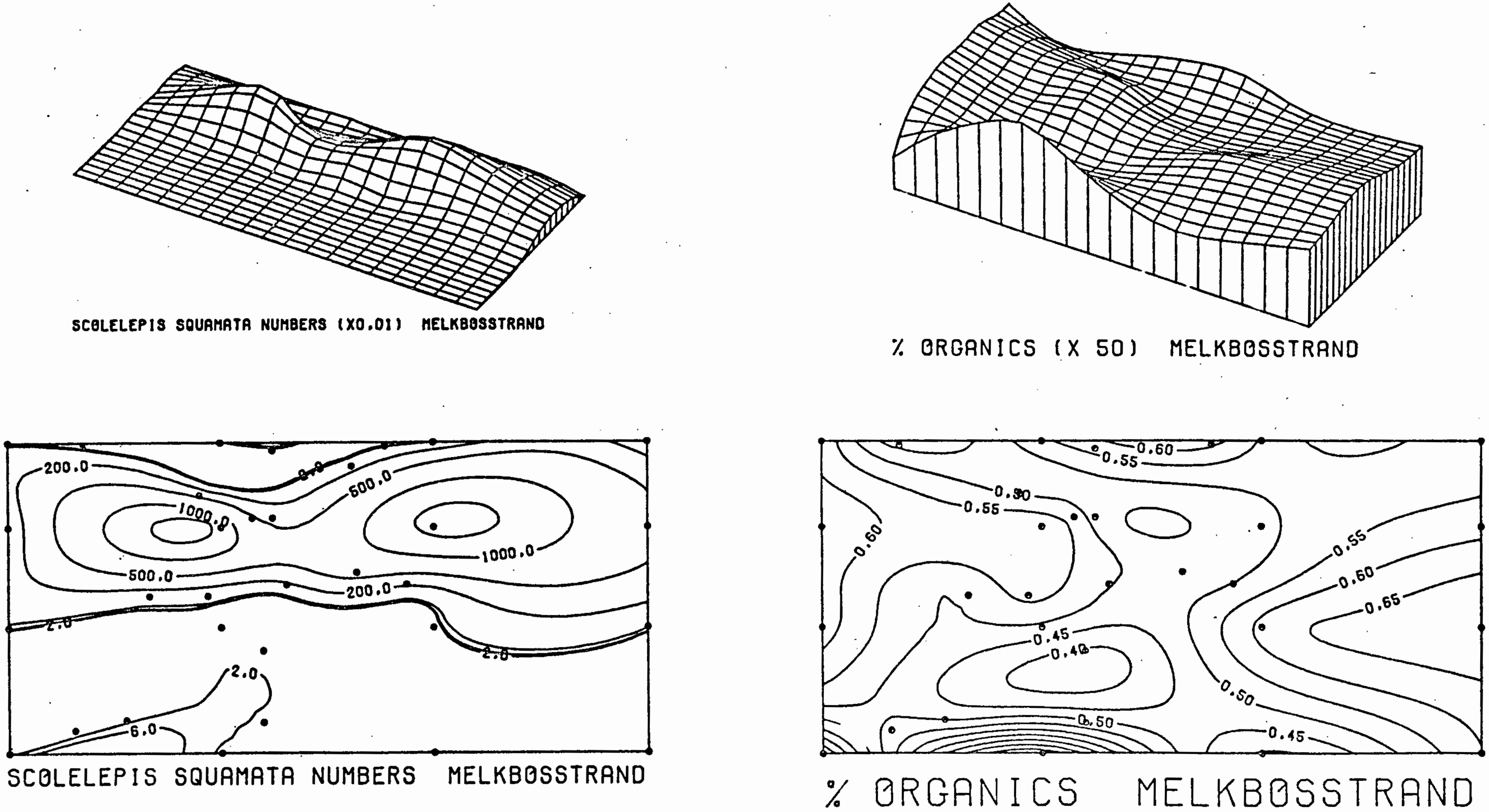
Scolelepis squamata

As mentioned above, *Scolelepis* is not found at Rocherpan due to the coarseness of the sand. The species is present on the other two finer beaches, although sand grain size does not appear to affect its distribution. The distribution of these animals does coincide, however, with areas of high organic content (see Figs. 8.10 and 8.11). This is an expected result, since these polychaetes are deposit feeders and would favour areas rich in organics. On the other hand, it is also possible that the polychaetes themselves increase the organic content of the sand by excretion, defacation and decomposition of dead organisms. Since these are largely sedentary organisms and the beach is a relatively mobile environment, patches "naturally" rich in organics may not remain so for very long.

It should be noted, however, that *Scolelepis* does move on the surface of the sand occasionally, possibly more frequently at night than in the daytime, leaving characteristic trails (Behrends and Michaelis, 1977). Which of the above alternatives operates operates would therefore depend on both the stability of sediment characteristics with time and the frequency with which *Scolelepis* shift their positions along the shore.

Pontogeloides latipes

At Melkbosstrand and Ysterfontein (Fig.s 8.12 and 8.13), *Pontogeloides* favours coarser sand, on the latter beach to a very marked degree. At Rocherpan (Fig. 8.14), no such trend was observed, although there was a slight correlation between distribution and areas of low organic content. On the two fine-grained beaches, this isopod favoured mean sand grain diameters of 2,20 - 2,22 phi and 2,40 - 2,45 phi at Melkbosstrand and Ysterfontein respectively, whereas at Rocherpan the requirement for



SCOLELEPIS SQUAMATA NUMBERS (X0.01) MELKBOSSTRAND

% ORGANICS (X 50) MELKBOSSTRAND

SCOLELEPIS SQUAMATA NUMBERS MELKBOSSTRAND

% ORGANICS MELKBOSSTRAND

Figure 8.10 The relationship between the distribution of *Scolelepis squamata* and percentage organics of the sediment at Melkbosstrand

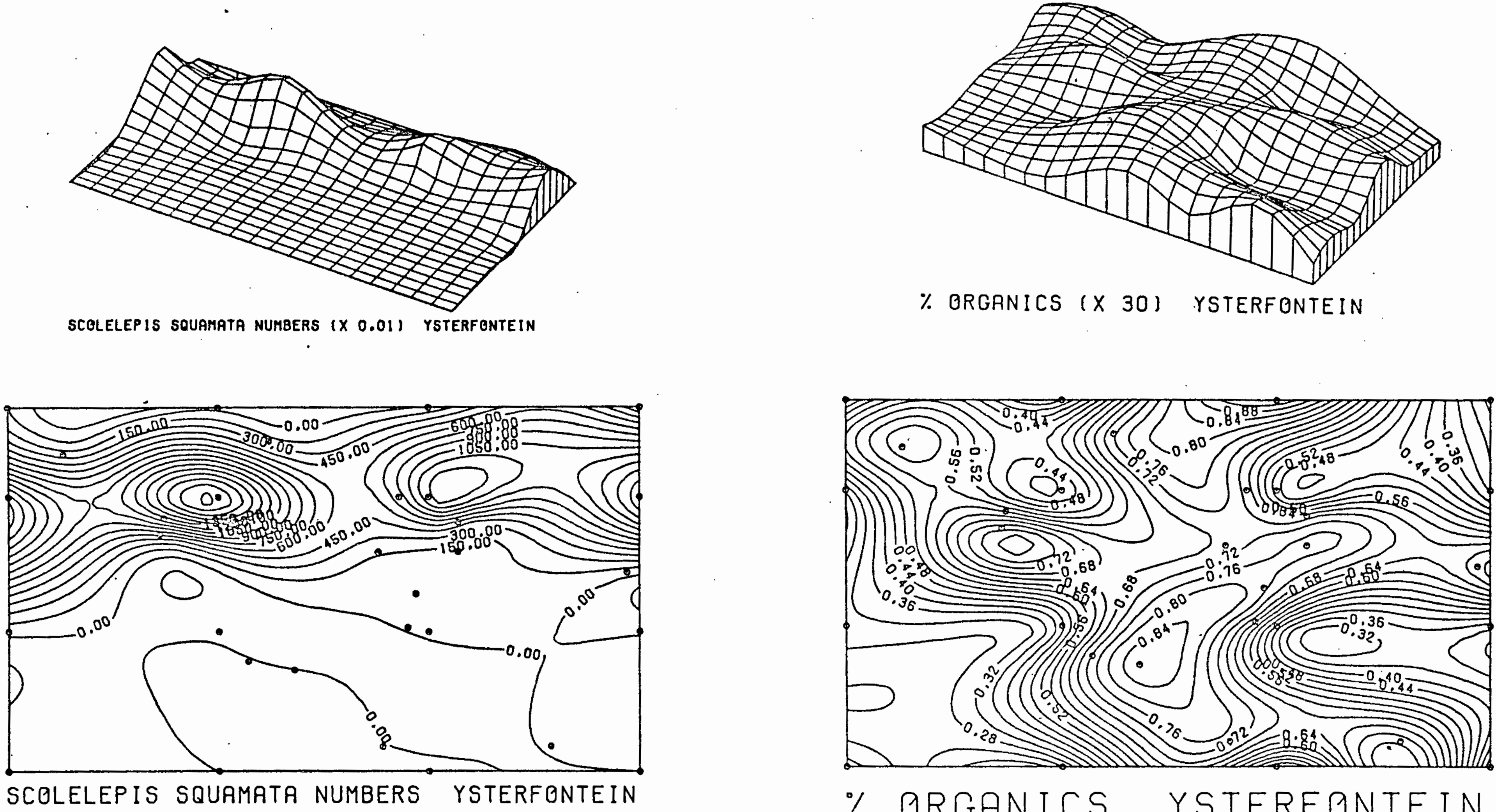
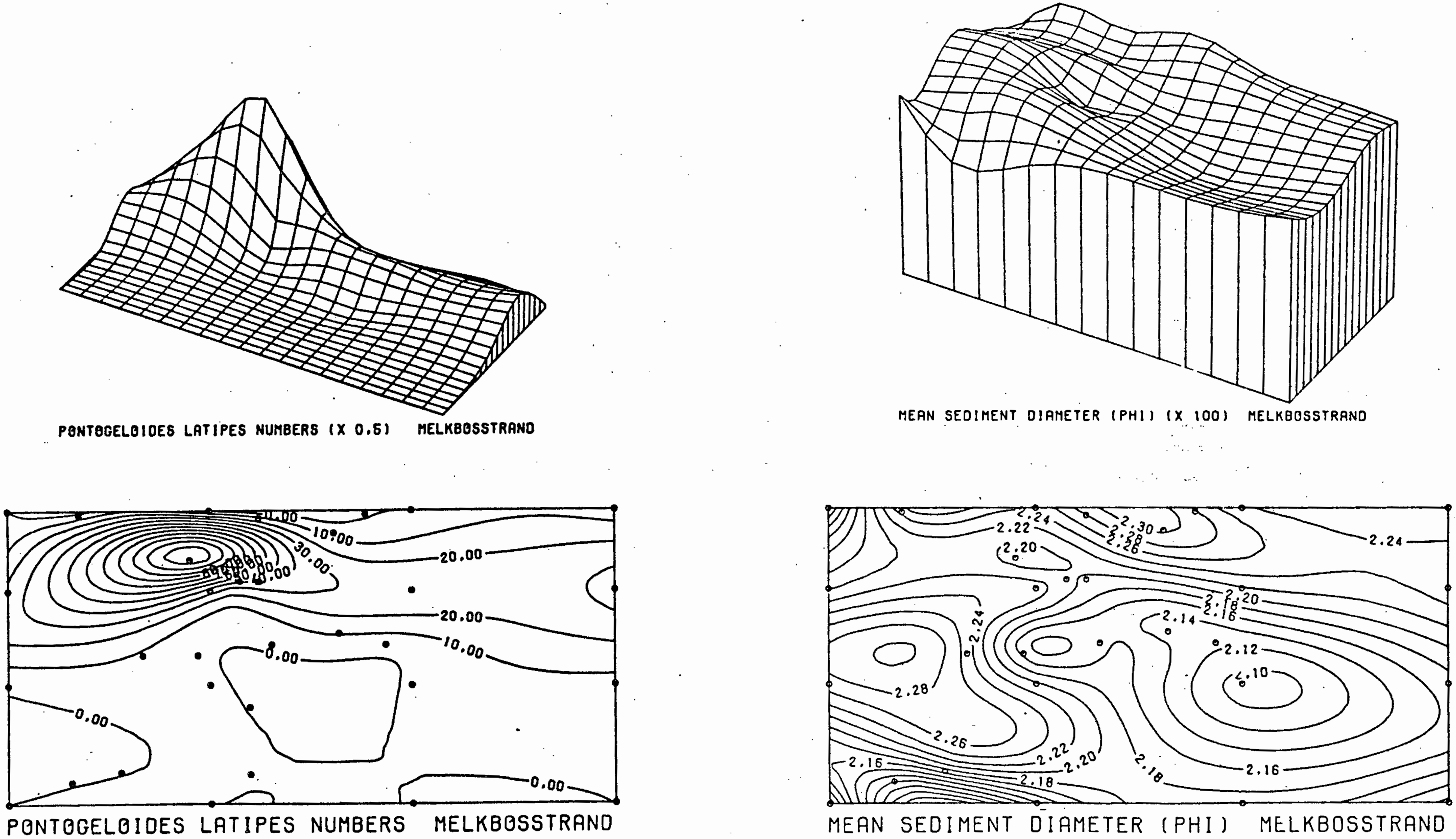


Figure 8.11 The relationship between the distribution of *Scolelepis squamata* and percentage organics of the sediment at Ysterfontein

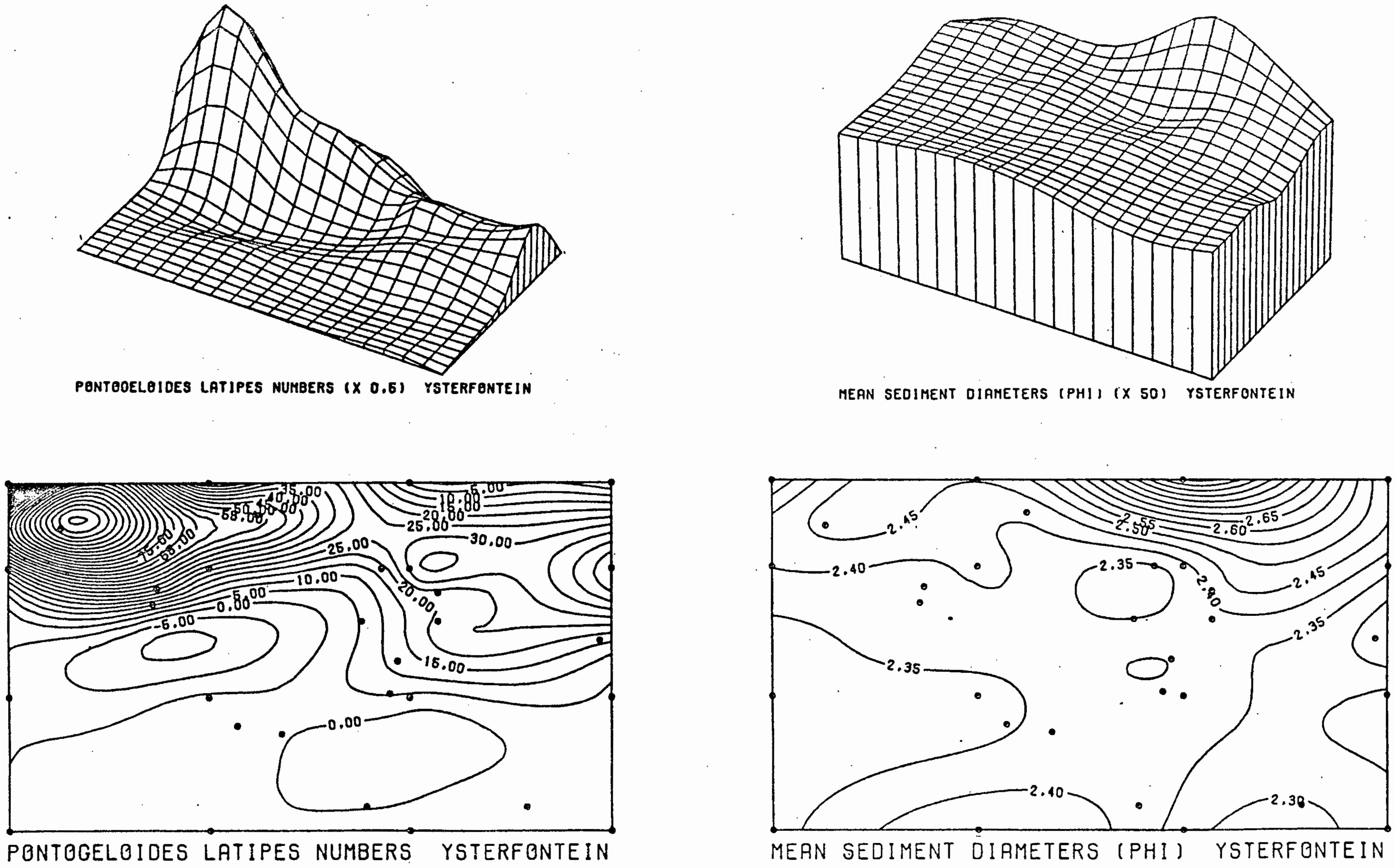

PONTOGELOIDES LATIPES NUMBERS (X 0.5) MELKBOSSTRAND

MEAN SEDIMENT DIAMETER (PHI) (X 100) MELKBOSSTRAND

PONTOGELOIDES LATIPES NUMBERS MELKBOSSTRAND

MEAN SEDIMENT DIAMETER (PHI) MELKBOSSTRAND

Figure 8.12 Relationship between distribution of *Pontogeloides latipes* and mean sediment diameter at Melbosstrand .



PONTOELOIDES LATIPES NUMBERS (X 0.5) YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) (X 50) YSTERFONTEIN

PONTOGELOIDES LATIPES NUMBERS YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) YSTERFONTEIN

Figure 8.13 Relationship between distribution of *Pontogeloides latipes* and mean sediment diameter at Ysterfontein

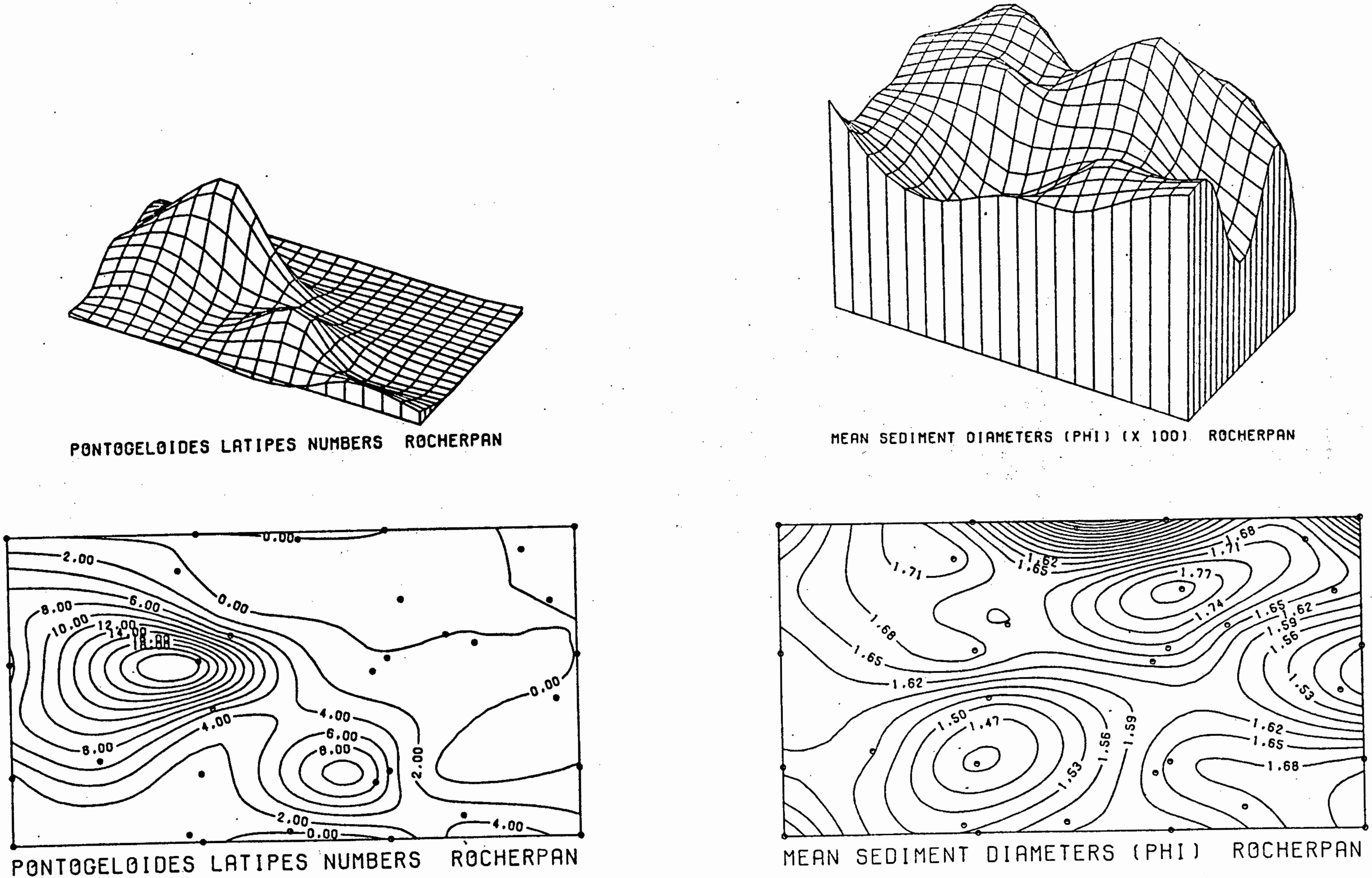


Figure 8.14 Relationship between distribution of *Pontogeloides latipes* and mean sediment diameter at Rocherpan

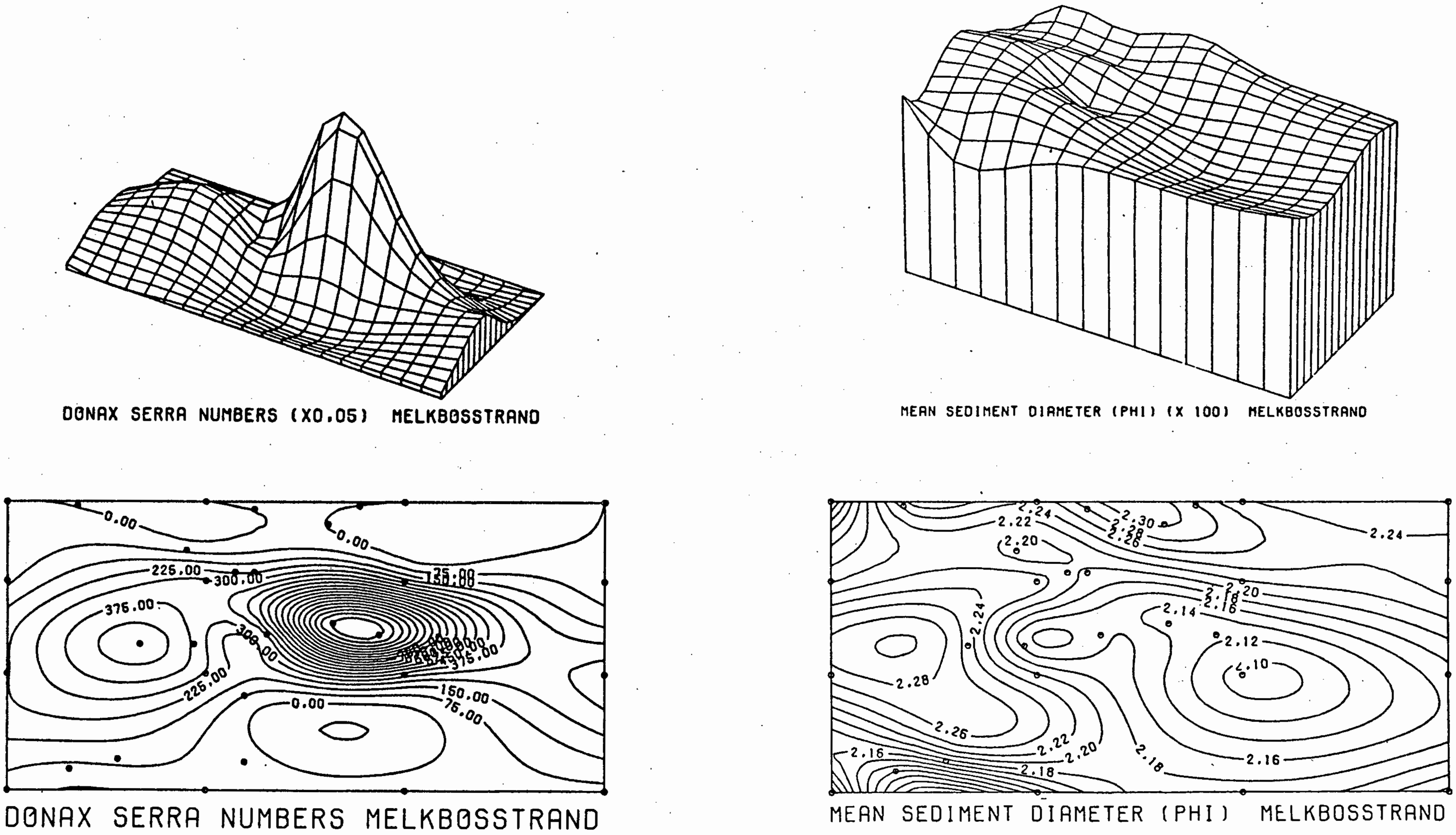
coarseness has apparently been satisfied. On the latter beach, *Pontogeloides* distribution peaks were found in sands of 1,56 - 1,68 phi, although both finer and coarser sands were available within the zone occupied by the species. At Rocherpan, the coarseness of the sand has also shifted the intertidal position occupied by *Pontogeloides* seawards relative to the zones occupied on the other two beaches.

Donax serra

At Melkbosstrand (Fig. 8.15) and Ysterfontein (Fig. 8.16), *Donax* distribution appears to be independent of sediment characteristics. At Rocherpan (Fig. 8.17), however, sediments just seaward to coarser sediments were favoured. This might be a function of the steepness of the beach and consequent high rates of erosion. Rocherpan was the only beach where *Donax* were observed being washed out of the beach by strong backwash. Where sand is coarser, the backwash is weaker, since coarse sand allows more water to percolate into the beach (Grant, 1948; Duncan, 1964), thereby making the areas selected energetically favourable for maintaining zonation. Because of the coarseness of the sand at Rocherpan, the position occupied by *Donax* is seaward to those occupied on the other two beaches. As was pointed out in chapter 3, however, wave action increases from the high-water mark to low water, so some compromise between energy expended on maintaining zonation and protection from desiccation is in operation.

Eurydice longicornis

This species, the dominant isopod in terms of numbers at Melkbosstrand (Fig. 8.18) and Ysterfontein (Fig. 8.19), shows a preference for fine-grained sand on these beaches. At Melkbosstrand this preference is very marked (finer than 2,18 phi), while at Ysterfontein, where the sediments are fairly uniform in the area occupied by *Eurydice*, the long shore edges of the distribution peaks coincide with an increase in



DONAX SERRA NUMBERS (X0.05) MELKBOSSTRAND

MEAN SEDIMENT DIAMETER (PHI) (X 100) MELKBOSSTRAND

DONAX SERRA NUMBERS MELKBOSSTRAND

MEAN SEDIMENT DIAMETER (PHI) MELKBOSSTRAND

Fogure 8.15 Relationship between distribution of *Donax serra* and mean sediment diameter at Melkbosstrand

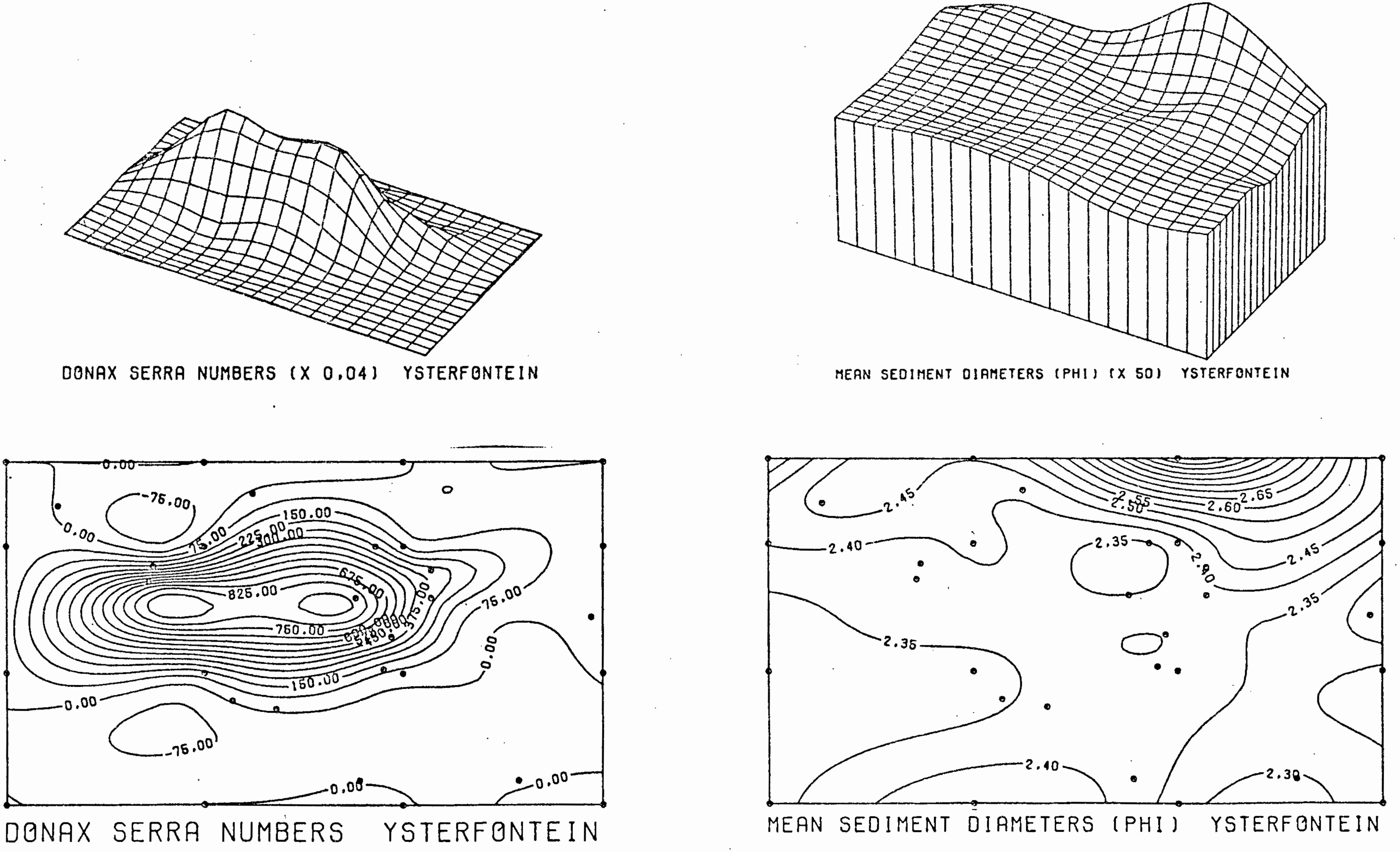
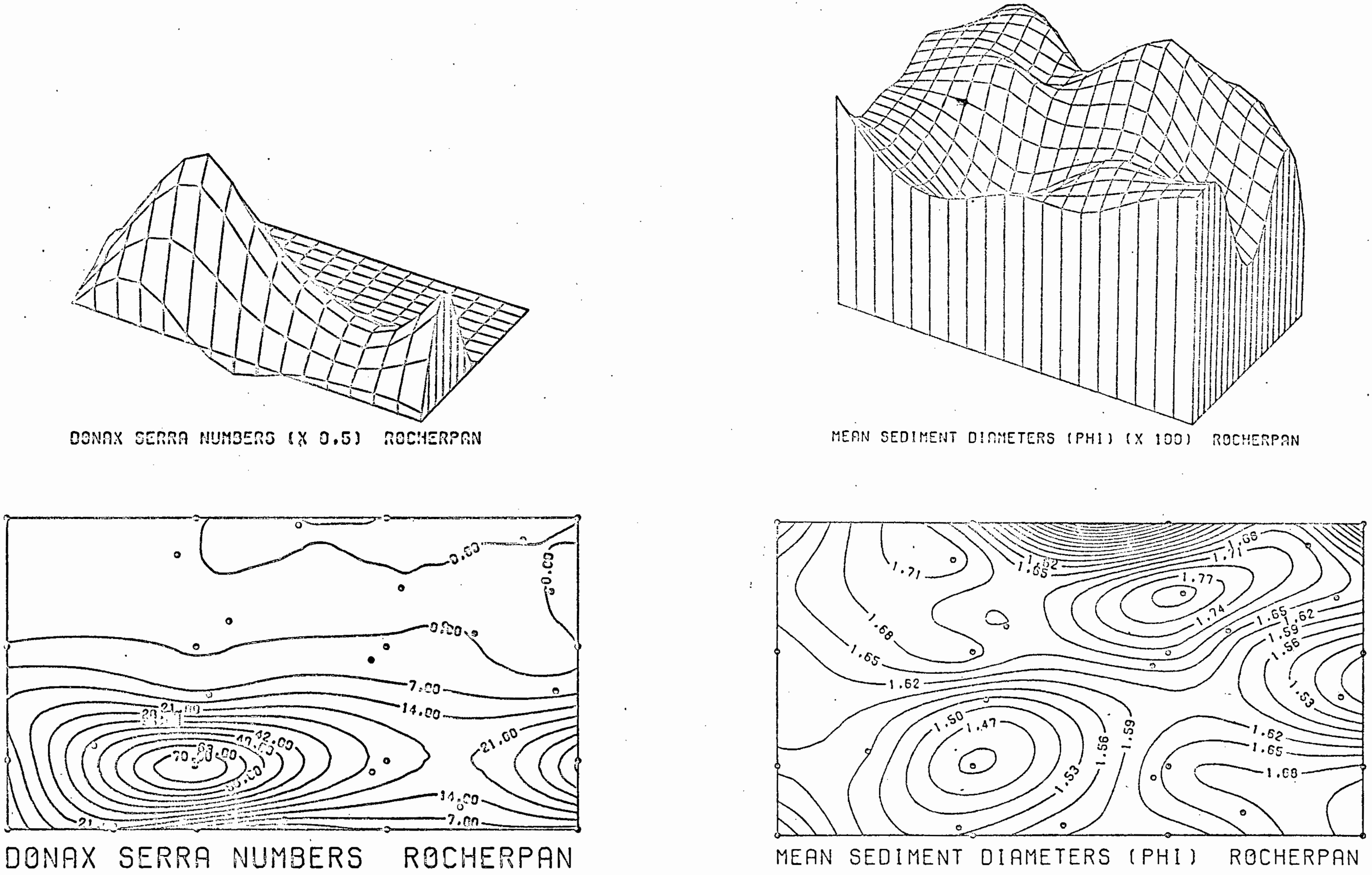


Figure 8.16 Relationship between distribution of *Donax serra* and mean sediment diameter at Ysterfontein


DONAX SERRA NUMBERS (X 0.5) ROCHERPAN

MEAN SEDIMENT DIAMETERS (PHI) (X 100) ROCHERPAN

DONAX SERRA NUMBERS ROCHERPAN

MEAN SEDIMENT DIAMETERS (PHI) ROCHERPAN

Figure 8.17 Relationship between distribution of *Donax serra* and mean sediment diameter at Rocherpan

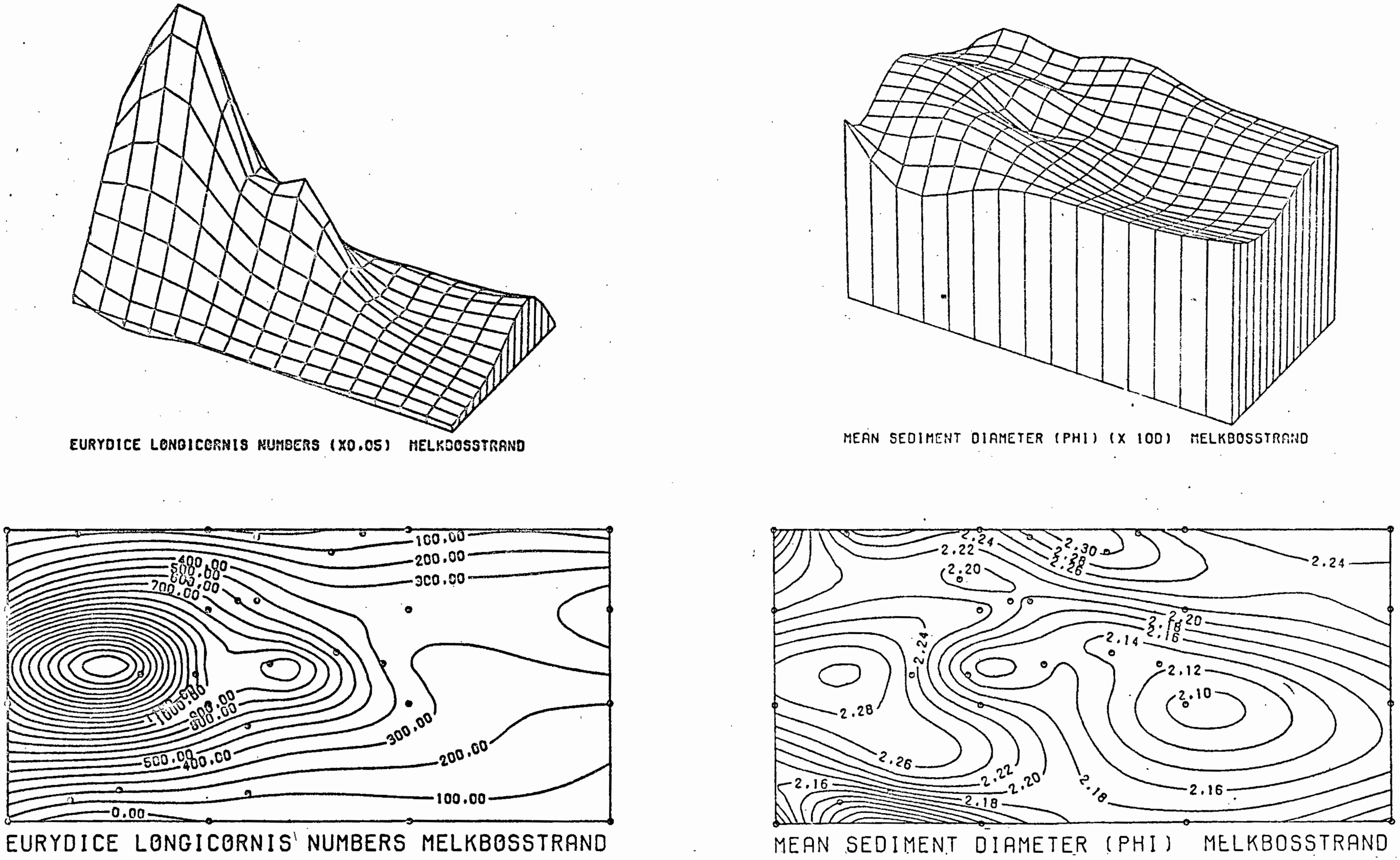
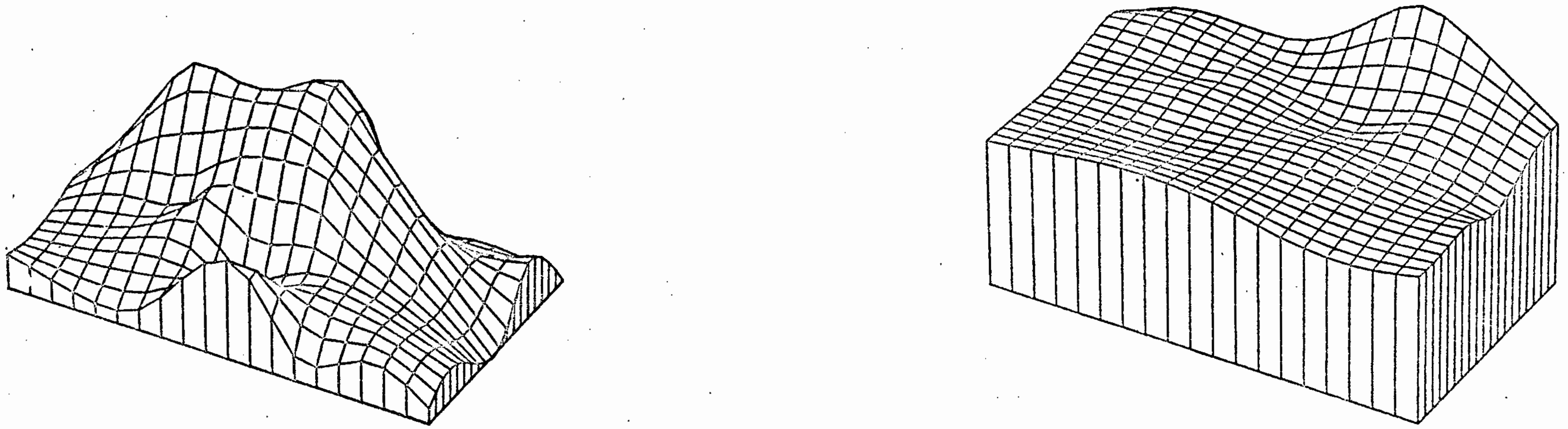
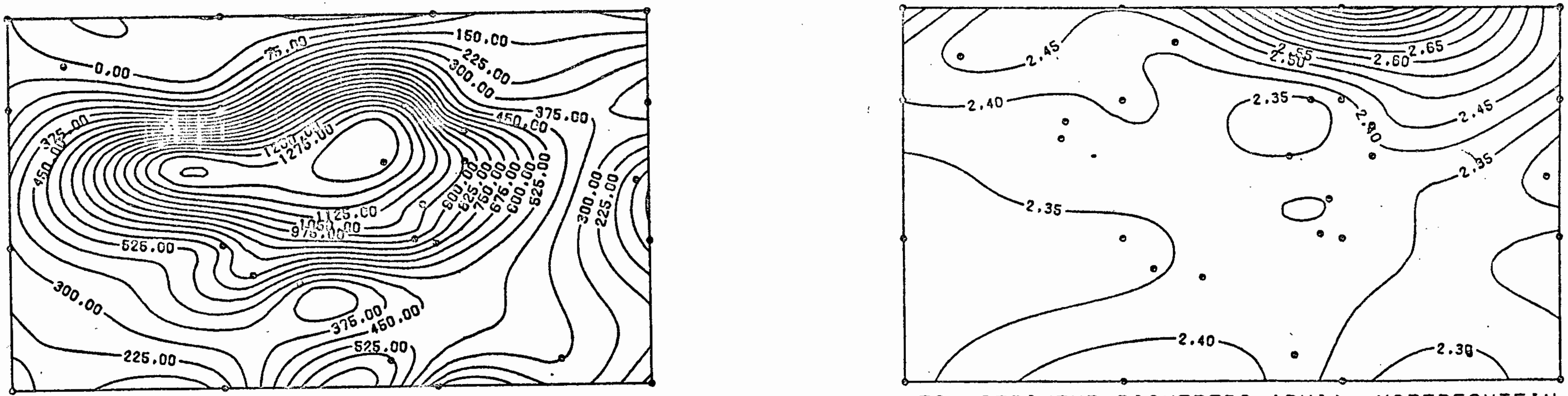


Figure 8.18 Relationship between distribution of *Eurydice longicornis* and mean sediment diameter at Melkbosstrand



EURYDICE LONGICORNIS NUMBERS (X 0.05) YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) (X 50) YSTERFONTEIN



EURYDICE LONGICORNIS NUMBERS YSTERFONTEIN

MEAN SEDIMENT DIAMETERS (PHI) YSTERFONTEIN

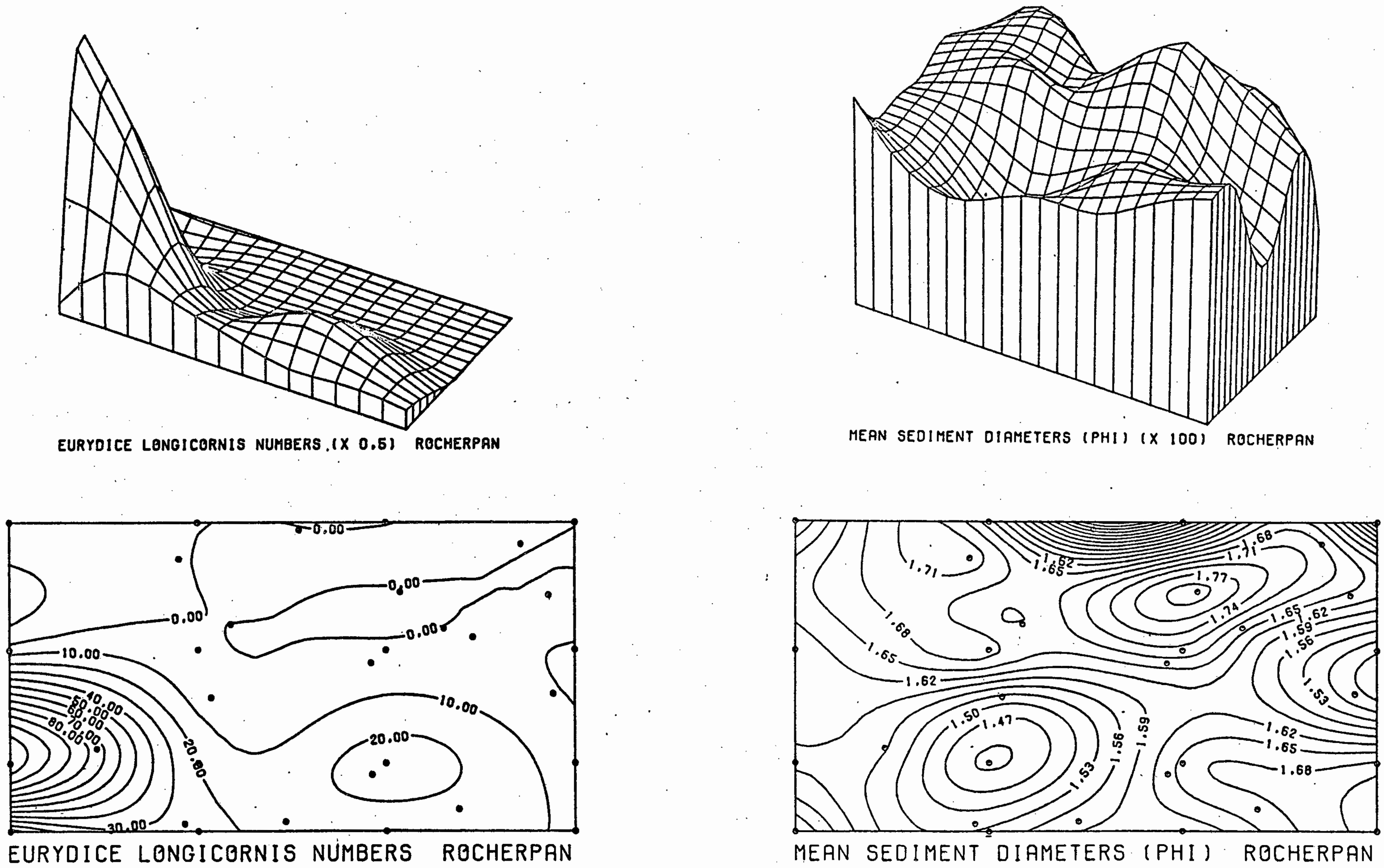
Figure 8.19 Relationship between distribution of *Eurydice longicornis* and mean sediment diameter at Ysterfontein the coarseness of the sand (coarser than 2,35 phi). Although this species is also found at Rocherpan (Fig. 8.20), it is no longer the dominant isopod species there. No correlation between sediment diameter and distribution is noted at Rocherpan, but, as in the cases of *Donax, Pontogeloides* and *Excirolana*, the zone occupied by *Eurydice* is shifted seawards relative to the other two beaches. The preference for fine sand is understandable in view of the small size of *Eurydice*, which measure and weigh approximately one tenth of *Pontogeloides* and *Excirolana*. As was noted in chapter 7, the patches at Melkbosstrand and Ysterfontein consist largely of juveniles, which would be expected to show a still greater preference for fine sand.

Gastrosaccus psammodytes

No clear correlation between sediment characteristics and distribution is apparent for this mysid at either Melkbosstrand or Ysterfontein. Although *Gastrosaccus* is also found at Rocherpan, only a single individual was found on the occasion that these collections were made. Brown and Talbot (1972) have shown that individuals of this species prefer coarse sediments with mean diameters of 0,55 - 0,75 mm (i.e. o,85 - 0,45 phi) as opposed to even coarser ones, but finer grades of sand were unfortunately not tested.

Nephtys capensis

Both at Melkbosstrand and Ysterfontein, no correlations were observed between sediment characteristics and distributions. This polychaete too is absent from Rocherpan, for the reasons outlined for *Sigalion*. *Nephtys* was also found in very much finer sand by Bally *et al.* (1980) on a sheltered beach in False Bay, where sediment diameters ranged from 3,08 to 3,61 phi.



EURYDICE LONGICORNIS NUMBERS (X 0.5) ROCHERPAN

MEAN SEDIMENT DIAMETERS (PHI) (X 100) ROCHERPAN

EURYDICE LONGICORNIS NUMBERS ROCHERPAN

MEAN SEDIMENT DIAMETERS (PHI) ROCHERPAN

Figure 8.20 Relationship between distribution of *Eurydice longicornis* and mean sediment diameter at Rocherpan

Pseudharpinia excavata

At Melkbosstrand (Fig. 8.21) this amphipod favoured finer sand of mean diameters less than 2,18 phi. At Ysterfontein (Fig. 8.22) the coarser beach sediments available were selected, although these, with a mean diameter of 2,30 phi were still finer than those at Melkbosstrand. Finally, at Rocherpan (Fig. 8.23), *Pseudharpinia* appeared to select the finer sediments in places. It would thus appear that the preferred diameter for this species lies between 2,18 and 2,30 phi.

Bullia digitalis

No correlations could be inferred between this species' distribution and the sedimentary characteristics studied, although Brown (1971b) found that juveniles of *Bullia digitalis* were unable to burrow into sand coarser than -0,49 phi. This is considerably coarser than any sediments found on the beaches studied. Although *Bullia* were collected on several occasions at Rocherpan, no individuals were found during this particular sampling session.

Other species

No correlations were found between sedimentary characteristics and the distribution of the nemertean *Cerebratulus fuscus* (which was only collected at Ysterfontein on this occasion although it normally also occurs on the other two beaches), the polychaete *Sigalion capensis*, the isopod *Excirolana natalensis*, and the amphipod *Talorchestia capensis*, while *Urothoe grimaldii* seemed to prefer areas of fine sediment at Melkbosstrand (Fig. 8.24). This species too, occurs on the other two beaches normally. Finally, the cumacean *Cumopsis robusta* is found on all three beaches, but on the occasion of these sampling sessions, a total of only five individuals were caught on all three beaches.

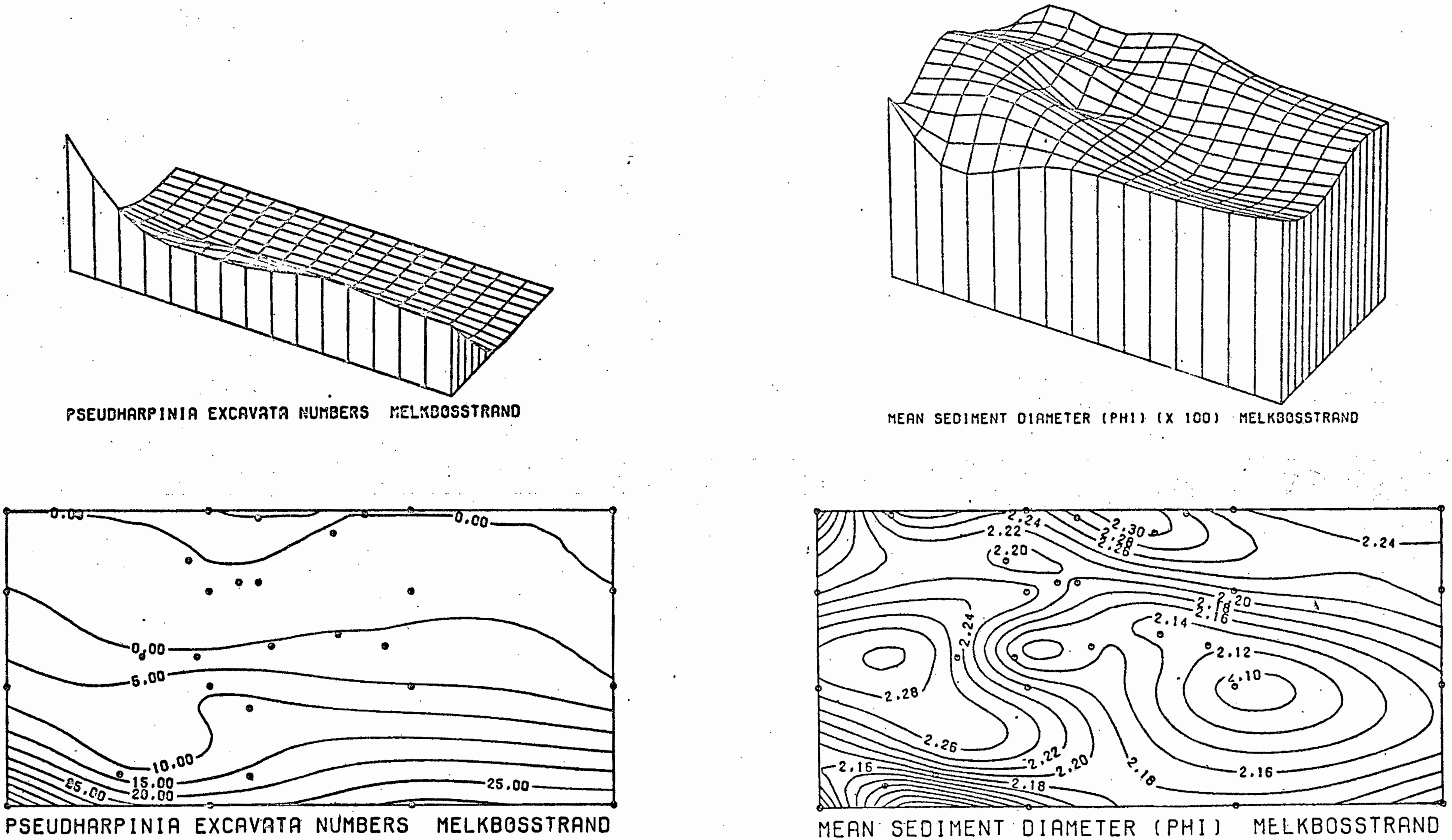


Figure 8.21 Relationship between distribution of *Pseudharpinia excavata* and mean sediment diameter at Melkbosstrand

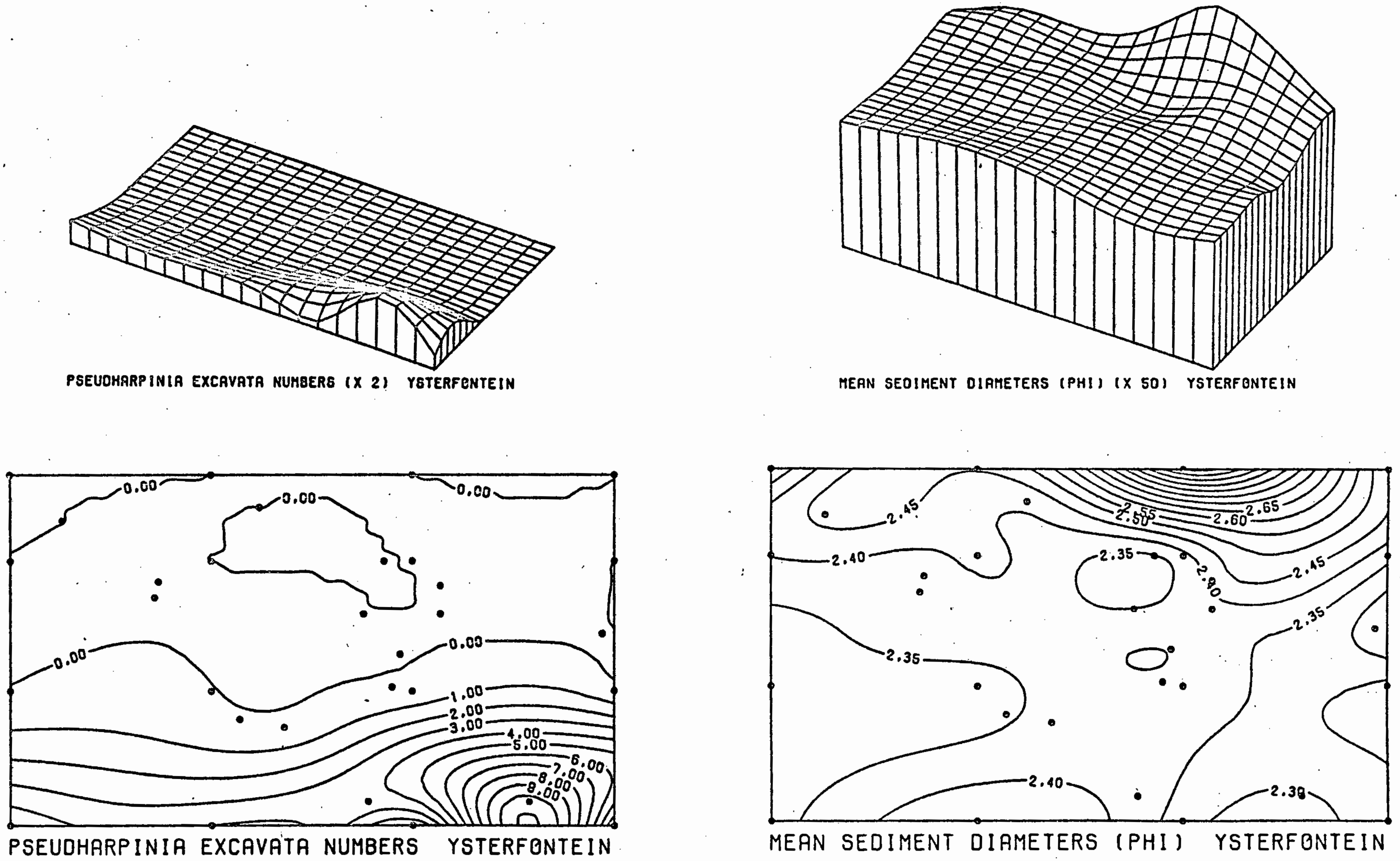


Figure 8.22 Relationship between distribution of *Pseudharpinia excavata* and mean sediment diameter at Ysterfontein

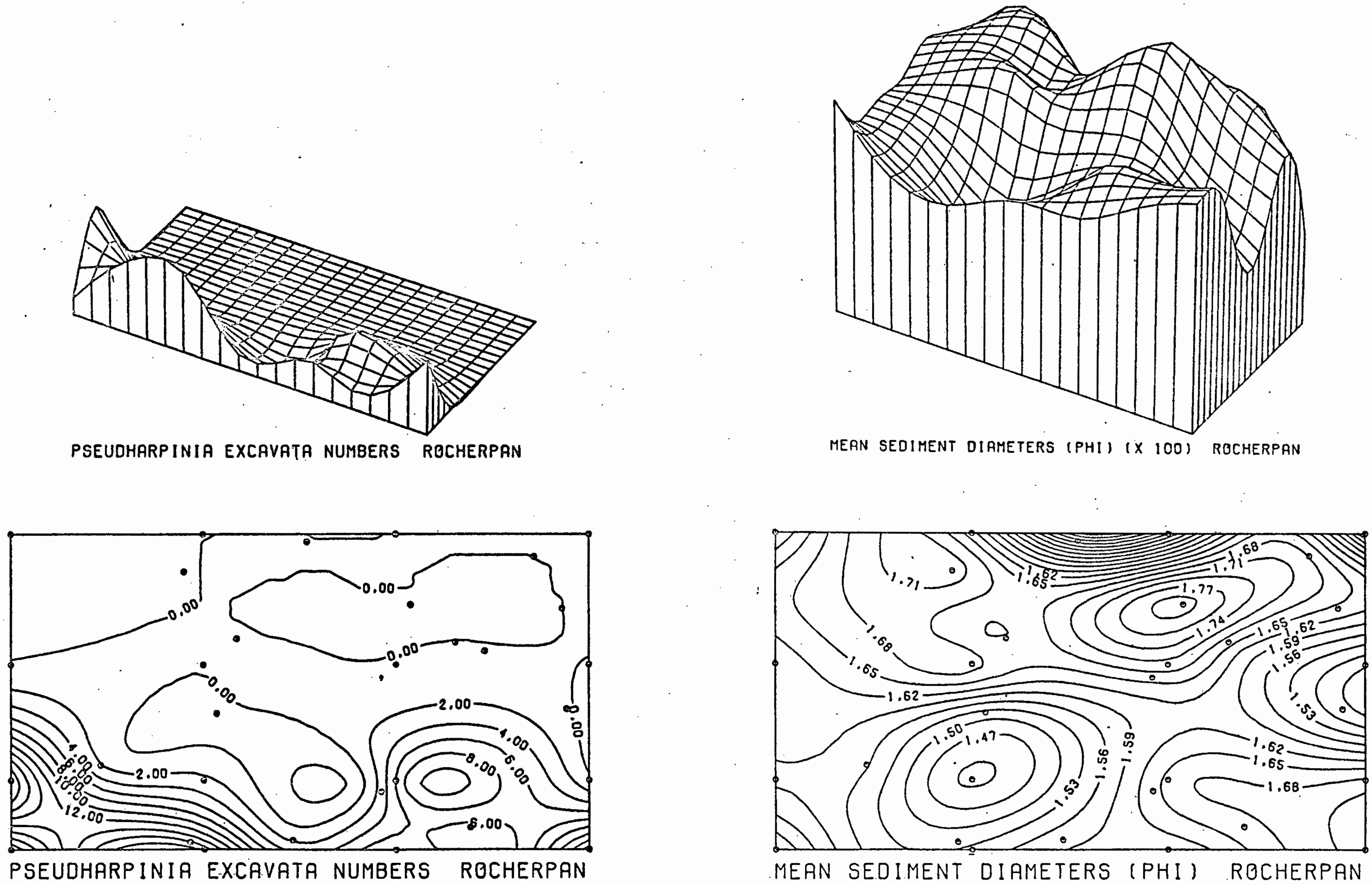
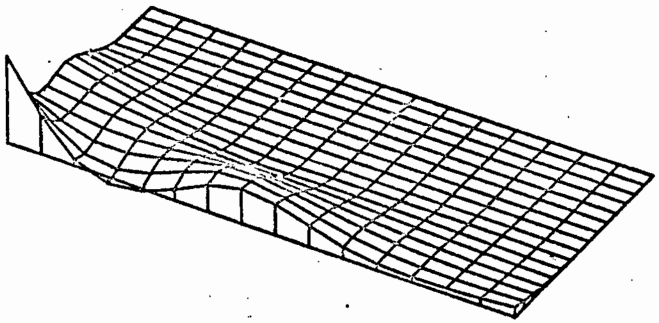
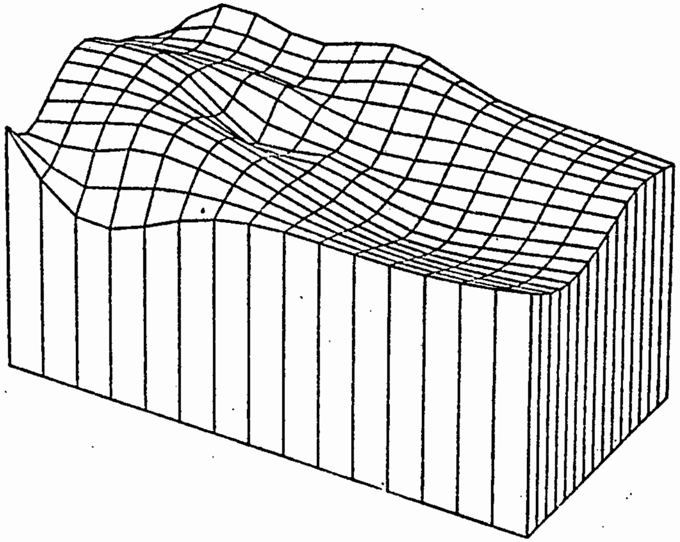


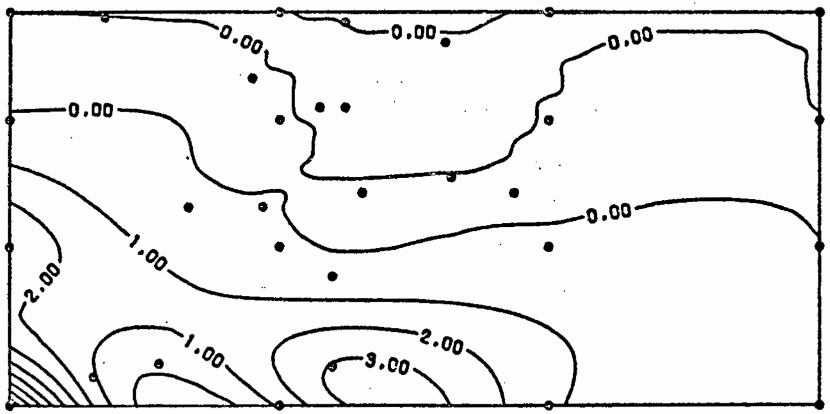
Figure 8.23 Relationship between distribution of *Pseudharpinia excavata* and mean sediment diameter at Rocherpan



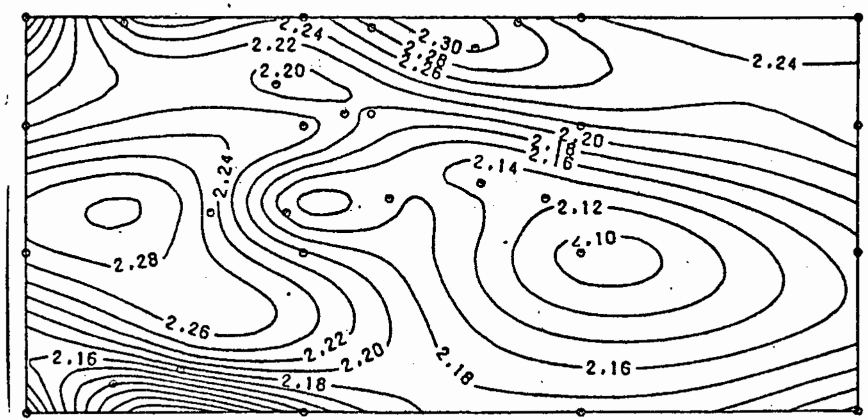
UROTHOE GRIMALDII NUMBERS (X3) MELKBOSSTRAND



MEAN SEDIMENT DIAMETER (PHI) (X 100) MELKBOSSTRAND



UROTHOE GRIMALDII NUMBERS MELKBOSSTRAND



MEAN SEDIMENT DIAMETER (PHI) MELKBOSSTRAND

Figure 8.24 Relationship between distribution of *Urothoe grimaldii* and mean sediment diameter at Melkbosstrand

These results show that there are two types of animal-sediment interactions to be found on intertidal sandy beaches. The first type is where gross differences from beach to beach, or possibly in areas of markedly differing aspect and exposure on a single beach, actually affect the presence, absence, dominance or loss of dominance of species. In these cases it is chiefly the sand-grain diameters that exert an influence. A more subtle interaction is the shifting landward or seaward of whole intertidal zones because of the influences exerted by sediments on the microenvironments of macrobenthos. Here organisms have no choice available to them. The environmental conditions of the beach either permit a species to occupy that beach, or they do not. This type of relationship in intertidal areas has been observed by Vader (1965), Withers (1977), Bloom *et al.* (1972) and Seed and Lowry (1973).

The second type of animal-sediment interaction occurs within individual beaches. In this case, the colonizing organisms on a beach are able to select sediment characteristics that vary over a comparatively small range and also within a relatively small area, easily covered by the highly mobile beach fauna. But it should be stressed that the selection of this second type of characteristics is of no immediate or short-term survival importance. Rather, it is over the longer term that such selection may give organisms the edge over competing individuals or species.

The latter type of animal-sediment relationship has not been described before for an exposed or high-energy beach. It is interesting to note that Grange (1977) in his study of animal-sediment relationships on the intertidal flats of Manakau Harbour, New Zealand, found that deposit feeders favour the finer sediments, carnivores and scavengers prefer the intermediate grades, while suspension feeders are more abundant in coarser sediments. This had been found previously in sub-tidal sediments by a number of workers, including Sanders (1958, 1960), and Young and Rhoads (1971). Grange found that in the intertidal zone, the preferred grain size of suspension feeders was 1,90 phi, rather coarser than had been found for subtidal benthic communities. The most important suspension feeder on west coast beaches, both in terms of numbers and biomass is *Donax serra* and in both finer grained beaches, no sediment preferences were observed. At Rocherpan, coarser sediments of 1,44 phi were preferred, although sediments of 1,71 phi (i.e. approaching Grange's optimum diameter) were available within the zone occupied by *Donax*.

On the other hand, on the occasion that this data was collected, both biomass and numbers of *Donax* were higher at Melkbosstrand, where grain size was 2,10 - 2,30 phi, than at Ysterfontein where the sand was finer (2,35 - 2,40 phi). This would be in agreement with Grange's findings.

The difference in optimum grain size for deposit and suspension feeders found by Grange was also apparent on west coast beaches. Densities of the deposit or detritus feeder *Scolelepis squamata* were higher at Ysterfontein (where sands of 2,40 phi were occupied) than at Melkbosstrand (2,30 phi). Grange (1977) calculated the optimal grain size for deposit feeders as 2,60 phi. Grange's optimum of 2,40 phi for scavengers and carnivores may apply to *Eurydice longicornis* which usually occurred in greater densities at Ysterfontein than at Melkbosstrand, although not on the occasion that the samples under consideration were collected. It does not apply to *Excirolana natalensis*, however, as has been discussed earlier, and no difference was noticed in densities of *Pontogeloides* on the two finer beaches, although this species was considerably less numerous at Rocherpan.

Conclusions

This chapter describes two different types of animal-sediment interactions. The first of these consists of the relationship between the whole beach (i.e. the gross characteristics of the beach sediments) and the organisms that colonize it. The second type involves sedimentary characteristics on a lesser scale that occur within a beach and which present colonizing organisms with limited choices.

Not all organisms were found to be affected by sedimentary characteristics within the range found on the beaches studied. The majority of the species did, however, show a relationship with the sediment of at least one of the two types, and these relationships have been described.

CHAPTER 9

BIOGEOGRAPHY

Introduction

The chapter on zonation (chapter 4) has already shown that particular types of animals can successfully colonize intertidal sand only within a range of environmental conditions and that this gives rise to characteristic intertidal zonation patterns. Since individual species also have restricted geographical distributions, the value of any ecological study decreases successively as it is applied to new sites more and more distant from the original site.

Fortunately, there is a way in which such effects can be minimized. On the crudest level, the earth can be divided latitudinally into a number of climatic regions, such as polar, temperate and tropical zones. Since organisms are adapted to their environments, one could not expect a specific result obtained from a polar region to hold true in the tropics, although it might be reasonable to expect a similar result at another polar site.

The environments inhabited by intertidal animals are much more subtle than the above crude climatic divisions. While temperature is generally regarded as the most important parameter determining distributions of marine organisms (Vermeij, 1978), the general latitudinal distinction between temperature regimes is often modified locally. For example, the west coasts of Africa and South America are washed by cold, northward-flowing currents that lower temperatures to such an extent that the distributions of temperate species extend well into the tropics.

Other natural constraints affecting the distribution of marine organisms in general are land barriers and salinity. In addition, benthic organisms are influenced by depth and type of substrate, as well as geographic barriers. Sandy beach animals are also affected by exposure, desiccation and other stresses imposed by tidal cycles. Any study of sandy beach faunal distributions that is based on the assumption that environmental factors affect distribution, must take the above factors into consideration.

One further factor is that species colonizing new sites can only do so provided that they can compete successfully with other, already resident species (Vermeij, 1978). Thus the distribution of a species can be limited by the presence of another species occupying a similar niche in adjacent areas.

The histories of the above-mentioned distributional barriers are of some importance as well, since these can account for many apparent paradoxes in biogeography. The isthmus of Panama, for example, has not been in uninterrupted exitence long enough (3,5 million years - Woodring, 1968; Saito, 1976) for taxonomically significant morphological differences to have developed between Atlantic and Pacific populations of the sand beach isopod *Excirolana braziliensis*. The same applies to a large number of molluscan species (Vermeij, 1978).

Biogeographers recognize a number of biogeographical provinces or regions in which the species assemblage of a particular environment remains relatively constant. This will define the limits within which an ecological study has the greatest relevance. Regions with similar or equivalent species assemblages will be valuable for comparative purposes, showing what sort of results might be expected from a similar system. Finally, a comparison of results from completely separate and different biogeographical provinces will place these into perspective relative to each other, from which a greater understanding of both systems and their differences may follow.

This particular study started with the purpose of mapping known distributions of the species found on South African west coast beaches. The next point of interest was to identify the factors controlling these distributions. Finally, it was decided to test the hypothesis of Bretsky and Lorenz (1970). This was based on a large body of evidence suggesting that environmental variability regulates genetic variability, and on Sanders's (1968) differentiation between physically-controlled communities with low species diversity and biologically accommodated communities with high diversity. Bretsky and Lorenz proposed that environmental stability promotes selection for homozygosity, i.e. genetic diversity is reduced. Heterogeneous and "unpredictable" environments would support species with a high genetic variability, as insurance for species survival. Long-term selection for homozygosity would lead to fine adjustment into specialised niches, but would also increase the vulnerability of species or populations to large-scale or local environmental changes respectively, thus leading to extinction of species or isolation of populations.

Since phenotypic differences usually express genotypic differences, it can be assumed that species described on taxonomic bases such as structures of mouthparts, shapes of appendages, etc. are genetically different to other, similarly described, species. Although certain features occasionally used by taxonomists may be environmentally induced; these usually have a genetic background as well (M. Picker, pers. comm.). Furthermore, since sandy beach genera tend to specialize for particular intertidal zones, and the intertidal area itself represents a very substantial environmental gradient, it was felt that a study of these genera, occupying as they do environments of different degrees of stability, would provide an ideal opportunity for substantiating or refuting the hypothesis put forward by Bretsky and Lorenz.

Such an approach would also provide considerable insight into the mechanics of speciation of benthic intertidal organisms, and from this into present-day distributions and diversities.

Methods

Total species lists for each of the genera found on sandy beaches on the west coast of South Africa were compiled and their distributions were drawn up after an extensive literature survey using Biological Abstracts and the Zoological Record back to 1864. The genera studied are listed in Table 9.1.

Where possible, the habitat occupied by the species was also noted. From hydrographic tables and world temperature and salinity charts, sea surface temperature and salinity values were collated. Mean monthly data were used, since monthly maximum and minimum values were not available for all areas. It was nevertheless felt that the range of mean monthly values would give some indication of actual ranges experienced by intertidal organisms. Air temperatures were not used since their effect on animals would vary firstly according to zonation, secondly according to local humidity and thirdly according to aspect and exposure of beaches. While air temperatures may be very important, it would require detail several orders of magnitude greater than is available for a study of this nature.

A number of environmental data characteristic of coastlines were added to this information. These were: annual precipitation, annual solar radiation, degree of prevalence of frost and tidal ranges, all within the distribution ranges of the species under consideration. Values for these categories were obtained from Davies (1972). In addition, the distributions were expressed in terms of latitudes and in terms of approximate extent of range in kilometres. When the genera were compared with each other, the number of species per genus and the percentage of species per genus occurring in Ekman's major biogeographic provinces (see Hedgpeth, 1957 for map) were also noted.

Similarity analysis was carried out on both species within genera and on the genera as entities themselves, using a computer programme that employs a Bray-Curtis similarity matrix. The values were all log-

TABLE 9.1 List of genera found on South African west coast beaches and the number of species per genus

Phylum/Sub-Phylum	Class/Order	Genus	Number of species per genus
Crustacea	Isopoda	*Tylos*	21
		Eurydice	35
		Excirolana	17
		Pontogeloides	2
	Amphipoda	*Pseudharpinia*	12
		Talorchestia	44
		Urothoe	32
	Mysidacea	*Gastrosaccus*	37
	Cumacea	*Cumopsis*	7
		Austrocuma	1
Mollusca	Gastropoda	*Bullia*	29
	Bivalvia	*Donax*	89
Annelida	Polychaeta	*Nephtys*	96
		Sigalion	16
		Scolelepis	27
Nemertea	Heteronemertea	*Cerebratulus*	93

transformed in order to even out the weighting between types of data consisting of low numbers and those with high values. The similarity analysis does not actually compare genera and species - rather it compares the environments that support them.

Certain reservations exist about the methods outlined above, and these should be borne in mind when considering the results. Firstly, distribution records are extremely patchy and incomplete. Certain areas such as western Europe, the United States, India and South Africa have been relatively well studied while very little data exists for areas such as China, Indonesia, Australia and large parts of South America and Africa. Secondly, the assignation of a species to a particular genus is often highly subjective. There is considerable debate among taxonomists as to the status of many species, especially among the polychaetes, but also among the other groups. Depending on the taxonomic view taken, the total number of species in a genus can fluctuate widely; where debate currently exists, the wider view was always taken in this study, since it was felt that even if some genera were actually complexes of genera, there must nevertheless exist a high degree of relatedness within those complexes.

A third problem is that the very existence of some species is doubtful. Species described from the 19th and early part of the 20th centuries were often so poorly characterized that it is sometimes impossible to identify them on the basis of modern taxonomic keys, especially in cases where the type specimens have been destroyed or lost.

Finally, it should be noted that certain groups have always been more popular among taxonomists than others. The reasons for this are many and include aesthetic appeal (molluscs), durability of identifiable features (molluscs and crustaceans), presence of taxonomically useful morphological features and size. Groups possessing one or more of these attributes have been relatively well studied. Fashions in working on various groups has also resulted in disproportionate attention being devoted to certain groups and this has been further complicated by the steadily increasing shortage of taxonomists in general.

While more and better data would be desirable in a study such as this, the best use must be made of what is available. As taxonomic and biogeographical knowledge improves, numbers of species will probably increase tne distribution ranges will certainly do so. Thus the results and conclusions that follow are based on a present minimum, which, with time and further study, can only improve in both quality and extent.

Results and Discussion

Table 9.1 shows the total number of species assigned to each genus. It can be seen that there is considerable variation in these numbers. The actual references and distributions for each species can be found in Appendix 2. The genera may cover a wide range of intertidal zones, but they can be divided essentially into three categories. These are: (1) Terrestrial genera (*Tylos* and *Talorchestia*); (2) intertidal and nearshore genera (*Excirolana, Pontogeloides, Cumopsis, Austrocuma, Scolelepis, Eurydice*); (3) genera to which the intertidal zone only represents the landward edges of their distributions (*Pseudharpinia, Urothoe, Gastrosaccus, Bullia, Donax, Nephtys, Sigalion* and *Cerebratulus*). Categories (2) and (3) could also be defined as follows: genera in which the majority of species are found intertidally and genera in which the majority of species occur subtidally, respectively.

The inclusion of *Donax* into the latter category requires a certain amount of explanation, since many of the species are truly intertidal. There are, however, many subtidal species and, in addition, many of the intertidal species spend only a part of the life cycle intertidally. Thus, in *Donax serra*, it is the juvenile stages that are intertidal (see chapter 4).

Finally, most of the tropical intertidal species migrate up and down the beach following the tides, which means that they must remain in the swash zone whatever the state of the tide. Although *Donax* does not entirely fit into category (3), therefore, this is nevertheless a more suitable category for this genus than (2).

As can be seen from Table 9.2 genera in category (3) consist of many more species than do those in category (2). Even in Monod's (1930) view is taken that *Pontogeloides* is a sub-genus of *Excirolana*, and

TABLE 9.2 Mean number of species per genus for three categories of intertidal sandy beach genera

where: (1) = Terrestrial genera; (2) = Intertidal and nearshore genera; (3) Sub-tidal and offshore genera

Category	Constituent Genera	Mean number of species per genus
(1)	*Tylos, Talorchestia*	33,0
(2)	*Excirolana, Pontogeloides, Eurydice, Scolelepis, Cumopsis, Austrocuma*	14,8
(3)	*Pseudharpinia, Urothoe, Gastrosaccus, Bullia, Donax, Nephtys, Sigalion Cerebratulus*	50,5

Austrocuma is omitted because it is only recently described and consists of a single species at present (Day, 1978), the mean number of species per genus in category (2) is 22, less than half the value for category (3). The difference between the means of these two categories is significant at the 95% confidence level.

Levinton (1973) and many other workers have investigated genetic variability in marine invertebrates from a wide range of environments. The evidence obtained suggests that environmental variability regulates genetic variability and this evidence led Bretsky and Lorenz (1970) to propose the hypothesis discussed earlier. The results listed in Table 9.3 lend substantial support to their theory. The genera of category (2) all experience desiccation and environmental variability vastly greater than do the animals of the third category. The first category could itself be subdivided, since *Tylos* live exclusively in the supratidal fringe and backing dunes (Roman (1977) calls *Tylos* a halophilous genus) and therefore occupy a region of considerably greater environmental variability and unpredictability than do *Talorchestia*, a genus including many truly terrestrial species (Hurley, 1968). Twice as many species of *Talorchestia* as *Tylos* have been described to date.

The number of species per genus in the above categories is important because, according to the hypothesis of Bretsky and Lorenz, the number of species in a genus is partly a function of the environmental stability which that genus enjoys. It can be safely assumed that all genera of more than a single species are derived from a single species - i.e. they are not of "polyphyletic" origin. The division and diversification of that single species into the constituent species of a genus as we now find it would therefore, according to the hypothesis, depend in part on the degree of environmental stability that the original species encountered. Species living in a stable environment would be more vulnerable to localized environmental disruptions resulting in local extinctions and isolation of populations. These isolated populations would then adapt to environmental

Table 9.3 Showing the effects of environments of different degrees of variability on the number of species in various taxonomic groups

Taxon	Number of species per genus (mean)		
	Category 1	Category 2	Category 3
Crustacea	33	12,4	27
Polychaeta	-	27	56
Amphipoda	45	-	22
Isopoda	21	18	-

conditions specific to the area they now occupy, and eventually evolve into distinct species. Thus an original species with a relatively wide distribution, could eventually give rise to a large number of localized species, each adapted to local conditions.

A "founder" species occupying a zone of considerable environmental instability, on the other hand, would be far less vulnerable to localized disruptions in its distribution, since the species would have had a high degree of heterozygosity in the first place, in order to cope with its unstable environment. This species would, therefore, possess a greater degree of genetic flexibility than the homozygous "founder" species from the stable environment with the result that, firstly, the distribution of the species is less likely to become fragmented resulting in isolation of populations, and secondly, even in the event of such interruptions, the species will have a greater ability to recolonize the decimated areas, thereby renewing contact with temporarily isolated populations.

For these reasons, relatively long-established genera would be expected to consist of a large number of species if inhabiting a relatively stable environment, and of a lower number of species if occupying a more diverse one. Similarly, the distribution ranges would be expected to be greater in the case of the heterozygous genera.

It could be argued that speciation rates might differ from one phylum or group to another. While there is no evidence to suggest this (palaeontological records are usually a function of the morphological suitability of the group to fossilization), it is a factor that should be borne in mind. Table 9.3 lists the within-group differences in the number of species per category.

These results merely show trends since in several of the above cases only single genera are involved. The trends are not substantially different to those shown previously, however, and it can be concluded that although there may be slight differences in the degree to which the environment influences speciation rates in various taxonomic groups, the general trends remain the same.

The environments occupied by the 14 genera investigated in this study varied to a certain extent. If the number of species occupying arctic, northern cold temperate, northern warm temperate, tropical southern warm temperate, southern cold temperate and antarctic zones are plotted, then the distribution is as shown in Figure 9.1. The only genus that does not occupy any of the northern zones is *Bullia*. The reason for this is that its distribution is confined to the northern, western and south-western Indian Ocean, with three species also extending up the west coast of South Africa, possibly as far as Angola.

All the other genera appear to have penetrated both hemispheres, and most are evenly distributed in these hemispheres. Only two of the genera studied have penetrated into both arctic and antarctic environments, however. The genus *Urothoe* shows an uneven distribution between the hemispheres and its distribution is of interest. According to Bousfield (1970), this is one of the more primitive groups of the Haustoriid amphipods, and, although it probably originated in the northern hemisphere, along what now is the coast of North America, it has been gradually displaced from that region by more effectively adapted amphipods of the sub-family Haustoriinae. While this replacement has been taking place, the genus has spread into the southern hemisphere, with the result that there are now more species there than in the north.

The genus *Bullia* has apparently not spread far from its centre of origin as yet. Most genera in Figure 9.1 have the greatest proportion of their species in tropical environments, a fact that would be expected from classical studies on diversity as related to environment. The actual values, however, vary considerably from one genus to the other. *Donax* and *Bullia* have 52 and 50% of their species occupying tropical environments respectively, but the other genera showing this type of distribution have considerably lower proportions of tropical

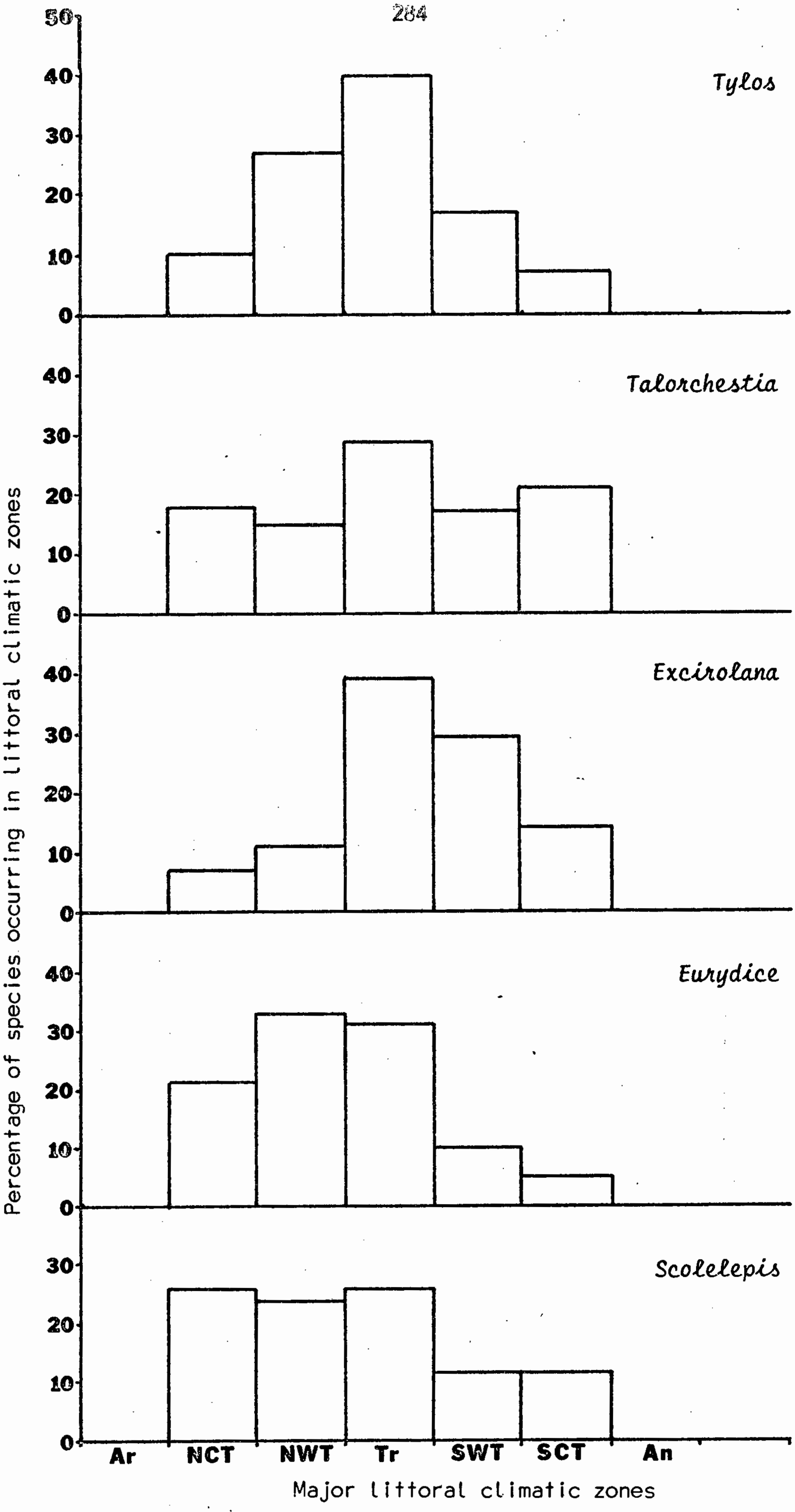


Figure 9.1 Distribution of species of the sandy beach genera found on west coast beaches in the major littoral climatic zones of the world.

Ar = Arctic; NCT = North Cold Temperate; NWT = North Warm Temperate; Tr = Tropical; SWT = South Warm Temperate; SCT = South Cold Temperate; An = Antarctic.

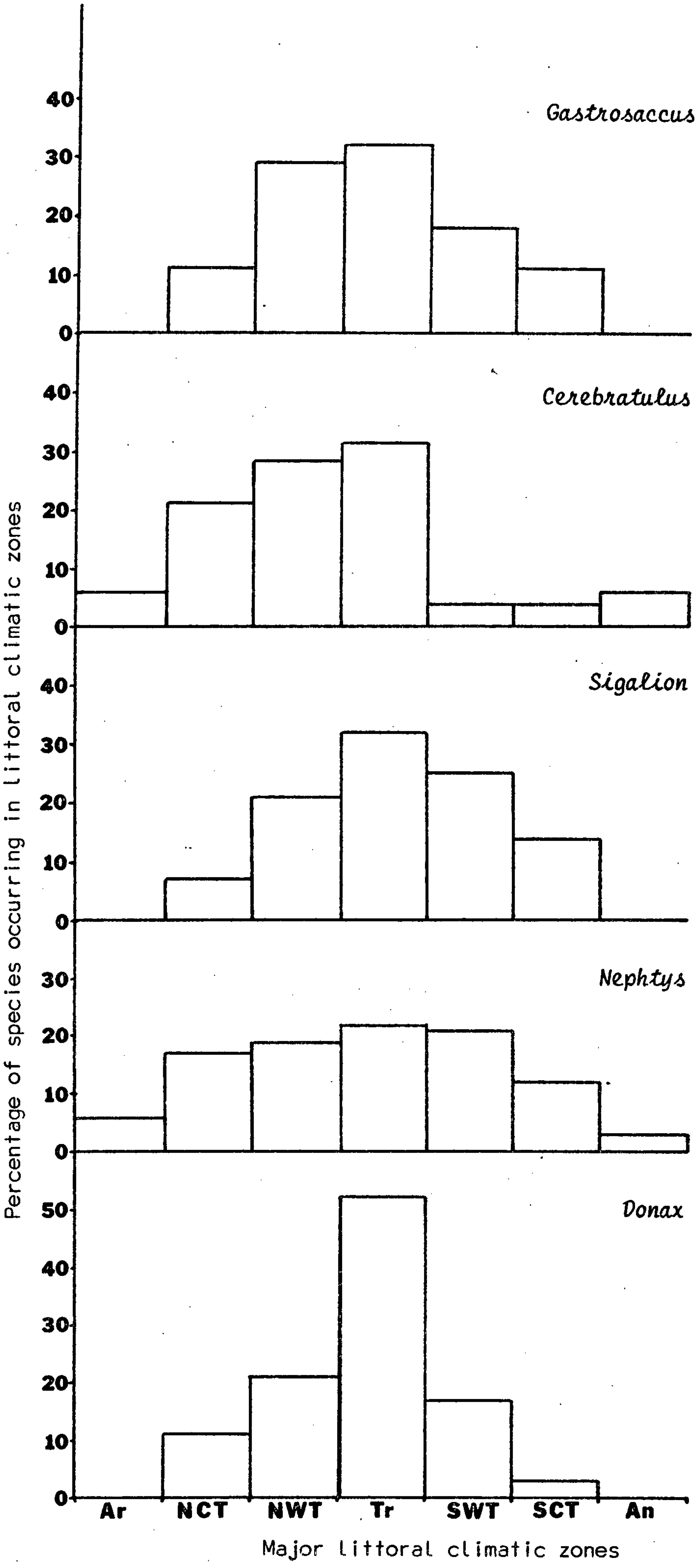


Figure 9.1 (contd.)

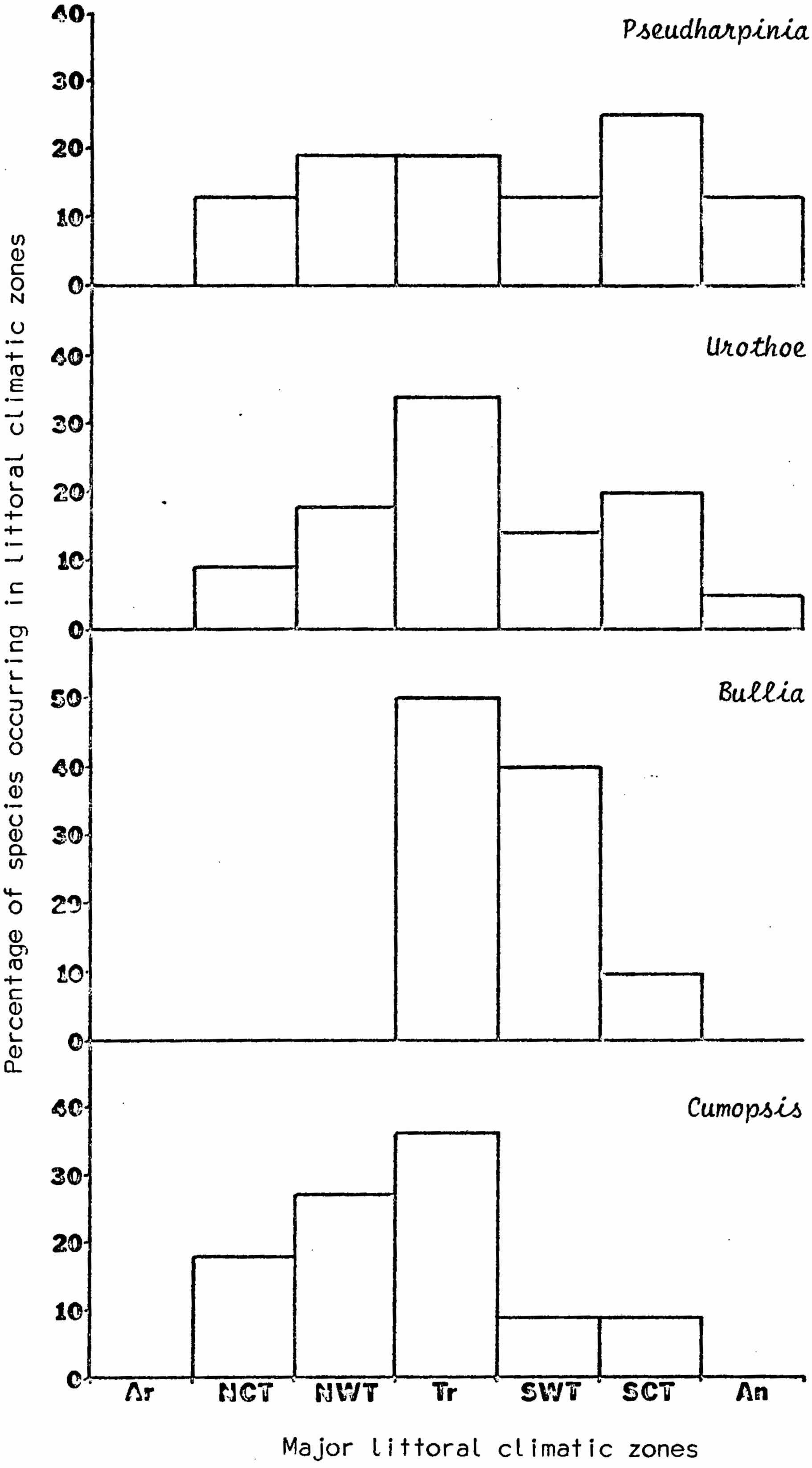


Figure 9.1 (contd.)

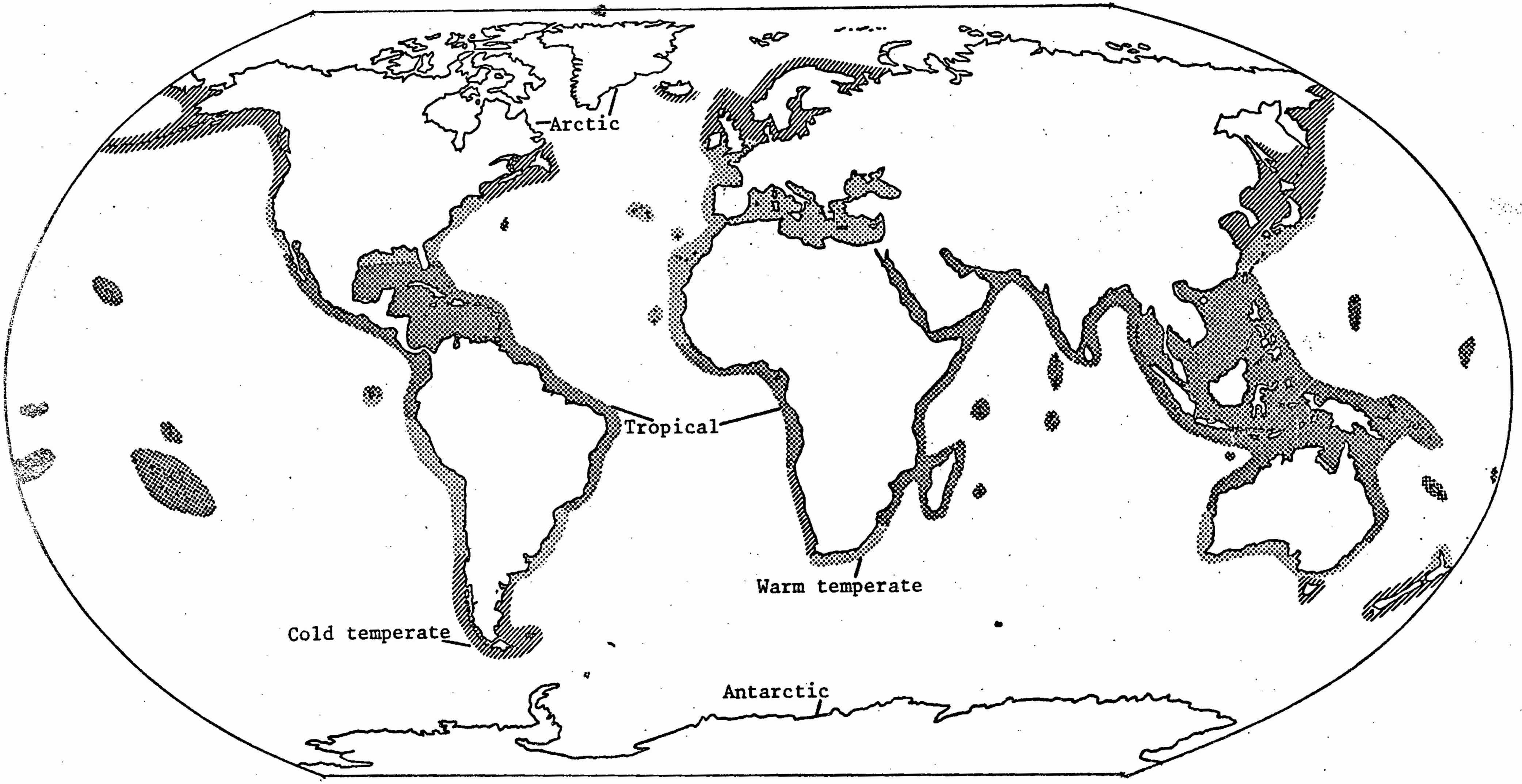


Figure 9.2 Distribution of major littoral provinces of the world (after Hedgpeth, 1957).

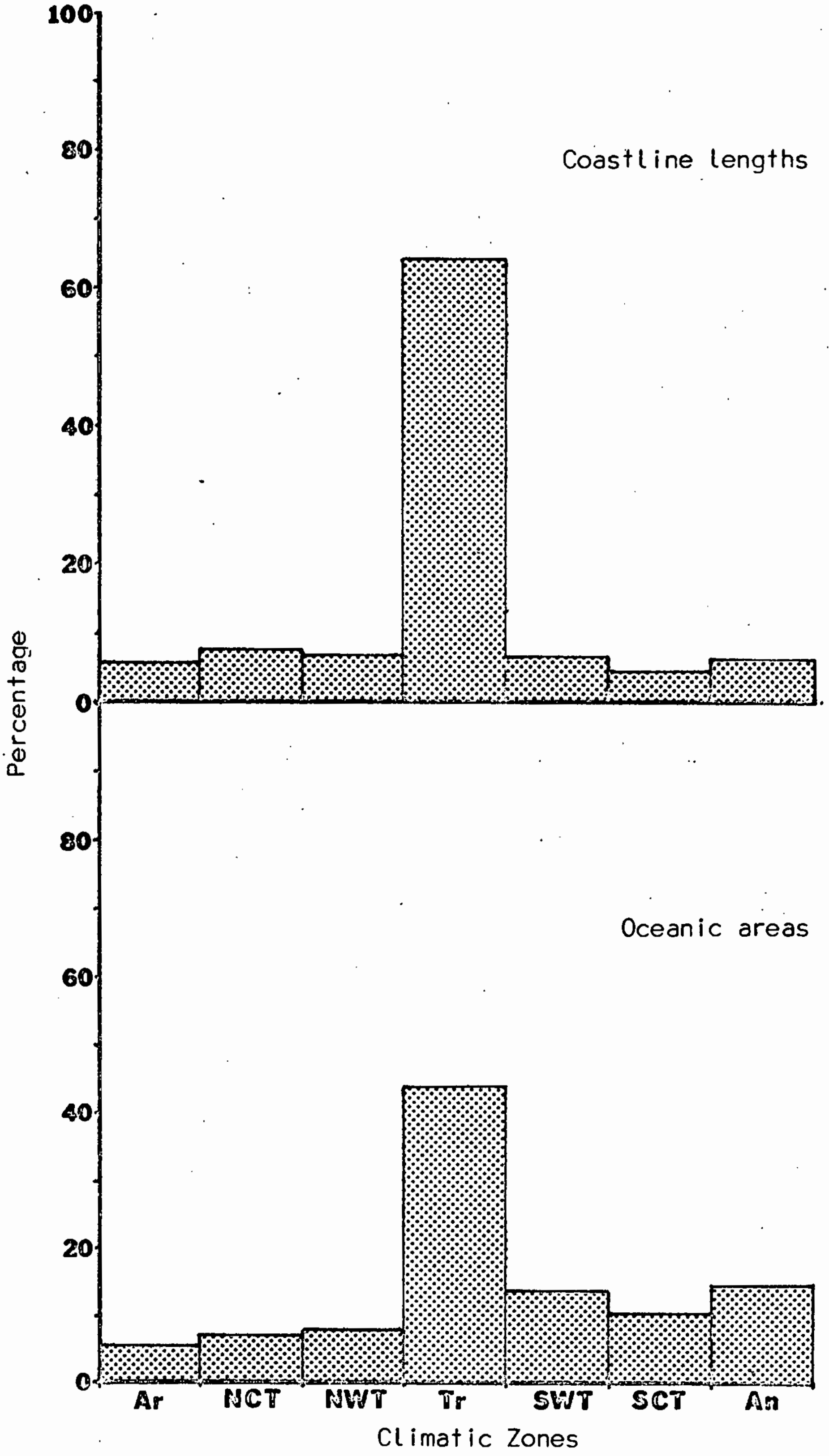


Figure 9.3 Relative distribution of total coastline length and oceanic areas in the major climatic zones of the world. Abbreviations as for Fig. 9.1.

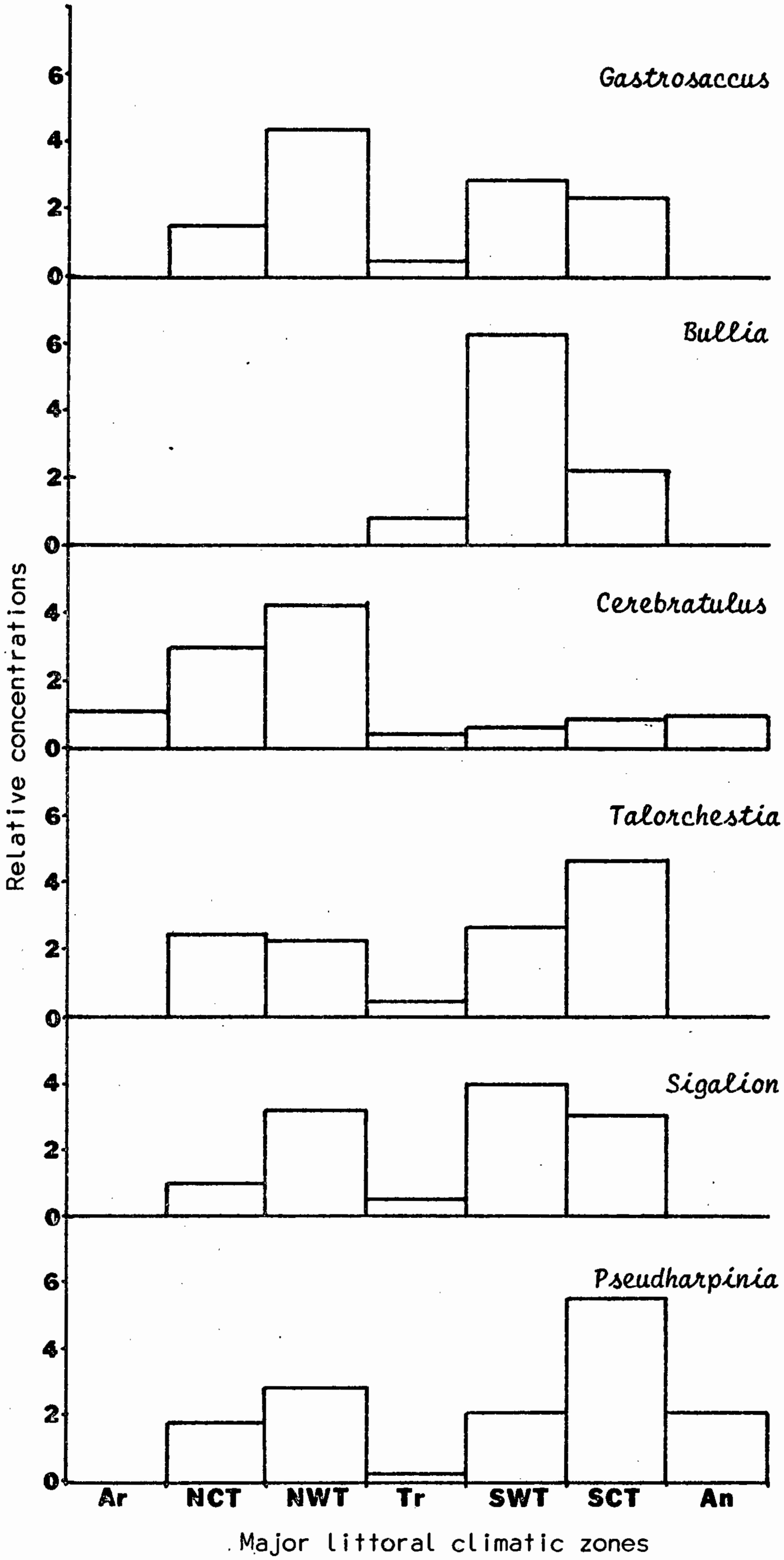


Figure 9.4a · Relative concentrations of species per length of coastline in major littoral climatic zones. Concentrations calculated as ratios of percentage species to percentage length of coastlines. Abbreviations as in Fig. 9.1.

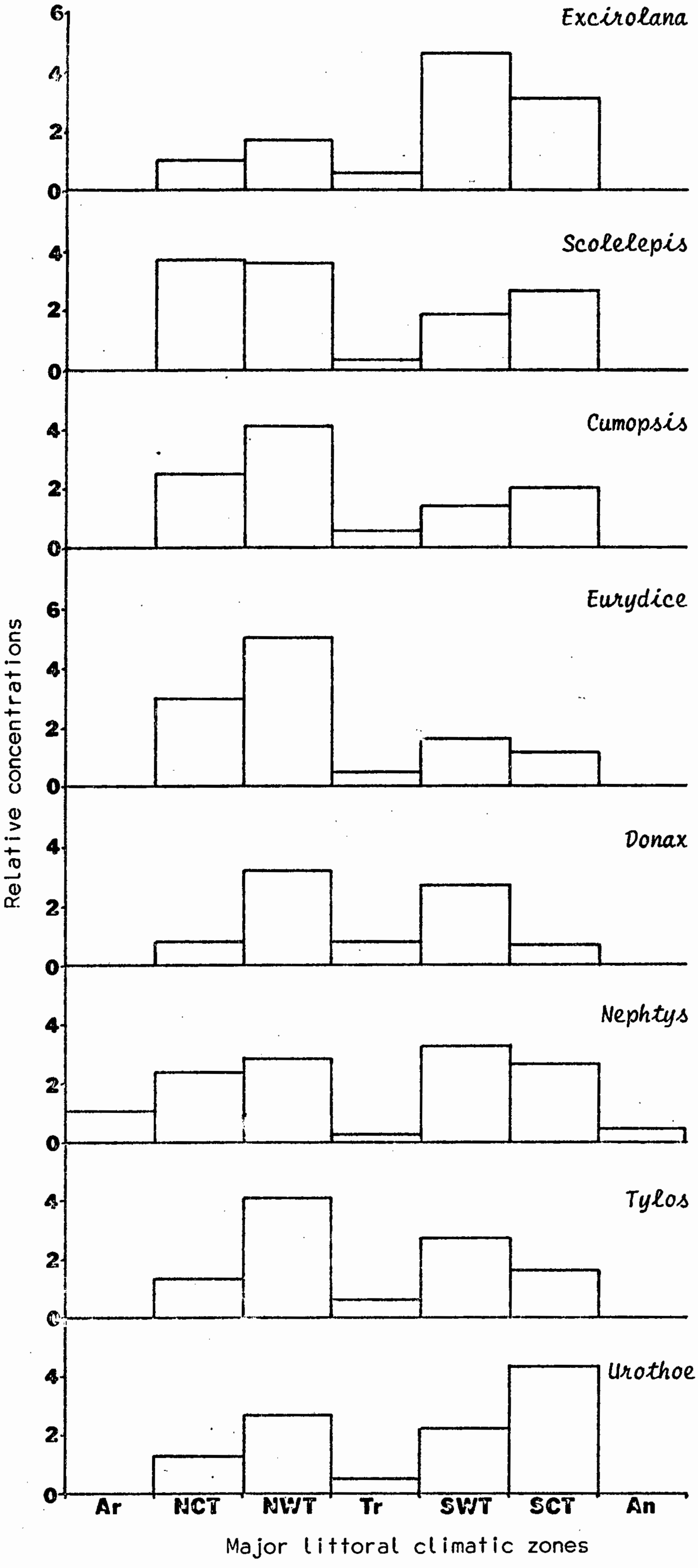


Figure 9.4a (contd.)

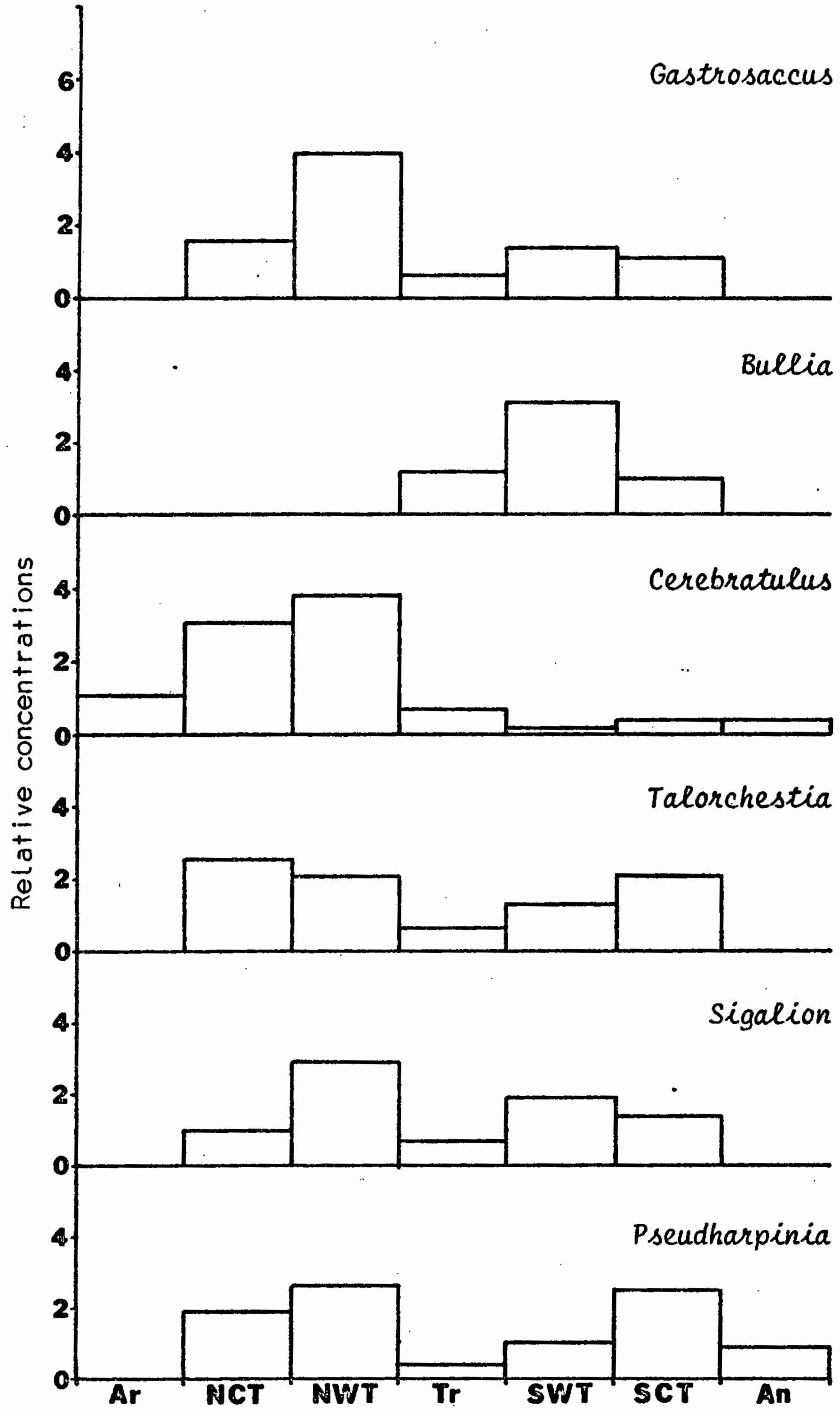


Figure 9.4b Relative concentrations of species per area of ocean in major climatic zones. Calculations as for Fig. 9.4a.

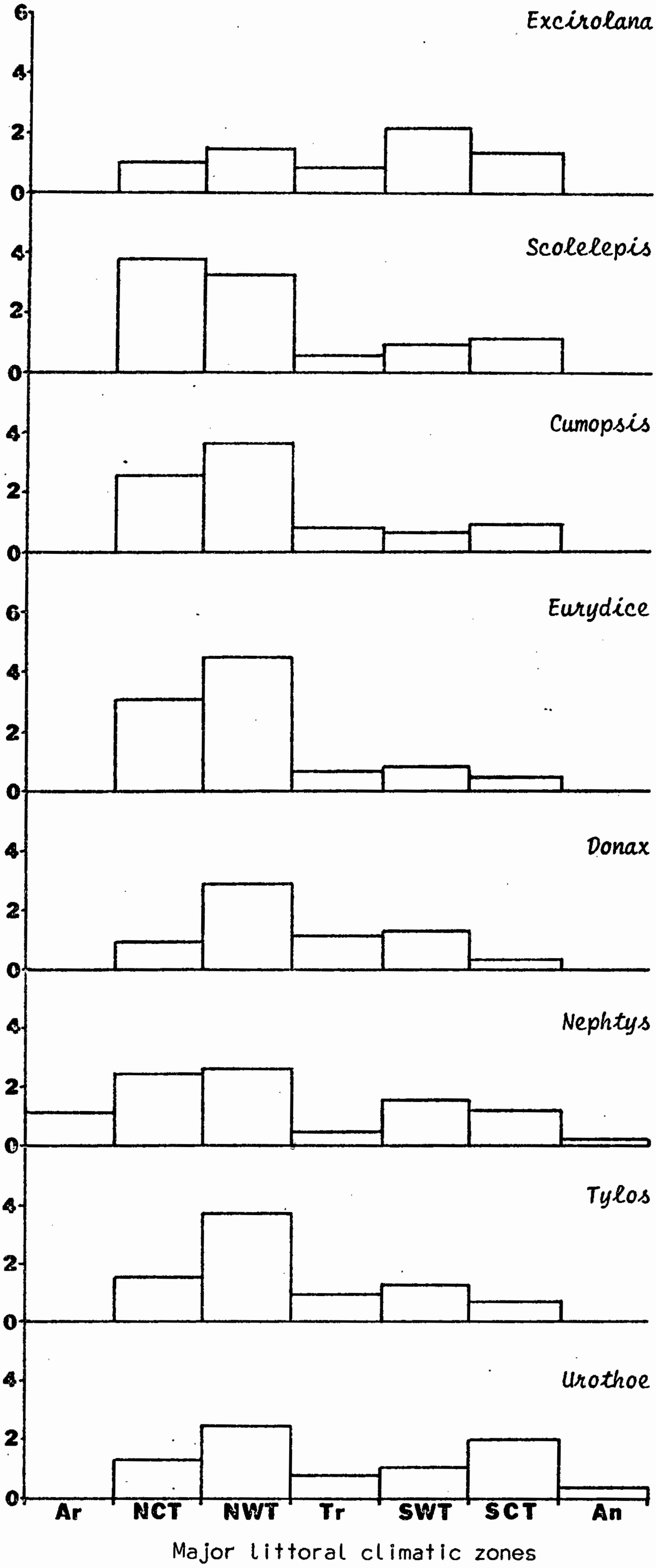


Figure 9.4b (contd.)

species. These are as follows: *Tylos* - 40%; *Excirolana* - 39% *Cumopsis* - 36%; *Urothoe* - 34%; *Gastrosaccus* and *Sigalion* - 32% *Cerebratulus* - 31%; *Talorchestia* - 29%; *Nephtys* - 22%. Tropical oceans and coastlines, however, both constitute over 40% of the total oceanic surface and coastlines of the world.

Thus only *Donax*, *Bullia* and possibly *Tylos* and *Excirolana* show any concentration of species in the tropical areas. The genus *Pseudharpinia* has its distributional focus in southern cold temperate latitudes, which are occupied by 25% of its species and in northern cold temperate regions (19%). *Eurydice* is concentrated in northern warm temperate environments (33% of its species), while *Scolelepis* is concentrated in northern cold temperate zones (26% of its species).

Figure 9.2 shows the distribution of the various zones described above (modified from Hedgpeth, 1957). Figure 9.3 shows the approximate percentages of the total world coastline and oceanic area in each zone. If Figure 9.1 is compared with Figure 9.3 the distribution of the genera studied in relation to the length of coastline and oceanic areas can be better understood. The ratios of percentage species to percentage coastlines and percentage of oceanic area are listed in Figure 9.4 and heighten the differences in distributions between these zones.

The reason both coastline length and oceanic areas have been plotted in the latter figure, is that certain species are associated with coastal environments, while others may be associated with abyssal ones. The results are essentially similar in both cases, however, although the actual values do differ slightly.

The most notable feature of Figure 9.4 is that none of the genera under consideration have undergone increased speciation in tropical areas. In fact, the majority of genera, show lower diversity in the tropics than in any other zone except the arctic and antarctic. It is always the temperate zones that show the greatest diversity proportional to area.

While this result is unexpected, it should be remembered that all the genera studied have species occurring in the cold temperate west coast of South Africa. There is thus a certain amount of bias towards the above finding. All these genera, therefore, show a marked degree of bipolarity, a common feature in genera adapted to temperate zones (Hedgpeth, 1957).

The results of the cluster analysis on species within genera, show findings similar to those described above, although finer sub-divisions of the climatic zones are apparent.

Figure 9.5 shows the results of the cluster analysis on the genera. Most notable is ***Bullia***, which has the lowest similarity to the other genera, largely because all its species are concentrated within a relatively small area, with comparatively little environmental variation. In fact, ***Bullia*** has the greatest concentration of species per unit area or unit of coastline of all the genera studied.

Nephtys and ***Cerebratulus*** show considerable similarity in the environments they occupy - both have worldwide distributions in all climatic zones. In the same way, ***Pseudharpinia*** and ***Urothoe*** are clustered together, since both genera are mainly distributed in the southern hemisphere and both extend into antarctic zones. Aside from these groupings, little additional information is yielded by the cluster analysis.

Although these results do not confirm Bretsky and Lorenz's hypothesis irrefutably, they do lend it considerable support. Perhaps the main criticism of both their hypothesis and that of Sanders (1968) is the use of the term "stability". A considerable amount of recent work has in fact shown that localized instabilities and disturbances may actually enhance diversity in an ecosystem. The general tenor of these recent findings has been that regular localized disruptions can result in the removal of a dominant species from a small area, giving the opportunity to less-successfully competing species to

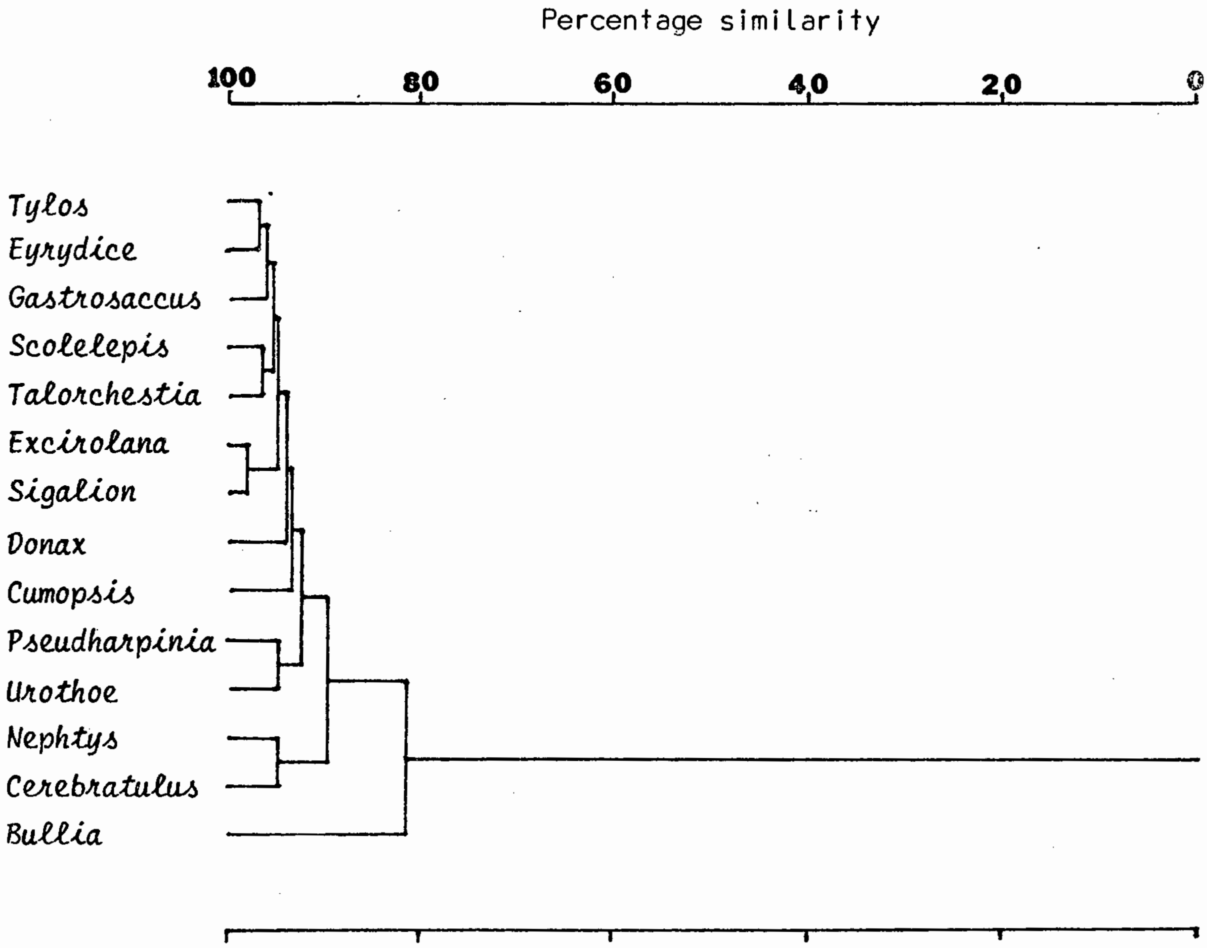


Figure 9.5 Cluster analysis on the environments occupied by the sandy beach genera studied.

settle and reproduce before being once again eliminated from that area by the dominant species. It has thus been argued that environmental instability actually promotes diversity and that Sanders's concept of the interaction between environmental stability and diversity is incorrect (see Dayton, 1971; Dayton and Hessler, 1972). This, however, is only because two independent meanings are being supplied to the term "stability".

On the one hand, Sanders used the word to denote a constant environment, in other words, the opposite to the type of environment where huge fluctuations of temperature, nutrients, etc. occur which result in sudden, short-lived blooms of organisms. The other sense in which stability has been used is to impart a condition of environmental placidity, peace and complete constancy. In this sense, wave-driven logs or storms which dislodge small colonies of a dominant species of barnacle from the intertidal zone are symbols of instability, and it is this instability which increases diversity, since it provides settling spaces for non-dominant species.

Perhaps a better term is needed to denote both these types of stability. A word expressing environmental regularity or predictability is required. The non-dominant species in the above example, after all, survive only because patches of dominant organisms are cleared by localized instabilities with sufficient regularity to enable generation after generation of non-dominant organisms to settle and reproduce. Since "environmental predictability" is a rather anthropomorphic term with teleological implications, I would suggest that "environmental regularity" be adopted and substituted for the word "stability" in Bretsky and Lorenz's hypothesis.

It should be stressed that regularity is not a term designed to apply only to areas such as intertidal zones, which Bretsky and Lorenz termed a "stable and rigorous" environment. The sequence of events described above can and does occur in non-rigorous environments such as coral reefs as well (Day, 1977).

Sandy beaches show both predictable and unpredictable environments. The macrofauna of high energy sandy beaches, however, generally enjoy a much less regular environment than does that of rocky shores. The reason for this is that sandy beaches themselves are not stable structures. Brown (1971a) mentions that certain beaches on the west coast of the Cape Peninsula may disappear completely in winter. While the beaches investigated in this study are permanent features of the coastline, they are nevertheless highly mobile environments. King (1951) has shown that up to 4 cm of sand may be removed by a single wave on high-energy beaches.

It is common knowledge that waves washing up shores are not regular in height and energy. Unusually high-energy waves normally occur several times an hour and these can deposit organisms high up the shore and, on a receding tide, leave them stranded for a considerable length of time. This undoubtedly occurs, despite the high mobility of the fauna. Those animals living high up the shore are particularly susceptible to such stranding, and it is to their advantage if they are able to tolerate a wide range of conditions, since extremes of desiccation and temperature are likely to be encountered while stranded.

Klapow (1972a) has shown that *Excirolana chiltoni*, living at the top of the shore, possesses extremely complex fortnightly moulting and reproductive cycles as well as a highly developed tidal rhythm. In chapter 6 it was shown that *E. natalensis*, also living at the top of the shore, had a substantially higher activity potential than did other cirolanid isopods living at lower levels. These facts indicate that animals living in less regular environments do evolve adaptations to these conditions.

The ability of a species to adapt to a varied environment or to a wide range of environments is not a function of a single set of genes that confers versatility to that species, it is rather a function of a wide range of genes extant within that species. Thus a wide genetic diversity within the species enables it to survive in an irregular environment.

The hypothesis put forward by Bretsky and Lorenz in 1970 caused a considerable amount of controversy, particularly those sections of it dealing with mass-extinctions. The main problem with the theory was the "lack of voluminous evidence" (Bretsky, 1973, p.157). Attempts to disprove the theory by Ayala *et al.* (1973) and Valentine *et al.* (1973) were considered inconclusive (Bretsky, 1973; Levinton, 1973).

Since then, further evidence has accumulated supporting both sides of the argument. Both Valentine and Ayala (1975) and Siebenaller (1978) found a relatively high degree of genetic variability in deep-sea environments that could be considered stable and non-rigorous in Bretsky and Lorenz's terms. Siebenaller does mention, however, that deep-sea organisms tend to be generalist feeders rather than specialized ones, suggesting that their food supply is irregular and varied at least, and perhaps that deep-sea environments are less regular for organisms than is assumed.

On the other hand, Levinton (1973) found differing genetic variabilities in molluscs from different depths and environments. Furthermore, Alexander (1979) reported differentiation of generic extinction rates in articulate brachiopods from the upper Ordovician-Devonian periods. Alexander attributed these differences to heterogeneity of the ecologies of the three taxa investigated. Narrow-niched reef genera had short longevities when compared with those of offshore non-reef genera.

There is no doubt that further conflicting evidence will yet be found. The evidence that does support Bretsky and Lorenz's hypothesis shows that the theory does explain certain events, while the other evidence highlights flaws and indicates that it is incomplete as it stands at present. The evidence presented in this thesis lends the theory a certain amount of support, but suffers from a paucity of genera and mainly a lack of ecological data on the species involved.

As is so often the case with problems of a biological nature, the information necessary for their resolution is largely lacking and researchers must content themselves with partial answers for the time being.

CHAPTER 10

SYNTHESIS

Sandy beaches as ecosystems

Sandy beaches are ecological systems that usually depend on imported carbon. Although some diatoms may be present and Wicks (1974) has reported the presence of the nitrogen-fixing bacterium *Azotobacter* on beaches in Florida, sandy beaches are generally poor in autotrophs. Thus beach food-chains are based on imported matter, rather than on carbon produced within the system. As a result, no direct grazers occur in sandy beaches; those herbivores that are found here feed on primary producers that have been imported from outside the system. These herbivores could thus be termed "herbivorous scavengers". This kind of primary consumer occurs within all three categories of organisms found on sandy beaches, i.e. macrofauna, meiofauna and microfauna.

The importance of the primary consumers on sandy beaches is thus directly dependent on the input of food into the beaches. On the west coast of South Africa, high energy beaches with both low and high primary producer inputs are found. Those beaches with a low input of such organic matter have been the subject of this thesis, while those with high inputs are found associated with kelp beds. Koop *et al.* (in press) have investigated the fate of stranded kelp on such beaches and have shown bacteria to be directly responsible for the mineralization of some 72-74% of the kelp beached. Although herbivores such as *Talorchestia* and *Tylos* consume considerable quantities of the kelp, as do the larvae of the kelp fly *Fucellia capensis* (Stenton-Dozey and Griffiths, 1980) much of this material is voided as faeces and is also consumed by bacteria. Bacterial carbon production is estimated at 26-28% of the beached kelp carbon.

Koop *et al's* figures indicate that bacteria are the major consumers on high primary producer input beaches. The role of bacteria on other beaches has yet to be investigated, but there is no reason to suppose that they are not important.

Two major differences are to be noted between these two types of beach, however. The first is the difference in inputs of organic material from primary producers discussed above. The second is the high biomass of primary consumers such as filter feeders and of secondary consumers on the low input beaches. As was shown in chapter 5, the carnivorous component constitutes up to 45% of the total biomass on these beaches, although it is usually in the region of 20%. While this is a high proportion, it should be stressed again that beaches are normally dependent on imported food and this applies to secondary consumers as well as primary consumers. The carnivores in fact double as scavengers on these beaches.

It is interesting to note that even some of the primary consumers (*Tylos* and *Talorchestia*) can and do feed on stranded animal material when this is available (Kensley, 1974; Muir, 1977). This high degree of opportunism is indicative of the unpredictability of the sandy beach environment for macrofauna. It also supports the idea of a system that is largely dependent on imported organic matter.

Work by Lewin and her colleagues on the chemistry and plankton of surf zones (e.g. Lewin *et al.*, 1975) has shown that cyclical blooms of phytoplankton (particularly diatoms) occur in certain circumstances. These surf-zone blooms appear mainly off sandy beaches as has been observed by both Gunter (1979) and McLachlan (1981). McLachlan has gone on to suggest that water circulation patterns off sandy beaches are sufficiently cellular to retain nitrogenous waste products excreted by beach fauna (see also McLachlan *et al.*, in press). The concentration of these waste products in the water is built up by the cellular circulation patterns until there is sufficient to produce a phytoplankton bloom. The phytoplankton organisms, both living and dead, form the bases of sandy beach food chains according to this hypothesis. McLachlan indicates that the above sequence of events is cyclical and occurs with sufficient frequency to maintain the entire ecosystem. While this pattern of events undoubtedly occurs wherever the conditions are suitable (such as along the northern coast of False Bay), no evidence of such cycles was encountered on west coast beaches. It would appear, therefore, that McLachlan's cyclical beach ecosystems are not the rule in sandy beaches. Indeed, beach macrofauna have not evolved any special forms to exploit such systems but have rather retained the ability to survive outside them.

On the three west coast beaches studied, kelp input was low and inshore circulation patterns did not appear to be cellular. These beaches thus appear to lie in between the types investigated by Koop and McLachlan, if they are classified on the basis of the origins of organic matter. The macrofauna is far more important in terms of both biomass and diversity than at Kommetjie, while the biomass is lower than was found on comparable Port Elizabeth beaches (McLachlan, 1977a, d).

Zonation on sandy beaches

As in the case of all organisms living between tide-marks, sandy beach fauna exhibit intertidal zonation. In this thesis four zones were demonstrated, corresponding to those described by Salvat (1964) and Pollock and Hummon (1971) on the basis of physical conditions. The subdivision of beaches into intertidal zones is only a convenient way of partitioning them into recognizable areas, since there are wide transitional areas between the zones. This is particularly the case in high energy sandy beaches where the fauna is mobile and indeed the zones themselves are mobile. All this mobility leads to a mixing of zones in the wide intermediate areas. Thus zones in the classical sense, of intertidal areas dominated by a few species optimally adapted to the environmental conditions found therein, are only evident in fairly narrow bands along the beach. On exposed sandy beaches, therefore, intertidal zonation as expressed by the macrofauna is made up of a gradual succession of one set of species by another along a gradient of physical conditions.

Although the zones shown by Pollock and Hummon (1971) have quite sharp cut-off points, these positions are only fixed at one particular moment. The zones migrate up and down the shore with the ebb and flow of tides and with the lunar tidal cycle. Since the macrofauna is mobile, it can follow these zones as they move up and down the beach (McLachlan *et al.*, 1979), thereby remaining in a relatively constant environment.

Adaptations of sandy beach organisms to the environment

In chapter 6 it was shown that closely-related isopod species from different intertidal levels showed adaptations in thier respiratory physiology appropriate to their intertidal zones of origin. This type of adaptation has already been shown in limpets (e.g. Branch & Newell, , 1978) on rocky shores, but it should be remembered that the majority of rocky shore organisms cannot follow the shifting tides. A greater degree of adaptation is required in rocky shore organisms, therefore, since each organism experiences what would constitute a range of intertidal zones to the mobile sandy shore animals. Of the sandy beach macrofauna, only *Scolelepis* is semi-sessile, and even these polychaetes can migrate up and down their burrows to follow the tidal cycles. McLachlan *et al.* (1977) have shown that meiofauna too, show a vertical migration in the sand in response to the lunar tidal cycle.

Most high-energy sandy beach organisms, therefore, have only been required to develop physiological adaptations of a relatively low degree, due to the particular physical nature of their environments. It is thus not surprising that cirolanid isopods, the dominant, most ubiquitous group on high-energy beaches worldwide, are also of the most primitive groups of isopods (Kussakin, 1973). These near-archetypal, scavenging isopods are in some ways the marine parallels of such primitive, omnivorous and unspecialized but highly successful and adaptable mammals, the opposums and rats. It is interesting that these mammals also become of great importance in disturbed, unpredictable environments.

There can be little doubt that sandy beaches constitute unpredictable environments even to the organisms that inhabit them. Some of the arguments for this are outlined in chapter 9, but there is one further factor to be taken into consideration. Excluding the dimension of time (a dimension which Klapow (1972a) and others have shown to be well-handled by beach fauna), sandy beach organisms live in a truly three-dimensional world. In their environment, these dimensions can be translated as: (1) depth burrowed into sand; (2) position occupied up the shore, and (3) position occupied along the shore.

While there are environmental cues enabling organisms to locate themselves in the first two of these dimensions, there are none for the last one. Indeed, long-shore currents and long-shore drift may cause entire populations to be washed off a beach and may account for the irregularity and frequent disappearance of populations reported by many workers.

Although there is considerable evidence that populations of sandy beach organisms can survive the effects of storms and hurricanes on their intertidal habitats (e.g. Croker, 1968; Saloman and Naughton, 1977; Yeo and Risk, 1979) despite the considerable damage to beaches and shore structures that accompany such events (Morton, 1976; Saloman and Naughton, 1977), I believe that the abovementioned longshore drift constitutes a much more insidious threat to the survival of populations of these animals. This drift could transport populations along the beach, possibly into areas that are less favourable for particular species and eventually right off the beach into hard shores.

It is difficult to imagine what environmental cues could be used by sandy beach organisms to detect their location in the longshore plane. The whole function of zonation is to permit organisms to select a particularly favourable environment, but the cues enabling animals to determine their intertidal position are virtually the same along the entire length of the beach. Different cues would therefore have to be used, such as sand grain size or degree of physical exposure. As was shown in chapter 8, however, there is patchiness or irregularity in the distribution of sediment characteristics along the beach so only major changes could be used as positional clues. Since the sediments themselves are mobile it is unlikely that such characteristics would be of value for this purpose. The degree of physical exposure is highly variable even at a single point along the beach because it is affected by the state of the tide and by the weather both inshore and offshore. Small organisms measuring at the most 8 cm in length (in the case of ***Donax***) would have no means of assessing the degree of exposure pertinent to their position along the beach. It thus appears that sandy beach organisms are not able to determine their along-shore positions.

A quotation from Gould's (1980) essay "Size and Shape" illustrates the problem involved in conceptualising microenvironments occupied by small animals in general:

> "We are prisoners of the perceptions of our size, and rarely recognize how different the world must appear to small animals. Since our relative surface area is so small at our large size, we are ruled by gravitational forces acting upon our weight.

> But gravity is negligible to very small animals with high surface to volume ratios; they live in a world dominated by surface forces and judge the pleasures and dangers of their surroundings in ways foreign to our experience". (Gould, 1980, p.173).

In chapter 8, it was shown that certain species have a distinct preference for particular grades of sand. The areas with the unfavoured sediments are, however, not devoid of organisms, they merely show lower concentrations. This may well be the result of circumstance such as a receding tide leaving individuals stranded in an area of less favoured sand. Such animals have no alternative but to cope with their new environment and it appears that they cope sufficiently well to survive. This may seem a contradiction of previous statements concerning the relative degrees of physiological adaptations undergone by rocky and sandy shore fauna. Random events such as stranding in areas of less favoured sediments may occur several times or even several dozen times in the lifetime of an organism. The ability to cope with such events is not a function of special adaptations but rather the reverse - a lack of specialization permitting the organism to remain a generalist.

This crucial distinction explains why, on rocky shores of the west coast of South Africa, there are some 80 common species of macrofauna and over 250 species altogether (McQuaid, 1980), while similarly exposed sandy beaches support only 15-20 species, and underlines a fundamental difference between the fauna of hard and soft shores. In any ecosystem, there are fewer niches for generalists than for specialists.

The biogeographical distributions of macrofaunal genera occurring on west coast beaches are examined in chapter 9 and the results of that study support the idea of sandy beach species being generalists. The relatively low numbers of species in the mainly intertidal genera as opposed to those of genera that are chiefly subtidal, indicates that sandy beach species tend to be "genetic generalists" as well. The apparent high degree of heterozygosity within these species may also be a consequence of the inconsistency of the sandy beach intertidal environment.

It was mentioned earlier that sandy beaches are dominated by fairly primitive, non-specialist groups such as the cirolanid isopods. In one part of the world, however, a more advanced group has appeared in recent geological time. This is along the east coast of North America, where haustoriid amphipods of the sub-family Haustoriinae have undergone adaptive radiation to a substantial degree and now occupy a wide range of filter-feeding niches (Bousfield, 1970). Bousfield notes that in the northern Gulf of Mexico, only one of ten species of this subfamily occurring there also occurs in beaches on the open Atlantic coast, while none of the other 16 Atlantic species are found in the Gulf. Since the intervening barrier (i.e. the Florida peninsula) dates only from the Pleistocene, Bousfield concludes that the species differences between these two regions have evolved over the last one million years.

This contrasts with the slow rates of evolution of species to either side of the Panama land barrier, which is at least 3 million years old. Here a considerable number of species, including members of the genera *Excirolana* and *Donax* have not diverged sufficiently to be considered morphologically distinct by taxonomists, despite noticeable differences in the Pacific and Caribbean marine environments (see Dexter, 1974, 1976).

The opportunity for adaptive radiation to take place in the Haustoriinae was probably provided by the development of the north Atlantic ocean from an estuarine basin, some 100 million years ago. This resulted in the isolation of the region from most competing crustacean types and adaptive radiation became possible as a consequence (Bousfield, 1970). Bousfield speculates that *Haustorius arenarius*, the only species of the group to have reached western Europe, may undergo adaptive radiation there, and eventually supplant more primitive groups along the eastern shores of the Atlantic as well. These developments, however, lie in the frustratingly distant future.

Factors influencing the distribution of beach organisms

The sedimentological studies discussed in chapter 3 show clearly that sandy beaches possess sedimentary characteristics that are intermediate to those of subtidal and supratidal sediments. Furthermore, these characteristics range from being very similar to those of subtidal sediments at the low water mark, to being very similar to the characteristics of dune sediments at the high water mark, and the transition between these two extremes can be observed across the intertidal zone. The very substance of sandy beaches, therefore, is affected by its intertidal position.

The relationships between sediment coarseness, beach slope and degree of exposure have often been misunderstood, and they are discussed in some detail in chapter 3. As a result of these interrelationships, it can be concluded that beaches of a given degree of exposure may be made up of either coarse or fine sand, depending on what is available. The slope will vary according to both the grain size and the energy of incoming waves; increasing grain size tending to result in steeper beach slopes, while increasing wave energy tends to flatten these, and at the same time favouring the deposition of sediments of increasing diameter. The degree of exposure also tends to affect the average size of the macrofauna that can settle successfully, as outlined in chapter 5. On exposed beaches there appears to be a lower size limit (which varies from species to species), below which organisms fail to remain in the sediment and are washed out to sea. Since this size limit increases with increasing exposure, the biomass of beaches is also affected by degree of exposure.

From a survey of beaches studied elsewhere, it appears that high energy beaches on the west coast of South Africa rank among the richest in terms of biomass and densities of macrofauna, possibly due to the nutrient subsidy that is provided by the Benguela upwelling system to the inshore waters of this coastline. As is usually the case, the meiofauna found in this study was considerably more important than the macrofauna in terms of biomass and production.

The distribution of organisms on sandy beaches has always presented a problem to investigators since the animals are not usually visible in their undisturbed natural environment. Because of the apparent uniformity of the sand surface, many workers have assumed equally uniform distributions of animals within the sand, although others have observed irregularities and patchiness in distributions. Chapter 7 shows just how prevalent and extensive this patchiness is, and emphasizes the dangers of biomass data based on results from single transects.

In chapter 8, some of the possible causes of this patchiness are discussed and it appears that different species are affected by different factors and criteria. These include exclusion from certain grades of sediment on the basis of structural limitations of the organisms, preference of certain sedimentary characteristics, competition, avoidance of areas of high predator concentrations, selection of areas of high prey concentrations and combinations of both these factors and zonation.

Further studies on patchiness need to be carried out before a complete understanding is achieved. These include the effects of sand humidity (which will partly reflect zonation) and measurements of interstitial oxygen and nutrients. Intensive studies over a period of several days would also yield information on the degrees of permanence and mobility of these patches.

With the present state of knowledge, however, it is possible to say that both sediment characteristics and macrofauna show irregular distributions superimposed on the basic zonational patterns described in chapters 3 and 4. In chapter 7, it was also shown that the composition of populations within species is irregular. Thus it seems that young animals of a species aggregate within an area that may be selected for its sediment characteristics, intertidal position or position relative to that of suitable prey or potential competitors and predators. As these cohorts grow, their preferences for particular sedimentary characteristics or their ability to compete or resist predation may change, resulting in a certain segregation of size-classes within that species. This gives rise to further complexities in the distribution pattern and presents additional problems in any attempts to study the population dynamics of beach macrofauna.

Mean sediment diameter was also found to affect the composition of the meiofauna (see chapter 5); nematodes become increasingly important with decreasing mean grain size, while the proportion of harpacticoid copepods becomes smaller.

Trends in sandy beach studies

Studies on sandy beaches have multiplied substantially over recent years. Not only are individual studies now becoming more numerous, but many new fields and techniques are being applied to these investigations. During the decade of the 'seventies, studies on energetics of individual species became fashionable, and energy budgets were determined for a variety of organisms (e.g. Hayes, 1974; Johnson, 1976a, b; Muir, 1977). The popularity of this kind of study is now fading in favour of studies covering entire systems (e.g. Edwards, 1973a, b; Ansell *et al.*, 1978; Munro *et al.*, 1978; McLachlan *et al.*, in press) and studies approaching problems from new angles. The studies of Koop *et al.* (in press) outlined earlier are an example of the latter type. Scanning electron microscopes, carbon analysers, gas-liquid chromatographs, settling columns and microbomb calorimeters all permit the analysis of large numbers of small samples, frequently also involving new and more sophisticated techniques, which ensure that results become more representative than has hitherto been possible.

Other examples include measurements of benthic metabolism such as those of Dye (1980b) who found a direct correlation between biological oxygen demand and the state of the tides, and Pamatmat *et al.* (1981) who studied heat production, ATP concentrations and electron transport activity in sandy beach sediments in order to determine the overall metabolism of the fauna and flora of such sands.

Most recent trends involve studies on the meio- and microfauna. This not only applies to intertidal benthic fauna but to subtidal ones as well. This is obviously an area that has been largely unstudied and the interrelationships between these categories will doubtless prove to be both varied and complex (see Tietjen, 1980 for a short review on existing knowledge). It is interesting that the studies on the meio- and microfauna are proceeding largely in the absence of detailed taxonomic information. This has necessitated the holistic approach to ecological studies advocated by Odum (1977). Although this is perhaps admirable, and knowledge is being gained on how these communities behave as entities, the underlying mechanisms will only become clear when a more reductionist approach can be adopted on the basis of more detailed taxonomic information.

APPENDIX 1

Results of detailed sedimentological analyses on sands collected seasonally from the beaches at Melkbosstrand, Ysterfontein and Rocherpan.

The letters M, Y and R represent the three beaches listed above respectively, while the last two letters and numbers are grid references. The last number represents the tidal level (1 = zone of drying, 2 = zone of saturation, 3 = zone of resurgence, 4 = zone of saturation). The letter X indicates a randomly taken sample.

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% CaCO$_3$
			25.8.76				
R1A1	1,575	1,603	0,291	0,154	0,616	0,117	2,943
R1B1	1,589	1,585	0,304	-0,126	0,180	0,123	3,729
R1C1	1,708	1,682	0,348	-0,154	0,133	0,094	3,308
R1D1	1,650	1,657	0,304	-0,087	0,660	0,105	1,891
R1A2	1,172	1,715	0,277	0,065	0,214	0,111	13,352
R1B2	1,837	1,844	0,240	-0,062	0,246	0,117	2,762
R1C2	1,519	1,540	0,306	0,067	-0,091	0,155	3,639
R1D2	1,744	1,763	0,235	0,234	0,063	0,089	1,517
R1A3	1,580	1,557	0,402	-0,127	0,542	0,237	6,806
R1B3	1,545	1,546	0,344	-0,015	0,361	0,177	5,234
R1C3		No Results					
R1D3	1,495	1,334	0,636	-0,309	0,242	0,316	17,896
R1A4	1,614	1,600	0,348	-0,066	0,373	0,125	5,381
R1B4	1,419	1,296	0,530	-0,133	-0,740	0,576	29,025
R1C4	1,364	1,311	0,430	-0,102	-0,481	0,302	13,449
R1D4	1,379	1,317	0,490	-0,095	-0,419	0,341	15,042
			27.7.76				
M1A1	2,285	2,279	0,282	-0,395	2,542	0,350	26,059
M1B1	2,255	2,243	0,298	-0,182	1,343	0,442	26,355
M1C1	2,237	2,220	0,318	-0,313	1,772	0,427	25,166
M1D1	2,311	2,313	0,284	0,045	0,770	0,321	27,671

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
				27.7.76 (contd)			
M1A2	2,283	2,279	0,262	-0,282	2,027	0,452	24,816
M1B2	2,265	2,256	0,320	-0,317	2,235	0,525	27,501
M1C2	2,300	2,305	0,287	-0,121	1,294	0,431	29,159
M1D2	2,288	2,248	0,352	-0,972	6,470	0,414	33,172
M1A3	2,143	2,154	0,315	0,114	-0,131	0,486	28,816
M1B3	2,200	2,178	0,302	-0,436	2,173	0,476	25,130
M1C3	2,155	2,159	0,330	-0,074	0,739	0,521	26,042
M1D3			No Results				
M1A4	2,212	2,160	0,394	-0,429	2,283	0,452	28,902
M1B4	2,246	2,228	0,323	-0,307	1,229	0,485	26,264
M1B4	2,246	2,228	0,323	-0,307	1,229	0,485	26,264
M1C4	2,280	2,260	0,303	-0,201	0,351	0,490	26,591
M1C4	2,280	2,260	0,303	-0,201	0,351	0,490	26,591
M1D4	2,289	2,317	0,243	0,254	0,433	0,469	24,402
				9.10.76			
Y1A1	2,324	2,335	0,261	-0,026	0,574	0,432	24,377
Y1B1			No Results				
Y1C1	2,237	2,208	0,356	-0,458	2,166	0,737	40,827
Y1D1	2,196	2,185	0,315	-0,036	-0,062	0,515	30,361

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
Y1A2	No Results						
Y1B2	2,329	2,307	0,293	-0,180	-0,008	0,654	50,415
Y1C2	2,359	2,332	0,327	-0,407	1,193	0,802	46,953
Y1D2	2,257	2,269	0,260	0,059	0,293	0,696	42,164
Y1A3	2,174	2,093	0,475	-0,288	0,062	0,998	42,550
Y1B3	2,074	2,064	0,458	-0,194	0,223	0,795	50,277
Y1C3	2,375	2,369	0,306	-0,265	1,338	0,873	50,439
Y1D3	2,287	2,295	0,324	-0,189	1,184	0,859	45,937
Y1A4	2,216	2,220	0,298	-0,070	0,104	1,435	40,538
Y1B4	2,222	2,190	0,377	-0,164	0,245	0,801	40,100
Y1C4	2,377	2,353	0,338	-0,282	1,203	0,916	50,882
Y1D4	2,269	2,257	0,350	-0,316	1,546	1,164	57,195
				7.11.76			
M2A1	2,400	2,409	0,229	0,049	0,889	0,480	25,272
M2B1	2,285	2,279	0,282	-0,395	2,542	-	-
M2C1	2,386	2,415	0,226	0,331	1,027	0,451	23,349
M2D1	2,400	2,420	0,208	0,173	0,328	0,473	24,027
M2A2	2,358	2,372	0,205	,040	0,676	0,360	25,446
M2B2	2,314	2,314	0,250	0,008	0,284	0,475	27,147
M2C2	2,375	2,371	0,283	01,007	8,976	0,484	26,259
M2D2	No Results						

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% CaCo$_3$
M2A3	2,299	2,289	0,270	-0,088	0,387	0,519	20,042
M2B3	2,325	2,314	0,272	-0,101	0,035	0,510	29,313
M2C3	2,368	2,376	0,217	0,012	0,171	0,503	25,155
M2D3	2,312	2,260	0,349	-0,477	1,681	0,547	32,212
M2A4	2,037	2,021	0,446	-0,122	0,031	0,603	35,609
M2B4	2,266	2,266	0,341	-0471	1,576	0,633	21,840
M2C4	2,285	2,267	0,294	-0,079	0,034	0,600	25,007
M2D4	2,253	2,242	0,306	-0,250	0,813	0,578	33,001
				22.11.76			
R2A1	1,741	1,735	0,280	-0,381	2,757	0,238	2,402
R2B1	2,158	2,320	0,468	0,537	-0,095	0,206	3,171
R2C1	1,643	1,661	0,319	0,367	1,188	0,208	3,509
R2D1	1,708	1,686	0,309	-0,303	1,448	0,248	4,386
R2A2	1,712	1,721	0,242	0,009	0,042	0,164	2,142
R2B2	1,885	2,001	0,471	0,688	1,712	0,120	1,486
R2C2	1,866	1,879	0,238	0,073	1,210	0,108	1,323
R2D2	1,763	1,772	0,342	0,129	3,291	0,116	1,407
R2A3	1,703	1,629	0,490	-0,481	1,043	0,310	13,542
R2B3	1,689	1,706	0,242	0,176	0,671	0,073	3,546
R2C3	1,689	1,552	0,525	-0,336	-0,025	0,290	1,187
R2D3	1,727	1,692	0,367	-0,534	1,883	0,158	5,473

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% CaCO$_3$
R2A4	1,678	1,614	0,442	-0,246	0,088	0,331	12,946
R2B4	1,570	1,521	0,402	-0,288	0,557	0,202	10,296
R2C4	1,642	1,564	0,461	-0,451	1,048	0,241	8,441
R2D4	1,635	1,638	0,284	-0,036	1,490	0,164	2,256
				7.12.76			
Y2A1	2,358	2,323	0,352	-0,928	8,071	0,799	39,580
Y2B1	2,397	2,410	0,254	0,313	1,509	0,786	39,347
Y2C1	2,229	2,243	0,369	- 0,012	0,229	0,628	29,782
Y2D1	2,201	2,204	0,350	-0,017	0,746	0,700	36,052
Y2A2	2,333	2,347	0,257	-0,021	0,585	0,544	37,245
Y2B2	2,388	2,401	0,199	0,079	0,294	0,889	41,844
Y2C2	2,167	2,154	0,332	-0,128	0,357	0,768	33,024
Y2D2	2,131	2,145	0,301	-0,104	1,064	0,702	33,276
Y2A3	2,264	2,265	0,319	-0,185	0,382	0,909	38,114
Y2B3	2,263	2,471	0,550	0,076	-1,370	0,838	37,753
Y2C3		No Results					
Y2D3	2,156	2,134	0,349	-0,336	1,708	0,732	34,329
Y2A4	2,281	2,290	0,313	-0,022	0,690	0,728	42,050
Y2B4	2,193	2,161	0,387	-0,196	0,089	0,589	33,928
Y2C4	2,198	2,176	0,338	-0,176	0,379	0,944	37,860
Y2D4	2,325	2,288	0,296	-0,332	0,437	1,024	41,434

22.1.77

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
M3A1	2,412	2,445	0,348	,064	0,431	0,502	24,817
M3B1	2,311	2,305	0,261	-0,017	0,514	0,656	25,029
M3A2	2,283	2,303	0,237	0,151	0,160	0,484	22,873

Other Samples Lost

5.2.77

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
R3A1	1,594	1,585	0,351	-0,366	2,026	0,143	2,131
R3B1	1,712	1,726	0,251	0,144	0,002	0,105	2,457
R3C1	1,695	1,724	0,257	0,267	0,828	0,102	1,354
R3D1	1,806	1,825	0,258	0,251	0,181	0,131	1,834
R3A2	1,696	1,723	0,332	0,368	1,931	0,137	3,213
R3B2	1,587	1,579	0,355	-0,079	-0,120	0,173	4,350
R3C2	1,748	1,775	0,263	0,172	1,039	0,106	1,545
R3D2	1,621	1,632	0,300	-0,019	0,492	0,146	3,973
R3A3	-	-	-	-	-	0,343	10,704
R3B3	1,596	1,594	0,346	-0,088	-0,213	0,218	5,176
R3C3	1,614	1,622	0,376	0,379	1,894	0,106	2,241
R3D3	1,764	1,776	0,259	0,018	1,177	0,177	6,821
R3A4	1,738	1,704	0,382	-0,258	0,251	0,321	4,902
R3B4	1,693	1,616	0,481	-0,333	0,935	0,334	6,543
R3C4	1,691	1,609	0,497	-0,318	0,691	0,317	5,410
R3D4	1,797	1,745	0,446	-0,272	0,345	0,269	5,104

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
			19.2.77				
Y3A1	2,398	2,414	0,224	0,071	0,317	0,451	37,378
Y3B1	2,359	2,381	0,250	0,107	0,367	0,713	38,421
Y3C1	2,360	2,389	0,235	0,080	0,069	0,696	39,155
Y3D1	2,349	2,374	0,245	0,210	0,339	0,710	38,187
Y3A2	2,437	2,441	0,261	-0,117	0,901	1,030	41,311
Y3C2	2,474	2,557	0,435	0,455	1,027	0,870	43,903
Y3D2	2,459	2,400	0,282	-0,075	0,808	0,634	44,914
Y3A3	2,365	2,359	0,308	-0,365	1,898	0,885	43,220
Y3B3	2,404	2,365	0,382	-0,566	2,476	0,855	44,989
Y3C3	2,349	2,372	0,258	0,182	0,283	-	-
Y3D3	2,354	2,379	0,252	-0,101	0,414	0,913	39,446
Y3A4	2,480	2,489	0,276	-0,271	2,603	0,948	48,705
Y3B4	2,425	2,448	0,362	-0,318	3,530	0,958	45,933
Y3C4	2,284	2,309	0,298	-0,136	0,496	0,465	38,863
Y3D4	2,467	2,477	0,258	0,017	0,974	0,866	41,036
			19.4.77				
M4A1	2,395	2,418	0,238	0,223	1,380	0,462	25,081
M4B1	2,442	2,460	0,219	0,262	1,309	0,533	25,182
M4C1	2,381	2,409	0,305	0,030	0,820	0,509	25,658
M4D1	2,450	2,480	0,325	0,197	-0,269	0,519	24,734

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
M4A2	2,303	2,412	0,187	0,152	0,268	0,599	23,345
M4B2	2,389	2,414	0,256	-0,065	2,364	0,310	23,507
M4C2	2,455	2,473	0,223	-0,122	1,607	1,408	22,308
M4D2	2,442	2,443	0,211	0,016	0,742	0,328	22,320
M4A3	2,303	2,291	0,279	-0,339	1,528	0,650	24,422
M4B3	2,338	2,344	0,253	-0,107	0,967	0,650	27,540
M4C3	2,377	2,396	0,249	0,225	0,375	0,534	27,248
M4D3	2,362	2,352	0,298	-0,114	0,638	0,628	25,778
M4A4	2,300	2,269	0,344	-0,378	1,249	0,598	32,089
M4B4	2,408	2,416	0,263	0,107	0,626	0,385	32,041
M4C4	2,285	2,238	0,384	-0,445	2,140	0,474	29,334
M4D4	2,211	2,131	0,404	-0,251	-0,235	0,744	29,279
4.5.77							
R4A1	1,549	1,544	0,347	-0,225	0,958	0,161	5,377
R4B1	1,700	1,700	0,298	-0,169	1,119	0,126	4,601
R4C1	1,574	1,593	0,289	0,010	0,222	0,185	4,835
R4D1	1,669	1,713	0,300	0,267	0,848	0,115	1,199
R4A2	1,577	1,604	0,291	0,142	0,778	0,128	3,341
R4B2	1,727	1,708	0,271	-0,413	2,419	0,122	2,959
R4C2	1,698	1,723	0,271	0,127	0,087	0,104	2,188
R4D2	1,744	1,769	0,243	0,234	0,676	0,132	1,601

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
R4A3	1,695	1,719	0,270	0,107	0,685	0,134	2,160
R4B3	1,694	1,684	0,255	-0,071	0,057	0,104	3,662
R4C3	1,568	1,555	0,381	-0,203	1,086	0,162	4,532
R4D3	1,679	1,710	0,243	0,223	-0,267	0,090	1,601
R4A4	1,577	1,577	0,309	-0,198	1,165	0,181	3,665
R4B4	1,582	1,589	0,348	-0,078	0,629	0,143	3,176
R4C4	1,714	1,697	0,344	-0,439	1,987	0,144	3,985
R4D4	1,687	1,705	0,320	0,185	0,721	0,160	3,281

18.5.77

Y4A1	2,299	2,321	0,265	0,030	0,003	0,561	38,713
Y4B1	2,229	2,247	0,311	0,045	0,514	0,721	35,032
Y4C1	2,299	2,314	0,289	-0,003	0,473	0,737	35,962
Y4D1	2,128	2,161	0,279	0,256	0,594	0,475	40,974
Y4A2	2,367	2,379	0,283	-0,119	0,316	0,914	41,003
Y4B2	2,297	2,305	0,265	-0,137	0,651	-	41,477
Y4C2	2,271	2,280	0,302	0,041	0,447	0,817	37,647
Y4D2	2,276	2,227	0,294	-0,279	1,809	0,678	36,540
Y4A3	2,411	2,426	0,288	0,030	0,255	0,925	43,262
Y4B3	2,383	2,371	0,340	-0,072	-0,068	0,879	44,538
Y4C3	2,212	2,151	0,388	-0,461	0,747	0,946	42,471
Y4D3	2,233	2,241	0,290	-0,168	0,281	0,829	32,794

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
Y4A4	2,485	2,467	0,285	-0,229	-0,008	1,181	54,395
Y4B4	2,230	2,152	0,496	-0,781	3,481	1,117	51,867
Y4C4	2,397	2,397	0,319	-0,369	1,897	1,055	44,173
Y4D4	2,299	2,285	0,325	-0,388	1,498	0,728	41,917
			18.7.77				
M5A1	2,229	2,186	0,372	-0,639	3,292	0,498	29,280
M5B1	2,277	2,273	-0,114	0,324	0,489	24,700	
M5C1	2,242	2,223	0,351	-0,368	1,954	0,482	29,345
M5D1	2,340	2,320	0,245	-0,341	1,046	-	24,920
M5A2	2,173	2,161	0,289	-0,269	1,053	0,470	26,651
M5B2	2,155	2,144	0,281	-0,164	0,549	0,492	28,015
M5C2	2,199	2,175	0,316	-0,085	-0,210	0,437	27,284
M5D2	2,104	2,090	0,408	-0,468	2,768	0,468	30,273
M5A3	2,196	2,187	0,293	-0,083	-0,490	0,319	28,210
M5B3	2,212	2,173	0,372	-0,275	1,165	0,601	29,988
M5C3	2,185	2,170	0,345	-0,116	1,007	0,527	29,705
M5D3	2,140	2,092	0,372	-0,279	0,694	0,537	29,623
M5A4	2,116	2,046	0,388	-0,406	0,581	0,510	28,903
M5B4	2,266	2,243	0,301	-0,354	1,170	0,560	30,075
M5C4	2,132	2,081	0,426	-0,774	4,747	0,585	30,737
M5D4	2,160	2,149	0,327	-0,206	0,579	0,572	30,664

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
				31.7.77			
R5A1	1,443	1,450	0,317	-0.093	0,246	0,179	3,362
R5B1	1,512	1,525	0,287	-.--4	-.636	0,112	2,391
R5C1	1,585	1,584	0,317	-0,109	1,103	0,110	3,233
R5D1	1,558	1,592	0,294	0,206	0,711	0,129	0,680
R5A2	1,519	1,518	0,317	-0,116	0,213	-	5,707
R5B2	1,385	1,386	0,365	-0,084	0,174	0,249	7,289
R5C2	1,328	1,274	0,422	-0,178	-0,332	-	-
R5D2	1,523	1,497	0,334	-0,316	0,952	0,153	3,014
R5A3	1,477	1,414	0,464	-0,179	-0,139	0,299	13,122
R5B3	1,358	1,274	0,521	-0,086	-0,541	0,355	17,969
R5C3	1,571	1,503	0,404	-0,298	-0,074	0,256	9,875
R5D3	1,488	1,440	0,394	-0,222	0,016	0,179	7,469
R5A4	1,224	1,194	0,459	0.000	-0,168	0,788	26,029
R5B4	1,077	1,089	0,601	0,027	-0,757	0,570	28,572
R5C4	1,634	1,568	0,424	-0,583	1,673	0,422	16,572
R5D4	1,447	1,454	0,383	0,112	0,555	0,269	6,994
				16.8.77			
Y5A1	2,285	2,297	0,295	0,149	0,649	0,642	35,310
Y5B1	2,337	2,363	0,265	0,109	0,837	0,642	34,846
Y5C1	2,287	2,305	0,233	0,216	0,159	0,403	44,534
Y5D1	2,311	2,355	0,239	-,404	0,705	0,668	34,599

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% CaCO$_3$
Y5A2	2,201	2,200	0,346	0,069	-0,102	0,558	33,315
Y5B2	2,184	2,197	0,366	0,192	0,488	0,548	33,481
Y5C2	2,268	2,298	0,274	0,343	1,228	0,647	32,444
Y5D2	2,286	2,308	0,330	0,208	0,464	0,636	33,487
Y5A3	2,259	2,271	0,311	0,053	0,261	0,484	36,205
Y5B3	2,299	2,307	0,225	0,121	-0,012	0,707	34,308
Y5C3	2,241	2,285	0,245	0,384	0,906	0,447	37,294
Y5D3	2,314	2,336	0,229	0,361	0,853	0,653	35,218
Y5A4	2,245	2,235	0,339	-0,271	1,142	0,750	40,643
Y5B4	2,204	2,204	0,298	-0,146	0,649	0,654	35,963
Y5C4	2,282	2,304	0,234	0,213	0,110	0,603	36,036
Y5D4	2,264	2,288	0,251	0,157	0,767	0,687	36,120
				13.10.77			
M6A1	2,090	2,074	0,431	-0,204	0,018	0,595	31,064
M6B1	2,337	2,227	0,313	-0,387	2,835	0,541	27,074
M6C1	2,224	2,238	0,281	0,002	0,977	0,535	26,941
M6D1	2,213	2,219	0,266	-0,076	0,508	0,529	27,390
M6A2	2,204	2,192	0,339	-0,526	3,233	0,655	26,377
M6B2	2,282	2,283	0,274	-0,190	3,446	0,622	26,061
M6C2	2,219	2,230	0,237	0,045	-0416	0,487	26,138
M6D2	2,225	2,255	0,260	0,423	2,079	0,580	26,343

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% CaCO$_3$
M6A3	2,261	2,274	0,254	-0,002	2,473	0,632	25,069
M6B3	2,187	2,208	0,312	0,166	1,435	0,505	29,232
M6C3	2,172	2,170	0,266	-0,084	0,360	0,700	27,267
M6D3	2,262	2,234	0,315	-0,410	1,336	0,245	29,290
M6A4	2,108	2,134	0,436	0,178	1,874	0,866	32,830
M6B4	2,052	2,072	0,308	0,092	0,067	0,641	27,333
M6C4	2,185	2,189	0,319	0,171	0,977	0,385	30,597
M6D4	2,265	2,246	0,258	-0,245	1,499	0,597	27,316

27.10.77

R6A1	1,533	1,553	0,349	0,246	1,825	0,144	2,376
R6B1	1,636	1,643	0,366	-0,070	1,987	0,190	7,150
R6C1	1,473	1,408	0,456	-0,304	-0,002	0,224	9,249
R6D1	1,411	1,405	0,351	-0,082	0,040	0,210	5,687
R6A2	1,605	1,594	0,350	-0,151	0,410	0,152	9,943
R6B2	1,726	1,729	0,307	-0,062	0,950	0,095	3,282
R6C2	1,703	1,721	0,367	0,198	1,219	0,100	2,809
R6D2	1,483	1,468	0,389	-0,074	0,106	0,228	3,301
R6A3	1,618	1,582	0,399	-0,233	0,119	0,219	9,351
R6B3	1,461	1,410	0,426	-0,228	0,108	0,207	6,958
R6C3	1,691	1,680	0,376	-0,112	0,150	0,293	5,443
R6D3	1,703	1,696	0,343	-0,160	0,683	0,251	5,902

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% CaCO$_3$
R6A4	1,743	1,686	0,477	-0,242	0,459	0,289	10,726
R6B4	1,639	1,599	0,441	-0,347	0,871	0,405	9,105
R6C4	1,645	1,594	0,426	-0,362	0,697	0,358	11,331
R6D4	1,745	1,722	0,357	-0,273	0,705	0,314	7,529
12.11.77							
Y6A1	2,311	2,296	0,302	-0,796	6,539	0,714	41,060
Y6B1	2,447	2,447	0,266	-0,589	5,724	0,763	42,347
Y6C1	2,460	3,038	0,982	0,397	-1,270	0,707	44,787
Y6D1	2,419	2,445	0,222	0,301	0,762	0,644	38,870
Y6A2	2,400	2,402	0,257	-0,173	0,737	0,862	47,446
Y6B2	2,42	2,432	0,254	0,143	0,774	0,818	42,159
Y6C2	2,349	2,351	0,271	-0,357	3,881	0,575	40,939
Y6D2	2,379	2,367	0,287	-0,754	6,704	0,578	43,793
Y6A3	2,323	2,300	0,309	-0,261	0,424	0,871	48,583
Y6B3	2,340	2,320	0,285	-0,243	0,148	0,888	51,402
Y6C3	2,356	2,376	0,256	0,163	0,289	0,884	47,173
Y6D3	2,373	2,371	0,285	-0,190	1,126	0,831	45,893
Y6A4	2,355	2,333	0,341	-0,195	-0,012	0,953	54,198
Y6B4	2,428	2,454	0,207	0,300	0,056	1,078	54,585
Y6C4	2,312	2,323	0,282	-0,050	0,242	1,046	55,477
Y6D4	2,345	2,350	0,279	-0,065	0,622	0,588	56,410

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
13.10.77							
M6X1	2,044	2,057	0,340	0,014	-0,094	0,534	30,350
M6X2	-	-	-	-	-	0,496	27,551
M6X3	-	-	-	-	-	0,364	32,069
M6X4	2,106	2,117	0,322	-0,017	0,630	0,483	27,367
M6X5	2,297	2,283	0,285	-0,184	0,337	0,869	28,243
M6X6	2,268	2,281	0,267	0,021	0,158	0,618	27,432
M6X7	2,250	2,230	0,272	-0,136	0,225	0,451	25,702
M6X8	2,153	2,172	0,263	-0,010	0,003	0,559	25,641
M6X9	2,250	2,230	0,307	-0,240	0,991	0,469	28,538
M6X10	2,242	2,276	0,261	0,165	0,329	0,477	26,343
M6X11	2,181	2,181	0,292	-0,047	0,534	0,489	26,216
M6X12	2,342	2,338	0,226	-0,047	0,063	-	27,657
M6X13	2,125	2,107	0,403	-0,089	0,140	0,481	27,204
M6X14	2,131	2,087	0,382	-0,380	1,159	0,597	27,427
M6X15	2,149	2,162	0,302	-0,101	1,830	0,470	26,480
M6X16	2,264	2,276	0,269	0,083	0,574	0,421	28,356
27.10.77							
R6X1	1,692	1,705	0,291	0,094	0,028	0,125	2,300
R6X2	1,652	1,645	0,356	-0,208	1,055	0,105	2,055
R6X3	1,689	1,670	0,349	-0,289	0,782	0,265	4,428
R6X4	1,667	1,644	0,387	-0,204	1,052	0,208	6,888
R6X5	1,673	1,586	0,490	-0,281	-0,239	0,401	11,834

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
R6X6	1,514	1,450	0,484	-0,150	-0,166	0,321	17,659
R6X7	1,575	1,577	0,330	-0,114	0,424	0,187	4,502
R6X8	1,533	1,496	0,379	-0,291	0,495	0,161	2,498
R6X9	1,649	1,628	0,345	-0,310	0,804	0,178	6,186
R6X10	1,744	1,753	0,308	-0,003	2,256	0,075	2,720
R6X11	1,326	1,292	0,449	-0,081	-0,048	0,257	12,863
R6X12	1,756	1,825	0,487	0,067	0,769	0,061	2,412
R6X13	1,864	1,859	0,310	-0,740	6,775	0,088	2,006
R6X14	1,644	1,650	0,364	-0,063	0,147	0,113	4,629
R6X15	1,505	1,468	0,438	-0,025	0,005	0,206	7,695
R6X16	1,640	1,659	0,318	0,056	0,755	0,117	2,084
				12.11.77			
Y6X1	2,382	2,382	0,287	-0,022	0,137	0,809	54,045
Y6X2	2,257	2,263	0,239	-0,033	0,129	0,741	43,942
Y6X3	2,299	2,287	0,316	-0,441	2,292	0,839	51,806
Y6X4	2,436	2,450	0,188	0,264	0,604	0,749	41,377
Y6X5	2,354	2,376	0,213	0,176	0,198	0,823	42,188
Y6X6	2,381	2,394	0,225	0,053	0,166	0,794	46,109
Y6X7	2,337	2,322	0,306	-0,640	4,606	0,572	45,210
Y6X8	2,361	2,367	0,275	-0,056	0,220	0,926	50,041
Y6X9	2,299	2,304	0,285	-0,270	2,254	0,763	41,033
Y6X10	2,383	2,388	0,243	-0,250	1,902	0,793	43,944
Y6X11	2,376	2,388	0,225	0,001	0,627	0,707	41,220

Sample	Median	Mean	Sorting	Skewness	Kurtosis	% Organic C	% $CaCO_3$
Y6X12	2,376	2,388	0,225	-0,080	0,074	0,900	43,370
Y6X13	2,344	2,339	0,299	-0,099	0,615	0,793	54,238
Y6X14	2,408	2,417	0,214	0,108	-0,146	0,812	47,989
Y6X15	2,336	2,359	0,209	0,162	0,087	0,857	43,627
Y6X16	2,330	2,345	0,230	0,024	0,979	0,658	46,533

APPENDIX 2

Species distribution list of west coast sandy beach genera.

Species	Distribution	References
Cerebratulus sordidus	Singapore	Punnett, 1900a
Cerebratulus bedfordii	Singapore	Punnett, 1900a
Cerebratulus insignis	Singapore	Punnett, 1900a
Cerebratulus ulatiformis	Singapore	Punnett, 1900a
Cerebratulus torresianus	Torres Straits	Punnett, 1900b
Cerebratulus queenslandicus	Torres Straits	Punnett, 1900b
Cerebratulus haddoni	Torres Straits	Punnett, 1900b
Cerebratulus viridis	Sri Lanka	Isler, 1900
Cerebratulus rigidus	Novaya Zemlya	Isler, 1900
Cerebratulus multiporatus	Wasin I., Kenya	Punnett & Cooper, 1910
Cerebratulus zebra	Sri Lanka	Punnett & Cooper, 1910
Cerebratulus melanorhynchus	Naples, Italy	Burger, 1895b
Cerebratulus cestoides	Naples, Italy	Burger, 1895b
Cerebratulus steineni	South Georgia	Burger, 1893
Cerebratulus subtilis	South Georgia	Burger, 1893
Cerebratulus validus	South Georgia	Burger, 1893
Cerebratulus boutani	Red Sea	Joubin, 1893
Cerebratulus acutus	Gulf of Naples, Italy	Burger, 1892
Cerebratulus anguillula	Gulf of Naples, Italy	Burger, 1892
Cerebratulus longifissus	Bergen, Norway	Punnett, 1903

Species	Distribution	References
Cerebratulus norvegicus	Bergen, Norway	Punnett, 1903
Cerebratulus melanops	Gulf of St Lawrence	Coe & Kunkel, 1903
Cerebratulus antillensis	Puerto Rico; Antilles	Coe, 1903
Cerebratulus greenlandicus	Greenland	Punnett, 1901b
Cerebratulus gracilis	Amboina, Indonesia	Staub, 1900
Cerebratulus latistomachus	Amboina, Indonesia	Staub, 1900
Cerebratulus laureolus	Amboina, Indonesia	Staub, 1900
Cerebratulus profundissimus	Amboina, Indonesia	Staub, 1900
Cerebratulus occidentalis	Alaska	Coe, 1901
Cerebratulus maldivensis	Maldive Is	Punnett, 1901a
Cerebratulus maculatus	Maldive Is	Punnett, 1901a
Cerebratulus gardineri	Maldive Is	Punnett, 1901a
Cerebratulus ischurus	Maldive Is	Punnett, 1901a
Cerebratulus natans	Singapore	Punnett, 1900a
Cerebratulus brunneus	Singapore	Punnett, 1900a
Cerebratulus robustus	Singapore	Punnett, 1900a
Cerebratulus erythrus	Singapore	Punnett, 1900a
Cerebratulus fuscus	Saldanha Bay to False Bay, South Africa; Tristan da Cunha I; Florida; Arctic regions	Coe, 1951; Day, 1974; Burger, 1903
Cerebratulus lacteus	Gulf of Mexico; North Carolina; Prince Edward I., Canada	Coe, 1951
Cerebratulus marginatus	New Brunswick; Mediterranean Sea; Greenland; Alaska to California; Japan	Iwata, 1954; Newcombe, 1935

Species	Distribution	References
Cerebratulus chilensis	Chile (41°24'S to 42°20S)	Friedrich, 1970
Cerebratulus bilineatus	Guernsey I.	Brehaut, 1973
Cerebratulus fissuralis	Iceland	Friedrich, 1958
Cerebratulus ventriporosus	Iceland	Friedrich, 1958
Cerebratulus leucopsis	Florida	Coe, 1951; Correa, 1961
Cerebratulus brevis	White Sea, U.S.S.R.	Uschakow, 1927
Cerebratulus alleni	Plymouth, England	Wijnhoff, 1913
Cerebratulus velatus	Gulf of Tonkin	Joubin, 1906
Cerebratulus krempfi	Gulf of Tadjourah (Red Sea)	Joubin, 1904
Cerebratulus charcoti	Antarctic	Joubin, 1904
Cerebratulus magelhoeniscus	Londonderry I. (Sub-Antarctic Is); Straits of Magellan; Falkland Is; Picton and Lemon Is	Bürger, 1904, 1895a
Cerebratulus signatus	Bering Sea	Coe, 1901
Cerebratulus linoleatus	California to Baja California; Florida	Coe, 1901, 1940
Cerebratulus californiensis	Mexico to Puget Sound	Coe, 1901, 1940; Correa, 1961
Cerebratulus latus	Alaska	Coe, 1901
Cerebratulus communis	Misaki and Tomioka, Japan	Iwata, 1952
Cerebratulus tageae	Brazil (300 km S.E. of Santos)	Correa, 1957
Cerebratulus ater	Curacao	Wijnhoff, 1925
Cerebratulus larseni	South Georgia	Wheeler, 1934
Cerebratulus malvini	52°25'S, 61°00'W to 52°10'S, 57°30'W; Falkland Is; 51°01'S, 58°54'W to 51°10'S, 62°10'W	Wheeler, 1934

Species	Distribution	References
Cerebratulus aureolus	Naples, Italy	Burger, 1892
Cerebratulus candida	Naples, Italy	Burger, 1892
Cerebratulus ferruginea	Naples, Italy	Burger, 1892
Cerebratulus fuscoides	Naples, Italy	Burger, 1892
Cerebratulus lividus	Naples, Italy	Burger, 1892
Cerebratulus notabilis	Naples, Italy	Burger, 1892
Cerebratulus simulans	Naples, Italy	Burger, 1892
Cerebratulus ventrosulcatus	Naples, Italy	Burger, 1892
Cerebratulus anas	New Caledonia	Joubin & Francois, 1892
Cerebratulus bicornis	New Caledonia	Joubin & Francois, 1892
Cerebratulus caledonicus	New Caledonia	Joubin & Francois, 1892
Cerebratulus aurostriatus	New Caledonia	Joubin & Francois, 1892
Cerebratulus auranticus	Devon, England	Garstang, 1892
Cerebratulus fasciolatus	Britanny, France	Chapuis, 1886
Cerebratulus modestus	Britanny, France	Chapuis, 1886
Cerebratulus cylindricus	Belles Amours, E. Canada	Packard, 1867
Cerebratulus angulatus	Britain	McIntosh, 1874
Cerebratulus macintoshi	Madeira	Langerhans, 1880
Cerebratulus hubrechti	Madeira	Langerhans, 1880

Species	Distribution	References
Cerebratulus aerugatus	Saldanha Bay	Wheeler, 1934
Cerebratulus johnstoni	Off S.W. Australia	Wheeler, 1940
Cerebratulus albifrons	Alaska to California	Coe, 1940
Cerebratulus corrugatus	South Georgia; S. Shetland Is; Independencia Bay, Peru	Coe, 1940
Cerebratulus herculeus	Bering Sea to S. California	Coe, 1940
Cerebratulus longiceps	Yakutat Bay, Alaska	Coe, 1940, 1901
Cerebratulus montgomeryi	Siberia; Bering Sea; Alaska to California	Coe, 1940
Cerebratulus penniger	Sagami Bay, Japan	Iwata, 1957
Cerebratulus superniger	Sagami Bay, Japan	Iwata, 1957
Cerebratulus formosus	Sagami Bay, Japan	Iwata, 1957
Cerebratulus albocinctus	Sagami Bay, Japan	Iwata, 1957
Cerebratulus barentsi	Barents Sea; Arctic regions	Burger, 1903, 1895a

Species	Distribution	References
Eurydice longicornis	Luderitz, Namibia to Transkei	Kensley, 1978; Branch & Grindley, 1979
Eurydice longispina	Aegean Sea	Jones, 1969
Eurydice longipes	Kenya	Jones, 1971
Eurydice peraticis	West coast of India; Arabian Gulf	Eleftheriou & Jones, 1976; Jones, 1974
Eurydice indicis	West coast of India	Eleftheriou & Jones, 1976
Eurydice caeca	South of Iceland	Jones & Naylor, 1967
Eurydice spinigera	Belgium; Cornwall; Atlantic France; Mediterranean; Black Sea; West Indies	Jones, 1969
Eurydice inermis	Isle of Man; Norway; Atlantic and Mediterranean coasts of France	Jones, 1969
Eurydice truncata	Norway; Britain to Mediterranean; S. of Saya de Malha Bank	Jones & Naylor, 1967; Stebbing, 1910
Eurydice grimaldii	Northeast Atlantic; Norway	Jones & Naylor, 1967
Eurydice rotundicaudata	Northeast Atlantic; France	Jones, 1969
Eurydice pulchra	Norway; Baltic Sea; Belgium; Britain to Morocco	Jones & Naylor, 1967
Eurydice affinis	Holland; Cornwall; Atlantic and Mediterranean France; Italy; Tunisia; Morocco	Jones & Naylor, 1967
Eurydice agilis	Kenya	Jones, 1971
Eurydice cavicaudata	Kenya	Jones, 1971
Eurydice chelifer	Kenya	Jones, 1971
Eurydice inornata	Kenya	Jones, 1971
Eurydice humilis	Solomon Is.	Stebbing, 1910
Eurydice convexa	Florida	Richardson, 1901

Species	Distribution	References
Eurydice elegantula	W. coast of Ireland	Jones & Naylor, 1967
Eurydice pontica	Black Sea to Spain	Jones, 1969
Eurydice caudata	California; Cocos Is.	Bowman, 1977
Eurydice dollfusi	Black Sea to Morocco	Jones, 1969
Eurydice subtruncata	New Zealand	Morton & Miller, 1971
Eurydice valkanovi	Gulf of Varna, Black Sea	Jones *et al.*, 1968
Eurydice racovitzai	Black Sea	Bacescu, 1949
Eurydice arabica	Arabian Gulf	Jones, 1974
Eurydice czerniavzky	Mediterranean France to Greece	Jones, 1969
Eurydice littoralis	South Brazil; Puerto Rico; Georgia; S. California	Moreira, 1972
Eurydice elongata	South Brazil (Rio and Sao Paulo Prov.)	Moreira, 1972
Eurydice emarginata	South Brazil	Moreira, 1972
Eurydice branchoporus	California	Menzies & Barnard, 1959
Eurydice orientalis	Great Barrier Reef; New Guinea; Indonesia; Philippines; Indochina; Sri Lanka	Bruce, 1980

Species	Distribution	References
Sigalion capense	West coast of South Africa to Natal	Day, 1974
Sigalion mathildae	Tropical Indian Ocean; Persian Gulf; Madagascar; Japan; Morocco; Britanny; Wales; Scotland	Day, 1967b, Pichon, 1967
Sigalion opalinum	Ivory Coast	Intes & Le Loeff, 1975
Sigalion cirriferum	Rio Grande do Sul, Brazil	Orensanz & Gianuca, 1974
Sigalion microantennata	Lobito, Angola	Hartmann-Schröder, 1974
Sigalion squamatum	Mediterranean to Scotland; Cape Verde Basin; Cape Province, South Africa	Day, 1967b. Cabioch *et al.*, 1967
Sigalion bandaensis	Solomon Is; East Indies; E. Australia	Gibbs, 1971
Sigalion arenicola	N.E. Brazil; Massachusetts; Atlantic U.S.A.	Nonanto & Luna, 1969; Hartman, 1959; Rullier & Amoureux, 1979
Sigalion ovigerum	New Zealand; New South Wales; Chatham I.; Chile	Monro, 1936; Wesenberg-Lund, 1961
Sigalion pourtalesii	Gulf of Mexico; South Florida	Chamberlin, 1919; Hartman, 1959
Sigalion amboiensis	Amboina, Indonesia	Hartman, 1959
Sigalion antillarum	Antilles; Cuba; West Indies	Hartman, 1959; Suarez & Fraga, 1978
Sigalion arenosum	Mediterranean	Hartman, 1959
Sigalion blainvilli	Naples, Italy	Hartman, 1959
Sigalion pergamentum	West Indies	Hartman, 1959

Species	Distribution	References
Talorchestia telluris	South Island, New Zealand	MacIntyre, 1963
Talorchestia chathamensis	Chatham I.	MacIntyre, 1963
Talorchestia kirki	Chatham I.	MacIntyre, 1963
Talorchestia dentata	Kapiti I., New Zealand	MacIntyre, 1963
Talorchestia spadix	New Zealand	MacIntyre, 1963; Hurley, 1956
Talorchestia novaehollandiae	Australia	Sheard, 1939
Talorchestia fritzi	Costa Rica; Cocos Is; Brazil	Stebbing, 1903 Schellenberg, 1938
Talorchestia kempii	East India	Tattersall, 1914
Talorchestia antennulata	New Caledonia	Chevreux, 1915
Talorchestia sinensis	Japan; Amoy, China	Morino, 1975
Talorchestia nipponensis	Japan	Morino, 1975
Talorchestia crassicornis	Kurile Is.	Kussakin, 1975
Talorchestia pachypus	Kurile Is.	Kussakin, 1975
Talorchestia zachsi	Kurile Is.	Kussakin, 1975
Talorchestia gracilis	Bay of Bengal	Rao, 1972
Talorchestia australis	Namibia to Mozambique	Griffiths, 1976
Talorchestia brito	England; France; Netherlands; Denmark; Norway; Tunisia; Morocco	Chevreux & Fage, 1925 Vader, 1970
Talorchestia frisiae	East Frisian Is.	Klein, 1969
Talorchestia spinifera	France; Morocco	Amanieu & Salvat, 1964; Elkaim, 1963

Species	Distribution	References
Talorchestia margaritae	Margarita I., West Indies	Stephensen, 1948
Talorchestia franchetti	Red Sea	Maccagno, 1937
Talorchestia affinis	Red Sea	Maccagno, 1937
Talorchestia patersoni	Stewart I., New Zealand	Stephensen, 1938
Talorchestia rectimana	Tahiti	Stephensen, 1935
Talorchestia capensis	Orange River, South Africa to Port St Johns, Transkei	Griffiths, 1976
Talorchestia quadrispinosa	Namibia to False Bay, South Africa	Griffiths, 1976
Talorchestia ancheidos	South African estuaries; West Africa; Cape Verde Is.	Day, 1974
Talorchestia dentata	New Zealand estuaries	Hurley, 1956
Talorchestia megalophthalma	Georgia to Gulf of St Lawrence	Fox & Byrnum, 1975
Talorchestia quoyana	New Zealand	Hurley, 1956
Talorchestia longicornis	Texas; Florida to Gulf of St Lawrence	Fox & Byrnum, 1975
Talorchestia marcuzzi	West Indies; Venezuela	Ruffo, 1951
Talorchestia quadrimana	New South Wales	Hurley, 1968
Talorchestia tricornuta	Congo estuary	
Talorchestia spinipalma	Micronesia; Queensland; Arabian Sea; Philippines	Barnard, 1965; Rao, 1972
Talorchestia dehayesii	Scandinavia; Baltic Sea; Holland; Portugal; Mediterranean; Black Sea	Chevreux & Fage, 1925
Talorchestia tumida	New Zealand	Hurley, 1956
Talorchestia cooki	New Zealand	Hurley, 1956
Talorchestia diemensis	S.W. Australia; Tasmania; New Caledonia	Hurley, 1968

Species	Distribution	References
Talorchestia laudanae	Cabinda, Angola	Schellenberg, 1925
Talorchestia japonica	Japan	Tattersall, 1922
Talorchestia malayensis	Singapore	Tattersall, 1922
Talorchestia bottae	Western Europe	Chevreux & Fage, 1925
Talorchestia martensii	Madascar; Kenya; Somalia; Arabian Sea; Red Sea; E. coast of India; Bay of Bengal; Indonesia; Thailand	Ledoyer, 1969; Rao, 1972; Scapini & Ercolini, 1973
Talorchestia skoogi	Angola	Griffiths, 1976

Species	Distribution	References
Gastrosaccus psammodytes	Lüderitz, Namibia to Kei River mouth, Transkei	Wooldridge, 1978
Gastrosaccus dunckeri	Morrumbene, Mozambique; India; Japan	Wooldridge, 1978
Gastrosaccus gordonae	Stompneus Bay to East London, South Africa	Wooldridge, 1978
Gastrosaccus brevifissura	Langebaan to St Lucia, South Africa	Day, 1974
Gastrosaccus sanctus	Black Sea; Mediterranean; Britain; Holland; Morocco; Canary Is; West Africa; South Africa	Moran, 1972; Tattersall, 1951; Wooldridge, 1978
Gastrosaccus spinifer	Scotland; Morocco; Mediterranean; Ghana; E. India; Helgoland	Tattersall, 1951; Gauld & Buchanan, 1956; Ehrenbaum, 1897
Gastrosaccus armatus	Mediterranean	Mauchline & Murano, 1977
Gastrosaccus lobatus	Mediterranean; Morocco	Mauchline & Murano, 1977
Gastrosaccus vulgaris	Japan	Wooldridge, 1978
Gastrosaccus mediterraneus	Mediterranean	Macquart-Moulin, 1977
Gastrosaccus roscoffensis	Britanny	Macquart-Moulin, 1977
Gastrosaccus olivae	Orange River, South Africa	Macquart-Moulin, 1977
Gastrosaccus normani	Black Sea; Libya; Morocco	Bacescu, 1976
Gastrosaccus magnilobatus	Libya; Naples, Italy	Bacescu, 1976
Gastrosaccus kempi	Kerala, India	Mauchline & Murano, 1977
Gastrosaccus muticus	Kerala, India	Mauchline & Murano, 1977

Species	Distribution	References
Gastrosaccus simulans	Kerala, India	Mauchline & Murano, 1977
Gastrosaccus erythraeus	Red Sea (Egypt and Gulf of Aqaba)	Macquart-Moulin, 1977
Gastrosaccus parerythraeus	Red Sea (Egypt)	Macquart-Moulin, 1977
Gastrosaccus indicus	India; Indonesia; Philippines; New South Wales	Tattersall, 1940, 1951
Gastrosaccus dakini	New South Wales	Tattersall, 1940
Gastrosaccus dissimilis	Brazil; Louisiana	Coifmann, 1937a; Tattersall, 1951
Gastrosaccus pusillus	Red Sea; Bay of Bengal	Coifmann, 1937b
Gastrasaccus johnsoni	Caribbean to North Carolina	Tattersall, 1937, 1951
Gastrosaccus australis	New Zealand	Tattersall, 1923; Mauchline & Murano, 1977
Gastrosaccus pacificus	Gilbert Is; Philippines; India	Tattersall, 1951
Gastrosaccus philippinensis	Philippines	Tattersall, 1951
Gastrosaccus mexicanus	Gulf of Mexico; Panama (Atlantic and Pacific coasts)	Tattersall, 1951
Gastrosaccus bengalensis	Bay of Bengal; Indonesia; Indochina; Japan	Mauchline & Murano, 1977
Gastrosaccus formosensis	Taiwan & Japan	Mauchline & Murano, 1977
Gastrosaccus hibii	East and South China Sea	Mauchline & Murano, 1977
Gastrosaccus msangii	Tanzania	Mauchline & Murano, 1977
Gastrosaccus ahshimai	Japan	Mauchline & Murano, 1977
Gastrosaccus parvus	Providence Is.	Mauchline & Murano, 1977
Gastrosaccus pelagicus	Japan	Mauchline & Murano, 1977
Gastrosaccus bispinosa	Mngazana, Transkei	Wooldridge, 1978
Gastrosaccus longifissura	Kei River mouth, Transkei	Wooldridge, 1978

Species	Distribution	References
Donax dorothea	Florida, U.S.A	Morrison, 1971
Donax gemmula	Rio Grande do Sul, Brazil	Morrison, 1971
Donax mediamericana	Guatamela (Caribbean)	Pilsbry, 1919
Donax striatellus	Australia	Hedley, 1913
Donax veruinus	Australia	Hedley, 1913
Donax mancorensis	Zorritos, Peru	Olsson, 1961
Donax ecuadorianus	Canoa, Ecuador	Olsson, 1961
Donax productus	Madagascar	Odhner, 1919
Donax epularis	South Yemen	Melvill, 1901
Donax politus	W. Europe	Lucas, 1967
Donax vellicatus	W. Caribbean Sea	Vermeij, 1978
Donax contusus	Pacific central America	Vermeij, 1978
Donax cayennensis	W. Caribbean Sea	Vermeij, 1978
Donax dussimeiria	Malabar and S.E. India	Bertin, 1881
Donax panamensis	Pacific coasts of Colombia, Panama and Costa Rica	Dexter, 1972, 1979
Donax gracilis	Peru to California	Cruz, 1977
Donax semigranosus	Japan; South China Sea; Indochina	Dautzenberg & Fischer, 1907
Donax conradi	Florida to New York	Tiffany, 1971
Donax deltoides	South Queensland to South Australia	Womersley & Edmonds, 1958
Donax rugosus	Senegal to Angola	Gauld & Buchanan, 1956; Sourie, 1957; Smith, 1971; Franca, 1955b
Donax navicula	Pacific Panama to Baja California, Mexico	Strong & Hertlein, 1940; Phillips, 1970

Species	Distribution	References
Donax dentifer	Costa Rica to Peru	Vegas-Velez, 1968
Donax punctatostriatus	Pacific coast of Mexico	Dexter, 1974
Donax obesulus	Central America to Peru	Schuster-Diedrichs, 1956
Donax striatus	Cuba to Brazil	Wade, 1967; Almeida Perez, 1974
Donax semistriatus	Mediterranean	Lucas, 1967
Donax peruvianus	Peru	Penchaszadeh, 1971
Donax hanleyanus	Buenos Aires Prov., Argentina to Sao Paulo, Brazil	Penchaszadeh & Olivier, 1975; Narchi, 1974
Donax carinatus	Pacific coasts of central America and Mexico	Vermeij, 1978
Donax aperittus	Iran (Gulf of Oman)	Melvill, 1897
Donax haesitans	New Guinea	Brancsik, 1895
Donax townsendi	Persian Gulf	Sowerby, 1894
Donax brasieri	New South Wales, Australia	Smith, 1891
Donax abbreviatus	Persian Gulf; S.E. India; Sri Lanka; Philippines	Melvill, 1910
Donax erythraensis	Red Sea	Bertin, 1881
Donax proximus	Japan	Bertin, 1881
Donax floridus	Borneo	Hanley, 1882
Donax impar	Baluchistan, Pakistan	Hanley, 1882
Donax mesodesmoides	Unknown	Hanley, 1882
Donax listeri	Unknown	Hanley, 1882
Donax dohrianus	Massawa, Ethiopia	Jickeli, 1882
Donax belardii	Italy	Tapparone-Canefri, 1869

Species	Distribution	References
Donax julianae	Black Sea - Romania and U.S.S.R.	Alyakrinskaya, 1972
Donax aperittus	Mauritius; W. India	Viader, 1951; Dwivedi *et al.*, 1973
Donax adriaticus	Adriatic Sea	Coen, 1937
Donax radians	Manila, Philippines	Tavolera & Faustino, 1933
Donax szemiani	S. Sumatra	Oostingh, 1931
Donax longissimus	Algoa Bay and Agulhas Bank, South Africa	Thiele & Jaekel, 1931
Donax fabula	Libya	Monteroserato, 1923
Donax venusutus	Black Sea (Caucasian coast)	Milaszewicz, 1909
Donax nuxfagus	Andaman Is.	Preston, 1908
Donax tiesenhauseni	Andaman Is.	Preston, 1908
Donax trigonalis	Andaman Is.	Preston, 1908
Donax variegatus	W. coast of France; Belgium; Mediterranean	Lucas, 1967
Donax dysoni	Indochina; South China Sea; S. and central Japan	Dautzenberg-Fischer, 1907; Lischke, 1871
Donax excavatus	Italy	Coen, 1925
Donax cacuminatus	New Caledonia	Sowerby, 1915
Donax laevigata	California	Moses, 1942
Donax assimilis	Pacific Panama	Strong & Hertlein, 1940
Donax denisi	Unknown	Fischer-Piette, 1941
Donax ticaoniscus	Philippines	Fischer-Piette, 1941
Donax purpurascens	Malay archipelago	Fischer-Piette, 1941
Donax victoris	Madagascar	Fischer-Piette, 1941

Species	Distribution	References
Donax euglyptus	Molucca Is., Indonesia	Dunker, 1865
Donax splendens	Australia	Dunker, 1865
Donax granosus	Amboina, Indonesia	Zelebor, 1886
Donax cattaniana	Adriatic Sea	Brusina, 1886
Donax saigonensis	Saigon, Viet-Nam	Crosse & Fischer, 1864
Donax bipartitus	Agulhas Bank, South Africa	Thiele & Jaekel, 1931
Donax kiusiuensis	Taiwan and Japan	Pilsbry, 1901
Donax serra	Lüderitz, Namibia to Transkei	Day, 1974; Branch & Grindley 1979
Donax faba	Natal, South Africa; Madagascar; East Africa; Seychelles; Maldive and Laccadive Is.; Red Sea; South Yemen; India; North Australia; Solomon Is.; Polynesian Is.; Philippines; South China Sea	Day, 1974; Rost & Soot-Ryen, 1955; Blackburn, 1974; Zhirmunsky & Chu, 1963; Morton & Challis, 1969
Donax madagascarensis	Natal, South Africa; Mozambique; Madagascar	Day, 1974
Donax trunculus	Algeria; Tunisia; Black Sea; Adriatic Sea; Sardinia; Mediterranean France	Lucas, 1967
Donax denticulatus	Caribbean Sea (except north coast); Venezuela to Brazil	Wade, 1967; Altena, 1971; Almeida-Perez, 1974
Donax variabilis	North Carolina to Texas; Gulf of Mexico; Venezuela	Dexter, 1974, 1976
Donax cuneatus	West India; Seychelles; South China Sea	Ansell *et al.*, 1972; Rost & Soot-Ryen, 1955; Zhirmunsky & Chu, 1963
Donax incarnatus	India; Mozambique	McLusky & Stirling, 1975
Donax sordidus	False Bay to East London, South Africa	Day, 1974; Wooldridge *et al.*, 1980
Donax vittatus	Baltic Sea; Norway to Portugal; Morocco; Mediterranean	Ansell, 1973
Donax tumidus	Texas, U.S.A.	Loesch, 1957
Donax gouldii	Southern California to El Salvador	Irwin, 1973

Species	Distribution	References
Donax spiculum	India	McLusky & Stirling, 1975
Donax pulchellus	Ghana	Gauld & Buchanan, 1956
Donax aemulus	Madagascar; Mozambique	Pichon, 1967
Donax elegans	Madagascar	Odhner, 1919
Donax acutangulus	Ghana	Gauld & Buchanan, 1956

Species	Distribution	References
Scolelepis indica	Great Barrier Reef, Australia; Sri Lanka; India; Madagascar	De Silva, 1965
Scolelepis agilis	Atlantic and Pacific coasts, Mexico to Colombia	Dexter, 1972, 1974, 1976
Scolelepis lefebvrei	Mozambique; Madagascar; Arabian Coast (Red Sea)	Hartmann-Schröder, 1974; Day, 1967; Jones, 1974
Scolelepis ciliata	Britanny; Scotland; Morocco	Cabioch *et al.*, 1967; Amoureux, 1972
Scolelepis fuliginosa	Denmark Strait; Isle of Man; Scotland; France (Atlantic and Mediterranean coasts)	Gandarsson, 1973; Southward, 1953
Scolelepis tridentata	Ireland	Pettibone, 1963
Scolelepis alaskensis	Alaska	Pettibone, 1963
Scolelepis squamata	South Africa; West Indies; Gulf of Mexico to Maine; British Columbia to southern California; Tunisia; Senegal; Mozambique; Saipan; Cook and Solomon Is; Scotland; Holland to Denmark; Namibia; Aldabra	Wade, 1967; Westeide, 1972; Croker, 1970; Behrends & Michaelis 1977; Light, 1977; Gibbs, 1971, 1972; Hughes & Gamble, 1977
Scolelepis texana	Texas to western Florida	Dauer & Simon, 1976
Scolelepis bonnieri	Germany; Holland; Marshall Is.	Hartman-Schröder & Stripp, 1968; Wolff, 1973; Reish, 1968
Scolelepis aitutakii	Cook Is.	Gibbs, 1972
Scolelepis perrieri	Lobito, Angola; Senegal	Hartman-Schröder, 1974
Scolelepis foliosa	Ireland; Channel; Holland; Naples, Italy; California	Wolff, 1973; Pettibone, 1963
Scolelepis cornifera	Kerguelen I.	Monro, 1939
Scolelepis girardi	Channel coast; North Sea	Cabioch *et al.*, 1967
Scolelepis vulgaris	Magellan Straits; Punta Arenas, Chile	Ehlers, 1897

Species	Distribution	References
Scolelepis glutea	Magellan Straits; Punta Arenas, Chile	Ehlers, 1897
Scolelepis bousfieldi	Gulf of St Lawrence; Massachusetts	Pettibone, 1963
Scolelepis antipoda	New Zealand	Pettibone, 1963
Scolelepis oligobranchia	Kurile Is.	Pettibone, 1963
Scplelepis williami	Sri Lanka	Pettibone, 1963
Scolelepis knight-jonesi	Sri Lanka	Pettibone, 1963
Scolelepis cantabra	France; Spain	Pettibone, 1963
Scolelepis pappillosa	Korea	Pettibone, 1963
Scolelepis arenicola	Central America (El Salvador)	Pettibone, 1963
Scolelepis gilchristi	South Africa	Pettibone, 1963
Scolelepis yamaguchii	Japan	Pettibone, 1963

Species name	Distribution	References
Camopsis robusta	South African West coast, False Bay	Day, 1975
Cumopsis longipes	South Wales, Britain, Mediterranean, Black Sea, Gulf of Gascogne	Withers, 1977, Macquart-Moulin, 1968
Cumopsis goodsiri	Britain, North Sea, Rhine estuary, Indo-Pacific (Annam)	Day, 1975
Cumopsis jonesi	Ivory Coast	Le Loeuff & Intes, 1972
Cumopsis fagei	French coast-Channel, Morocco	Bacescu, 1956; Day, 1975
Cumopsis wafri	West Africa	Day, 1975
Cumopsis elongata	West Africa	Day, 1975

Species	Distribution	References
Nephtys trissophyllus	South Georgia	Rioja, 1944
Nephtys phyllobranchia	Delaware Bay	Hartman, 1942
Nephtys stammeri	Adriatic Sea	Augener, 1932
Nephtys panamensis	Gulf of California to Panama; Cocos Is.	Monro, 1928; Hartman, 1940
Nephtys spiribranchis	Aru and Kei Is., Indonesia	Ehlers, 1918
Nephtys abranchiata	Antarctica	Ehlers, 1913
Nephtys tabogensis	Taboga I.	Monro, 1933
Nephtys phyllocirra	Rio Hacha (Caribbean Sea)	Augener, 1933
Nephtys schmittii	N.E. Pacific	Hartman, 1938
Nephtys ectopa	Aguja Point, Peru (5°46'S)	Chamberlin, 1919
Nephtys posterobranchus	Chile (42°-72°S); South Georgia, S. Shetland and S. Orkney Is.	Rozbaczylo & Castilla, 1974
Nephtys glossophylla	Chile	Rozbaczylo & Castilla, 1974
Nephtys imbricata	Valparaiso, Chile	Rozbaczylo & Castilla, 1974
Nephtys impressa	Chile (32°-40°S)	Rozbaczylo & Castilla, 1974
Nephtys monilibranchiata	Chile (32°-40°S)	Rozbaczylo & Castilla, 1974
Nephtys oculata	El Salvador to Chile (37°S)	Rozbaczylo & Castilla, 1974
Nephtys serratifolia	Falkland Is.; South Atlantic; South Chile to Valparaiso	Rozbaczylo & Castilla
Nephtys modesta	Uruguay; Straits of Magellan; Kerguelen I.	Ehlers, 1901; Rozbaczylo & Castilla, 1974
Nephtys discors	Maine	Banse, 1972

Species	Distribution	References
Nephtys digitifera	6°13'S, 104°9'E	Augener, 1933
Nephtys polybranchia	W. India; Taleh-Sap (Cambodia); Sri Lanka; Shanghai, China; Ryukyu Is, Japan	Fauvel, 1953; Okuda, 1940; De Silva, 1965; Imajima, 1967
Nephtys sinensis	Amoy (China); Gulf of Pe-Chou-Li	Okuda, 1940
Nephtys munamorii	Solomon Is	Gibbs, 1971
Nephtys palatii	Solomon Is; Red Sea	Gibbs, 1971; Gravier, 1906
Nephtys rubella	Norway to Portugal; North Sea; W. Mediterranean	Forêt-Montardo, 1969
Nephtys inermis	Gulf of Suez; South Arabia; Maldive Is; Mediterranean; Caribbean; Panama (Pacific)	Fauvel, 1933, 1953
Nephtys dibranchis	California to Ecuador; New Guinea; New Zealand; Australia; Indian Ocean; Gulf of Oman	Monro, 1933; Hartman, 1940; Fauvel, 1953; Paxton, 1974
Nephtys verrilli	New Zealand; Queensland; India; California to Panama	Paxton, 1974
Nephtys ciliata	Baltic; North Sea; Siberian coast; Sea of Japan; Bering Sea; Yellow Sea; Alaska to Washington; New England	Banse & Hobson, 1974; Hartman, 1938; Fauchald, 1963
Nephtys cornuta	British Columbia to Mexico	Banse & Hobson, 1974
Nephtys ferruginea	California to Chile; Shag Rocks (S. Atlantic); British Columbia	Rozbaczylo & Castilla, 1974; Banse & Hobson, 1974
Nephtys punctata	Alaska to Washington	Banse & Hobson, 1974; Hartman, 1938
Nephtys rickettsi	Alaska to Washington; N.E. Pacific	Banse & Hobson, 1974; Hartman, 1938
Nephtys lyrochaeta	Morocco; Senegal; Congo; Persian Gulf	Day, 1967
Nephtys malmgreni	Kara Sea; Novaya Zemlya, Arctic Ocean to 179°W; Bering Sea; Sea of Okhotsk; Shikotin I, Greenland; Norway; Portugal; Mediterranean; Bay of Bengal; Andaman Is.	Day, 1967; Ditvelsen, 1937; Fauchald, 1963; Fauvel, 1953
Nephtys sphaerocirrata	Namibia to Persian Gulf; Solomon and Marshall Is	Day, 1967; Gibbs, 1971

Species name	Distribution	References
Nephtys dussumieri	Malabar, India	Fauvel, 1953
Nephtys assimilis	Pacific Guatamela	Hartman, 1940
Nephtys lobophora	San Juan Bay, Peru	Hartman, 1940
Nephtys sukumoensis	Sukumo Bay, Seto Inland Sea, Japan	Kitamori, 1960
Nephtys ehlersi	Baltic Sea	Heinen, 1911
Nephtys multicirrata	Peru	Hartmann-Schröder, 1960
Nephtys mirasetis	Philippine Is.	Hoagland, 1920
Nephtys hudsonica	Hudson Bay, Canada	Chamberlin, 1920
Nephtys jeffresii	Japan	McIntosh, 1901
Nephtys pansa	Norway	McIntosh, 1901
Nephtys canadiensis	Gulf of St Lawrence	McIntosh, 1900
Nephtys lawrencii	Gulf of St Lawrence	McIntosh, 1900
Nephtys quatrefagesi	Cuba; West Indies	Suarez & Fraga, 1978
Nephtys bilobatus	Gulf of California	Kudenov, 1975
Nephtys furcifera	El Salvador	Hartman-Schröder, 1959
Nephtys brevibranchis	El Salvador	Hartman-Schröder, 1959
Nephtys elamellata	Kermadec Trench; 29°48'N, 17°30'W to 30°05'N, 17°18'W and 40°33'N, 35°24'W to 40°34'N, 35°52'W	Eliason, 1951; Kirkegaard, 1956
Nephtys parva	San Francisco Bay, California	Clark & Jones, 1955
Nephtys serratus	Falkland Is.	Hartman, 1953
Nephtys oligobranchia	Central China; Taleh-Sap (Cambodia); Bay of Bengal	Okuda, 1943

Species name	Distribution	References
Nephtys picta	Gulf of Mexico to Long Island, New York	Kinner & Maurer, 1978
Nephtys capensis	Cape Province, South Africa	Day, 1967
Nephtys bucera	North Carolina to Maine	Fauchald, 1963
Nephtys incisa	Georgia to Massachusetts; Greenland; Norway to Portugal; Menorca; Corsica	Fauchald, 1963
Nephtys hombergii	Novaya Zemlya; Iceland; Norway to Morocco; Adriatic Sea; Black Sea; Indo China; Angola to Natal, South Africa	Clark *et al.*, 1962; Forêt-Montardo, 1969; Day, 1967
Nephtys caeca	Novaya Zemlya; Kurile Is; Greenland; N. Atlantic and Pacific Oceans; Korea; Japan; Baltic Sea; Britain	Fauchald, 1967
Nephtys longosetosa	Korea; Greenland; New Hampshire; Norway; Britain; N. Atlantic and Pacific Oceans	Ditvelsen, 1937; Fauchald, 1963
Nephtys cirrosa	Eastern U.S.A.; Baltic Sea; Britain to Morocco; N. Mediterranean and Aegean Seas	Amoureux, 1972; Forêt-Montardo, 1969
Nephtys tulearensis	Port Elizabeth to Mozambique; Madagascar; Arabian Gulf	Day, 1967
Nephtys macroura	Bouvet I.; Tierra del Fuego; South Georgia; Antarctic and Sub-Antarctic Is; New Zealand; Australia; Tasmania; Chile; New England	Day, 1967; Rozbaczylo & Castilla, 1974
Nephtys dibranchis	Arabian Gulf; Madagascar; Natal; Tropical Indian Ocean and E. Pacific Ocean; Colombia to S. California	Hartman, 1938, 1940; Pichon, 1967; Day, 1967
Nephtys singularis	Pacific: Colombia to Mexico	Dexter, 1974, 1976; Fauchald, 1977
Nephtys hystricis	Baltic Sea; North Sea to Morocco; Adriatic Sea; Eastern U.S.A.; Western U.S.A.; Bering Sea; Sea of Japan; Kara and Okhotsk Seas	Forêt-Montardo, 1969; Mare, 1942; Riedl, 1970
Nephtys caecoides	Northern Mexico to British Columbia	Banse & Hobson, 1974
Nephtys monroi	Pacific Panama	Fauchald, 1977

Species name	Distribution	References
Nephtys californicus	British Columbia to N. Mexico; Gorgona I.	Banse & Hobson, 1974
Nephtys squamosa	Morocco; Panama (Pacific & Atlantic); Mexico (Pacific & Atlantic); California; Colombia; Brazil to Florida	Amoureux, 1972; Nonanto & Luna, 1970; Fauchald, 1977; Hartman, 1940; Suarez & Fraga, 1978
Nephtys minuta	White Sea, USSR	L'Vova, 1976
Nephtys acrochaeta	Ubatuba, Brazil to Uruguay	Fauchald, 1977; Hartman, 1940 Suarez & Fraga, 1978
Nephtys magellanica	Chile to California; Magellan Straits; Ubatuba, Brazil	Fauchald, 1978; Rozbaczylo & Castilla, 1974; Hartman, 1940
Nephtys fluviatilis	Uruguay; Rio del Plata; Rio Grande do Sul (Brazil)	Monro, 1937; Orensanz & Gianuca, 1974
Nephtys californiensis	Peru to California; Kurile Is.	Hartman, 1938, 1940; Kussakin, 1975
Nephtys vikingensis	New South Wales, Australia	Paxton, 1974
Nephtys paradoxa	Greenland; North Atlantic; Norway; Sweden; Mediterranean; Maine; Massachussetts; Bering Sea; Chile; Tierra del Fuego; New South Wales, Australia	Rozbaczylo & Castilla, 1974; Paxton, 1974 Paxton, 1974
Nephtys australiensis	South Australia; Yorke Peninsula; West Australia;	Paxton, 1974; Augener, 1913; Fauvel, 1953
Nephtys gravieri	South Australia; Yorke Peninsula; West Australia; Bay of Bengal	Paxton, 1974; Augener, 1913; Fauvel, 1953
Nephtys longipes	?	?
Nephtys assignis	British Columbia to California; Kamchatka Peninsula	Banse, 1972; Banse & Hobson, 1974
Nephtys brachycephala	British Columbia; Washington; Bering Sea; Miura Peninsula (Japan)	Banse & Hobson, 1974

Species	Distribution	References
Nephtys ambrizettana	Angola	Day, 1967
Nephtys erectanoides	Central Chile (40°S)	Rozbaczylo & Castilla, 1974
Nephtys foliosus	South Sandwich Is; Falkland Is; Cape Horn	Rozbaczylo & Castilla, 1974
Nephtys heteroserrata	Central Chile	Rozbaczylo & Castilla, 1974
Nephtys lutrea	Otter Is; Patagonia	Rozbacqylo & Castilla, 1974
Nephtys ornatus	Sandwich Is; Antarctic Peninsula; Scotia Sea	Rozbaczylo & Castilla, 1974
Nephtys peruana	Peru to South Chile	Rozbaczylo & Castilla, 1974
Nephtys polyphara	Peru and Chile	Rozbaczylo & Castilla, 1974

Species	Distribution	References
Bullia digitalis	Lüderitz, Namibia to Port Alfred, South Africa	Kensley, 1973
Bullia annulata	Saldanha Bay to Port Alfred, South Africa	Brown, 1971; Kensley, 1973
Bullia callosa	Angola to Natal, South Africa	Brown, 1971; Kensley, 1973
Bullia diluta	False Bay, South Africa to Maputo, Mozambique	Brown, 1971
Bullia laevissima	Lüderitz, Namibia to Algoa Bay, South Africa	Brown, 1971; Kensley, 1973
Bullia mozambicensis	Natal, South Africa to Mozambique	Kensley, 1973
Bullia natalensis	Natal, South Africa to Mozambique	Brown, 1971
Bullia osculata	East London to Zululand, South Africa	Brown, 1971; Kensley, 1973
Bullia pura	False Bay to Port Alfred, South Africa	Kensley, 1973
Bullia rhodostoma	False Bay, South Africa to Maputo, Mozambique	Brown, 1971
Bullia similis	East London to Zululand, South Africa	Brown, 1971; Kensley, 1973
Bullia tenuis	False Bay to Natal, South Africa	Kensley, 1973
Bullia trifasciata	Still Bay to Port Alfred, South Africa	Kensley, 1973
Bullia sendersi	Kenya	Kilburn, 1978
Bullia vittata	East India and Sri Lanka	Crichton, 1943
Bullia livida	Madras, India	Chrichton, 1943
Bullia aikeni	Mozambique (13°S - 21°40'S)	Kilburn, 1978
Bullia nitida	Pakistan	Kilburn, 1978
Bullia belangeri	India	Kilburn, 1978
Bullia nuttalli	Mozambique (24°S)	Kilburn, 1978
Bullia tricolor	-	Kilburn, 1978

Species	Distribution	References
Bullia ancillaeformis	False Bay; E. Cape Province to Natal	Conolly, 1974
Bullia cataphracta	Mozambique (24°S)	Kilburn, 1978
Bullia melanoides	Arabian Gulf, W. India	Trueman and Brown, 1976
Bullia strenaria	Arabian Gulf	Kilburn, 1978
Bullia cinerea	Sri Lanka	Preston, 1903
Bullia tranquebarica	Madras, India	Crichton, 1943
Bullia townsendi	Gulf of Oman	Melvill, 1912
Bullia granulosa	Cabinda (Angola)	Franca 1955a

Species	Distribution	References
Tylos granulatus	False Bay, South Africa to northern Namibia	Kensley, 1978
Tylos capensis	False Bay, South Africa to Transkei	Kensley, 1978; Wooldridge *et al.*, 1980
Tylos latrielli	Brazil; Puerto Rico; Bahamas; Venezuela; Nicaragua; Azores; Canary Is; Cape Verde Is; Dakar, Senegal to Britanny; Florida; Bermudas; Mediterranean coast	De Castro, 1952; Hayes, 1969
Tylos algerinus	Algeria	Hayes, 1969
Tylos cilicius	Sicily; Turkey	Hayes, 1969
Tylos europaeus	Corsica; Sardinia; Elba; North Atlantic	Hayes, 1969
Tylos niveus	Florida; Caribbean Is and coastline; Bermuda; Massachusetts	Hayes, 1969
Tylos spinulosus	Tierra del Fuego; Central Chile; Atlantic central America	Schultz, 1970
Tylos punctatus	Southern California to central Mexico	Schultz, 1970
Tylos punctatus insularis	Galapagos Is.	Schultz, 1970
Tylos neozelandicus	North Island, New Zealand	Hayes, 1969
Tylos granuliferus	Japan and Borneo; Solomon Is; Kurile Is.	Hayes, 1969; Kussakin, 1975
Tylos nudulus	Christmas I.	Hayes, 1969
Tylos opercularis	Philippines	Hayes, 1969
Tylos albidus	Nicobar Is; Western Malaya	Hayes, 1969
Tylos minor	Seychelles	Hayes, 1969
Tylos exiguus	Red Sea (Egypt and Saudi Arabia)	Hayes, 1969; Jones, 1974
Tylos ponticus	Black Sea; Adriatic Sea	Hayes, 1969
Tylos wagneri	Venezuela	Schultz, 1970
Tylos ochri	South-west Madagascar; Penang I., Malaysia	Roman, 1977; Jones, 1979
Tylos africanus	Somalia	Ferrara, 1974

Species	Distribution	References
Urothoe marina	Atlantic France; Britain; Shetland Is.; Kattegat	Chevreux & Fage, 1925
Urothoe brevicornis	Isle of Man; Wales; Britanny	Withers, 1977
Urothoe grimaldii	South Africa; Ghana; Morocco; France; Holland; Wales; India	Griffiths, 1976; Rabindranath, 1971; Gauld & Buchanan, 1956
Urothoe elegans	Madagascar; Indian Ocean; Red Sea; Mozambique; Orange River, South Africa; Mediterranean	Griffiths, 1976
Urothoe coxalis	Natal to Saldanha Bay, South Africa	Griffiths, 1976
Urothoe planata	Mozambique to False Bay, South Africa	Griffiths, 1976
Urothoe platypoda	Knysna, South Africa	Griffiths, 1976
Urothoe pulchella	Mozambique to Lambert's Bay, South Africa; Atlantic Ocean; Senegal; Western Mediterranean Sea; France; Scotland	Chevreux & Fage, 1925; Griffiths, 1976
Urothoe serrulidactylus	Kosi Bay, South Africa; S.W. Indian Ocean; Madagascar	Griffiths, 1976
Urothoe tumorosa	Natal to False Bay, South Africa	Griffiths, 1976
Urothoe dentata	Ghana	Schellenberg, 1925
Urothoe denticulata	Monaco	Bellan-Santini, 1965
Urothoe ruber	Arabian Sea; India; Bay of Bengal	Barnard, 1965
Urothoe spinidigitus	South Viet-Nam; Bay of Bengal; India; Arabian Sea	Barnard, 1966b
Urothoe vavarini	North Pacific; S. Sakhalin I.; S. California	Barnard, 1966a
Urothoe vemae	S. Sandwich Trench and Cape Basin	Barnard, 1962
Urothoe abbreviata		Barnard, 1966b
Urothoe irrostrata	Indonesia and North Australia	Barnard, 1966b
Urothoe poucheti	Azores Is.	Stebbing, 1895

Species	Distribution	References
		Barnard, 1966b
Urothoe leone	Red Sea	Barnard, 1966b
Urothoe pestai	Falkland Is.; Argentina	Lowry & Bullock, 1976
Urothoe orientalis	Sea of Okhotsk and Sea of Japan; Viet Nam	Barnard, 1966b
Urothoe rotundifrons	Cape Basin	Barnard, 1962
Urothoe simplignathia	Angola Basin	Barnard, 1962
Urothoe oniscoides	Bransfield Strait	Lowry & Bullock, 1976
Urothoe carda	Bay of Nha-Trang, Viet-Nam	Imbach, 1967
Urothoe cuspis	Bay of Nha-Trang, Viet-Nam	Imbach, 1967
Urothoe gelasina	Bay of Nha-Trang, Viet-Nam	Imbach, 1967
Urothoe platydactyla	Kerala, India	Rabindranath, 1971
Urothoe corsica	Corsica	Bellan-Santini, 1965
Urothoe norvegica	Shetland Is.; Norway	Stebbing, 1895

Species	Distribution	References
Pseudharpinia excavata	Bay of Biscay; False Bay to Lambert's Bay, South Africa; Southern Ocean	Griffiths, 1976
Pseudharpinia dentata	Lagotowia; Tierra del Fuego	Barnard and Drummond, 1978
Pseudharpinia abyssalis	Flores Sea and Macassar Straits	Barnard & Drummond, 1978
Pseudharpinia ayutlanta	Pacific coast of Panama	Barnard & Drummond, 1978
Pseudharpinia birjulini	Kurile Is.	Barnard, 1960
Pseudharpinia brevirostris	Bay of Biscay; Cap Blanc	Barnard, 1960
Pseudharpinia cariniceps	South Orkneys; South Shetlands; Palmer archipelago	Barnard, 1960
Pseudharpinia cinca	Off Namibia	Barnard & Drummond, 1978
Pseudharpinia latipes	Outer Hebrides; Morocco; S.W. Spain	Barnard, 1960
Pseudharpinia obtusifrons	Kerguelen I.; Antarctic	Barnard, 1960
Pseudharpinia vallini	Ross Sea	Barnard, 1960
Pseudharpinia wandichia	Valdivia basin	Lowry & Bullock, 1976

Species	Distribution	References
Excirolana natalensis	S.W. Madagascar; Natal to Lamberts Bay, South Africa	Pichon, 1967; Kensley, 1978; This study
Excirolana braziliensis	Brazil to Mexico; Caribbean Sea; Mexico to Chile; Galapagos Is.	Glynn *et al.*, 1976
Excirolana armata	Rio de Janeiro, Brazil to Buenos Aires, Argentina	De Castro & Brum, 1969
Excirolana orientalis	Madagascar; Kenya; Red Sea; Arabian Gulf; Nicobar Is.; Malaya; Borneo; Philippines; New Guinea; N.E. Australia	Jones, 1974
Excirolana japonica	Japan; Kurile Is.	Kussakin, 1975
Excirolana linguifrons	California	Johnson & Juskevice, 1965
Excirolana chiltoni	California	Klapow, 1972a
Excirolana hirsuticauda	Central and southern Chile	Carvacho, 1977
Excirolana monodi	Central Chile	Carvacho, 1977
Excirolana geniculata	Kenya	Jones, 1971
Excirolana chilensis	Lota, Chile	Carvacho, 1977
Excirolana bicornis	Off Natal	Kensley, 1978
Excirolana kumari	Malaysia	Bowman, 1971
Excirolana mesopotamica	Shatt al Arab, Iraq	Ahmed, 1971
Excirolana mesopotamicoides	Shatt al Arab, Iraq	Ahmed, 1971
Excirolana mayana	Baja California, Mexico; Galapagos Is.; Antilles	De Castro & Brum, 1969
Excirolana kincaidi	Puget Sound, U.S.A.	Monod, 1976

Species name	Distribution	References
Pontogeloides latipes	Mozambique, South Africa, Namibia, Congo, Cameroon, Ghana, Spanish Sahara, Brazil	Kensley, 1978; Brian & Darteville, 1949; Monod, 1928; Gauld & Buchanan, 1956; De Castro & Brum, 1969
Pontogeloides affinis	Kenya	Jones, 1971

REFERENCES

Ansell, A.D., McLusky, D.S., Stirling, A. and Trevallion, A. 1978. Production and energy flow in the macrobenthos of two sandy beaches in south west India. Proc. roy. Soc. Edinburgh 76B: 269-296.

Ansell, A.D., Sivadas, P., Narayanan, B., Sankaranarayanan, V.N. and Trevallion, A. 1972. The ecology of two sandy beaches in south west India. Seasonal changes in physical and chemical factors, and in the macrofauna. Mar. Biol. 17: 38-62.

Ansell, A.D. and Trevallion, A. 1969. Behavioural adaptations of intertidal molluscs from a tropical sandy beach. J. exp. mar. Biol. Ecol. 4: 9-35.

Augener, H. 1913. Polychaeta. I. Errantia. In: Die Fauna Südwest Australiens. 4(5): 63-304.

Augener, H. 1932. Die Polychaeten und Hirudineen des Timavogebietes in der Adriatischen Karstregion. Zool. Jb. Jena (Syst.) 63: 657-681.

Augener, H. 1933. Polychaeten aus den Zoologischen Museen von Leiden und Amsterdam. Zool. Meded. Leiden 15: 177-260.

Ayala, F.J., Hedgecock, D., Zumwalt, G.S. and Valentine, J.W. 1973. Genetic variation in Tridacna maxima, an ecological analog of some unsuccessful evolutionary lineages. Evolution 27: 177-191.

Bacescu, M. 1949. Quelques malacostracés nouveaux pour la faune marine de la Roumanie (avec la description d'une espèce nouvelle, Eurydice racovitzai n.sp.). Bull. scient. Acad. R. P. Roum. 1: 165-170.

Bacescu, M. 1956. Cumopsis fagei n.sp. Cumacé nouveau provenant des eaux du littoral francais de la Manche. Vie Milieu 7: 357-365.

Bacescu, M. 1976. Contribution to the knowledge of Mysidacea (Crustacea) of the Lybian coast, with descriptions of two new species. Rev. Roum. Biol. 21: 85-91.

Bally, R., Grindley, J.R. and Eagle, G.A. 1980. The environmental effects of effluent from a food canning factory on a sandy beach ecosystem in False Bay. School of Environmental Studies, University of Cape Town.

Banks, D.J. 1975. The effects of zinc on behaviour and respiration in Bullia digitalis (Prosobranchiata). Unpublished project, Zoology Dept., University of Cape Town.

Banse, K. 1972. On some species of Phyllodocidae, Syllidae, Nephtydae, Gonianidae, Apistobranchidae and Spionidae (Polychaeta) from the northeast Pacific Ocean. Pacific Sci. 26: 191-222.

Banse, K. and Hobson, K.D. 1974. Benthic errantiate polychaetes of British Columbia and Washington. Bull. Fish. Res. Bd. Canada 185: 1-111.

Barnard, J.L. 1960. The amphipod family Phoxocephalidae in the eastern Pacific Ocean, with analyses of other species and notes for a revision of the family. Allan Hancock Pacific Exped. 18: 175-375.

Barnard, J.L. 1962. South Atlantic abyssal amphipods collected by R.V. Vema. Abyssal Crustacea 1: 1-78.

Barnard, J.L. 1965. Marine amphipoda of atolls in Micronesia. Proc. U.S. natn. Mus. 117: 459-552.

Barnard, J.L. 1966a. Submarine canyons of southern California: Part V Systematics: Amphipoda. Allan Hancock Pacific Exped. 27(5): 1-166.

Barnard, J.L. 1966b. Benthic Amphipoda of Monterey Bay, California. Proc. U.S. natn. Mus. 119: 1-41.

Barnard, J.L. and Drummond, M.M. 1978. Gammaridean Amphipoda of Australia. Part III: the Phoxocephalidae. Smithson. Contrib. Zool. 245: 1-551.

Bascom, W.N. 1951. The relationship between sand size and beach-face slope. Trans. Am. geophys. Un. 32: 866-874.

Behrends, G. and Michaelis, H. 1977. Zur Deutung der Lebenspuren des Polychaeten Scolelepis squamata. Senckenberg. marit. 9: 47-57.

Bell, S.S. and Coull, B.C. 1978. Field evidence that shrimp predation regulates meiofauna. Oecologia 35: 141-148.

Bellan-Santini, D. 1965. Contribution a l'étude des amphipodes de la Mediterranée (parages de Monaco - côtes de Corse). Bull. Inst. oceanogr. Monaco 1355: 1-16.

Bertin, V. 1881. Revision des Donacidées du Muséum d'Histoire naturelle. N. Arch. Mus. 4(2): 57-121.

Biernbaum, C.K. 1979. Influence of sedimentary factors on the distribution of benthic amphipods of Fishers Island Sound, Connecticut. J. exp. mar. Biol. Ecol. 38: 201-223.

Blaber, S.J.M. 1976. The food and feeding ecology of Mugilidae in the St Lucia lake system. Biol. J. linn. Soc. 8: 267-277.

Blackburn, H. 1974. Fauna survey of the Port Essington district, Cobourg Peninsula, Northern Territory of Australia: marine molluscs. Aust. C.S.I.R.O. Div. Wildl. Res. Tech. Pap. 28: 49-62.

Blatt, H., Middleton, G. and Murray, R. 1972. Origin of sedimentary rocks. Prentice-Hall, Englewood Cliffs, New Jersey.

Bloom, S.A., Simon, J.L. and Hunter, V.D. 1972. Animal-sediment relations and community analysis of a Florida estuary. Mar. Biol. 13: 43-56.

Boaden, P.J.S. 1968. Water movement - a dominant factor in interstitial ecology. Sarsia 34: 125-136.

Boaden, P.J.S. 1980. Meiofaunal thiobios and "the Arenicola negation". Case not proven. Mar. Biol. 58: 25-30.

Boland, J. 1974. The ecology of Noordhoek beach. Unpublished project, Zoology Dept., University of Cape Town.

Bousfield, E.L. 1970. Adaptive radiation in sand-burrowing amphipod crustaceans. Chesapeake Sci. 11: 143-154.

Bowman, T.E. 1971. Excirolana kumari, a new tubiculous isopod from Malaysia. Crustaceana 20: 70-76.

Bowman, T.E. 1977. Isopod crustaceans (except Anthuridae) collected on the Presidential Cruise of 1938. Proc. biol. Soc. Wash. 89: 653-666.

Brady, F. 1943. The distribution of the fauna of some intertidal sands and muds on the Northumberland coast. J. Anim. Ecol. 12: 27-41.

Branch, G.M. 1979. Respiratory adaptations in the limpet Patella granatina: a comparison with other limpets. Comp. Biochem. Physiol. 62A: 641-647.

Branch, G.M. and Grindley, J.R. 1979. Ecology of southern African estuaries. Part XI. Mngazana: a mangrove estuary in Transkei. S. Afr. J. Zool. 14: 149-170.

Branch, G.M. and Newell, R.C. 1978. A comparative study of metabolic energy expenditure in the limpets Patella cochlear, P. oculus and P. granularis. Mar. Biol. 49: 351-361.

Brancsik, K. 1895. Contributiones ad faunam Molluscarum insulae Papua. Jahres. Ver. Trencsen 17: 209-288.

Brehaut, R. 1973. Report of the zoological section. Rep. Trans. Soc. Guernesey 19: 139-140.

Bretsky, P.W. 1973. A reflection on genetics, extinction and the "killer clam". Geology 1: 157.

Bretsky, P.W. and Lorenz, D.M. 1970. An essay on genetic-adaptive strategies and mass extinctions. Bull. geol. Soc. Am. 81: 2449-2456.

Brian, A. and Darteville, E. 1949. Contribution à l'étude des isopodes marins et fluviatiles du Congo. Ann. Mus. Congo Belge Sect. C Ser. 3,3 1: 1-205.

Briggs, J.C. 1974a. Marine zoogeography. McGraw-Hill, New York.

Briggs, J.C. 1974b. Operation of zoogeographic barriers. *Syst. Zool.* *23*: 248-256.

Brown, A.C. 1958. The ecology of South African estuaries. Part 9: notes on the estuary of the Orange River. *Trans. roy. Soc. S. Afr.* *35*: 463-473.

Brown, A.C. 1961. Physiological-ecological studies of two sandy beach Gastropoda from South Africa; *Bullia digitalis* Meuschen and *Bullia laevissima* (Gmelin). *Z. Morph. Okol. Tiere* *49*: 629-657.

Brown, A.C. 1964. Food relationships on the intertidal sandy beaches of the Cape Peninsula. *S. Afr. J. Sci*. *60*: 35-41.

Brown, A.C. 1971a. The ecology of sandy beaches of the Cape Peninsula, South Africa. Part 1: Introduction. *Trans. roy. Soc S. Afr.* *39*: 247-279.

Brown, A.C. 1971b. The ecology of sandy beaches of the Cape Peninsula, South Africa. Part 2: The mode of life of *Bullia* (Gastropoda: Prosobranchiata). *Trans. roy. Soc. S. Afr.* *39*: 281-320.

Brown, A.C. 1973. The ecology of sandy beaches of the Cape Peninsula, South Africa. Part 4: Observations on two intertidal Isopoda; *Eurydice longicornis* (Studer) and *Exosphaeroma truncatitelson* Barnard. *Trans. roy. Soc. S. Afr.* *40*: 381-404.

Brown, A.C. 1978. Oxygen consumption of the sandy beach whelk *Bullia digitalis* Meuschen at different levels of activity. *Comp. Biochem. Physiol.* *62A*: 673-675.

Brown, A.C. 1979a. Respiration and activity in the sandy-beach whelk *Bullia digitalis* (Dillwyn) (Nassariidae). *S. Afr. J. Sci*. *75*: 451-452.

Brown, A.C. 1979b. The energy cost and efficiency of burrowing in the sandy beach whelk *Bullia digitalis* (Dillwyn) (Nassariidae). *J. exp. mar. Biol. Ecol.* *40*: 149-154.

Brown, A.C. In press. The biology of sandy-beach whelks of the genus *Bullia* (Nassariidae). *Oceanogr. mar. Biol. Ann. Rev.* *20*.

Brown, A.C., Ansell, A.D. and Trevallion, A. 1978. Oxygen consumption by *Bullia* (Dorsanum) *melaniodes* (Deshayes) and *Bullia digitalis* Meuschen (Gastropoda, Nassariidae) - an example of non-acclimation. *Comp. Biochem. Physiol.* *61A*: 123-125.

Brown, A.C., Baissac, P. de B. and Leon, B. 1974. Observations on the effects of crude oil pollution on the sandy beach snail *Bullia* (Gastropoda: Prosobranchiata). *Trans. roy. Soc. S. Afr.* *41*: 19-24.

Brown, A.C. and Currie, A.B. 1973. Tolerance of *Bullia digitalis* (Prosobranchiata) to solutions of ammonium nitrate in natural seawater. *S. Afr. J. Sci.* *69*: 219-220.

Brown, A.C. and Jarman, N. 1978. Coastal marine habitats. In: Werger, M.J.A. (ed.) Biogeography and ecology of Southern Africa. Junk, The Hague.

Brown, A.C. and da Silva, F.M. 1978. The effects of temperature on oxygen consumption in Bullia digitalis (Gastropoda, Nassariidae). Comp. Biochem. Physiol. 62A: 573-576.

Brown, A.C. and Talbot, M.S. 1972. The ecology of sandy beaches of the Cape Peninsula. Part 3: A study of Gastrosaccus psammodytes Tattersall (Crustacea; Mysidacea). Trans. roy. Soc. S. Afr. 40: 309-333.

Bruce, N.L. 1980. Cirolanidae (Crustacea: Isopoda) of Australia. Heron Island and Capricorn group. Bull. mar. Sci. 30: 108-130.

Brusca, G.J. 1966. Studies on the salinity and humidity tolerances of five species of isopods in a transition from marine to terrestrial life. Bull. Sth. Calif. Acad. Sci. 65: 146-154.

Brusina, K. 1866. Fauna Moll. Dalmat. 1866: 42. Reference incomplete, see Zoological Record, 1866.

Burger, O. 1892. Zur Kenntnis der Nemertinen des Golfes von Neapel. Vorlaüfige Mitt. Nachr. Ges. Göttingen 1982: 137-178.

Burger, O. 1893. Sudgeorgische und andere exotische Nemertinen. Zool. Jb. (Syst.) 7: 207-240.

Burger, O. 1895a. Beitrage zur Anatomie, Systematik und geographischen Verbreitung der Nemertinen. Z. wiss. Zool. 61: 16-37.

Burger, O. 1895b. Die Nemertinen des Golfes von Neapel und den angrenzenden Meeres-Abschnitte. Fauna u. Flora d. Golfes v. Neapel 22: 743.

Burger, O. 1903. Die Nemertinen. Fauna Arctica 3: 57-64.

Burger, O. 1904. Nemertinien. In: Expedition Antartique Belge, Résultats du voyage du S.Y. Belgica. Rapports Scientifiques, Zoologie, Anvers.

Cabioch, L., L'Hardy, J-P. and Rullier, F. 1967. Inventaire de la faune marine de Roscoff: Annelides (nouvelle édition). Trav. Stn. biol. Roscoff 17: 1-94.

Cameron, C.L., Cameron, I.F. and Paterson, C.G. 1979. Contribution of organic shell matter to biomass estimates of unionid bivalves. Can. J. Zool. 57: 1666-1669.

Carpenter, E.J. 1976. Plastics, pelagic tar and other litter. In: Goldberg, E.D. (ed.) Strategies for marine pollution monitoring. Wiley Interscience, New York.

Carr. C.E. 1976. Distribution pattern of the intertidal macrofauna at Langebaan Lagoon. Unpublished project, Zoology Dept., University of Cape Town.

Carvacho, A. 1977. Isopodes intertidaux des côtes du centre et du nord du Chili. 1. Familles des Cirolanidae, Excorallanidae et Corallanidae. *Crustaceana* *32*: 27-44.

Cassie, R.M. 1954. Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. mar. Freshwat. Res.* *5*: 513-522.

Chamberlin, R.V. 1919. Reports of the Scientific Research Expeditions of the U.S. Fishery steamer "Albatross" 1891, 1899-1900 and 1904-1905. The Annelida Polychaeta. *Mem. Mus. comp. Zool. Harvard* *48*: 1-514.

Chamberlin, R.V. 1920. Polychaeta. *Rep. Can. arct. Exped., 1913-18, Ottawa* *9*: 1-41.

Chapman, G. 1949. The thixotropy and dilatancy of a marine soil. *J. mar. biol. Ass. U.K.* *28*: 123-140.

Chapuis, F. 1886. Note sur quelques nêmertes rêcoltées à Roscoff dans le courant du mois d'Aout, 1885. *Arch. Zool. exp.* *1*: 21-24.

Chevreux, E. 1915. Amphipodes de la Nouvelle Caledonie et des Îles Loyalty. *J. Nov. Caled. Zool.* *2*: 1-14.

Chevreux, E. and Fage, L. 1925. *Faune de France. 9: Amphipodes.* Le Chevalier, Paris.

Clark, R.B., Alder, J. and McIntyre, A.D. 1962. The distribution of *Nephtys* on the Scottish coast. *J. Anim. Ecol.* *31*: 359-372.

Clark, R.B. and Jones, M.L. 1955. Two new *Nephtys* (Annelida Polychaeta) from San Fransisco Bay. *J. Wash. Acad. Sci.* *45*: 143-146.

Clifton, H.E., Hunter, R.E. and Phillips, R.L. 1971. Depositional structures and processes in the non-barred high-energy nearshore. *J. sedim. Petrol.* *41*: 651-670.

Coe, W.R. 1901. Papers from the Harriman Alaska Expedition. 20: the nemerteans. *Proc. Wash. Acad.* *3*: 1-110.

Coe, W.R. 1903. The nemerteans of Porto Rico. *Bull. U.S. Fish. Comm.* *20*: 225-229.

Coe, W.R. 1940. Revision of the nemertean fauna of the Pacific coasts of North, Central and Northern South America. *Reps. Allan Hancock Pacific Exped., 1932-38* *22*(13): 247-322.

Coe, W.R. 1951. The nemertean faunas of the Gulf of Mexico and of southern Florida. *Bull. mar. Sci. Gulf Caribbean* *1*: 149-186.

Coe, W.R. 1955. Ecology of the bean clam, *Donax gouldii* on the coast of southern California. *Ecology* *36*: 512-514.

Coe, W.R. and Kunkel, B.W. 1903. A new species of nemertean (*Cerebratulus melanops*) from the Gulf of St Lawrence. *Biol. Bull.* *4*: 119-124.

Coen, G. 1925. Sul _Donax excaratus_ Krauss. _Atti Acc. scient. veneto-trent. Padova Ser. 3_ _15_: 44-45.

Coen, G. 1937. Nuovo saggio di una Sylloge molluscorum adriaticorum. _R. Com. talassogr. Ital. Mem. Venezia_ _240_: 1-173.

Coifmann, I. 1937a. Misidacei raccolti dalla R. Corvetta "Vettor Pisani" negli anni 1882-85. _Annu. Mus. Zool. Univ. Napoli_ _7_(3): 1-14.

Coifmann, I. 1937b. Misidacei de Mar Rosso. Studio del materiale raccolto dal Prof. L. Sanzo durante la campagna idrografica della R. Nave Ammiraglio Magnaghi (1923-24). _Mem. Com. talassogr. Ital. Venezia_ _233_: 1-52.

Colvin, P.M. 1969. On the determination of dissolved oxygen in sandy beaches. Unpublished project, Zoology Dept., University of Cape Town.

Connolly, C.M. 1974. _Bullia ancillaeformis_ found in False Bay. _Strandloper_ _168_: 6.

Corey, S. 1970. The quantitative distribution of Cumacea (Crustacea; Peracarida) in Kames Bay, Scotland. _Can. J. Zool._ _48_: 925-930.

Correa, D.D. 1957. Nemertinos do litoral brasileiro: VI. _Anais Acad. bras. Cienc._ _29_: 251-272.

Correa, D.D. 1961. Nemerteans from Florida and the Virgin Islands. _Bull. mar. Sci. Gulf Caribbean_ _11_: 1-44.

Crichton, M.D. 1943. Some notes on the Madras _Bullia_. _Proc. malac. Soc. Lond._ _25_: 143-146.

Croker, R.A. 1968. Distribution and abundance of some intertidal sand beach amphipods accompanying the passage of two hurricanes. _Chesapeake Sci._ _9_: 157-162.

Croker, R.A. 1970. Intertidal sand macrofauna from Long Island, New York. _Chesapeake Sci._ _11_: 134-137.

Croker, R.A., Hager, R.P. and Scott, K.J. 1975. Macroinfauna of northern New England marine sand. II Amphipod-dominated intertidal communities. _Can. J. Zool._ _53_: 42-51.

Crosse, V. and Fischer, J. 1864. Faune malacologique de Cochinchine. Premier supplement. _J. Conch., Paris_ _11_: 322-338.

Cruz, M.P. 1977. Bivalvos de la platforma continental de la region norte de Ecuador. _Publ. Inocar._ _1_: 1-55.

Cummins, K.W. and Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. _Mitt. int. Verein theor. angew. Limnol._ _18_: 1-158.

Currie, B. and Cook, P.A. 1975. Report on biological investigations for the proposed ESCOM nuclear power station at Duynefontein. Unpublished report, Zoology Dept., University of Cape Town.

Cuthbert, K.C., Brown, A.C. and Orren, M.J. 1976a. Cadmium concentration in the tissues of Bullia digitalis (Prosobranchiata) from the South African west coast. S. Afr. J. Sci. 72: 57.

Cuthbert, K.C., Brown, A.C. and Orren, M,J. 1976b. Toxicity of cadmium to Bullia digitalis (Prosobranchiata, Nassariidae). Trans. roy. Soc. S. Afr. 42: 203-208.

Dahl, E. 1952. Some aspects of the ecology and zonation of the fauna on sandy beaches. Oikos 4: 1-27.

Dale, N.G. 1974. Bacteria in intertidal sediments; factors related to their distribution. Limnol. Oceanogr. 19: 509-518.

Dales, R.P. 1967. Annelids. Hutchinson, London.

Dame, R.F. and Vernberg, F.J. 1978. The influence of constant and cyclic acclimation temperatures on the metabolic rates of Panopeus herbstii and Uca pugilator. Biol. Bull. 154: 188-197.

Dauer, D.M. and Simon, J.L. 1975. Lateral or along-shore distribution of the polychaetous annelids of an intertidal, sandy habitat. Mar. Biol. 31: 363-370.

Dauer, D.M. and Simon, J.L. 1976. Habitat expansion among polychaetous annelids repopulating a defaunated marine habitat. Mar. Biol. 37: 169-177.

Dautzenberg, P. and Fisher, H. 1907. Contribution à la faune malacologique de l'Indo-Chine. J. Conch. Paris 54: 145-226.

Davies, J.L. 1972. Geographical variation in coastal development. Oliver and Boyd, Edinburgh.

Davis, R.A. 1979. The beach and the nearshore zone. In: Davis, R.A. (ed.) Coastal sedimentology environments. Springer, New York.

Day, J.A. 1975. Southern African Cumacea. Part 1: family Bodotriidae, subfamily Vaunthompsoniinae. Ann. S. Afr. Mus. 66: 177-220.

Day, J.A. 1978. Southern African Cumacea. Part 2: family Bodotriidae, subfamily Bodotriinae. Ann. S. Afr. Mus. 75: 159-290.

Day, J.H. 1959. The biology of Langebaan Lagoon: a study of the effects of shelter from wave action. Trans. roy. Soc. S. Afr. 35: 475-547.

Day, J.H. 1967a. The biology of Knysna estuary, South Africa. In: Lauff, J.H. (ed.) Estuaries. American Association for the Advancement of Science, Washington.

Day, J.H. 1967b. A monograph on the Polychaeta of South Africa. British Museum, London.

Day, J.H. 1974. A guide to marine life on South African shores. 2nd ed. A.A. Balkema, Cape Town.

Day, J.H. (ed.). 1981. The estuaries of southern Africa. A.A. Balkema, Cape Town.

Day, R.W. 1977. Two contrasting effects of predation on species richness in coral reef habitats. Mar. Biol. 44: 1-6.

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351-389.

Dayton, P.K. and Hessler, R.R. 1972. Role of biological disturbances in maintaining diversity in the deep sea. Deep Sea Res. 19: 199-208.

De Castro, A.L. 1952. Sobre a occurrencia do genero Tylos latreille no litoral Brasileiro (Isopoda, Tylidae). Bolm. Mus. nac. Rio de Janeiro, Brasil, N.S. Zool. 107: 1-17.

De Castro, A.L. and Brum, I.N.da S. 1969. On the species of Excirolana Richardson of the Altantic littoral of the Americas (Isopoda, Cirolanidae). Bolm. Mus. nac. Rio de Janeiro, Brasil, N.S. Zool. 271: 1-21.

De Silva, P.H.D.H. 1965. New species and records of polychaeta from Ceylon. Proc. zool. Soc., Lond. 144: 537-563.

De Villiers, G. 1975a. Reproduction of the white sand mussel Donax serra Röding. Investl. Rep. Sea Fish. Branch S. Afr. 102: 1-33.

De Villiers, G. 1975b. Growth, population dynamics, a mass mortality and arrangement of white sand mussels, Donax serra Röding. Investl. Rep. Sea Fish. Branch S. Afr. 109: 1-31.

Dexter, D.M. 1969. Structure of an intertidal sandy-beach community in North Carolina. Chesapeake Sci. 10: 93-98.

Dexter, D.M. 1972. Comparison of the community structures in a Pacific and Atlantic Panamanian sandy beach. Bull. mar. Sci. 22: 449-462.

Dexter, D.M. 1974. Sandy beach fauna of the Pacific and Atlantic coasts of Costa Rica and Colombia. Revta. biol. Trop. 22: 51-66.

Dexter, D.M. 1976. The sandy beach fauna of Mexico. Southwest. Nat. 20: 479-485.

Dexter, D.M. 1977. Natural history of the Pan-American sand beach isopod _Excirolana braziliensis_ (Crustacea: Malacostraca). _J. Zool., Lond._ _183_: 103-109.

Dexter, D.M. 1979. Community structure and seasonal variation in intertidal Panamanian sandy beaches. _Estuar. coastl. mar. Sci._ _9_: 543-558.

Ditvelsen, H. 1937. Polychaeta. The Godthaab Expedition, 1928. _Medd. Grønland._ _80_(4): 1-64.

Driscoll, E.G. 1967. Experimental field study of shell abrasion. _J. sedim. Petrol._ _34_: 1117-1123.

Driscoll, E.G. 1975. Sediment-animal-water interaction, Buzzards Bay, Massachusetts. _J. mar. Res._ _33_: 275-302.

Duncan, J.R. 1964. The effects of water table and tide cycle on swash-backwash sediment distribution and beach profile development. _Mar. Geol._ _2_: 186-197.

Dunker, W. 1865. Part 9. In: Pfeiffer, L. and Dunker, W. (eds.) _Novitates Conchologicae._ Fischer, Cassel.

Dwivedi, S.N., Ayyappan Nair, S. and Rahim, A. 1973. Ecology and production of intertidal macrofauna during monsoon in a sandy beach at Calangute, Goa. _J. mar. biol. Ass. India_ _15_: 274-284.

Dye, A.H. 1978a. An ecophysiological study of the meiofauna of Swartkops estuary. 1. Physical and chemical features. _Zool. afr._ _13_: 1-18.

Dye, A.H. 1978b. Diurnal vertical migrations of meiofauna in an estuarine sand flat. _Zool. afr._ _13_: 201-206.

Dye, A.H. 1978c. Seasonal fluctuations in the vertical distribution of meiofauna in estuarine sediments. _Zool. afr._ _13_: 207-212.

Dye, A.H. 1979a. The effect of acute and long term temperature changes on the respiration of two sand-dwelling bivalves. _Comp. Biochem. Physiol._ _63A_: 405-409.

Dye, A.H. 1979b. Measurement of biological oxygen demand in sandy beaches. _S. Afr. J. Zool._ _14_: 55-60.

Dye, A.H. 1980a. Aspects of the respiratory physiology of _Gastrosaccus psammodytes_ Tattersall (Crustacea: Mysidacea). _Comp. Biochem. Physiol._ _65A_: 187-191.

Dye, A.H. 1980b. Tidal fluctuations in biological oxygen demand in exposed sandy beaches. _Estuar. coastl. mar. Sci._ _11_: 1-18.

Dye, A.H., Erasmus, T. and Furstenberg, J.P. 1978. An ecophysiological study of the meiofauna of the Swartkops estuary. 3. Partition of benthic oxygen consumption and the relative importance of the meiofauna. _Zool. afr._ _13_: 187-200.

Dye, A.H. and Furstenberg, J.P. 1978. An ecophysiological study of the meiofauna of the Swartkops estuary. 2. The meiofauna: composition, distribution, seasonal fluctuation and biomass. Zool. afr. 13: 19-32.

Dye, A.H. and McGwynne, L. 1980. The effect of temperature and season on the respiratory rates of three psammolittoral gastropods. Comp. Biochem. Physiol. 66A: 107-111.

Dye, A.H., McLachlan, A. and Wooldridge, T. 1980. The ecology of sandy beaches in Natal. Unpublished manuscript.

Eagle, G.A., Fricke, A.H., Gledhill, W.J., Greenwood, P.J., Orren, M.J. and Mazure, H. 1977. Camps Bay beach: a pollution survey. S. Afr. J. Sci. 73: 342-345.

Edgren, R.E. 1959. Coquinas (Donax variabilis) on a Florida beach. Ecology 40: 498-502.

Edwards, D.C. 1969. Zonation by size as an adaptation for intertidal life in Olivella biplicata. Am. Zoologist 9: 399-417.

Edwards, G.A. and Irving, L. 1943. The influence of temperature and season upon the oxygen consumption of the sand crab Emerita talpoida Say. J. cell. comp. Physiol. 21: 169-182.

Edwards, R.R.C. 1973a. Production ecology of two Caribbean marine ecosystems. I. Physical environment and fauna. Estuar. coastl. mar. Sci. 1: 303-318.

Edwards, R.R.C. 1973b. Production ecology of two Caribbean marine ecosystems. II. Metabolism and energy flow. Estuar. coastl. mar. Sci. 1: 319-333.

Efford, I.E. 1976. Distribution of the sand crabs in the genus Emerita (Decapoda, Hippidae). Crustaceana 30: 169-183.

Ehlers, E. 1897. Polychaeta. Hamb. Maghaelanische Sammelreise 1: 1-148.

Ehlers, E. 1901. Die Polychaeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. Festschrift zur Feier des 150 jahrigen Bestehens des koniglichen Gesellschaft der Wissenshaften zur Göttingen. Abh. Math.-Phys. Berlin, Wiedmannsche Buchhandlung: 1-232.

Ehlers, E. 1913. Die Polychaeten-Sammlung der Deutcher Südpolar-Expedition, 1901-03. D. Südpolar-Exped. 13: 397-598.

Ehlers, E. 1918. Polychaete Anneliden von den Aru- und Kei-Inseln. Frankfurt-am-Main Abh. Senckenberg. Ges. 35: 227-250.

Ehrenbaum, E. 1897. Beitrage zur Meeresfauna von Helgoland. VIII. Die Cumaceen und Schizopoden von Helgoland, nebst neuern Beobachtungen uber ihr Vorkommen in der deutchen Bucht und in der Nordsee. Wiss. Meeresunters. 2: 401-435.

Ekman, S. 1953. Zoogeography of the sea. Sidgwick and Jackson, London.

Eliason, A. 1951. Polychaeta. Rep. Swedish Deep-Sea exped. Zool. 2(11): 1-98.

Eleftheriou, A. and Jones, D.A. 1976. The genus Eurydice on the west coast of India. J. Zool., Lond. 178: 385-394.

Eleftheriou, A. and Nicholson, M.D. 1975. The effects of exposure on beach fauna. Cah. Biol. mar. 16: 695-710.

Elkaim, B. 1963. Présence au Maroc de Talorchestia spinifera. Bull. Soc. Sci. nat. Maroc 43: 169-191.

Enright, J.T. 1963. The tidal rhythm of activity of a sand-beach amphipod. Z. vergl. Physiol. 46: 276-313.

Enright, J.T. 1965. Entrainment of a tidal rhythm. Science 147: 864-867.

Enright, J.T. 1972. A virtuoso isopod: circa-lunar rhythms and their tidal fine structure. J. comp. Physiol. 77: 141-162.

Epelde-Aguirre, A. and Lopez, M.T. 1975. Zonacion en el sustrato arenoso de Playa Blanca, Bahia de Coronel y observaciones sobre crustaceos poco frecuentes. Bol. Soc. biol. de Concepcion 49: 161-170.

Fauchald, K. 1963. Nephtyidae (Polychaeta) from Norwegian waters. Sarsia 13: 1-32.

Fauchald, K. 1977. Polychaetes from intertidal areas in Panama with a review of previous shallow-water records. Smithson. Contrib. Zool. 221: 1-81.

Fauvel, P. 1933. Mission Robert Ph. Dollfus en Egypte. Annélide Polychètes. Mém. Inst. égypt. 21: 31-83.

Fauvel, P. 1953. Annelida: Polychaeta. In: Sewell, R.B.S. (ed.) Fauna of India. Indian Press, Allahabad.

Ferrara, F. 1974. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 3: Terrestrial isopods. Monitore zool. ital., Suppl. 5: 191-220.

Fincham, A.A. 1971. Ecology and population studies of some intertidal and sub-littoral sand-dwelling amphipods. J. mar. biol. Ass. U.K. 51: 471-488.

Fincham, A.A. 1974. Intertidal sand-dwelling peracarid fauna of Stewart Island. N.Z. J. mar. Freshwat. Res. 8: 1-14.

Fincham, A.A. 1977. Intertidal sand-dwelling peracarid fauna of North Island, New Zealand. N.Z. J. mar. Freshwat. Res. 11: 677-696.

Fischer-Piette, E. 1941. Description de nouvelles espèces de Donax et Heterodonax. Bull. Mus. Hist. nat. Paris 13: 556-560.

Fish, J.D. and Fish, S. 1972. The swimming rhythm of Eurydice pulchra Leach and a possible explanation of intertidal migration. J. exp. mar. Biol. Ecol. 8: 195-200.

Fish, S. 1970. The biology of Eurydice pulchra (Crustacea: Isopoda). J. mar. biol. Ass. U.K. 50: 753-758.

Flemming, B.W. 1977. Depositional processes in Saldanha Bay and Langebaan Lagoon. Univ. Cape Town mar. Geosci. Grp. Bull. 8: 1-215.

Forêt-Montardo, P. 1969. Etude systematique et ecologie des Nephtydidae des parages de Marseille. Tethys 1: 80-832.

Fox, R.S. and Byrnum, K.H. 1975. The amphipod crustaceans of North Carolina estuarine waters. Chesapeake Sci. 16: 223-237.

Franca, M.L.P. 1955a. Contribuçāo para o conhecimento da fauna malacologia de Angola. Gasteropodes testáceos. Trab. Miss. Biol. Mar., Lisbon.

Franca, M.L.P. 1955b. Contribuçāo para o conhecimento da fauna malacologia de Angola. Moluscos bivalves. Trab. Miss. Biol. Mar., Lisbon.

Fricke, A.H. 1980. Meiofauna extraction efficiency by a modified Oostenbrink apparatus. Helgoländer wiss. Meeresunters. 32: 436-443.

Fricke, A.H., Hennig, H.F-K.O., Greenwood, P.J. and Eagle, G.A. Submitted for publication. Relationships between meiofaunal population densities and physico-chemical properties of unpolluted sand beaches.

Friedrich, H. 1958. Nemertini. In: Fridrikson et al. (eds.) Zoology of Iceland. Reijkjavik.

Friedrich, H. 1970. Nemertinen aus Chile. Report No. 47 of the Lund University Chile expedition, 1948-1949. Sarsia 40: 1-80.

Gandarsson, A. 1973. Nyjungar um isleuzka burstaorma. Natturufroedingurinn 43: 77-91.

Garstang, W. 1892. On some new or rare marine animals recently discovered on the coast of Devonshire. Rep. Trans. Devon Ass. 24: 381-383.

Gaudette, H.E., Flight, W.R., Toner, L. and Folger, D.W. 1974. An inexpensive titration method for the determination of organic carbon in Recent sediments. J. sedim. Petrol. 44: 249-253.

Gauld, D.T. and Buchanan, J.B. 1956. The fauna of sandy beaches in the Gold Coast. Oikos 7: 293-301.

Gehman, H.H. 1962. Organic matter in limestones. Geochim. Cosmochim. Acta 26: 885-897.

Gerlach, S.A. 1971. On the importance of marine meiofauna for benthos communities. Oecologia 6: 176-190.

Gerlach, S.A. 1977. Attraction to decaying organisms as a possible cause for patchy distribution of nematodes in a Bermuda beach. Ophelia 16: 151-165.

Gibbs, P.E. 1971. The polychaete fauna of the Solomon Islands. Bull. Br. Mus. nat. Hist. (Zool.) 21: 101-211.

Gibbs, P.E. 1972. Polychaete annelids from the Cook Islands. J. Zool., Lond. 168: 199-220.

Giere, O. 1975. Population structure, food relations and ecological role of marine oligochaetes, with special reference to meiobenthic species. Mar. Biol. 31: 139-156.

Giere, O. 1979. Some apparatus for preference experiments with meiofauna. J. exp. mar. Biol. Ecol. 41: 125-131.

Glynn, P.W., Dexter, D.M. and Bowman, T.E. 1976. Excirolana braziliensis, a Pan-American sand beach isopod: taxonomic status, zonation and distribution. J. Zool., Lond. 175: 509-521.

Gould. S.J. 1980. Ever since Darwin. Reflections in natural history. Pelican Books, Harmondsworth.

Grange, K.R. 1977. Littoral benthos-sediment relationships in Manakau Harbour, New Zealand. N.Z. J. mar. Freshwat. Res. 11: 111-123.

Grant, U.S. 1948. Influence of the water table on beach aggradation and degradation. J. mar. Res. 7: 655-660.

Gravier, C. 1906. Contribution a l'étude des annélides polychètes de la Mer Rouge. Nouv. Archs. Mus. Hist. nat., Paris (Ser 4) 8: 123-272.

Gray, J.S. 1971. Factors controlling population locatizations in polychaete worms. Vie Milieu Supp. 22: 702-722.

Gray, J.S. and Rieger, R.M. 1971. A quantitative study of the meiofauna of an exposed sandy beach at Robin Hood's Bay, Yorkshire. J. mar. biol. Ass. U.K. 51: 1-19.

Gregory, M.R. 1977. Plastic pellets on New Zealand beaches. Mar. Poll. Bull. 8: 82-84.

Griffiths, C.L. 1976. Guide to the benthic marine amphipods of southern Africa. South African Museum, Cape Town.

Griffiths, C.L. and Stenton-Dozey, J. In press. Stranded kelp its fauna and degradation. Estuar. coastl. Shelf Sci.

Griffiths, D. 1977. Caloric variation in crustacea and other animals. J. Anim. Ecol. 46: 593-605.

Griffiths, R.J. 1977. Thermal stress and the biology of Actinia equina L. (Anthozoa). J. exp. mar. Biol. Ecol. 27: 141-154.

Gunter, G. 1979. Notes on sea beach ecology. Food sources on sandy beaches and localized diatom blooms bordering Gulf beaches. Gulf Res. Reps. 6: 305-307.

Halcrow, K. and Boyd, C.M. 1967. The oxygen consumption and swimming activity of the amphipod Gammarus oceanicus at different temperatures. Comp. Biochem. Physiol. 23: 233-242.

Hanekom, N. 1975. a study of Donax serra in the eastern Cape. Unpublished M.Sc. thesis, University of Port Elizabeth.

Hanley, S. 1882. Descriptions of new species of Donax. J. linn. Soc. 16: 539-541.

Harding, J.P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. mar. biol. Ass. U.K. 28: 141-153.

Hart, T.J. and Currie, R.I. 1960. The Benguela current. Discovery Reps. 31: 127-297.

Hartman, O. 1938. Review of the annelid worms of the family Nephtydae from the northeast Pacific, with descriptions of five new species. Proc. U.S. natn. Mus. 85: 143-158.

Hartman, O. 1940. Polychaetous annelids. Part II. Chrysopetalidae to Gonianidae. Reps. Allan Hancock Pacific Exped., 1932-38. 7: 173-287.

Hartman, O. 1942. Report on the scientific results of the Atlantic expeditions to the West Indies under the auspices of the University of Havana and Harvard University. The polychaetous annelida. Mem. Soc. cub. Hist. nat. Felipe Poey 16: 89-104.

Hartman, O. 1953. Non-pelagic polychaeta of the Swedish Antarctic Expedition, 1901-1903. Further zool. Results Swed. Antarct. Exped. 4(11): 1-83.

Hartman, O. 1959. Catalogue of the polychaetous annelids of the world. Part 1. Allan Hancock occ. Pap. 23: 1-650.

Hartmann-Schröder, G. 1959. Zur Okologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador. Beitr. neotrop. Fauna 1: 69-183.

Hartmann-Schröder, G. 1960. Zur Polychaeten-Fauna von Peru. Beitr. neotrop. Fauna 2: 1-44.

Hartmann-Schröder, G. 1971. Annelida, Borstenwurmer, Polychaeta. In: Dahl, F. (ed.) Die Tierwelt Deutschlands. Fischer, Jena.

Hartmann-Schröder, G. 1974. Zur kenntnis des Eulitorals der Afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der Afrikanischen Ostküste von Südafrika und Mozambique unter besonderer Beruksichtigung der Polychaeten und Ostracoden. Teil 2. Die Polychaeten des Untersuchungsgebietes. Mitt. Hamb. zool. Mus. Inst. 69(Suppl.): 5-94.

Hartmann-Schröder, G. and Stripp, K. 1968. Beitrage zur Polychaetenfauna der Deutschen Bucht. Veroff. Inst. Meeresforsch. Bremerh. 11: 1-24.

Hayes, W.B. 1969. Ecological studies on the high-beach isopod Tylos punctatus, Holmes and Gay. Unpublished Ph.D. thesis, University of California, San Diego.

Hayes, W.B. 1974. Sand-beach energetics: importance of the isopod Tylos punctatus. Ecology 55: 838-847.

Hayes, W.B. 1977. Factors affecting the distribution of Tylos punctatus (Isopoda, Oniscoidea) on beaches in southern California and northern Mexico. Pacific Sci. 31: 165-186.

Hedgpeth, J.W. 1957. Marine biogeography. Geol. Soc. Am. Mem. 67: 359-382.

Hedley, C. 1913. Studies on Australian mollusca. Part 11. Proc. linn. Soc. N.S.Wales 38: 258-339.

Heinen, A. 1911. Die Nephtydeen und Lycorideen der Nord- und Ostsee, einschliesslich der verbindenden Meeresteile. Wiss. Meeresunters. Kiel Abt. Kiel N. F. 13: 1-87.

Hemmingsen, A.M. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rep. Steno meml. Hosp. 9: 7-110.

Hibbert, C.J. 1977. Biomass and production of a bivalve community on an intertidal mud-flat. J. exp. mar. Biol. Ecol. 25: 249-262.

Hoagland, R. 1920. Polychaetous annelids collected by the U.S. Fisheries steamer Albatross during the Philippine expedition of 1907-1909. Smithson. Inst. U.S. natn. Mus. Bull. 100: 603-634.

Hodgson, A.N. In prep. Studies on wound healing and regeneration of the siphons of the bivalve Donax serra (Röding).

Holanov, S.H. and Hendrickson, J.R. 1980. The relationship of sand moisture to burrowing depth of the sand beach isopod Tylos punctatus. J. exp. mar. Biol. Ecol. 46: 81-88.

Holland, A.F. and Polgar, T.T. 1976. Seasonal changes in the structure of an intertidal community. Mar. Biol. 37: 341-348.

Hulings, N.C. and Gray, J.S. 1976. Physical factors controlling abundance of meiofauna on tidal and atidal beaches. Mar. Biol. 34: 77-83.

Hummon, W.D., Fleeger, J.W. and Hummon, M.R. 1976. Meiofauna -macrofauna interactions: 1. Sand beach meiofauna affected by maturing Limulus eggs. Chesapeake Sci. 17: 297-299.

Hurley, D.E. 1956. Studies on New Zealand amphipodan fauna. No. 13. Sandhoppers of the genus Talorchestia. Trans. roy. Soc. N.Z. 84: 359-389.

Hurley, D.E. 1961. A checklist and key to the crustacean Isopoda of New Zealand and subantarctic islands. Trans. roy. Soc. N.Z. (Zool.) 1: 259-292.

Hurley, D.E. 1968. Transition from water to land in amphipod crustaceans. Am. Zool. 8: 327-353.

Imajima, M. 1967. Errant plychaetous annelids from Tsukumo Bay and vicinity of Noto Peninsula, Japan. Bull. natn. Sci. Mus. Tokyo 10: 403-441.

Imbach, M.C. 1967. Gammaridean amphipoda from the South China Sea. Naga Rep. 4: 39-167.

Intes, A. and Le Loeuff, P. 1975. Les annēlides polychētes de Cȏte D'Ivoire. 1. Polychētes errantes - compte rendu systēmatique. Cah. Off. Rech. scient. tech. Outre-Mer (Oceanogr.) 13: 267-321.

Irwin, T.H. 1973. The intertidal behaviour of the bean clam, Donax gouldii Dall 1921. Veliger 15: 206-212.

Isler, E. 1900. Beitrage zur Kenntnis der Nemertinen. Zool. Anz. 23: 177-180.

Iwata, F. 1952. Nemertini from the coasts of Kyusyu. J. Fac. Sci. Hokkaido Univ. (4) Zool. 11: 126-148.

Iwata, F. 1957. Nemerteans from Sagami Bay. Publ. Akkeshi mar. biol. Sta. 7: 1-31.

James, C.J. and Gibson, R. 1980. The distribution of the polychaete Capitella capitata (Fabricius) in dock sediments. Estuar. coastl. mar. Sci. 10: 671-683.

Jickeli, C.F. 1882. Diagnosen neuer Conchylien. Z. Berl. mal. Ges. 9: 336-370.

Johnson, R.G. 1965. Temperature variation in the infaunal environment of a sand flat. Limnol. Oceanogr. 10: 114-120.

Johnson, R.G. and Juskevice, J.A. 1965. Check list of marine invertebrates of the Tomales Bay region, Marin County, California. Pacific mar. Sta. Res. Rep. 5: 1-78.

Johnson, W.S. 1976a. Biology and population dynamics of the intertidal isopod Cirolana harfordi. Mar. Biol. 36: 343-350.

Johnson, W.S. 1976b. Population energetics of the intertidal isopod Cirolana harfordi. Mar. Biol. 36: 351-357.

Jones, D.A. 1969. The genus Eurydice (Crustacea: Isopoda) in the Aegean Sea, including E. longispina sp. nov. Cah. Biol. mar. 10: 15-29.

Jones, D.A. 1971. The systematics and ecology of some sand beach isopods (Crustacea: Eurydicidae) from the coast of Kenya. J. Zool., Lond. 165: 201-207.

Jones, D.A. 1974. The systematics and ecology of some sand beach isopods (family Cirolanidae) from the coasts of Saudi Arabia. Crustaceana 26: 202-211.

Jones, D.A. 1979. The ecology of sandy beaches in Penang, Malaysia, with special reference to Excirolana orientalis (Dana). Estuar. coastl. mar. Sci. 9: 677-682.

Jones, D.A., Knight-Jones, E.W., Moyse, J., Babbage, P.C. and Stebbing A.R.D. 1968. Some biological problems in the Aegean. Underwater Ass. Rep. 1968: 73-78.

Jones, D.A. and Naylor, E. 1967. The distribution of Eurydice (Crustacea: Isopoda) in British waters, including E. affinis new to Britain. J. mar. biol. Ass. U.K. 47: 373-382.

Jones, D.A. and Naylor, E. 1970. The swimming rhythm of the sand beach isopod Eurydice pulchra. J. exp. mar. Biol. Ecol. 4: 188-199.

Joubin, L. 1893. Note sur un Cerebratulus de la Mer Rouge. Rev. biol. Nord France 5: 66-69.

Joubin, L. 1904. Note sur quelques némertes receuillies par M. Ch. Gravier dans le Golfe de Tadjourah, Mer Rouge. Bull. Mus. Paris 6: 326-343.

Joubin, L. 1906. Notes sur un némertien receuilli au Tonkin par M. Louis Boutan. Bull. Soc. zool. Paris 30: 144-147.

Joubin, L. and François, P. 1892. Notes sur quelques némertes de Nouméa. Rev. Biol. 4: 161-172.

Kay, D.G. and Knights, R.D. 1975. The macroinvertebrate fauna of the intertidal soft sediments of south east England. J. mar. biol. Ass. U.K. 55: 811-832.

Kensley, B.F. 1972. Behavioural adaptations of the isopod Tylos granulatus Krauss. Zool. afr. 7: 1-4.

Kensley, B.F. 1973. Sea-shells of southern Africa. Gastropods. Maskew Miller, Cape Town.

Kensley, B.F. 1974. Aspects of the biology and ecology of the genus Tylos. Ann. S. Afr. Mus. 65: 401-471.

Kensley, B.F. 1978. Guide to the marine isopods of southern Africa. South African Museum, Cape Town.

Kilburn, R.N. 1978. Four new Bullia species (Mollusca: Gastropoda: Nassariidae) from Kenya and Mozambique. Ann. Natal Mus. 23: 297-303.

King, C.A.M. 1951. Depth of disturbance of sand on sea beaches by waves. J. sedim. Petrol. 21: 131-140.

King, J. 1974. Oil pollution and the beach-hopper, Talorchestia. Unpublished project, Zoology Dept., University of Cape Town.

Kinner, P. and Maurer, D. 1978. Polychaetous annelids of the Delaware Bay region. U.S. natn. mar. fish. Serv. Fish. Bull. 76: 209-224.

Kirkegaard, J.B. 1956. Benthic polychaeta from depths exceeding 6,000 metres. Galathea Rep. 2: 63-78.

Kitamori, R. 1960. Two new species of cirratulid and Nephthydidae (Annelida: Polychaeta). Bull. Jap. Soc. sci. Fish. 26: 1082-1085.

Klapow, L.A. 1972a. Fortnightly molting and reproductive cycles in the sand-beach isopod Excirolana chiltoni. Biol. Bull. 143: 568-591.

Klapow, L.A. 1972b. Natural and artificial rephasing of a tidal rhythm. J. comp. Physiol. 79: 233-258.

Klein, G. 1969. Amphipoden aus der Wesermündung und der Helgoländer Bucht, mit Beschreibung von Talorchestia frisiae n. sp. Veroff. Inst. Meeresforsch. Bremerh. 11: 173-194.

Komar, P.D. 1978. Relative quantities of suspension versus bed-load transport on beaches. J. sedim. Petrol. 48: 921-932.

Koop, K. 1979. Biology and ecological energetics of the supralittoral isopod Ligia dilatata. Unpublished M.Sc. thesis, University of Cape Town.

Koop, K. and Field, J.G. 1980. The influence of food availability on population dynamics of a supralittoral isopod Ligia dilatata Brandt. J. exp. mar. Biol. Ecol. 48: 61-72.

Koop, K. and Griffiths, C.L. In prep. The relative significance of macro-, meio- and microfauna on an exposed sandy beach.

Koop, K., Newell, R.C. and Lucas, M.I. In press. Biodegradation and carbon flow based on kelp debris (Ecklonia maxima) in a sandy beach microcosm. Mar. Ecol. Prog. Ser.

Kudenov, J.D. 1975. Two new species of errant polychaetes from the Gulf of California, Mexico. Bull. Sth. Calif. Acad. Sci. 74: 75-80.

Kuhn, M. 1978. The ecology of wading birds on east Cape beaches. Unpublished project, Zoology Dept., University of Port Elizabeth.

Kussakin, O.G. 1973. Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep-sea fauna origin. Mar. Biol. 23: 19-34.

Kussakin, O.G. 1975. A list of the macrofauna in the intertidal zone of the Kurile Islands, with remarks on the zoogeographical structure of the region. Publ. Seto mar. biol. Lab. 22: 47-74.

Langerhans, P. 1880. Zur Wurmfauna der Madeira. IV. Z. wiss. Zool. 34: 86-143.

Lasserre, P. and Renaud-Mornant, J. 1973. Resistance and respiratory physiology of intertidal meiofauna to oxygen-deficiency. Neth. J. Sea Res. 7: 290-302.

Ledoyer, M. 1969. Amphipodes gammariens de quelques biotopes de substrat meuble de la region de Tuléar. Etudes systématique et ecologique. Rec. Trav. Sta. mar. Endoume, Fasc. h-s. Suppl. 8: 15-62.

Leech, G. 1974. Semantics. Pelican Books, Harmondsworth.

Le Loeuff, P. and Intes, A. 1972. Les cumacés du plateau continental de Côte D'Ivoire. Cah. Off. Rech. scient. tech. Outre-Mer (Oceanogr.) 10: 19-46.

Levine, D.M. 1978. A Monte Carlo study of Kruskal's variance-based measure on stress. Psychometrika 43: 307-315.

Levinton, J. 1973. Genetic variation in a gradient of environmental variability: marine Bivalvia (Mollusca). Science 180: 75-76.

Lewin, J., Hruby, T. and Mackas, D. 1975. Blooms of surf zone diatoms along the coast of the Olympic Peninsula, Washington. V. Environmental conditions associated with the blooms. Estuar. coastl. mar. Sci. 3: 229-241.

Lewis, J.R. 1964. Ecology of rocky shores. The English Universities Press, London.

Light, W.J. 1977. Spionidae (Annelida: Polychaeta) from San Fransisco Bay, California: a revised list with nomenclatural changes, new records and comments on related species from the northeastern Pacific Ocean. Proc. biol. Soc. Wash. 90: 66-88.

Lischke, C.E. 1871. Japanische Meeres-Conchylien. (Zweiter Theil). Cassel.

Loesch, H.C. 1957. Studies on the ecology of two species of Donax on Mustang Island, Texas. Publ. Inst. mar. Sci. Univ. Texas 4: 201-207.

Lowry, K. and Bullock, S. 1976. Catalogue of the marine gammaridean Amphipoda of the Southern Ocean. Bull. roy. Soc. N.Z. 16: 1-187.

Lucas, M. 1967. Révision des Donacidae des côtes européennes. Naturalistes belg. 48: 271-281.

L'Vova, T.G. 1976. The dynamics of the stepwise acclimation of the White Sea polychaete Nephtys minuta to the reduction of environmental salinity. Zool. Zh. 55: 921-923.

Maccagno, T. 1937. Crostacei di Assab: decapodi, stomatopodi, Anfipodi. Ann. Mus. Stor. nat. Genova 59: 171-186.

MacIntyre, R.J. 1963. The supralittoral fringe of New Zealand sand beaches. Trans. roy. Soc. N.Z. Gen. 1: 89-105.

MacNae, W. and Kalk, M. 1962. The fauna and flora of sand flats at Inhaca Island, Mozambique. J. Anim. Ecol. 31: 93-128.

Macquart-Moulin, C. 1968. Les cumacés bentho-planktoniques du Golfe de Marseille: étude des differentes espèces receuillies au cours des pêches planktoniques nocturnes effectuées durant les années 1963-1964. Rec. Trav. Sta. mar. Endoume, Bull. 43: 285-309.

Macquart-Moulin, C. 1977. Le contrôle de l'émergence et des nages nocturnes chez les péracarides des plages de Mediterranée. Eurydice affinis Hansen (Isopoda), Gastrosaccus mediterraneus Bacescu, Gastrosaccus spinifer (Goes) (Mysidacea). J. exp. mar. Biol. Ecol. 27: 61-81.

Mare, M. F. 1942. Study of a marine benthic community with special reference to the microorganisms. J. mar. biol. Ass. U.K. 25: 517-554.

Marsh, B.A. and Branch, G.M. 1979. Circadian and circatidal rhythms of oxygen consumption in the sandy beach isopod Tylos granulatus Krauss. J. exp. mar. Biol. Ecol. 37: 77-89.

Mason, C.C. and Folk, R.L. 1958. Differentiation of beach, dune and aeolian flat environments by size analysis, Mustang Island, Texas. J. sedim. Petrol. 28: 211-226.

Masson, H. and Marais, J.F.K. 1975. Stomach content analyses of mullet from the Swartkops estuary. Zool. afr. 10: 193-208.

Mauchline, J. and Murano, M. 1977. World list of the Mysidacea, Crustacea. J. Tokyo Univ. Fish. 64: 39-88.

Maynard, N.G. 1968. Aquatic foam as an ecological habitat. Z. allg. Mikrobiol. 8: 119-126.

McIntosh, W.C. 1874. A monograph of the British annelids. Pt 1. Ray Society, London.

McIntosh, W.C. 1900. Nephthydidae. Ann. Mag. nat. Hist. 7: 254-268.

McIntosh, W.C. 1901. On Japanese annelids, Nephtys, Eteone. Notes Gatty mar. Lab. 21: 220-222.

McIntyre, A.D. 1970. The range of biomass in intertidal sand, with special reference to the bivalve Tellina tenuis. J. mar. biol. Ass. U.K. 50: 561-575.

McIntyre, A.D. and Eleftheriou, A. 1968. The bottom fauna of a flatfish nursery ground. J. mar. biol. Ass. U.K. 48: 113-142.

McLachlan, A. 1977a. Composition, distribution, abundance and biomass of the macrofauna and meiofauna of four sandy beaches. Zool. afr. 12: 279-306.

McLachlan, A. 1977b. The larval development and population dynamics of Derocheilocaris algoensis (Crustacea: Mystacocarida). Zool. afr. 12: 1-14.

McLachlan, A. 1977c. Studies on the psammolittoral fauna of Algoa Bay, South Africa. 1. Physical and chemical evaluation of the beaches. Zool. afr. 12: 15-32.

McLachlan, A. 1977d. Studies on the psammolittoral fauna of Algoa Bay, South Africa. 2. The distribution, composition and biomass of the meiofauna and macrofauna. Zool. afr. 12: 33-60.

McLachlan, A. 1977e. Effects of ore dust pollution on the physical and chemical features, and on the meiofauna and microfauna, of a sandy beach. Zool. afr. 12: 73-88.

McLachlan, A.D. 1978. Sediment particle size and body size in meiofaunal harpacticoid copepods. S. Afr. J. Sci. 74: 27-28.

McLachlan, A. 1979a. Growth and reproduction of Donax sordidus Hanley on an open sandy beach in Algoa Bay. S. Afr. J. Zool. 14: 61-66.

McLachlan, A. 1979b. Volumes of sea water filtered through eastern Cape sandy beaches. S. Afr. J. Sci. 75: 75-79.

McLachlan, A. 1980a. Intertidal zonation of the macrofauna and stratification of meiofauna on high energy beaches in the eastern Cape, South Africa. Trans. roy. Soc. S. Afr. 44: 213-223.

McLachlan, A. 1980b. Occurrence of the ghost crabs Ocypode spp. in the eastern Cape. S. Afr. J. Zool. 15: 57-58.

McLachlan, A. 1980c. The definition of sandy beaches in relation to exposure: a simple rating system. S. Afr. J. Sci. 76: 137-138.

McLachlan, A. 1981. Exposed sandy beaches as semi-closed ecosystems. Mar. environ. Res. 4: 59-63.

McLachlan, A., Cooper, C. and van der Horst, G. 1979. Growth and production of Bullia rhodostoma on an open sandy beach in Algoa Bay. S. Afr. J. Zool. 14: 49-53.

McLachlan, A., Dye, A.H. and Van der Ryst, P. 1979. Vertical gradients in the fauna and oxidation of two exposed sandy beaches. S. Afr. J. Zool. 14: 43-47.

McLachlan, A., Erasmus, T., Dye, A.H., Wooldridge, T., van der Horst, G., Rossouw, G., Lasiak, T.A. and McGwynne, L. In press. Sand beach energetics: an ecosystem's approach towards a high energy interface. Estuar. coastl. Shelf Sci.

McLachlan, A., Erasmus, T. and Furstenberg, J.P. 1977. Migrations of sandy beach meiofauna. Zool. afr. 12: 257-278.

McLachlan, A. and Furstenberg, J.P. 1977. Studies on the psammolittoral fauna of Algoa Bay, South Africa. 3. A quantitative analysis of the nematode and crustacean communities. Zool. Afr. 12: 61-72.

McLachlan, A. and Grindley, J.R. 1974. Distribution of macrobenthic fauna of soft substrata in Swartkops estuary. Zool. afr. 9: 211-233.

McLachlan, A. and Hanekom, N. 1979. Aspects of the biology, ecology and seasonal fluctuations in biochemical composition of Donax serra in the East Cape. S. Afr. J. Zool. 14: 183-193.

McLachlan, A. and van der Horst, G. 1979. Growth and reproduction of two molluscs from an exposed sandy beach. S. Afr. J. Zool. 14: 194-201.

McLachlan, A., Wooldridge, T. and Dye, A.H. 1980. The ecology of sandy beaches in southern Africa. Unpublished manuscript.

McLachlan, A., Wooldridge, T., Schramm, M. and Kuhn, M. 1980. Seasonal abundance, biomass and feeding of shore birds on sandy beaches in the eastern Cape, South Africa. Ostrich 51: 44-52.

McLachlan, A., Wooldridge, T. and van der Horst, G. 1979. Tidal movements of the macrofauna on an exposed sandy beach in South Africa. J. Zool., Lond. 187: 433-442.

McLusky, D.S., Nair, S.A., Stirling, A. and Bhargava, R. 1975. The ecology of a central west Indian beach, with particular reference to Donax incarnatus. Mar. Biol. 30: 267-276.

McLusky, D.S. and Stirling, A. 1975. The oxygen consumption and feeding of Donax incarnatus and Donax spiculum from tropical beaches. Comp. Biochem. Physiol. 51A: 943-947.

McNulty, J.K., Work, R.C. and Moore, H.B. 1962. Some relationships between the infauna of the level bottom and the sediment in South Florida. Bull. mar. Sci. Gulf Caribbean 12: 322-332.

McQuaid, C.D. 1980. Spatial and temporal variations in rocky intertidal communities. Unpublished Ph.D. thesis, University of Cape Town.

Meadows, P.S. and Anderson, J.G. 1966. Microorganisms attached to marine and freshwater sand grains. Nature 212: 1059-1060.

Meadows, P.S. and Anderson, J.G. 1968. Microorganisms attached to marine sand grains. J. mar. biol. Ass. U.K. 48: 161-175.

Melvill, J.C. 1897. Descriptions of thirty-four new species of marine mollusca from the Arabian Sea, Persian Gulf and Gulf of Oman. Mem. Manchester Soc. 41: 1-25.

Melvill, J.C. 1901. A few furhter remarks upon the Erythraean molluscan fauna, with descriptions of seven species from Aden, in the collection of Cmdr. E.R. Shopland, R.I.M. Ann. Mag. nat. Hist. 7: 550-556.

Melvill, J.C. 1910. Report on the marine mollusca obtained by J. Stanley Gardiner, F.R.S. among the islands of the Indian Ocean in 1905. Reference incomplete.

Melvill, J.C. 1912. Descriptions of thirty-three new species of Gastropoda from the Persian Gulf, Gulf of Oman and North Arabian Sea. Proc. malac. Soc., Lond. 10: 240-254.

Menzies, R.J. and Barnard, J.L. 1959. Marine Isopoda on coastal shelf bottoms of southern California: systematics and ecology. Pacific Nat. 1: 3-36.

Meyer-Riel, L-A., Dawson, R., Liebezeit, G. and Tiedge, H. 1978. Fluctuations and interactions of bacterial activity in sandy beach sediments and overlying waters. Mar. Biol. 48: 161-171.

Meyer-Riel, L-A. and Faubel, A. 1980. Uptake of organic matter by meiofauna organisms and interrelationships with bacteria. Mar. Ecol. Prog. Ser. 3: 251-256.

Milaszewicz, K.O. 1909. Liste des mollusques marins collectionnés en 1908 par K.P. Jagodovsky dans la Mer Noire près des côtes du Caucase. St Petersbourg Ann. Mus. zool. Ac. Sc. 14: 310-318.

Monod, T. 1928. Crustacea IV. Decapoda (excl. Palaemonidae, Atyidae et Potamonidae). In: Monod, T. (ed.) Contribution à l'étude de la faune du Cameroun. Faune des Colonies Françaises.

Monod, T. 1930. Contribution à l'étude des Cirolanidae. Annls. Sci. nat. Zool. Ser. 10 8: 129-183.

Monod, T. 1976. Remarques sur quelques Cirolanides (Crustaces, Isopodes). Bull. Mus. natn. Hist. nat., Paris Zool. 251: 133-161.

Monro, C.C.A. 1928. Papers from Dr. Th. Mortensen's Pacific expedition, 1914-16. XLV. On the Polychaeta collected by Dr. Th. Mortensen off the coast of Panama. Vidensk. Medd. naturh. Foren. Kobehavn 85: 75-103.

Monro, C.C.A. 1933. The Polychaeta Errantia collected by Dr. C. Crossland at Colon, Panama and the Galapagos Islands during the expedition of the S.Y. "St George". Proc. zool. Soc., Lond. 1933: 1-96.

Monro, C.C.A. 1936. Polychaete worms II. *Discovery Reps.* *12*: 59-198.

Monro, C.C.A. 1937. On some freshwater polychaetes from Uruguay. *Ann. Mag. nat. Hist., London (10)* *20*: 241-250.

Monro, C.C.A. 1939. Polychaeta. *Rep. B.A.N.Z. Antarctic Res. Exped., 1929-31* *4B*(4): 89-115.

Monteroserato, D. 1923. Molluschi delle coste cirenaiche raccolti dall' Ing. Camillo Crema. *R. Com. talassogr. Ital., Venezia* *107*: 1-14.

Moran, S. 1972. Ecology and distribution of the sand-dwelling mysid *Gastrosaccus* *sanctus* (van Beneden, 1961) along the Mediterranean sandy shore of Israel. *Crustaceana Suppl.* *3*: 357-361.

Moreira, P.S. 1972. Species of *Eurydice* (Isopoda, Flabellifera) from southern Brazil. *Bol. Inst. Oceanogr.* *21*: 69-92.

Morino, H. 1975. Studies on the Talitridae (Amphipoda, Crustacea) in Japan. 2. Taxonomy of sea-shore *Orchestia*, with notes on the habitats of Japanese sea-shore talitrids. *Publ. Seto mar. biol. Lab.* *22*: 171-193.

Morrison, J.P.E. 1971. Western Atlantic *Donax*. *Proc. biol. Soc. Wash.* *83*: 545-568.

Morton, J.E. and Challis, D.A. 1969. The biomorphology of Solomon Islands shores, with a discussion of zoning patterns and ecological terminology. *Phil. Trans. roy. Soc. Lond.* *255B*: 459-516.

Morton, J.E. and Miller,M.C. 1968. *The New Zealand sea shore.* Collins, London.

Morton, R.A. 1976. Effects of Hurricane Eloise on beach and coastal structures, Florida Panhandle. *Geology* *4*: 277-280.

Moses, R.H. 1942. Foreign shells at Sandwich. *J. Conch., London* *21*: 314.

Moueza, M. and Chessel, D. 1976. Contribution à l'étude de la biologie de *Donax* *trunculus* L. (Mollusque: Lamellibranche) dans l'Algerois: analyse statistique de la dispersion le long d'une plage en Baie de Bou Ismail. *J. exp. mar. Biol. Ecol.* *21*: 211-221.

Muir, D.G. 1977. The biology of Talorchestia capensis (Amphipoda, Talitridae) including a population energy budget. Unpublished M.Sc. thesis, University of Cape Town.

Munro, A.L.S., Wells, J.B.J. and McIntyre, A.D. 1978. Energy flow in the flora and meiofauna of sandy beaches. *Proc. roy. Soc. Edinburgh* *76B*: 297-315.

Myren, R.T. and Pella, J.J. 1977. Natural variability in distribution of an intertidal population of Macoma balthica subject to potential oil pollution at Port Valdez, Alaska. Mar. Biol. 41: 371-382.

Narchi, W. 1974. Aspectos ecologicos e adaptotivos de algunos bivalves do litoral paulista. Papeis avuls. Dep. Zool. Sao Paulo 27: 235-262.

Newcombe, C.L. 1935. Certain environmental factors of a sand beach in the St Andrews region, New Brunswick, with a preliminary designation of the intertidal communities. J. Ecol. 33: 334-355.

Newell, P.F. and Brown, A.C. 1977. The fine structure of the osphradium of Bullia digitalis Meuschen (Gastropoda, Prosobranchia). Malacologia 16: 197-205.

Newell, R.C. 1976. Adaptation to environment. Butterworths, London.

Newell, R.C. 1979. Biology of intertidal animals. 3rd ed. Marine Ecological Surveys, Faversham.

Newell, R.C. In press. The maintenance of energy balance in marine invertebrates exposed to changes in environmental temperature. In: "Animals and environmental fitness". Proc. 1st Conf. europ. Soc. comp. Physiol. Biochem.

Newell, R.C., Johnson, L.G. and Kofoed, L.M. 1977. Adjustment of the components of energy balance in response to temperature change in Ostrea edulis. Oecologia 30: 97-110.

Newell, R.C. and Roy, A. 1973. A statistical model relating the oxygen consumption of a mollusk (Littorina littorea) to activity, body size, and environmental conditions. Physiol. Zool. 46: 252-275.

Newell, R.C., Roy, A. and Armitage, K.B. 1976. An analysis of the factors affecting the oxygen consumption of the isopod Ligia oceanica. Physiol. Zool. 49: 109-137.

Nonanto, E.F. and Luna, J.A.C. 1970. Anelidos poliquetos do nordeste do Brasil. 1. Poliquetos bentonicos da costa de Alagoas e Sergipe. Bolm. Inst. Oceanogr. Sao Paulo 19: 57-130.

Odhner, N. 1919. Contribution à la faune malacologique de Madagascar. Ark. Zool., Stockholm 12: 52.

Odum, E.P. 1977. The emergence of ecology as a new integrative discipline. Science 195: 1289-1293.

Okuda, S. 1940. Polychaetous annelids from the Ryukyu Islands. Bull. biogeogr. Soc. Japan 10: 1-24.

Okuda, S. 1943. Occurrence of a freshwater polychaete in central China. J. Shanghai Sci. Inst. N.S. 2(3): 99-103.

Oliff, W.D., Berrisford, C.D., Turner, W.D., Ballard, J.A. and McWilliam, D.C. 1967. The ecology and chemistry of sandy beaches and nearshore submarine sediments of Natal. Water Res. 1: 115-129.

Oliff, W.D., Gardner, B.D., Turner, W.D. and Sharp, J.B. 1970. The chemistry of the interstitial water as a measure of conditions in a sandy beach. Water Res. 4: 179-188.

Olsson, A.A. 1961. Molluscs of the tropical eastern Pacific, particularly from the southern half of the Panamic-Pacific faunal province (Panama to Peru). In: Panamic-Pacific Pelecypoda. Paleontological Research Institute, Ithaca, N.Y.

Oostingh, C.H. 1931. Beitrag zur Kenntnis der Molluskenfauna von Süd-Sumatra. Arch. Molluskenk. 63(6): 1-255.

Orensanz, J.M. and Gianuca, N.M. 1974. Contribucão ao conhecimento dos anelidos poliquetos do Rio Grande do Sul, Brasil. 1. Lista sistematica preliminar et descricão de três novas especies. Comm. Mus. Cienc. P.U.C.R.G.S. (Zool.) 4: 1-37.

Orren, M.J. and Eagle, G.A. 1979. Tar ball distribution along the Cape of Good Hope tanker route. S. Afr. J. Sci. 75: 465.

Orren, M.J., Eagle, G.A., Fricke, A.H., Gledhill, W.J., Greenwood, P.J. and Hennig, H.F-K.O. In press. The chemistry and meiofauna of some unpolluted sandy beaches in South Africa. Water S. A.

Packard, A.S. 1867. Observations on the glacial phenomena of Labrador and Maine, with a view of the recent invertebrate fauna of Labrador. Mem. Boston Soc. nat. Hist. 1: 210-303.

Page, H.G. 1955. Phi-millimetre conversion table. J. sedim. Petrol. 25: 285-292.

Paine, R.T. 1966. Endothermy in bomb calorimetry. Limnol. Oceanogr. 11: 126-129.

Pamatmat, M.M., Graf, G., Bengtsson, W. and Novak, C.S. 1981. Heat production, ATP concentration and electron transport activity of marine sediments. Mar. Ecol. Prog. Ser. 4: 135-143.

Paxton, H. 1974. Contribution to the study of Australian Nephtyidae (Polychaeta). Rec. Aust. Mus. 29: 197-208.

Pearse, A.S., Humm, H.J. and Wharton, G.W. 1942. Ecology of sand beaches at Beaufort, North Carolina. Ecol. Monogr. 13: 322-374.

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.

Penchaszadeh, P.E. and Olivier, S.R. 1975. Ecologia de una poblacion de "berberecho" (Donax hanleyanus) en Villa Gesell, Argentina. Malacologia 15: 133-146.

Pettibone, M.H. 1963. Revision of some genera of polychaete worms of the family Spionidae, including the description of a new genus of Scolelepis. Proc. biol. Soc. Wash. 76: 89-104.

Philip, K.P. 1974. The intertidal fauna of the sandy beaches of Cochin. Proc. Ind. natn. Sci. Acad. B 38: 317-328.

Phillips, T. 1970. Notes on the predation of the asteroid Luidia on Donax navicula at the Plaza Almejas, Baja California del Norte, Mexico. Tabulata 3: 16-18.

Phillipson, J. 1966. Ecological energetics. Edward Arnold, London.

Pichon, M. 1967. Contribution à l'étude des peuplements de la zone intertidale sur sables fins et sables vaseux non fixes dans la région de Tuléar. Rec. Trav. Sta. mar. Endoume Suppl. 7: 57-100.

Pilsbry, H.A. 1901. New mollusca from Japan, the Loo-Choo Islands and Formosa. Proc. Acad. Philadelphia 1: 193-201.

Pilsbry, H.A. 1919. Mollusca from central America and Mexico. Philadelphia Proc. Acad. nat. Sci. 71: 212-223.

Platt, H.M. 1977. Ecology of free-living nematodes from an intertidal sand flat in Strangford Lough, Northern Ireland. Estuar. coastl. mar. Sci. 5: 685-693.

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.

Preston, H.B. 1903. Descriptions of four new species of marine shells, probably from Ceylon. Proc. malac. Soc. Lond. 7: 34-35.

Preston, H.B. 1908. Descriptions of new species of land, marine and freshwater shells from the Andaman Islands. Rec. Ind. Mus. Calcutta 2: 187-210.

Price, T.J., Thayer, G.W., La Croix, M.W. and Montgomery, G.P. 1976. The organic content of shells and soft tissues of selected estuarine gastropods and pelecypods. Proc. natn. Shellfish. Ass. 65: 26-31.

Prus, T. 1970. Calorific value of animals as an element of bioenergetical considerations. Pol. Arch. Hydrobiol. 17: 183-199.

Punnett, R.C. 1900a. On a collection of nemerteans from Singapore. Quart. J. micr. Sci. 44: 117-139.

Punnett, R.C. 1900b. On some nemerteans from Torres Straits. Proc. zool. Soc. Lond. 1900: 825-831.

Punnett, R.C. 1901a. Nemerteans. In: Gardiner, J.S. (ed.) Fauna and geography of the Maldive and Laccadive Islands. Reference incomplete, see Zoological Record, 1901.

Punnett, R.C. 1901b. On some Arctic nemerteans. Proc. zool. Soc., Lond. 2: 90-107.

Punnett, R.C. 1903. On the nemerteans of Norway. Bergens Museum, Aarborg.

Punnett, R.C. and Cooper, C.F. 1910. On some nemerteans of the eastern Indian Ocean. Trans. linn. Soc. Zool. Ser. 2 13: 1-15.

Puttick, G.M. 1979. Foraging behaviour and activity budgets of curlew sandpipers. Ardea 67: 111-122.

Rabindranath, P. 1971. Haustoriid amphipods from India. Hydrobiologia 38: 521-539.

Rao, K.V.S. 1972. Intertidal amphipods from the Indian coast. Proc. Ind. natn. Sci. Acad. B 38: 190-205.

Ravenel, W.S. and Thistle, D. 1981. The effect of sediment characteristics on the distribution of two subtidal harpacticoid copepod species. J. exp. mar. Biol. Ecol. 50: 289-301.

Reed, W.E., Le Fever, R. and Moir, G.J. 1975. Depositional environment interpretations from settling velocity (Psi) distributions. Bull. geol. Soc. Am. 86: 1321-1328.

Rees, C.B. 1939. Notes on the ecology of the sandy beaches of North Donegal. Proc. roy. Irish Acad. 45: 215-229.

Reish, D.J. 1968. The polychaetous annelids of the Marshall Islands. Pacific Sci. 22: 208-231.

Richardson, H. 1901. Key to the isopods of the Atlantic coast of North America, with descriptions of new and little-known species. Proc. U.S. Mus. 23: 494-579.

Riedl, R. 1970. Fauna und Flora der Adria. Verlag Paul Parey, Berlin.

Riese, K. 1979. Moderate predation on meiofauna by the macrobenthos of the Wadden Sea. Helgoländer wiss. Meeresunters. 32: 453-465.

Riese, K. and Ax, P. 1979. A meiofauna "thiobios" limited to the anaerobic sulfide system of marine sand does not exist. Mar. Biol. 54: 225-237.

Riese, K. and Ax, P. 1980. Statement on the thiobios-hypothesis. Mar. Biol. 58: 31-32.

Rioja, E. 1944. Estudios anelidologicos X. Estudio de algunos poliquetos del Museo Argentino de Ciencias Naturales. An. Inst. biol. Mexico 15: 115-138.

Roll, H.U. 1965. Physics of the marine atmosphere. Academic Press, New York.

Roman, M-L. 1977. Les oniscoides halophiles de Madagascar (Isopoda, Oniscoidea). Beaufortia 26: 107-152.

Rost, H. and Soot-Ryen, T. 1955. Pelecypods from the Seychelles Islands collected by Mr. W.V. Hasselberg. Acta Borealis (A) 8: 1-23.

Rozbaczylo, N. and Castilla, J.C. 1974. La familia Nephtydae en Chile. (Annelida, Polychaeta). Stud. neotrop. Fauna 9: 179-206.

Ruffo, S. 1951. Studi sui crostacei anfipodi.XXII. Anfipodi di Venezuela raccolti dal Dott. G. Marcuzzi. Mem. Mus. Stor. nat. Verona 2: 44-65.

Rullier, F. and Amoureux, L. 1979. Annêlides polychêtes: campagnes de la Calypso au large des côtes atlantiques de l'Amerique du Sud (1961-62). Ann. Inst. oceanogr. Monaco Fasc. suppl. 55: 145-206.

Saito, T. 1976. Geologic significance of coiling direction in the planktonic foraminifera Pulleniatina. Geology 4: 305-309.

Saloman, C.H. and Naughton, S.P. 1977. Effect of Hurricane Eloise on the benthic fauna of Panama City Beach, Florida, U.S.A. Mar. Biol. 42: 357-363.

Salvat, B. 1964. Les conditions hydrodynamiques interstitielles des sêdiment meubles intertidaux et la rêpartition verticale de la faune endogêe. C. R. 259: 1576-1579.

Salvat, B. 1966. Eurydice pulchra Leach 1815 et Eurydice affinis Hansen 1905 (Isopodes: Cirolanidae). Taxonomie, êthologie, rêpartition verticale et cycle reproducteur. Acta Soc. linn. Bordeaux A 193: 1-77.

Salvat, B. 1967. La macrofaune carcinologique endogêe des sêdiments meubles intertidaux (Tanaidaces, Isopodes et Amphipodes): êthologie, bionomie et cycle biologique. Mem. Mus. natn. Hist. nat. Ser. A 45: 1-275.

Sanders, H.L. 1958. Benthic studies in Buzzards Bay 1. Animal-sediment relationships. Limnol. Oceanogr. 3: 245-258.

Sanders, H.L. 1960. Benthic studies in Buzzards Bay 3. The structure of the soft-bottom community. Limnol. Oceanogr. 5: 138-153.

Sanders, H.L. 1968. Marine benthic diversity: a comparative study. Am. Nat. 102: 243-282.

Scapini, F. and Ercolini, A. 1973. Research on the non-visual orientation of littoral amphipods: experiments with young born in captivity and adults from a Somalian population of Talorchestia martensii Weber (Crustacea Amphipoda). Monitore zool. ital. Suppl. 5: 23-30.

Schellenberg, A. 1925. Crustacea VIII: In: Michaelsen (ed.) Beitrage zur Kenntnis der Meeresfauna Westafrikas. Reference incomplete, see Zoological Record, 1925.

Schellenberg, A. 1938. Brasilianische Amphipoda, mit biologischen Bemerkungen. Zool. Jb., Jena (Syst.) 71: 203-218.

Scherba, S. and Gallucci, V.F. 1976. The application of systematic sampling to a study of infauna variation in a soft substrate environment. Fish. Bull. 74: 937-948.

Schiffman, A. 1965. Energy measurements in the swash-surf zone. Limnol. Oceanogr. 10: 255-260.

Schmidt-Nielsen, K. 1975. Animal physiology: adaptation and environment. Cambridge University Press, London.

Schultz, G.A. 1970. A review of the genus Tylos Latreille from the New World (Isopoda, Oniscoidea). Crustaceana 19: 297-305.

Schuster-Diedrichs, O. 1956. Die Makrofauna am sandigen Brandungsstrand von El Salvador. Senckenberg. biol. 37: 1-56.

Seed, R. and Lowry, B.J. 1973. The intertidal macrofauna of seven sandy beaches of County Down. Proc. roy. Irish Acad. Sect. B 73: 217-230.

Shafir, A. 1978. Population dynamics and ecological energetics of Cirolana imposita. Unpublished M.Sc. thesis, University of Cape Town.

Sheard, K. 1939. Regeneration in the amphipod Talorchestia novaehollandiae Stebbing. Aust. J. Sci. 2: 29-30.

Shepard, F.P. and Young, R. 1961. Distinguishing between beach and dune sands. J. sedim. Petrol. 31: 196-214.

Shillington, F.A. 1978. Preliminary report on surface wind wave prediction in Cape waters. S. Afr. J. Sci. 74: 220-223.

Shumway, S.E. 1979. The effects of body size, oxygen tension and mode of life on the oxygen uptake rates of polychaetes. Comp. Biochem. Physiol. 64A: 273-278.

Sibert, J.R. 1979. Detritus and juvenile salmon production in the Nanaimo estuary: II. Meiofauna available as food to juvenile chum salmon (Oncorhynchus keta). J. Fish. Res. Bd. Canada 36: 497-503.

Sikora, J.P., Sikora, W.B., Erkenbrecher, C.W. and Coull, B.C. 1977. Significance of ATP, carbon and caloric content of meiobenthic nematodes in partitioning benthic biomass. Mar. Biol. 44: 7-14.

Siebenaller, J.F. 1978. Genetic variation in deep-sea invertebrate populations: the bathyal gastropod Bathybembix bairdii. Mar. Biol. 47: 265-275.

Skjoldal, H.R. and Bakke, T. 1978a. Anaerobic metabolism of the scavenging isopod Cirolana borealis (Lilljeborg). Adenine nucleotides. In: McLusky, D.S. and Berry, A.J. (eds.) Twelfth European symposium on marine biology. Pergamon Press, Oxford.

Skjoldal, H.R. and Bakke, T. 1978b. Relationships between ATP and energy charge during lethal metabolic stress of the marine isopod Cirolana borealis. J. biol. Chem. 253: 3355-3356.

Smith, D.A.S. 1971. Polymorphism and population density in Donax rugosus (Lamellibranchiata: Donacidae). J. Zool., Lond. 164: 429-441.

Smith, E.A. 1891. Descriptions of new species of shells from New South Wales, New Guinea, the Caroline and Solomon Islands. Proc. zool. Soc., Lond. 1891: 486-491.

Solomon, M.E. 1976. Population dynamics. Edward Arnold, London.

Sourie, R. 1957. Etude ecologique des plages de la côte Senegalaise aux environs de Dakar. Ann. Ec. sup. Sci. Dakar 3: 1-110.

Southward, A.J. 1953. The fauna of some sandy and muddy shores in the south of the Isle of Man. Proc. Trans. Liverpool biol. Soc. 59: 51-71.

Sowerby, G.B. 1894. Descriptions of four new shells from the Persian Gulf and Bay of Zaila. Proc. malac. Soc., Lond. 1: 160-161.

Sowerby, G.B. 1915. Descriptions of new species of mollusca from various localities. Ann. Mag. nat. Hist., Lond. Ser. 8 15: 164-170.

Stander, G.H. 1968. The "Esso Essen" incident. S. Afr. Ship. News Fish. Indust. Rev. 1968(8): 41-45.

Staub, J. 1900. Neue Nemertinen aus Amboina. Semon. zool. Forsch. Denkschr. Ges. Jena 7: 591-614.

Stebbing, T.R.R. 1895. On the genus Urothoe and a new genus Urothoides. Trans. zool. Soc., Lond. 13: 1-30.

Stebbing, T.R.R. 1903. Amphipoda from Costa Rica. Publ. U.S. Mus. 26: 925-931.

Stebbing, T.R.R. 1910. Isopoda from the Indian Ocean and British East Africa. Trans. linn. Soc. Ser. 2 Zool. 14: 83-118.

Stenton-Dozey, J. and Griffiths, C.L. 1980. Growth, consumption and respiration by larvae of the kelp-fly Fucellia capensis (Diptera: Anthomyiidae). S. Afr. J. Zool. 15: 280-283.

Stephen, A.C. 1929. Studies on the Scottish marine fauna: the fauna of the sandy and muddy areas of the tidal zone. Trans. roy. Soc. Edinburgh 56: 291-306.

Stephen, A.C. 1930. Studies on the Scottish marine fauna. Additional observations on the fauna of the sandy and muddy areas of the tidal zone. Trans. roy. Soc. Edinburgh 56: 521-535.

Stephensen, K. 1935. Talorchestia rectimana (Dana) from Tahiti and Moorea. Bull. Bishop Mus. Honolulu 113: 143-147.

Stephensen, K. 1938. Amphipoda, Tanaidacea and Pycnogonida. Senckenbergiana 20: 236-264.

Stephensen, K. 1948. Amphipods from Curacao, Bonaire, Aruba and Margarita. Natuurw. Stud. Suriname en Curacao 5: 1-20.

Stephenson, T.A. and Stephenson, A. 1949. The universal features of zonation between tide-marks on rocky coasts. J. Ecol. 37:289-305.

Stephenson, T.A. and Stephenson, A. 1972. Life between tide-marks on rocky shores. W.H. Freeman, San Fransisco.

Strong, E.M. and Hertlein, L.G. 1940. Marine molluscs from Panama collected by the Allan Hancock expedition to the Galapagos Islands, 1931-32. Rep. Allan Hancock Pacific Exped. 2(12): 177-245.

Suarez, A.M. and Fraga, R. 1978. Poliquetos bentosicos Cubanos. I: Lista de poliquetos errantes. Univ. Habana, Cienc. Invest. mar. Ser. 8 33: 1-59.

Summers, R.W., Pringle, J.S. and Cooper, J. 1976. The status of coastal waders in the south-western Cape, South Africa. Western Cape Wader Group, Cape Town.

Tankard, A.J. 1976. Pleistocene history and coastal morphology of the Ysterfontein-Elands Bay area, Cape Province. Ann. S. Afr. Mus. 69: 73-119.

Tapparone-Canefri, C. 1869. Indice sistematico dei molluschi testacei dei dintorni di Spezia e del suo Golfo. Att. Soc. Ital. Sci. nat. 12: 261-406.

Tattersall, W.M. 1914. Zoological results of the Abor expedition, 1911-12. Crustacea, Amphipoda. Rec. Ind. Mus. Calcutta 8: 449-453.

Tattersall, W.M. 1922. Zoological results of a tour in the Far East. Part VII. Amphipoda, with notes on an additional species of isopod. Mem. asiatic Soc. Bengal 6: 435-459.

Tattersall, W.M. 1923. Crustacea Part VII. Mysidacea. Nat. Hist. Rep. Brit. Antarctic (Terra Nova) Exped. 1910 Zool. 3(10): 273-304.

Tattersall, W.M. 1937. New species of mysidasid crustaceans. Smithson. misc. Coll. 91(26): 1-18.

Tattersall, W.M. 1940. Report on a small collection of Mysidacea from the coastal waters of New South Wales. Rec. Aust. Mus. Sydney 20: 327-340.

Tattersall, W.M. 1951. A review of the Mysidacea of the United States National Museum. Bull. U.S. natn. Mus. 201: 1-292.

Tavolera, F. and Faustino, L.A. 1933. Edible mollusks of Manila. Philipp. J. Sci. 50: 1-48.

Thiele, J. and Jaeckel, S. 1931. Muscheln der Deutchen Tiefsee-Expedition . Wiss. Erg. Deutch. Tiefsee-Exped. 21: 161-268.

Thijssen, R., Lever, A.J. and Lever, J. 1974. Food composition and feeding periodicity of O-group plaice (Pleuronectes platessa) in the tidal area of a sandy beach. Neth. J. Sea Res. 8: 369-377.

Tietjen, J.H. 1980. Microbial-meiofaunal interrelationships: a review. Microbiology 1980: 335-338.

Tiffany, W.J. 1971. The tidal migration of Donax varaibilis Say (Mollusca: Bivalvia). Veliger 14: 82-85.

Trevallion, A. 1971. Studies on Tellina tenuis Da Costa. III Aspects of general biology and energy flow. J. exp. mar. Biol. Ecol. 7: 95-122.

Trevallion, A., Ansell, A.D., Sivadas, P. and Narayanan, B. 1970. A preliminary account of two sandy beaches in south west India. Mar. Biol. 6: 268-279.

Trevor, J.H. 1978. The dynamics and mechanical energy expenditure of the polychaetes Nephtys cirrosa, Nereis diversicola and Arenicola marina during burrowing. Estuar. coastl. mar. Sci. 6: 605-619.

Trueman, E.R. and Brown, A.C. 1976. Locomotion, pedal retraction and extension, and the hydraulic systems of Bullia (Gastropoda, Nassaridae). J. Zool., Lond. 178: 365-384.

Underhill, L.G., Cooper, J. and Waltner, M. 1980. The status of waders (Charadrii) and other birds in the coastal region of the southern and eastern Cape, summer 1978/79. Western Cape Wader Group, Cape Town.

Uschakow, P. 1927. In: Derjugin, K.M. (ed.) Zur Fauna des Weisses Meeres. Trav. Soc. Nat. Sect. Zool. Leningrad 57: 104-119.

Vader, W.J.M. 1965. Intertidal distribution of haustoriid amphipods in the Netherlands. Bot. Gothoburg. 3: 233-246.

Vader, W.J.M. 1970. Talorchestia brito Stebbing (Amphipoda, Talitridae): Notes on distribution, taxonomy, and biology. Sarsia 42: 83-96.

Valentine, J.W. and Ayala, F.J. 1975. Genetic variation in Frieleia halli, a deep-sea brachiopod. Deep Sea Res. 22: 37-44.

Valentine, J.W., Hedgecock, D., Zumwalt, G.S. and Ayala, F.J. 1973. Mass extinctions and genetic polymorphism in the "killer clam" Tridacna. Geol. Soc. Am. Bull. 84: 3411-3414.

Van As, D., Fourie, H.O. and Vleggaar, C.M. 1975. Trace element concentrations in marine organisms from the Cape west coast. S. Afr. J. Sci. 71: 151-154.

Vegas-Velez, M. 1968. Revision taxonomica y zoogeographica de algunos gasteropodes y lamellibranquios marinos del Peru. An. Cient., Lima 6: 1-29.

Velimirov, B. 1980. Formation and potential trophic significance of marine foam near kelp beds in the Benguela upwelling system. Mar. Biol. 58: 311-318.

Vermeij, G.J. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge, Mass.

Viader, R. 1951. New or unrecorded shells from Mauritius and its dependencies. Mauritius Inst. Bull. 3: 127-155.

Vohra, F.C. 1971. Zonation on a tropical sandy shore. J. Anim. Ecol. 40: 679-708.

Wade, B.A. 1967. Studies on the biology of the West Indian beach clam Donax denticulatus Linné. 1. Ecology. Bull. mar. Sci. 17: 149-174.

Walger, E. 1962. Die Korngrossenverteilung von Einzellagen sandiger Sedimente und ihre genetische Bedeutung. Geol. Rundschau 51: 494-507.

Warwick, R.M. and Davies, J.R. 1977. The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to the substrate. Estuar. coastl. mar. Sci. 5: 267-288.

Warwick, R.M. and Price, R. 1975. Macrofauna production in an estuarine mud-flat. J. mar. biol. Ass. U.K. 55: 1-18.

Washburn, E.W. 1928. The vapor pressures of ice and water up to 100°C. Internat. crit. Tab. 3: 210-212.

Watkin, E.E. 1940. The swimming and burrowing habits of the amphipod Urothoe marina (Bate). Proc. roy. Soc. Edinburgh 60: 271-280.

Watkin, E.E. 1942. The macrofauna of the intertidal sand at Kames Bay, Millport, Buteshire. Trans. roy. Soc. Edinburgh 60: 543-561.

Webb, J.E. 1958. The ecology of Lagos Lagoon. V. some physical properties of lagoon deposits. Phil. Trans. roy. Soc. Lond. 241B:393-419.

Webber, H.H. 1979. The intertidal and shallow subtidal benthos of the west coast of Whidbey Island, spring 1977 to winter 1978. N.O.A.A. tech. Mem. E.R.L. MESA-37: 1-108.

Wesenberg-Lund, E. 1961. Report of the Lund University Chile expedition, 1948-49. 43. Polychaeta errantia. Acta Univ. Lund N. S. Avd. Zool. 57(12): 1-139.

Westheide, W. 1972. La faune des polychètes et des archiannélides dans les plages sableuses â ressac de la côte mediterranéenne de la Tunisie. Bull. Inst. natn. scient. tech. Oceanogr. Pêche. Salammbo 2: 449-468.

Wheeler, J.F.G. 1934. Nemerteans from the South Atlantic and Southern Oceans. Discovery Reps. 9: 215-294.

Wheeler, J.F.G. 1940. Nemerteans of Kerguelen and the Southern Ocean. Rep. B.A.N.Z. Antarctic Res. Exped., 1929-31 4B(8): 235-256.

Wicks, S.R. 1974. Presence of Azotobacter in marine sand beaches. Florida Scient. 37: 167-169.

Wiener, S. Lowenstam, H.A. and Hood, L. 1976. Characterisation of 80 million-year old mollusk shell proteins. Proc. natn. Sci. Acad. U.S.A. 73: 2541-2545.

Wieser, W. 1975. The meiofauna as a tool in the study of habitat heterogeneity. Cah. Biol. mar. 16: 647-670.

Wijnhoff, G. 1913. List of nemertenans collected in the neighbouhood of Plymouth from May-September, 1910. Plymouth J. mar. biol. Ass. 9: 407-434.

Wijnhoff, G. 1925. On a collection of nemerteans from Curaçao. Bijdr. Dierk. 24: 97-120.

Winterbottom, R. 1967. A preliminary investigation of the fauna of the Muizenberg surf zone. Unpublished project, Zoology Dept., University of Cape Town.

Withers, R.G. 1977. Soft-shore macrobenthos along the south-west coast of Wales. Estuar. coastl. mar. Sci. 5: 467-484.

Wolcott, T.G. 1978. Ecological role of ghost crabs, Ocypode quadrata (Fabricius) on an ocean beach: scavengers or predators? J. exp. mar. Biol. Ecol. 31: 67-82.

Wolff, W.J. 1973. The estuary as a habitat: analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. Zool. Verh., Leiden 126: 1-242.

Wood, D.H. 1968. An ecological study of a sandy beach near Aukland, New Zealand. Trans. roy. Soc. N.Z. 10: 89-115.

Woodring, W.P. 1966. The Panama land bridge as a sea barrier. Amer. phil. Soc. Proc. 110: 425-433.

Wooldridge, T. 1978. Two new species of *Gastrosaccus* (Crustacea, Mysidacea) from sandy beaches in Transkei. Ann. S. Afr. Mus. 76: 309-327.

Wooldridge, T. 1981. Zonation and distribution of the beach mysid, *Gastrosaccus psammodytes*. J. Zool., Lond. 193: 183-189.

Wooldridge, T., Dye, A.H. and McLachlan, A. 1980. The ecology of sandy beaches in Transkei. Unpublished manuscript.

Wormersley, H.B.S. and Edmonds, S.J. 1958. A general account of the intertidal ecology of South Australian coasts. Aust. J. mar. Freshwat. Res. 9: 217-260.

Yeo, R.K. and Risk, M.J. 1979. Intertidal catastrophes: effects of storms and hurricanes on intertidal benthos of Minas Basin, Bay of Fundy. J. Can. Fish. Res. Bd. __: 667-669.

Young, D.K. and Rhoads, D.C. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. 1. A transect study. Mar. Biol. 11: 242-251.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

Zelebor, V. 1886. Faun. Moll. Dalmat. 1886: 42. Reference incomplete, see Zoological Record, 1886.

Zhirmusnky, A.V. and Chu, L-C. 1963. the cell thermostability of sympatric species of Donax in relation to the temperature condition of their habitat. Acta zool. Sinica 15: 21-27.

Zwaan, A. de. and Skjoldal, H.R. 1979. anaerobic energy metabolism of the scavenging isopod *Cirolana borealis* (Lilljeborg). J. comp. Physiol. 129: 327-331.