SAND INUNDATION ON ROCKY SHORES:
ITS EFFECTS ON SPECIES RICHNESS AND THE STRUCTURE OF SPECIES ASSEMBLAGES.

by

KATHERINE MARY DOWER

THESIS

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ABSTRACT

Although sand deposits are present on many intertidal rocky shores, their effects on species richness, zonation and trophic structure have often been overlooked. This study is the first to recognise sand as an important abiotic factor on South African rocky shores.

Rocky shores in the eastern Cape Province of South Africa are subject to extensive sand inundation and are composed of two hard substrata of differing topographies. Four sites on one substratum and six on the other were sampled quantitatively using quadrats. The biota were identified, counted and/or weighed to provide a matrix of species biomass and numbers in separate zones. This matrix was then analysed using ordination and classification.

A total of 321 species were identified which is more than local rocky or sandy shores. While the intermediate disturbance hypothesis would predict high species richness on these shores, it does not fully explain this richness nor the distribution of species assemblages.

Habitat heterogeneity, including the dynamics of sand deposits, is strongly influenced by substratum topography and is the most important factor generating species richness. Abrasion by sand (sand scour) causes local reductions in richness but the presence of semi-permanent sand deposits allows habitation by psammophilic and sand-dependent species. As a result the biota of a sand

inundated rocky shore includes both a full rocky shore and a large sandy beach component.

Substratum topography controls patterns of sand deposition and retention and community analysis showed that samples were clustered primarily according to species richness and secondarily according to substratum type. Ordination of species identified an arc of species assemblages of decreasing levels of sand tolerance. These corresponded to sample groupings so that the assemblages found in various habitats were characterised by particular levels of sand tolerance.

The presence of sand has a negative effect on the biomass of primary producers and filter feeders but a positive effect on the biomass of deposit feeders. Because sand is retained to different degrees in different zones, trophic structure varies between zones and to a lesser extent, between rock types. In general, however, the trophic structure of sand inundated rocky shores is similar to that of non-inundated shores.

A DUNE ROCK

B SANDSTONE

Figure 1.1: Photographs of the two substratum types showing the topography of each. A) The wave-cut platform characteristic of dune rock shores (Three Sisters) and B) the ridges and sand-filled gulleys characteristic of sandstone shores (Beacon Rocks).

CHAPTER ONE - INTRODUCTION

Ecological communities can be characterised by the number of species present and their abundances. The sequential development of a community through changes in the relative abundances of the dominant species, theoretically leads ultimately to a stable climax community. The climax community is characterised by low species diversity and is often dominated by a single species (Huston and Smith, 1987). This process is known as succession. Stability is the ability of a community at any stage during succession to persist despite continual disturbances, or to recover from a disturbance (May, 1979). Disturbances which upset the normal balance of a community, sometimes removing the dominant species, may be biotic or abiotic. They include both regular and completely unpredictable events and may be varied in form and scale. Disturbances include intense predation, fallen trees in tropical forests, landslides, and log battering or the scouring of pack-ice on intertidal shores.

The "intermediate disturbance hypothesis" postulates a peak in species diversity "at an intermediate stage in succession after a large disturbance or with smaller disturbances that are neither very frequent nor very infrequent" (Connell, 1979). It was presented first by Connell in 1978. This hypothesis has been used to successfully predict species richness in a variety of terrestrial and aquatic ecosystems including tropical forests, coral reefs and intertidal boulder fields (Paine and Vadas, 1969;

Connell, 1978,1979; Sousa, 1979a,b; Dethier, 1984). In some cases (Huston, 1979; Armesto and Pickett, 1985; Menge and Sutherland, 1987) the intermediate disturbance hypothesis has been found to be unsatisfactory when used to predict the diversity of the system studied.

In this context 'richness' and 'diversity' are generally regarded as synonyms (Menge and Sutherland, 1976; Connell, 1978) and will be used as such in this study.

In intertidal systems the irregular deposition of sand on rocky shore communities constitutes a very common though little studied form of disturbance. The possible effects of sand deposition on rocky shores were first pointed out by Stephenson (1943a) when he wrote "...there is little doubt that the proximity of any considerable body of sand to a rocky area affects the population of the adjacent rock". Few rocky shores are devoid of any trapped sediments and on many their effect on community structure is negligible. Nevertheless, on some rocky shores sand deposits are present in sufficient quantity to influence directly the communities present. For the purposes of this study such rocky shores are referred to as 'mixed shores'.

The world-wide understanding of these shore types is remarkably scant and the only detailed studies to date on mixed shores have been carried out in the United States of America. The majority of these studies involve the effects of sand on algae only (Markham, 1973; Devinny and Volse, 1978; Stewart, 1983; D'Antonio, 1986) while few studies have been done on whole communities (Daly and Mathieson, 1977; Taylor and Littler, 1982; Littler *et al.*, 1983).

Sand presence may be viewed as an abiotic factor when defining habitat heterogeneity. Gradients of sand cover, ranging from sand free areas to stable sand deposits, allow the separation of species on the basis of sand tolerance in the same manner in which high shore species may be separated from low shore species on the basis of their tolerance of emersion. Sand presence may also be viewed as a catastrophic event, as are ice scouring (Wethey, 1985), log damage (Dayton, 1971) or severe wave action (Paine, 1974; Menge, 1979; Underwood, 1980; Paine and Suchanek, 1983; Sousa, 1984,1985; Ebeling *et al.*,1985), when large amounts of sand are either deposited or eroded over a very short (diurnal), neap-spring or longer time period resulting in the removal or loss of organisms. Such catastrophes provide free space for colonisation. This is important as space is often a primary limiting factor in intertidal systems (Paine and Vadas, 1969; Dayton, 1971; Paine and Levin, 1981; Branch, 1984). The area of the shore in which a species assemblage is found could be indicative of the levels of sand tolerance of those species (Brown, pers. comm.). Fluctuation between sand free and sand inundated states in certain areas, by catastrophic or less severe events, may therefore be expected to influence species assemblages.

Although zones are easily identified in the intertidal region over large areas, it is often found that within a zone much small scale differentiation occurs. These small areas of specific habitats are caused by small scale changes in spatial and temporal factors and are known as patches. The concept of patchiness on rocky shores and on sandy beaches is well known and has been well documented (Stephenson, 1943a; Chapman, 1946; Brown, 1971; Menge and Sutherland, 1976; McLachlan, 1977a; Sousa, 1979a; Hartnoll and Hawkins, 1980; Dye *et al.*,1981; McLachlan *et al.*, 1981a; Robles, 1982; McQuaid *et al.*, 1985; Pickett and White, 1985). Sand presence constitutes an additional temporal and spatial variable on mixed shores so that the size and permanency of a sand deposit appear to play a role in determining community structure (Bally *et al.*, 1984). Patchiness is exhibited in time, due to the frequency and intensity of sand inundation, and with respect to space in terms of the topography of the substratum and the patterns in which the sand is trapped. As a result of this temporal and spatial patchiness, mixed shores maintain populations of some rocky shore species in sand free areas and at the same time permit the presence of sand-tolerant, sand-dependent and sand-loving (psammophilic) species in sand patches (Brown, pers.comm.; Littler *et al.* ,1983).

Sand inundation is often unpredictable and sand may be deposited or eroded in varying amounts at different times (Daly and Mathieson, 1977). In general there is usually a net deposition during either the winter months (Taylor and Littler, 1982; Littler *et al.*, 1983) or the summer months (Markham, 1973; Daly and Mathieson, 1977; Stewart, 1983; D'Antonio, 1986; Brown unpubl. data; Dower, unpubl. data), with erosion occurring during the other half of the year. The age of a sand deposit or the period for which an area of hard substratum remains clear of sand has important consequences in terms of succession and the intermediate disturbance hypothesis. Mixed shores may constitute a mosaic of fluctuating successional stages (Littler *et al.*, 1983), similar in theory to the boulder beaches described by Osman (1977) and Sousa (1979a), with separate successional stages occurring in sand and rock.

Shores of mixed rock and sand comprise over 31% of the South African and Namibian coastline (Underhill and Cooper, 1982 in Bally *et al.*, 1984). Being neither homogeneous rock or sand these areas include a large range of shore types from those with small amounts of rock dispersed along sandy beaches to rocky shores with varying amounts of sand deposits. In the eastern Cape the coastline consists of considerable stretches of 'rock-free' sandy beaches as well as rocky shores most of which are mixed shores, subject to frequent sand scour or deposition.

It may be expected that intertidal topography has a direct effect on the deposition and retention patterns of sand. In this region two rock types with very different topographies occur: consolidated dunes (aeolian calcarenites) and hard quartzitic sandstone (Figure 1.1).

The extreme topographic differences displayed between these two substratum types could result in substratum-specific species assemblages caused by different patterns of sand deposition. The first aim of this study was, therefore, to derive a basic understanding of the effects of substratum topography on species assemblages (i.e. their richness and trophic structure), and to discuss to what extent patterns of sand deposition may affect these assemblages. The second aim was to examine the validity of the intermediate disturbance hypothesis when applied to these sand inundated rocky shores.

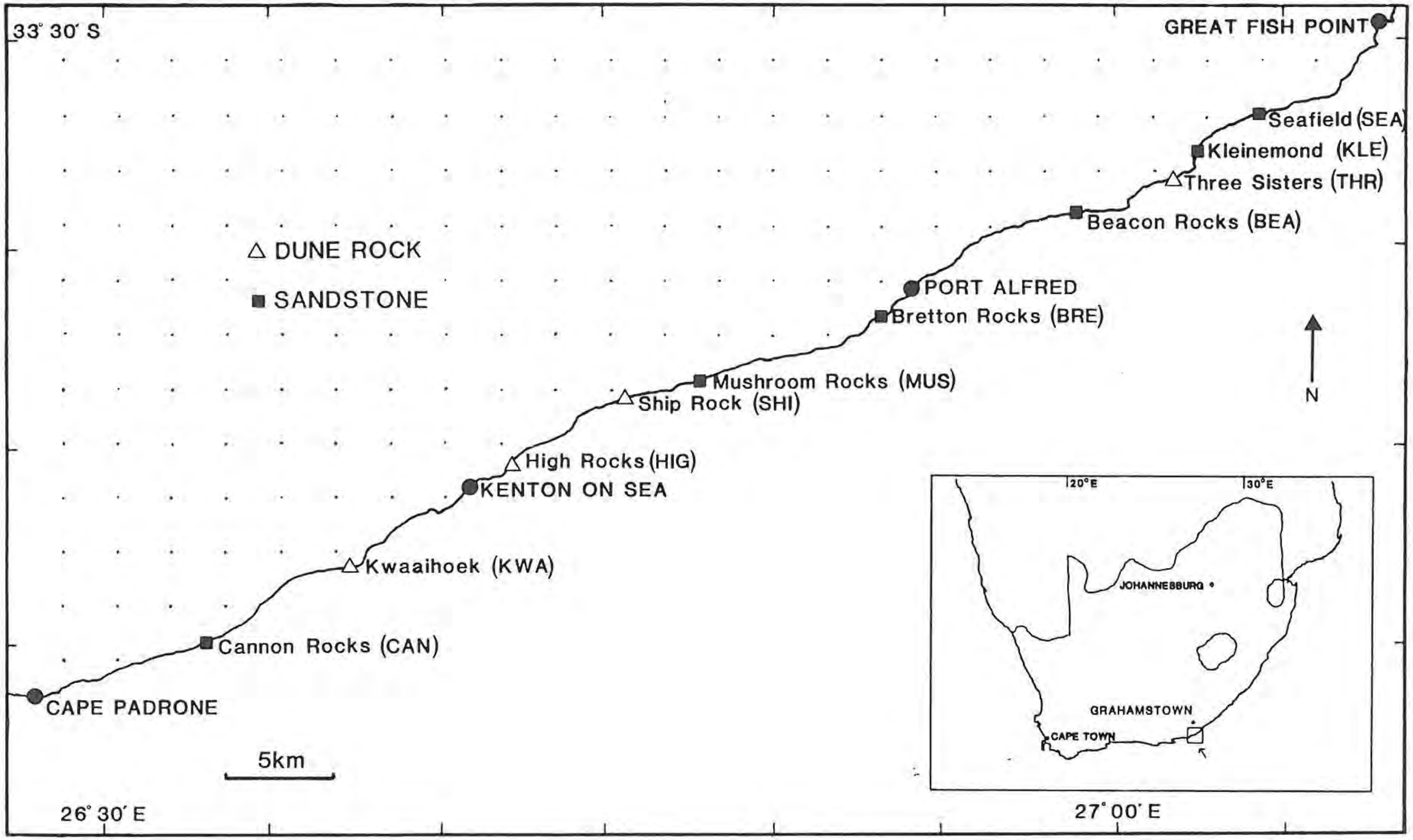


Figure 2.1: Map of the study area showing four dune rock and six sandstone sampling sites.

CHAPTER TWO - STUDY AREA

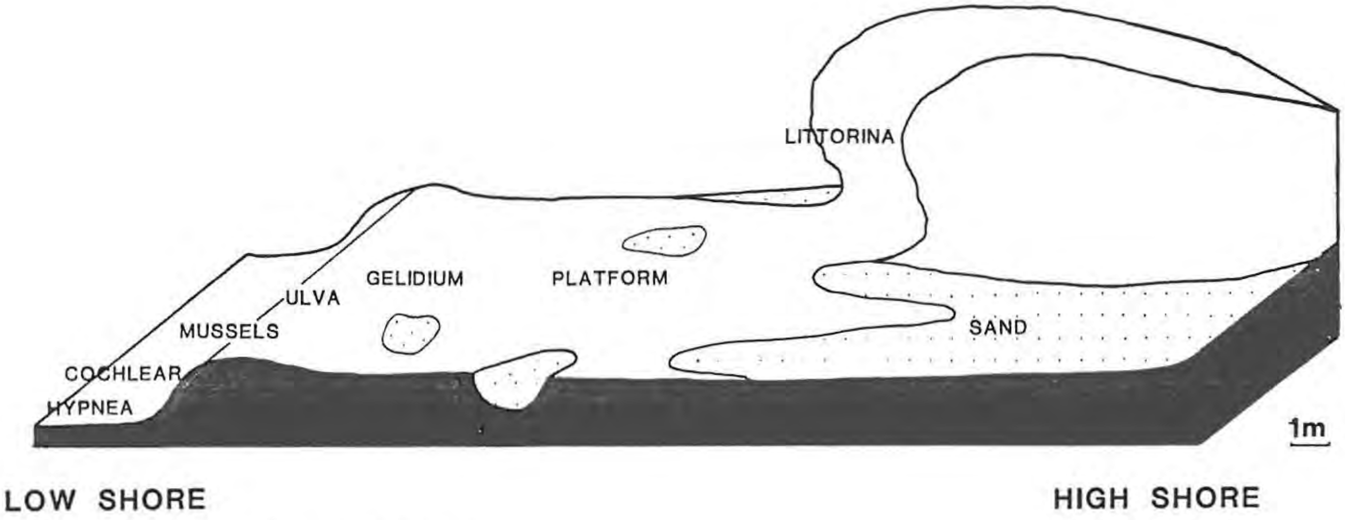
Shores of mixed rock and sand include a spectrum of shores with varying proportions of rock and sand ranging from "sand free" rocky shores to "rock free" sandy beaches (Bally *et al.*, 1984). Before detailed sampling could begin it was necessary to carry out a survey of the local coastline to ascertain the extent to which these shores are subjected to sand inundation. This would allow the preliminary classification of shore types and the selection of specific sites for a more detailed study.

Using four wheel drive vehicles the coastline of the eastern Cape province of South Africa was surveyed from Cape Padrone (33^{o} 46.3' S: 26^{o} 27.5' E) to Great Fish Point (33^{o} 31.3' S: 27^{o} 06.8' E) and areas of rock, sand inundated rock and "rock free" sandy beaches were noted (Figure 2.1). At various localities along this 80km stretch of coast sand deposits and rocky areas were subjectively sampled. Without using quantitative sampling methods, patches of substratum were scraped, larger organisms were noted, sand was sifted and small rocks and boulders were overturned. Specimens were then returned to the laboratory for identification.

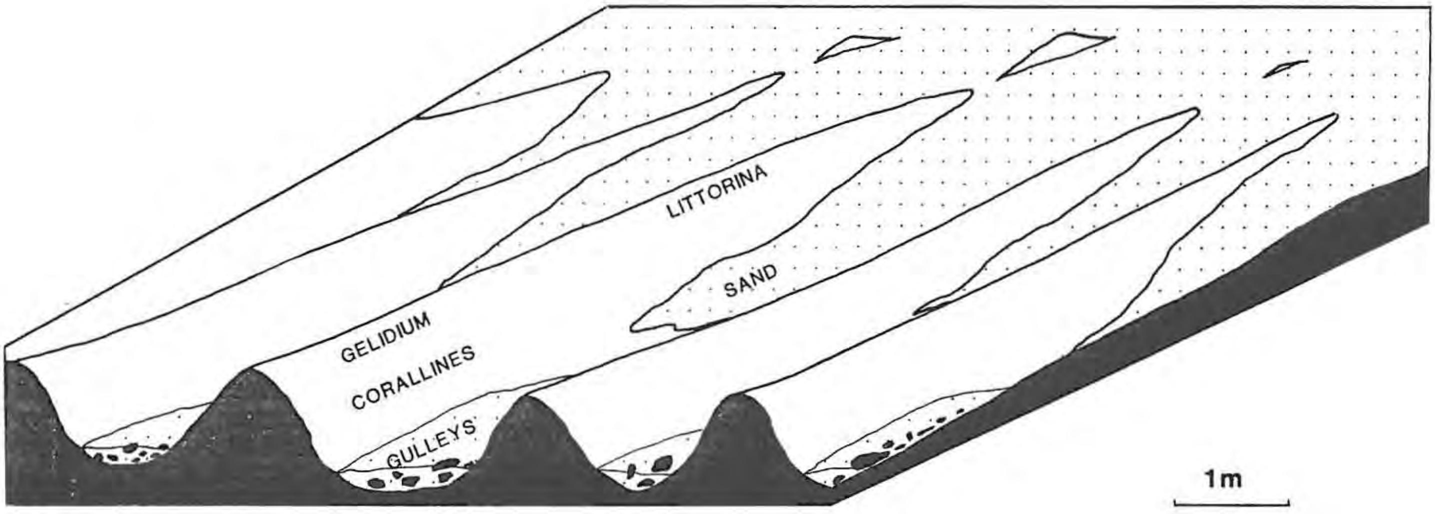
Although considerable stretches of sandy beach lacking any rock component were found, there were no rocky shores without considerable sand deposits. The fact that rocky and sandy areas did not always correspond fully to those shown on detailed ordinance survey maps indicates that large amounts of sand may be eroded and deposited in some areas.

Sand inundated rocky outcrops along this coast are made up of one of two substrata. Highly eroded, consolidated dunes form aeolian calcarenite (hereafter referred to as "dune rock" following Tinley, 1985) is the less common of the two substrata. Dune rock is characterised by an eroded wave cut platform which may or may not be backed by an overhanging cliff-face ("undercut visor", Tinley, 1985) (Figure 1.1). Vertical zonation is typically parallel to the shore (Figure 2.2). The surface, although heavily pitted and with many pools and small potholes, is fairly homogeneous. Sand is found predominantly in the mid shore and high shore areas as well as in the pools and in small pits in the rock.

The second, more common rock type is quartzitic sandstone, a hard rock characterised by jagged parallel ridges running perpendicular to the sea (Figure 2.2). The ridges are separated by wide gulleys which can contain deep sand deposits and sometimes small rocks or boulders as well. The crests of the ridges remain predominantly sand free. The topography of the sandstone appears to provide a higher level of spatial heterogeneity than that of dune rock. Vertical zonation follows the form of the ridges and, although there are noticeable low shore, mid shore and high shore regions parallel to the sea, there is also marked zonation up the sides of the ridges and thus perpendicular to the sea. For example *Littorina africana africana*



A DUNE ROCK



B SANDSTONE

Figure 2.2: Diagrammatic representation of each shore type. A) a dune rock shore showing the position of all the zones and B) a sandstone shore showing the zones in the mid and upper shore regions.

and *L. a. knysnaensis*, two gastropods usually associated with the splash zone, are often found low down on the shore but along the crests of ridges.

Both shore types show zonation superficially similar to that described by Brown and Jarman (1978) for the warm temperate South Coast Province and by Branch and Branch (1981) for the South Coast. Expansive beds of the red alga, *Hypnea spicifera*, dominate the infratidal (sublittoral) fringe zone. A narrow *cochlear* zone characterised by the limpet *Patella cochlear*, is present in a few areas and large beds of the brown mussel, *Perna perna*, are found in the lower balanoid (lower mid littoral) zone.

Farther upshore there are more noticeable differences in zonation. On sandstone sand-filled gulleys are found, followed by a zone of coralline algae which precedes a zone dominated by the red alga, *Gelidium pristoides*. On dune rock gulley and coralline zones do not occur. A zone of the green alga, *Ulva rigida* is sometimes found and the *Gelidium* zone is less marked than on sandstone. Higher up the shore is an apparently impoverished platform zone. A high shore sand and a *Littorina* zone occur on both shore types although distinct differences in species composition can be shown for these two zones.

Observations made in the preliminary study were important in focusing on various aspects of sand inundation that may affect species assemblages. Amongst these was the effect of substratum type. The topography of the two substrata appeared to have a direct effect on sand deposition patterns and thus an indirect effect on species assemblages. Patterns of deposition may influence benthic species assemblages as some species are more tolerant of sand presence or burial than others. Different subcommunities may thus be found within the same intertidal zone on shores of different substrata. With this in mind, sites were selected according to rock type for more detailed sampling.

CHAPTER THREE - MATERIALS AND METHODS

3.1 STUDY SITES

Sandstone was the most common of the two hard substrata between Cape Padrone and Great Fish Point whereas relatively few outcrops of dune rock were found (Figure 2.1). The four major outcrops of dune rock were sampled. These were (from W-E):

1. Kwaaihoek (KWA)
2. High Rocks (HIG)
3. Ship Rock (SHI)
4. Three Sisters (THR)

Six outcrops of sandstone were also sampled:

1. Cannon Rocks (CAN)
2. Mushroom Rocks (MUS)
3. Bretton Rocks (BRE)
4. Beacon Rocks (BEA)
5. Kleinemond (KLE)
6. Seafield (SEA)

Virtually no shores along this coast are sheltered from wave action and all the study sites experience similar degrees of wave exposure.

3.2 SAMPLING AND LABORATORY ANALYSIS

Each of the ten sites was divided into subjectively chosen species assemblages or zones, characterised by various conspicuous species e.g. *Hypnea spicifera* or coralline algae. Intertidal pools were not sampled at either shore type. The size of each zone varied greatly between the sites and not all zones occurred on each shore. Sampling was carried out during spring low tides.

A total of 66 zones were sampled at the ten sites (Appendix A). Zones that were sampled at three or more sites included *Hypnea spicifera* (*Hypnea*), *Patella cochlear* (*cochlear*), *Perna perna* (mussels), gulleys, coralline algae (corallines), *Gelidium pristoides* (*Gelidium*), wave cut platform (platform), high shore sand (sand) and high shore rocks (*Littorina*).

Quantitative sampling of each zone was done using three quadrats for each sample. Metal quadrats of 50cm x 50cm and 50cm x 25cm were used for most of the shore. Smaller quadrats of 20cm x 20cm and 10cm x 10cm were used for mussel beds and high shore rocks respectively. In the case of very small quadrats (10cm x 10cm) a minimum of five samples were taken. The substratum was scraped clean and the organisms were collected in plastic bags.

High shore sand was sampled using 50cm x 50cm and 50cm x 25cm quadrats. Sand of approximately 10cm in depth was sifted through a sieve of mesh size 1.0mm. All organisms were removed from the sieve and placed in containers for preservation.

In the laboratory specimens were fixed in 4% Formalin in sea water. After a minimum of three days they were transferred to 10% Phenoxytol in sea water for preservation. Later, sorting and identification took place. All specimens were then counted and subsequently dried in an oven at 60°C for a minimum of 24 hours after which they were weighed to 0.0001g. Limpets were removed from their shells before drying. All calcareous molluscs, decapods and echinoderms (excluding ophiuroidea) were acidised in 1M HNO_3 before drying. The non-calcareous component of the shells and carapaces was included in the final mass. Coralline algae were not acidised.

Two species, the bivalve *Perna perna* and the gastropod, *Eatoniella nigra*, were either too numerous or too small to weigh individually. *Perna perna* of >10mm were therefore measured and the following length/mass regression equation was calculated and used to derive dry mass:

$Y = 0,000023\ X^{2.42}$ $\qquad n = 40\ ;\ r^2 = 0.973$

where Y = shell free dry mass

X = maximum shell length

For small mussels (<10mm) a mean mass of 0.0011g per individual was assumed (X = 5mm). Individuals were counted and shell free dry mass was derived by extrapolation.

The gastropod, *Eatoniella nigra*, was too small to measure accurately (maximum length = 2mm). Ten samples of 100 individuals each were acidised and a mean mass per individual of 0.045mg was obtained. Samples of *E. nigra* were subsequently counted and acidised dry mass was derived by extrapolation.

Mean biomass and abundance data for each species were obtained for each set of quadrats, for each zone, at each site, and converted to biomass and abundance per m^2. A sample therefore represents the meaned data for three or five quadrats from one zone at one site. Raw data matrices of sample by species were drawn up for biomass and numbers per m^2. Basic statistical analyses such as t-tests were done using the computer package STATGRAPHICS.

3.3 COMMUNITY ANALYSIS

Multivariate analysis is used in ecology in order to generate hypotheses which may then be tested by other statistical means (Gauch, 1982). Two methods of multivariate analysis, ordination and classification, were used to summarise and define structure in the present data.

3.3.1 Ordination

Ordination is a way of showing, in as few dimensions as possible, the ecological relationships between species and samples (Gauch, 1982). Various techniques for ordination are currently in use by ecologists. These include direct gradient analysis, weighted averages, principle components analysis, nonmetric multidimensional scaling, reciprocal averaging (a synonym for correspondence analysis) and detrended correspondence analysis (Gauch and Whittaker, 1972; Gauch, 1982; Digby and Kempton, 1987).

Detrended correspondence analysis, DCA, is at present used extensively in ecology and appears to be the most popular method of ordination (Peet *et al.*, 1988). It is derived from reciprocal averaging techniques (see Hill (1973) for detailed methods). During reciprocal averaging a range of arbitrarily chosen 'starting scores' is allocated to the samples. Species scores are derived by averaging the total sample scores of the samples in which a particular species occurs. A second, new set of sample scores is then obtained by averaging the newly derived species scores. The second sample scores are then rescaled according to the following formula :

$$S_{i2} \text{ (rescaled)} = R_1 \text{ X } \frac{(S_{i2} - S_{2min})}{R_2}$$

where : R_1 = the range of the original arbitrarily defined scores

S_{i2} = the second sample score for species i

S_{2min} = the lowest second sample score for species i to n

R_2 = the range of the second sample scores for species i to n

This gives rescaled values for each sample, the range of which is equal to that of the original arbitrary sample scores.

These rescaled sample scores are used to calculate a new set of species scores which in turn are rescaled in the same manner and used to recalculate new sample scores. After repeated iterations of this reciprocal averaging the rescaled scores stabilise. These stabilised scores make up the first ordination axis.

Sample scores for the second axis are not arbitrary. A set of rescaled scores which are 'close' to the final stabilised set is used. Before iteration these must be adjusted by subtracting an estimated multiple of the final stabilised set of the first axis. These adjusted scores then undergo reciprocal averaging to obtain the second axis. This process is continued until the required number of axes has been obtained.

Unfortunately two fundamental problems arise from this method (Gauch, 1982; Kenkel and Orloci, 1986; Wartenberg *et al.*, 1987; Peet *et al.*, 1988) :

1) An 'arch effect' develops in the summarised data resulting from the dependence of one axis on the previous axis, and

2) Axis scaling is arbitrary and the ends of the axis are contracted. As a result, points at the ends of the axes, once scaled, are closer together than if they had occurred in the middle.

By detrending, using DCA, the first problem is avoided as there is in no relationship between the first and subsequent axes. This is achieved by dividing the first axis into segments. In each segment the final sample scores are adjusted so as to have a mean equal to zero. These detrended sample scores are then used to calculate the next axis (Hill, 1979a).

To account for undefined axis scaling, DCA uses an arbitrary method to provide uniform units of length by rescaling the final species scores and then the final sample scores of each axis, and rids the axes of distortion found mainly in the form of compression at the extremes (Dargie, 1986; Peet *et al.*, 1988).

Wartenberg *et al.* (1987) criticise the removal of the 'arch effect' by DCA as well as the method of rescaling. They state that the 'arch effect' which is referred to as a 'mathematical artifact' by some (e.g. Hill, 1979a), may in fact contain valuable information and may be representative of the data. 'Flattening' by DCA is therefore inappropriate. Wartenberg *et al.* (1987) also argue that rather than using an arbitrary rescaling method, rescaling should be done with respect to the observed data so that, for example, rescaling based on biomass data would, and should, differ from that based on abundance.

In defending DCA, Peet *et al.* (1988) emphasise that Wartenberg *et al.* (1987) address only one-dimensional gradients while DCA is most useful when applied to multi-dimensional gradients. Peet *et al.* (1988) argue that since there is, at present, no adequate alternative to DCA that is without problems of its own, the use of this technique should be encouraged as long as the user is aware of the possible drawbacks. They add that, although the rescaling of axes is arbitrary, all methods are in fact arbitrary and the axes produced by rescaling are as interpretable as those produced by any other method. Kenkel and Orloci (1986) advise the complementary use of reciprocal averaging and DCA in order to establish the extent to which DCA alters the result.

In general it appears that DCA is the most useful method in use at present. A DCA program, DECORANA (DEtrended CORrespondence ANAlysis, produced by Cornell Ecology Programs, (Hill, 1979a) was used for the purposes of this study. Reciprocal averaging can also be run using this program and was applied to monitor the 'flattening' properties of DCA, which were found to be minimal. Therefore only the DCA option of the program is referred to in the final results and discussion. For classification (see below) only a method based on reciprocal averaging was available.

3.3.2 Classification

Classification is the formation of clusters of similar entities (Gauch, 1982). Three kinds of classification are frequently used: table arrangement, nonhierarchical classification and hierarchical classification. For this study hierarchical classification was appropriate. This involves placing similar samples or species into groups and then arranging these in a hierarchical pattern which illustrates the relationships between these groups (Gauch, 1982).

The hierarchical classification program applied to this study, TWINSPAN (Two-Way INdicator SPecies ANalysis; Hill, 1979b), uses polythetic divisive methods for the ordering of classes (Gauch, 1982). Polythetic division implies that there is initially one large group which is repeatedly divided until a set number of smaller groups is reached (cf. agglomerative). This division uses all the information supplied for the species and samples and is not based solely on presence or absence data (cf. monothetic). TWINSPAN creates a hierarchical dendrogram for samples from an ordination based on reciprocal averaging.

TWINSPAN first classifies samples into groups and then classifies species according to their 'fidelity' to these groups (Hill, 1979b). Species classification is therefore dependent on the original sample classification. TWINSPAN has been used mainly to ensure easier interpretation of the three dimensional plot derived from the DCA ordination as presented by DECORANA.

3.3.3 Using DECORANA and TWINSPAN

The raw data consisted of two matrices, one of species abundance based on number of individuals (excluding algae) (66 zones X 281 species) and a second of species biomass (66 zones X 321 species). In a few specified cases rare species (arbitrarily defined as species occurring in only one sample) were ommitted for clarity and to minimise the effect of the program bias toward rare species. Biomass data (algae included) were transformed to a presence/absence matrix for which dendrograms were also calculated.

The transformation or scaling of the data for the TWINSPAN program into 'pseudospecies cut levels' (Hill, 1979), referred to here as data groups, was obligatory and so these transformations were simulated for the DECORANA program as well. Transformations are presented in Table 3.1.

	DECORANA	TWINSPAN			DECORANA AND TWINSPAN	
	Value	Value	Group		Value	Group
Biomass (grams)	0.01	0.00	1	Abundance	1	1
	0.10	0.10	2		10	2
	1.00	1.00	3		100	3
	10.00	10.00	4		1000	4
	100.00	100.00	5		10000	5

Table 3.1: Transformations used by the DECORANA and TWINSPAN programs.

For both programs, data are allocated to groups which are defined by cut-off values. Within each group individual data values are assigned a group score. The procedure for score assignment is slightly different for the two programs.

In the case of DECORANA, data values below the lowest or above the highest cut-off values are given group scores of 1 and 5 respectively. Data which fall between the cut-off values for any group are given real number group scores on a linear scale. For example, 11g falls into group 4 with a group score of 4.01 and 110g falls into group 5 with a score of 5.

TWINSPAN ignores all data less than the lowest cut-off value given and includes data greater than the highest cut-off value into group 5. Intermediate data are assigned integer group scores. For example, 11g falls into group 4 with a score of 4.

This discrepancy in transformation methods did not have any appreciable effects on the results produced by the two multivariate techniques.

CHAPTER FOUR - RESULTS

A full data set is housed in the Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa.

4.1 SPECIES RICHNESS

A total of 321 species, including 40 species of algae, was found at the ten sites (Appendix B). Of these, 284 were found on sandstone (x = 142.2 ± 24.9 per site) and 199 were found on dune rock (x = 118.5 ± 27.9 per site) (Table 4.1). The two rock types had 162 species in common. Although sandstone shores appear to have a far higher species richness than dune rock, these figures are not significantly different (t-test, $P>0.05$). Species richness per site ranged from 171 and 170 species at Kleinemond and Seafield respectively (both sandstone shores) to 83 species at High Rocks (dune rock). The three sites with the highest richness were all at the eastern end of the sampled coastal region (Figure 4.1).

SUBSTRATUM TYPE	NUMBER OF SITES	TOTAL RICHNESS	MEAN RICHNESS PER SITE ± S.D.	NUMBER OF RARE SPECIES
SANDSTONE	6	284	142.2 ± 24.9	66
DUNE ROCK	4	199	118.5 ± 27.8	30

Table 4.1: Total richness, mean richness and number of rare species (those found in one sample only) for six sandstone and four dune rock sites.

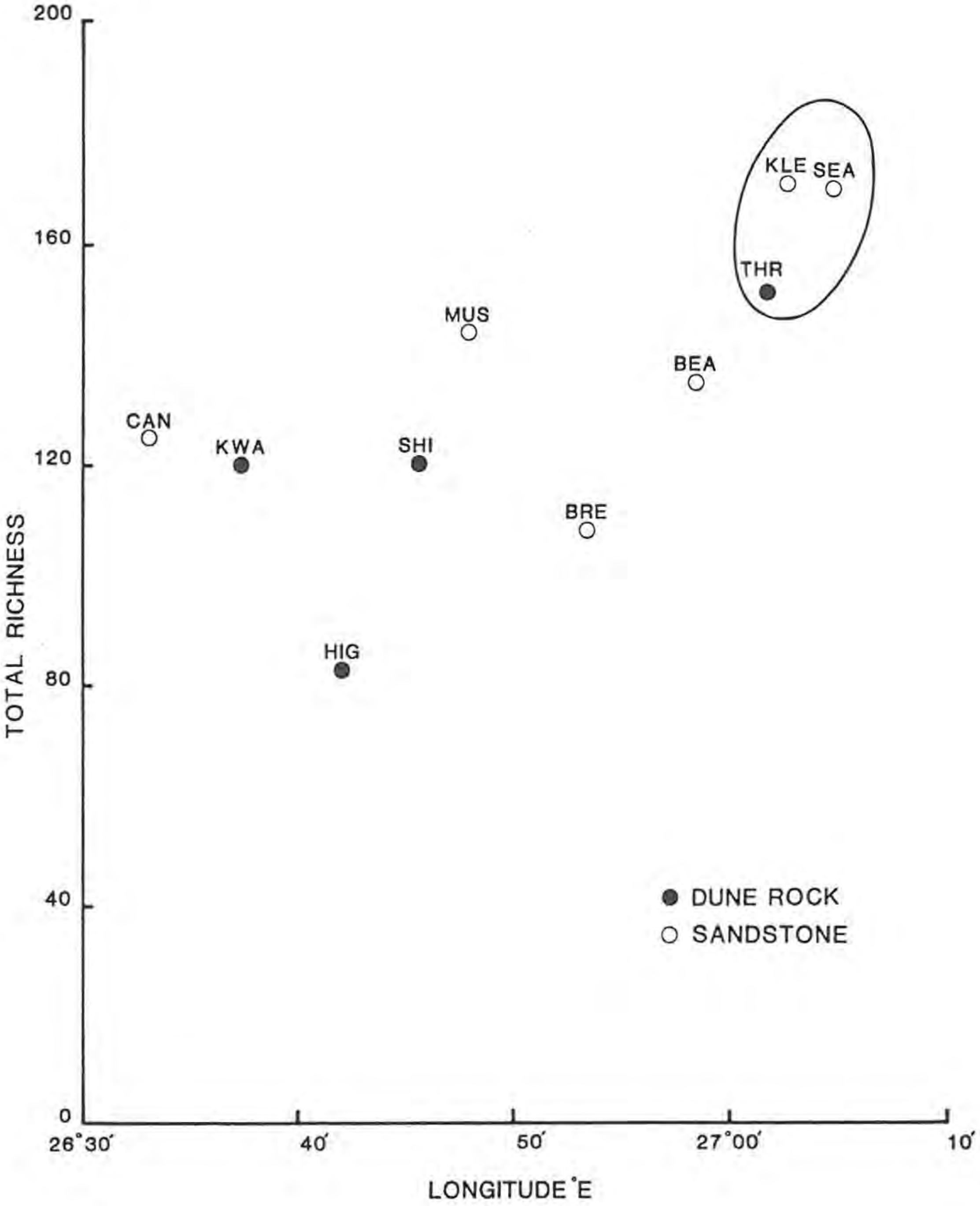
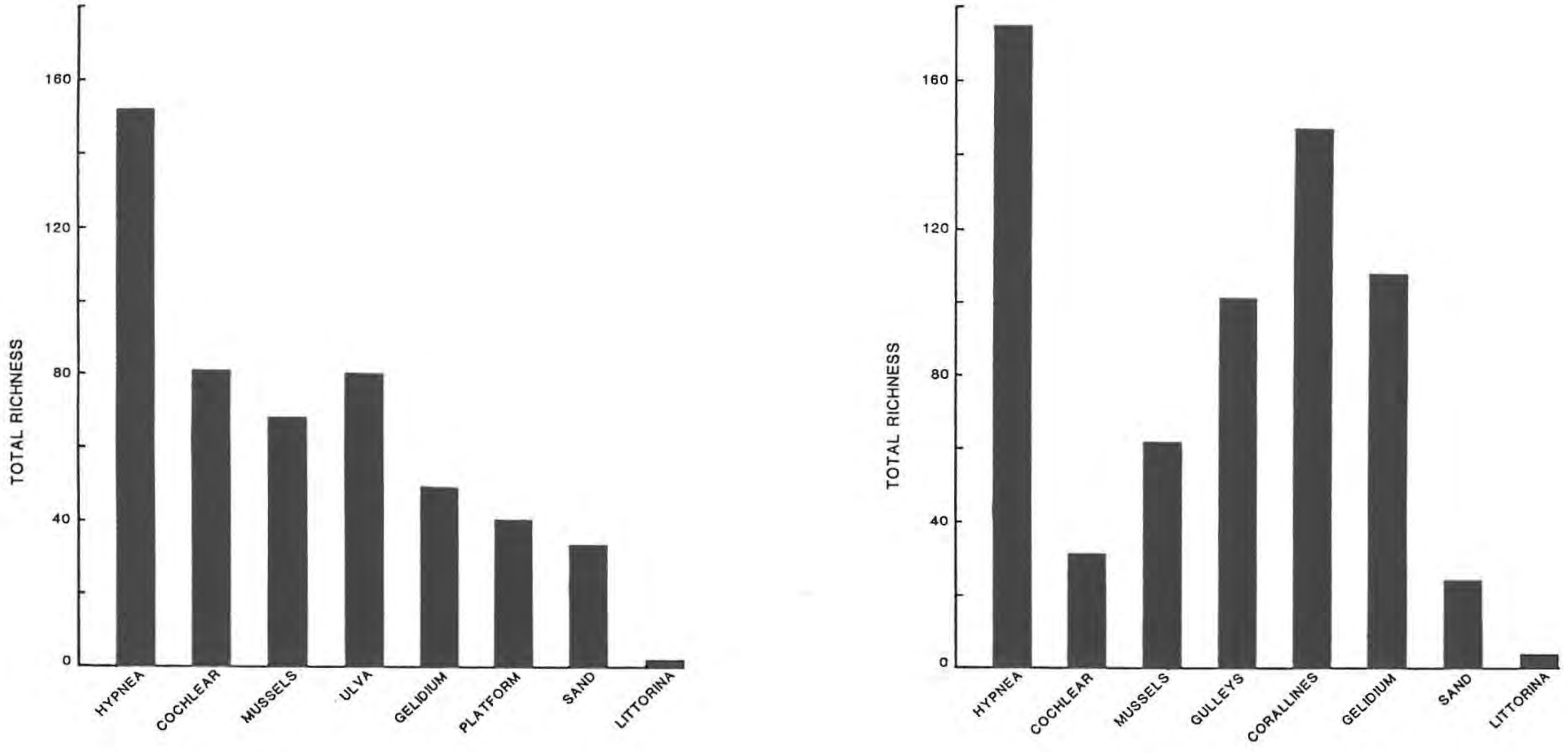


Figure 4.1: The relationship between total species richness at each site and longitude (°E). The three sites with highest richness have been circled.

BEA-Beacon Rocks, BRE-Bretton Rocks, CAN-Cannon Rocks, HIG-High Rocks, KLE-Kleinemond, KWA-Kwaaihoek, MUS-Mushroom Rocks, SEA-Seafield, SHI-Ship Rock, THR-Three Sisters.



A DUNE ROCK

B SANDSTONE

Figure 4.2: Total species richness for each zone. Zones are ordered from lowest on the shore (*Hypnea*) to highest (*Littorina*).

The sublittoral fringe, or *Hypnea* zone, characterised by the rhodophyte *Hypnea spicifera*, had the highest richness for any one zone. A total of 222 species was found in this zone; 152 and 175 species on dune rock and sandstone respectively (Figure 4.2). The two substrata shared 105 species and sixty-eight species were exclusive to this zone. The coralline zone, which was only found on sandstone shores, had the second highest total richness; 147 species. Of these, 27 were exclusive to the coralline zone. Mean richness was also highest for these two zones on both rock types combined: 74.3 ± 25.4 for *Hypnea* and 68.4 ± 21.8 for the coralline algae (Table 4.2).

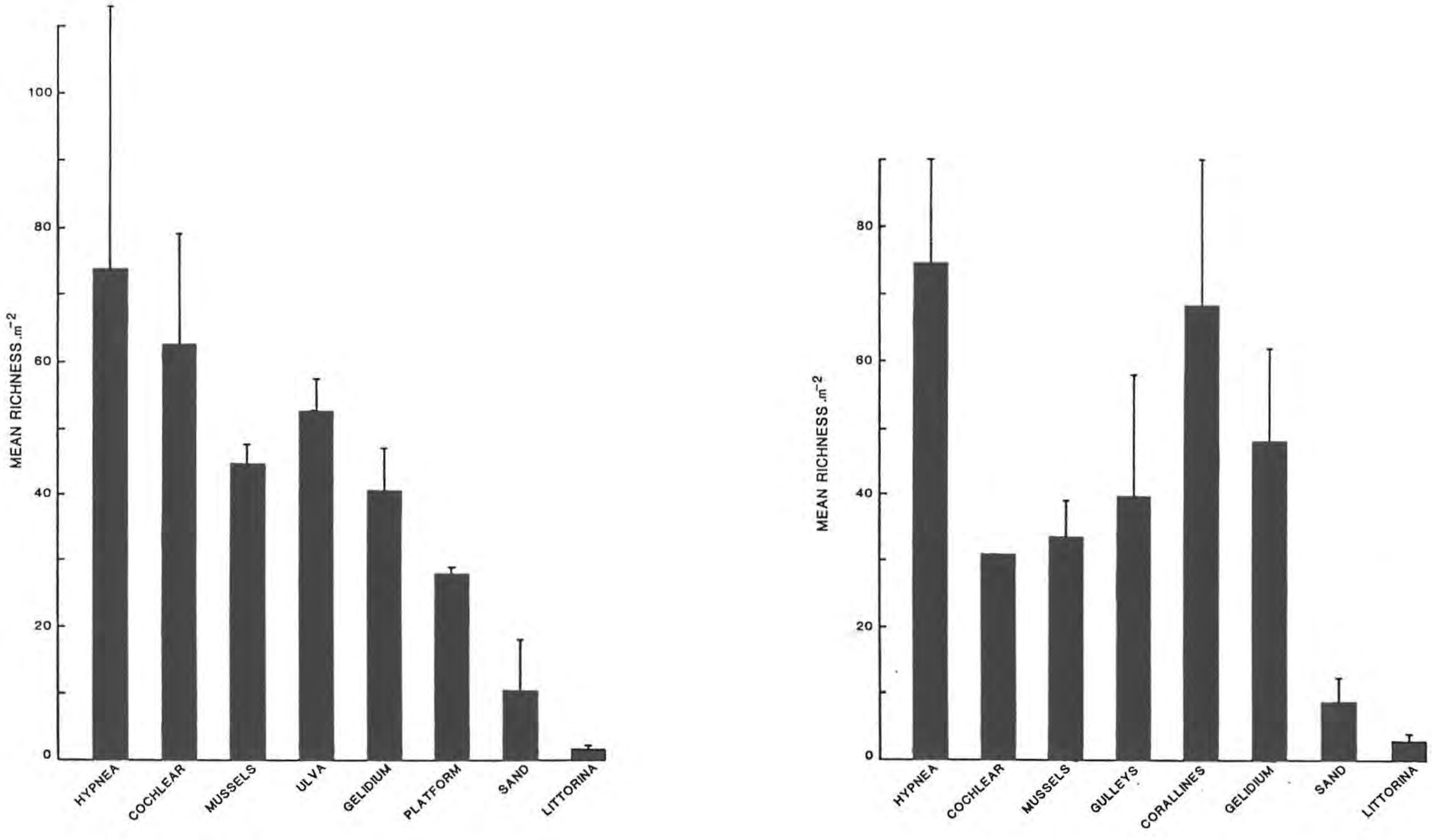
REGION	ZONE	TOTAL RICHNESS	MEAN RICHNESS PER ZONE ± S.D.	MEAN BIOMASS PER ZONE ± S.D.
LOW SHORE	*HYPNEA*	222	74.3 ± 25.4	572.35 ± 195.93
	COCHLEAR	86	52.0 ± 21.5	271.27 ± 131.21
	MUSSELS	84	38.3 ± 07.2	488.32 ± 341.63
	GULLEYS (sandstone only)	101	39.8 ± 18.2	100.17 ± 69.92
MID SHORE	CORALLINES (sandstone only)	147	68.4 ± 21.8	155.55 ± 126.06
	GELIDIUM	110	46.4 ± 12.7	222.06 ± 73.84
	PLATFORM (dune rock only)	40	28.0 ± 01.0	28.69 ± 21.91
HIGH SHORE	SAND	44	09.7 ± 05.9	3.47 ± 4.35
	LITTORINA	4	02.6 ± 01.1	33.62 ± 32.42

Table 4.2: Total richness, mean richness and mean biomass for all zones listed from lowest to highest on the shore.

A steady decrease in total species richness up the shore was found on dune rock (Figure 4.2). On sandstone there was a sharp decrease in total richness in the *cochlear* zone (31 species) which was followed by a steady increase in the mussel (68 species) and gulley (101 species) zones to a peak of 147 species in the coralline algae zone. Richness then decreased farther up the shore (Figure 4.2).

Richness in zones that were found on both shore types was similar in most cases except the *cochlear* and *Gelidium* zones. A distinct *cochlear* zone was found on only one sandstone and two dune rock shores. The *Gelidium* zone on dune rock is much poorer than on sandstone (49 and 108 species respectively). This is probably due to the fine layer of mobile sand which appears to scour the wave-cut platform on dune rock. Trends similar to those for total richness per zone were found for mean richness per zone on each rock type (Figure 4.3).

The zones on each shore were then grouped together as low, mid and high shore zones (Table 4.3). Distinction between the three regions was made using information in the available literature on zonation on the eastern Cape coastal region (Stephenson, 1943b; Branch and Branch, 1981; Lubke, 1988). Sand-filled gulleys on sandstone became covered with water at the same stage of the tide as the low shore *Ulva* zone on dune rock and were thus included in the low shore zones.



A DUNE ROCK

B SANDSTONE

Figure 4.3: Mean species richness and standard deviations for each zone. Zones are ordered from lowest on the shore (*Hypnea*) to highest (*Littorina*).

There was no significant difference in total richness between sandstone and dune rock in any of the pooled low, mid and high shore groups (t-tests, P>0.05, in all cases). Total richness for low, mid and high shore regions for all shores combined showed a distinct decrease up the shore (Table 4.3).

REGION	DUNE ROCK	SANDSTONE	TOTAL RICHNESS
LOW SHORE	*HYPNEA* *COCHLEAR* MUSSELS *ULVA*	*HYPNEA* *COCHLEAR* MUSSELS GULLEYS	278
MID SHORE	*GELIDIUM* PLATFORM	CORALLINES *GELIDIUM*	188
HIGH SHORE	SAND *LITTORINA*	SAND *LITTORINA*	44

Table 4.3: The low, mid and high shore zones on dune rock and sandstone shores, showing total richness for each region.

An even balance of richness between the phyla Annelida, Arthropoda and Mollusca was found. These taxonomic groups contributed 26.5%, 27.7% and 25.9% respectively (a cumulative total of 80.1%) to the total richness (Figure 4.4).

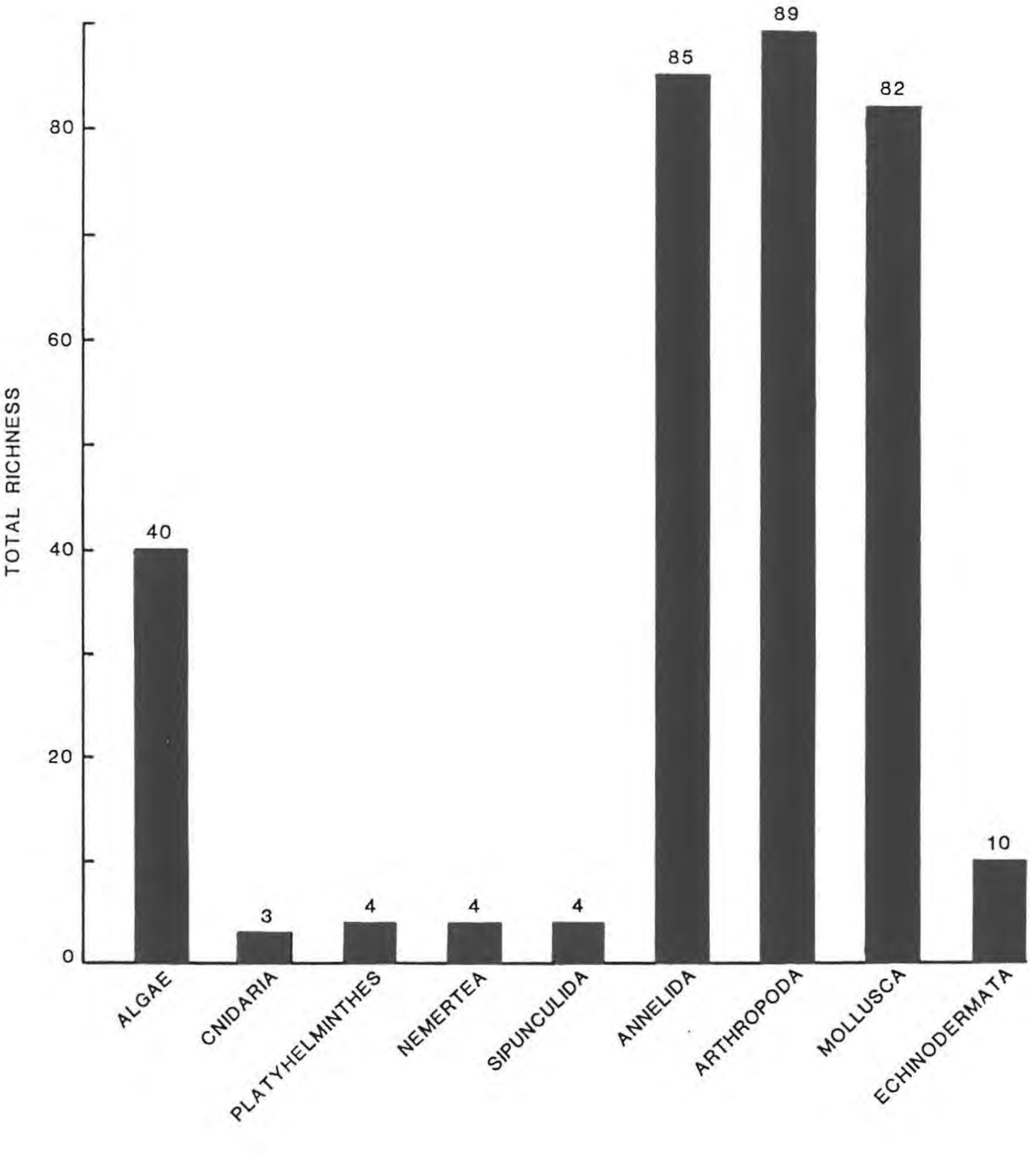


Figure 4.4: Total species richness of algae and each animal phylum.

4.2 ABUNDANT SPECIES

The five most abundant species in the major zones are given in Table 4.4, totalling 26 species for all nine zones. In most zones juvenile or small herbivores and filter feeders dominated numerically e.g. the small (2mm) gastropod *Eatoniella nigra* (*Hypnea*, coralline, *Gelidium* and platform zones), the mussel *Perna perna* (*Hypnea*, *cochlear*, mussel and *Gelidium* zones), the chiton *Acanthochitona garnoti* (platform and sand zones), the herbivorous errant polychaete *Platynereis dumerilii* (*cochlear* and coralline zones) and the barnacle *Chthamalus dentatus* (mussel and *Gelidium* zones). Gulleys were numerically dominated by the deposit feeding polychaete *Scoloplos johnstonei* and the gastropod *Haminoea alfredensis*. Some of these numerically dominant species are epifaunal or live among the byssal threads of mussels or the thalli of macroalgae e.g. the mussel worm *Pseudonereis variegata* and *E. nigra*. Only four of these numerically dominant species are sedentary.

4.3 INDICATOR SPECIES FOR SUBSTRATUM AND RARE SPECIES

Species found only on one substratum type and in more than one sample were defined as indicator species for substratum type (Appendix B). Far more indicator species were found on sandstone then on dune rock. Of the 284 species found on sandstone, 122 (43.0%) were not found on dune rock, but 66 of these were rare species. Rare species are those found in one sample only, most of which were, in fact, found in only one quadrat of a sample. Of

Table 4.4: The five most abundant animals in each zone. Zones are listed from lowest to highest on the shore. Species are listed in taxonomic order. Trophic category of each species is given. (S) indicates sedentary of slow-moving species. P-primary producer, H-herbivore, O-omnivore, C-carnivore, S-scavenger, D-deposit feeder, F-filter feeder.

ZONE	FIVE MOST ABUNDANT SPECIES IN EACH ZONE	TAXONOMIC GROUP	TROPHIC LEVEL	
HYPNEA	*Dynamenella huttoni*	ISOPODA	S	
	Hyale grandicornis	AMPHIPODA	H	
	Perna perna	PELECYPODA	F	(S)
	Eatoniella nigra	GASTROPODA	H	
	Tricolia capensis	GASTROPODA	H	
COCHLEAR	*Nereis willeyi*	POLYCHAETA	O	
	Platynereis dumerilii	POLYCHAETA	H	
	Pseudonereis variegata	POLYCHAETA	O	
	Perna perna	PELECYPODA	F	(S)
	Patella cochlear	GASTROPODA	H	(S)
MUSSELS	*Pseudonereis variegata*	POLYCHAETA	O	
	Chthamalus dentatus	CIRRIPEDIA	F	(S)
	Tetraclita serrata	CIRRIPEDIA	F	(S)
	Hyale grandicornis	AMPHIPODA	H	
	Perna perna	PELECYPODA	F	(S)
GULLEYS (sandstone only)	*Cerebratulus* sp.1	NEMERTEA	C	
	Scoloplos johnstonei	POLYCHAETA	D	
	Exosphaeroma truncatitelson	ISOPODA	S	
	Ischnochiton oniscus	AMPHINEURA	H	
	Haminoea alfredensis	GASTROPODA	D	
CORALLINES (sandstone only)	*Platynereis dumerilii*	POLYCHAETA	H	
	Cymodocella pustulata	ISOPODA	S	
	Hyale grandicornis	AMPHIPODA	H	
	Lysianassa ceratina	AMPHIPODA	S	
	Eatoniella nigra	GASTROPODA	H	
GELIDIUM	*Chthamalus dentatus*	CIRRIPEDIA	F	(S)
	Tetraclita serrata	CIRRIPEDIA	F	(S)
	Dynamenella huttoni	ISOPODA	S	
	Perna perna	PELECYPODA	F	(S)
	Eatoniella nigra	GASTROPODA	H	
PLATFORM (dune rock only)	*Perinereis falsovariegata*	POLYCHAETA	O	
	Acanthochitona garnoti	AMPHINEURA	H	
	Lasaea adansoni turtoni	PELECYPODA	F	(S)
	Eatoniella nigra	GASTROPODA	H	
	Littorina a. knysnaensis	GASTROPODA	H	
SAND	*Lumbrineris tetraura*	POLYCHAETA	C	
	Eurydice longicornis	ISOPODA	O	
	Exosphaeroma truncatitelson	ISOPODA	S	
	Acanthochitona garnoti	AMPHINEURA	H	
	Siphonaria concinna	GASTROPODA	H	
LITTORINA	Only four species in total.			
	Chthamalus dentatus	CIRRIPEDIA	F	(S)
	Littorina africana africana	GASTROPODA	H	
	Littorina a. knysnaensis	GASTROPODA	H	
	Siphonaria concinna	GASTROPODA	H	

the 57 indicator species found on sandstone, 22 were found in three or more samples. They included five polychaete and five gastropod species, four isopod species, two amphipod species, two chitons and one species each of Ostracoda, Pelecypoda, Holothuroidea and algae (Appendix B). Of the 199 species found on dune rock, 37 (18.6%) did not occur on sandstone; 30 of these were rare. Only five of the 37 species found exclusively on dune rock were indicators, none of which were found at more than two sites. They are thus much less reliable as indicator species than those recorded for sandstone.

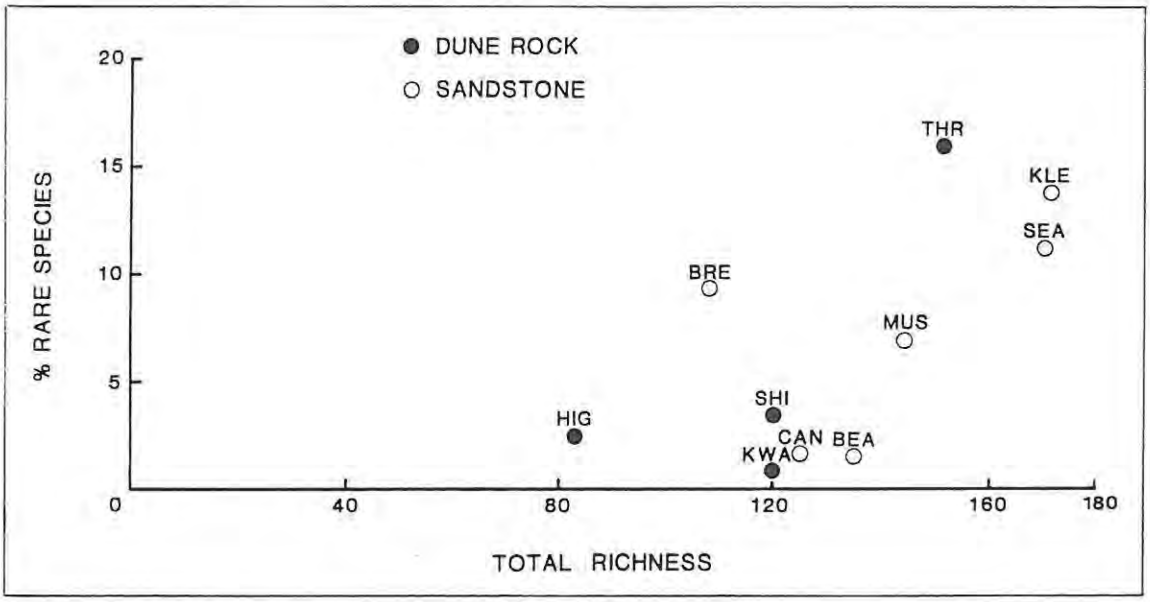


Figure 4.5: The relationship between total species richness and the proportion (%) of rare species (those species found in only one sample) at each site.

The percentage of rare species was calculated for each site and each zone. The highest proportion of rare species (15.9%) was found at Three Sisters (THR) (Figure 4.5). At this site 20 of the 24 rare species recorded were from the *Hypnea* zone. Sandstone

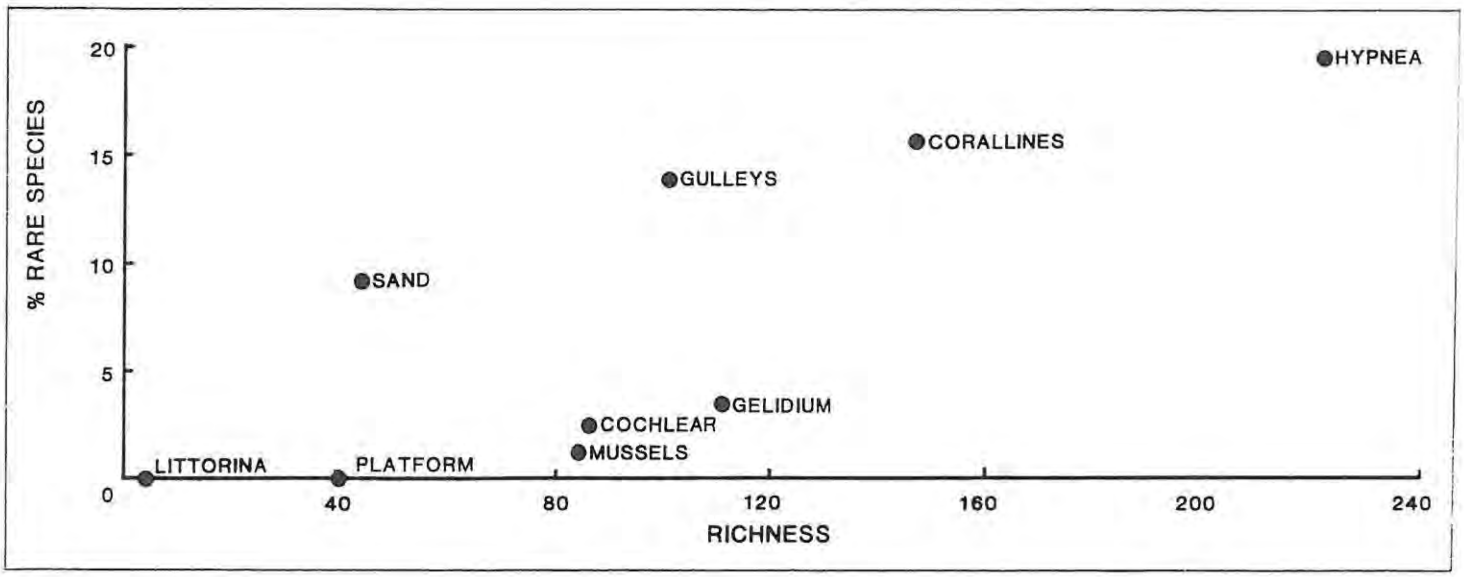
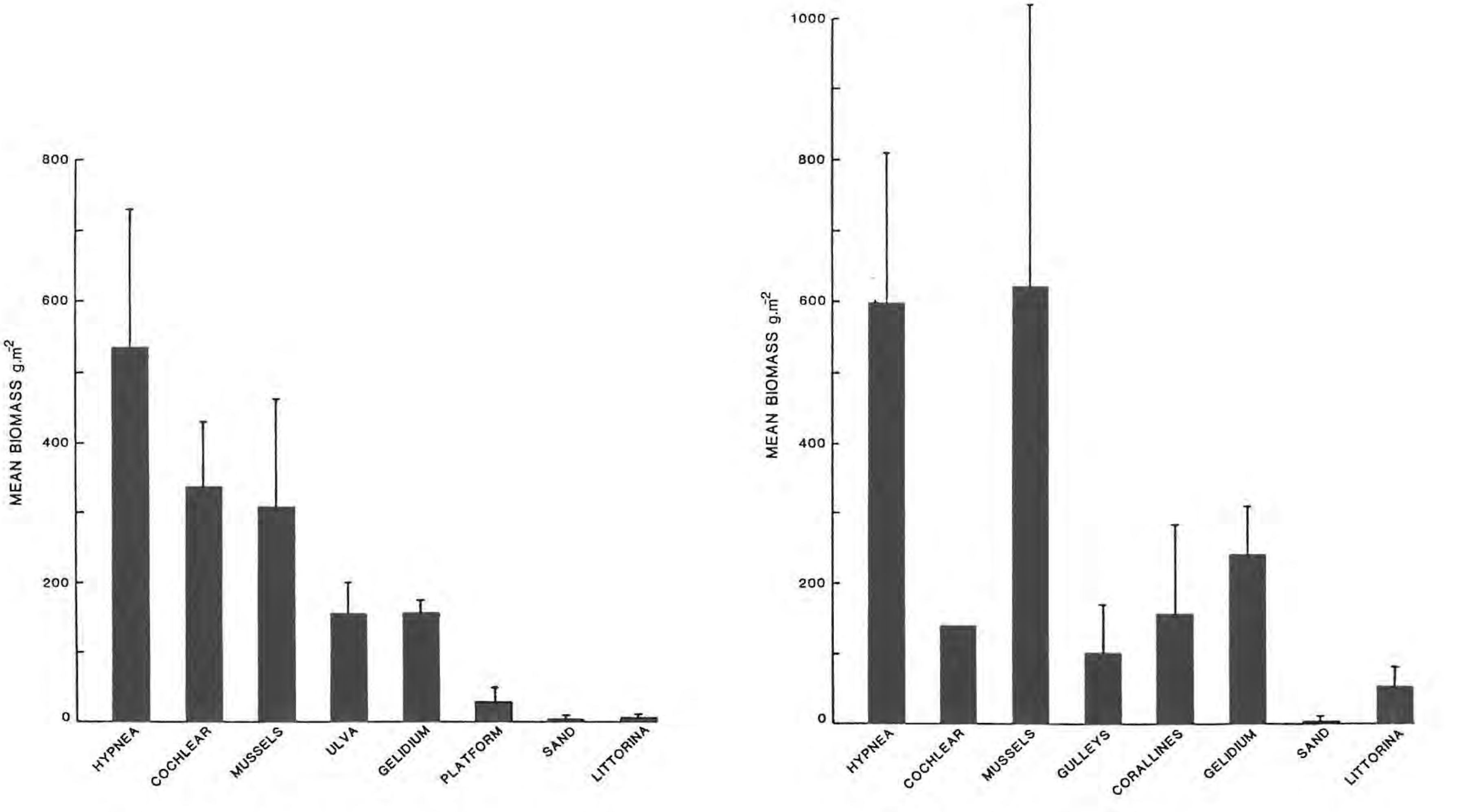


Figure 4.6: The relationship between total species richness and the proportion (%) of rare species (those species found in one sample only) in each zone.

shores showed slightly higher overall proportions of rare species than dune rock. The *Hypnea* zone had the greatest proportion of rare species (19.4%) of all the zones. Together, the *Hypnea*, gulleys, corallines and sand zones had significantly larger proportions of rare species than did the remaining zones ($t=6.69$, $P<0.05$) (Figure 4.6). Within each of these two groups there is a tendency towards an increase in percent rare species as richness increases.

4.4 BIOMASS

On both shore types mean biomass.m^{-2} per zone decreased up the shore (Figure 4.7). On dune rock the decrease up the shore was regular and similar to that described for total richness (Figure 4.2). On sandstone peaks in mean biomass per m^2 occurred in mussel and *Gelidium* samples. Note that the standard deviation for the mussel zone was high, indicating large differences between sites in mussel bed densities. Biomass in the *Gelidium* zone was greater on sandstone than on dune rock. Despite apparent differences in biomass in the *cochlear*, *Gelidium* and mussel zones between the two rock types, low degrees of freedom and considerable variance render these differences statistically significant only for the *Littorina* zone ($t=3.305$, $P<0.05$). On sandstone this zone was dominated in both numbers and biomass by dense populations of the barnacle, *Chthamalus dentatus*, while on dune rock populations of the gastropods, *Littorina africana africana* and *L. a. knysnaensis* and the pulmonate limpet, *Siphonaria concinna* were found. The presence of *C. dentatus* was



A DUNE ROCK

B SANDSTONE

Figure 4.7: Mean biomass and standard deviation for each zone. Zones are ordered from lowest on the shore (*Hypnea*) to highest (*Littorina*).

not associated with a significant decrease in the populations of the *Littorina* spp. on sandstone shores.

Although highest biomass was found in the mussel zone on sandstone, when the data for both rock types are combined, *Hypnea* had the highest mean biomass (572.35 ± 195.93 $g.m^{-2}$ per site) (Table 4.2), 94% of which was formed by primary producers. Mean biomass for this zone was slightly higher on sandstone (597.73 ± 210.71 $g.m^{-2}$) than on dune rock (534.27 ± 194.81 $g.m^{-2}$) (Figure 4.7). Five of the most important species in terms of biomass were *Hypnea spicifera*, *Perna perna*, two errant polychaetes, *Lysidice natalensis* (a deposit feeder) and *Platynereis dumerilii* (a herbivore), and the isopod, *Dynamenella huttoni* (a scavenger) (Table 4.5). Mussel beds had the second highest mean biomass for both shore types (488.33 ± 341.62 $g.m^{-2}$), (Table 4.2). The filter feeding brown mussel, *P. perna*, accounted for approximately 80% of this. On sandstone mean biomass for mussel beds was almost twice that on dune rock : 623.39 ± 400.85 and 308.23 ± 154.79 $g.m^{-2}$ respectively (Figure 4.7). Apart from *P. perna*, the red alga, *Gelidium pristoides*, the mussel worm, *Pseudonereis variegata*, the patellid limpet, *Patella granularis* and the barnacle *Chthamalus dentatus* consistently exhibited high biomass (Table 4.5).

Lowest mean biomass was found in high shore sand (3.47 ± 4.35 $g.m^{-2}$) (Table 4.2). The major portion of biomass in the sand samples consisted of the algae *Centroceras clavulatum* and *Ulva rigida*, which grew on rocks buried beneath the sand, as well as

Table 4.5: The five species exhibiting highest biomass, in each zone. Zones are listed from lowest to highest on the shore. Species are listed in taxonomic order. Trophic category of each species is given. (S) indicates sedentary or slow-moving species. P-primary producer, H-herbivore, O-omnivore, C-carnivore, S-scavenger, D-deposit feeder, F-filter feeder.

ZONE	THE FIVE SPECIES EXHIBITING HIGHEST BIOMASS	TAXONOMIC GROUP	TROPHIC LEVEL	
HYPNEA	*Hypnea spicifera*	ALGA	P	(S)
	Lysidice natalensis	POLYCHAETA	D	
	Platynereis dumerilii	POLYCHAETA	H	
	Dynamenella huttoni	ISOPODA	S	
	Perna perna	PELECYPODA	F	(S)
COCHLEAR	*Arthrocardia carinata*	ALGA	P	(S)
	Pseudonereis variegata	POLYCHAETA	O	
	Perna perna	PELECYPODA	F	(S)
	Patella barbara	GASTROPODA	H	(S)
	Patella cochlear	GASTROPODA	H	(S)
MUSSELS	*Gelidium pristoides*	ALGA	P	(S)
	Pseudonereis variegata	POLYCHAETA	O	
	Chthamalus dentatus	CIRRIPEDIA	F	(S)
	Perna perna	PELECYPODA	F	(S)
	Patella granularis	GASTROPODA	H	
GULLEYS (sandstone only)	*Ulva rigida*	ALGA	P	(S)
	Jania crassa	ALGA	P	(S)
	Polysiphonia cf. *savatieri*	ALGA	P	(S)
	Lumbrineris tetraura	POLYCHAETA	C	
	Ischnochiton oniscus	AMPHINEURA	H	
CORALLINES (sandstone only)	*Ulva rigida*	ALGA	P	(S)
	Arthrocardia carinata	ALGA	P	(S)
	Cheilosporum sp.1	ALGA	P	(S)
	Jania crassa	ALGA	P	(S)
	Lysidice natalensis	POLYCHAETA	D	
GELIDIUM	*Gelidium pristoides*	ALGA	P	(S)
	Tetraclita serrata	CIRRIPEDIA	F	(S)
	Perna perna	PELECYPODA	F	(S)
	Burnupena lagenaria	GASTROPODA	S	
	Patella oculus	GASTROPODA	H	
PLATFORM (dune rock only)	*Perinereis falsovariegata*	POLYCHAETA	O	
	Acanthochitona garnoti	AMPHINEURA	H	
	Brachidontes semistriatus	PELECYPODA	F	(S)
	Oxystele tabularis	GASTROPODA	H	
	Siphonaria capensis	GASTROPODA	H	
SAND	*Ulva rigida*	ALGA	P	(S)
	Centroceras clavulatum	ALGA	P	(S)
	Lumbrineris tetraura	POLYCHAETA	C	
	Eurydice longicornis	POLYCHAETA	O	
	Exosphaeroma truncatitelson	ISOPODA	S	
LITTORINA	Only four species in total:			
	Chthamlus dentatus	CIRRIPEDIA	F	(S)
	Littorina africana africana	GASTROPODA	H	
	Littorina a. knysnaensis	GASTROPODA	H	
	Siphonaria concinna	GASTROPODA	H	

two isopods *Eurydice longicornis* and *Exosphaeroma truncatitelson* and an errant polychaete, *Lumbrineris tetraura* (Table 4.5). Juvenile *Acanthochitona garnoti*, *Siphonaria capensis* and *S. concinna* (all herbivores) were sometimes found attached to rocks beneath the sand.

The majority of the abundant species were mobile and small (76.9%), while those exhibiting greatest biomass were more often sedentary or slow moving (54.5%) (Tables 4.4 and 4.5). This is particularly relevant to the algal species which unfortunately cannot be included in the abundance data. If the biomass data are considered, macroalgal species are among the top five contributing species in all zones except the platform zone on dune rock (which mainly supported large herbivorous molluscs) and the *Littorina* zone.

4.5 TROPHIC COMPOSITION

Carnivorous species and scavengers had the highest richness of all the trophic levels (67 and 54 species respectively). Omnivores showed lowest richness of 25 species (Figure 4.8).

The abundance of trophic categories in the different zones was considered starting at the bottom of the shore. These trophic categories were defined as primary producers, herbivores, omnivores, carnivores, scavengers, deposit feeders and filter feeders. Each species was assigned to a trophic category and histograms of cumulative percentages of the biomass of each category were drawn up. This was repeated for each zone on each rock type and for pooled low, mid and high shore data for each rock type (Figures 4.9 and 4.10).

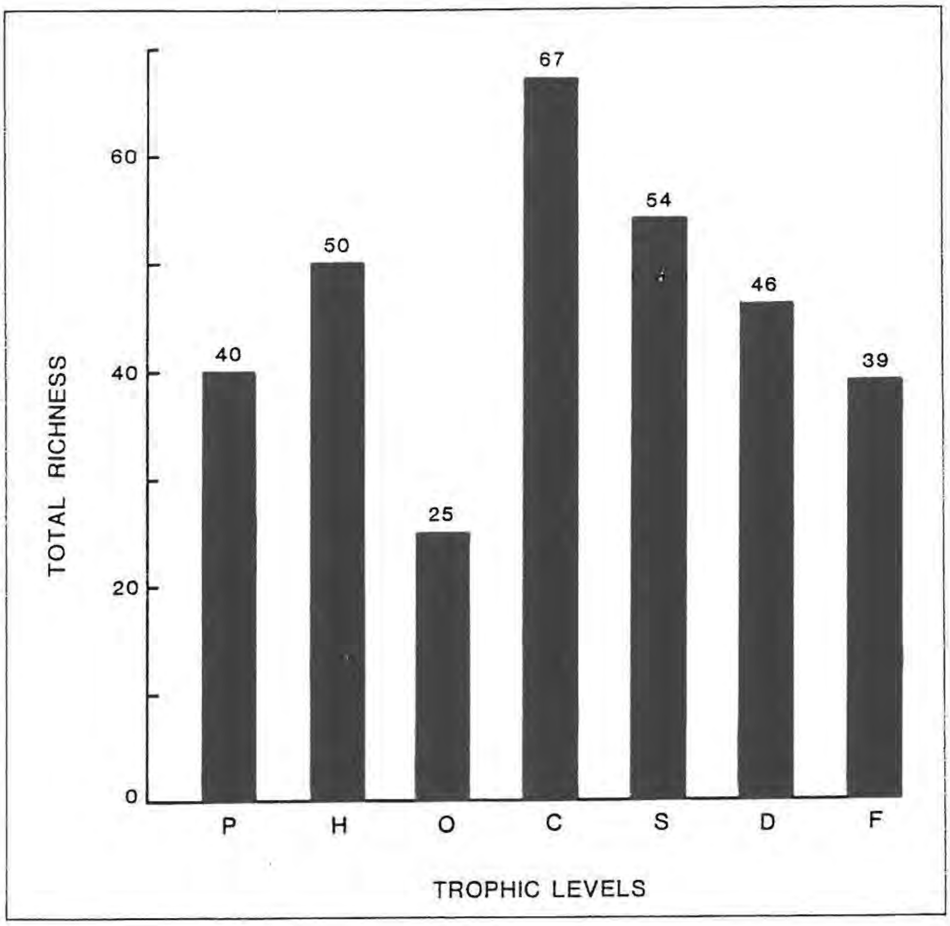


Figure 4.8: Total species richness of each trophic category. P-primary producers, H-herbivores, O-omnivores, C-carnivores, S-scavengers, D-deposit feeders, F-filter feeders.

When considered separately the zones on the two shore types showed some marked differences in their respective proportions of feeding categories. This was most obvious in the *cochlear*, mussel, sand and *Littorina* zones (Figure 4.9). In the *cochlear* zone herbivores contributed 81.5% to the biomass on sandstone whereas on dune rock the biomass was more evenly shared between primary producers, herbivores and filter feeders (28.4%, 32.6% and 29.8% respectively). The majority of biomass in most zones was made up of primary producers, herbivores and filter feeders. Mussel beds were more dense on sandstone, resulting in a greater proportion of filter feeders in this zone on these shores. Scavengers, mainly small crustaceans, contributed far more to the biomass of sand samples on dune rock than on sandstone where primary producers dominated. Only herbivores (100.0%) were found in the *Littorina* zone on dune rock whereas biomass in this zone consisted of 95.9% filter feeders on sandstone.

Other differences between these two shore types were evident in the gulley, coralline, *Ulva* and platform zones, none of which occurred on both shore types. Sandstone gulleys showed a high biomass of the opportunistic green algae, *Ulva rigida* and *Enteromorpha* sp., and the coralline alga, *Jania crassa* (Table 4.5). These were found on the surface of boulders lying in the gulleys rather than buried in the sand. The turf forming red alga, *Polysiphonia* cf. *savatieri* was often found on the underside of these boulders. After algae, which contributed 75.0% to the biomass in this zone, omnivores showed highest biomass (18.0%).

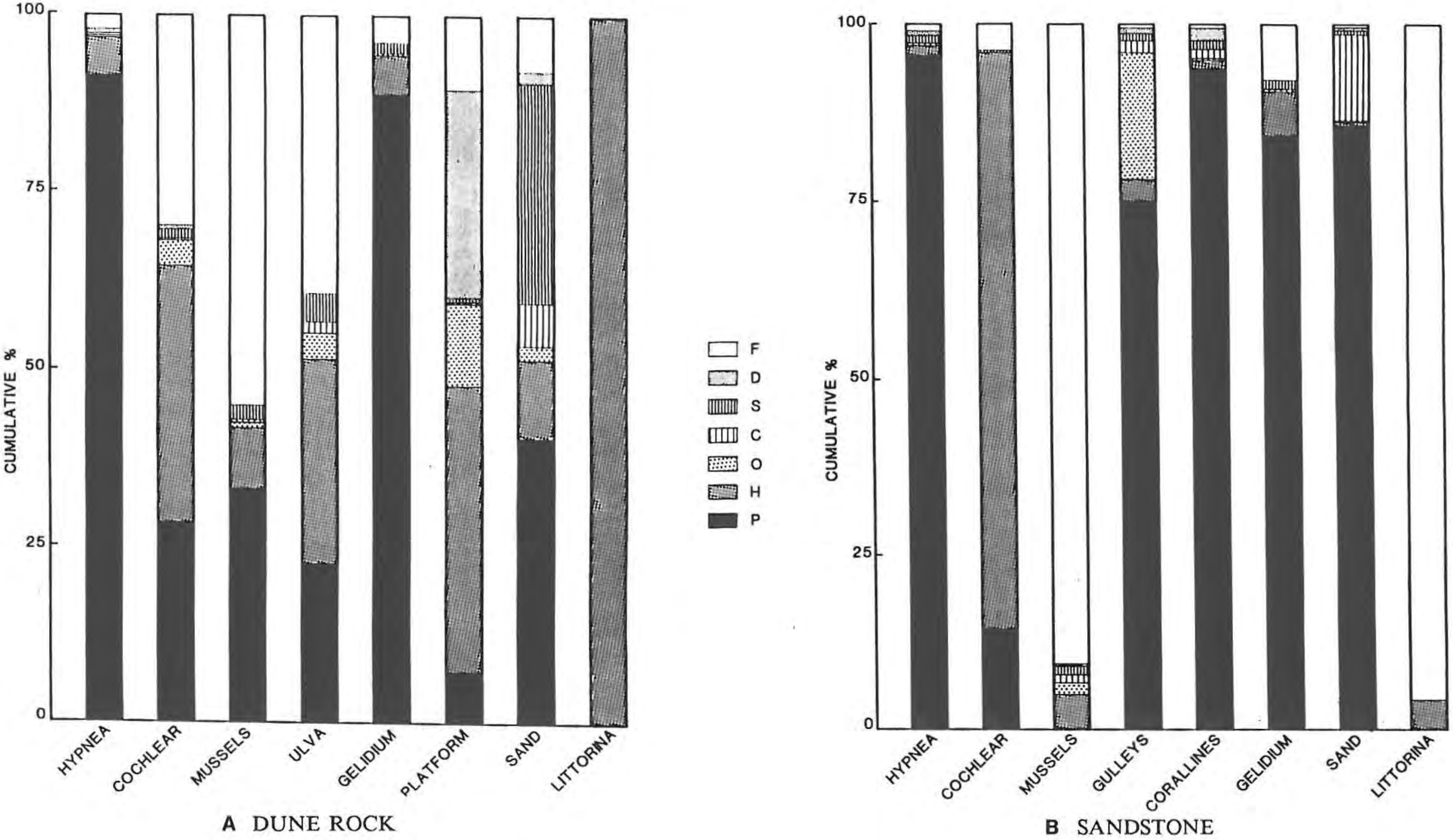


Figure 4.9: Cumulative percentages of trophic category biomass for each zone. Zones are ordered from lowest on the shore (*Hypnea*) to highest (*Littorina*).
P-primary producers, H-herbivores, O-omnivores, C-carnivores, S-scavengers, D-deposit feeders, F-filter feeders.

On sandstone, algae formed most of the biomass in the mid shore coralline and *Gelidium* zones (93.7% and 84.2% respectively) (Figure 4.9). These were dominated by corallines, *Arthrocardia carinata*, *Jania crassa* and *Cheilosporum* sp. 1, and *Gelidium pristoides* (Table 4.5).

The *Gelidium* zone on dune rock was also dominated mainly by *Gelidium pristoides* and other primary producers (88.9%). The poorly colonised platform zone which had a mean biomass of only 28.68 ± 21.91 $g.m^{-2}$ (Figure 4.7), was dominated by the herbivores *Siphonaria capensis*, *Acanthochitona garnoti* and *Oxystele tabularis* which contributed to the total herbivore biomass of 40.8%. Deposit feeders, mostly the sipunculid, *Themiste minor*, formed 29.2% of the biomass in this zone.

Despite differences between zones, pooled low shore data showed proportions of each trophic category to be very similar on the two rock types (Figure 4.10). In both cases primary producers and filter feeders dominated. In the mid shore the coralline zone on sandstone raised the contribution of primary producers marginally while there were slightly more herbivores on dune rock. Differences were most noticeable in the high shore area where filter feeders on sandstone dominated contributing 91.3% to the total biomass whereas on dune rock herbivores formed 62.3% of the total biomass (Figure 4.10).

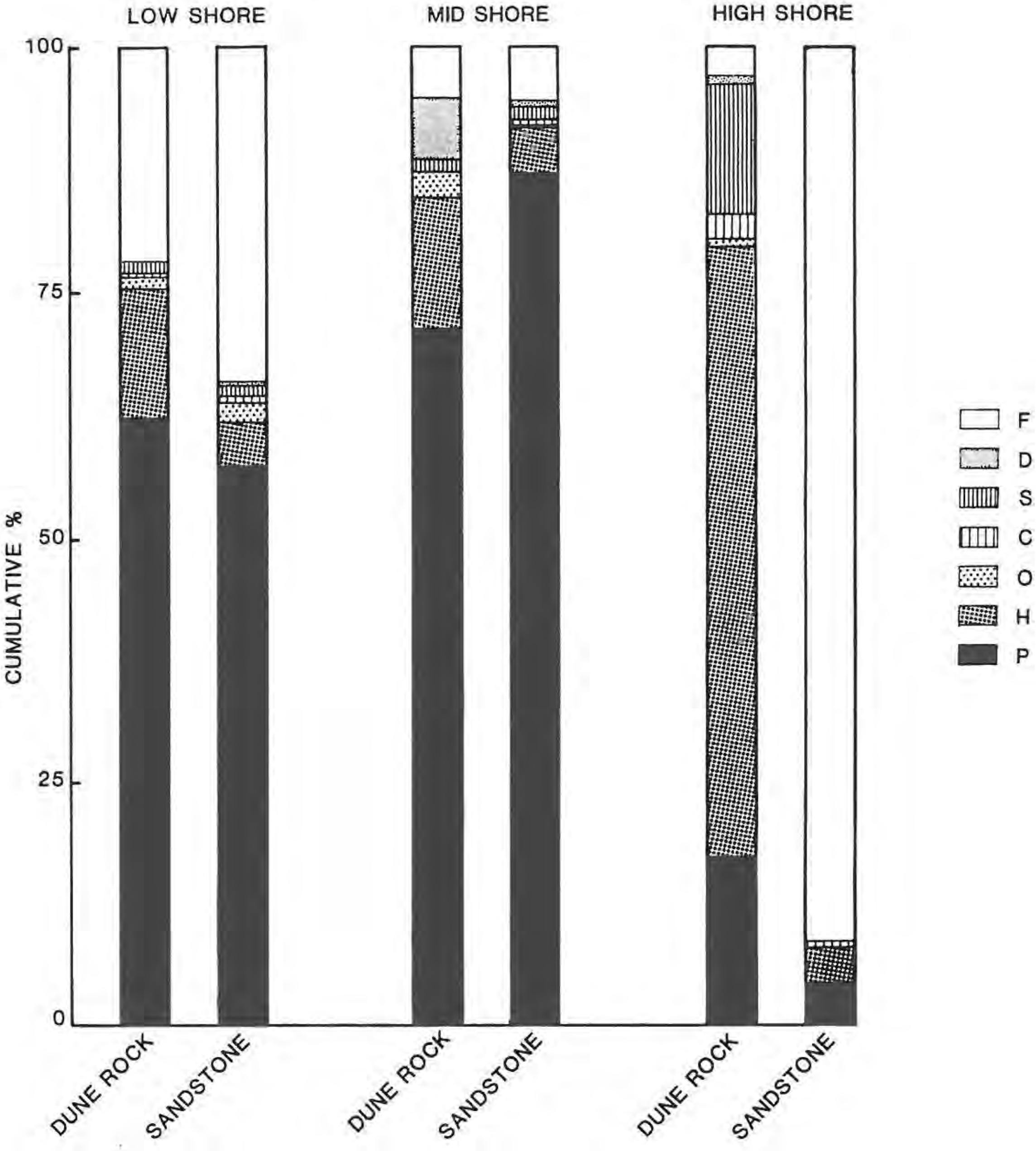


Figure 4.10: Cumulative percentages of trophic category biomass for both sandstone and dune rock. Data have been pooled to give mean low, mid and high shore values.

P-primary producers, H-herbivores, O-omnivores,

C-carnivores, S-scavengers, D-deposit feeders,

F-filter feeders.

4.6 COMMUNITY ANALYSIS

Two-dimensional ordinations were calculated from the raw data using DECORANA. Classification using TWINSPAN, from which dendrograms were drawn, was carried out subsequently. The dendrograms provided a more practical and succinct display of the data for interpretation. Although dendrograms are more interpretable, relevant data may be lost because of oversimplification. Where this seems to be the case reference is made to the original ordination.

Ordinations were performed using different data matrices: presence/absence; species abundance and biomass data. There were only minor differences between the results obtained using these different matrices and further analyses were based on biomass data. Rare species were included in the samples by samples ordination and dendrogram but were omitted from the species by samples analyses for clarity. These species only occur in one sample and therefore contribute no meaningful data to such analyses.

The dendrogram presented by TWINSPAN is made up of levels representing increasing similarity. At the first division (i.e. at level one) the similarity between the two groups derived is lowest i.e. they are the most dissimilar. As later divisions at higher levels are derived the groups increase in similarity. The distances between levels are equal. Levels are thus arbitrary measures of the similarities between samples or species.

4.6.1 Analysis of samples

The samples by samples dendrogram was summarised into five levels (Figure 4.11). At the first level of division of the samples TWINSPAN divided the 66 samples of the various zones into two groups. The first consisted of the ten samples from the *Littorina* zone (group 1). These samples had a total richness of only four species. *Littorina africana knysnaensis* was common to all ten of these samples.

At the second division the remaining 56 samples were divided into one group of seven samples of high shore sand (group 2) and a second group consisting of all the low and mid shore samples as well as two sand samples. It can be seen from the ordination of samples (Figure 4.12) that these two samples (42 and 49), although isolated, are closest to the mid shore samples and are clearly separated from the other sand samples.

At the third division the remaining 49 samples were divided into one group of 22 samples which were composed of those with the highest richness i.e. *Hypnea*, corallines and gulleys, and a second group of lower richness samples from mussel, *cochlear*, *Gelidium*, platform zones plus the remaining two sand samples.

At the fourth division the three coralline samples with highest species richness were grouped with the ten *Hypnea* samples (group 4) and the two with lowest richness were grouped with the seven remaining samples including those of the gulley zone (group 3).

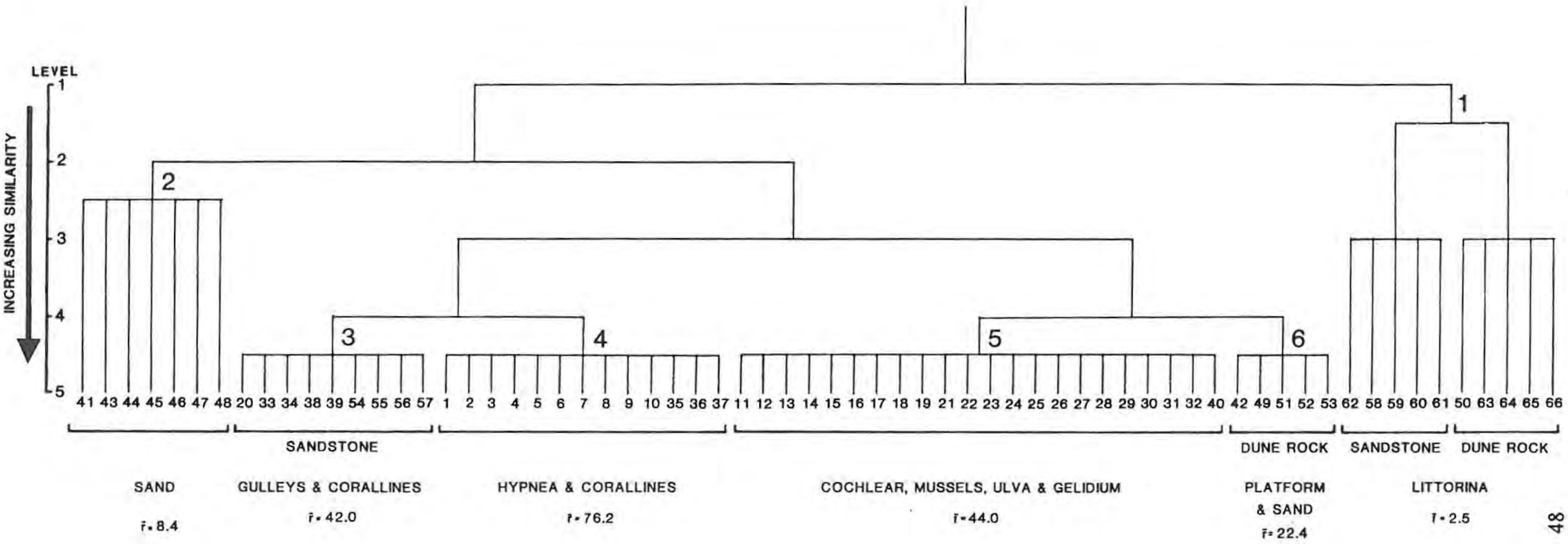


Figure 4.11: Summarised dendrogram showing classification of samples. Samples are coded by number according to Appendix B. r = mean richness per cluster.

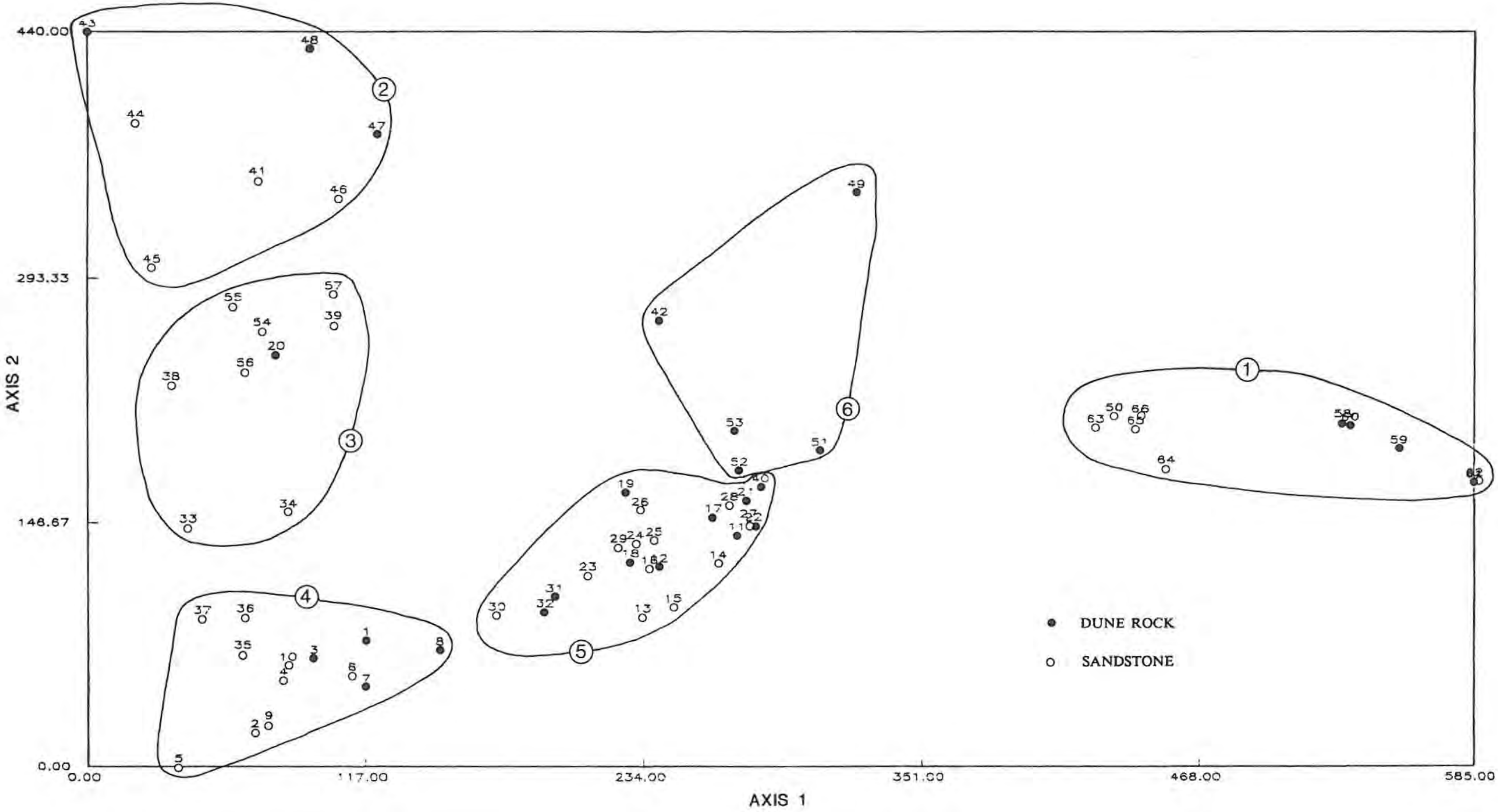


Figure 4.12: Ordination of samples. Sample numbers correspond to those in Appendix A and the group numbers correspond to those in Figure 4.11.

At the same level mid shore samples and the two sand samples formed one cluster of five samples (group 6) and mussel, *cochlear* and *Gelidium* samples formed the other group of 22 samples (group 5). Further splitting produced less interpretable groups except for group 5. At the fifth division group 5 was divided further into one cluster of low shore mussels and *cochlear* and one of mid shore *Gelidium* samples.

Clustering in this case appears to depend largely on overall species richness in a sample though it may be related to a less obvious factor that is correlated with richness. The groups presented by TWINSPAN in the dendrogram show the zones to be well defined as in most cases the majority of samples in one zone are grouped into the same cluster. Groups 3 and 4 and groups 5 and 6 are most similar to one another and therefore most tightly clustered. Groups 3 and 4 have high algal biomass and high species richness in common whereas groups 5 and 6 have low algal biomass and relatively lower species richness in common (Figure 4.11).

At a lower level of similarity (level 3) these two large groups (groups 3 and 4 and groups 5 and 6) are joined together to form one large group of samples made up of the low and mid shore zones. At the following level the less similar high shore sand samples join this group. Lastly the *Littorina* samples, which are unlike any of the others, join the cluster at level one.

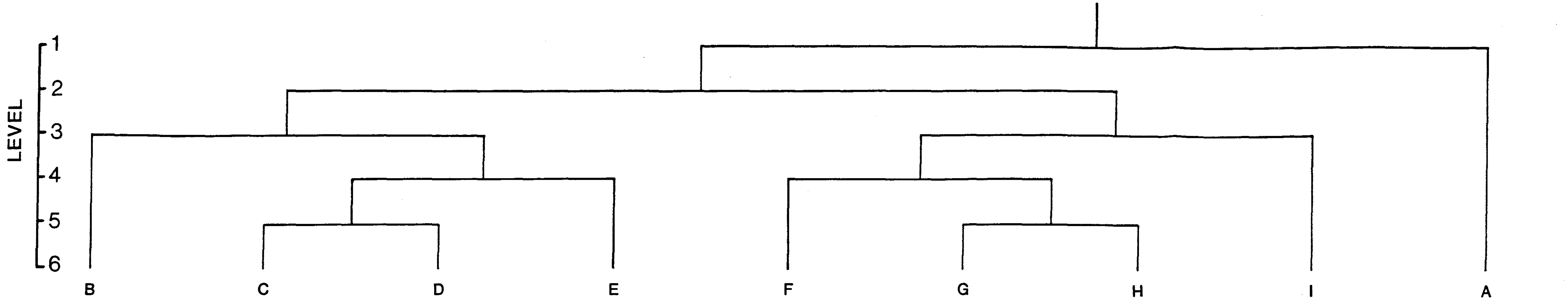
The primary overall factor that determined clustering was richness. A secondary factor was substratum or shore type. Samples that were in groups 1, 2, 4 and 5 were found on both shore types. Group 1 split according to rock type while group 3 consisted of samples from sandstone only and group six consisted of samples from dune rock only.

4.6.2 Analysis of species

The cluster analysis of samples, was used to cluster the species (see page 21). The final dendrogram was divided into nine major groups of species and is summarised in Figure 4.13. Where possible, each species was assigned to one of four categories relating to its observed ability to withstand burial in sand. The four categories were:

1) sand-intolerant (or psammophobic) species found only on rocky shores;
2) sand-tolerant species which are normally associated with rocky shores and are able to withstand sand scour but not burial;
3) sand-dependent species which require hard substrata for attachment but are normally found under sand and
4) psammophilic species which are normally associated with sandy beaches and live in the sand column.

Group A, which is separated from the others at the first level of division, consists of only four species. These four, *Littorina africana africana*, *L. a. knysnaensis*, *Chthamalus dentatus* and *Siphonaria concinna*, were the only species found in the *Littorina* zone. This cluster of species corresponds to the first level of



Ps & Sd
(16)

15 *Arabella iricolor caerulea*
23 *Goniadopsis incerta*
31 *Lumbrineris tetraura*
89 *Scoloplos uniramus*
114 *Cymodocella sublevis*
125 *Eurydice longicornis*
128 *Exosphaeroma truncatitelson*
164 *Gastrosaccus psammodytes*
196 *Gregariella simplicifilis*
240 *Natica tecta*
282 *Cladophora* cf. *virgata*
293 *Arthrocardia* sp.b
297 *Centroceras clavulatum*
304 *Gelidium caespitosum*
309 *Jania crassa*
313 *Polysiphonia* cf. *savatieri*

Ps & Sd
(31)

52 *Syllidia armata*
35 *Marphysa depressa*
37 *Marphysa sanguinea*
66 *Branchiomma nigromaculata*
69 *Cirriformia tentaculata*
81 *Piromus arenosus*
88 *Scoloplos johnstonei*
103 *Cymodoce natalensis*
105 *Cirolana cranchi*
119 *Dynamenella macrocephala*
123 Sphaeromatidae (Eubr. nol)
137 *Pseudosphaeroma barnardi*
140 *Ampelisca* cf. *spinicaudata*
143 *Aora kergueleni*
160 *Urothoe tumorosa*
178 *Portumnus biguttatus*
180 *Endeis clipeatus*
181 *Queubus jamesianus*
185 *Chaetopleura papilio*
186 *Chaetopleura pertusa*
189 *Dinoplax fossus*
194 *Choromytilus meridionalis*
238 *Nassarius capensis*
239 *Natica forata*
257 *Peristernia fuscotincta*
273 *Roweia f. frauenfeldi*
288 *Amphiroa beauvoisii*
301 *Cheilosporum sagittatum*
302 *Cheilosporum* sp.1
314 *Polyzonia elegans*
321 *Ovalipes punctatus*

Sd & St
(58)

4 Polyclad sp.1
20 *Eulalia capensis*
21 *Eulalia sanguinans*
28 *Lumbrineris* cf. *oculata*
30 *Lumbrineris coccinea*
36 *Marphysa posteriobranchia*
44 *Paronuphis antarctica*
48 *Pseudactinia varia*
51 *Sthenelais boa*
68 *Cirriformia* cf. *saxatilis*
71 *Cirratulus filiformis*
73 *Flabelligera affinis*
75 *Hyboscolex longiseta*
76 *Jasmineira elegans*
77 *Megalomma quadrioculatum*
79 *Nicolea v. venustula*
85 *Potamilla torelli*
87 *Sabellaria s. alcocki*
95 *Thelepus pequenianus*
102 Ostracod
104 *Cirolana bovina*
108 Sphaeromatidae (Hemi. nol)
111 *Cymodocella eutylos*
113 *Cymodocella pustulata*
121 *Dynamenella taurus*
122 *Dynamenella ovalis*
127 *Exosphaeroma porrectum*
129 *Haliophasma foveolata*
131 *Leptanthura agulhaensis*
132 *Mesanthura catenula*
142 *Ampithoe ramondi*
154 *Jassa falcata*
158 *Podocerus africana*
167 *Paguristes barnardi*
169 *Antilibinia smithi*
172 *Dehaanius dentatus*
173 *Leucisca squalina*
176 Xanthidae
187 *Chiton tulipa*
193 *Cardita variegata*
201 *Neocardia africana*
206 *Afrocominella elongata*
207 *Alcira elegans*
208 *Amblychilepas scutella*
209 *Anachis kraussi*
213 *Burnupena cincta*
218 *Clionella rosaria*
219 *Clionella semicostata*
220 *Crepidula aculeata*
263 *Turbo cidaris cidaris*
267 *Amphioplus integer*
278 *Flabellifera* sp.1
287 *Amphiroa anceps*
292 *Arthrocardia* sp.A
299 *Cheilosporum cultratum*
300 *Cheilosporum multifidum*
303 *Gelidium amansii*
308 *Hypnea spicifera*

Si
(42)

1 *Actinia equina*
3 *Planocera gilchristi*
7 *Lineus lacticapitatus*
8 *Lineus olivaceus*
16 *Autolytus tuberculatus*
18 *Bhawania goodei*
22 *Eulalia trilineata*
27 *Lepidonotus semitectus*
33 *Lysidice natalensis*
40 *Nereis operta*
41 *Nereis willeyi*
43 *Odontosyllis polycera*
49 *Platynereis dumerilii*
54 *Syllis prolifera*
56 *Brania furcelligera*
57 Hesionidae sp.1
59 *Syllis* cf. *taprobanensis*
60 *Syllis* sp.1
78 *Naineris laevigata*
98 *Balanus amphitrite*
107 *Cirolana v. venusticauda*
112 *Cymodocella magna*
117 *Dynamenella dioxus*
141 *Ampithoe africana*
148 *Eusiroides monoculoides*
155 *Lysianassa ceratina*
157 *Paramoera capensis*
182 *Tanystylum brevipes*
184 *Callochiton castanea*
190 *Ischnochiton oniscus*
198 *Kellia rotunda*
211 *Aplysia spuria*
221 *Crepidula porcellana*
228 *Haminoea alfredensis*
242 *Nucella squamosa*
253 *Patella miniata*
262 *Tricolia capensis*
266 *Patiriella exigua*
268 *Parechinus angulosus*
271 *Pseudocnella sinorbis*
289 *Amphiroa bowerbanki*
290 *Arthrocardia carinata*

St & Si
(19)

26 *Lepidonotus durbanensis*
42 *Bunodosoma capensis*
46 *Phyllodoce castanea*
55 *Syllis variegata*
74 *Gunnarea capensis*
96 *Thelepus plagiostoma*
118 *Dynamenella huttoni*
133 *Paranthura punctata*
152 *Hyale grandicornis*
177 *Plagusia chabrus*
205 *Afrocardium shepstonensis*
223 *Eatoniella nigra*
224 *Fisurella mutabilis*
231 *Helcion pruinosus*
232 *Heliacus d. alfredensis*
245 *Oxystele sinensis*
249 *Patella barbara*
269 *Aslia spyridophora*
270 *Aslia tetracentriophora*

Si
(23)

2 *Notoplana patellarum*
9 *Lineus ornatus*
32 *Lysidice collaris*
34 *Marphysa corallina*
50 *Pseudonereis variegata*
96 *Proscoloplos cygnochaetus*
100 *Octomeris angulosus*
135 *Parisocladus stimpsoni*
195 *Crassostrea margaritacae*
197 *Hiatella arctica*
202 *Perna perna*
203 *Petricola bicolor*
225 *Fisurella natalensis*
230 *Helcion pectunculus*
241 *Nucella dubia*
244 *Onchidella capensis*
247 *Oxystele variegata*
248 *Patella argenvillei*
250 *Patella cochlear*
251 *Patella granularis*
252 *Patella longicosta*
272 *Pseudocnella sykion*
306 *Gigartina paxillata*

Si
(23)

12 *Themiste minor*
19 *Eteone foliosa*
62 *Opisthosyllis brunnea*
65 *Boccardia polybranchia*
84 *Pomatoleios kraussi*
101 *Tetraclita serrata*
134 *Parisocladus perforatus*
156 *Megaluropus* sp.1
159 *Urothoe elegans*
175 *Metopograpsus messor*
179 *Telmatogeton minor*
192 *Brachidontes semistriatus*
199 *Lasaea turtoni adansoni*
214 *Burnupena lagenaria*
222 *Cynisca granularis*
229 *Helcion dunkeri*
246 *Oxystele tabularis*
255 *Patella oculus*
258 *Siphonaria aspera*
261 *Siphonaria oculus*
285 *Iyengaria stellata*
305 *Gelidium pristoides*
310 *Nothogenia erinacea*

Ps & Sd
(4)

6 *Cerebratulus* sp.1
45 *Perinereis falsovariegata*
53 *Syllis* cf. *armillaris*
115 *Dynamenella australis*
136 *Pontogeloides latipes*
183 *Acanthochitona garnoti*
259 *Siphonaria capensis*
284 *Ulva rigida*

Si
(8)

99 *Chthamalus dentatus*
235 *Littorina a. africana*
236 *Littorina a. knysnaensis*
260 *Siphonaria concinna*

Figure 4.13: Summarised dendrogram showing classification of species. The predominant level of sand tolerance is given for each group and the number of species in each group is given in parentheses.

division in the samples by samples cluster analysis where the ten *Littorina* zone samples were separated from the others. *S. concinna* is a sand-tolerant species but the other three are all rocky shore species (Appendix B).

At the second level of division, groups B to E were separated from groups F to I. Groups B to E were characterised by species predominantly present in zones of high richness (except for high shore sand) e.g. *Hypnea* and corallines. Groups F to I were characterised by species from zones of low richness e.g. the platform zone.

Group B was separated from groups C to E at the third level of division. This group was made up of 16 species which were found mainly in high shore sand. Most of these species are psammophilic and many are normally associated with the macrofauna of sandy beaches (e.g. the mysid, *Gastrosaccus psammodytes*, the isopods, *Eurydice longicornis* and *Exosphaeroma truncatitelson* and the errant polychaete, *Lumbrineris tetraura*). The algae in this group are sand-dependent turf-forming species such as *Centroceras clavulatum* and *Polysiphonia* cf. *savatieri*. Some of the species in group B (e.g. the bivalve, *Gregariella simplicifilis*) were also found in low shore sand filled gulleys, *Hypnea* and coralline algae.

Group C consisted of 31 psammophilic and sand-dependent species associated with gulleys and coralline algae. Some less common species found in coralline algae and *Hypnea* samples were also included. Two species, the sedentary filter feeding polychaete, *Branchiomma nigromaculata*, and the isopod, *Cymodoce natalensis*, were found only in coralline algae samples. One species, the 'three-spot swimming crab', *Ovalipes punctatus*, which is also common on sandy beaches, was found only in sand-filled gulleys. The most abundant species in this group, *Cirriformia tentaculata*, is a deposit feeding sedentary polychaete.

The fourth and largest group, group D, was most similar to group C and was dominated by the 25 species found only in the *Hypnea* zone. The remaining 33 species in group D were found in both *Hypnea* and coralline algae samples. Two isopods, *Exosphaeroma porrectum* and *Haliophasma foveolata* were found only in coralline algae. None of these species are psammophilic but the majority are either sand-dependent or sand-tolerant species.

Group E consisted of 42 abundant species common to most low shore zones, in particular *Hypnea* and mussels. Many were also found in the coralline algae. They are mainly rocky shore, sand-intolerant species, and many are closely associated with the common coralline alga, *Arthrocardia carinata.*

Group F, the first group of the low richness samples, consisted of 19 rocky shore and sand tolerant species that were found over a wide range of low and middle shore samples. These included the errant polychaete, *Syllis variegata*, the isopod, *Dynamenella huttoni*, the amphipod, *Hyale grandicornis* and the gastropod, *Eatoniella nigra*. Also in this group were many less common species found in the low shore zones.

The seventh group, group G (23 species), consisted mainly of animals associated with *Perna perna*, which was abundant, not only in the mussel beds, but also in the *cochlear* and *Gelidium* zones. Many sand-intolerant species were found in this group. Common species included the flat worm, *Notoplana patellarum*, the mussel worm, *Pseudonereis variegata*, the gastropod, *Oxystele variegata* and patellid limpets: *Patella cochlear*; *P. granularis* and *P. longicosta.* One species, the oyster *Crassostrea margaritacea*, was found only in the *cochlear* zone.

Group H consisted of 23 species associated with *Gelidium pristoides*, the majority of which inhabit areas with little or no sand. These included the filter feeding sedentary polychaete, *Pomatoleios kraussi*, the barnacle, *Tetraclita serrata*, the limpets, *Patella oculus* and *Siphonaria aspera.*

The final group consisted of only eight species all of which were associated with sand presence and were common to most zones, especially *Gelidium* and the platform zone on dune rock. Two psammophilic species, the nemertine, *Cerebratulus* sp.1 and the isopod *Pontogeloides latipes* were found in this group. Other common species included *Ulva rigida*, *Acanthochitona garnoti*, the errant polychaete, *Perinereis falsovariegata* and *Siphonaria capensis.*

As expected, these species groups were less defined in the ordination (Figure 4.14). A large amount of overlap between the

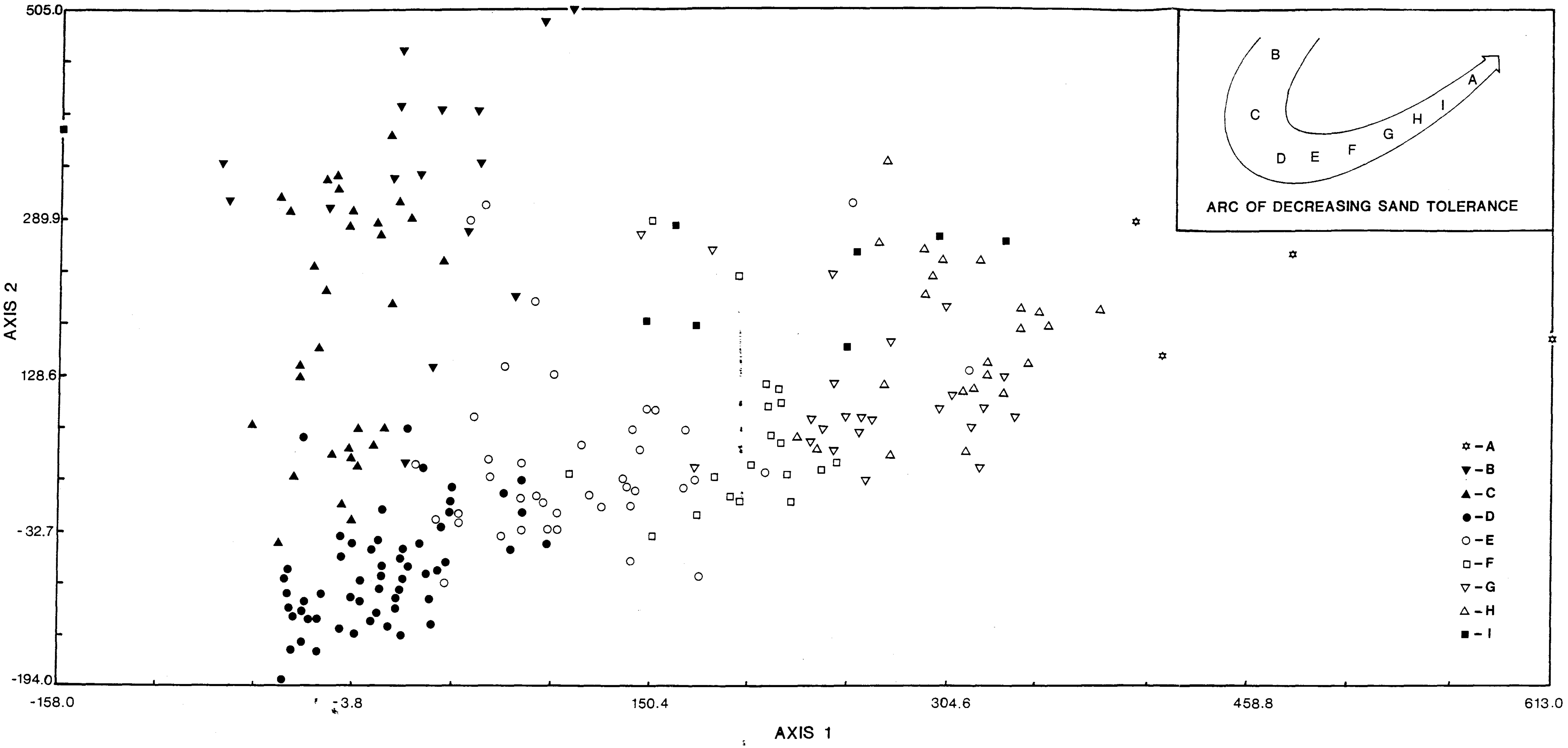


Figure 4.14: Ordination of species. Symbols correspond to the groups shown in the dendrogram (Figure 4.13). Groups with low sand tolerance have been allocated open symbols. Rare species have been omitted for clarity.

groups was found but in general the species groups closely followed the same pattern as samples groups. This is not unexpected as the sample groups were used as a base for setting the species groups. Species appear in general to be grouped according to the richness of the zones in which they were found and their respective levels of sand tolerance. The most similar groups were groups C and D and groups G and H. Species found in groups C and D were psammophilic and sand-dependent species found predominantly in group 4 of the samples by samples dendrogram i.e. in the high richness *Hypnea* and coralline zones. Species found in groups G and H were sand-intolerant species found predominantly in group 6 of the samples by samples dendrogram i.e. in *Gelidium*, mussel and *cochlear* zones.

4.7 SUMMARY

1. Richness on sandstone shores was higher than on dune rock shores. No significant difference in biomass was found between rock types except in the *Littorina* zone where biomass was higher on sandstone due to the presence of *Chthamalus dentatus*.
2. The *Hypnea* zone had the highest richness, the highest number of rare species and the highest mean biomass of all the zones.
3. The phyla Annelida, Arthropoda and Mollusca each formed over 25% of the total richness (i.e. over 80% in total).
4. More indicator species and rare species were found on

sandstone than on dune rock. A significantly higher proportion of rare species were found in the *Hypnea*, gulley, coralline and sand zones.

5. In most zones, juvenile and small herbivores and filter feeders were most abundant, although highest total richness was found for carnivores.
6. The three most abundant trophic levels were primary producers, herbivores and filter feeders. Algae were among the five species exhibiting highest biomass in terms of biomass in all zones except the platform zone on dune rock.
7. Trophic levels showed greatest differences between rock type in the high shore region.
8. The primary factor influencing the clustering of samples was the total richness of each sample. Groups were secondarily grouped according to rock type.
9. Species were grouped according to the richness of the sample groups in which they were found and their levels of sand tolerance.

CHAPTER FIVE - DISCUSSION

The discussion has been divided into three sections. The first section involves a detailed examination of the effects of sand on richness, zonation and trophic composition of the shores studied. Secondly, the possible classification of mixed shores using community analysis is discussed and finally, the intermediate disturbance hypothesis is applied to sand inundated rocky shores, in particular, eastern Cape mixed shores.

5.1 SPECIES RICHNESS, ZONATION AND TROPHIC STRUCTURE

Until recently sand deposition on rocky shores has normally been ignored as a factor determining species distribution, richness and intertidal zonation patterns. Sand can occur as semi-permanent deposits between rocks, in gulleys or trapped in the holdfasts of algae or as a thin layer of mobile, scouring sand. Consequently, the spatial heterogeneity or topographic complexity of the substratum may play a major role in determining the ultimate effect of sand inundation on the distribution of intertidal communities. Different patterns of retention on shores of different topography have implications for the distribution of species assemblages.

The influence of sand as a common disturbance factor in intertidal systems has also only recently received attention (Daly and Mathieson, 1977; Robles, 1982; Taylor and Littler, 1982; Littler *et al.*, 1983; Stewart, 1983; D'Antonio, 1986). Its effects have been noted to be both detrimental (Daly and Mathieson, 1977; Devinny and Volse, 1978) and beneficial (Foster, 1975; Taylor and Littler, 1982; Littler *et al.*; 1983) to local species richness. The effects of sand on richness, zonation and trophic and species composition of eastern Cape shores will be examined and discussed in more detail below.

5.1.1 Species richness

Few detailed ecological studies on intertidal flora and fauna have been carried out in the eastern Cape region of South Africa where sand deposits are often extensive. Stephenson (1943b) recorded 318 species in total for the South African intertidal coastline. He divided the intertidal biota into three components - west coast, south coast and east coast and noted a distinct trend of decreasing richness from Durban, on the east coast, to Port Nolloth, on the west coast (Figure 5.1). This trend, which Stephenson attributed to the east - west decrease in water temperature, was more noticeable for fauna than it was for algae.

In a detailed study done in the Cape Peninsula a total of 310 species of fauna and flora at 12 sites was recorded (McQuaid and Branch, 1984; McQuaid *et al.*, 1985). This study concluded that the high richness value was related to an overlap of the south and west coast biota as noted by Stephenson (1943b). McLachlan *et al.* (1981a) recorded a total of 120 species for two rocky shores near Port Elizabeth. However, a low richness could be expected from the latter study as sponges, isopods, amphipods and epifauna

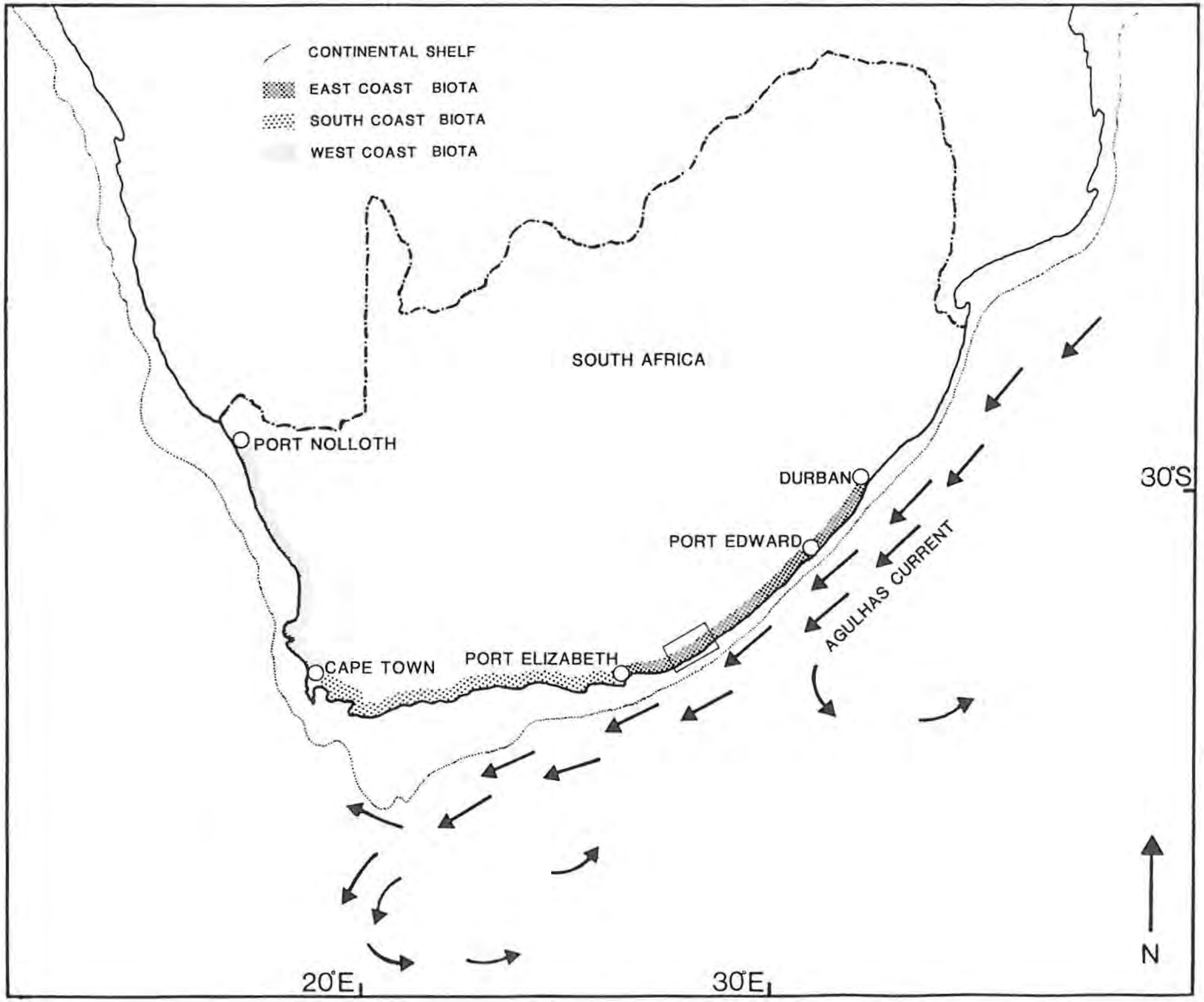


Figure 5.1: Map of the South African coastline, showing Stephenson's (1943b) three biotic regions and the Agulhas Current (after Branch and Branch, 1981).

were omitted. Nevertheless, this total seems unrealistically low when compared with Stephenson (1943b) and Munnik (1987) who identified over 110 species of algae alone at three sites near Port Elizabeth.

The total of 321 species recorded for the ten sites sampled during this study therefore seems remarkably high compared to the richness values for the Cape Peninsula, the Port Elizabeth area and the whole of the South African coastline.

Three possible reasons can be given for the high richness in this area : 1) this study was more taxonomically thorough and detailed than any previously carried out in this region, 2) overlap of the south and east coast biota in this area is responsible for increased richness, as is found in the Cape Agulhas to Cape Point region and 3) sand deposits in this area increase overall species richness through disturbance and by increasing spatial and temporal heterogeneity.

It is presumed that the first two points alone could account for higher richness. Firstly, greater taxonomic detail, where sampling was thorough and each organism was identified to species level where possible, must reveal greater species richness than a more general study such as that carried out by McLachlan *et al.* (1981a). In the latter study isopods and amphipods were omitted while in the present study these two groups alone contributed more than 60 species to the total richness. Only 40 species of algae were identified in this study. Munnik's (1987) record of

110 algae in Port Elizabeth suggests that algae here are underestimated and thus richness should be even greater.

Secondly, a peak in richness was recorded in the regions of overlap of the three biota described by Stephenson (1943b). This was especially marked between Cape Point and Cape Agulhas where "the eastern warm-water component of the population has not yet become reduced to its minimum, the western cold-water component is still strong, and the south coast component is still at its maximum" (Stephenson 1943b). The east coast/south coast overlap of biota i.e. Port Edward to Port Elizabeth, showed a very slight and less interpretable peak in richness.

The coastal region from Port Edward to Port Elizabeth (these are not necessarily the exact boundaries) has been considered an overlap area for many years (Stephenson, 1943b; Brown and Jarman, 1978; Kilburn and Rippey, 1982; Lubke, 1988). As the warm Agulhas current turns away from the coast in a more southerly direction the east coast warm water runs into cooler south coast water (Figure 5.1). The exact point of deflection of this current changes and therefore so too does the western boundary of the east coast component (Lubke, 1988). This results in an undefined transitional zone between the east coast and the south coast biota. Since there is a trend towards decreased richness from Durban (warm water) to Port Nolloth (cold water), lower richness should, theoretically, be found in a cold water overlap region (southern and western Cape) than in a warm water overlap region (eastern Cape). The three sites with highest richness in this study (Seafield, Kleinemond and Three Sisters) were all at the eastern end of the study area (Figure 4.1). This may therefore be a biogeographical trend resulting from a slight increase in water temperature towards the east. Highest richness recorded for an individual shore in the western Cape was 137 species (McQuaid *et al.*, 1985). This is lower than the richness of any of the three sites mentioned above and it is therefore apparent that biogeographic effects are indeed partially responsible for the higher richness.

The final possible reason for high richness in this area is the influence of sand deposits and the effects of substratum heterogeneity. Changes in biological or physical factors over short periods of time (ecological time) or over long periods of time (evolutionary time) increase the temporal variation in a system (Menge and Sutherland, 1976). Spatially heterogeneous surfaces have been shown to enhance species richness on rocky shores due to increased habitat variation (Menge *et al.*, 1985). Heterogeneity provides refuges in time and space, where species are protected from competition and predation, and therefore provides more niches and allow more species to colonise an area. Prey species and competitors are able to avoid local extinction thereby maintaining diversity (Menge, 1976; Lubchenco, 1978; Lubchenco and Menge, 1978; Woodin, 1978; Williams, 1981; Menge *et al.*, 1985).

In many natural systems spatial heterogeneity and frequent disturbances are important in structuring biological communities (Hastings, 1978; May, 1979; White, 1979; Turner, 1985; Feinsinger *et al.*, 1988). Many forms of physical disturbance have been documented for intertidal rocky shores. These include intense wave action and wave driven logs (Dayton, 1971, 1975), scouring ice sheets (Wethey, 1985), wave driven boulders (Osman, 1977; Sousa, 1979a,b) and fresh water runoff from the land (Connell, 1978).

Disturbances cause environmental patchiness resulting in a mosaic of recently disturbed patches as well as patches that have remained undisturbed for a long time (White, 1979; Pickett and White, 1985; Feinsinger *et al.*, 1988). The effects of sand inundation and the patchiness resulting from this type of disturbance have only recently been considered in intertidal systems and the results are often contradictory. Sand inundation has been reported to decrease species richness through smothering or scouring (Brown, in prep.; Daly and Mathieson, 1977). Low species richness can also result from the presence of sand deposits which provide an unstable substratum and reduce available space for colonisation by sand-intolerant rocky shore species (Devinny and Volse, 1978). Apart from the inability of macroalgae to colonise rocks covered by sand, sand deposits may also reduce colonisation of algal species by preventing spore settlement, smothering the sporelings or causing reduced oxygen concentrations (Devinny and Volse, 1978).

Alternatively sand inundation may provide refuges from consumers and competitors or facilitate the growth of sand-tolerant, sand-dependent or psammophilic algae (Markham, 1973; Devinny and Volse, 1978; Stewart, 1983; D'Antonio, 1986). Burial by shifting sediments has also been found to be responsible for the promotion of subtidal and intertidal species diversity. Burial clears space for recolonisation, removes effective predatory species and prevents domination by competitively superior invertebrate or algal species. Colonisation by, and development of, assemblages of competitively inferior sand-tolerant and psammophilic species are thus enhanced (Foster, 1975; Littler, 1980; Robles, 1982; Taylor and Littler, 1982; Littler *et al.*, 1983).

It is now necessary to consider the results of the present study in the light of the previously predicted and recorded effects of sand inundation on rocky shores in other parts of the world.

Species richness values recorded for the present study are, in fact, in the same range as those recorded by Stephenson *et al.*, 1938; Stephenson, 1943b) for individual sites in the eastern Cape region and are thus comparable. Richness on dune rock shores examined in this study ranged from 83 at High Rocks to 151 at Three Sisters while on sandstone shores richness was higher, ranging from 108 at Bretton Rocks to 171 at Kleinemond (Figure 4.1)

Although the difference in species richness on sandstone and dune rock shores was not statistically significant, this difference was initially thought to be due to greater spatial heterogeneity resulting from more complex topography and the effects of accumulated sand deposits on sandstone. The ridges and gulleys of sandstone shores provide habitats not found on the more homogeneous wave-cut platforms of dune rock. A detailed examination of zonation, species distribution patterns and trophic composition on each rock type can therefore lead to a better understanding of the community structure of mixed shores.

5.1.2 Zonation

On mixed shores general zonation patterns can be explained by the biotic and abiotic factors that are normally associated with rocky shores. However, an additional abiotic factor, sand inundation, also plays a part in zonation patterns.

The upper limits of an intertidal species' vertical zonation are normally considered to be set by its physiological tolerance to the physical stress imposed by emersion and desiccation (Connell, 1972; Paine, 1974; Littler *et al.*, 1983; Malusa, 1986). Lower limits, however, tend to be set by biological interactions involving predation, herbivory and competition for space (Dayton, 1971; Connell, 1972; Paine, 1974; Lewis, 1977; Littler *et al.*, 1983; Malusa, 1986). However, these two generalisations regarding upper and lower limits of distribution are often derived from small-scale experiments and no data exist to confirm these facts for the majority of intertidal species (Underwood and Denley, 1984; Underwood, 1985). Larval recruitment, rates of colonization and the order in which species colonise, especially low down on the shore, have often been overlooked and are fundamental to explaining species interactions and the real effects of physical factors.

For example, Littler *et al.* (1983) decribe a community for which the lower limits are set by the smothering of sand and not, in fact, by biological constraints. Likewise in the present study the limits of distribution of some species can be explained by the smothering and scouring action of sand. There was an overall decrease in richness and biomass from low shore to high shore on dune rock shores and a peak in richness in the gulley and coralline zones on sandstone shores (Figure 4.2). These phenomena can probably be explained by biological interactions and changes in physical heterogeneity and physical stress including the effects of sand inundation.

Sand deposits range from almost zero on the lower shore to total inundation during the late summer months on the middle and upper shore (Dower, unpubl. data). The amount of sand deposited may fluctuate slightly with each tide or may alter irregularly in much greater quantities with storm activity. The influence of sand on zonation and community composition varied according to local topographical features and was more marked on sandstone shores because of their greater topographic complexity. Sandstone shores are characterised by ridges and gulleys which run perpendicular to the shore line and increase spatial heterogeneity. On dune rock a homogeneous wave-cut platform characterises the mid shore and high shore areas. The differences in zonation and community composition between these two shore types occurred predominantly in the mid shore and high shore regions.

5.1.2.1 Low shore

The low shore region on both rock types was similar to that found on rocky shores and sand effects appeared to be minimal. Wave action seems to keep the low shore relatively clear of sand although sand deposits were found which had been stabilised by the subtidal green alga *Caulerpa filiformis*. Sand is also found trapped amongst the holdfasts of the red alga *Hypnea spicifera*.

a) The *Hypnea* zone

Algae-dominated zones are usually high in richness as many faunal species are associated with microhabitats provided by the algae (McQuaid *et al.*, 1985). It is therefore not surprising that the *Hypnea* zone had the highest richness and biomass on these shores (Figures 4.2 and 4.7). The physical heterogeneity offered by the algae was responsible for the high richness, while the density of the *Hypnea spicifera* plants added significantly to the biomass. The sand that was trapped in the entangled thalli of the *H. spicifera* plants facilitated the survival of sand-tolerant, sand-dependent and psammophilic species which were associated with the understorey and together made up more than 35% of the richness of this zone. Such species include the turf-forming algae *Polysiphonia* cf. *savatieri* and *Centroceras clavulatum* and the errant polychaetes *Lumbrineris tetraura* and *Marphysa depressa.*

b) The *cochlear* zone

Richness decreased in the *cochlear* and mussel zones which lie immediately upshore of the *Hypnea* zone and are dominated by herbivores and filter feeders respectively (Figures 4.2 and 4.9). The eastern limit of distribution of the limpet *Patella cochlear* is at Port Edward (Day, 1969; Kilburn and Rippey, 1982) and it occurs intermittently in this region forming a distinct zone on only three shores. Despite this, limpet densities were high. Densities at Seafield, the only sandstone shore with a clearly delineated *cochlear* zone, were extremely high ($1341.m^{-2}$) but total richness for the zone was low (31 species). The two dune rock shores where *P. cochlear* was sampled, Ship Rock and Kwaaihoek, had densities of $433.m^{-2}$ and $240.m^{-2}$ respectively. There was a significant, negative correlation ($P<0.05$) between the density of *P. cochlear* and species richness in the zone (Figure 5.2).

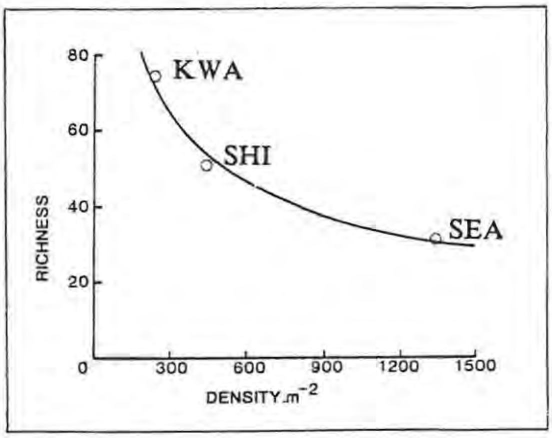


Figure 5.2: The relationship between the richness of each *cochlear* sample and the density.m^{-2} of the dominant limpet *Patella cochlear* ($n=3$, $r^2=0.991$, $Y=1092.981\ X^{-0.497}$).

At densities greater than 450.m^{-2} *Patella cochlear* suffers the effects of intense intraspecific competition (Branch and Griffiths, 1988). Most juveniles are found to settle on the shells of adults and there is an overall decrease in growth rates, maximum sizes and the reproductive output of individuals (Branch, 1975; Branch and Griffiths, 1988). This could account for the almost equal biomass values recorded for the high density populations of Seafield and the low density populations of Kwaaihoek. Biomass was approximately 114g.m^{-2} and 117g.m^{-2} respectively. *P. cochlear* grazes heavily on algal spores and encrusting species of algae and thus prevents algal species from becoming established (McQuaid *et al.*, 1985). Low richness recorded for these zones may therefore be partially the result of the absence of macroalgae as well as the direct effects of limpet grazing.

c) The mussel zone

The mussel zone exhibited very high biomass because of the dense beds of the brown mussel *Perna perna*. McQuaid *et al.* (1985) found that dense beds of filter feeders were associated with high richness because of the large number of microhabitats available. This was not found in the present study although many understorey species were found among the byssal threads of the mussels. The dominance of this space-occupying species resulted in decreased richness - a similar trend to that found in the *cochlear* zone (Figure 4.2). On dune rock herbivores (limpets) and primary producers formed the majority of the biomass whereas on sandstone no primary producers were found and filter feeders dominated (Figure 4.9).

Major differences between the two rock types seem to be attributable to topographic effects and were first apparent at the top of the low shore. Wave action is no longer able to keep this area sand free. Sand becomes trapped in the gulleys on sandstone and has a scouring effect on the dune rock platform. Low shore sand-filled gulleys and a mid shore coralline zone are both characteristic of sandstone shores (Figure 2.2).

d) The gulley zone

An increase in richness was found in the gulley zone followed by a further increase up the shore in the coralline zone (Figure 4.2). During periods of deposition gulleys become inundated first (pers. obs.). Adjacent gulleys can be of different depths and therefore subjected to different patterns or cycles of sand deposition. Although sand is present in most of these gulleys all the time, the depth of sand varies according to the steepness or 'holding capacity' of individual gulleys. Small rocks or boulders which are present in most gulleys, help to stabilise the sand. The resulting patchiness or substratum heterogeneity facilitates the intermingling of species assemblages which contain populations representing different successional stages. A mosaic of early succession, subclimax and mature species assemblages is found which augments within-habitat richness. The presence of sand, in fact, does not appear to exclude any species but rather augments richness by providing habitats for species that are otherwise not found on sand-free rocky shores including many psammophilic and sand-dependent species.

The small rocks found in sand-filled gulleys harbour many sand-dependent and sand-tolerant organisms. Irregular burial and exhumation of individual rocks increases both patchiness and richness. Two habitats, unburied rock surfaces and the rock/sand interface, provide niches for a number of species, especially sand-dependent species which are usually found only on hard substrata buried in sand. These include the sea cucumber *Roweia frauenfeldi frauenfeldi*, the chitons *Dinoplax fossus* and *Ischnochiton oniscus* and the isopod *Cirolana cranchi*. The surfaces of these rocks, if recently exposed, may be bare but are often covered by beds of the fugitive algae *Ulva rigida* and *Enteromorpha* sp. Many faunal species are associated with these algae and add substantially to total richness.

Although there is a net increase in the deposition of sand during the summer, reaching a maximum in the late summer months of March and April (Dower, unpubl. data), changes in sand level can occur over a single tidal cycle, a neap-spring cycle or over a couple of months. Continual, low level disturbance created by sand deposition and removal may also contribute to the high richness found in the gulleys.

The overall effect of inundation in gulleys is similar to the effect of wave action on boulders (Osman, 1977; Sousa, 1979a,b). The variation in age of patches in the gulleys (both sand and rock patches) equates with the variation in size of boulders. Young patches are similar to small boulders and have low richness, consisting of mainly fugitive species. Old patches resemble large boulders and have low richness. In sand patches, space is not limiting and low-richness climax communities of psammophilic species are never attained.

5.1.2.2 Mid shore

a) The coralline zone

Sand burial may occasionally be extensive enough to inundate this zone because of its close proximity to sand-filled gulleys (Figure 2.2). This is not as frequent or as regular as inundation in the gulleys. Coralline algae are rarely buried (pers. obs.) but tend to retain large amounts of sand among their thalli for long periods. This adds to the heterogeneity provided by these algae and enhances recruitment and survival of sand-tolerant, sand-dependent and psammophilic species living in the understorey. This and occasional inundation may be responsible for the high richness in this zone.

There were strong similarities between the corallines, *Hypnea* and gulleys, all of which fall into groups 3 and 4 on the samples dendrogram (Figure 4.11). The coralline algae and *Hypnea* zones have high richness because of the spatial heterogeneity provided by the algae. Although 100 of the 147 species found in the coralline zone were also found in the *Hypnea* zone, some important differences in trophic composition between these two zones were found. The majority of the remaining 47 species were carnivores and deposit feeders while the species found in the *Hypnea* zone and not in the coralline zone were mainly primary producers and herbivores. The sand deposits trapped by the corallines play an important role in determining the component species of this zone, almost 10% of which were psammophilic.

The coralline zone had 60 species in common with the gulley zone, 49 of which were exclusive to these two zones. The majority of these species were scavengers, carnivores or deposit feeders.

b) The *Gelidium* zone

The greatest differences in species richness and biomass between the two shore types were found in the mid shore area. Sand scouring is particularly detrimental to richness. Richness in the sand-free *Gelidium* zone on sandstone was higher than that in the same zone on dune rock which was subjected to moderate sand scour. This zone in turn had greater richness than the platform zone on dune rock which was subjected to more intense sand scour (Figure 4.2).

The *Gelidium* zone on sandstone was confined to the steep sides of the ridges (Figure 2.2) and consequently permanently sand free with no apparent effects of sand scour. Sixty-four percent of the species found in this zone on sandstone were also found in the adjacent coralline zone. Most of those not found in the coralline zone were sand-intolerant filter feeders (in particular the barnacle *Tetraclita serrata*) and sand-intolerant herbivores such as the two patellids *Patella oculus* and *P. granularis* and three species of the periwinkle *Oxystele*.

When describing the *Gelidium* and platform zones on dune rock it is necessary to consider the different effects of sand deposition and scour or abrasion. On dune rock shores coralline algae are present in high densities in sandy-bottomed pools in the *Gelidium* zone. The corallines grow towards the top of the pool sides, away from the bottom sand. They appear to be unaffected by sand trapped in their thalli, but unable to tolerate scour. Hence they are not found lower down the sides of the pools where the pool sand would have a scouring effect or on the platform zone which is often subjected to intense sand scour. Two species of coralline algae, *Jania crassa* and *Arthrocardia carinata*, which were abundant in the *Gelidium* zone on sandstone (and even occurred under high shore sand) were absent from the same zone on dune rock. Although it has been suggested that the calcified thalli of coralline algae offer protection from abrasion (Stewart, 1983), the exclusion of these algae on dune rock seems likely to be due to sand scour.

Littler *et al.* (1983) regarded the effects of smothering and scouring to be separable. They viewed smothering as a predictable "sand-induced stress" equivalent to desiccation, and scouring as an unpredictable disturbance. However, sand which is smothering is also a disturbance because of stochastic variations in sand quantities. On a scale of disturbance frequency, smothering equates with rare to intermediate disturbances while scour equates with a high level of disturbance frequency.

The accumulation of sand may exclude some species by smothering (i.e. reduced oxygen or light levels) but at the same time it promotes habitation by other species physiologically able to survive in this habitat as in gulleys and corallines. The effects of scour are different and although some species are able to survive sand scour its overall effect on the dune rock platform is detrimental. D'Antonio (1986) states that the red alga *Rhodomela larix*, which survives scour, will succumb if sand scour is too great.

On dune rock the *Gelidium* zone occurred at the seaward edge of the wave-cut platforms and was impoverished, having a richness of only 49 species, less than half that on sandstone (Figure 4.2). In this region sand had a scouring rather than accumulating effect, as wave action prevented the accumulation of sand deposits. The species that were excluded were mainly polychaetes, herbivorous molluscs and deposit feeding echinoderms. The three most common echinoderms on the middle and lower shore (the urchin *Parechinus angulosus*, the starfish *Patiriella exigua* and the brittle star *Amphioplus integer*) were not found in this zone on dune rock.

In the *Gelidium* zone scouring reduced not just species richness but also total biomass. Although the proportion of total biomass formed by primary producers in this zone was higher on dune rock than on sandstone (Figure 4.9) the actual value was much lower; mean of 139.5 and 202.8g.m^{-2} respectively.

c) The platform zone

More intense sand scour over the rest of the wave-cut platform had an even greater effect on richness and biomass. Only three of the 40 species recorded for the platform zone were not found in the *Gelidium* zone. These were a rare errant polychaete (*Brania furcelligera*), a psammophilic sedentary polychaete (*Boccardia polybranchia*), also found in coralline algae samples, and a psammophilic gastropod (*Natica tecta*), also found in sand, gulley and coralline samples. *Gelidium pristoides* and the green alga *Ulva rigida* were absent, and the brown alga *Iyengaria stellata* was the only species of macroalgae found. Stewart (1983) suggested that the internal reinforcing filaments found in the algal family Gelidiaceae (including *Gelidium pristoides*) protect the species in this family from abrasion. This does not appear to be the case for *G. pristoides* which is notably affected by sand scour on dune rock shores.

Some organisms on the platform zone escape abrasion by burrowing into the substratum. Dune rock is soft and a large proportion of the biomass of this zone consisted of the deposit feeding sipunculid *Themiste minor*, which lives under the surface of the rock to a depth of approximately 10mm. Molluscs such as the chiton *Acanthochitona garnoti*, which excavates shallow pits, and the pulmonate limpets *Siphonaria capensis* and *S. concinna* are able to withstand abrasion and contributed to the high herbivore proportion of the biomass of this zone. Two omnivorous polychaetes *Perinereis falsovariegata* and *Pseudonereis variegata*, which are also found in burrows in the rock, made up 12% of the total biomass for this zone (Figure 4.9).

The platform zone was not always uniformly flat and on several shores small hummocks a few centimeters high occurred. Some species escaped abrasion by inhabiting such small refuges or 'islands' of raised substratum as described by Littler (1980) and Littler *et al.* (1983). Although *Siphonaria capensis* appears to tolerate sand scour, aggregations of this limpet were found on these 'islands', where sand scour was apparently reduced.

SPECIES	*GELIDIUM* sandstone	*GELIDIUM* dune rock	PLATFORM dune rock
Patella granularis	17.0 ± 37.2	6.0 ± 2.8	0
Patella oculus	14.1 ± 3.9	4.5 ± 0.7	0
Siphonaria capensis	7.7 ± 11.0	51.0 ± 43.8	323.0 + 222.0
Siphonaria concinna	20.1 ± 17.4	8.5 ± 4.9	150.5 ± 154.9
Acanthochitona garnoti	28.2 ± 14.1	84.5 ± 74.2	625.0 ± 530.3

Table 5.1: Mean densities.m^{-2} (± S.D) for five herbivorous molluscs in three mid shore zones with varying degrees of sand scour. On the platform zone, where scour is greatest, the patellid species were absent.

Unlike siphonarid limpets, members of the Patellidae cannot tolerate sand inundation (Marshall and McQuaid, 1989) and *Patella oculus* and *P. granularis* were excluded from this zone. Both species are major herbivores in the *Gelidium* zone and their absence from the platform zone allows the above-mentioned sand-tolerant species to increase in abundance. Densities of *Acanthochitona garnoti*, in particular, were higher in this zone than in the adjacent *Gelidium* zone (Table 5.1). Low degrees of freedom and large variance meant that none of these increases were statistically significant (t-tests, $P>0.05$).

5.1.2.3 Upper shore

a) The high shore sand zone

Superimposed on the 'rocky shore' species associated with hard substrata, were 'sandy shore' species associated with extensive sand deposits on the high shore. These were similar on both shore types.

McLachlan (1977a,b), McLachlan *et al.* (1981b) and Wooldridge *et al.* (1981) have recorded a total of 21 sandy beach macrofaunal species for the south coast biota. Between four and 11 species are recorded for each individual shore. This range is similar to that found for this study. Most of the molluscs recorded for sandy beaches (*Bullia* spp. and *Donax* spp.) are found near the low water mark. Other species, mainly crustacea such as *Talorchestia quadrispinosa* and *Tylos capensis*, occur high up the shore in the foredune area. The sand sampled for mixed shores corresponded to the mid to upper shore zone of sandy beaches, excluding these major groups. Although 26 psammophilic species were recorded across the entire mixed shore, only ten of these had previously been recorded by McLachlan and co-workers for sandy beaches in this area.

Mobile psammophilic species such as the mysid *Gastrosaccus psammodytes*, the isopods *Exosphaeroma truncatitelson*, *Pontogeloides latipes* and *Eurydice longicornis* and the errant polychaetes *Arabella iricolor caerulea* and *Lumbrineris tetraura* were found in the sand column and may have migrated from adjacent sandy beaches. Most of these were found elsewhere in sand deposits on the shore and only *P. latipes* and four rare species were exclusive to this zone. Although Brown (1973) noted that this species was more common in a habitat of mixed rock and sand than in one of pure sand, it was not found in the gulleys on sandstone shores. The isopod *Exosphaeroma truncatitelson* is a west coast species which has been collected at densities of up to 532 individuals.m^{-2} (Brown, 1973), but has not previously been recorded for this region. It was, however, found in this study at densities of up to 2192 individuals.m^{-2}.

Some 'rocky shore' species with a high degree of sand tolerance were found at low densities attached to rocks beneath the sand deposits. These included sand-tolerant coralline algae such as *Jania crassa* and *Arthrocardia* sp.b and sand-dependent species such as turf-forming algae (*Polysiphonia* cf. *savatieri*, *Cladophora virgata* and *Centroceras clavulatum*). They also include sand-dependent animals such as the bivalves *Brachidontes semistriatus* and *Gregariella simplicifilis*, the chitons *Acanthochitona garnoti* and *Ischnochiton oniscus* and the pulmonate limpets *Siphonaria capensis* and *Siphonaria concinna.*

The physiological mechanisms and life history strategies which allow some species a high degree of tolerance to sand inundation have been investigated for very few species (Markham, 1973; Stewart, 1983; D'Antonio, 1986; Marshall and McQuaid, 1989). For example, the ability of the pulmonate limpet *Siphonaria capensis*, to withstand smothering appears to be linked to its ability to tolerate hypoxia. *S. capensis* has been shown to respire anaerobically under conditions of low oxygen tension and is thus able to survive beneath the sand for long periods of time whereas a species such as the patellid limpet *Patella granularis* is not able to do this and is thus absent from sand inundated areas (Marshall and McQuaid, 1989).

Almost 60% of the species found in the sand samples were also found in the sand-filled gulleys. All of these species were either sand-dependent or psammophilic. Some species that were recorded by McLachlan and co-workers but were not found in the high shore sand did occur in gulleys. The difference in total richness between the present study and that of McQuaid *et al.* (1985) could be due to the presence of a "psammophilic component" on eastern Cape mixed shores (Figure 5.3). It seems that a mixed shore is in fact a very heterogeneous rocky shore with a sandy beach component which acts to enhance overall species richness.

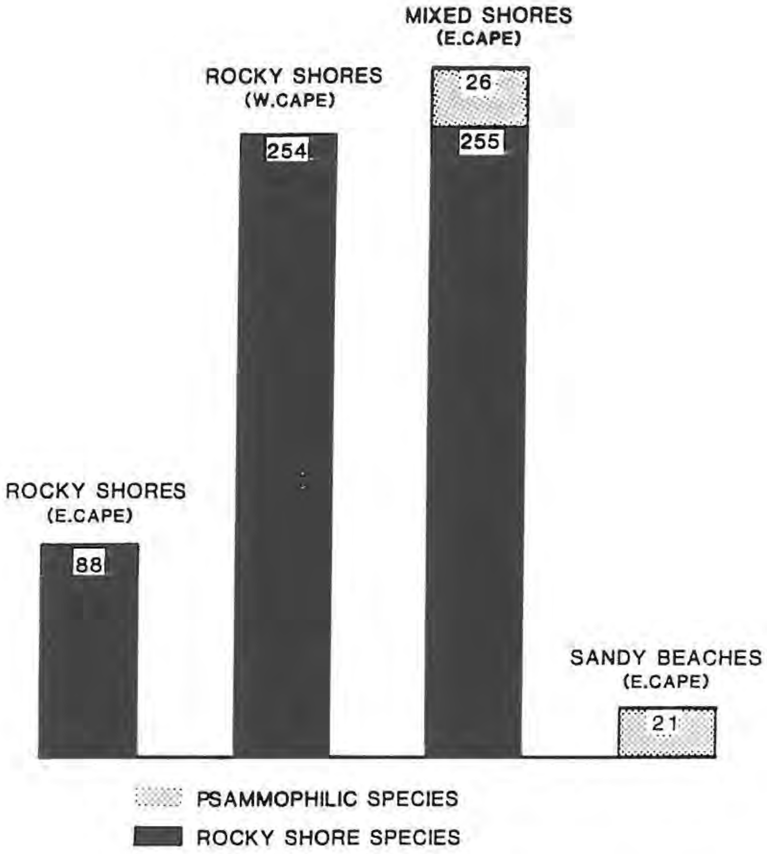


Figure 5.3: Species richness of rocky shore (sand-intolerant, sand-tolerant and sand-dependent) and psammophilic species in the eastern Cape and western Cape. Primary producers have been omitted because they were not sampled in as much detail as the fauna in the present study and in McLachlan *et al.* (1981a).

Rocky shores (E.Cape) - McLachlan *et al.* (1981a)
(W.Cape) - McQuaid (1980)
Mixed shores (E.Cape) - present study
Sandy beaches (E.Cape) - McLachlan (1977a,b)
McLachlan *et al.* (1981b)
Wooldridge *et al.* (1981)

On sandy beaches macrofaunal richness decreases as exposure to wave action increases (McLachlan *et al.*, 1981b). It could be said that high disturbance frequency and intensity maintains a low diversity. Movement patterns of high shore sand on mixed shores are poorly understood but subsequent studies (Dower, unpubl. data) have shown large variations within two week cycles and this sand must move across the shore in substantial quantities. Low richness in high shore sand, resulting from maximum disturbance similar to that found on sandy beaches, is thus not unexpected.

Turf-forming algae and small scavenging crustaceans made up the most of the biomass for the high shore sand on dune rock shores. Unusually high densities of the isopod *Exosphaeroma truncatitelson* at Kwaaihoek and Ship Rock were responsible for this high proportion of scavengers (Figure 4.9). On sandstone, high shore sand was dominated by turf-forming algae and carnivorous polychaetes. The errant polychaete *Lumbrineris tetraura* was found to have a particularly high biomass at Mushroom Rocks which increased the total biomass for carnivores considerably. Turf-forming algae are known to persist in, and are often associated with, stressed habitats (Hay, 1981).

b) The *Littorina* zone

On dune rock the *Littorina* zone consisted of only the two gastropods *Littorina africana africana* and *L. a. knysnaensis*. On sandstone these two species were present in similar densities to those on dune rock but large beds of the barnacle *Chthamalus dentatus* and a few juvenile *Siphonaria concinna* were also found.

These differences may be due to sand deposition. On sandstone, upper shore ridges run inland until they are covered high up the shore by dunes (Figure 2.2). On dune rock the upper shore rocks form an almost vertical 'back wall' at the top of the shore and are always sand free. Periodic removal of sand from sandstone rocks provides free space for colonisation by available propagules of opportunistic species; in this case *C. dentatus*. No macroalgae occurred in this zone. The reason for the absence of *C. dentatus* from the *Littorina* zone on dune rock is unclear but may be related to the inability of the larvae to colonise this area.

5.1.3 Trophic structure

This section describes the vertical zonation of trophic biomass on sandy beaches and rocky shores and then examines the trophic structure of mixed shores in greater detail.

At least 90% of the biomass on sandy beaches can be accounted for by filter feeding molluscs (*Donax* spp.) and by scavenging molluscs (*Bullia* spp.) which occur primarily in the low shore region near the swash line (McLachlan *et al.*, 1981b). Scavenging crustacea are found in the mid shore and high shore regions. No macroalgae occur on sandy beaches.

Two rocky shores studied in the eastern Cape (McLachlan *et al.*, 1981a) showed a very high herbivore biomass coinciding with very high primary producer biomass. This does not agree with a study done in the western Cape (McQuaid and Branch, 1985) or with the

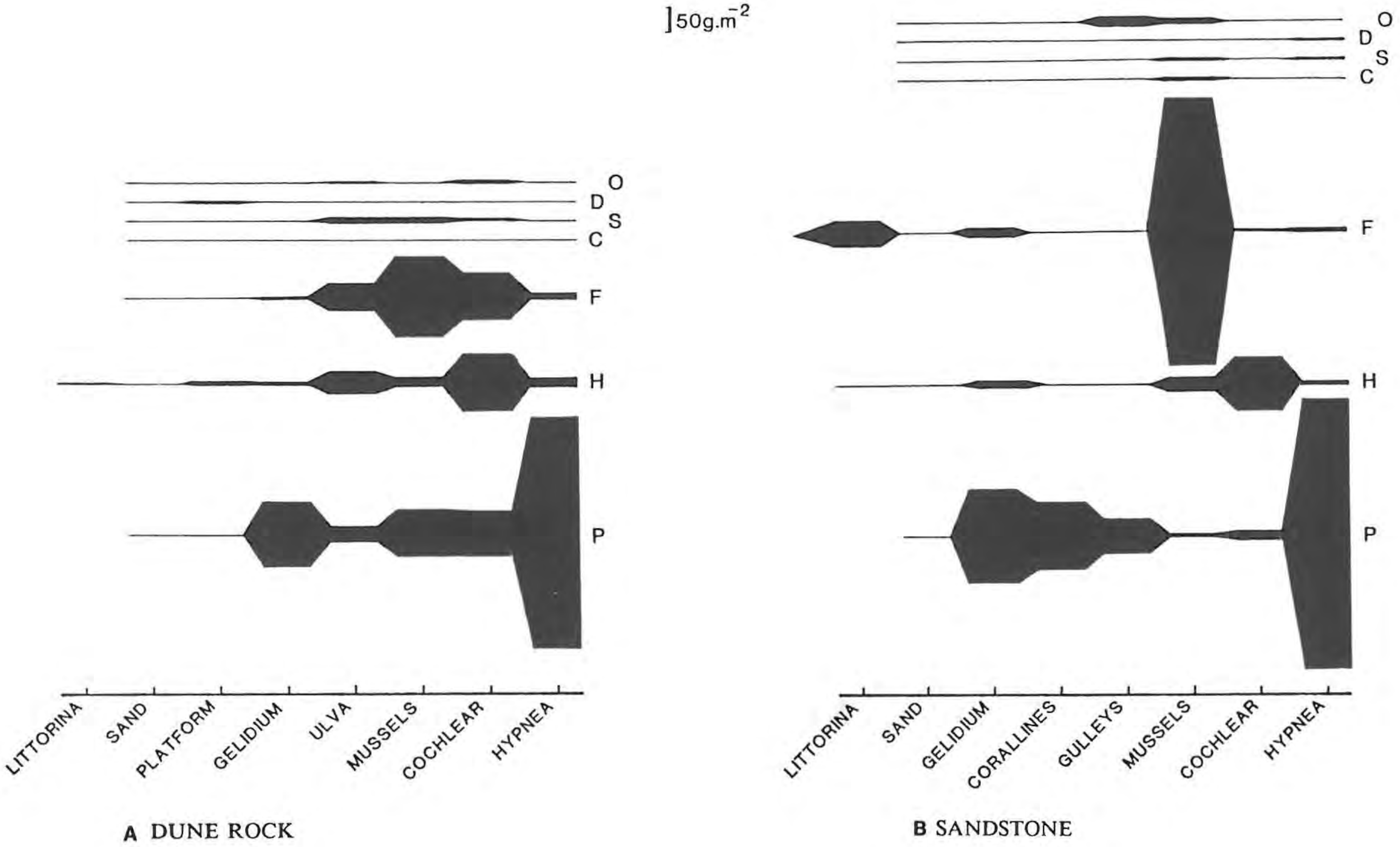


Figure 5.4: Vertical distribution of biomass for each trophic level from the low shore *Hypnea* zone to the high shore *Littorina* zone. P-primary producers, H-herbivores, F-filter feeders, C-carnivores, S-scavengers, D-deposit feeders, O-omnivores.

present study where biomass of herbivores is inversely related to that of primary producers (Figure 5.4). However, McLachlan *et al.* (1981a) sampled the algae two years after the faunal survey, so that trophic biomass values were not concurrent.

If the profiles of biomass distribution presented for these two shores (McLachlan *et al.*, 1981a) are modified so that sampling points in pools are removed, then a steady upshore decrease in both primary producer and herbivore biomass can be seen. The more exposed of the two shores had greatest biomass of filter feeders in the low shore region. Filter feeders decreased up the shore with a slight increase in the barnacle zone higher up the shore. The sheltered shore had fewer filter feeders but slightly more deposit feeders. The authors mention incidentally that sand deposits were present on this shore, and it is possible that this could account for the increase in biomass of deposit feeders.

McQuaid and Branch (1985) examined the trophic composition of 12 exposed and sheltered rocky shores in the western Cape and found differences related to the degree of wave exposure. On sheltered shores algal biomass decreased steadily up the shore. Herbivore biomass, although far lower, showed a similar upshore trend while omnivores, deposit feeders, scavengers and carnivores were present throughout but contributed very little to the biomass in all zones. On exposed shores algae decreased initially in the herbivore-dominated *cochlear* zone, increased in the lower balanoid and then decreased further up the shore. Herbivore biomass appeared to be inversely related to algal biomass. It has been found that herbivores often feed on algal sporelings rather than on full grown plants (McQuaid and Branch, 1985; Menge and Sutherland, 1987). Herbivores may also be ineffective in controlling stable beds of perennial macroalgae through grazing (Dayton, 1975). This results in space being unavailable for the establishment of ephemeral algae. The absence of competitive ephemerals further enhances the persistence of the dominant algae thereby substantially increasing primary producer biomass (Lubchenco and Menge, 1978). Of the other trophic categories on exposed shores filter feeders showed extremely high biomass in the low shore and again in the upper balanoid, corresponding with mussel and barnacle zones respectively. All other trophic levels were present throughout in small quantities.

On mixed shores each zone can be characterised by certain species or species assemblages which are determined by the presence or absence of sand. Alternatively, zones can also be characterised by trophic levels.

All zones were dominated by primary producers, herbivores and/or filter feeders in terms of both numbers and biomass (Figure 4.9 and Tables 4.4, 4.5). This is similar to rocky shores (McLachlan *et al.*, 1981a; McQuaid and Branch, 1985). The highest biomass recorded was for primary producers in the *Hypnea* zone. On dune rock algal biomass decreased steadily up the shore while on sandstone the effects of the topography and sand resulted in a second concentration of primary producer biomass in the sand-free

Gelidium zone (Figure 5.4). The existence of the gulley and coralline zones on sandstone shores does not greatly influence the trophic composition of the whole shore except with respect to primary producers. Bally *et al.* (1984) predicted that primary producers on mixed shores would have a biomass less than that on rocky shores. This does appear to be the case. McQuaid and Branch (1985) recorded a low shore biomass of algae three times that recorded for this study.

Herbivore biomass on both rock types was highest in the *cochlear* zone and then decreased steadily up the shore. An inverse relationship between primary producer and herbivore biomass similar to that recorded for rocky shores by McQuaid and Branch (1985), was found for mixed shores (Figure 5.4). Highest filter feeder biomass was found in the low shore with a maximum in the mussel zone. On sandstone, barnacles present in the *Gelidium* and *Littorina* zones accounted for a second and third rise in filter feeder biomass respectively (Figure 5.4). The presence of scouring sand almost completely eliminates filter feeders from the middle and upper shore on dune rock (Figure 5.4).

Scavengers, omnivores, carnivores and deposit feeders were again present throughout (usually contributing less than five percent to the total biomass) except in the *Littorina* zone where none of these trophic categories were present (Figure 5.4). Although carnivores showed greatest richness (Figure 4.8), they were neither very abundant nor did they exhibit high biomass. The only carnivorous species of significance in terms of abundance and biomass was the psammophilic errant polychaete *Lumbrineris tetraura* which was found in gulleys and was common in high shore sand. McQuaid and Branch (1985) found a positive correlation between carnivore biomass and filter feeder biomass. A similar relationship was not found in this study.

In comparing the structure of mixed shores to other intertidal systems, two differences between rocky shores and sandy beaches are of particular relevance. Firstly, on rocky shores many herbivores appear to graze microalgae rather than macroalgae (McQuaid and Branch, 1985; Menge and Sutherland, 1987), whereas on sandy beaches macroalgae and herbivores are both absent. Secondly, on sandy beaches the meiofauna is far more diverse and abundant than the macrofauna (McLachlan, 1977a,b; McLachlan *et al.*, 1981b), and it has been found that on rocky shores of the western Cape, meiofauna are also more abundant and can account for 25% of the secondary production (Gibbons and Griffiths, 1986). Mixed shores certainly support macro- and microalgae and herbivores are abundant but no information on meiofauna is available.

5.1.4 Indicator and rare species

Indicator species for sandstone shores were abundant. Twenty-two species were found to be common on sandstone but were never found on dune rock (Appendix B). Only four of these indicator species were not found in either coralline algae or gulleys. Most of the indicator species were polychaetes, crustaceans or molluscs. This is not surprising as these three groups each contributed just over 25% to the total richness (Figure 4.4). McQuaid and Branch (1984) found far fewer indicator species for degree of wave exposure or temperature regime. One indicator species was found for wave exposed shores but none for sheltered shores while six and 11 species of indicators were found for cold and warm water respectively. The sites sampled for the present study are all subject to a similar degree of wave exposure and their temperatures were presumed to be equal.

The most useful indicator, because of its large size, was the U-shaped sea-cucumber *Roweia frauenfeldi frauenfeldi*. Adults and juveniles of this species were found under the rocks in the sand filled gulleys while only juveniles were found in the sandy understorey of the coralline algae. The giant chiton *Dinoplax fossus*, although only recorded from sandstone shores, was seen in pools (which were not sampled) on dune rock. This species was very common under rocks in the gulleys.

A significantly higher proportion of rare species was found in the *Hypnea*, gulley, coralline and sand zones (Figure 4.6). The reason for this is unknown but there may be some relationship between richness and rare species which could also be linked to the spatial heterogeneity and the heterogeneity offered by the macroalgae within a zone (Figure 4.9). This does not apply to the sand samples which had low richness and a low level of spatial heterogeneity. The generally high proportion of rare species on sandstone shores (Figure 4.5) could be attributed to greater heterogeneity and the presence of the gulley and coralline zones.

5.2 COMMUNITY ANALYSIS

It was suggested earlier that greater richness on sandstone shores is due to greater spatial heterogenetiy, in particular the presence of sand deposits. Although there is a decrease in the number of sand-intolerant species on dune rock because of the absence of sand-free habitats, the increase in sand-dependent and psammophilic species on sandstone (reflecting larger and more permanent sand deposits) has a greater influence on the relative richness on the two rock types (Table 5.2). This is compounded by an increase in rare species on sandstone, presumed to be a further consequence of greater spatial heterogeneity (Figure 4.6). The large number of rare species on sandstone also influences the relative proportions of the other species.

SAND TOLERANCE LEVEL	DUNE ROCK	SANDSTONE
SAND-INTOLERANT	47 (23.6)	57 (20.1)
SAND-TOLERANT	48 (24.1)	54 (19.0)
SAND-DEPENDENT	20 (10.1)	30 (10.6)
PSAMMOPHILIC	15 (07.5)	23 (08.1)
RARE	30 (15.1)	66 (23.2)
UNKNOWN	39 (19.6)	54 (19.0)
TOTAL	199 (100.0)	284 (100.0)

Table 5.2: Number of species exhibiting each level of sand tolerance on dune rock and sandstone shores. Percentages are in parenthesis.

In section 5.1 of the Discussion reference was made to species assemblages corresponding to various levels of sand tolerance. The classification of mixed shores with respect to substratum type has also previously been discussed. Community analysis was carried out to ascertain whether substratum type could be used to classify sand inundated rocky shores and whether species assemblages representing a variety of levels of sand tolerance are distinguishable on a quantitative basis. Because many species were rare and the sand tolerance levels of many others were unknown, classification of species according to these levels could only be done with about half of the species.

5.2.1 Analysis of samples

Analysis by ordination and classification clearly indicates that zones are related to one another primarily on the basis of richness and secondarily according to rock type.

The *Littorina* zone was clearly different from all the other zones and was the first group of samples to form a distinct cluster in the classification (group 1, Figure 4.11). This zone is characterised by very low richness (four species) and extremely low biomass. Within this group, at the second division, the samples split into one group of sandstone samples, characterised by the presence of the barnacle *Chthamalus dentatus* and one of dune rock samples. In other words a group defined by richness is composed of two substratum specific sub-groups.

Following the separation of the *Littorina* samples, seven of the nine sand samples form a single cluster at the second division (group 2, Figure 4.11). These samples are also characterised by a low richness species assemblage which is distinct from that of any other group of samples but further divisions revealed no clear sub-groups.

The remaining samples were more clearly linked to one another but as the third division were again grouped primarily according to richness. High richness samples of *Hypnea*, coralline and gulley zones (groups 3 and 4) were separated from lower richness *cochlear*, mussel, *Gelidium* and platform zones as well as the remaining two sand samples (groups 5 and 6).

One division further, substratum specific zones can again be recognised. Within the high richness cluster the gulley and coralline zones, characteristic of sandstone shores, are separated from the *Hypnea* zone which occurred at all sites. The separation between *Hypnea* and gulleys is distinct but the coralline samples are split according to richness. The high richness coralline samples are grouped with the *Hypnea* zone (group 4) and the low richness samples with the gulley zone (group 3, Figure 4.11).

The large group of low richness samples also splits according to substratum at the fourth level (groups 5 and 6, Figure 4.11). Group 6 is substratum-specific and is characteristic of dune rock shores. The three platform samples are separated from the remaining samples of mixed richness and substratum type. Included in group 6 with the platform samples are the two remaining sand samples. Both of these were from dune rock shores and both had more sand-dependent species attached to the rock beneath the sand than the seven other sand samples. Some of these sand-dependent species such as the chiton *Acanthochitona garnoti*, the pulmonate limpets *Siphonaria capensis* and *S. concinna* and the bivalves *Gregariella simplicifilis* and *Brachidontes semistriatus* were also found in platform samples which explains the inclusion of these sand samples in this group.

Just as gulleys, and perhaps coralline algae, present a basis for the classification of mixed shores, so too does the platform zone on dune rock. While *Hypnea*, *cochlear*, mussel and *Gelidium* zones can be found on rocky shores, and high shore sand samples closely resemble the same zones on sandy beaches; gulleys, corallines and dune rock platforms are characteristic of mixed shores. The vast difference in richness and biomass between the *Gelidium* zone on sandstone and the same zone on dune rock was not apparent in the ordination or classification results and the two sample types were grouped together (group 5, Figure 4.11).

5.2.2 Analysis of species

Classification of species according to samples confirmed that zones, and therefore in some cases also substrata, can be defined by assemblages of species which are characterised by their level of sand tolerance.

The species analysis is based on the results of the sample analysis (see Methods) and the major divisions in the ordination and the classification are consequently very similar to those in Figures 4.11. The first group (group A) consists of the four species associated with the *Littorina* zone. At the second division two major clusters corresponding to high richness (groups B-E) and low richness (groups F-I) zones are found. Each major group contains four smaller clusters (Figure 4.13).

The four zones represented by the first of these two groups are sand, *Hypnea*, corallines and gulleys all of which had a significantly greater proportion of rare species than the remaining zones (Figure 4.6). The first cluster within this group (group B) consists entirely of an assemblage of psammophilic and sand-dependent species associated with high shore sand. It was mentioned earlier that two sand samples were grouped with the platform zone because of a group of sand-dependent species common to those samples. None of these species appeared in this group. Most of the psammophilic species have been recorded for sandy beaches (McLachlan, 1977a,b; McLachlan *et al.*, 1981b) while the sand-dependent species consisted mainly of turf-forming algae.

The next cluster to be separated from this major group is one of predominantly sand-intolerant species associated mainly with the *Hypnea* zone (group E). Most of these species are abundant and were found in more than two zones. These species were found in the *Hypnea* itself but group E also contained a few sand-tolerant species found in the sand trapped in the holdfasts of the algae.

At the fifth division (Figure 4.13) group C consists of sand-tolerant, sand-dependent and a few psammophilic species. This group is characteristic of the gulley zone and over a third of the species in this cluster are indicators for sandstone shores. Thus this group, or assemblage, of species is characteristic of not only the gulley zone or sandstone shores but also of mixed shores in general.

Group D consists predominantly of those species found in both the coralline and the *Hypnea* zones. This is a heterogeneous group but the majority of species are sand-dependent or sand-tolerant.

Completely separate from the clusters described above is the second major group presented at the second division of the classification (groups F-I). Except for group I, these species are mostly sand-intolerant (with some sand-tolerant species in group F) and appear to be clustered according to the zones in which they were found (Figure 4.13). These zones include *cochlear*, mussels, and *Gelidium* which are all basically rocky shore zones with minimal sand influence.

Group I consists of psammophilic and sand-dependent, or perhaps abrasion-tolerant, species which were found in the platform zone and in the two remaining sand samples. Note that there are no patellid limpets in this group while the sand-tolerant chiton *Acanthochitona garnoti* and pulmonate limpet *Siphonaria capensis* are found here.

Although, because of the large number of species involved, a lot of generalisations have had to be made, it is still possible to distinguish species assemblages on the basis of sand tolerance. From the whole ordination or classification at least two distinct species assemblages can be identified which are exclusive to mixed shores. The first is that representing gulleys and therefore also sandstone shores (group 3), and the other is that representing the platform zone and thus also dune rock shores (group I).

An arc of species groups which approximates to a gradient of decreasing sand tolerance can be fitted to the ordination of species (Figure 4.14). Psammophilic and sand-dependent species associated with high shore sand, gulleys and corallines are found closest to the Y-axis on the left of the ordination (groups B, C and D). A mixture of sand-tolerant and sand-intolerant species are found farther to the right (groups E, F). These species are mainly from the low shore region and the *Gelidium* zone. Still farther to the right are the sand-intolerant species of groups G and H. The four species most isolated and furthest along the X-axis are the four sand-intolerant species associated with the *Littorina* zone.

In conclusion, while sample grouping was based primarily on richness, three groups can be identified according to substratum type and therefore provide a means for classifying mixed shores. In the species analysis species are classified according to the zones in which they were found and in many cases according to their respective sand tolerance levels as well.

5.3 THE INTERMEDIATE DISTURBANCE HYPOTHESIS AND PATCH DYNAMICS

Implications of the intermerdiate disturbance hypothesis have already been suggested in the first section of this chapter. Here, the effectiveness of this hypothesis in predicting species richness in general will be discussed with particular emphasis on its application to mixed shores.

The intermediate disturbance hypothesis predicts maximum species richness for communities when they are subject to an intermediate level of disturbance (Connell, 1978,1979), where disturbance is defined as the removal of space occupying organisms (Connell, 1978; Dethier, 1984; Gaines and Roughgarden, 1985). This hypothesis, although widely accepted, has received much critisism and provoked much discussion in the literature (Huston, 1979; Armesto and Pickett, 1985; Connell and Keough, 1985; Denslow, 1985; Pickett and White, 1985; Menge and Sutherland, 1987).

One difficulty with the intermediate disturbance hypothesis is that it is too generalised to provide a testable hypothesis. Sousa (1979a,b) found low diversity on small, frequently disturbed and large infrequently disturbed intertidal boulders. High diversity was found on medium-sized boulders which were subject to intermediate levels of disturbance. This appeared to satisfy the predictions made by the intermediate disturbance hypothesis. However, Menge and Sutherland (1987) note that the sides of the boulders were subjected to intense grazing pressure by sea urchins while grazing effects of these herbivores on the boulder tops was minimal. Different grazing patterns of the sea urchins could therefore be responsible for Sousa's (1979a) results.

Huston (1979) has put forward a second hypothesis which states that the balance between the rate at which one species displaces another through competition, and the frequency of disturbance, maintains species diversity. The intermediate disturbance hypothesis and Huston's hypothesis are fundamental to disturbance and diversity theory but cannot alone explain community composition and species diversity on intertidal hard substratum (Pickett and White, 1985).

One fundamental problem is that the search for a uniform measure of disturbance is futile as each disturbance, and the community it affects, has its own specific characteristics. Perhaps the definition of disturbance as "removal of space occupying organisms" is too vague. A more satisfactory and complete definition is given by White and Pickett (1985 page 7): "...a disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment".

A second problem is that the intermediate disturbance hypothesis assumes a competitive hierarchy in which one species is consistently competitively superior to a second species (Connell and Keough, 1985). Maximum richness is predicted to occur at certain levels of frequency and severity of disturbance. However, these levels will depend on species abundances, competitive abilities and interactions (Connell and Keough, 1985; Armesto and Pickett, 1985). It has also been found that the final stage of succession following a single disturbance may not be a single dominant species in a low-richness community but may consist of a continually changing variety of species (with no clear dominant) with overall high species richness (Connell and Keough, 1985).

Apart from the properties of the disturbance itself, its effects depend on a number of factors involving the state of a community at the time of disturbance. Where the disturbance is in the form of sand inundation, the following are important (Armesto and Pickett, 1985; Turner 1985) :

1. time since last inundation,
2. pre-inundation successional state of the community,
3. the life history stages of the dominant and the component species,
4. the season of inundation,
5. spatial and temporal variations within the area inundated and
6. the physiological tolerance of sand of the organisms in the community.

The distribution and abundance of organisms described for eastern

Cape mixed shores have been shown, by zonation and community analysis, to represent apparent responses to increased spatial heterogeneity and the presence of sand. It appears that sand inundation of intermediate frequency and intensity, rather than maintaining or increasing richness through its effects on the patches inundated, increases within-habitat diversity on rocky shores and creates local patches at different successional stages.

On these shores competitors for space are only prominent on the low shore. Space occupying species such as the algae *Caulerpa filiformis* (subtidal) and *Hypnea spicifera*, the mussel *Perna perna* and the limpet *Patella cochlear* are dominant in the low shore. In the middle and upper shore regions relatively few competitors for space were present. Free space is always found in these regions and even species such as the barnacle *Chthamalus dentatus*, which exhibits 100% space occupancy in small patches, has bare areas between patches. Disturbance as "the removal of space occupying species" is thus irrelevant in this context.

In a study on a mixed shore in California, U.S.A., space in the middle to upper shore was obviously limiting (Taylor and Littler, 1982). The sand-tolerant anemone, *Anthopleura elegantissima*, depended on the mortality of the competitively superior tube worm, *Phragmatopoma californica*, in order to colonise the area. Exposure to air, sand inundation and sand scouring were responsible for the mortality of the tube worm resulting in the provision of free-space which the anemone was then able to colonise (Taylor and Littler, 1982). The only species exhibiting similar dominance in this study was the sand-tube worm *Gunnarea capensis*. Extensive colonies of this species were often found in predominantly sand-free areas especially on sandstone shores. It is apparent that on eastern Cape mixed shores sand causes local extinctions of only a few sand-intolerant species. Overall diversity (whole shore diversity) was seldom affected by the elimination of competitors for space.

Apart from the effects predicted by the intermediate disturbance hypothesis, D'Antonio (1986) describes several means by which sand inundation may increase species abundance. Some of these could also be used to explain changes in species richness:

1. Sand provides a refuge from grazers or predators. Where a species of alga can tolerate sand, but is not dependent on it for survival, sand might provide a refuge for that species from large herbivores.

   In this study sand did not appear to facilitate the growth of any species of alga except perhaps the turf-forming species. Although sand-tolerant herbivores may derive protection from predators while buried under sand, they would probably die of starvation due to the absence of primary producers. The only herbivore found in this study, known to survive sand burial for any considerable length of time is the pulmonate limpet *Siphonaria capensis*. This limpet can reduce its metabolic rate during periods of sand stress and can therefore live off food reserves for long periods (Marshall, unpubl. data). Also, sand-intolerant predators may be replaced by sand-tolerant predators so that the protection offered by sand deposits would be doubtful. The psammophilic whelks *Natica forata* and *N. tecta*, found in the present study, are such predators.

2. Sand inundation may eliminate some potential herbivores, predators or competitors from the shore.

Five large herbivores are found in the *Gelidium* zone on sandstone. These included two patellid limpets, *Patella oculus* and *P. granularis*, two siphonarid limpets, *Siphonaria capensis* and *S. concinna* and a chiton, *Acanthochitona garnoti.* On dune rock, where the effects of the sand are greater, lower numbers of the two patellid species are found (Table 5.1). On dune rock platforms, where even more sand is found, these patellids are absent. The remaining three species are sand-tolerant and are thus common on dune rock shores.

On sandstone shores all five species co-occur with no evidence of competitive exclusion. Therefore, where some species are excluded by physical factors, the others simply become more abundant (Table 5.1).

An example directly contrary to D'Antonio's suggestion is provided by local mussel populations. Approximately 50 kilometers west of this study Phillips (unpubl. data) has found that where the mussel zone is heavily inundated with sand, the invasive mussel *Mytilus galloprovincialis* is common, or even numerically dominant. It is absent where little or no sand is found, and *Perna perna* forms monospecific mussel stands. The presence of sand seems to allow for more effective competition by *M. galloprovincialis*.

3. Sand inundation may protect some species from other physical stresses such as exposure.

   The only species in this study to which this may apply are the turf-forming algae such as *Centroceras clavulatum* and *Polysiphonia* cf. *savatieri*. As Hay (1981) points out, turf-forming species are characteristic of stressed environments and are adapted to exposure to air. Therefore protection from sand in this way would be minimal.

4. Sand inundation may restrict recruitment by less tolerant but competitively superior species thereby allowing space dominance by competitively inferior sand-tolerant species.

   Denslow (1985) comments that the preservation of patch structure and competitive conditions, upon which some species depend for survival, is more important than the allowance of dominance by competitively inferior species. Since space does not appear to be limiting in the areas most affected by sand on these shores it is unlikely that any species are being suppressed by competitively superior species. In the case of the limpets described (presumably competitors for food), removal of apparently competitively superior species (*Patella* spp.) is associated with and increase in density of the siphonarid species and the chiton but at the same time an overall decrease in richness. In this study, patchiness resulting from sand inundation, is more likely to cause increased richness than the successful colonisation and co-existence of competitively inferior species such as the mussel *Mytilus galloprovincialis.*

It can be concluded that D'Antonio's (1986) suggestions are overall not important in this case. Of greater importance is the enhancement of richness by the presence of psammophilic species in sand deposits. Sand depth in the gulleys varies considerably (Dower, unpubl. data) but there is very seldom no sand present and richness here is augmented by the presence of psammophilic species.

Similarly, some sand-dependent rocky shore species only occur where there is sand even though they require hard substata for attachment. Where there is no sand these species are absent e.g. the sea-cucumber *Roweia frauenfeldi frauenfeldi* and the giant chiton *Dinoplax fossus.*

Co-existence of psammophilic, sand-dependent and sand-tolerant species assemblages is a function of habitat heterogeneity created by sand deposits. Very few species appear to be excluded on a large scale and only small scale extinctions occur.

Other factors such as protection by sand from consumers, competitors or physical stress will perhaps lead to increased abundance of species but will not necessarily result in the actual exclusion or inclusion of species.

Some of the apparent structure of these species assemblages can be explained by the presence of sand and there does seem to be a correlation between habitat heterogeneity and species richness but more detail is required. Further investigations involving long term, large scale monitoring of changes in sand levels and small scale measurements of patch size and depth; life history strategies of the component species and the physiological tolerances (of sand and of other physical stresses) of the dominant sand-tolerant, sand-dependent and psammophilic species will have to be made. A more accurate account of patch dynamics, successional stages and community composition can then be obtained.

The results of such investigations would reveal the extent to which factors such as succession, competition, grazing and predation, as functions of sand inundation, play a part in determining species richness.

CHAPTER SIX - SUMMARY

1) The presence of sand on rocky shores can have a positive or negative effect on species richness. Sand scour reduces richness on a local scale (eg. in the *Gelidium* and platform zones), but very few species are excluded from the shore as a whole. The positive effect of sand on richness seems more important and is related to the heterogeneity of the habitat.

2) The intermediate disturbance hypothesis is relevant to mixed shores but does not fully explain the distribution of species assemblages. The present study indicates that patch structure, where habitat heterogeneity is increased, is the most important factor in generating species richness on eastern Cape mixed shores (see Denslow, 1985).

3) The topography of the substratum is important through its influence on the deposition and retention of sand. As topography determines the nature of sand deposits, it indirectly affects species richness. Wave exposure is also important in preventing the accumulation of sand deposits, particularly in the low shore region.

4) Community analysis indicates that sand promotes the presence and abundance of sand-tolerant, sand-dependent and psammophilic species so that assemblages of these species are found in a variety of habitats according to the degree of sand inundation. Mixed shores in the eastern Cape can be classified

according to rock type on the basis of the existence of three substratum-specific zones - gulleys, coralline algae and platforms. Two substratum-specific assemblages, one for gulleys and a second for platforms, have been identified and could also be used to classify mixed shores.

5) A small number of indicator species for substratum type occur only on mixed shores (e.g. *Roweia frauenfeldi frauenfeldi*). Each species is found in a particular habitat, such as mixed rock and sand (gulleys), and is always associated with sand deposits.

6) Trophic structure varies greatly between zones and between rock types. Sand presence particularly affects the biomass of primary producers, filter feeders and deposit feeders. Macroalgae on the low shore have much lower biomass than in the same zones on rocky shores (c.f. McQuaid and Branch, 1985). In the mid shore region they exhibit very high biomass on sandstone while on dune rock their biomass is low. Sand presence also reduces the numbers and biomass of filter feeders while the biomass of deposit feeders increases. Nevertheless, trophic structure for the whole shore is basically similar to that for rocky shores rather than for sandy shores.

CHAPTER SIX - REFERENCES

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APPENDIX A

List of the site, zone and substratum type of each sample.

BEA - Beacon Rocks,	BRE - Bretton Rocks,
CAN - Cannon Rocks,	HIG - High Rocks,
KLE - Kleinemond,	KWA - Kwaaihoek,
MUS - Mushroom Rocks,	SEA - Seafield,
SHI - Ship Rock,	SIS - Three Sisters.

MISCELLAN. - Miscellaneous sample i.e. sampled at one site only.

SAMPLE	SITE	ZONE	SUBSTRATUM
1	SIS	*HYPNEA*	DUNE ROCK
2	KLE	*HYPNEA*	SANDSTONE
3	KWA	*HYPNEA*	DUNE ROCK
4	MUS	*HYPNEA*	SANDSTONE
5	SEA	*HYPNEA*	SANDSTONE
6	BEA	*HYPNEA*	SANDSTONE
7	SHI	*HYPNEA*	DUNE ROCK
8	HIG	*HYPNEA*	DUNE ROCK
9	BRE	*HYPNEA*	SANDSTONE
10	CAN	*HYPNEA*	SANDSTONE
11	SHI	MUSSELS	DUNE ROCK
12	HIG	MUSSELS	DUNE ROCK
13	BEA	MUSSELS	SANDSTONE
14	CAN	MUSSELS	SANDSTONE
15	SEA	MUSSELS	SANDSTONE
16	BRE	MUSSELS	SANDSTONE
17	SIS	MUSSELS	DUNE ROCK
18	KWA	*ULVA*	DUNE ROCK
19	SIS	*ULVA*	DUNE ROCK
20	HIG	MISCELLAN.	DUNE ROCK
21	SHI	*GELIDIUM*	DUNE ROCK
22	KWA	*GELIDIUM*	DUNE ROCK
23	BEA	*GELIDIUM*	SANDSTONE
24	KLE	*GELIDIUM*	SANDSTONE
25	SEA	*GELIDIUM*	SANDSTONE
26	CAN	*GELIDIUM*	SANDSTONE
27	BRE	*GELIDIUM*	SANDSTONE
28	MUS	*GELIDIUM*1	SANDSTONE
29	MUS	*GELIDIUM*2	SANDSTONE
30	SEA	*COCHLEAR*	SANDSTONE
31	KWA	*COCHLEAR*	DUNE ROCK
32	SHI	*COCHLEAR*	DUNE ROCK
33	BEA	CORALLINES	SANDSTONE
34	CAN	CORALLINES	SANDSTONE
35	SEA	CORALLINES	SANDSTONE
36	MUS	CORALLINES	SANDSTONE
37	KLE	CORALLINES	SANDSTONE
38	KLE	GULLEYS	SANDSTONE
39	BRE	MISCELLAN.	SANDSTONE
40	HIG	MISCELLAN.	DUNE ROCK
41	BRE	SAND	SANDSTONE
42	SIS	SAND1	DUNE ROCK
43	HIG	SAND	DUNE ROCK
44	BEA	SAND	SANDSTONE
45	KLE	SAND	SANDSTONE
46	MUS	SAND	SANDSTONE
47	KWA	SAND	DUNE ROCK
48	SHI	SAND	DUNE ROCK
49	SIS	SAND2	DUNE ROCK
50	BRE	*LITTORINA*	SANDSTONE
51	SIS	MID SHORE	DUNE ROCK
52	SHI	MID SHORE	DUNE ROCK
53	KWA	MID SHORE	DUNE ROCK
54	BEA	GULLEY	SANDSTONE
55	SEA	GULLEY	SANDSTONE
56	CAN	GULLEY	SANDSTONE
57	BRE	GULLEY	SANDSTONE
58	KWA	*LITTORINA*	DUNE ROCK
59	SIS	*LITTORINA*	DUNE ROCK
60	SHI	*LITTORINA*	DUNE ROCK
61	HIG	*LITTORINA*	DUNE ROCK
62	SEA	*LITTORINA*	SANDSTONE
63	KLE	*LITTORINA*	SANDSTONE
64	BEA	*LITTORINA*	SANDSTONE
65	MUS	*LITTORINA*	SANDSTONE
66	CAN	*LITTORINA*	SANDSTONE

APPENDIX B

List of all 321 species including 40 species of algae. Species number, species name, trophic level and sand tolerance level are given in that order. Rare species (R) and indicator species (I) are also shown (* - common indicator species). Species that were neither rare nor indicators were found on both substratum types.

Trophic levels: P - primary producer, H - herbivore, O - omnivore, C - carnivore, S - scavenger, D - deposit feeder, F - filter feeder.

Sand tolerance levels: Ps - psammophilic, Sd - sand-dependent,St - sand-tolerant, Si - sand-intolerant, Un - unknown.

Substratum type: d.r. - dune rock, s.s. - sandstone.

ALGAE - **Chlorophycophyta** -

280	CAULERPA FILIFORMIS	P	-	R, d.r.
281	CLADOPHORA RUGULOSA	P	-	R, s.s.
282	CLADOPHORA cf. VIRGATA	P	Un	
283	ENTEROMORPHA SP.	P	St	
284	ULVA RIGIDA	P	St	
- **Phaeophycophyta** -				
285	IYENGARIA STELLATA	P	St	
286	ZONARIA SUBARTICULATA	P	-	R, s.s.
- **Rhodophycophyta** -				
287	AMPHIROA ANCEPS	P	Un	I, s.s. *
288	AMPHIROA BEAUVOISII	P	Un	I, s.s.
289	AMPHIROA BOWERBANKI	P	Un	
290	ARTHROCARDIA CARINATA	P	Un	

291	ARTHROCARDIA DUTHIAE	P	-	R, d.r.
292	ARTHROCARDIA cf. FLABELLATA	P	Un	I, s.s.
293	ARTHROCARDIA SP.B.	P	Un	
294	CALLITHAMNION STUPOSUM	P	-	R, d.r.
295	CALLITHAMNION SP.1.	P	-	R, d.r.
296	CALLITHAMNION SP.2.	P	-	R, s.s.
297	CENTROCERAS CLAVULATUM	P	Sd	
298	CERAMIUM OBSOLETUM	P	-	R, d.r.
299	CHEILOSPORUM CULTRATUM	P	Un	
300	CHEILOSPORUM MULTIFIDUM	P	Un	
301	CHEILOSPORUM SAGITTATUM	P	Un	
302	CHEILOSPORUM SP.A	P	Un	
303	GELIDIUM AMANSII	P	Si	
304	GELIDIUM CAESPITOSUM	P	Un	
305	GELIDIUM PRISTOIDES	P	Si	
306	GIGARTINA PAXILLATA	P	Un	
307	HALIPTILON SUBULATA	P	-	R, s.s.
308	HYPNEA SPICIFERA	P	St	
309	JANIA CRASSA	P	St	
310	NOTHOGENIA ERINACEA	P	Un	I, s.s.
311	PLAEOPHORA BINDERI	P	-	R, s.s.
312	PLATYSIPHONIA MINIATA	P	-	R, d.r.
313	POLYSIPHONIA cf. SAVATIERI	P	Sd	
314	POLYZONIA ELEGANS	P	Un	I, s.s.
315	PTEROSIPHONIA CLOIOPHYLLA	P	-	R, d.r.
316	PTEROSIPHONIA cf. SPINIFERA	P	-	R, d.r.
317	PTEROSIPHONIA SP.A	P	-	R, d.r.

318	RHODYMENIA NATALENSIS	P	-	R, s.s.
319	STREBLOCLADIA SP.A	P	-	R, s.s.
CNIDARIA - Actinaria -				
1	ACTINIA EQUINA	C	Un	
42	BUNODOSOMA CAPENSIS	C	Si	
48	PSEUDACTINIA VARIA	C	St	
PLATYHELMINTHES -				
2	NOTOPLANA PATELLARUM	C	St	
3	PLANOCERA GILCHRISTI	C	St	
4	POLYCLAD SP.1	C	St	
5	POLYCLAD SP.2	C	-	R, s.s.
NEMERTEA -				
6	CEREBRATULUS SP.1	C	Ps	
7	LINEUS LACTICAPITATUS	C	Sd	
8	LINEUS OLIVACEUS	C	Sd	
9	LINEUS ORNATUS	C	St	
SIPUNCULIDA -				
10	GOLFINGIA CAPENSIS	D	-	R, s.s.
11	PHASCOLOSOMA SPP.	D	-	R, s.s.
12	THEMISTE MINOR	D	St	
13	THEMISTE STEPHENSONI	D	-	R, s.s.
ANNELIDA- Polychaeta - Errantia -				
14	APHRODITIDAE	C	-	R, s.s.
15	ARABELLA IRICOLOR CAERULEA	C	Sd	
16	AUTOLYTUS TUBERCULATUS	C	Un	
17	AUTOLYTUS cf. BONDEI	C	-	R, d.r.

APPENDIX B contd.:

18	BHAWANIA GOODEI	C	Si	
56	BRANIA FURCELLIGERA	C	Un	I, d.r.
19	ETEONE FOLIOSA	O	St	
61	ETEONE SIPHODONTA	O	-	R, s.s.
20	EULALIA CAPENSIS	O	St	
21	EULALIA SANGUINEA	O	St	
22	EULALIA TRILINEATA	O	St	
23	GONIADIOPSIS INCERTA	C	Ps	I, s.s.
24	POLYCHAETE NO.1	O	-	R, s.s.
57	HESIONIDAE SP.	C	Un	
25	LEOCRATES CLAPAREDII	C	-	R, s.s.
26	LEPIDONOTUS DURBANENSIS	C	St	
27	LEPIDONOTUS SEMITECTUS	C	Sd	
28	LUMBRINERIS cf. OCULATA	C	St	
29	LUMBRINERIS CAVIFRONS	C	-	R, s.s.
30	LUMBRINERIS COCCINEA	C	Si	
31	LUMBRINERIS TETRAURA	C	Ps	
32	LYSIDICE COLLARIS	D	Sd	
33	LYSIDICE NATALENSIS	D	St	
34	MARPHYSA CORALLINA	C	Ps	I, d.r.
35	MARPHYSA DEPRESSA	C	Ps	I, s.s. *
36	MARPHYSA POSTERIOBRANCHIA	C	Ps	I,s.s.
37	MARPHYSA SANGUINEA	D	Ps	I, s.s. *
38	NEPHTYS CAPENSIS	O	-	R, s.s.
39	NEREIS FALSA	O	-	R, d.r.
40	NEREIS OPERTA	O	Si	
41	NEREIS WILLEYI	O	Si	

43	ODONTOSYLLIS POLYCERA	C	Un	
62	OPISTHOSYLLIS BRUNNEA	C	Ps	
44	PARONUPHIS ANTARCTICA	C	St	
45	PERINEREIS FALSOVARIEGATA	O	Sd	
46	PHYLLODOCE CASTANEA	O	St	
47	PHYLLODOCIDAE SP.1	O	-	R, s.s.
49	PLATYNEREIS DUMERILII	H	St	
50	PSEUDONEREIS VARIEGATA	O	Sd	
51	STHENELAIS BOA	C	Sd	
52	SYLLIDIA ARMATA	C	Ps	I, s.s.
53	SYLLIS ARMILARIS	C	St	
54	SYLLIS PROLIFERA	C	Si	
59	SYLLIS cf. TAPROBANENSIS	C	Un	
55	SYLLIS VARIEGATA	C	St	
60	SYLLIS SP.1	C	St	
- **Sedentaria** -				
65	BOCCARDIA POLYBRANCHIA	D	Ps	
66	BRANCHIOMMA NIGROMACULATA	F	Un	I,s.s.
320	CAPITELLIDAE	D	-	R, s.s.
67	CAULERIELLA CAPENSIS	D	-	R, d.r.
68	CIRRIFORMIA cf. SAXATILIS	D	Sd	
69	CIRRIFORMIA TENTACULATA	D	Sd	
70	CIRRIFORMIA SP.A.	D	-	R, d.r.
71	CIRRATULUS FILIFORMIS	D	Sd	
72	DIPLOCIRRUS CAPENSIS	D	-	R, s.s.
277	DISPIO MAGNA	D	-	R, d.r.

APPENDIX B contd.:

64	DODECACERIA LADDI	D	-	R, s.s.
73	FLABELLIGERA AFFINIS	D	Sd	I, s.s.
74	GUNNAREA CAPENSIS	F	St	
75	HYBOSCOLEX LONGISETA	D	Sd	
76	JASMINIERA ELEGANS	F	Si	I, s.s.
77	MEGALOMMA QUADRIOCULATUM	F	Si	
78	NAINERIS LAEVIGATA	D	Sd	
79	NICOLEA VENUSTULA VENUSTULA	D	Un	
80	NOTOMASTUS ABERANS	D	-	R, s.s.
83	PHYLO CAPENSIS	D	-	R, s.s.
81	PIROMUS ARENOSUS	D	Sd	I, s.s. *
82	PISTA QUADRILOBATA	D	-	R, s.s.
84	POMATOLEIOS KRAUSSI	F	Si	
85	POTAMILLA TORELLI	F	St	
86	PROSCOLOPLOS CYGNOCHAETUS	D	Ps	
87	SABELLARIA SPINULOSA ALCOCKI	F	Sd	
63	SABELLARIDAE SP.	F	-	R, d.r.
88	SCOLOPLOS JOHNSTONEI	D	Ps	
89	SCOLOPLOS UNIRAMUS	D	Ps	I, s.s.
90	SERPULINAE SP.A.	F	-	R, d.r.
91	SERPULINAE SP.B.	F	-	R,d.r.
276	SPIO FILICORNIS	D	-	R, d.r.
92	STREBLOSOMA HESSLEI	D	-	R, s.s.
93	TEREBELLIDAE SP.	D	-	R, s.s.
94	TEREBELLA PTEROCHAETA	D	-	R, s.s.
95	THELEPUS PEQUENIANUS	D	St	I, s.s. *
96	THELEPUS PLAGIOSTOMA	D	St	I,s.s. *

97	THELEPINAE SP.1.	D	-	R, d.r.
58	THELEPINAE SP.2.	D	-	R, s.s.

ARTHROPODA- Crustacea - Cirripedia -

98	BALANUS AMPHITRITE	F	Si	
99	CHTHAMALUS DENTATUS	F	Si	
100	OCTOMERIS ANGULOSA	F	Si	
101	TETRACLITA SERRATA	F	Si	

- Ostracoda -

102	OSTRACODA SP.	F	Sd	I, s.s. *

- Isopoda -

104	CIROLANA BOVINA	C	Un	
105	CIROLANA CRANCHI	C	Si	I, s.s. *
106	CIROLANA IMPOSITA	C	-	R, s.s.
107	CIROLANA VENUSTICAUDA VENUSTICAUDA	C	St	
103	CYMODOCE NATALENSIS	S	Un	I, s.s.
110	CYMODOCE ZANZIBARENSIS	S	-	R, s.s.
111	CYMODOCELLA EUTYLOS	S	Un	
112	CYMODOCELLA MAGNA	S	Un	
113	CYMODOCELLA PUSTULATA	S	Si	
114	CYMODOCELLA SUBLEVIS	S	Si	
115	DYNAMENELLA AUSTRALIS	S	Un	
116	DYNAMENELLA AUSTRALOIDES	S	-	R, d.r.
117	DYNAMENELLA DIOXUS	S	Si	
118	DYNAMENELLA HUTTONI	S	Si	
119	DYNAMENELLA MACROCEPHALA	S	St	
122	DYNAMENELLA OVALIS	S	Un	
120	DYNAMENELLA SCABRICULA	S	-	R, s.s.

121	DYNAMENELLA TAURUS	S	Un	
125	EURYDICE LONGICORNIS	O	Ps	
126	EXOSPHAEROMA PALLIDUM	S	-	R, s.s.
127	EXOSPHAEROMA PORRECTUM	S	Si	I, s.s.
128	EXOSPHAEROMA TRUNCTATITELSON	S	Ps	
278	FLABELLIFERA SP.	S	Un	
129	HALIOPHASMA FOVEOLATA	C	Un	I, s.s.
130	JAEROPSIS STEBBINGI	S	-	R, s.s.
131	LEPTANTHURA AGULHAENSIS	C	Sd	I, s.s.
132	MESANTHURA CATENULA	C	Un	I, s.s.
133	PARANTHURA PUNCTATA	C	Un	I, s.s. *
134	PARISOCLADUS PERFORATUS	S	Un	
135	PARISOCLADUS STIMPSONI	S	Un	
136	PONTOGELOIDES LATIPES	S	Ps	
137	PSEUDOSPHAEROMA BARNARDI	S	Un	I, s.s. *
138	SPHAERAMENE MICROTYLOS	S	-	R, s.s.
123	SPHAEROMATIDAE (EUBRANCHIATE) NO.1	S	Un	I, s.s. *
124	SPHAEROMATIDAE (EUBRANCHIATE) NO.2	S	-	R, d.r.
108	SPHAEROMATIDAE (HEMIBRANCHIATE) NO.1	S	Un	I, s.s.
109	SPHAEROMATIDAE (HEMIBRANCHIATE) NO.2	S	-	R, s.s.
139	SYNIDOTEA VARIEGATA	S	-	R, s.s.
- **Amphipoda** -				
140	AMPELISCA SP. cf. SPINICAUDATA	D	Ps	I, s.s.
141	AMPITHOE AFRICANA	F	Un	
142	AMPITHOE RAMONDI	F	St	
143	AORA KERGUELENI	F	Un	I, s.s. *
144	ATYLUS GRANULOSA	S	-	R, s.s.

145	CYPROIDEA ORNATA	S	-	R, s.s.
146	ELASMOPUS PECTINICRUS	F	-	R, d.r.
275	ERIOPISA SP.	F	-	R, s.s.
147	EUPARIAMBUS FALLAX	S	-	R, s.s.
148	EUSIROIDES MONOCULOIDES	C	St	
149	GAMMAROPSIS SP.1	F	-	R, s.s.
150	GAMMARIDAE	F	-	R, s.s.
151	HIPPOMEDON NORMALIS	S	-	R, s.s.
152	HYALE GRANDICORNIS	H	St	
153	ISCHYROCERUS ANGUIPES	D	-	R, s.s.
154	JASSA FALCATA	D	Un	
155	LYSIANASSA CERATINA	S	St	
156	MEGALUROPUS SP.	F	Un	I, s.s. *
157	PARAMOERA CAPENSIS	S	St	
158	PODOCERUS AFRICANA	C	Si	I, s.s.
159	UROTHOE ELEGANS	D	Ps	I, d.r.
160	UROTHOE TUMOROSA	D	Ps	
161	UNKNOWN AMPHIPOD NO.1	S	-	R, s.s.
279	UNKNOWN AMPHIPOD NO.2	S	-	R, d.r.
- **Tanaidacea** -				
162	APSEUDOMORPHA AVICULARIA	C	-	R, s.s.
163	TANAIS PHILETAERUS	C	-	R, s.s.
- **Mysidacea** -				
164	GASTROSACCUS PSAMMODYTES	D	Ps	I, s.s.
- **Decapoda** - **Macrura** -				
174	UNKNOWN MACRURA	S	-	R, s.s.

- Anomura -				
165	EMERITA AUSTROAFRICANA	D	-	R, d.r.
166	PAGURIDAE	S	-	R, s.s.
167	PAGURISTES BARNARDI	S	Un	I, s.s.
168	UPOGEBIA CAPENSIS	D	-	R, s.s.
- Brachyura -				
169	ANTILIBINIA SMITHI	S	Un	
170	CLEISTOSOMA EDWARDSII	S	-	R, s.s.
171	CYCLOGRAPSUS PUNCTATUS	S	-	R, d.r.
172	DEHAANIUS DENTATUS	S	St	
173	LEUCISCA SQUALINA	S	Sd	
175	METOPOGRAPSUS MESSOR	S	St	
321	OVALIPES PUNCTATUS	S	Ps	I, s.s.
177	PLAGUSIA CHABRUS	S	Si	
178	PORTUMNUS BIGUTTATUS	S	Sd	
176	XANTHIDAE	S	Si	
- Insecta -				
179	TELMATOGETON MINOR	H	St	
- Arachnida - Pycnigonida -				
180	ENDEIS CLIPEATUS	C	Si	
181	QUEUBUS JAMESIANUS	C	Si	I, s.s.
182	TANYSTYLUM BREVIPES	C	Si	
MOLLUSCA - Amphineura -				
183	ACANTHOCHITONA GARNOTI	H	St	
184	CALLOCHITON CASTANEA	H	Un	I, d.r.
185	CHAETOPLEURA PAPILIO	H	Si	I, s.s.
186	CHAETOPLEURA PERTUSA	H	Si	I, s.s. *

187	CHITON TULIPA	H	Si	
189	DINOPLAX FOSSUS	H	Sd	I, s.s. *
190	ISCHNOCHITON ONISCUS	H	Sd	
191	NOTOPLAX PRODUCTUS	H	-	R, d.r.
- Pelecypoda -				
205	AFROCARDIUM SHEPSTONENS	F	Sd	I, s.s. *
322	BARBATIA OBLIQUATA	F	-	R, s.s.
192	BRACHIDONTES SEMISTRIATUS	F	Un	
193	CARDITA VARIEGATA	F	Sd	I, s.s.
194	CHOROMYTILUS MERIDIONALIS	F	Sd	I, s.s.
195	CRASSOSTREA MARGARITACAE	F	Sd	I, d.r.
196	GREGARIELLA SIMPLICIFILIS	F	Sd	
197	HIATELLA ARCTICA	F	Si	
198	KELLIA ROTUNDA	F	St	
199	LASAEA ADANSONI TURTONI	F	St	
200	MUSCULUS CUNEATUS	F	-	R, s.s.
201	NEOCARDIA AFRICANA	F	Un	
202	PERNA PERNA	F	Si	
203	PETRICOLA BICOLOR	F	Sd	I, s.s.
204	VENERUPIS CORRUGATA	F	-	R, s.s.
- Gastropoda -				
206	AFROCOMINELLA ELONGATA	C	Sd	I, s.s.
207	ALCIRA ELEGANS	O	Un	I, s.s. *
208	AMBLYCHILEPAS SCUTELLA	H	St	
209	ANACHIS KRAUSSI	O	Un	
210	ANACHIS KRAUSSI `KITCHINGI`	O	-	R, s.s.
211	APLYSIA SPURIA	H	Si	

APPENDIX B contd.:

212	AUSTROMITRA RHODARION	C	-	R, s.s.
213	BURNUPENA CINCTA	S	Si	
214	BURNUPENA LAGENARIA	S	Si	
215	BURNUPENA PUBESCENS	S	-	R, s.s.
216	CERITHIOPSIS FOVEOLATA	F	-	R, d.r.
217	CINGULINA TRACHEALIS	C	-	R, s.s.
218	CLIONELLA ROSARIA	C	St	I, s.s.
219	CLIONELLA SEMICOSTATA	C	St	I, s.s. *
220	CREPIDULA ACULEATA	H	Un	I, s.s.
221	CREPIDULA PORCELLANA	H	Si	I, s.s.
222	CYNISCA GRANULOSA	H	Un	
223	EATONIELLA NIGRA	H	St	
224	FISURELLA MUTABILIS	H	Si	
225	FISURELLA NATALENSIS	H	Si	
226	GIBBULA CICER	H	-	R, s.s.
227	HALIOTUS SPADICEA	H	-	R, d.r.
228	HAMINOEA ALFREDENSIS	D	Ps	
229	HELCION DUNKERI	H	Si	
230	HELCION PECTUNCULUS	H	Si	
231	HELCION PRUINOSUS	H	Si	
232	HELIACUS DORSUOSUS ALFREDENSIS	C	Un	
233	LATIRUS ROUSI	C	-	R, s.s.
234	LIENARDI GRAYI	C	-	R, s.s.
235	LITTORINA AFRICANA AFRICANA	H	Si	
236	LITTORINA AFRICANA KNYSNAENSIS	H	Si	
237	MITRELLA FLOCATA	O	-	R, s.s.
238	NASSARIUS CAPENSIS	S	Ps	

APPENDIX B contd.:

239	NATICA FORATA	C	Ps	I, s.s. *
240	NATICA TECTA	C	Ps	
241	NUCELLA DUBIA	C	Un	
242	NUCELLA SQUAMOSA	C	Si	
243	OCENEBRA FENESTRATA	H	-	R, d.r.
244	ONCHIDELLA CAPENSIS	H	St	I, s.s.
245	OXYSTELE SINENSIS	H	Si	I, s.s.
246	OXYSTELE TABULARIS	H	Si	
247	OXYSTELE VARIEGATA	H	Si	
248	PATELLA ARGENVILLEI	H	Si	
249	PATELLA BARBARA	H	Si	
250	PATELLA COCHLEAR	H	Si	
251	PATELLA GRANULARIS	H	Si	
252	PATELLA LONGICOSTA	H	Si	
253	PATELLA MINIATA MINIATA	H	Si	I, d.r.
254	PATELLA MINIATA SANGUINANS	H	-	R, d.r.
255	PATELLA OCULUS	H	Si	
256	PATELLA TABULARIS	H	-	R, s.s.
257	PERISTERNIA FUSCOTINCTA	C	Si	I, s.s.
258	SIPHONARIA ASPERA	H	Si	
259	SIPHONARIA CAPENSIS	H	St	
260	SIPHONARIA CONCINNA	H	St	
261	SIPHONARIA OCULUS	H	St	
262	TRICOLIA CAPENSIS	H	St	
263	TURBO CIDARIS CIDARIS	H	St	I, s.s. *
264	TURBO CIDARIS NATALENSIS	H	-	R, s.s.

ECHINODERMATA - **Asteroidea** -				
265	PATIRIELLA BURTONI	H	-	R, s.s.
266	PATIRIELLA EXIGUA	H	St	
- **Ophiuroidea** -				
267	AMPHIOPLUS INTEGER	D	St	
- **Echinoidea** -				
268	PARECHINUS ANGULOSUS	D	St	
- **Holothuroidea** -				
269	`ASLIA` SPYRIDOPHORA	O	Un	
270	`ASLIA` TETRACENTRIOPHORA	O	Un	I, s.s.
271	PSEUDOCNELLA SINORBIS	O	Un	
272	PSEUDOCNELLA SYKION	O	Un	
273	ROWEIA FRAUENFELDI FRAUENFELDI	O	Sd	I, s.s. *
274	ROWEIA STEPHENSONI	O	-	R, s.s.