

**The Biogeography and Biodiversity
of the Namibian Intertidal
Seaweed Flora**

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Abstract

There have been very few intertidal studies carried out on the Namibian coast. With respect to seaweeds in particular there have been a number of species lists and shore descriptions, but very little research into the biogeography, diversity or ecology. One of the reasons for the lack of research is probably that much of the 1500 km coast is inaccessible. The coastline is relatively straight with few inlets or bays and comprises mostly sandy beaches, with few rocky shores. Estimates range from 5-16% of rocky shores for the total coast length, and as a result there is relatively little substrate on which seaweed can attach. The dominant current is the northward, slow-flowing Benguela current. Upwelling also occurs here due to long shore winds, which bring cool, nutrient-rich water to the surface.

In this study the Namibian coast was divided into three regions, largely governed by accessibility to the coast, viz. southern, central and northern Namibian. Most of the Namibian coast is subject to severe wave action, as a result wave-exposed shores were predominantly chosen. The degree of wave exposure was determined by the degree to which the site was open to the ocean. Sites that were completely or largely protected from incoming swells were not included. Three sites in the southern region were semi-exposed, in that they occurred within relatively large bays and were partially protected from dominant winds, they were however relatively exposed to the open ocean. Two to three transect lines were taken on each shore, along which quadrats were sampled at regular intervals. The material was taken back to the laboratory, sorted and analysed. Multivariate techniques were used as diagnostic tools in the interpretation of the data. Detailed seaweed species data were collected from all samples (biomass of individual species as well as general species collections), while data on major sessile invertebrate groups and amount of sand were also collated.

The biogeographical affinity of the Namibian flora was analysed with respect to the entire flora of southwestern Africa (from southern Angola to Cape Agulhas, South Africa, the southern-most point of Africa). Angola was found to be very distinct from the Namibian flora, whereas Namibia showed marked similarities to the southwestern coast of the South Africa flora, as part of the Benguela marine province. A general decrease in species richness was noted in a south-north direction. This was suggested to be due to a number of factors including: a decrease in habitat availability and heterogeneity, increase in average sea surface temperature, and a number of

stochastic events that occur in the central and northern regions of Namibia, viz. El Niño water events, southwesterly-bound counter-currents of the Angolan current and hot, desiccating east wind conditions. Multivariate techniques indicated the dividing of the Benguela marine province into two sub-provinces, this division being primarily due to the decrease in species numbers in the northern reaches of the province and secondarily to the presence of different species.

The composition of the three main seaweed divisions, namely Chlorophyta, Phaeophyta and Rhodophyta, was examined with respect to family and genus richness in eight defined regions within the Benguela marine province and southern Angola, as well as numbers of species. The general pattern of attenuation in species richness as one moves north was seen in all three divisions, although less clearly with the Chlorophyta. The ratio among the three seaweed divisions showed a relative decrease in the proportion of Phaeophyta, in a northerly direction. A relationship was observed between species richness and both family and genus richness, and as a result the use of these higher taxa as a surrogate for species richness was investigated. Each division's predictiveness in determining its species richness from the genus and family richness, as well as predicting the total seaweed species richness was examined. The use of family richness as surrogates for species richness had relative low r^2 values (0.5 - 0.87), whereas genus richness mostly had r^2 values greater than 0.8. The best correlate with total species richness was a correlation of the combined genera of the three divisions with species richness (r^2 - 0.96). The accuracy of the various surrogates was tested. It was found that as the number of species to genera ratio increased the accuracy decreased. Despite many of these correlations having high correlation coefficients of determination, the accuracy of these surrogates was found to be relatively low with a 10% degree of error at best.

The α -diversity of seaweeds within the lower eulittoral zone was examined in relation to two physical factors (wave exposure and degree of sand inundation), and three biological factors (the abundance of mussels, limpet and whelks). Seaweed diversity was found to be controlled by a number of interacting factors. Sand inundation was found to be a dominant factor determining species diversity within the lower eulittoral, but only at quantities over 5.6 kg.m^{-2} . Sand inundation seemed to lower equitability by increasing the dominance of certain species. In areas where sand inundation was less than 5.6 kg.m^{-2} , mussel biomass was the most important determinant of seaweed diversity. Wave exposure was found to have a negative influence on seaweed species diversity largely because of its positive effect on mussel biomass. Thus, the degree of wave

exposure is indirectly related to seaweed species richness. In areas where mussels were absent, however, wave action had a positive effect on seaweed diversity. The effect of limpets and whelks in the lower eulittoral zone was found to be non-significant in determining seaweed diversity, owing to relatively low abundances of these animals.

The vertical zonation patterns in the three Namibian regions were objectively examined. The presence of each species as a percentage of total biomass in each quadrat was calculated. Species that represented 10% or more of the quadrat biomass were considered dominant / abundant. The average percentage abundances for each species were then mapped according to their height above the spring low water mark. Southern Namibia had a similar zonation pattern for exposed shores as is found on the South African west coast. The central and northern regions, however, had a different composition of dominant species. These species largely comprised turf-forming, opportunistic algae or those with persistent basal portions. This was attributed to the moderate to high sand inundation levels in these regions. This change in dominant seaweed species between southern and central Namibia reinforced the biogeographic decision to divide the Benguela marine province into two sub-provinces at this point. There appeared to be a break down in clearly defined zonation patterns in central Namibia. This was considered indicative of a disturbance factor, namely sand inundation. The northern region sites were also found to be more varied than the central Namibian regions; this was attributed to the increase in habitat heterogeneity in the north.

The final chapter deals with β -diversity on various scales: transects, sites and regions. β -diversity is a measure of species turn-over and therefore is indirectly a measure of similarity. β -diversity was calculated at the various scales indicated above. To test if the difference between species composition of sites was due to random assortment, a number of hypothetical shores were generated and the results compared with the observed data. Southern and central Namibia had less variation in species composition than would be expected by random assortment, this means that there are more species in common between these shores than expected. A number of non-abundant species therefore have a wider distribution even though they constitute a small percentage of the biomass. The data from northern Namibia, however, could be explained by random assortment of species. This region covers a wide variety of habitats, as well as experiencing environmental perturbation. These two factors would probably result in the more even distribution of propagules, hence giving rise to the random assortment pattern. To see how close the observed regional richness approached

its upper limit, regional species richness was estimated using three non-parametric methods, viz. the Chao 2, 1st Order Jackknife, and 2nd Order Jackknife Estimators. Analysis of the three Namibian regions indicated that only 70-80% of the intertidal flora had been sampled within each area. It is believed that southern Namibia has had the least number of habitats sampled, out of the three regions, and is therefore likely to yield a greater regional species richness with further research.

Five appendices, dealing with additional site and species (animal and plant) information, have been included. Appendix A maps a vertical cross-section of the shores sampled, as well as a table containing the angle of wave-exposure and dominant onshore winds. Appendix B lists the seaweed species (with authorities) found within the Benguela marine province and their distribution within the eight defined regions of the province. Appendix C is a species list with authorities of the sessile invertebrates that occurred within the biomass samples. Appendix D is a break down of the three main seaweed divisions into their component families. These families have been further subdivided into families that appear to have cosmopolitan, cool temperate or warmer water affinities. Appendix E contains a list of 58 species which are additions to the Namibian flora. This list includes the reference numbers of the specimens collected, position on shore and location, occasional taxonomic notes have been made on selected species.

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Chapter 1

Introduction

Namibia is situated north of South Africa on the southwestern side of Africa. It has a coastline that is approximately 1500 km long, which stretches from the Orange River, on its southern South African border, to the Cunene river, on its Angolan northern border. Much of the coast is inaccessible as it is bordered by the Namib desert on one side and treacherous seas with few natural harbours on the other. Also, almost 50% of the coast falls under diamond mine control (in particular the regions either side of Lüderitz) and as a result has restricted entry. There are also few roads leading to or travelling along the coast. The areas sampled are around Lüderitz, in the south, Swakopmund, in central Namibia, and within the Skeleton Coast National Park which includes most of the northern coastline. The northern reaches of the latter is also a restricted area, where a permit is required and an accompanying Nature Conservation officer / Sea Fisheries official. As a result, a substantial proportion of the Namibian coast is conserved environmentally, either directly or indirectly.

The shores of Namibia are home to a number of marine and coastal vertebrates. A number of relatively large Cape Fur seal and sea bird colonies may be found here. Hyaenas (strandwolf) and jackals are the dominant predators and are often associated with these colonies. Many of the seabirds as a result have settled on the near offshore islands. These islands had accumulated extensive amounts of guano over hundreds of years, but much of the material has already been removed for commercial purposes. Guano platforms were built in the Walvis Bay - Swakopmund area as a commercial venture, where they provide a home for thousands of cormorants and gannets. The Benguela current, with its upwelling phenomenon, is nutrient-rich and as a result supports a highly productive system (Field & Griffiths, 1991). As a result fishing contributes a major part to the gross domestic product in this country, as well as providing recreation and tourism in the form of angling (mostly between Swakopmund - Terrace Bay). Excessive commercial fishing of pilchards in the 1950's-1970's led to a drastic drop in African penguins and Cape gannets, which depend on this food source. There are also three relatively large sheltered areas on the Namibian coast - Lüderitz lagoon, Sandwich Harbour, and Walvis Bay - that provide a haven for wading

birds. These areas cover a mere 30km² but support thousands of migrating birds, including 75 % of southern Africa's population of flamingoes. Most of the Namibian coast is however sandy beaches with only a small percentage being rocky shores. There is thus relatively little substrate for the attachment of seaweed or sessile invertebrates on this coast.

Namibian seaweeds have received little attention by phycologists. This is largely due to the inaccessibility of the coast. The only accounts published on the Namibian seaweeds are those of Foslie (1893), Pilger (1908), Wynne (1986) and Lawson et al. (1990). Foslie (1893) described the new species *Laminaria schinzii*. Wynne (1986) provides an annotated species list of the seaweeds collected over a three day period in April 1983 whilst in the Swakopmund area. This study added a significant number of previously unrecorded species to the Namibian flora. Lawson et al. (1990) described the littoral zonation patterns in Lüderitz and Swakopmund areas, as well as giving a description of the phytogeography of the Namibian coast. They recorded a total of 136 species for the Namibian coast; this list comprised all previous records including the species listed in Wynne (1986). Lawson et al. (1990) is largely a descriptive study, but it includes a detailed account of the phytogeographical positioning of Namibian seaweed flora. Some reference is made to seaweeds in the papers of Kensley & Penrith (1980) and Penrith & Kensley (1970 a,b), but these are largely zoological works. There is no quantitative account of seaweed communities in any of these studies. Other than these very little is known about this coast. A number of other references cite algal species which occur in Namibia e.g. Stephenson (1948), Simons (1970). This information is largely descriptive or taxonomic and includes information on the composition, biogeography and diversity of the Namibian marine flora.

“When we observe the environment, we necessarily do so on only a limited range of scales; therefore, our perception of events provides us with only a low-dimensional slice through a high-dimensional cake” (Levin, 1992). This thesis examines the biogeographical and biodiversity trends and patterns that occur on the Namibian coast at various scales, from a flora level to a local site level. Local sites are subsets of the regional species pools, but the factors that are responsible for their composition and community structure are not usually the same ones responsible for the regional patterns. The major factors having impact at these different scales will be examined.

In Chapter 2 the sampling methods, data collection, basic analysis, general statistics and a brief description of the regions and sites sampled are outlined. More specific methods are given in the relevant chapters.

Chapter 3 deals with the biogeography of the Namibian seaweed flora, which was examined with respect to gradients of changes in species composition along the coast of south-western Africa and also proposing affinities to other adjacent southern African regions. The broad scale patterns within this phytogeographic range and the possible factors responsible for them will be examined. The concept of species richness is introduced in this chapter and will be developed in the following chapter.

Chapter 4 looks at the broad scale of species, genus and family richness within the three main seaweed divisions. It also examines the possibility of using higher taxa as a means of estimating species richness, as well as looking at the efficacy of such a measure. The reason for the relationship between species richness and higher taxa in seaweed floras in other parts of the world is also examined.

Chapter 5 focuses on a smaller scale, looking at factors that may be responsible for generating α -diversity at a local level. A basic ecological model has been derived to explain the patterns in the number of species that are found in a local area along this coast.

Whereas Chapter 5 is primarily concerned with factors responsible for 'patterns in numbers', Chapter 6 looks at the actual community structure. The latter examines the zonation patterns along the Namibian coast. These are discussed in the light of zonation patterns on the South African west coast and the biotic controlling factors outlined in the preceding chapters.

Chapter 7 examines the rate of species turnover (β -diversity), at various scales, on the Namibian coast. It also looks at the possibility of using β -diversity as a tool for evaluating sampling methods. This chapter will be followed by a concluding chapter (Chapter 8) which summarises the findings of the thesis and suggests possible directions for future work.

Chapter 2

General Methods

The Namibia coast was divided into three equal areas based on practical accessibility to the coast, viz. Southern (SNAM), Central (CNAM) and Northern (NNAM) Namibia. Southern Namibia comprises the area around Lüderitz, which stretches from Elizabeth Bay in the south to Agate Beach in the north (also included in the general collection data is material obtained on a trip into Sperrgebiet¹ 2, which went as far north as Spencer Bay (Fig.2.1)). Central Namibia included sites from Langstrand to Myl 8; while northern Namibia included the Skeleton Coast from Toscanini to False Cape Fria. Several sites were sampled from these three regions, seven from Lüderitz, five from Swakopmund and six from the Skeleton Coast (Fig.2.1, 2.8; Table 2.1.). Samples were collected during two seasons, viz. spring (18 September to 3 December 1990) and autumn (15 March to 18 April 1992). Descriptions of the sampling methods and the three regions sampled are given below, for additional information refer to: Penrith & Kensley, 1970a, b; Kensley & Penrith 1980; Lawson *et al.*, 1990.

Table 2.1: Legend for the coding of the various sites sampled along the Namibian coast. (Sites in **bold** were sampled in both 1990 (Spring) & 1992 (Autumn))

Code	Site No.		Site	Code	Site No.		Site
	1990	1992			1990	1992	
ESB	1		Elizabeth Bay	CNAM	MY4	10	Myl 4
GSB	2	16	Grossebucht		MY8	11	21 Myl 8
KBF	3		Kleinbogenfels		TOS	12	Toscanini
SNAM ESB	4		Essy Bay		TOR	13	22 Torra Bay
DZP	5	17	Diaz Point	NNAM	TER	14	23 Terrace Bay
SKI	6		Shark Island		MOW	15	24 Möwe Bay
L&A	7	18	Agate Beach		RPR		25 Rocky Point
CNAM LGS	8	19	Langstrand		FCF		26 False Cape Fria
VIN	9	20	Vineta Beach				

¹ Sperrgebiet - German word for "restricted area". There are two main such areas in the Lüderitz area, viz. Sperrgebiet 1 (south of Lüderitz) and Sperrgebiet 2 (north of Lüderitz). Permission from the mining authorities and police clearance are required to enter these areas.

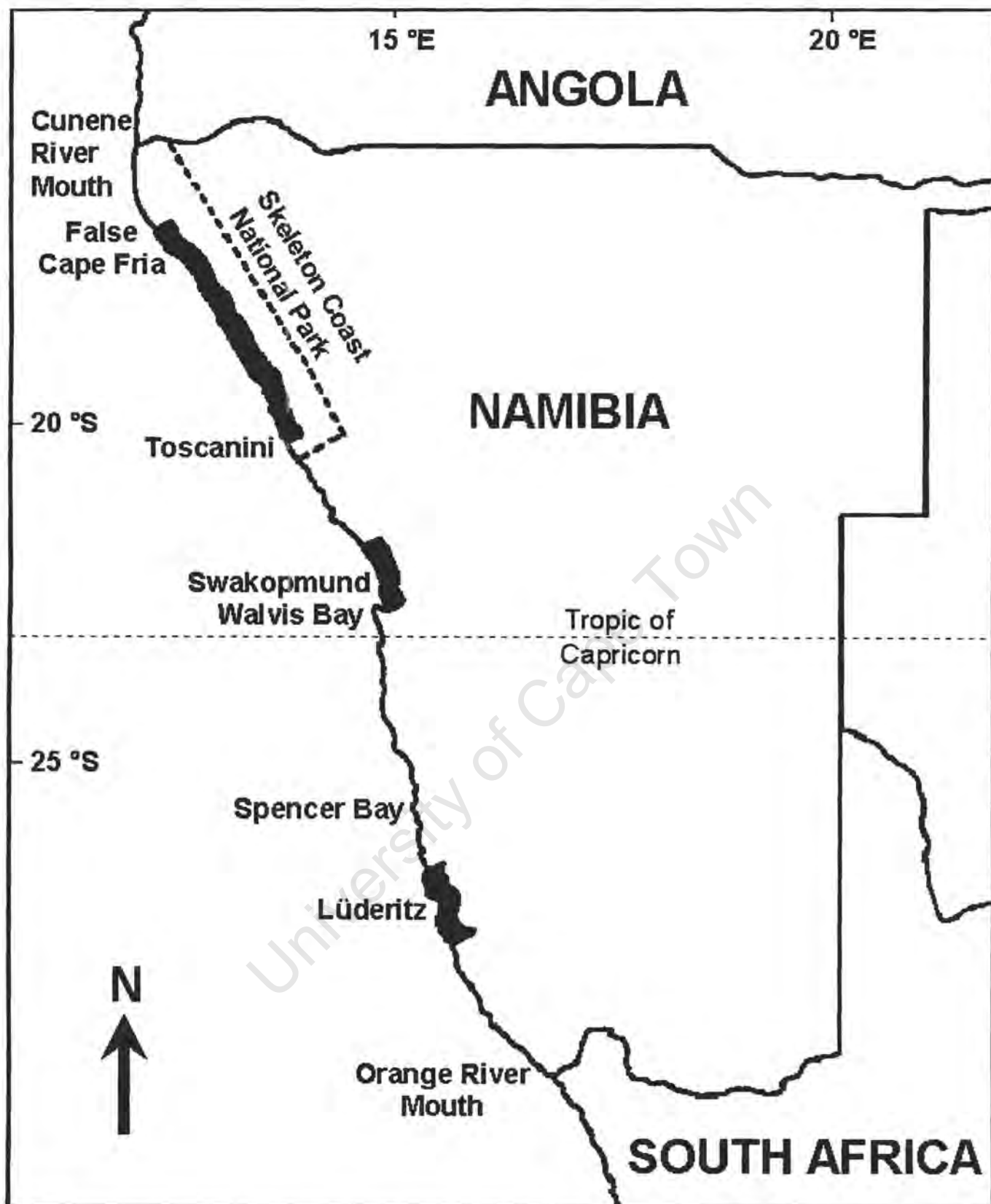
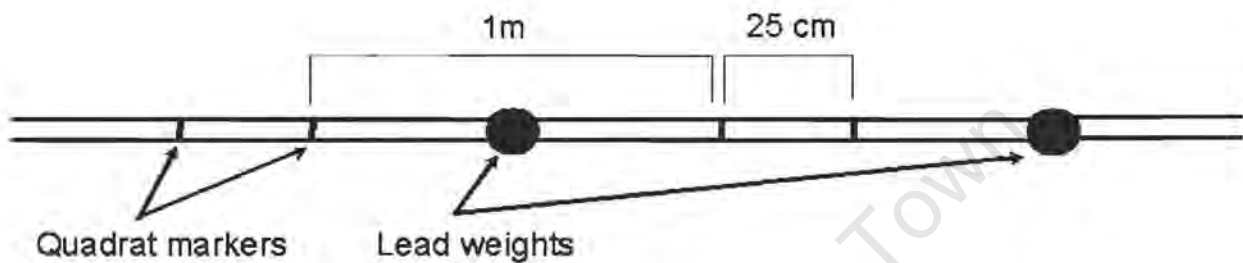


Fig. 2.1: Map of Namibia showing the areas sampled (thickened lines).

Sampling

Sampling comprised two parts, namely a general collection of seaweed species and biomass component. The former included not only intertidal material, but samples collected from intertidal rock-pools and beach cast material. These were preserved in 5% formaldehyde in seawater, identified and made into herbarium specimens. The biomass sampling is outlined below.

A 30 m transect line consisting of a weighted polypropylene rope (lead weights every 1.25 m), with quadrat markers between the weights as in the diagram below, was used to sample the shore. The transect rope also had a weight anchor at either end to keep the rope straight.



Two transect lines were taken at each site, running perpendicular to the incoming waves. The only exceptions were Essy Bay (1 transect - due to bad weather) and Agate Beach (3 transects - a relatively short shore). The transect line was placed at the bottom of the eulittoral zone and placed in a straight line up the shore to the upper limit of the eulittoral zone. The lower and upper eulittoral boundaries are referred to as the spring low water mark (SLWM) and spring high water mark (SHWM) respectively. Biological indicators were used for establishing SLWM, and this point coincided mostly with the appearance / beginning of the kelp beds. If kelp was not present at the site, then the first quadrat would fall at the start of the zone containing the limpet, *Patella argenvillei*, or the red seaweed, *Chondria capensis*, two characteristic organisms of the lower eulittoral zone in Namibia. The latter species, in particular, is abundant in areas with high sand inundation. Non-sessile invertebrates (mostly amphipods and isopods) and crustose coralline red algae were not sampled owing to practical constraints. All material (i.e. animals, plants and sand) was removed from 25cm X 25cm quadrats at regular intervals (1 m between successive quadrats) along each transect.

The reason for using a 25cm X 25 cm quadrat is that this is a standard quadrat size used on southern African shores for biomass sampling as the tidal range is relatively small and as a result the intertidal zones compressed. This size reduces the likelihood of zone overlap. An increase in quadrat area would have to be in a rectangular shape in order to reduce this problem of overlapping

zones. A species area curve was looked at in a pilot study in 1990 demonstrated that due to the relatively high turnover in the lower reaches of the shore the quadrat size would have to be too large for a biomass survey. The 25cm X 25 cm quadrats incorporated on average 80% of the species in the respective zone. As numerous samples were taken in each zone, most of the species, found in a particular site were included.

The removed material was labelled, preserved in 5 % formaldehyde in seawater, and transported to the laboratory in Cape Town, South Africa, for sorting and identification. Both seaweeds and sessile invertebrates were identified to species level, with the exception of actinarians (sea anemones) and holothuroideans (sea cucumbers), which were classified as such. The authorities for all the species are given in Appendix B and C. The wet and dry mass was ascertained for each species (animals and plants). The latter was obtained by drying each species in an oven at 60°C for 24 hours.

The sand found in each quadrat was oven dried at 60°C for 24 hours and weighed, as an indication of the relative degree of sand inundation. The sand was then sifted through a 250µm diameter mesh sieve to ascertain the relative ratio of coarse sand to silt ratio (coarse sand $\geq 250\mu\text{m}$ diameter particles; silt $< 250\mu\text{m}$). Other environmental data collected included distance from SLWM, angle of exposure (compass measurement), gradient of shore (clinometer) at each quadrat point and rock type. The height above the SLWM was calculated using the formula below (Fig. 2.2):

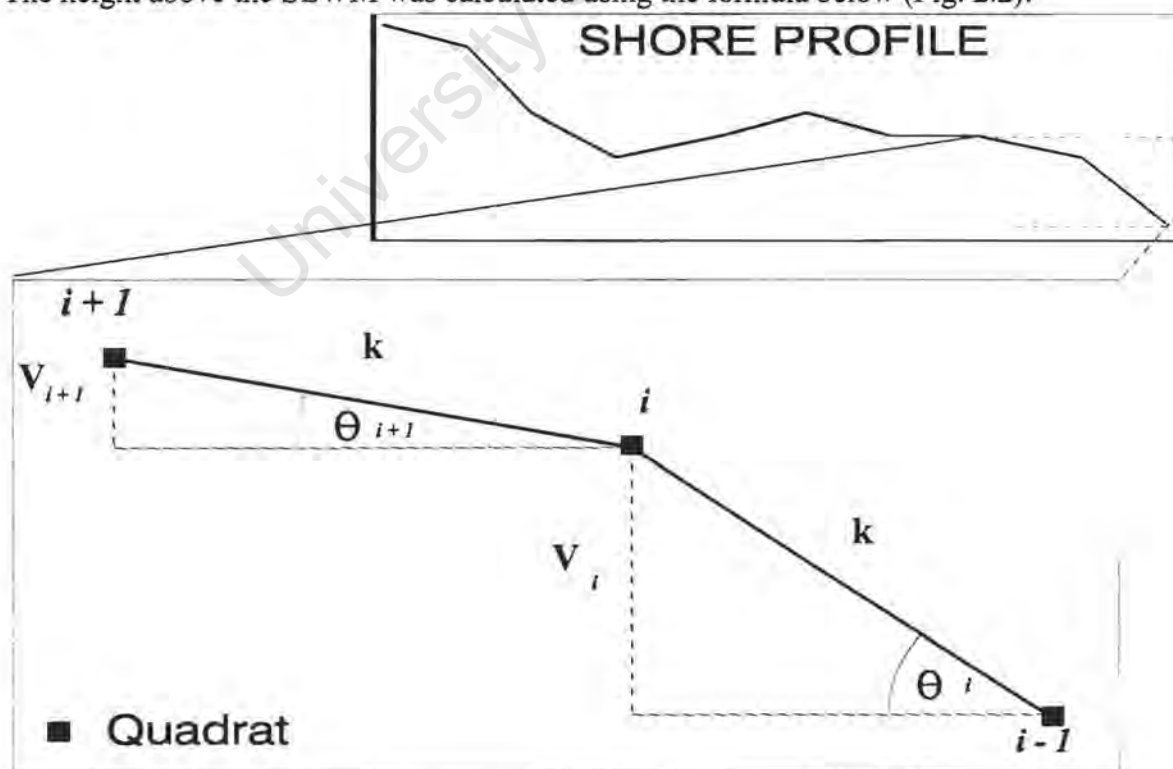


Fig. 2.2: Diagram illustrating method used to calculate height above SLWM.

$$V_q = \sum_{i=2}^q k \sin \theta_i$$

V_q - Vertical height of quadrat q

q - Quadrat number in question (quadrat number starts at 1 at SLWM and has an increment every 1.25 m until the top of the shore)

k - Length of quadrat + distance between two successive quadrats

(Constant - 1 m + 0.25 m = 1.25 m) ($k = 0$ when $q = 1$)

θ - Gradient of shore between two successive quadrats (radians)

i - Quadrat number (quadrat nearest SLWM = 1)

Quadrat number one is given a slope of 0 and as a result has a vertical height of 0 mm. The angle θ for quadrat i is determined as the angle of slope between quadrat i and $i - 1$ (Hence $i = 2$ in formula, since quadrat 1 has no slope by definition). (For detailed profiles of each shore see **Appendix A.**)

Wind speed and sea surface temperature were obtained from the South African Centre for Oceanography (Council for Scientific and Industrial Research), Stellenbosch - Cape Town. Data comprising mean monthly averages for the period 1985 - 1992, in degree blocks along the Namibian coast, were acquired and averaged for each month. Degree of wave exposure was ascertained by means of the following formula:

$$W = G \times A \times M$$

W - Wave exposure co-efficient

G - Slope of shore (i.e. $\frac{\text{Height above SLWM}}{\text{Distance from SLWM}}$)

A - Angle of exposure to open ocean (radians)

M - Maximum mean monthly wind speed for the preceding three months (windiest month)

This wave exposure index was based on the factors outlined in Lobban & Harrison (1994) as being important in determining wave size. A factor not taken into account was the slope of the immediate subtidal as this information was not available. The latter would enable one to estimate wave size more accurately. A long, gently sloping subtidal would cause a wave to break earlier and lose much of its force, as opposed to a steeply sloping subtidal.

Multivariate Methods

The purpose of using multivariate techniques is set out in Randerson (1993) as being threefold:

- to search for pattern or structure within a data set;
- to reduce the data matrix into a more manageable form; and
- to search for possible relationships between organisms and their environment.

Multivariate methods are inductive and there are two approaches used to detect pattern in data, viz. classification or ordination. Classification assigns an individual, species, or site to a group on the basis of its similarity to the other members in that group. Hence, the results of such an analysis are hierarchical and form discrete groups, or basically a classification (Bridge, 1993). Ordination, on the other hand, displays data as a point in low dimensional space. As a result, the points which are closest together show greatest similarity. This method therefore displays the data in a continuous manner.

This study has made use of two commonly used multivariate packages to analyse the data, **Two-Way INDicator SPecies ANalysis (TWINSpan)**(Hill, 1979), and **Detrended Correspondence Analysis (DCA)**(Ter Braak, 1991). TWINSpan is a classification method programme which results in a final dendrogram for species and sites. This form of analysis is particularly useful for dividing data into related groups. This method is complemented by the DCA analysis, and may act as a confirmation of the results obtained (Randerson, 1993). For more information on classification techniques and methods see Bridge (1993).

The DCA is an eigen vector ordination method (James & McCulloch, 1990), which works best with counts data (which includes presence / absence data), although it is used extensively in phytosociological studies (Randerson, 1993). The results are given as values of four axes. These axes represent hypothetical factors that may be responsible for the pattern of separation. Axis 1 represents the primary factor, Axis 2 the secondary factor, etc. The relative importance of the different axes are indicated by eigen values. These values range from 0 - 1, with 1 representing maximum agreement between the axis in question and the data. These axes may then be plotted in two or three dimensional space. Axes 1 and 2 are usually used, as these explain the greatest amount of variance within the data. Where abundance data were used with this method, the results obtained were checked against another multivariate technique for congruency, viz. Principal Components Analysis (PCA). For further information on these methods and techniques see: Hill (1979); Ter Braak (1991); James & McCulloch (1990); Randerson (1993).

Diversity Indices

These indices will be discussed in more detail in the relevant chapters.

α -Diversity Measures

α -Diversity is species richness or diversity at a local level. Species richness is the number of species in a defined area, whereas diversity is a more complex measure which may include a measure of relative abundance (Ludwig & Reynolds, 1988; Magurran, 1988) or relatedness of the species (Vane-Wright *et al.* 1991; Colwell & Coddington, 1995; Warwick & Clark, 1995). The latter concept will not be examined in this thesis.

(i) Species Richness

S = Number of species per defined area (quadrat)

(ii) Shannon-Wiener Index (Shannon & Wiener, 1963):

$$H' = - \sum_{i=1}^S p_i \log_2 p_i$$

H' - Shannon-Wiener Index

S - Species Richness (i.e. number of species)

i - The i -th species

p_i - The proportional abundance of the i -th species (In this study p_i represented the proportion of the i -th species of seaweed with respect to the total seaweed biomass in the quadrat (wet weight))

The Shannon-Wiener index is a composite measure of diversity that incorporates species richness and equitability (degree of evenness of occurrence). It is one of the most widely used indices in the field of community ecology (Ludwig & Reynolds, 1988). The index starts at zero but does not have an upper limit, although the values rarely exceed 4.5 (Margalef, 1972). When only one species is present H' is equal to zero, while it increases with increasing species richness and evenness.

(iii) Simpson's Dominance Index (Simpson, 1949):

$$\lambda = \frac{S}{\sum_{i=1}^S p_i^2}$$

λ - Simpson's Dominance Index

Simpson's Dominance Index ranges from 0 - 1, where 0 represents a state of maximum evenness (i.e. all the species are found in equal quantities/proportions) and 1 represents dominance by a single species. The inverse of this index is a measure of the number of 'very abundant' species (Ludwig & Reynolds, 1988). As the name suggests this index is a measure of dominance and is therefore heavily weighted towards the most abundant species and less sensitive to species richness (Magurran, 1988).

(iv) Modified Hill's Ratio (Alatalo, 1981):

$$E = \frac{\lambda^{-1} - 1}{2H - 1}$$

The Modified Hill's Ratio is an equitability ratio. It also ranges from 0 - 1, however the reverse explanation applies. As the community approaches a state of dominance by a single individual the ratio approaches 0, while a value of one equals a state where all the species present are in equal quantities. This ratio is independent of species richness and is therefore not biased by the addition of rare species, as is Simpson's Dominance Index.

β -diversity Measures

β -diversity is the species turnover between adjacent areas / sites along a habitat or environmental gradient. The following formula of Wilson & Shmida (1984) was used to calculate this rate of change:

$$\beta = \frac{(g_E + l_E)}{2S}$$

Where,

- β - β -diversity;
- g_E - Number of species gained along gradient E ;
- l_E - Number of species lost along gradient E ;
- S - Mean sample richness of all samples along the gradient.

This method is independent of both α -diversity and sampling intensity. Species missing from intermediate sites / regions are not assumed to be present. The concept of β -diversity is discussed in more depth in Chapter 7.

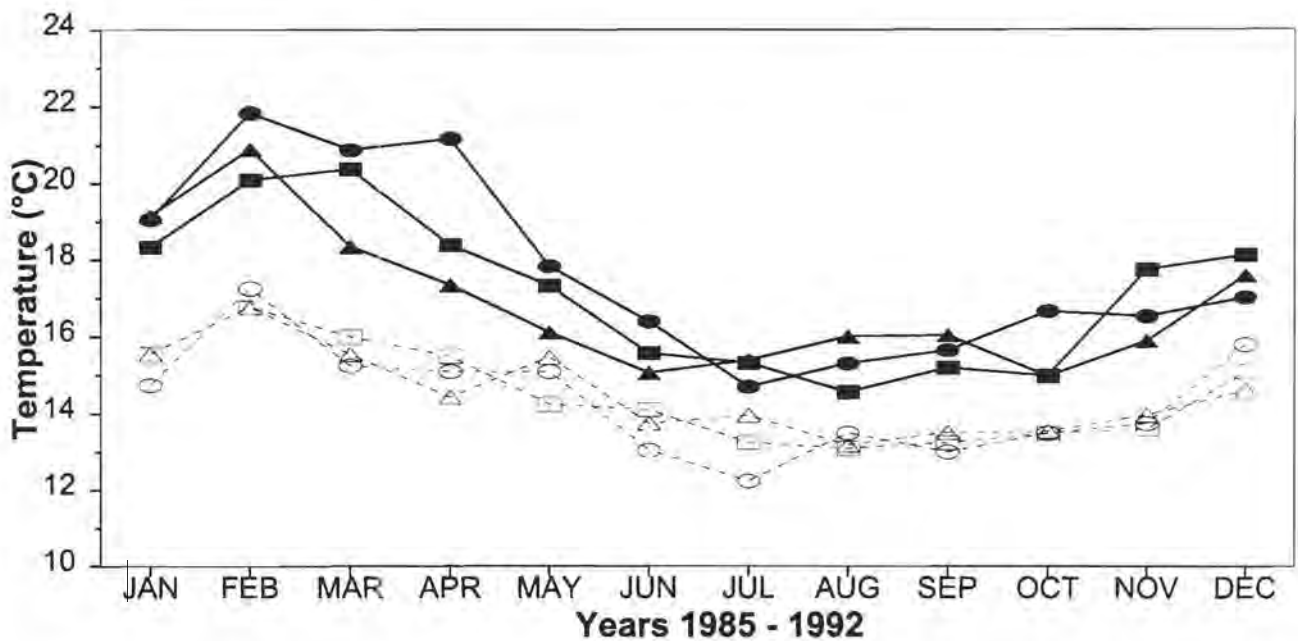
Study Area

Upwelling

Namibia lies between the latitudes 17°30'S and 28°20'S on the south-western coast of Africa, bisected by the Tropic of Capricorn (Fig.2.1). Despite being largely within the tropics the coast is climatically temperate. This is predominantly due to the upwelling of the cool, nutrient-rich, central water of the Benguela current. This is a broad slow moving current, flowing northwards along the south western coast of Africa. Upwelling occurs as a result of long shore winds, corresponding to south and south-easterly winds. These winds predominate during the summer months on the west coast of South Africa, but they are less seasonal in Namibia. The resulting effect is that upwelling on the Namibian coast occurs throughout the year (Shillington, 1986). According to Shannon (1985), the Lüderitz area constitutes the primary upwelling cell within the Benguela system with secondary cells around Walvis Bay (Fig.2.1) and Hondeklip Bay (30°19'S; 17°16'E), South Africa. The Benguela current travels northwards to Cape Fria (18°26'S; 12°0'E) in northern Namibia (Shannon, 1985), where it turns westward into the Atlantic ocean. Upwelling of cooler water has been reported from further north (Hart & Currie, 1960; Stander, 1964). Shannon (1985) attributes the latter to the uplifting of warmer saline waters close inshore, and not to the effects of local winds.

Surface Sea Water Temperature

Namibia is exposed to upwelling along its coast-line which brings cool Antarctic bottom water to the surface. As was mentioned above there is a primary upwelling cell off Lüderitz in the south, which keeps this area relatively cold throughout the year. According to Molloy (1990) the mean monthly average sea surface temperatures for Lüderitz range from 12 - 14.8°C, whilst Swakopmund further north has a range from 12 - 18.4°C. The mean monthly sea surface temperatures taken from ships data logs for the years 1985 -1992, obtained from the South African Centre for Oceanography, are plotted in Fig. 2.3. As can be seen there is a shift to warmer mean monthly sea surface temperatures from southern to central Namibia. The Namibian coast occasionally also receives a number of warm water events. These events are often associated with the El Niño phenomenon, or southward bound counter-current tongues of warm water from the Angolan current. These warm water events may increase the sea water surface temperatures to 21°C while, within sheltered areas like Lüderitz lagoon, temperatures may reach 28°C (Molloy, pers.comm.)



Angola - Central Namibia ● 17-18S, 11-12E ■ 19-20S, 12-13E ▲ 22-23S, 13-14E
Southern Namibia - Northwestern South Africa ○ 25-26S, 14-15E △ 26-27S, 14-15E □ 29-30S, 15-16E

Fig. 2.3: Mean monthly sea surface temperatures for degree blocks on the coast of Namibia for the years 1985 - 1992. (Data - South African Centre for Oceanography, Stellenbosch). Numbers in the legend refer to degrees South and East; while the letters in **bold** indicate the areas concerned.

General Wind speed and Direction along the Coast

There is a decrease in inshore wind speed from southern to northern Namibia, as well as frequency (Jury, 1993). Wind speeds of 8 m.s^{-1} or more have a

- 32% probability of occurring in Lüderitz;
- 17% probability of occurring in Walvis Bay;
- 13% probability of occurring in Möwe Bay.

The strongest winds occur in spring and summer and these are predominantly south and south-southwesterly winds. Southerly winds often reach gale force strength in southern Namibia (Jury, 1993). Another wind which may be of considerable importance to understanding seaweed distribution, is the east wind. This wind is strongest and most frequent during the months April to September (from data in Jury, 1993). These winds blow directly off the Namib desert, and are therefore very hot and dry ($30 - 40^\circ\text{C}$, pers.obs.). Large patches of bleached / dead seaweed have been observed in Swakopmund after such an event has coincided with a spring low tide.

Wave Exposure

Shillington (1993), looking at the physical oceanography of Namibia, pointed out the extreme lack of information with respect to Namibian inshore current patterns, although a fair amount of information is known about the off-shore patterns. He notes a decrease in wave height as one moves northwards, with no seasonal variation in height north of Walvis Bay, as opposed to Lüderitz which exhibits greater heights in spring. These patterns coincide with the wind patterns outlined by Jury (1993) (see above).

The west coast of South Africa and Namibia is mostly exposed to extreme wave action (Branch & Griffiths, 1988; Molloy, 1990; Field & Griffiths, 1991; John & Lawson, 1991), with few sheltered areas. There are a number of bays and inlets on the Namibian coast in the Lüderitz area, with Sandwich Harbour and Walvis Bay being the only other significant bays on an otherwise straight coastline.

Substrate Availability and the amount of Sand Inundation

A mere 80 km (5.3%), of the 1500 km coastline, comprises extensive rocky outcrops, the remainder of the coast being predominantly composed of sandy beaches (Molloy, 1990). Slightly different proportions are given by Campbell (1993), who attributes 80% to sandy beaches, 16% to rocky shores, and 4% to mixed shores. The basic pattern is however largely the same. These rocky outcrops are concentrated mostly around the Lüderitz area, while smaller outcrops are found in the central and northern regions of Namibia. Many of the latter are low lying and flanked by sandy beaches. As a result, many of these rocky shores are periodically covered by sand. The only other notable rocky outcrops on the Namibian coast are Möwe Bay and Rocky Point, in northern Namibia.

In this study the average amount of sand per quadrat per site was ascertained for the two sampling trips (Fig. 2.4). As can be seen, there is a low degree of sand inundation in the southern Namibia sites, a moderate to high degree in central Namibia, and a range in northern Namibia ranging from low to high. There is also a seasonal variation between some of the sites. In southern Namibia most of the sites have levels of sand less than 10 g/quadrat; this is very low, so differences are probably not significant. The Agate Beach (L&A) site does however show a marked increase in the

autumn sample. The sites in central Namibia have less sand in the autumn (1992) data set. The seasonal difference between these sites could be related to the size of the rocky outcrop. Langstrand (LGS) is the biggest rocky outcrop of the three, with the least difference in sand quantity, whilst Myl 8 (MY8) is the smallest outcrop with the biggest difference in sand quantity. The latter site is low lying and flanked by sandy beaches and therefore sand inundation on these rocks is probably more variable. Vineta Beach (VIN) has a moderately sized rocky outcrop and a moderate difference in sand inundation. The differences between sampling occasions in northern Namibia are slight, greatest in Möwe Bay (MOW), which has low sand quantities. There is also a fundamental difference in the ratio of sand particle size (Fig. 2.5). The ratio was calculated as follows:

The ratio of coarse sand : silt, i.e. coarse sand weight / silt weight, was calculated for each quadrat containing sand. This scale is uneven with respect to the two components, i.e. if the ratio is:

1 - coarse sand = silt

>1 - coarse sand > silt

<1 - coarse sand < silt

As a result values of ">1" can range from $1 \rightarrow \infty$; but values of "<1" are only between $0 \rightarrow 1$.

Therefore, for a more equal scale, values "<1" were inverted and made negative. Values >1 are coarse sand dominant, and values <1 are silt dominant. Standard deviation was then calculated for each site. Results are displayed in Fig. 2.5.

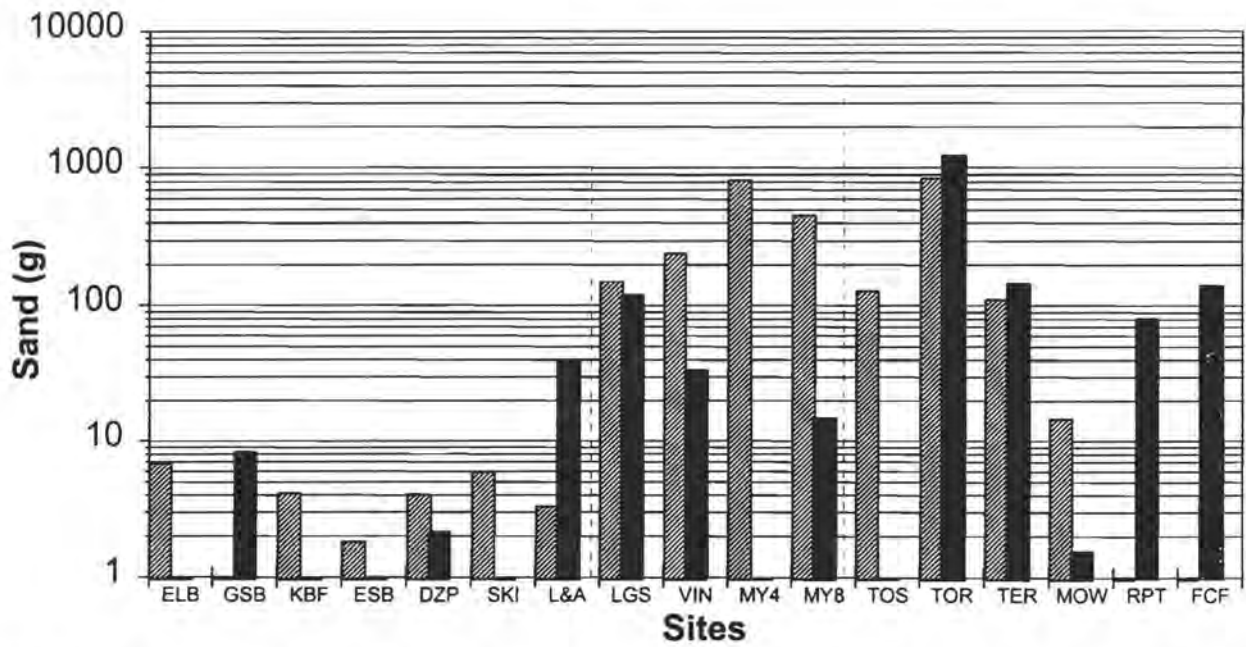


Fig. 2.4: Average sand weight / quadrat per site. The three areas have been divided by means of two vertical dashed lines. Hatched pattern - 1990 samples - Spring; Dotted pattern - 1992 samples - Autumn.

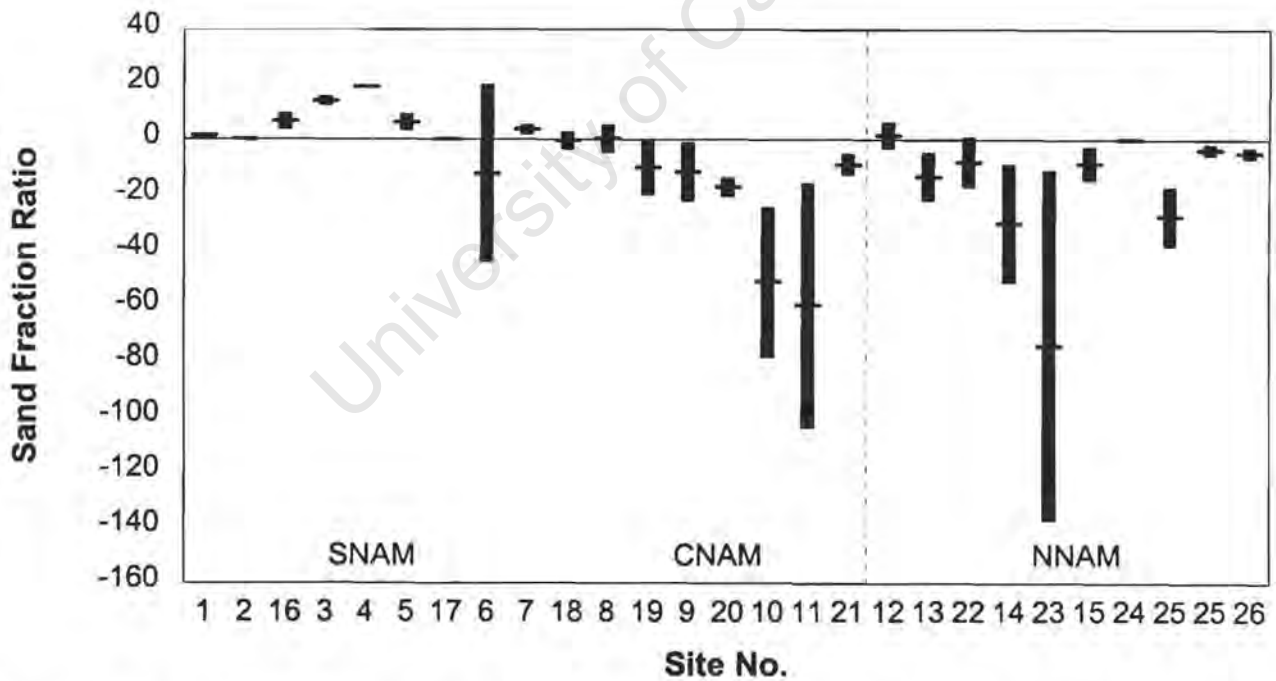


Fig. 2.5: Ratio of coarse sand : silt, for the various sites sampled. Horizontal lines - means, vertical lines - standard deviation.

As can be seen from Fig. 2.5 the sand composition in central and northern Namibia has a higher silt component than at sites further south. The only site in the south to have relatively high silt ratios is that of Shark Island (SKI, #6). This site occurred within Lüderitzbucht (bay / lagoon) and therefore higher levels of silt may be expected, although the Elizabeth Bay (#1) and Agate Beach (#7, 18) samples did not show this trend.

Tidal Pattern

The tidal range on this coast is relatively small at approximately 0.42 -1.88m above Chart Datum (Molloy, 1990). Many of the low-lying rocky outcrop sites, in central and northern Namibia, are completely immersed during neap high tide. As a result the upper shore zonation is absent from these sites. Spring low tides always occurs during the morning and late afternoon, when air temperatures are relatively low (except during east wind conditions when a hot wind blows off the desert).

Fog

Another factor that may be important to understanding seaweed distribution is the occurrence of fog which occurs predominantly between April and September. During this period approximately 50% of the days in Walvis Bay and on only 30% of the days in Lüderitz (Jury, 1993). The fog is usually present in the morning or late afternoon. This coincides with spring low tides, thus reducing the rate of desiccation of seaweeds, although it should be borne in mind that the fog is not present during east wind conditions.

Gradient of Shores

The relationship between gradient and zone length are examined below in Fig. 2.6:

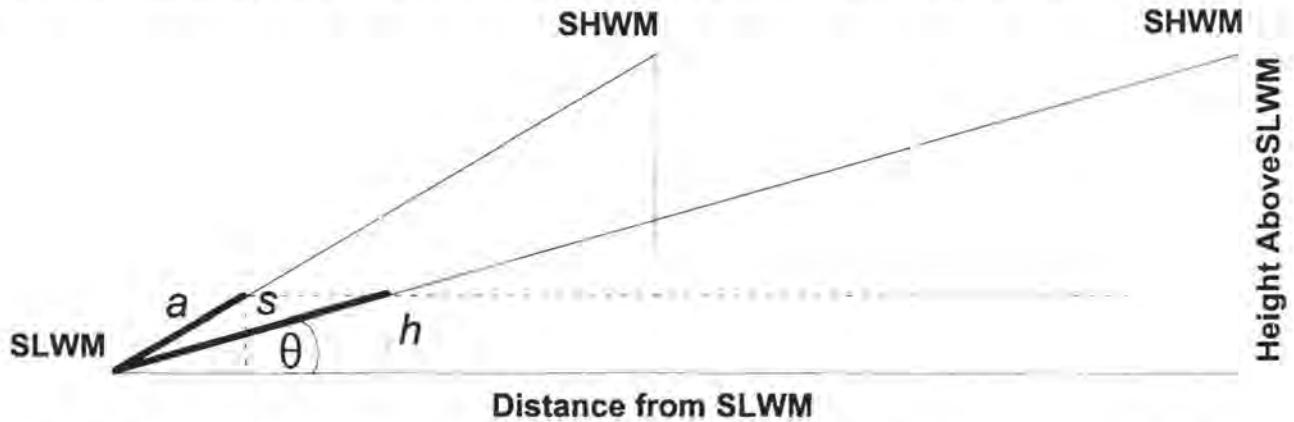


Fig. 2.6: Hypothetical shores with the same height but differing gradients. SLWM - spring low water mark; SHWM - spring high water mark; s - zone length at height h ; a - zone length at height h ; θ - angle of slope of shore.

$$h/s = \sin \theta$$

$$s/h = \operatorname{cosec} \theta$$

therefore

$$s = h \operatorname{cosec} \theta$$

$$\text{Also, } \operatorname{cosec}^2 \theta = 1 + \cot^2 \theta$$

$$\text{Therefore, } \operatorname{cosec} \theta = \sqrt{1 + \cot^2 \theta}$$

$$= \sqrt{1 + \frac{1}{\tan^2 \theta}}$$

$$\text{Let the gradient} = m$$

$$\text{Therefore, } m = \tan \theta$$

$$= h \cdot \sqrt{1 + \frac{1}{m^2}}$$

$$= h \frac{m^2 + 1}{m}$$

$$\text{Therefore, } s'(m) = h \left[\frac{1}{2} (m^2 + 1)^{-\frac{1}{2}} (2m)m - (m^2 + 1)^{-\frac{1}{2}} \right]$$

$$= h \left[\frac{m^2}{m^2 + 1} - \frac{1}{m^2 + 1} \right]$$

$$= \frac{h(m^2 - 1)}{m^2 + 1}$$

$s'(m)$ - Rate of change of the length 's' with the gradient 'm'

The above derived equation looks at the rate of change of 'zone length' (s) with respect to gradient (m). As can be seen, s decreases as m increases, i.e. the zone length decreases as the gradient becomes steeper. The ' h ' component of the equation represents the height of a zone, sub-zone within the intertidal, or SHWM of chart datum. The rate at which the 'zone length' decreases is exponential to the gradient. Therefore a relatively small change in gradient between two sites with a shallow gradient can have a marked effect on zone length; whereas a similar change in gradient on a steep shore will have relatively little effect on zone length.

A frequency histogram of the gradients of the transects at the various sites, for the three areas, was plotted (Fig. 2.7). Southern Namibia has a wide array of shore gradients, with a tendency towards relatively moderate to steep shores. Central Namibia has low lying rocky shores with gentle slopes; while northern Namibia has gentle to moderately sloping shores. As a result, the eulittoral zone within the central and northern reaches of Namibia is generally wider.

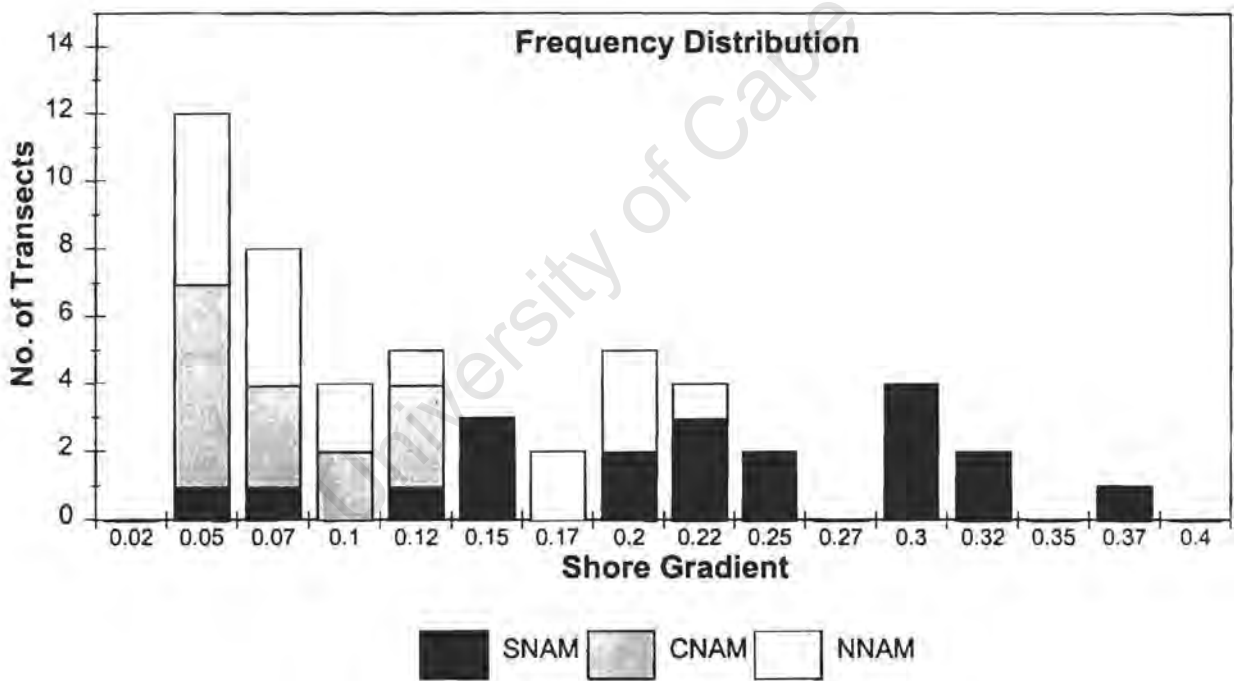


Fig. 2.7: A frequency histogram of shore gradients for the various transects along the Namibian coast.

A short description of the sites sampled is given below. Appendix A contains the shore profiles for the various sites, as well as the onshore wind directions which may affect these shores.

Southern Namibia

The area referred to as southern Namibia is largely restricted to the area immediately around the town Lüderitz. This area has a considerable rocky shore component, largely composed of sedimentary rock and in some places conglomerate (at some sites within the Lüderitz lagoon). There are a number of small bays and inlets, which provide a certain degree of shelter, but most of the coast in this area is exposed to strong wave action. Most of the shores sampled had kelp beds extending from the spring low water mark to 20 - 100 m out (*Ecklonia maxima* (proximally) and *Laminaria schinzii* (distally)). Sand inundation in the immediate Lüderitz vicinity is relatively low (Fig. 2.4), although sites within the lagoon tend to have some degree of sand / silt deposition. Areas to the south and north of Lüderitz do have shores which exhibit mixed sandy-rocky shores, but owing to access restriction these sites were not sampled during this study. A subsequent investigation of the intertidal, for the diamond company, allowed me access to some of these areas. This study formed part of an environmental impact assessment carried out in 1995 by the CSIR. I was invited along as a seaweed specialist to help identify the local seaweed species. Permission to use the data was obtained from the environmental officer of NamDeb. Only two of the islands sampled are used in this study, viz. Possession and Pamona Islands. These data are however, of a different form and can not be directly compared to the biomass data set. A brief description of the methods is given below.

Three transects were taken at each site and a number of zones subjectively chosen with respect to visible vertical zonation patterns (usually 5 zones). Within each zone two quadrats (0.5 m²) were randomly chosen and the percentage cover of the various animals and plants ascertained. The latter was done by means of an intersection grid system (consisting of 120 intersection points); the organism occurring under the intersection point was recorded and later its percentage presence was calculated for the entire quadrat. This method is adequate for looking at the most abundant organisms in a zone or community, but is unreliable with respect to species richness.

A brief description for each of the sites sampled in the Lüderitz area (Fig.2.8), is given below.

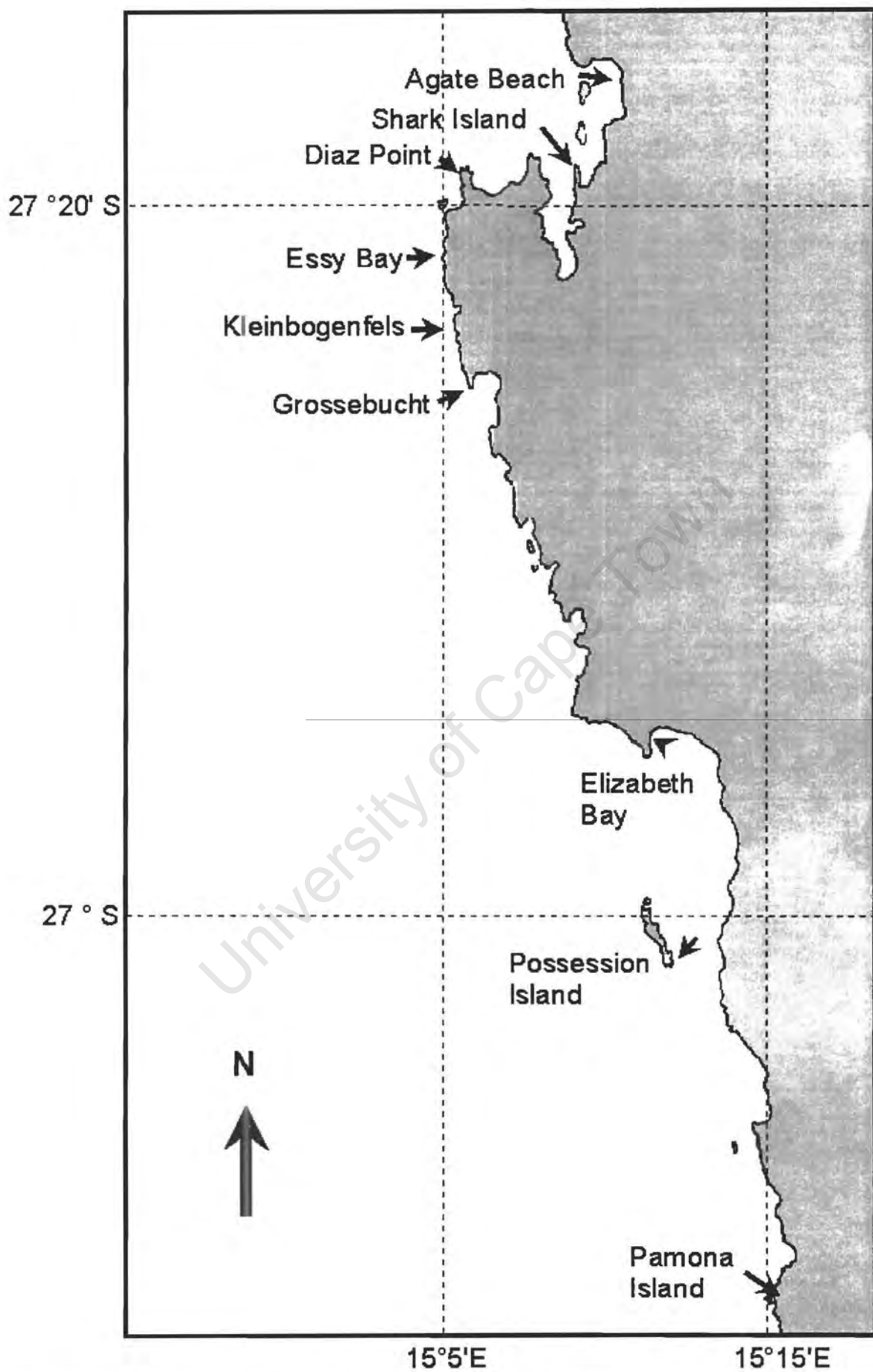


Fig. 2.8: Map of the Lüderitz area sampled in 1990, 1992, and 1995.

Elizabeth Bay

This site occurs within the NamDeb diamond area, Sperrgebiet 1, and, as a result there is restricted access. In 1990 I was allowed to sample in the north east corner of the Bay, while in 1992 access to the area was denied due to a bureaucratic error and no samples could be collected. Due to the restriction of movement in the area I was only allowed to work in one corner of the Bay, which is not representative of the southern Namibian flora for the following reasons.

Elizabeth Bay was an old diamond mining area that was last mined in 1933, reducing it to a “ghost town”. In 1990 mining operations were resumed, which resulted in large amounts of processed sediment being pumped into the bay. The site that was sampled had considerable fine silt in the water column, although as can be seen from Fig. 2.4 & 2.5, very little was present on the rocky shore itself. The effluent being pumped into the sea is high in fine sediment and may also contain ferro-silicon, a chemical used in the diamond sorting process (although it is claimed that this substance is reclaimed before the effluent is pumped into the sea). The site sampled was relatively sheltered; access to the more exposed shores at the northern point of the bay was prohibited at that time.

The site sampled had a gradual slope and the topography was relatively flat, although there were numerous fissures and cracks in the rocks. On the lower reaches of the shore there were extensive beds of *Gunnerea capensis* (tube worm) with numerous tufts of *Centroceras clavulatum*. In the intertidal fringe of one of the transects there was an abundance of *Codium isaacii* / *C. duthiae*, possibly an indication of the extreme shelter. Subsequent visits to the area (1995) revealed that the 1990 sample site was totally covered by sand / silt and that the entire sandy beach had moved forward due to the sediment dumping in the bay, and as a result this site could not be sampled.

Grossebucht

This is the southern-most bay in Lüderitz to which there is public access. It has both an exposed and semi-sheltered side, but only the exposed side was sampled. The sampled area comprised a gneiss substrate which was relatively flat with a moderately sloping gradient. The area is moderately wave exposed.

Kleinbogenfels

The slope of the shore at this site is moderate, with an intertidal shore length of approximately 11 m. Despite being in a slight embayment, and only being exposed to northwesterly onshore winds, this area appeared to have a relatively high wave exposure.

Essy Bay

Owing to the rough weather conditions and high swell, only one transect was possible at this site. The shore has a relatively low slope, with a high degree of wave exposure. This shore is exposed to south and southwesterly winds.

Diaz Point

This site was extremely exposed, probably second only to Grossebucht. The slope of the shore was also extremely steep. This site was exposed to both southwesterly and northwesterly winds. The intertidal zones on these shores were very compact.

Shark Island

This site is situated within Lüderitzbucht, which affords it some degree of shelter from the open ocean. It is, however, not entirely sheltered as it is near to the 'mouth' of the lagoon. The transects sampled on this island were taken at the exposed point of the island. These transects are sheltered from the southwesterly winds. The island is connected to the mainland by means of a causeway.

Agate Beach

This site was not strictly taken at Agate Beach, but half way between the latter and the Lalandii crayfish factory (hence the site abbreviation: L&A). It is situated more deeply within the Lüderitzbucht lagoon than the previous site, thus making it relatively more sheltered. Further shelter is provided by two islands, viz. Penguin and Seal Island, which are situated between the site and the lagoon 'mouth'. This site has a relatively steep gradient; this combined with the slightly sheltered nature results in a very short eulittoral zone.

Possession Island

This island is just south of Elizabeth Bay and has a sheltered and exposed side. Information from the sheltered side only was used in this study. The sheltered site was in a small cove on the southeast side of the island. The most abundant organisms at this site were seaweeds and very few filter feeders were present. There was a small amount of silt but sand inundation seemed to be negligible. The gradient was gentle to moderate.

Pamona Island

This site was also part of the above mentioned survey in 1995. This island is joined to the mainland during low tide by means of a sand bar. The transects sampled here were taken in a semi-exposed position in close proximity to the sandy beach / dune area. As a result there was some degree of sand inundation in this area. The slope of the shore was moderate to low.

Central Namibia

There are very few rocky outcrops in central Namibia, and the ones that do exist are low lying (Fig. 2.7, Appendix A). As a result they are mostly totally covered during neap high tide, and the upper zones of the rocky shore intertidal are therefore absent. These shores exhibit a moderate to high degree of sand inundation. This is probably due to two factors:

- (1) The shores are low lying, small and flanked by sandy beaches. As a result, sand is carried onto the rocks from adjacent areas; and / or
- (2) the shores abut sand dunes and sandy beaches / plains, and this sand is blown onto the rocks by off-shore winds.

The coast in this area is relatively straight and apparently open to the full force of the incoming waves. The degree of wave exposure however, may not be as severe as further south since the wind frequency and strength is lower in the central and northern reaches of Namibia as mentioned above. A gradually sloping subtidal would cause the wave to break a distance away from the shore thereby reducing the impact and energy of the waves before they reach the eulittoral zone.

The overall appearance of the shore changes from sites further south, as different species become abundant in the central and northern parts of Namibia. The brown mussel, *Perna perna*, and a small introduced black mussel, *Semimytilus algosus*, are often dominant components on these shores. The first record I encountered on the introduced mussel, *Semimytilus algosus*, is that of Penrith & Kensley (1970 b)(I do not know the way or how long ago this species was introduced).

Langstrand

This site is just south of Swakopmund and it lies directly north of the beach Langstrand (22°45'S, 14°32'E), on the rocky outcrop. The slope of the shore is gentle, and the shore comprises a broken up platform with numerous crevices, interspersed with numerous low lying boulders. This site has a moderate amount of sand inundation.

Vineta Beach

This site lies adjacent to the town of Swakopmund, just north of the mole (22°40'S, 14°32'E). The latter may give a certain degree of shelter to this site, but this is probably negligible. The rocky outcrop takes the form of large, flat-topped boulders.

Myl 4

This site is situated four miles to the north of Swakopmund (22°34'S, 14°32'E). It has a similar rocky shore topography to Langstrand, however, the sand inundation at this site is nine fold greater than the latter. This shore is not as extensive as Langstrand and is flanked by sandy beaches.

Myl 8

This site is situated eight miles north of Swakopmund (22°45'S, 14°32'E). It is characteristic of the numerous small rocky outcrops that are found along this part of the coast. It is a very small rocky outcrop, separated from its nearest neighbour by a number of kilometers. These sites are low lying and are probably periodically buried in sand. The topography of the shore was that of jagged and boulder-type rocks which lie obliquely to the incoming waves.

Skeleton Coast

The shores of the Skeleton Coast National Park, which encompasses the entire shoreline of northern Namibia, are very similar in appearance to those in central Namibia, although they exhibit a greater habitat heterogeneity. There are two relatively large rocky outcrops in this area, viz. Möwe Bay and Rocky Point, as well as some smaller but still substantial ones at Torra Bay, Terrace Bay and False Cape Fria. As was seen in Fig. 2.4, the sampled sites also have a variable degree of sand inundation. The two sites north of Möwe Bay, Rocky Point and False Cape Fria, were only sampled in 1992 as access was not possible in 1990. The reasons for this were three fold, firstly this area is a nature conservation restricted area and a permit is required; secondly, a 4-wheel drive

vehicle is required; and thirdly, you have to be accompanied by a Nature Conservation officer. In 1990 the first two conditions were met, but unfortunately no Nature Conservation officer was available at that stage to accompany me into the area.

Toscanini

Toscanini is situated in the southern part of the Skeleton Coast National Park, and comprises a relatively small rocky outcrop. It is topographically similar to Myl 8. This shore was dominated by animals, in particular the filter feeders (*Perna perna* being the most dominant). The site also appeared to be very wave exposed.

Torra Bay

Torra Bay is the site of an angling camping site. It has a gently sloping rocky platform which stretches for 50 - 60m to the subtidal fringe. The shore has a high degree of sand inundation, the composition of which is moderately silty. The most abundant organisms on the shore are algae, in particular filamentous and turf-forming species. Despite being exposed to the south-westerly and northwesterly winds, this site appeared to be slightly sheltered. The gently sloping intertidal rock substrate probably extends for a distance into the subtidal region, thus causing the waves to break further out to sea.

Terrace Bay

This is another angling campsite, north of Torra Bay. The rocky substrate is composed of broken boulders and small rock platforms. The exposure at this site appeared to be greater than that found at Torra Bay. Sand inundation was moderate at this site and the biotic composition was a balance of fauna and flora. There was a small boulder rock beach near by but it appeared to be largely devoid of living organisms.

Möwe Bay

This was the most northern site accessible by road. The sites further north had to be reached by means of 4-wheel drive vehicles. Möwe Bay comprised a relatively large boulder type rocky outcrop, which extended above the SHWM. Sand inundation in this area was low and the wave exposure high. The slope of the shore was moderate to slightly steep in parts. The lower intertidal was dominated by crustose and articulated coralline red algae, and a number of filamentous species.

Rocky Point

This site lies to the north of Möwe Bay and comprises a substantial rocky promontory. An exposed site, comprising a red basalt substrate which was hard and smooth, was chosen. The gradient was moderate to high and the sand inundation moderate.

False Cape Fria

The northernmost site sampled on the Namibian coast was False Cape Fria approximately 110 km from the Angolan border. This site is situated near a Cape Fur Seal colony. It comprised a small red basalt rocky outcrop with a topography of smooth flat topped boulders. Sand inundation was moderate, while wave exposure seemed to be moderately high. The diversity on these rocks was low, consisting mainly of filter feeders, *Ulva sp.*, and *Grateloupia longifolia*. The *Grateloupia* may however be seasonal.

University of Cape Town

The Biogeography of the Seaweed Flora of Namibia

Introduction

Namibia forms the northern half of the south-western African marine phytogeographical province (Lawson *et al.*, 1990; Lüning, 1990; Field & Griffiths, 1991), which stretches from Moçamêdes (southern Angola, 15°10'S) to Cape Agulhas (southern-most tip of Africa). The same region is referred to as the Benguela marine province by Bolton & Anderson (1997) and the West Cape by Hommersand (1986). The former authors however, mark the southern cut off point as Cape Point on the Cape Peninsula as opposed to Cape Agulhas. The reason for the name, the Benguela marine province, is that this province is coincident with the Benguela Current (Shannon, 1985). The region between Cape Point and Cape Agulhas is seen as a transition region between the Benguela province and the Agulhas province (Stephenson, 1948; Stegenga & Bolton, 1992; Bolton & Anderson, 1997).

This region has also been investigated from a zoological perspective, and the findings are similar with respect to the biological boundaries of this province, although there seems to be some dissension with respect to the use of specific classification of the region. Stephenson (1948), who looked at the distribution of 318 common intertidal species (a third of these species being algae) around the South African coast, referred to this region as the cold temperate, west coast marine province. He also designated a similar southern cut off point as Bolton and Anderson (1997). The transition region between his west and south coast marine provinces was termed the western overlap. Emanuel *et al.* (1992) suggested the splitting of the Benguela province into two distinct biogeographical units based on the results of a zoogeographical multivariate analysis of invertebrates. They mooted the separation of a cool temperate southwest coast (Namaqua province) from a cool temperate north west coast (Namib province), with Lüderitz marking the border between these two provinces. The findings in this chapter will offer an alternative explanation for their findings.

The Benguela province is bordered on either side by warm currents, viz. the Angolan current (towards the north) and the Agulhas current (towards the south). As a result it abuts directly onto the Tropical West African marine province; the rapid transition between Namibia and Angola is

discussed by Lawson *et al.* (1990). Hommersand (1986) and Lawson *et al.* (1990) also noted that there is an attenuation in species number in a northerly direction towards Angola. Hommersand (1986) partly attributed this to a lack of data collections, while Lawson *et al.* (1990) stated that it could be the result of decreased relative wind stress and concomitant water circulation patterns in the northern regions. (This trend will be discussed further).

There has been much controversy as to whether this region is a cold temperate (Stephensen, 1948; Hedgepeth, 1957; Knox, 1960) or warm temperate marine province (Ekman, 1953; Briggs, 1974; van den Hoek, 1984; Bolton, 1986; Lüning, 1990; Bolton & Anderson, 1997; Stegenga *et al.*, 1997). The protagonists of the cold temperate marine province, in particular Stephensen (1948), based this designation on the fact that there is kelp in this region and that the cold temperate areas in other places in the world have kelp species present. As Bolton (1986) has pointed out this is specious reasoning, since the kelp species concerned have higher growth and reproductive temperature optima than those found in cold temperate waters elsewhere. Lawson (1988), in support of the concept of a warm temperate province, points out that the south-western African phytogeographical province (Benguela marine province) has more in common with the warm temperate Uruguayo-Bonearensis and Uruguay floras in South America than the cold temperate flora of Patagonia. Emanuel *et al.* (1992) refer to the Benguela province as 'cool temperate' but fail to explain what they mean by the concept. Bolton & Anderson (1997) would seem to agree with this designation on the basis that the temperature regime, within this province, falls between warm and cold temperate temperature categories. This debate does not affect the delineation of this area as a phytogeographical province but is important when comparing it to other provinces elsewhere.

This chapter will comprise two main sections:

- (1) The south-western African region's status as a phytogeographical province, as well as ascertaining the extent of a region of transition between this province and the tropical west African province; and
- (2) Phytogeographical trends within this province, in particular with respect to species richness.

Methods

Numerous seaweed collections from various sources were used in these analyses. These include my own collections from field trips (1990, 1992, 1995); Wynne (1986); Lawson *et al.* (1990); Penrith & Kensley (1970 a, b); Kensley & Penrith (1973, 1980); John *et al.* (1975); Lawson *et al.* (1975); and detailed distribution data for the South African west coast from Stegenga *et al.* (1997). Data include both intertidal and subtidal seaweed species (a full list is given in Appendix B.)

The change in species richness along the west coast of southern Africa was determined as follows: Eight regions of comparable size (except False Bay & South of False Bay to Agulhas) were chosen between Cape Agulhas (South Africa) and São Nicolau (14°12'S; 12°E, Angola)(Table 3.1; Fig.3.1) and their species richness calculated.

Table 3.1: The regions sampled, their number and code name.

Region No.	Code	Ranges
1	ANG	Southern Angola (São Nicolau - Kunene River mouth)
2	NNAM	Northern Namibia (Kunene river mouth - Cape Cross)
3	CNAM	Central Namibia (Cape Cross - Black Rocks)
4	SNAM	Southern Namibia (Black Rocks - Oranjemund)
5	NWC	North Western Cape (Oranjemund - Groen river)
6	SWC	South Western Cape (Groen River - Cape Point)
7	FB	False Bay (Cape Point - Cape Hangklip)
8	SFB	South-east of False Bay to Cape Agulhas

The reason why False Bay is not of comparable size is that it is a unique bay along the South African west coast (Bolton *et al.* 1991). It is a relatively shallow bay and as a result the water temperature within this big bay heats up, resulting in a temperature gradient around the bay. This allows for a greater variety of organisms with different temperature requirements to survive in this region. There is also a wide variety of habitats within the bay: sheltered to exposed shores; topographic gradients (shallow - steep sloping shores); variety of substrate types and structure; as well as 'mixed' sand/rocky shores (Bolton *et al.* 1991). If this region were included in an analysis as part of the 'south western Cape' region or the 'south of False Bay' region, it would artificially inflate species richness levels and obscure biogeographic patterns. With respect to the 'south of False Bay to

Agulhas' region, as was noted in the introduction, this region has been regarded as forming the transition region between the Benguela and Agulhas provinces. It therefore seems logical to keep it separate from the other defined regions.

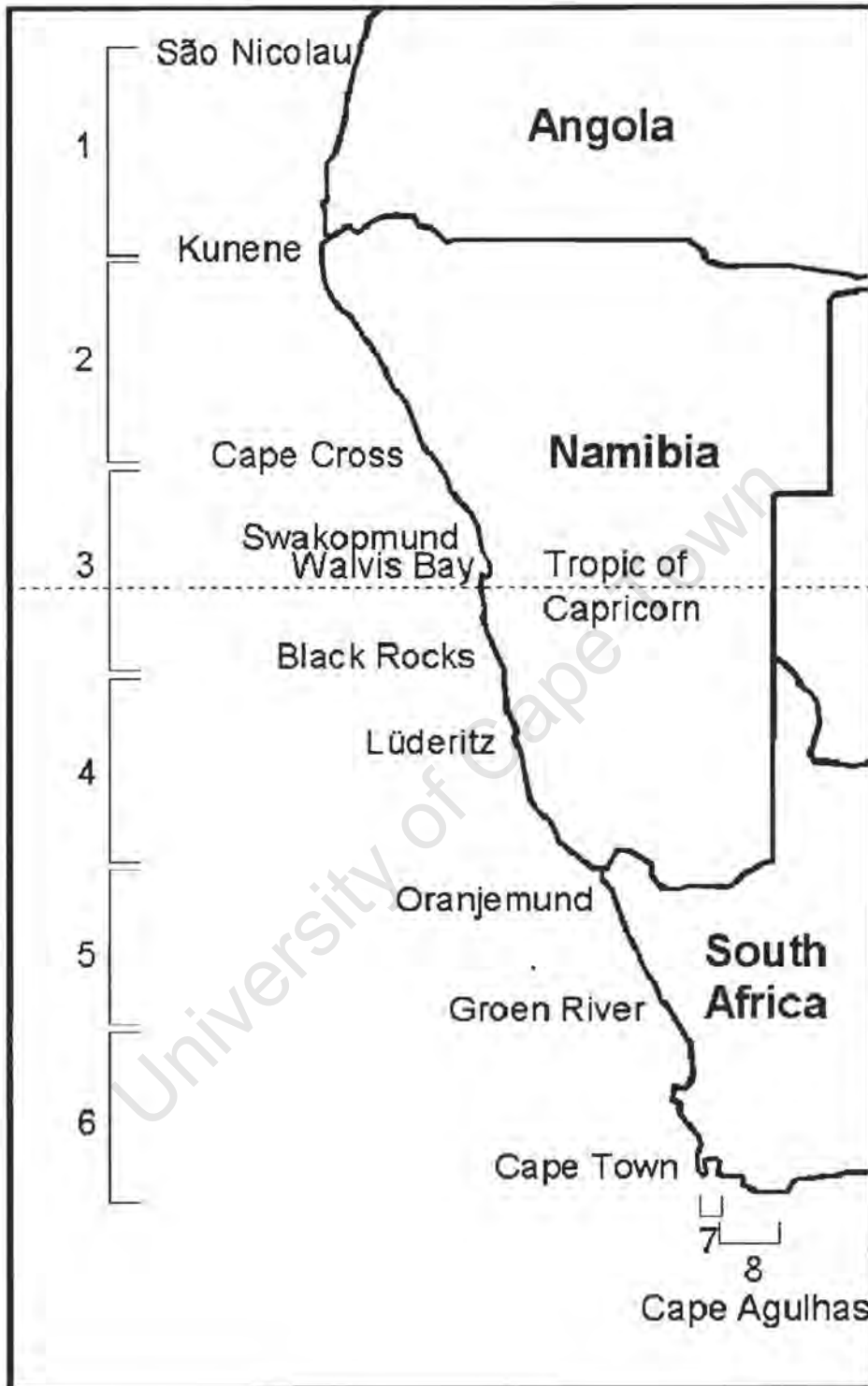


Fig. 3.1: Map of the south western coast of Africa showing the eight defined regions.

Two multivariate packages were used to analyse the data, viz. **Two-Way INDicator SPecies ANalysis (TWINSpan)**(Hill, 1979), and **Detrended Correspondence Analysis (DCA)**(Ter Braak, 1991)(see Chapter 2, General Methods). The data matrices comprised presence / absence values for species occurring in the above regions.

β -diversity was also determined to establish the rate of species turnover between adjacent regions using Wilson & Shmida (1984) (see General Methods) and was represented graphically. Table 3.2 relates comparison numbers to regions compared. The scale at which β -diversity will be looked at is at a regional level; in a later chapter I will look at β -diversity at a site level.

Table 3.2: Comparison numbers for the various regions compared.

Comparison No.	Regions Compared
1	ANG & NNAM
2	NNAM & CNAM
3	CNAM & SNAM
4	SNAM & NWC
5	NWC & SWC
6	SWC & FB
7	FB & SFB

Results

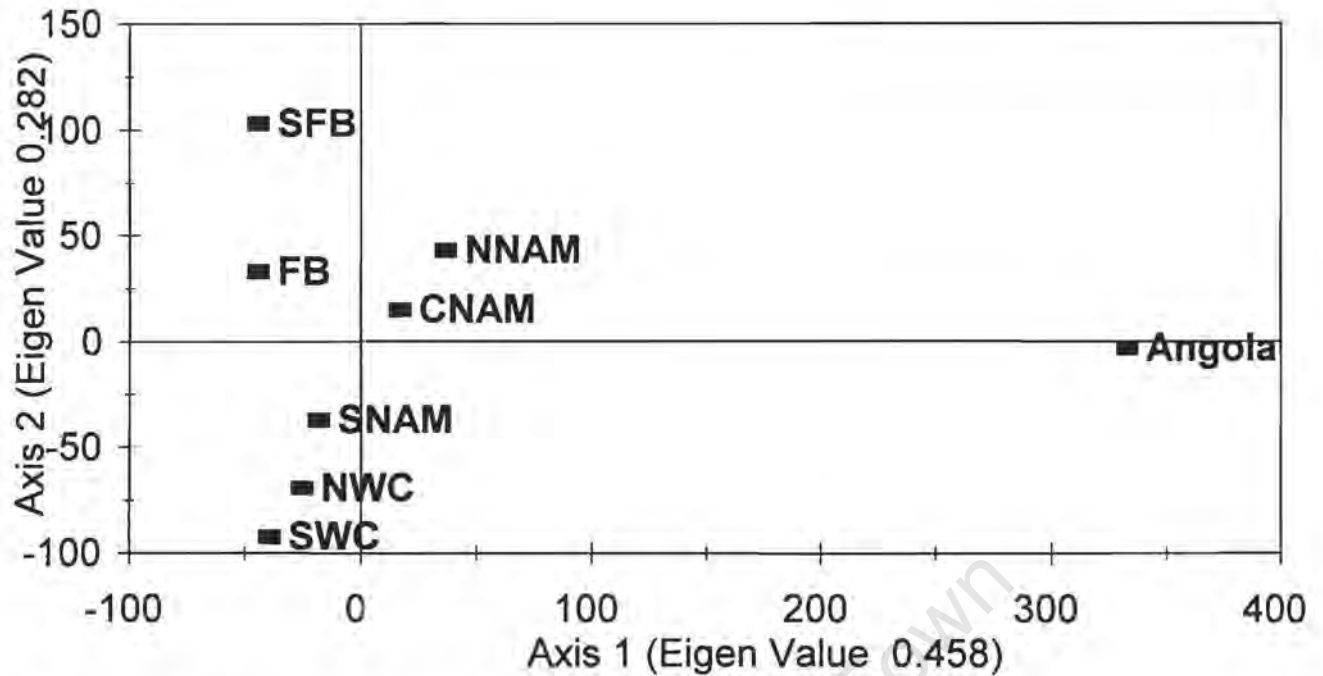


Fig. 3.2: DCA of Regions 1 - 8 as outlined in Table 3.1.

Fig. 3.2 represents the arrangement of the various regions based on a DCA of the species presence / absence data. It can be seen that the southern Angolan flora is extremely distinct from that of the other regions based on its species composition. The analysis was repeated with the exclusion of the Angolan data, and the results are represented in Fig. 3.3. As can be seen from the graph, False Bay and south-east of False Bay to Agulhas are separated from the rest of the south-western African coast flora along Axis 1. Note the Eigen value is not particularly large - indicating that much of the variance is not explained in terms of this axis, although the differences are significant. Also, there is a separation of data points along Axis 2, which follows in geographical position order, i.e. regions follow in a south - north order from bottom to top.

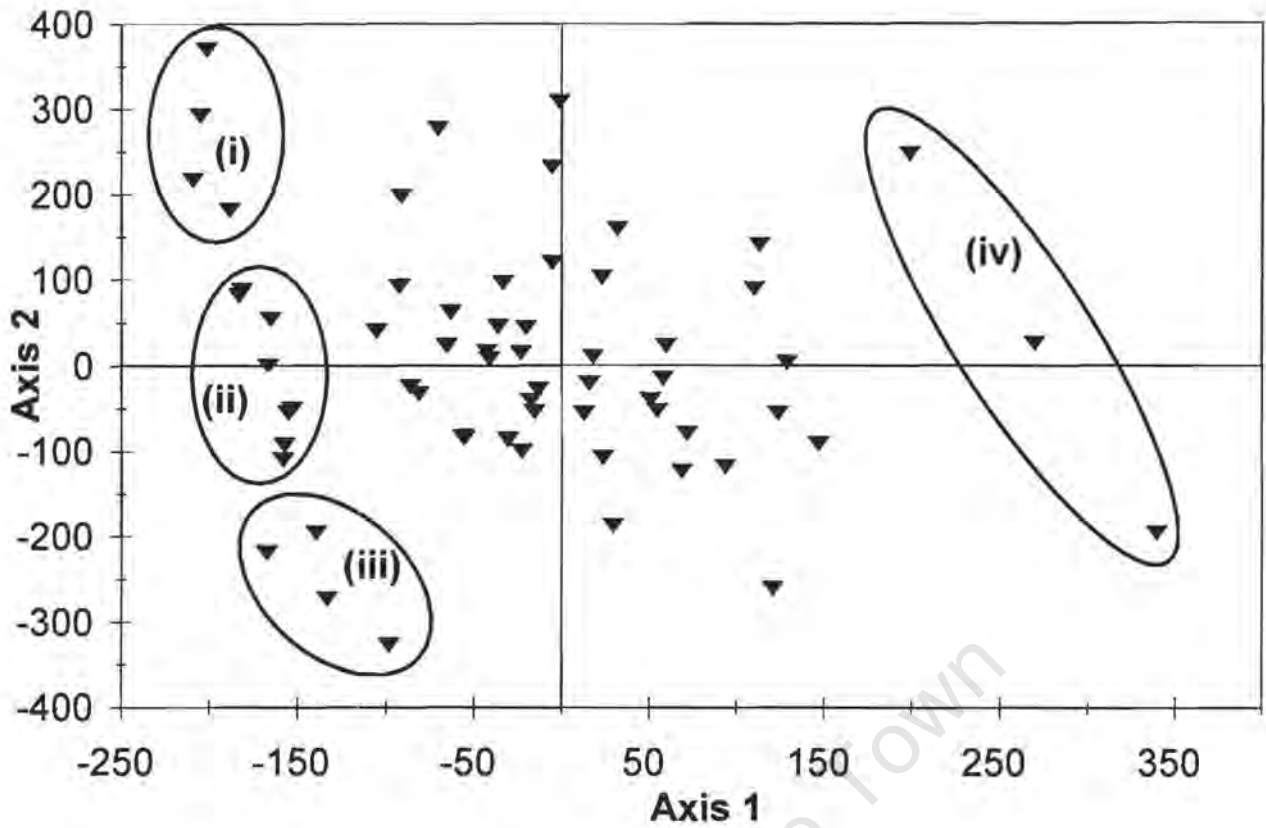


Fig. 3.4: Distribution of species groups of a DCA of Regions 2 - 8 (Table 3.1), with the exclusion of southern Angola

Fig. 3.4 represents the species distribution for the same DCA in which each point represents a group of species that had the same co-ordinates for Axis 1 and 2. As with the regions graph (Fig. 3.3), a number of species have grouped in a vertical / diagonal line on the left and right margins of the graph. Four clusters have been subjectively identified, viz. i - iv, these will be discussed later. There is also a more diffuse cluster of species located in the centre of the graph.

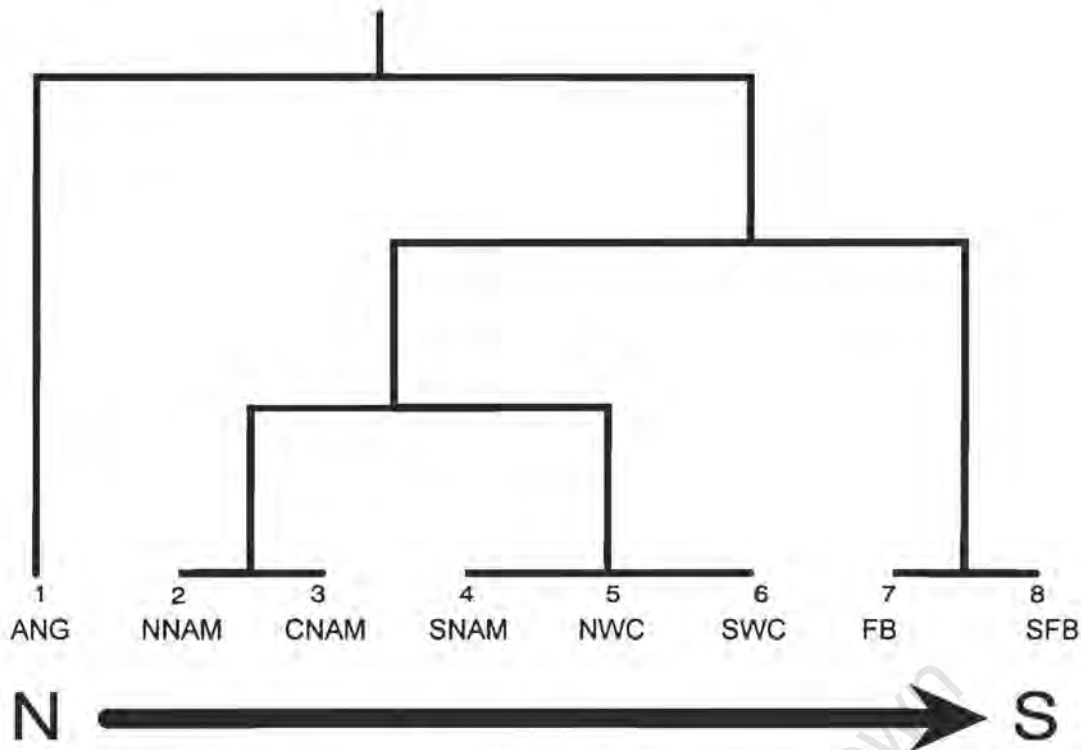


Fig. 3.5: Dendrogram of regions 1 - 8 (Table 3.1) from a TWINSpan Analysis.

Fig. 3.5 is a dendrogram representing the results of a TWINSpan analysis. As was found in the DCA, southern Angola is separated from the other regions. Next, False Bay and the region southeast of False Bay to Cape Agulhas are separated from the south-western African coast flora. In the last division southern Namibia and the western Cape are separated from northern and central Namibia.

Tables 3.3 A & B represents a composite of species results from the DCA and TWINSpan analyses. The table is divided into four categories. The species in Table 3.3 A are those located within the groupings indicated (i) - (iv) whilst the species in Table 3.3 B are placed in the 'best-fit' region. The latter group are derived from the species in the central region of Fig. 3.4. Due to the fact that many species have not been recorded over the entire region range, as set out in Table 3.3, alignment took place on the basis of best fit of geographical range and where the species was most abundant. The first category (i) represents species found from central Namibia northwards (Table 3.3A), whilst the species in Table 3.3B had a similar distribution in the northern regions as well as a disjunct distribution in False Bay and/or southeast of False Bay.

Table 3.3 A: Primary representative species of the various regions - a composite assembly from DCA and TWINSPAN analyses.

ANG - CNAM (i) Warmer water species	NNAM & CNAM - FB(ii) West Coast Cosmopolitan species	SNAM & NWC - SWC (iii) Cold water species	FB - SFB (iv) Warmer water species	
<i>Codium decorticatum</i> <i>Enteromorpha tubulosa</i> <i>Ulva nematoidea</i> <i>Basispora africana</i> <i>Ectocarpus rhodochorionoides</i> <i>Laminaria schinzii</i> <i>Anthamnon leptocladum</i> <i>Audouinella hypneae</i> <i>Ceramium diaphanum</i> <i>Chondracanthus teedii</i> <i>Cryptopleura calophylloides</i> <i>Flauhalitia appendiculata</i> <i>Gelidium pusillum</i> <i>Plocamium vulgare</i> <i>Pterosiphonia parasitica</i>	<i>Cladophora contexta</i> <i>Codium isaacii</i> <i>Enteromorpha atroviridis</i> <i>Enteromorpha bulbosa</i> <i>Ulvella</i> sp. <i>Myriogloea abbreviata</i> <i>Papenfussiiella gracilis</i> <i>Petalonia fascia</i> <i>Ahnfeltiopsis complicatus</i> <i>Ballia sertularoides</i> <i>Callithamnion hookeri</i> <i>Ceramium atrorubescens</i> <i>Ceramium capense</i> <i>Colaconema plumosum</i> <i>Hildenbrandia rubra</i> <i>Myriogramme livida</i> <i>Nothogenia ovalis</i>	<i>Stromatella monostromatica</i> <i>Urospora media</i> <i>Axillariella constricta</i> <i>Compsomena cf. sessile</i> <i>Ectocarpus acutus</i> <i>Streblonema nemastomae</i> <i>Streblonema transfixum</i> <i>Zeacarpa tetomorpha</i> <i>Acrochaetium tenuissimum</i> <i>Anthamnonella tormentosa</i> <i>Audouinella balliae</i> <i>Audouinella desmarestiae</i> <i>Ballia callitricha</i> <i>Botryocladia</i> sp. <i>Callithamnion decompositum</i> <i>Cataglossa lepriouri</i> <i>Colaconema monorhiza</i> <i>Delisea flaccida</i> <i>Haematocelis</i> sp. <i>Neevea repens</i> <i>Nemastoma pulchrum</i> <i>Platyclinia</i> sp. <i>Platythamnion capense</i> <i>Pleonosporium paternoster</i> <i>Pleonosporium ramulosum</i> <i>Rhodoglossum</i> sp. <i>Spyridia plumosa</i>	<i>Caulerpa bartoniae</i> <i>Caulerpa filiformis</i> <i>Caulerpa holmesiana</i> <i>Cladophora dalmatica</i> <i>Codium extricatum</i> <i>Codium lucasii</i> <i>Codium papenfussii</i> <i>Codium platylobium</i> <i>Enteromorpha flexuosa</i> <i>Ulothrix speciosa</i> <i>Aglaozonia</i> sp. <i>Anthophycus longifolius</i> <i>Bachelotia antillarum</i> <i>Carpomitra filiformis</i> <i>Cystophora fibrosa</i> <i>Dichopteris longifolia</i> <i>Dichyota dichotoma</i> <i>Dichyota liturata</i> <i>Dichyota naevosa</i> <i>Ecklonia radiata</i> <i>Lobophora variegata</i> <i>Myrionema magnusii</i> <i>Phloiocaulon squamulosum</i> <i>Sargassum elegans</i> <i>Sargassum heterophyllum</i> <i>Sphacelaria brachygonia</i> <i>Sphacelaria rigidula</i> <i>Sporochnus pedunculus</i> <i>Streblonema codii</i> <i>Zonaria harveyana</i> <i>Zonaria subarticulata</i> <i>Acrosorium cincinnatum</i> <i>Amphiroa beauvoisii</i> <i>Amphiroa capensis</i>	<i>Griffithsia subbionica</i> <i>Gymnothamnion elegans</i> <i>Herposiphonia prorepens</i> <i>Herposiphonia secunda</i> <i>†.tenella</i> <i>Heterosiphonia arenaria</i> <i>Holmesia capensis</i> <i>Hypnea rosea</i> <i>Jania adharens</i> <i>Jania capillacea</i> <i>Jania crassa</i> <i>Jania verrucosa</i> <i>Laurencia flexuosa</i> <i>Laurencia natalensis</i> <i>Laurencia obtusa</i> <i>Laurencia</i> sp. <i>Laurenciophila minima</i> <i>Lomathamnion capense</i> <i>Membranella</i> sp. <i>Nienburgia serrata</i> <i>Pachychaeta cryptoclada</i> <i>Pleonosporium caribaeum</i> <i>Pollexfenia minuta</i> <i>Polysiphonia cf. repida</i> <i>Pterosiphonia spinifera</i> <i>Pterosiphonia stangerii</i> <i>Rhodomelopsis africana</i> <i>Rhodophysema feldmannii</i> <i>Sarcodia dentata</i> <i>Scinaia capensis</i> <i>Spyridia filamentosa</i> <i>Symphyocladia marchantioides</i> <i>Tiffaniella schmitziana</i> <i>Wrangelia purpurifera</i>

Table 3.3 B: Secondary representative species of the various regions - a composite assembly from DCA and TWINSPAN analyses.

ANG - CNAM (i)		NNAM & CNAM - FB (ii)		SNAM & NWC -SWC (iii)		FB - SFB (iv)	
Warmer water species		West Coast Cosmopolitan species		Cold water species		Warmer water species	
<i>Codium duthieae</i>	<i>Chaetomorpha aerea</i>	<i>Arthrocardia</i> spp.	<i>Mazzaella capensis</i>	<i>Enteromorpha intestinalis</i>	<i>Cladophora radiosa</i>		
<i>Ulva fasciata</i>	<i>Chaetomorpha robusta</i>	<i>Botryocarpa prolifera</i>	<i>Microcladia gloria-spei</i>	<i>Ecklonia maxima</i>	<i>Percusaria percursa</i>		
<i>Ulva rhacodes</i>	<i>Cladophora capensis</i>	<i>Carpoblepharis minima</i>	<i>Nothogenia erinacea</i>	<i>Gigartina polycarpa</i>	<i>Ulothrix flacca</i>		
<i>Endarachne binghamiae</i>	<i>Cladophora flagelliformis</i>	<i>Caulacanthus ustulatus</i>	<i>Ophiodocladus simpliciusculus</i>	<i>Halopteris funicularis</i>	<i>Feldmannia irregularis</i>		
<i>Acrochaetium moniliforme</i>	<i>Cladophora isaacii</i>	<i>Centroceras clavulatum</i>	<i>Pachymenia carnosa</i>	<i>Laminaria pallida</i>	<i>Iyengarita stellata</i>		
<i>Antithamnion reductum</i>	<i>Cladophora mirabilis</i>	<i>Ceramium arenarium</i>	<i>Pachymenia cornea</i>	<i>Leathesia difformis</i>	<i>Myriocladia capensis</i>		
<i>Antithamnion diminutum</i>	<i>Codium fragile</i>	<i>Ceramium papenfussianum</i>	<i>Chondria capensis</i>	<i>Myriogloea papenfussii</i>	<i>Acrosorium uncinatum</i>		
<i>Bornetia repens</i>	<i>spp. capense</i>	<i>Chondria capensis</i>	<i>Chylocladia capensis</i>	<i>Scytosiphon lomentaria</i>	<i>Antithamnion</i>		
<i>Erythrotrichia boryana</i>	<i>Enteromorpha compressa</i>	<i>Chylocladia capensis</i>	<i>Colaconema daviesii</i>	<i>Splachnidium rugosum</i>	<i>pseudoarmatum</i>		
<i>Erythrotrichia welwitschii</i>	<i>Enteromorpha linguata</i>	<i>Colaconema daviesii</i>	<i>Corallina</i> spp.	<i>Sporochnus pedunculatus</i>	<i>Bostrychia intricata</i>		
<i>Gracilariaopsis lemaneiformis</i>	<i>Enteromorpha prolifera</i>	<i>Corallina</i> spp.	<i>Epymentia capensis</i>	<i>Botryoglossum platycarpum</i>	<i>Ceramium tenerrimum</i>		
<i>Hypnea tenuis</i>	<i>Ulva capensis</i>	<i>Epymentia capensis</i>	<i>Epymentia obtusa</i>	<i>Ceramium obsoletum</i>	<i>Colaconema nemalione</i>		
<i>Peyssonnelia capensis</i>	<i>Ulva lactuca</i>	<i>Erythrocladia</i>	<i>Erythrocladia</i>	<i>Champia lumbricalis</i>	<i>Gonimophyllum africanum</i>		
<i>Pleonosporium filicinum</i>	<i>Ulva rigida</i>	<i>polystromatica</i>	<i>Gigartina bracteata</i>	<i>Dasya scoparia</i>	<i>Gymnogongrus intermedius</i>		
<i>Plocamium corallorhiza</i>	<i>Chordariopsis capensis</i>	<i>Gigartina bracteata</i>	<i>Gracilaria gracilis</i>	<i>Delesseria papenfussii</i>	<i>Helminthocladia papenfussii</i>		
<i>Plocamium glomeratum</i>	<i>Colpomenia sinuosa</i>	<i>Gracilaria gracilis</i>	<i>Grateloupia doryphora</i>	<i>Eupitilota pappana</i>	<i>Helminthocladia furcellata</i>		
<i>Plocamium subrii</i>	<i>Desmarestia firma</i>	<i>Grateloupia doryphora</i>	<i>Grateloupia filicina</i>	<i>Gelidium capense</i>	<i>Herposiphonia falcata</i>		
<i>Pollexfenia laciniata</i>	<i>Ectocarpus fasciculatus</i>	<i>Grateloupia filicina</i>	<i>Grateloupia longifolia</i>	<i>Gelidium micropterum</i>	<i>Laurencia glomerata</i>		
<i>Polysiphonia scopulorum</i>	<i>Hinckia granulosa</i>	<i>Griffithsia confervoides</i>	<i>Gymnogongrus dilatatus</i>	<i>Herposiphonia didymosporangia</i>	<i>Mazzaella convoluta</i>		
	<i>Ralfsia verrucosa</i>	<i>Gymnogongrus dilatatus</i>	<i>Haraldtophyllum</i>	<i>Herposiphonia heringii</i>	<i>Placophora binderi</i>		
	<i>Acrochaetium catenulatum</i>	<i>Haraldtophyllum</i>	<i>bonnemaisonii</i>	<i>Heterosiphonia pellucida</i>	<i>Platythamnion recurvatum</i>		
	<i>Acrochaetium secundatum</i>	<i>Heringia mirabilis</i>	<i>Heringia mirabilis</i>	<i>Hymenena venosa</i>	<i>Portieria hormemanni</i>		
	<i>Acrosorium acrospermum</i>	<i>Heterosiphonia dubia</i>	<i>Heterosiphonia dubia</i>	<i>Hypnea ecklonii</i>	<i>Scinaia salicornioides</i>		
	<i>Acrosorium maculatum</i>	<i>Kallymenia agardhii</i>	<i>Kallymenia schizophylla</i>	<i>Hypnea spicifera</i>	<i>Stromatocarpus parasiticus</i>		
	<i>Aeodes orbitosa</i>	<i>Lomathamnion humile</i>	<i>Lomathamnion humile</i>	<i>Nemastoma lanceolatum</i>			
	<i>Ahnfeltiopsis glomerata</i>			<i>Neuroglossum binderianum</i>			
	<i>Ahnfeltiopsis polyclada</i>			<i>Placophora monocarpa</i>			
	<i>Ahnfeltiopsis vermicularis</i>			<i>Plocamium maxillosum</i>			
	<i>Anotrichium tenue</i>			<i>Polyopes constrictus</i>			
	<i>Aristothamnion collabens</i>			<i>Pugetia harveyana</i>			
				<i>Sarcothalia scutellata</i>			
				<i>Sarcothalia stirtata</i>			
				<i>Trematocarpus flabellatus</i>			
				<i>Trematocarpus fragilis</i>			

The second category are those species which are found throughout the Benguela marine province. Category (iii) are those species which are found between southern Namibia and the south-western Cape (Table 3.3 B species include those that may be found in False Bay). The fourth category (iv) are those species that are represented in and south of False Bay; Table 3.3 B species include those found in the south-western Cape region only.

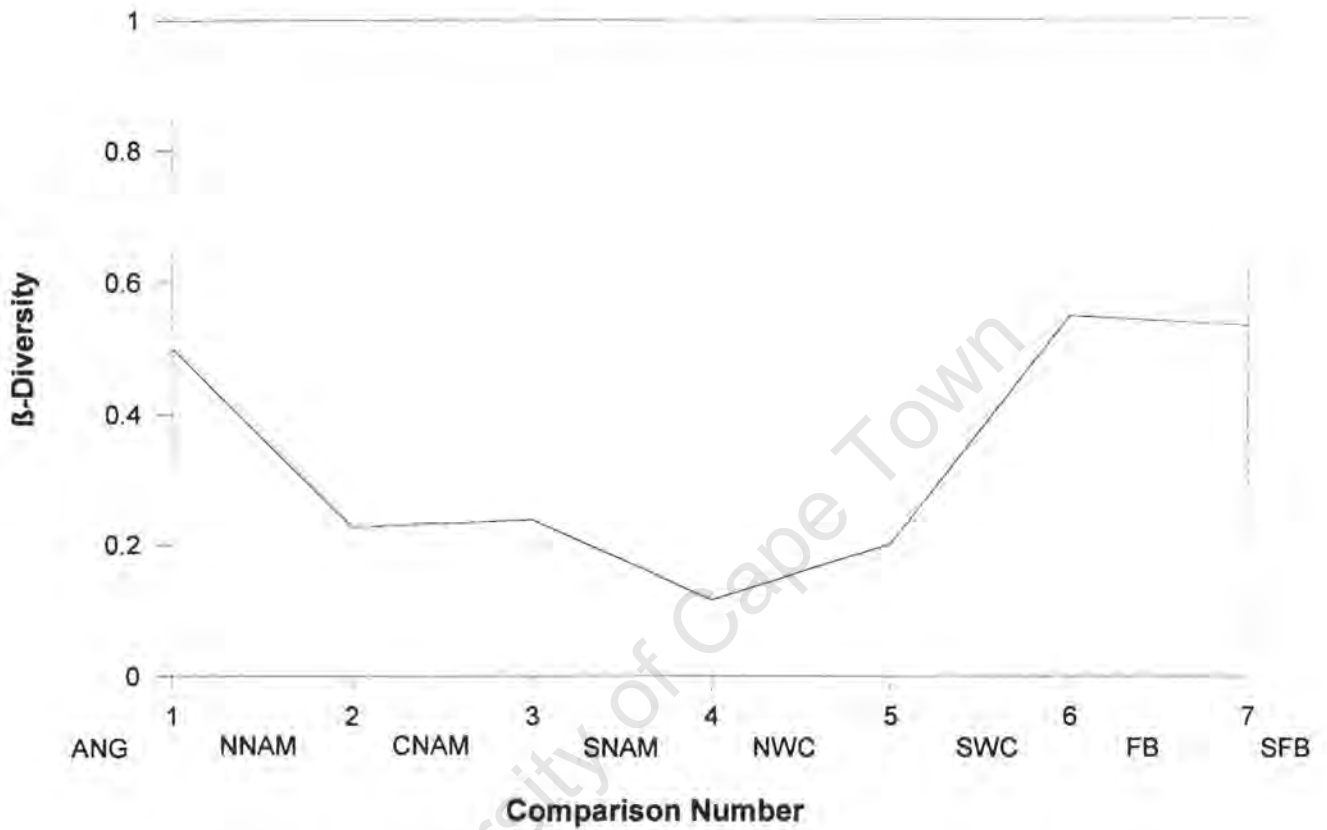


Fig. 3.6: Change in β -Diversity between adjacent regions, from Angola to Cape Agulhas (comparisons in a north to south direction)

The β -diversity values (Fig. 3.6) show that there are three regions of relatively high turnover, viz. 1, 6 and 7. These are between the regions southern Angola and northern Namibia, south-western Cape and False Bay, and False Bay and the region south-east of False Bay to Cape Agulhas. There is very little species turnover between the other regions, with comparison 4 (between southern Namibia and north-western Cape) representing the least difference.

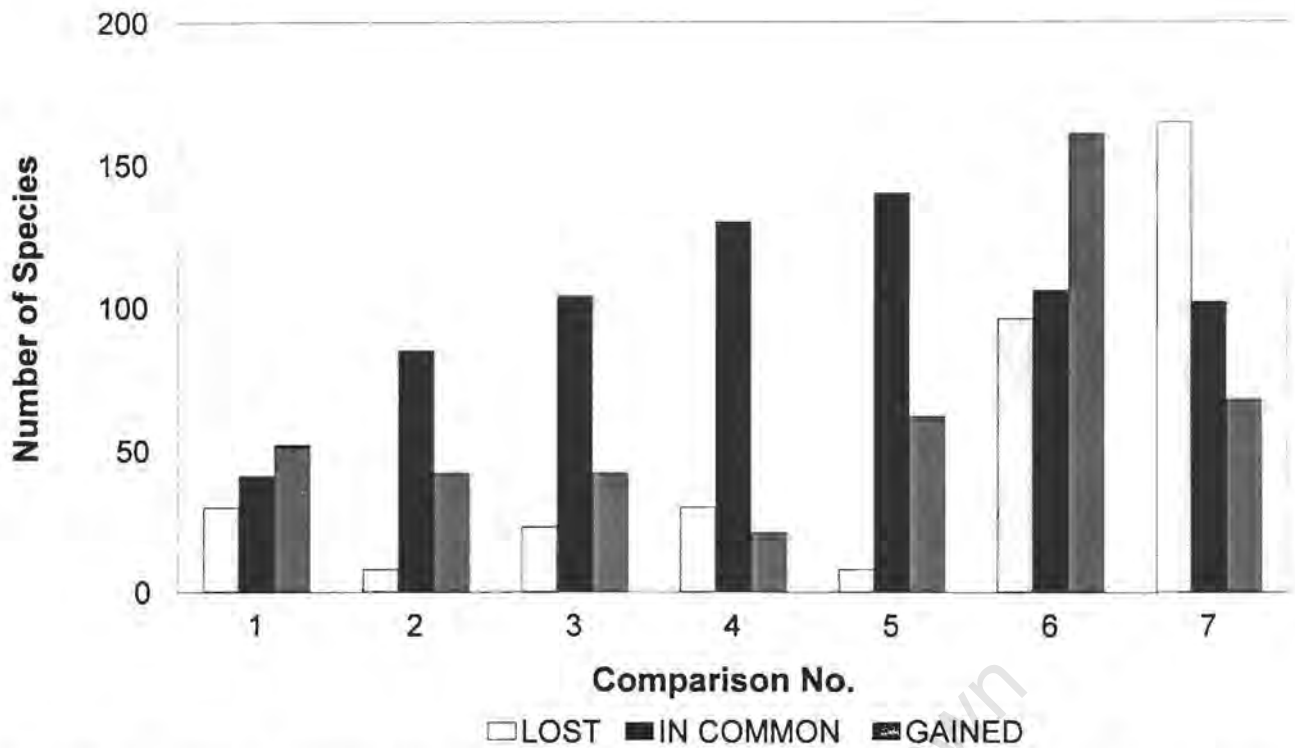


Fig. 3.7: Number of Species Lost, In Common, and Gained between adjacent regions, from Angola to Cape Agulhas. (comparisons in a north to south direction)

Fig. 3.7 illustrates the number of species lost, in common, and gained in each successive comparison, in a north to south direction. It should be noted that there are more species gained in each comparison than lost, resulting in an increase in species richness in a southward direction, except for comparison 7. As can be seen, numerous species are gained as one enters False Bay (Comparison 6) and many lost as one leaves False Bay (Comparison 7). This indicates a specialized region.

The percentage similarity between regions with respect to species composition was based on the following formula:

$$\% \text{ Similarity} = \frac{\text{Species in Common}}{\text{The smaller of the two regions Total Number of Species}}$$

Reasoning behind formula:

If there are two regions, viz. "A" and "B", where "A's" species richness is greater than "B's", then, hypothetically speaking, all "B's" species may be present in "A", thus making "B" 100% represented in "A". "B" would therefore be a subset of "A". This formula is looking at the real degree of overlap between the two regions. The two regions are not actually 100% similar as the one has more species than the other.

As was seen in Fig. 3.8 not all regions have the same species richness. Due to the reason given above, the differences in species richness would result in percentage similarity values less than 100%, even though all the species present in a region of low species richness are present in the region of high species richness. This enables one to evaluate how similar a region of smaller species richness is to a region of greater species richness. In this way one can evaluate whether species are being excluded from a region or being replaced by other species.

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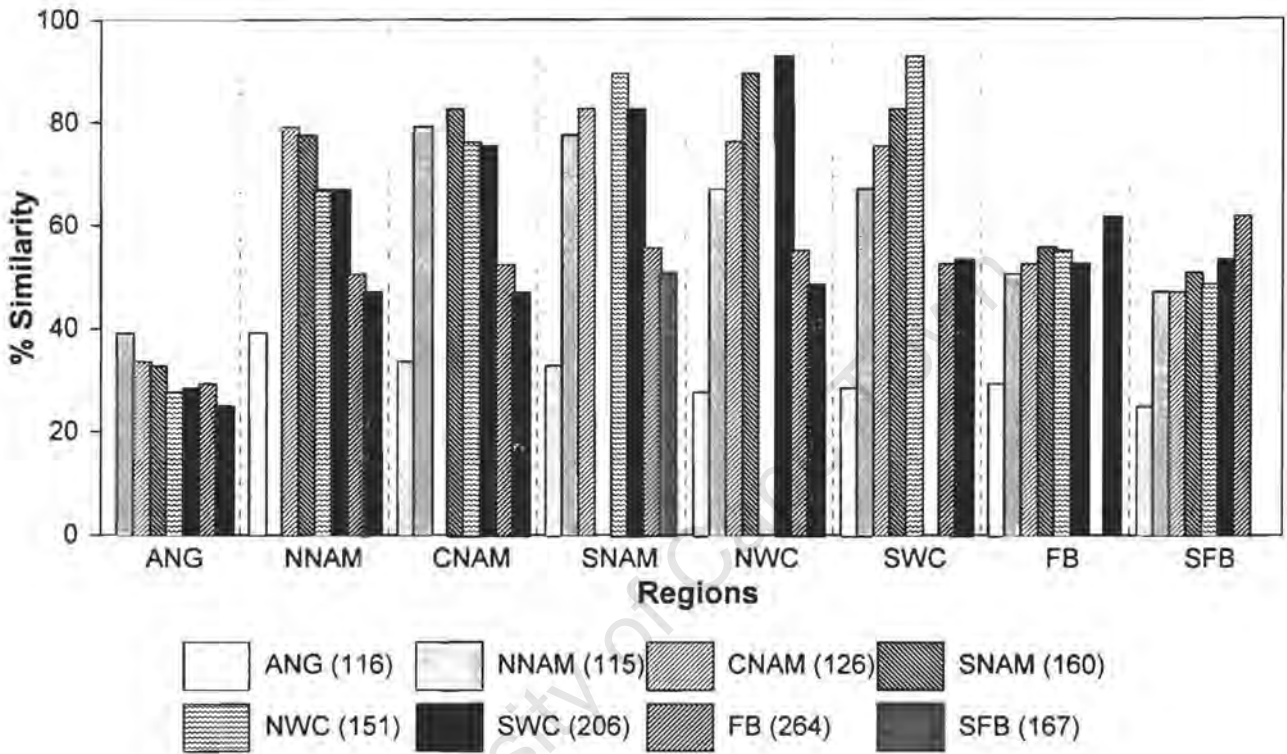


Fig. 3.9: Percentage Similarity between the various regions, as a function of the region with the smaller species richness.

Fig. 3.9 represents the percentage similarity as outlined above. There is a relatively low percentage similarity between southern Angola and the regions further south. But, almost 40% of the species found in southern Angola are shared with northern Namibia. There is a high degree of similarity between regions Northern Namibia to South-western Cape, while only a 50% similarity between these regions and the regions False Bay to Agulhas.

Discussion

The discussion will comprise two main areas of focus: Firstly, I will look at the status of the Benguela province and its structural composition and, secondly, look at the trend in species richness within the province, and suggest possible explanations for this trend.

Phytogeography

It is clear from the results presented that the Benguela province is distinct and separate from Angola, as described by Lüning (1990) and Lawson (1978, 1988). Both multivariate methods separated southern Angola out as being different from the other regions (Fig. 3.2 & Fig. 3.5). These findings were reinforced by the relatively high degree of species turnover between northern Namibia and southern Angola (Fig. 3.6 & Fig. 3.7). But as was noted with respect to percentage similarity between the various regions (Fig. 3.9), almost 40% of the species in northern Namibia are represented in southern Angola. If the south-western African flora is looked at in its entirety, approximately 50% of the species found in southern Angola are represented in this flora. Northern Namibia and southern Angola could therefore be described as a transition zone between the two regions, but due to the rapid turnover of species the difference between the two floras are still quite striking. This may be attributed to the marked difference in sea surface temperature between the two regions. The mean monthly sea surface temperatures for northern Namibia range from 18-21°C (Fig. 2.3, ■), as opposed to the 24°C summer isotherm which meets the coast just north of Moçamêdes in southern Angola (Lawson *et al.* 1975). This temperature difference is due to the fact that the northward flowing Benguela current turns westward into the Atlantic just north of Cape Fria, where it meets the warmer south flowing Angola current. There is also some degree of upwelling in northern Namibia (Shannon, 1985), which would serve to lower the sea surface temperature in this region, further increasing the temperature difference between these two regions. The regions, apart from southern Angola, constitute a relatively cohesive group, making up what has been referred to as the Benguela marine province.

The Benguela marine province, as was seen in Figs. 3.3 and 3.5, clearly separates into two parts, viz. a northern Namibia to south-western Cape part and a False Bay to Cape Agulhas part. False Bay, as was mentioned in the methods section, is a unique area with a sea surface temperature gradient within the Bay. As a result both colder and warmer water species are able to survive here. False Bay is considered to be an overlap between the Benguela and Agulhas marine provinces (Lüning,

1990; Bolton *et al.*, 1991; Jackelman *et al.*, 1991; Emanuel *et al.*, 1992). This is strongly supported by the percentage similarity data (Fig. 3.9) where False Bay only has around 50% similarity to other south-western African regions. This is surprising in that the percentage similarity formula was designed in such a way that the high species richness of this region would not affect the resulting value, i.e. a value of 100% could theoretically be obtained. This means that not all the seaweed species encountered within the Benguela province are found within False Bay. Likewise, False Bay only shows a 60% similarity to the region Cape Hangklip to Cape Agulhas (SFB). If the 50% from the Benguela province and the 60% from the Agulhas Transition region are accounted for, then approximately 25% of the False Bay seaweeds are not accounted for by either of these two regions. False Bay therefore not only contains species from the south-western coast on one side and Cape Hangklip to Cape Agulhas on the other side, but also other species with disjunct distributions. Many species find their distribution extremes within this Bay.

The stretch of coast south-east of False Bay to Cape Agulhas also shows a relatively low percentage of similarity, <50%, to regions northern Namibia to south-western Cape (Fig. 3.9). This is quite a substantial difference considering that the distance separating these two regions is relatively small. False Bay, as was seen above, is a unique habitat and only represents a small hiatus between these two regions. Therefore there seems to be agreement with Bolton and Anderson (1997) who place the boundary of the Benguela province as Cape Point, with the region south of False Bay being a transitional zone between the Benguela and the Agulhas marine province.

The last region under consideration is that of northern Namibia to the south-western Cape. Fig. 3.5 shows that it is split into two regions, viz. a northern part consisting of northern and central Namibia (North-west sub-province), and a southern part comprising southern Namibia to south-western Cape (South-west sub-province). This is a similar finding to Emanuel *et al.* (1992), who wanted to divide the province into two separate provinces. This 'discontinuity' in the flora is not only a result of different species in these regions, but is also due to the decrease in species richness as one travels northwards (Fig. 3.8). The multivariate packages are only concerned with presence or absence and do not make the distinction of species being lost along a latitudinal gradient. Emanuel *et al.* (1991) noted a decline in species richness of marine invertebrates, although they nevertheless maintain that there is a replacement of species based on the Bray-Curtis similarity index. The latter, however, shows a 70% similarity between their proposed provinces.

As can be seen from Fig. 3.9, northern and central Namibia show a relatively high degree of similarity to the southern Namibia to south-western Cape regions (range from 67-83%). The remaining species which are not accounted for in these latter regions are derived from two sources. Some are from Angola and some represent disjunct distributions with False Bay to Cape Agulhas (Table 3.3, (i)). The reason for this is that the central and northern parts of Namibia are warmer than the southern regions (see Bolton, 1986), which would allow for stenothermic warmer water species to occur in these regions. This gradient is reflected in Fig. 3.2 and 3.3, where Axis 2 in both graphs would seem to represent a temperature gradient. This would explain why False Bay is relatively closely aligned with central and northern Namibia in Fig. 3.2, and with Axis 2 values in Fig. 3.3. Temperature data for False Bay and Walvis Bay sites are relatively similar (Bolton, 1986); also, as was noted in Fig. 2.3, there appears to be a mean monthly temperature discontinuity between southern and central Namibia. There is a difference, therefore, between the central and northern regions of Namibia, and the rest of the Benguela marine province. Floristically the difference is small, but a difference nevertheless based on a marked temperature difference. This rise in temperature possibly results in the exclusion of temperature sensitive species from further south.

Van den Hoek (1975) defines a phytogeographical province as a region with a relatively homogeneous flora. Noting that the difference that between the south-western Cape and False Bay to Cape Agulhas is far greater than that between southern and central Namibia (Fig. 3.6 & 3.9), and faced with the above evidence, the Benguela marine province does not constitute two phytogeographical provinces but a single one. The northern reaches of this province may therefore be described as a species poor sub-province of the Benguela marine province with a small number of warmer water species from Angola and False Bay.

Bolton and Anderson (1997) have divided the Benguela marine province into three sub-provinces, viz. the Namib (NNAM-CNAM), Namaqua (SNAM-NWC) and Southwestern Cape (SWC) sub-provinces. The TWINSPLAN analysis (Fig. 3.5) however, split the Benguela marine province into only two parts, a northern (NNAM-CNAM) and southern (SNAM-SWC) part. Bolton and Anderson (1997) base the separation on the greater species richness in the southern regions with a marked drop off in species numbers between the borders of the sub-provinces. This is supported by Fig. 3.8 but, as shown in Chapter 7, there is reason to believe that the Lüderitz area in southern Namibia is under-collected. The northwestern Cape region is also probably under collected (J.J.Bolton, pers. comm.), however, this region will be dealt with in a little more detail below. If these regions are under collected, then as the difference between the Namaqua and Southwestern Cape sub-provinces becomes smaller the sub-division becomes more artificial.

Species Richness

As was noted in Fig. 3.8 there is a gradual decrease in species richness as one moves from False Bay towards Angola. There are numerous possible reasons for the observed paucity in the flora. The reason given by Hommersand (1986), viz. lack of collected material, is partly true but sufficient material has been collected in this study to validate the general trend. Lawson *et al.* (1990) proposed a decrease in wind stress and the related water circulation patterns but do not elaborate on how this would affect species richness. The reasons I deem to be important are outlined below.

Firstly, as mentioned earlier, there is a sudden transition in sea surface temperature between Namibia and Angola. As a result of this rapid transition few tropical seaweed species can establish in Namibia and *vice versa*, unless they are eurythermal. It should also be noted that the general sea current direction on the Namibian coast is in a northerly direction, which would probably reduce the likelihood of seaweeds migrating south.

Not only is there a temperature discontinuity at the northern extreme, but as was mentioned earlier, there is an increase in temperature at Walvis Bay (Fig. 2.3; Bolton, 1986). The average temperature of the southern regions of the Benguela province is approximately 12-13°C with a range of 11.5-14°C i.e. mean monthly temperatures (Bolton, 1986); while in the Walvis Bay area the monthly mean is approximately 16°C with a range of 12 - 18.4°C (Molloy, 1990). Bolton (1996) hypothesized that a narrow temperature range and a long geological period of prevailing conditions in a warm temperate sea would result in high diversity due to the coexistence of both stenothermic and eurythermic species. This change in temperature in central Namibia has probably resulted in halting the spread of more 'cold' water adapted stenothermal species (Table 3.3, Column (iii)) from venturing further north.

Unlike the northern reaches of the Benguela marine province, the southern part of the province abuts another warm temperate province (the Agulhas marine province). The latter has slightly higher temperatures on average than the former. As a result some species from the Agulhas province are able to survive in southern part of the Benguela marine province for several reasons. The latter area is very heterogeneous with respect to physical environment. Therefore there are micro habitats or sites in this habitat heterogeneous region (e.g. not all areas experience upwelling - Table Bay, Cape Town). Another reason may be that the species that do live in these southern parts are eurythermal

or at their temperature limits and, being near a propagule source (viz. False Bay), are able to recolonize an area if it becomes locally extinct.

As mentioned earlier, the Namibian coast is subject to upwelling of cool central water. This is particularly prevalent in Lüderitz, and to a lesser extent further north. The coastal waters also receive counter-current tongues of warm water from the Angolan current as well as warm water events caused by the El Niño phenomenon. These may increase the sea surface temperature up to 21°C, while parts of Lüderitz lagoon may reach temperatures of 28°C, for periods of one to three weeks (Molloy pers.comm.). These warm water events may serve as a limiting factor to the spread or establishment of various algae that could potentially occur here. It is also a less stable situation than that found on the west coast of South Africa (which has a much narrower temperature range and seasonal variation, Bolton (1986)). As a result seaweeds along this coast are exposed to cool water for most of the year, with occasional warm water events which are tropical in nature. The sea temperature is therefore generally too cold to allow the establishment / survival of tropical species and occasionally too warm for relatively “stenothermal” warm temperate species, thus limiting the geographical spread of South African west coast and Angolan species.

Owing to the relatively young age of the Benguela current (Shannon, 1985) and the ephemeral nature of the warm water intrusions, it is plausible that few species have evolved to cope with this phenomenon. Although, the evolution of *Laminaria pallida* into *L. schinzii* may be due to these environmental changes, *L. pallida* is more abundant in the southern reaches of the Benguela marine province, while *L. schinzii* is more abundant in the central and northern parts. Likewise, *Ecklonia maxima* has been shown to have a relatively high temperature optima for growth and reproduction of both the gametophyte and sporophyte stage (Bolton & Anderson, 1987). The reason why this occurs very occasionally in central and northern Namibia is that it is probably near its upper temperature limit for growth and is outcompeted by other seaweed species, including *L. schinzii*. There would therefore appear to be some indication of adaptation in some species, although I believe this to be more the exception than the rule as there are no recorded endemic species in the central and northern reaches of this province.

As was seen in the phytogeography section above, some ‘warmer’ water species show a disjunct distribution between False Bay (including the region to Cape Agulhas), and central and northern Namibia. These regions have a similar temperature range. The question is, why are there not more

species represented from the species rich False Bay in the northern reaches of the flora? Part of the reason is probably that the long intervening coastline is too cold and stable, thus acting as an effective barrier to dispersal. Other important factors are the lack of habitat heterogeneity and suitable substrate.

Secondly, there is a decrease in habitat heterogeneity on a micro and macro scale as one moves northward. Lüderitz, in southern Namibia, comprises a lagoon, a number of bays, numerous inlets and extensive rocky outcrops ranging from sheltered to extremely exposed. As one moves north of Lüderitz there is a tailing off of the above and the coast becomes relatively straight, with Sandwich Harbour and Walvis Bay being the only inlets in the central reaches of the country. The Skeleton coast consists of long sandy beaches with small rocky outcrops, which are often completely submerged during neap tides. As a result the central and northern parts of Namibia are exposed to severe wave action with very few or no sheltered habitats. Likewise on a micro-scale there is a plethora of habitats in the south. The rocky outcrops in the Lüderitz region usually extend above the spring high water mark and are diverse in texture, type, morphology and aspect; having numerous rock pools (at all tidal levels), gullies of various dimensions, rocks of various sizes, etc. This diversity is present to a lesser extent further north. Thus there is a greater variety of habitats available in the south, allowing for the establishment of a wider range of species.

The above argument may also be used to explain the 'difference' between Bolton & Anderson's (1997) sub-provinces, viz. Namaqua and Southwestern Cape. The latter region, as a percentage of the total coastline, has greater habitat heterogeneity and substrate availability than the former region, which may give rise to the observed greater species richness in the south. But as mentioned earlier this species difference may not be as pronounced as it appears, even though the drop in species number in the northwestern Cape is probably a real one, for the reasons given above. The region of southern Namibia is reasonably heterogeneous in habitats and it has a relatively substantial rocky shoreline (although not as much as southwestern Cape). Another component which has not been considered are the off-shore islands of southern Namibia, which represent further habitat heterogeneity and which have not been extensively researched (with respect to seaweeds or intertidal communities).

Thirdly, there is not only a decrease in habitat heterogeneity with a decrease in latitude but, as was mentioned above, a decrease in habitat availability as well. In the central and northern regions of Namibia the rocky out-crops are small, few and separated by long expanses of sandy beaches. The

rocky shores would therefore act as small islands, and the sand a barrier to dispersal i.e. not a suitable substrate for the attachment of seaweeds.

Fourthly, sand/silt inundation of rocky shores is more prevalent in the central and northern reaches of the Namibian coast. Thus one would expect to find predominantly sand-tolerant species (e.g. *Ahnfeldtiopsis* spp., *Mazzaella capensis*, *Caulacanthus ustulatus*) with the exclusion of sand-intolerant species (e.g. *Aeodes orbitosa*, *Chaetomorpha robusta*). This, together with increased temperature conditions and possible related increases in herbivory, could account for the predominance of turf-forming seaweeds in the central and northern parts of the coast.

Fifthly, there is the potential for mass destruction of seaweeds and other intertidal organisms during east wind conditions on the coast of Namibia. As was mentioned in Chapter 2 (General Methods), east winds are hot dry winds which blow off the desert onto the rocky shore. If these winds coincide with low tides they may have potentially devastating effects on the intertidal organisms. The bleaching of many intertidal seaweeds was noticed during such an event in Swakopmund (central Namibia). The severe desiccating effects of a similar wind in southern California was noted by Seapy & Littler (1982). The effect of this wind may have a profound affect on the intertidal diversity and species richness in that it may cause "local extinction" of species. This, coupled with the fact that potential propagule sources, viz. close unaffected rocky shores, are relatively rare in the central and northern Namibian regions, means that recolonization of these shores is severely restricted.

The reduced species richness of the central and northern reaches of Namibia can be attributed to the above. Temperature in conjunction with habitat (including wave action) and propagule source would set the range of species that could potentially survive in the given region. This range is further influenced by the ability of species to tolerate stochastic events such as sand-inundation, warm water intrusion and low tide, east wind events.

Conclusions

In conclusion my data support the opinion of Lüning (1990) and Lawson *et al.* (1990), amongst others, that the Namibian flora is an extension of the South African west coast flora, with minor tropical influences in the extreme northern regions. It would also appear that the Benguela marine province comprises three regions, viz. one transition region and two sub-provinces:

- (1) a southern coast transitional region (False Bay - Cape Agulhas), between the south-western African and Agulhas marine provinces;
- (2) a characteristic “cool” water adapted southwestern coast region (southern Namibia - southwestern Cape); which may be further split into two sub-provinces in the future, but the evidence at this stage is not conclusive;
- (3) a depauperate “warm” water adapted North-west coast region (northern Namibia - central Namibia).

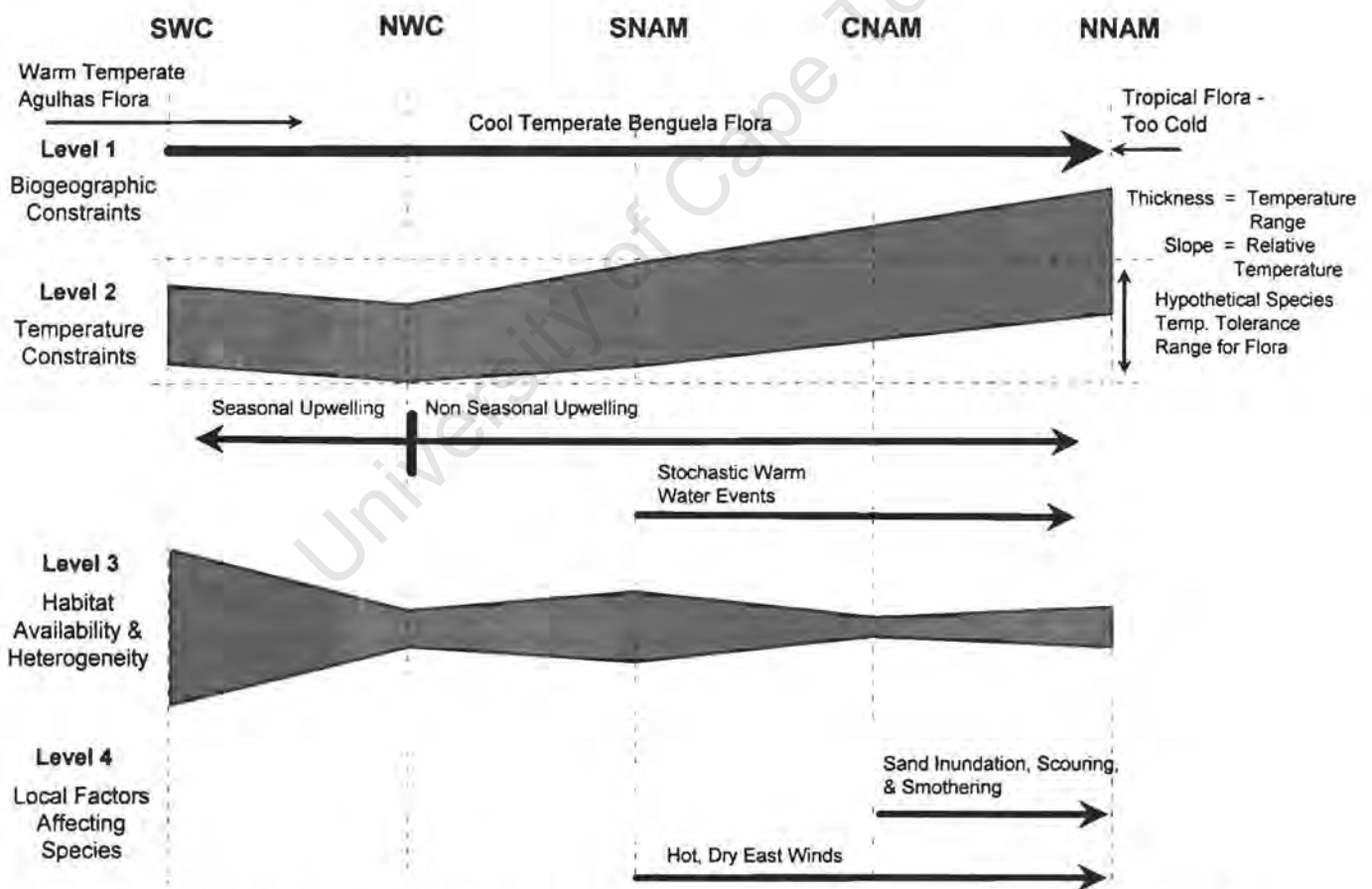


Fig. 3.10: Schematic diagram modeling the major factors affect seaweed species richness along the Benguela marine province.

The general decline of species in a south-north direction may be attributed to the factors outlined in the above schematic model of the Benguela marine province (Fig. 3.10). A number of factors determines what species can survive in each area and it should be noted that all these factors are responsible for the biogeographic patterns observed. Level 1 describes the biogeographic and oceanographic constraints, i.e. the flora abuts a warm temperate flora on its southern border and a tropical flora on its northern border. Thus, in the south some species from the Agulhas province are able to survive in ecologically similar microhabitats and sites in the southern reaches of the province, but very few species from the Angolan flora are able to establish in northern Namibia. The Benguela current also moves in a northerly direction. Level 2 follows on from level 1, looking more specifically at the temperature constraints faced by the species within the flora. Within this level there is a general increase in unpredictability and greater need for eurythermal tolerance as one moves north. Level 3 shows the decline in habitat availability and heterogeneity towards the north, and level 4, the deleterious effects of sand inundation and low tide east wind events in central and northern Namibia. All these factors contribute to a declining species richness northwards, especially the paucity in species richness in the northern regions of the province.

Distribution of the three main seaweed divisions in the Benguela Marine Province, and the use of higher taxa as a surrogate measure for species richness

Introduction

The increase in public awareness of environmental issues has caused a resurgence in the interest of marine biodiversity (Ray, 1991; Ray and Grassle, 1991; Steele, 1991; Hawkes, 1991, 1992; Andersen, 1992; Bolton, 1994; Williams & Gaston, 1994; Norton *et al.*, 1996; John & Lawson, 1997). Sustainability of natural resources and biodiversity have gained greater impetus in many countries since the signing of the United Nations conference on Environment and Development Conference in Rio de Janeiro in June 1992 (John & Lawson, 1997). This conference has given political expression to environmental sustainability and management. In most developed and some developing countries, an environmental impact assessment (EIA) is mandatory before any development can take place. These EIA's usually require an assessment of biodiversity.

What is biodiversity? Biodiversity refers to variety within the living world. In its broadest sense it represents the number, variety and variability of living organisms. This variety may be measured using various units e.g. genes, species, ecosystems, etc., but the most utilised of these is the species. This unit has a number of problems, especially surrounding the philosophical debate as to the definition of the species concept. Despite the problems associated with this unit, it is still the most pragmatic way at this stage to assess biological diversity / variety. Williams & Gaston (1994) have pointed out, however, that this is not only very time consuming but also impacts heavily on strapped conservation budgets. The use of a surrogate measure for estimating biodiversity, which was simpler to estimate, would therefore be a more cost-effective way of determining species richness.

Williams & Gaston (1994) reviewed two and tested a third surrogate method for assessing species richness. The two most studied methods are environmental variables and indicator groups. The third method is the use of higher taxa in estimating the species richness of an area. I will briefly discuss the various methods below.

Environmental variables would make an excellent surrogate for establishing biodiversity largely because they are easily obtained and at relatively low costs. Currie (1991) posed the following question: “*Why, in a given environment, does one find n different species, not more or fewer, and why does n vary so greatly among environments?*” Many ecologists have sought to answer this question by investigating local and global patterns in species richness, and have tried to explain these trends in terms of environmental factors (Menge & Sutherland, 1976; Schall & Pianka, 1978; Wright, 1983; Currie & Paquin, 1987; Turner *et al.* 1988; Fresco, 1988; Currie, 1991; Rosenweig, 1992; Bolton, 1994; Tilman, 1986, 1996; Tilman *et al.*, 1996). The problem with many of these measures are that they require ground-truthing to verify the relationship between the physical factor and the number of species predicted. The three of the most well known theories to explain diversity patterns thus far are:

1. The energy hypothesis (Currie & Paquin, 1987; Currie, 1991);
2. The resource competition hypothesis (Tilman, 1986);
3. Ecological hypotheses.

The energy hypothesis predicts that in a region of approximately equal size, the energy flux per unit area will be the prime determinant of species richness (Currie, 1991). Local potential evapotranspiration (a measure of energy) was found to be the best indicator of vertebrate species richness, whereas actual evapotranspiration was the best correlate for primary producers. This theory however appears to break down in some high biomass environments which have very low species richness. The theory is able to explain why there is an upper limit to species richness but is unable to explain the reason for the number of species present. Similarly, the resource competition theory bases species richness levels on the amount and availability of resources within an area. Both these hypotheses are relatively good at explaining broad scale patterns, but are not always reliable when explaining patterns on a more local scale. Ecological hypotheses, which include factors like habitat heterogeneity and disturbance regimes (MacArthur & MacArthur, 1961; Connell, 1978; Boulinier *et al.*, 1998; Cowling *et al.*, 1992), have been found to explain local diversity values more accurately. These ecological aspects will be looked at in more detail in the following chapter.

The second surrogate method is indicator groups. Here the species richness of a particular group would be reflective of the diversity of other groups (May, 1988). As Williams & Gaston (1994) point out, this method makes bold extrapolations which need to be based on thorough and accurate data. The unit / group which is selected as an indicator must also be ubiquitous for application in other places. It may be more appropriate to look at functional groups than phylogenetic assemblages

e.g. mammalian herbivores as opposed to antelope species. The reason for this is that different groups of organisms have radiated (with respect to speciation) in different parts of the world and it thus seems unlikely that one group would have an even pattern of species radiation. An example from seaweeds would be the species radiation of the Cystoseiraceae (Phaeophyta) in southern Australia. This method I believe to be too broad to be of much help in elucidating species diversity. It would also require extensive 'ground truthing' which would make this exercise expensive.

The last surrogate method I will discuss is using higher taxa as a means of estimating species richness. If it is possible to show a relationship between higher taxa and species richness, then it would be possible to use spatial distribution of higher taxa to estimate species richness for these areas. Williams & Gaston (1994) looking at four groups of organisms, namely ferns, butterflies, passerine birds and bats, found that >79% of the variance was accounted for when using families as a surrogate for species richness. They found that species poor areas tended to have more species clumped in larger families and conversely, species rich areas had the species spread over a wider variety of families. They indicated that it was possible to use higher taxa as an estimate for species richness. However, Prance (1994) looking at biodiversity in the neotropics, found that this method did not adequately identify species hotspots and was therefore useless in the neotropics as a conservation tool. Andersen (1995), working on Australian ant faunas, found that the number of genera acted as a surrogate for species richness, but states that the method was confounded by biogeographic factors and strongly influenced by sampling intensity and area.

This chapter will focus on the distribution of the three main seaweed divisions, Chlorophyta, Phaeophyta and Rhodophyta, within the Benguela marine province. It will investigate the relationship between number of species, genera and families of these three divisions within the Benguela marine province, as well as the relative composition of these three divisions to one another. It will also examine whether higher taxa, genera and families, can be used as a surrogate for estimating species richness.

Methods

The raw data used in this chapter are the same as that used in Chapter 3. The species have been divided in the three principal seaweed divisions, viz. Chlorophyta, Phaeophyta and Rhodophyta. They were further divided into families and the information displayed graphically in Appendix D. The raw data for these analyses may be found in Appendix B.

The relative ratios of these three divisions were looked at to see any interaction of these taxa as one moves from Angola to Cape Agulhas. The following formula was used (Cheney, 1977; Kapraun, 1980; Bolton, 1986):

$$\text{ratio} = (R + C)/P$$

where

- R* - Number of Rhodophytes species
- C* - Number of Chlorophytes species
- P* - Number of Phaeophytes species

To see whether numbers of genera or families could be used as a surrogate measure for species richness, a number of floras were compared. They were divided into the three major seaweed divisions and the results displayed on an XY-scatter graph. The result obtained show an initial linear increase, which starts to flatten out with increasing diversity. The X-Axis, species richness, was then subjected to a square root transformation to obtain a better linear relationship.

The following floras were used:

- (1) Namibia (Wynne, 1986; Lawson *et al.*, 1990; personal data)
- (2) South Africa West Coast (Stegenga *et al.*, 1997);
- (3) Tristan da Cunha (Baardseth, 1941);
- (4) Tropical West Africa (Lawson & John, 1987);
- (5) Southern Australia (Womersley, 1984, 1987, 1994, 1996);
- (6) New Zealand (Adams, 1994);
- (7) Macquarie Island (Ricker, 1987)
- (8) Chile (Santelices, 1989);
- (9) North Eastern USA (Taylor, 1957);
- (10) South Eastern USA (Schneider & Searles, 1991);
- (11) California (Abbott & Hollenberg, 1976);

The Benguela marine province was divided into three groups of increasing size, viz. NNAM-SWC, NNAM-FB and NNAM-SFB. The reason for doing this is that:

1. The NNAM-SWC represents the Benguela marine province proper, and is therefore an accurate representation of this flora; and,
2. To test whether the inclusion of False Bay (FB - a floristic 'hiatus') and the transition zone with the Agulhas flora (SFB) had an effect on the overall pattern.

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Results

Fig. 4.1 (A-C) illustrates the number of species, genera and families found in the three divisions of seaweeds for the eight regions outlined in Table 3.1. The species richness pattern observed in Fig. 3.7 of decreasing total seaweed species richness from south to north along the Benguela marine province, is reflected within each of the three seaweed divisions. It should be noted that the pattern within the Chlorophyta (Fig. 4.1 A) is not as pronounced as in the Phaeophyta and Rhodophyta.

The Chlorophyta (Fig. 4.1 A) in general have approximately two genera per family, and three species per genus. The pattern of species richness is strongly mirrored with respect to the genera, and to some extent within the families, of this group. There appears to be a slight dip in species richness in the northwestern Cape, and a slight rise in southern Angola.

The Phaeophyta (Fig. 4.1 B) have marginally more species than genera, and about one and a half genera per family. As a result the genera and families closely follow the general species richness pattern along the coast. There is a significant increase in brown algae between northern Namibia and southern Angola.

Rhodophyta (Fig. 4.1 C), having the greatest species richness, reflect the general pattern most clearly, as would be expected. The genera closely follow the species richness pattern at an approximate rate of one and a half species per genus, whereas the number of families do not differ substantially between regions. There is a slight increase in families in the southwestern Cape and False Bay. The slight dip in species richness in the northwestern Cape which was noted in the Chlorophyta, is also reflected within the Rhodophyta.

Table 4.1. lists the ratio of the above three divisions to one another from Angola to Cape Agulhas. As can be seen the ratio is not consistent within the Benguela marine province; there is an increase in the ratio as one moves north, largely related to the drop in numbers of Phaeophyta. Note that northern and central Namibia are considerably higher than the other values, while southern Angola is similar to northwestern Cape to False Bay.

Table 4.1: Ratio of the three seaweed divisions to one another as one moves from north to south.

$(R + C)/P$	ANG	NNAM	CNAM	SNAM	NWC	SWC	FB	SFB
Species	6.31	10.50	10.45	7.89	6.19	6.36	6.16	4.09

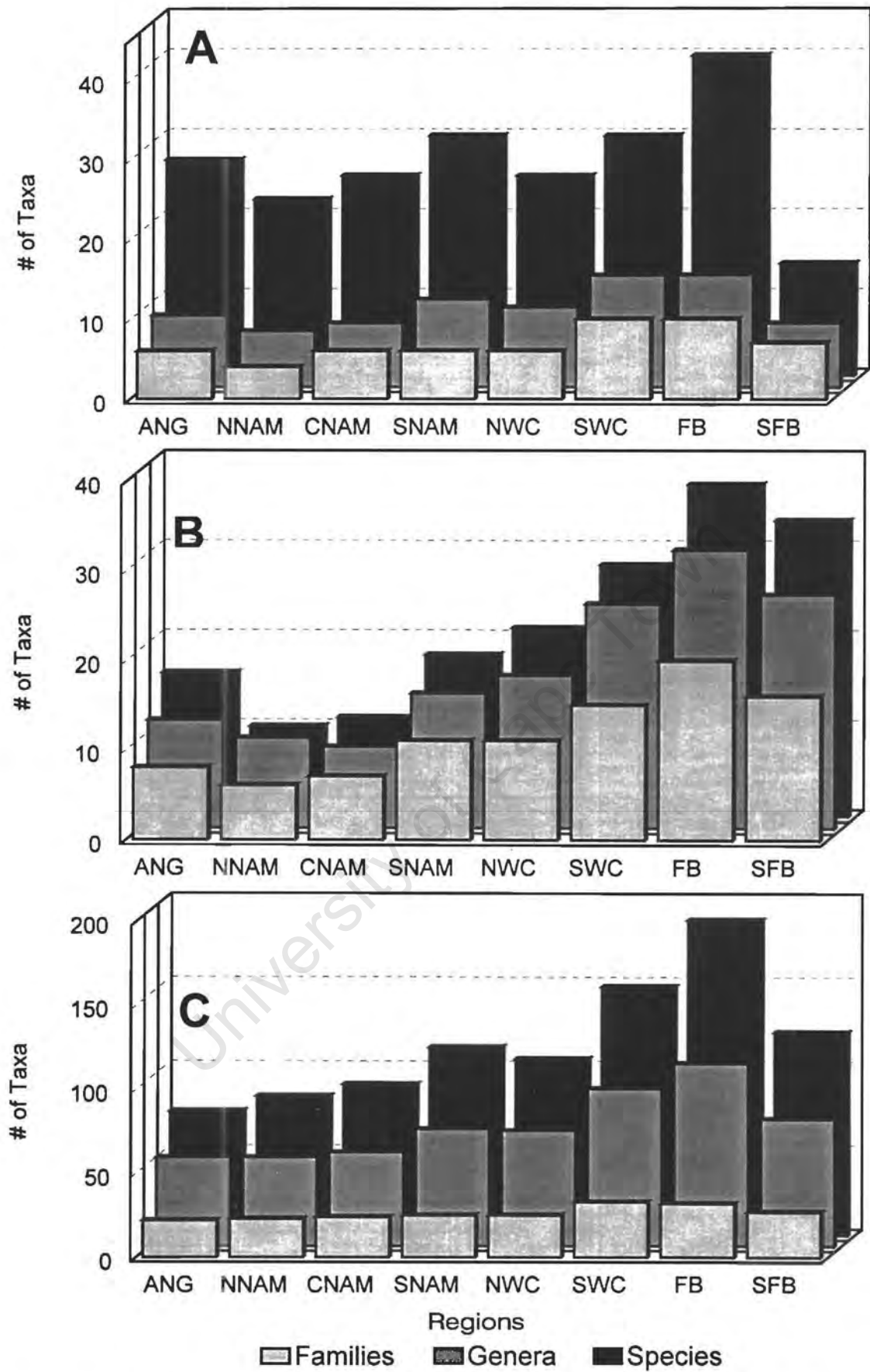


Fig. 4.1 : Number of taxa found at species, genus and family levels, for the various regions of the Benguela marine province (Table 3.1). A - Chlorophyta; B - Phaeophyta; C - Rhodophyta.

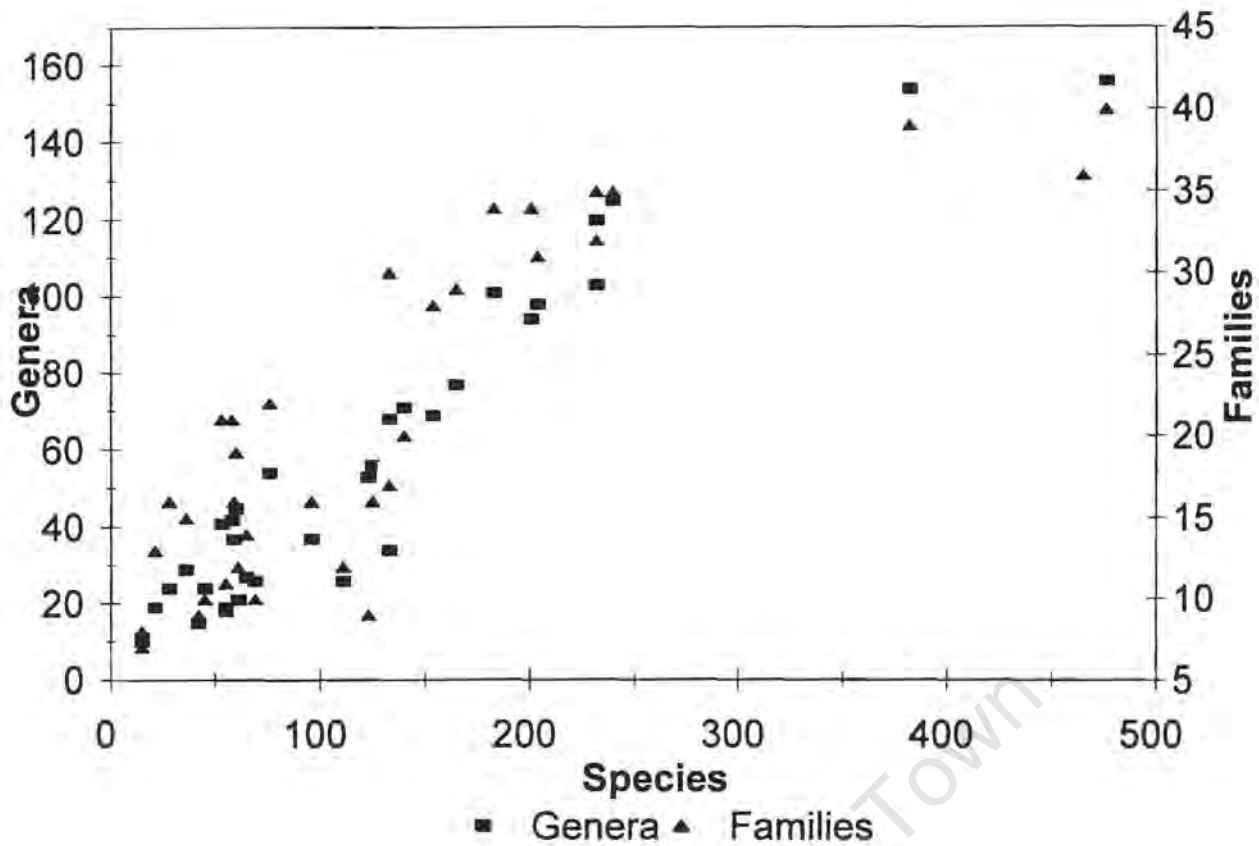


Fig. 4.2: Relationship between species richness and genera (Axis - Y1) and families (Axis - Y2), for 11 florae (see Methods).

There is thus an apparent relationship between number of species and genera in Fig. 4.1, and to a lesser extent between species and families. Fig. 4.2 shows this relationship for the eleven world seaweed florae listed earlier. As can be seen there appears to be an initial linear relation between species richness and genera and families for the various florae. Above a certain species number (ca. 250 species) the number of species per higher taxon appears to plane-out gradually.

The species data were then transformed using a square root transformation. The transformed species richness was then regressed against number of genera and families, Figs. 4.3 & 4.4 respectively. Separate regressions were performed on the three divisions, i.e. the relation between the number of species within the genera or family of the specific division, as well as for the combined divisions. The regressions were set to intercept the Y-axis at "0", since when there are "0" species there will be "0" families. The results of these correlations are given in Table 4.2.

For the purpose of predicting species richness the regressions were repeated for species vs genera (within the respective division), and the Y-intercept was calculated. Even though these regressions do not pass through the origin, an alternative explanation may be argued. As families, genera and

species are discrete entities, i.e. one does not get half a family for example, a more feasible starting point for the regression would be a Y-axis (i.e. the family or genus axis) value of 1. It is also unlikely that an area would only comprise one family or genus. In the latter's case it would be more practicable to simply count all the species. The use of a surrogate measure would have its greatest applicability within areas of large species diversity. Towards this purpose total species richness for the various floras were regressed against the number of genera within each division. This would determine if there is a possibility of assessing total seaweed species richness using just one indicator group. One could theoretically use Rhodophyta genus richness to predict total species richness for an area / region. These results are listed in Table 4.2.

Table 4.2: Results of regression analysis in Figs. 4.3 & 4.4 below, for species richness vs genera and families. The r^2 value, Degrees of Freedom (DOF), Gradient, and Y intercept are given.

	All	Chlorophyta	Phaeophyta	Rhodophyta
Genera				
<i>Surrogacy for Divisio</i>				
<i>Spp. Richness</i>				
r^2	0.87	0.82	0.90	0.91
DOF	11	11	11	11
Gradient	9.8	3.0	5.7	7.6
<i>Y - computed</i>				
r^2	0.96	0.84	0.96	0.95
Gradient	12.0	3.5	7.4	9.4
Y intercept	-49.7	-4.7	-17.3	-30.6
<i>Surrogacy for Total</i>				
<i>Spp. Richness</i>				
r^2	0.96	0.66	0.80	0.84
Gradient	12.0	1.34	3.85	6.85
Y intercept	-49.7	-2.64	-26.78	-20.32
Families				
<i>Surrogacy for Divisio</i>				
<i>Spp. Richness</i>				
r^2	0.71	0.73	0.57	0.5
DOF	11	11	11	11
Gradient	3.2	1.46	2.2	2.0
<i>Y - computed</i>				
r^2	0.87	0.79	0.64	0.83
Gradient	2.3	1.2	1.7	1.3
Y intercept	20.1	2.7	5.1	12.8

(All regressions significant to $p < 0.005$)

As can be seen from Table 4.2 even though families are significantly correlated with species richness to $p < 0.005$ the r^2 values are relatively low compared to the genera values. The predictive value of these regressions would therefore also be low. For the Genera vs Species Richness the r^2 values are, however, very high, above 0.80. The r^2 values for the computed y-intercept considerably improve the predictive ability of these correlations. Of particular note are the relatively high r^2 values for Phaeophyta and Rhodophyta surrogate regressions for total species richness. The Phaeophyta and Rhodophyta both have r^2 values ≥ 0.8 which may be sufficient to use as surrogate measures, while the Chlorophyta value of 0.66 is probably too low. By far the best measure is the one that uses *all* three divisions generic richness (0.96).

Figures 4.3 & 4.4 graphically illustrate the above regressions, i.e. where $y = 0$. In Fig. 4.3, the Rhodophyta has a greater genus:species ratio than the other two divisions. With respect to the family:species ratio (Fig.4.4) the Phaeophytes have the largest ratio. In both Figures 4.3 & 4.4 the Chlorophytes show the smallest genus:species and family:species ratios. The Benguela marine province is positioned close to the regression lines and within the 95% confidence limits. This indicates that the various ratios do not differ from the regression line, thus the addition of FB and SFB did not affect the general correlation.

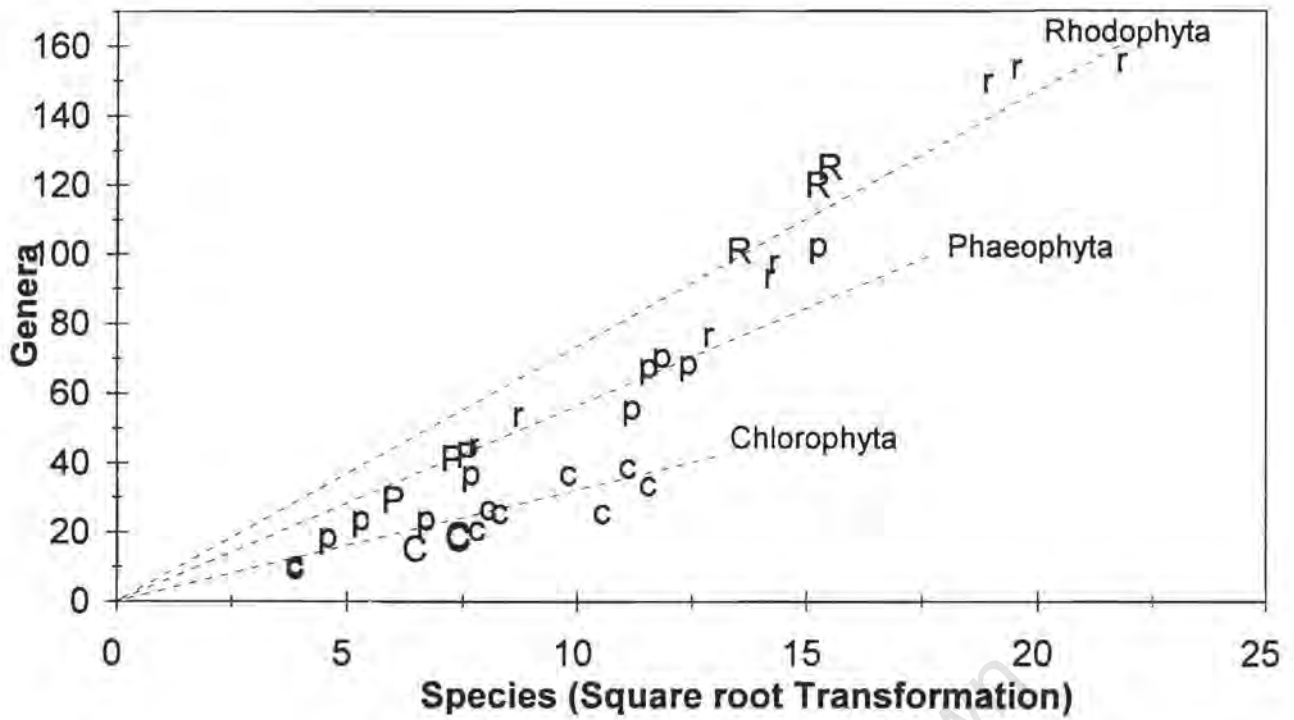


Fig. 4.3: Relationship between species richness and number of genera for various floras. C - Chlorophyta; P - Phaeophyta; R - Rhodophyta. Capital letters indicate the Benguela marine province groupings, viz. NNAM - SWC; NNAM - FB; & NNAM - SFB.

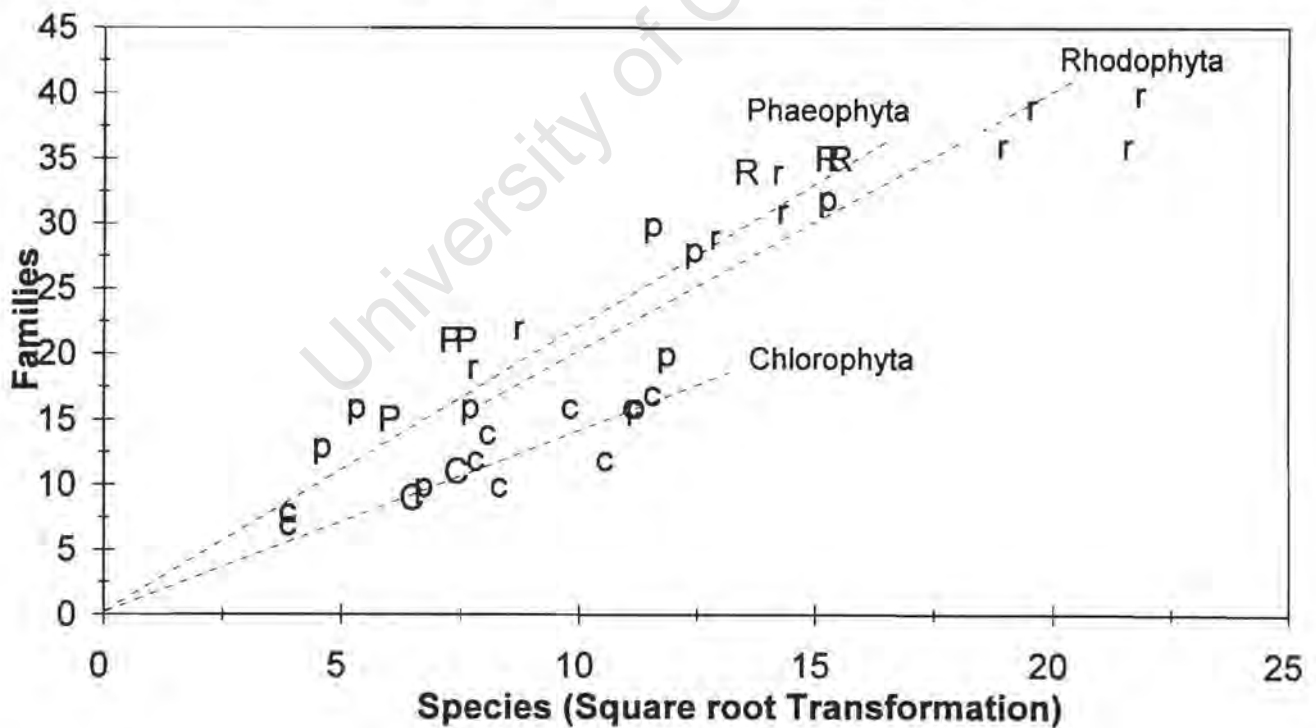


Fig. 4.4: Relationship between species richness and number of families for various floras. C - Chlorophyta; P - Phaeophyta; R - Rhodophyta. Capital letters indicate the Benguela marine province groupings, viz. NNAM - SWC; NNAM - FB; & NNAM - SFB.

As can be seen in Table 4.2 the division Chlorophyta r^2 values are lower than those for the other two divisions. I investigated this with respect to the eight defined areas of the Benguela marine province and divided the data into the following categories:

- 1 - 1 species / genus
- 2 - 2 species / genus
- 3 - 3 species / genus
- ≥ 4 - 4 or more species / genus

I then worked out what percentage each category comprised for each area. These values were then plotted on an accumulative graph for each division (Fig. 4.5).

As can be seen from Fig. 4.5, the Phaeophyta and Rhodophyta for all the different regions show a consistent pattern, with very little variation between regions Angola to Cape Agulhas, whereas the Chlorophyta show a clear difference in composition between regions. The regions in the Chlorophyta may be divided into three relatively loose groupings:

- (1) Angola to central Namibia (ANG - CNAM);
- (2) Southern Namibia, northwestern Cape and False Bay (SNAM - NWC & FB); and
- (3) Southwestern Cape and the south coast transition zone (SWC & SFB).

The relative rate of increase for the three divisions should also be noted. The Chlorophytes, as previously noted, have a relatively high species to genus level, whereas, the Rhodophytes have relatively few genera ($\pm 10\%$) with three or more species. The Phaeophytes have an even lower ratio, with most of the genera being represented by a single species.

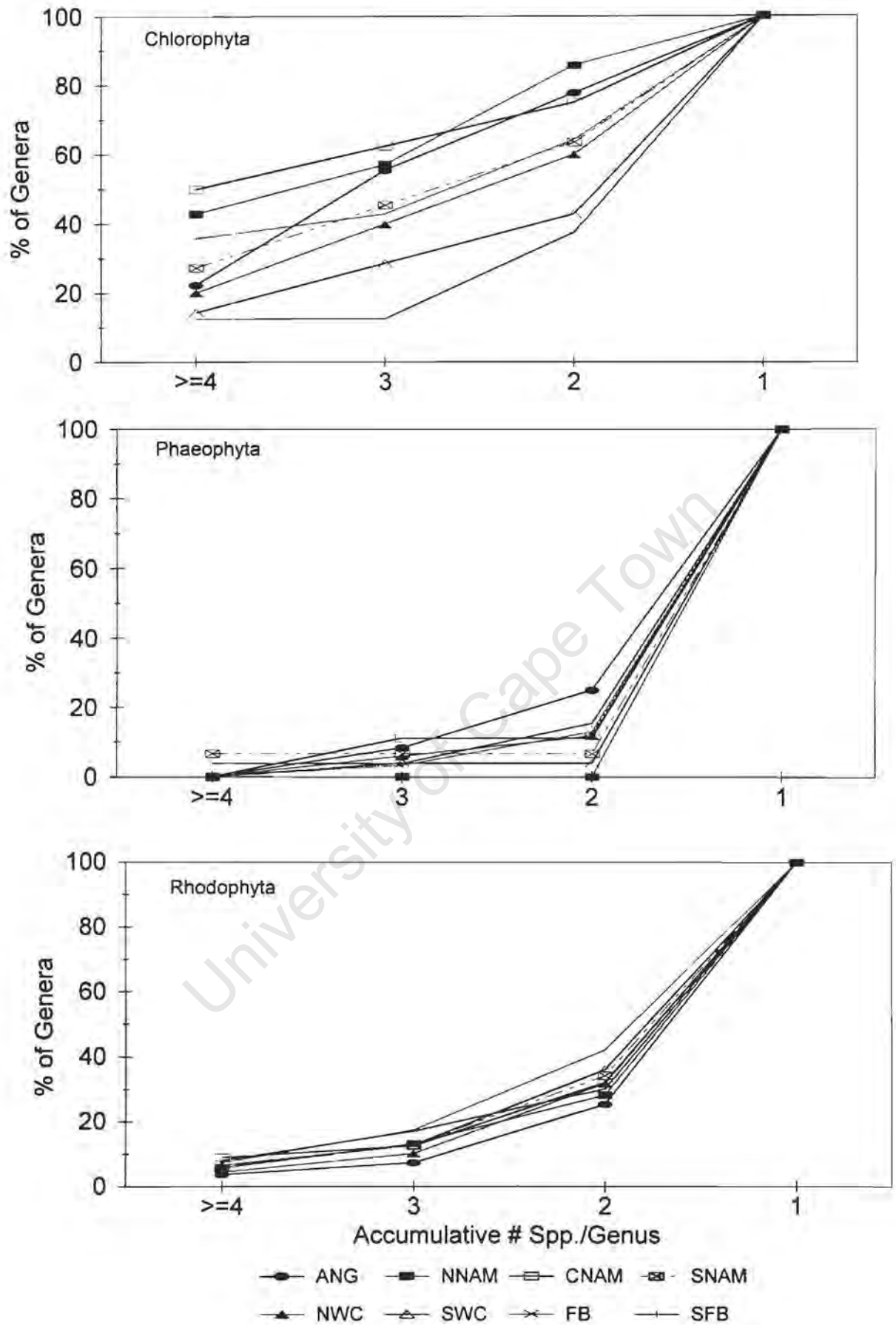


Fig.4.5: Accumulative percentage of number of genera in each of the categories, outlined above, for the eight regions defined in Table 3.1.

Discussion

The patterns observed within the three seaweed divisions (Fig. 4.1) are the same as the generalised picture of species richness along the coast (Fig. 3.7). A slight dip however was noted in the Chlorophytes and Rhodophytes within the northwestern Cape. This may be partly due to under collection in this area, although as was seen in Chapter 3 (Fig. 3.10) this region lacks the habitat heterogeneity and availability of the adjacent regions. The 'dip' is therefore probably a true reflection of the low species richness in this region. This 'dip' is not reflected within the Phaeophytes, but there are not many of these species present in this region so it is probably not a good indicator at such low species richness.

The Chlorophytes have a high proportion of species to genera and families (Fig. 4.1, 4.5), and this appears to represent a global pattern (Fig. 4.3 & 4.4). The r^2 values (coefficient of determination) for the species richness versus genera and families correlations were also relatively high (Table 4.2). The fact that this division has a high species richness to family ratio and a good coefficient of determination makes it a good candidate for surrogacy. The accuracy of this surrogate measure is tested later in this discussion.

The Phaeophytes have a relatively close association between species and higher taxonomic levels. This is largely due to the fact that there are very few species within each genus and few genera within each family on average in any particular flora (Fig. 4.1 B, 4.3, 4.4, 4.5). It should be noted, however, that the brown algae show the weakest correlation between species and family richness (Table 4.2 - computed y-axis). Andersen (1995), however, points out that even though a low species:genus ratio may give a reliable surrogate, it also limits its value with respect to surveying (discussed in more detail below).

The species richness of Phaeophyta declines very steeply from south to north within the Benguela marine province. This pattern is also seen in Table 4.1, where the high ratios obtained for northern and central Namibia are partly due to the disappearance of the fucoids and other brown seaweeds which occur further south. Most of the Benguela marine province is devoid of fucoids (Bolton, 1994). Prof. J. J. Bolton (pers.comm.) believes that as the fucoids are not good dispersers, and if they are removed from an environment recolonization will be slow. As was noted in Chapter 3 (Fig. 3.10), there is greater instability and lack of substrate as one moves north. Thus the local extinction of a fucoid would make recolonization an unlikely event. The distribution of fucoids in the Benguela marine province also does not extend much further than the southern end of the flora.

This would seem to imply a temperature limitation, in that these plants are at the end of their distribution range. The ratios in Table 4.1 are also indicative of the TWINSPAN and DCA results obtained in Chapter 3. The northern and central regions are not floristically different as was seen in the previously noted, but the relative species proportions of the three seaweed divisions found there is markedly different from areas further south. This again supports the designation of a sub province in this area.

Within the Rhodophyta, in the Benguela marine province, only 10 - 15% of the genera had ≥ 3 species per genus (Fig. 4.5). About the same amount had two species per genus; while the remainder only had a single species per genus. This would again seem to be a more general pattern within the division (Fig. 4.3), where the regression line is close to a 1.5 species to genus ratio (on average). The species to genus ratio for the Benguela marine province is even smaller in the Phaeophyta (Fig. 4.5), with most of the genera being represented by a single species. On a more global level, however, the ratio of species to genus, on average, is slightly higher than those of the Rhodophyta. It would nevertheless appear that both these divisions have relatively low species to genus ratios, and therefore the potential use as surrogate measures is diminished, despite having very high coefficients of determination.

The observed relationship between species and higher taxonomic levels (Fig. 4.1) was the motivation behind investigating higher taxa as a surrogate for species richness. As was noted in the results, there is a good correlation between species richness and number of genera, and a poorer relationship between species richness and families (despite the latter being significant). Combining the entire flora data gave a greater r^2 value for the families regression than separating the individual divisions. The correlation between species and families is interesting but the use of families for predicting species richness would be relatively useless for the reason given above. The practicality of using seaweed families is potentially problematic as the systematics of these higher taxa are often controversial.

The relationship however between species and genera seemed to be more promising as a predictive tool than that between species and families. This taxonomic level is a more attractive surrogate as genera are often easier to determine within the algae than families, as characters that are used to define algal families are often vague and not easily observed. The r^2 values obtained are very high for all groups, indicating that most of the variance is explained by the regression line. As was seen in Table 4.2, better r^2 values were obtained from regressions where the regression line was not forced through the origin (reasons as to why these results may be more applicable are given in the results

section). The major purpose of using this method as a surrogate would be to gain a relatively accurate estimate of species richness in the shortest and cheapest manner possible.

To test the accuracy of the various surrogate measures obtained, the actual species richness of the various areas were compared with the predicted species richness calculated using the results obtained from the regression analyses (Table 4.2). The percentage error was calculated as follows:

$$\% \text{ Error} = \frac{\text{Difference between Actual and Predicted Species Richness}}{\text{Actual Species Richness}} \times 100$$

The percentages were then arcsine transformed, the mean and standard deviation calculated, and the results transformed back to percentages. The results of the percentage error, standard deviation and the associated species : genus ratios are displayed in Table 4.3. This percentage error can occur on either side of the actual species richness. The measures for the three division's 'ability to determine' their respective division's species richness by means of genera was tested, as well as the ability of these divisions to individually predict total seaweed species richness. As can be seen from Table 4.3, the predictions are relatively inaccurate as a species richness indicator for a particular division, as well as for the total species richness. The best predictors of total species richness was the Additive and the All Genera surrogacy measures. Both of these methods generated relatively similar average percentage errors, although the additive method had a greater margin of error (s^2). It would therefore probably be more accurate to use the All Genera method.

Table 4.3: Comparison of the species : genus ratios, % error on average and the standard deviation around that average of the various surrogate measures. (**Bold** - a measure of the total species richness, i.e. total species richness : specific Division(s) genus richness; **Non-Bold** - a measure of the species richness of the respective Division : genus richness of that Division; **Additive** - the sum of the 3 divisions calculated separately).

Genera Surrogate Measure	Spp:Genus ratio	% Error on Average	
		%	s^2
Additive	2.0	9.7	2.4
Chlorophyta	2.8	20.7	3.1
Phaeophyta	1.7	10.5	1.8
Rhodophyta	2.1	9.3	1.0
All Genera	2.0	9.9	1.9
Chlorophyta	16.9	ERR	
Phaeophyta	8.4	20.5	4.5
Rhodophyta	3.5	15.4	2.3

(ERR - Some of the values exceeded 100 % and could not be arcsine transformed)

As was mentioned above, a problem associated with using higher taxa as surrogate measures is that predictability is dependant on the species : higher taxon ratio. The reason is that taxa are positive integers (e.g. you can not find 6.34 families in an area, there are either 6 or 7) and, as a result, a single family represents a number of species. Therefore, the bigger the ratio of the higher taxonomic level relative to the species richness the more imprecise the species richness estimate (Table 4.3). The use of this method would therefore be dependant on the purpose and degree of precision required. There is however, a relatively large degree of error. Since the error is a percentage, as the total species richness increases, the actual number of species unaccounted or over estimated for increases substantially e.g.

10% error on a species of 50 = 5 species either way i.e. a range of 45 - 55 species.

500 = 50 species either way i.e. a range of 450 - 550 species

The value of such surrogate measures are therefore doubtful in practical terms, as its greatest potential usage would be in areas of large species richness.

The question as to why there should be any relation between species richness and higher taxonomic levels nevertheless poses an interesting conundrum. The first idea that came to mind was that taxonomists divide things up into "boxes" and continue to fill them until the "boxes" get too full,

they then redistribute and / or divide up those “boxes” into smaller “boxes”. As a result there is a relatively even spread of organisms in the various “boxes”. This is not entirely the case, although there may be some degree of truth. As a result I looked at the relative proportions of the number of species to families in various floras to see whether there was any general pattern, worldwide.

The method was as follows:

1. The data set comprised species lists obtained for the 10 floras listed above;
2. The number of species (n_f) in any particular family (f) was divided by the total species richness of its flora (S) to find the percentage of the Flora accounted for by family “ f ” i.e. $(n_f / S) \times 100$
3. A frequency histogram with an interval of 1 % was then employed to group the above data into classes, to see the spread of the relative size of different families with respect to the Flora. This value may be referred to as Frequency f (F_f).
4. To standardize the “ F_f ” values for various floras, as there was a variable number of families per Flora, “ F_f ” was converted to a percentage of its own Flora’s number of families (ΣF).
i.e. $(F_f / \Sigma F) \times 100$
5. The percentage data obtained in step 4 were arc sine transformed (Zar, 1984) and the mean and standard deviation was calculated for each frequency class for all the Floras, and the results sine transformed back to percentage data (Table 4.4). All family frequency values exceeding 7 were combined. It was noticed that in all the floras there was a continuous decline in values from percentages 1 - 7, after which there were usually only 1 - 2 families represented between the frequencies 8 - 16 for the various Floras. The last category was therefore established to group these last remaining families.

Table 4.4: The average percentage of families in a flora with a specified species / family frequency category.

<i>Frequency Category</i>	<i>Average Percentage</i>	<i>Standard Deviation</i>
1	50.28	0.21
2	17.10	0.23
3	8.12	0.17
4	5.43	0.16
5	1.55	0.66
6	1.18	0.45
7	1.01	0.39
>7	3.81	0.17

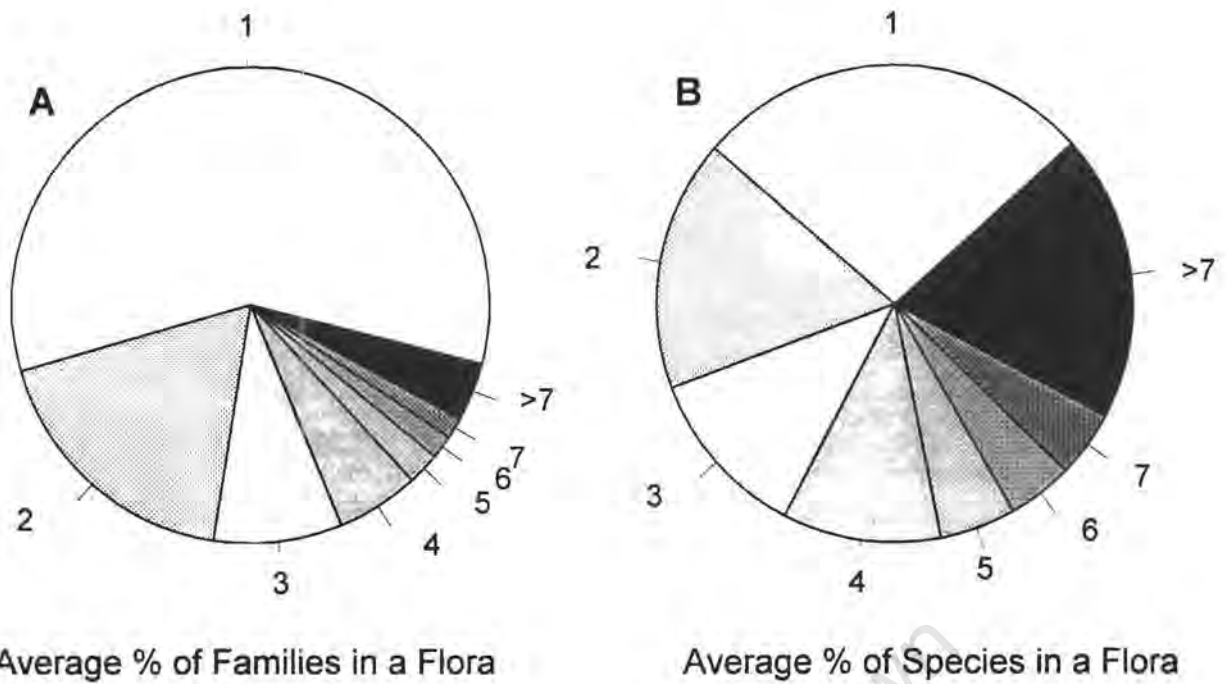


Fig. 4.6: The percentage of families and species present on average in a seaweed flora. **A** - represents the average proportion of families with a specified percentage (numbers 1 - >7) of the floras species richness (n_f/S); **B** - represents the proportion of species that are found in the specified family frequency categories (1 - >7).

As can be seen from Fig. 4.6A most of the families present in a flora represent families with a low proportion of the floras species richness, and relatively few families with a high proportion of the floras species richness. Fig. 4.6B shows the proportion of species, in a flora, represented by the specific family frequency categories. Comparing diagrams A and B, it becomes evident that category “>7”, which represents only a small percentage of the total number of families (A), comprises approximately 25 % of the total species richness of a Flora (B). Conversely, category “1”, which represents 60% of the families (A), only comprises 25% of the total species richness (B). The surprising fact about Fig. 4.6A is that there is a definite structure to seaweed floras, with very little variation around average (Table 4.4). This would imply that Flora structure is independent of geographical location or conditions.

The formation of a hypothetical flora would be dependant on:

1. How isolated it is from a propagule source, which may be seen as the rate of colonization of species into the new area; and / or
2. The ability of the colonizing species to speciate.

It can be assumed that there is an upper limit to the species richness in any particular area (Currie, 1991), and as a result a concomitant number of niches to fill. As a new area is colonized it is likely to be filled by those species that belong to groups which are good dispersers and/or able to speciate rapidly. Assuming two areas have the same colonization and speciation rates, but differ with respect to upper limits to species richness, then the area with low species richness limits would be under-represented with respect to families, since the niche space is rapidly filled by these two groups of organisms and the number of niche space left for other groups is considerably reduced. In areas with a high species richness limit, it takes a longer period for the niche space to be saturated and therefore allows more families to colonize / speciate (e.g. southern Australia). As a result, there are more families than would be found on average in these areas. This pattern has been found by Williams & Gaston (1994).

In conclusion it should be noted that the above relation between species richness and number of genera or families is directly related to the structure of the Flora. As was seen in Table 4.1 and published literature (Cheney, 1977; Kapraun, 1980; John & Lawson, 1997), the relative ratios of Rhodophyta, Phaeophyta and Chlorophyta differ within a flora and from region to region. This would explain why using a division as a surrogate for species richness was not very accurate (Table 4.3) as the relative taxonomic abundance of the three divisions vary between floras. Despite the relative ratio of the major seaweed divisions varying from place to place, the 'Flora Family Structure' remains similar. As a result looking at the relation between a select few families and interpolating species richness from them may result in inaccurate findings if these select groups do not reflect the "Flora Structure" above. The more a sampled area reflects this structure the greater the accuracy. It can be assumed, based on the above hypothetical scenario, that if all the dominant families (i.e. those with the high species richness) are sampled first and the minor families later then the overall 'Flora structure' will be approached. This may be a problem in that an abundant family with respect to species is not necessarily an abundant with respect to biomass. If a family comprises species / genera which are relatively small and / or live in interstitial habitats (e.g. Ceramiaceae - a large family with many physically small genera - *Pleonosporium*, *Ceramium*, *Callithamnion*, *Gymnothamnion*, *Lomathamnion*, etc.) these taxa may go undetected. Although with the above method, only a single species of the genus would need to be detected as the surrogate measure is

genus dependant and not species. If a dominant family is left out, for whatever reason, it could have a big effect on the accuracy of the prediction. The reason is that its place in the 'Flora structure' will be 'filled' by a family with a lower species : family ratio, this would result in an over estimation of species richness for the sampled groups.

Species richness can be estimated using a number of genera as a surrogate, but there are complications with using this method. As has been pointed out, the accuracy is dependant on the species : genus ratio, and as a result, as this ratio goes up the value of the measure goes up but the accuracy decreases. The use of this method would therefore be dictated by the purpose of the measure required. At best it could give a crude estimate of species richness within an area.

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The Effect of Wave Action, Sand Inundation, Mussels, Limpets and Whelks on Seaweed α -Diversity within the Lower Eulittoral Zone in Namibia

Introduction

As was seen in the previous chapter, there is much interest in biodiversity, its quantification and explanation of patterns observed. Much ecological work has been done in the marine intertidal with respect to factors affecting community composition and interaction in time and space (e.g. Paine, 1966; Menge & Sutherland, 1976, 1987; Connell, 1972; Branch, 1984). Species richness and diversity have, to a limited extent, been looked at on a community scale. Some authors have focused on the diversity of all the macro-organisms occurring on the shore (e.g. Paine, 1971, 1974; Lubchenco, 1978; Hawkins & Hartnoll, 1980; Seapy & Littler, 1982; Branch, 1984; McQuaid & Branch 1984, 1985); others have concentrated on specific groups of organisms such as meiofauna (Gibbons, 1988); limpets (Branch, 1981); and seaweed (Daly & Mathieson, 1977). The latter paper deals with the effects of sand inundation on intertidal seaweeds and some invertebrates, and alludes to its effects on seaweed diversity but does not deal with it specifically. Seaweeds, as a functional group, have been little studied with respect to their diversity patterns or the factors responsible for them.

Species diversity largely consists of two components, viz. species richness (i.e. the number of species per unit area) and equitability (or evenness of composition). Two communities with the same species richness will not necessarily have the same diversity, as the latter would be dependant on the relative abundance of the various species in each community. A diverse community would therefore not only have a high species richness, but also have the species evenly spread with respect to abundance. Conversely a community which is dominated by a single or a few species would have a low diversity, despite having numerous rare species.

Species diversity may also be studied on various scales, namely α -, β -, γ -diversity (Whittaker, 1972; Cody, 1975, 1983; Westoby, 1985). α -diversity looks at species richness / species diversity at a local level, i.e. it is the number of species present in a homogeneous community. β -diversity looks

at species turnover along an environmental or habitat gradient (Cowling *et al.* 1992). This level of diversity will be looked at in Chapter 7. γ -diversity or Δ -diversity (Whittaker, 1972) compares species of equivalent habitats from different geographical regions. The latter has been tackled in the marine environment, to a certain extent, by Bolton (1994) and Norton *et al.* (1996). Bolton, in particular, looked at the species richness of various floras on a global scale, where he compared species richness to latitudinal positioning. Seaweeds, unlike most terrestrial and marine organisms, do not follow the pattern of greatest diversity within the tropics decreasing into temperate regions. The lack of this pattern within seaweeds was also commented on by Norton *et al.* (1996), who reviewed algal biodiversity.

At the α -diversity level, a number of models exist to explain the co-existence of species. These include niche differentiation, regeneration niche theory, disturbance, mass effects, history and regional species pool size. These theories are not mutually exclusive but interact at various levels, and may be used to describe the complex patterns observed within biotic communities.

Niche differentiation theory states that co-existing species are dissimilar enough for competitive exclusion not to occur, i.e. the number of species present in an area is therefore limited by the number of niches available (Newman, 1982; Crawley, 1986). Niche space is dependant on micro-habitat heterogeneity, this may take the form of abiotic as well as biotic structure. In the rocky shore intertidal, the topography of the rocks, slope of the shore, degree of sand inundation, and community structure all play a role in creating niche space. As was seen in the previous chapter, this process may be responsible for the family structure observed for the various seaweed floras tested.

The regeneration niche hypothesis states that species which have overlapping requirements may co-exist if they differ in their regeneration requirements (Grubb, 1977). This theory is primarily concerned with the life history strategies of the plant species in the community.

Disturbance may also play an important role in maintaining species richness by preventing the exclusion of 'competitively weaker' species. Providing the disturbance is not too severe, as to be deleterious to the species, an intermediate level of disturbance will maintain maximum species richness (Connell, 1978; Fox, 1979; Huston, 1979; Walker & Peet, 1983; Denslow, 1985). Disturbances which may be applicable to the intertidal marine environment are: the degree of wave exposure, sand inundation, heavy rains during low tides, herbivory, etc.

Species which are not able to sustain a presence in a community are often able to persist due to the continual rain of propagules from adjacent areas (Shmida & Ellner, 1984; Shmida & Wilson, 1985). This may explain the existence of some *Ulva* spp., often primary succession plants, in late succession intertidal communities. These 'r' selected plants (MacArthur & Wilson, 1967) are able to produce large numbers of spores that germinate and grow quickly, therefore being able to take advantage of any spaces that are made available.

The history and size of the regional species pool are also fundamental in explaining the species richness of an area (Ricklefs, 1987; Caley & Schluter, 1997; Hugueny, 1997). If a region has a low species richness, any local homogenous sub-group will also have a low species richness. The reason for a low or high regional species richness may often be the result of the historical past. An example is the depauperate seaweed flora of tropical west Africa. It has been proposed by van den Hoek (1975) that during the Pleistocene glaciation the winter 20°C isotherm was shifted approximately 15-20° towards the equator. This would have led to the local extinction of the east Atlantic tropical flora, while leaving the west Atlantic flora relatively unaffected. The rich seaweed flora of southern Australia has also been partially attributed to historical factors, namely the long geological period of stable sea surface temperatures (van den Hoek, 1984; Bolton, 1996).

This chapter will look at the intertidal communities on the Namibian coast and examine the factors which may be controlling seaweed α -diversity within the lower eulittoral zone. Understanding diversity at a more local level may help us to understand the patterns at larger scales.

As was seen in the preceding chapters the seaweed flora of Namibia forms the northern part of the Benguela marine province (Lüning, 1990; Engledow *et al.* 1992; Bolton & Anderson, 1997). A decline in seaweed species numbers occurs as one moves from southwestern Cape (South Africa) through to northern Namibia (Chapters 3 & 4). This chapter will attempt to establish what local factors are responsible for affecting species richness / diversity. Two physical factors (sand inundation and degree of wave exposure) and three biological factors (the abundance of limpets, mussels and whelks) are investigated.

The degree of wave action was chosen since it is an important determinant of biomass (McQuaid & Branch 1984) and trophic composition on the South African west coast (McQuaid & Branch, 1985; McQuaid *et al.* 1985). As was seen in chapter 2 the level of sand inundation varies along the

Namibian coast, being more extreme in the central and northern regions of the coast. An increase in sand inundation has been found to decrease seaweed species diversity and biomass (Littler, 1980; Seapy & Littler, 1982), and it would therefore appear to be a good factor to consider within this study.

The biological factors, of limpets and mussels, were chosen since they comprise the dominant herbivores and space competitors within the low-eulittoral zone respectively (Branch, 1981, 1984, 1985; Branch & Griffiths, 1988), therefore having an affect through herbivory and resource allocation. The whelks were also examined, not because they formed a dominant component of the shore, or affected the seaweeds directly, but because they are predatory on the other two animals mentioned above. They would therefore have an indirect effect on the seaweeds by their effect on the limpets and mussels.

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Method

The quadrat biomass data were used for this analysis. Only those quadrats occurring within the vertical height 0 - 50 cm were used in this analysis. This zone was selected as:

- (1) It has the greatest diversity with respect to seaweeds in the intertidal;
- (2) The tidal range varies little in the region sampled, but as was noted in the General Methods chapter (Chapter 2), there is a considerable difference in the gradients of shores. This would result in differential zone size between shores of different slopes. The 0-50 cm height range encompassed the lower intertidal “seaweed” zone on all the shores or part thereof, thus making the zone comparable from site to site;
- (3) The quadrat size is relatively small and unlikely to span more than one “zone”, even on the steepest shores;
- (4) This chapter is concerned with number and diversity of species present in a particular unit area, not the actual species concerned. Therefore, so long as the sample is drawn from a relatively homogeneous set, the results are comparable.

The most abundant animal species that comprised the three defined groups, limpets, mussels and whelks, are set out in the Table 5.1 below.

Table 5.1: List of animal species within each of the categories: limpets, mussels and whelks.

Limpets	Mussels	Whelks
<i>Patella argenvillei</i>	<i>Aulacomya ater</i>	<i>Burnupena catarrhacta</i>
<i>Patella granatina</i>	<i>Choromytilus meridionalis</i>	<i>Burnupena cincta</i>
<i>Patella granularis</i>	<i>Mytilus galloprovincialis</i>	<i>Nucella cingulata</i>
<i>Patella miniata</i>	<i>Semimytilus algosus</i>	<i>Nucella dubia</i>
<i>Patella barbara</i>	<i>Perna perna</i>	<i>Nucella squamosa</i>
<i>Patella safiana</i>		
<i>Helcion</i> spp.		
<i>Crepidula</i> spp.		
<i>Fissurella mutabilis</i>		

Statistics

The data were analysed using the following statistics

(Computer package - Statgraphics version 6; For details on statistics see Zar, 1984):

- (i) Linear regression (Two-tailed test);
- (ii) Stepwise multiple regression (Two-tailed test);
- (iii) One-way Analysis of Variance (with Multiple Range Test).

The following indices were used as indicators of seaweed diversity: (See General Methods)

- (i) Species Richness;
- (ii) Shannon-Wiener Index (Shannon & Wiener, 1963);
- (iii) Simpson's Dominance Index (Simpson, 1949);
- (iv) Modified Hill's Ratio (Alatalo, 1981).

The data were analysed as a number of different units. Initially the entire data set comprising all those quadrats found in the 0 - 50 cm category were analysed for overall trends. The data set was then divided into quadrats with sand inundation greater than or less than 350 g/quadrat (5.6 kg.m⁻²) (See Results for explanation). The latter category was further divided into quadrats with or without mussels and/or limpets. As the whelks do not form a substantial component of Namibian shores with respect to abundance, therefore have been omitted from the major analyses. A short description of the impacts of whelks are given at the end of the results section.

RESULTS

Broad Scale Patterns

Seaweed species richness was positively correlated with total seaweed biomass ($r = 0.50$; $p < 0.05$; $n = 183$) and negatively correlated with Simpson's Dominance Index ($r = 0.5$; $p < 0.05$; $n = 183$). A stepwise regression analysis revealed that seaweed biomass and dominance seemed to be the best correlates for explaining seaweed species richness ($r = 0.66$; $p < 0.05$; $n = 183$). An interactive coefficient was designed, viz. Seaweed Biomass / Dominance Index, and regressed against Species richness (Log-Log Graph). The interaction of these three variables accounted for 60 % of the variance ($r = 0.78$; $n = 183$). The next step was to ascertain what factors were affecting seaweed dominance and/or biomass.

Table 5.2: The relationship between wave exposure and sand on seaweed species richness and diversity, and seaweed, mussel and limpet biomass (Correlation sign and r ; n in parenthesis; 2-Tailed test).

	WAVE EXPOSURE r	SAND > 0g (Log) r
Species Richness	-0.18 (183)	0.8 n.s. (102)
Shannon-Wiener Index	-0.13* (183)	0.12 n.s. (102)
Simpson's Index	0.12* (183)	-0.11 n.s. (102)
Algal Biomass (Log)	-0.18 (183)	0.5 n.s. (102)
Mussel Biomass >0g (Log)	0.24 (139)	0.11 n.s. (75)
Limpet Biomass >0g (Log)	0.7 n.s. (119)	-0.25 * (55)

(**Bold** = $p < 0.05$; * = $p < 0.10$; **n.s.** = Not Significant)

Species richness and algal biomass were found to be negatively correlated with degree of wave exposure (Table 5.2); however, the Shannon-Wiener Index and Simpson's Dominance Index were not significantly correlated ($p < 0.10$). Mussel biomass was positively correlated with wave exposure, while limpet biomass was negatively correlated with sand inundation to the $p < 10\%$

significance level (only quadrats containing limpets and mussels were used in these calculations). Sand inundation was, however, not correlated with seaweed species richness, diversity or algal, limpet or mussel biomass, for the entire data set. This result came as surprise since there visibly seemed to be some effect observed whilst sampling. I therefore plotted seaweed diversity against sand inundation (Fig. 5.1). It became apparent from the figure that sand inundation had no effect on seaweed diversity or abundance below a certain critical level of sand.

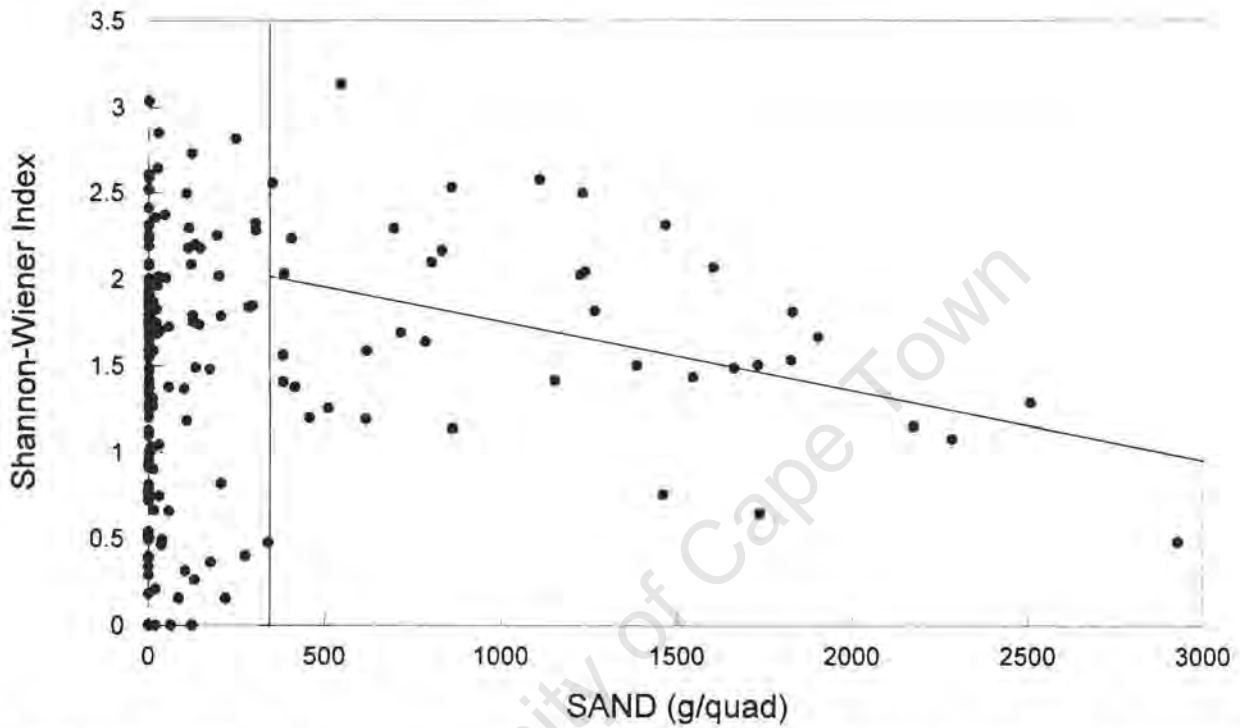


Fig. 5.1: The relationship between seaweed diversity and degree of sand inundation. The vertical line indicates the sand quantities below which sand does not have an effect.

Sand inundation was strongly correlated with species diversity (Shannon-Wiener Index) and Simpson's Dominance Index in quadrats with sand greater than 350 g/quadrat (5.6 kg.m⁻²) (Fig.5.1, Table 5.3). The data were therefore divided into two major categories, namely sand greater and less than 5.6 kg.m⁻².

Sand Quantities > 5.6 kg.m⁻² (Table 5.3)

Table 5.3: Correlation sign and *r* for seaweed richness and diversity in quadrats with sand quantities > 5.6 kg.m⁻² (2-Tailed test)

	Sand n = 39	Wave Exposure n = 39	Seaweed Biomass (Log) n = 39	Mussel Biomass >0g (Log) n = 24	Limpet Biomass >0g n = 13
Species Richness	-0.28*	-0.31*	0.27*	0.09 n.s.	-0.64
Species Diversity					
Shannon-Wiener	-0.42	0.19 n.s.	0.29*	0.47	-0.41 n.s.
Equitability					
Simpson's Dominance Index	0.45	-0.30*	-0.35	-0.49	0.34 n.s.
Hill's Index	-0.27*	0.44	0.26	0.43	0.07 n.s.

(**Bold** = $p < 0.05$; * = $p < 0.10$; **n.s.** = Not Significant)

Species richness was not significantly correlated with sand; however, a stepwise multiple regression revealed that the combined effect of sand inundation and wave exposure were the best factors in describing the species richness in these quadrats (Adjusted $r = 0.39$, $p < 0.05$; $n = 39$). Wave exposure was positively correlated with Hill's Equitability Index, while seaweed biomass was negatively correlated with Simpson's Dominance Index. Thus wave exposure and seaweed biomass both appear to affect the equitability of seaweed diversity. Mussel biomass was positively correlated with seaweed diversity and Hill's Index, and negatively correlated with seaweed dominance. This is as a result of the inverse relationship between sand inundation and seaweed diversity, since mussel biomass is negatively correlated with sand inundation ($r = 0.52$, $n = 22$, $p < 0.011$). Limpet biomass was significantly correlated with seaweed species richness; however, limpet biomass was found to be negatively correlated with increased sand inundation, and these quadrats had relatively low limpet biomass (average = 2.28g; median = 0g; mode = 0g; maximum value = 29.39g). At such low biomass values limpets would have little to no effect on the intertidal seaweed.

Sand Quantities < 5.6 kg.m⁻²

The following section deals with the factors that are responsible for seaweed diversity and richness values obtained in quadrats with sand less than 350g / quadrat.

Table 5.4: Correlation sign and *r* values for seaweed richness and diversity in quadrats with sand quantities < 5.6 kg.m⁻².

	Wave Exposure <i>n</i> = 144	Seaweed Biomass (Log) <i>n</i> = 144	Mussel Biomass >0g <i>n</i> = 115	Limpet Biomass > 0g <i>n</i> = 106
Species Richness	-0.16*	0.37	-0.19	0.19
Species Diversity Shannon-Wiener	-0.16*	0.38	-0.31	0.24
Equitability Simpson's Index	-0.53	-0.32	0.31	-0.19
Hill's Index	-0.03 n.s.	-0.11 n.s.	0.14 n.s.	-0.03 n.s.

(**Bold** = $p < 0.05$; * = $p < 0.10$; **n.s.** = Not Significant)

In Table 5.4 species diversity and richness are negatively correlated with mussel biomass and positively correlated with limpet and seaweed biomass. Mussel biomass was positively correlated with Simpson's Dominance Index, which is negatively correlated with species richness. Mussels are therefore probably having an effect on seaweed diversity by affecting seaweed dominance, and not by affecting the seaweed biomass (since there was no significant correlation between seaweed and mussel biomass). Mussel biomass was also correlated with degree of wave exposure ($r = 0.22$, $n = 115$). Wave exposure is correlated with species richness to the 6 % significance level (Table 5.4); despite this correlation being non significant (at the 5% significance level) in this sand category, it is highly significant in the subcategory mussel biomass greater than 0g/quadrat ($r = 0.29$, $p < 0.05$; $n = 115$). Simpson's index is also correlated with the degree of wave action, however the results obtained for wave action are not representative of the factor since wave exposure is a covariate of mussel biomass. To see the effect of wave action, all those quadrats where mussels were absent were regressed against seaweed diversity and equitability. Species diversity was positively correlated with wave exposure in all quadrats where mussels were absent ($r = 0.39$, $p < 0.05$; $n = 43$) and Simpson's Index was negatively correlated ($r = 0.36$, $p < 0.05$; $n = 43$).

Mussel and Limpet Effect on Seaweed Diversity

Table 5.5: Results of an Analysis of Variance's (ANOVA) Multiple Range Test and the correlation slope coefficient for seaweed diversity versus mussel and limpet biomass under various treatments.(MUSSELS > 0 (+LIM) = All quadrats where mussels present; MUSSELS > 0 (-LIM) = All quadrats where mussels were present but limpets were absent; etc.)(Sand < 350g/Quadrat)

	One-way ANOVA Multiple Range Test	Regression Slope Coefficients Seaweed Diversity vs	
		Mussels	Limpets
	Homogeneous Groups		
Mussels > 0 (+LIM)	A	-0.0015	0.0065 n.s.
Limpets > 0 (+MUS)	A	-0.0013	0.0061
Mussels + Limpets > 0	A	-0.0015	0.0065
Mussels > 0 (-LIM)	A	-0.0015 n.s.	-----
Limpets > 0 (-MUS)	B	-----	0.008 n.s.

(**Bold** = $p < 0.05$; **n.s.** = Not Significant)

The analysis was taken one step further in looking at the specific interaction among mussel biomass, limpet biomass and species diversity. The data analysis comprised those quadrats with sand < 350 g/quadrat and containing mussels and/or limpets. The results in Table 5.5 assume no interaction between mussels and limpets, or their combined effect on seaweed diversity.

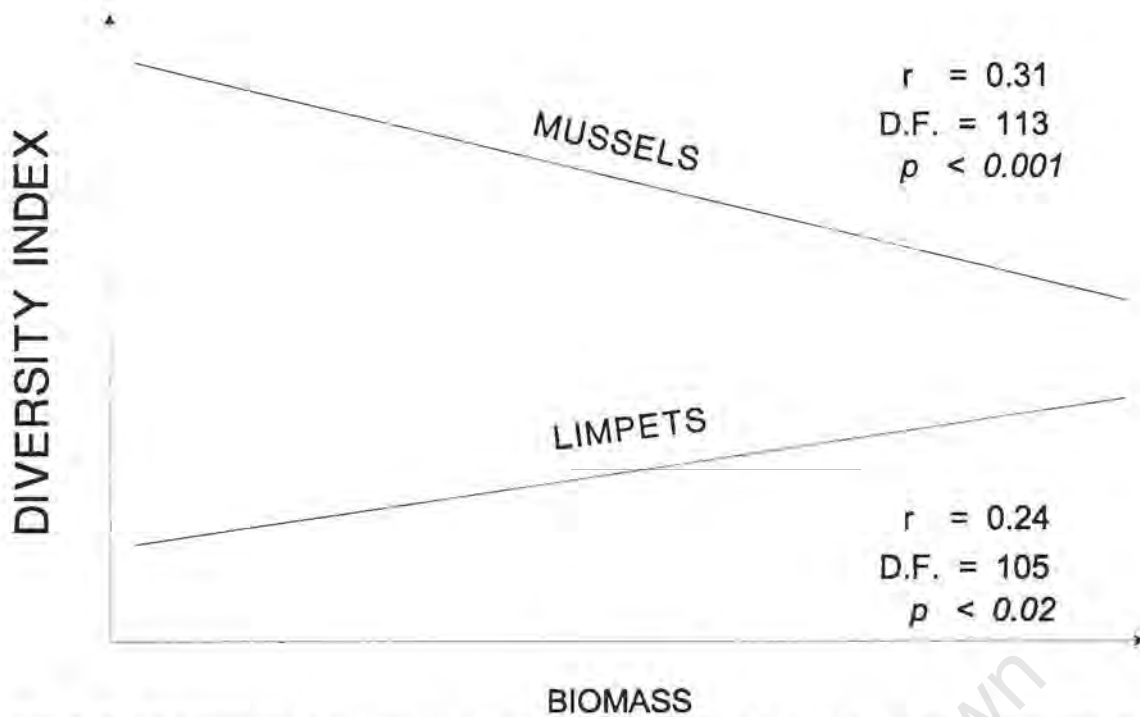


Fig. 5.2: Diagrammatic representation of the relationship between limpet and mussel biomass against seaweed diversity (Shannon-Wiener Index).

Mussel biomass is negatively correlated with seaweed species diversity, while limpet biomass is positively correlated with species diversity (Fig. 5.2). The latter correlation was found to be spurious for three main reasons. Firstly, limpet and/or mussel biomass > 5 g/quadrat were significantly negatively correlated to each other. This is probably owing to the fact that they compete with one another for space. Secondly, only 7 quadrats out of 106 possessed limpets only, the remaining 99 contained mussels. Therefore, the relationship between limpet biomass and species diversity is the result of an inverse relationship between mussel biomass and species diversity, as there is correlation between mussels and limpets. Thirdly, the validity of the mussel vs seaweed relationship was confirmed by means of a one-way ANOVA and multiple range test, which included analysis of quadrats with and without limpets and mussels (Table 5.5). A stepwise multiple regression also confirmed mussel biomass as being the single most important factor (i.e. after seaweed biomass and dominance were removed).

The impact of whelks on intertidal organisms

As was pointed out in the introduction to this chapter, whelks would probably have an effect on seaweed diversity through their effect as predators on the limpets and mussels. There was however, no correlation between whelk biomass and mussel or limpet biomass. Whelks were only present in 18% of the quadrats sampled, and 85% of these had biomass values < 10g / quadrat (wet weight). 50% of the sites sampled had whelks present, but only two of these sites had them in amounts greater than 10g / quadrat. Both these sites occurred in relatively sheltered areas within the Lüderitz region, viz. Elizabeth Bay and Agate Beach. Whelks were found to be negatively correlated with degree of wave exposure ($r = 0.31, p < 0.05; n = 33$) and positively correlated with seaweed biomass ($r = 0.29, p < 0.05; n = 33$). This group of organisms was present in 10 % of quadrats with sand levels in excess of 350 g/quadrat; these quadrats came from sites of moderate exposure and sand inundation and the whelks were in relatively low abundance (<10g / quadrat).

Discussion

Seaweed species richness in the lower eulittoral zone on the Namibian coast may be explained by two factors which are intrinsic components of diversity, namely the degree of dominance by a single or a few species, and the total seaweed biomass present. These factors however do not provide a mechanism for the control of species richness/diversity. The following discussion will attempt to isolate those factors that may be important in providing a mechanism for seaweed species diversity on this coast.

Broad scale patterns

There appeared to be one major factor affecting species richness, diversity or equitability, the degree of wave exposure. Wave exposure would affect seaweed species richness and diversity by controlling the amount of seaweed biomass. Wave exposed shores on the west coast of southern Africa tend to be dominated by filter-feeders (McQuaid & Branch, 1984, 1985; Branch, 1984, 1985). The latter are known to out-compete seaweeds for space in wave exposed areas (McQuaid & Branch, 1985), which would result in decreased algal biomass. The next most important factor appeared to be the degree of sand inundation. As was seen in Fig. 5.1, the relationship between sand and seaweed diversity only occurred after the levels of sand exceeded 5.6 kg.m^{-2} .

Sand quantities > 5.6 kg.m^{-2}

Sand inundation directly affects species diversity by controlling dominance. Areas with increased sand tend to be dominated by a few sand tolerant species (Daly & Mathieson, 1977). There would be exclusion of less resilient, psammophobic species owing to the physical stresses of sand scouring and smothering, and the competition for suitable space from other seaweed or sessile invertebrate species. Seaweeds that often survive these physical forces are usually tough and wiry, e.g. *Ahnfeldtiopsis* sp.. Sand would also favour those seaweed species with perennial crustose bases or rhizomatous holdfasts which would be able to spread without the need to reproduce (Vermeij, 1978; Littler *et al.*, 1983). A local example would be *Mazzaella capensis* which has a long-lived crust (Bolton & Joska, 1993). Daly and Mathieson (1977) point out that perennial psammophilic seaweeds exhibit incomplete or asexual life histories, which would ensure a stable genetic base. These could partially account for the increased dominance values in areas of high sand inundation.

The degree of wave exposure and sand inundation emerged as the dominant factors affecting species richness / diversity. The synergistic combination of these two factors could increase the effect that the sand would have on the seaweed diversity. Not only would it have a smothering effect, but also a scouring one, dependent on the degree of wave action. As a result only those species which are tolerant of these stressful conditions would be able to survive in these areas.

Mussel biomass was correlated with seaweed dominance and diversity, but as was pointed out this is a spurious correlation (see Results). It would therefore seem that seaweed diversity and species richness in areas with a mid to high degree of sand inundation could be explained by the mechanism outlined above.

Sand quantities < 5.6 kg.m⁻²

In areas with sand inundation below 5.6 kg.m⁻², mussel biomass seems to be the dominant determinant of seaweed diversity. Mussel biomass was shown to be dependent on the degree of wave exposure. As a result, an increase in wave exposure would result in an increase in mussel biomass and a concomitant decrease in seaweed diversity.

Mussel and limpet effect on seaweed diversity

Space is recognized as the primary limiting resource to sessile organisms in the lower eulittoral zone (Paine, 1966; Connell, 1961; Dayton, 1971, 1975; Branch, 1984). As mussels and seaweeds are sessile organisms that compete for this resource, some effect on seaweed diversity is expected. Mussels were found to be positively correlated with degree of wave exposure. Therefore, an increase in wave exposure would result in an increase in mussel biomass and a concomitant decrease in seaweed biomass (owing to competition for space). The algae could theoretically grow on the mussel shells, and some do, but the data seems to indicate that this is not a significant quantity. This could be due to the some property of the mussel shell (e.g. exfoliation of the outter-layer) or an anti-fouling agent released by the mussel. Mussels are also effective filter-feeders and probably reduce the number of spores settling by removing them from the water column. Unlike McQuaid and Branch (1984, 1985) the current study found that seaweed biomass was positively correlated with seaweed diversity; therefore a decrease in seaweed biomass would result in a low seaweed diversity. Mussels could affect diversity through favouring species with specific life-

history / form traits. Since mussels are filter feeders, seaweed species that produce gametes / spores which settle and attach quickly after release or are released during low tide will be better able to establish than those that do not. Species that rely on a mass propagule production (see Introduction) may be disadvantaged in areas with high mussel densities, as their reproductive success is dependant on high numbers of spores or propagules.

In quadrats without mussels however, an increase in the degree of wave exposure results in an increase in seaweed species diversity. As long as the wave action remains non-deleterious in the force it exerts i.e. intermediate disturbance hypothesis (Connell, 1978; Fox, 1979), it could serve to increase seaweed biomass by increasing nutrient availability with increasing wave action (Mann & Lazier 1991).

The results also indicate that wave exposure has a negative effect on Simpson's Index. This means that increased wave exposure reduces the probability of dominance by a single species of seaweed. Conceptually, increased water movement could result in increased randomness of recruitment, thus preventing dominance of a single species. Wave action could also clear space within the intertidal allowing new species to recruit and preventing dominance by a single species (i.e. creating a disturbance regime). Wave action therefore negatively affects seaweed diversity indirectly through its effect on mussel biomass, while having a direct positive effect when mussels are absent.

Limpets were found to have no significant effect on seaweed diversity within the zone tested. Limpet biomass was relatively low in most quadrats however, which would account for no apparent effect observed on seaweed diversity.

The Effect of whelks within the lower intertidal

As was seen from the results whelks do not seem to have an effect on seaweed diversity through their impact on the sessile invertebrates, limpets and mussels. This is largely due to the fact that most of the shores sampled and others observed on the south western coast of South Africa and Namibia are extremely exposed. Whelks are not able to remain attached under these conditions, and are therefore restricted to calmer waters. This was confirmed by the results obtained, showing a negative correlation between whelk biomass and degree of wave exposure. It was also noted that there was a strong positive correlation between seaweed biomass and whelks. This could be due to the seaweeds providing refugia for the whelks against water movement and possibly desiccation. The whelks did not seem to affect the limpet or mussel populations in the lower intertidal significantly. This could be because these organisms are highly mobile and are probably feeding on the extensive limpet populations higher up on the shore and living on the lower shore during low tide. The whelks were also virtually absent from quadrats with sand > 350 g / quadrat, showing an intolerance to sand. Despite being found on at least 50 % of the sites sampled, the relative abundance in these areas was very small. Whelks, in conclusion, may have an effect on sheltered shores within another zone on the shore; but do not appear to have a significant affect within the lower intertidal. They also do not seem to have a great effect on the Namibian coast in general, as most of the coast is inhospitable to these whelk species, i.e. being mostly wave exposed, sand inundated or a combination of both.

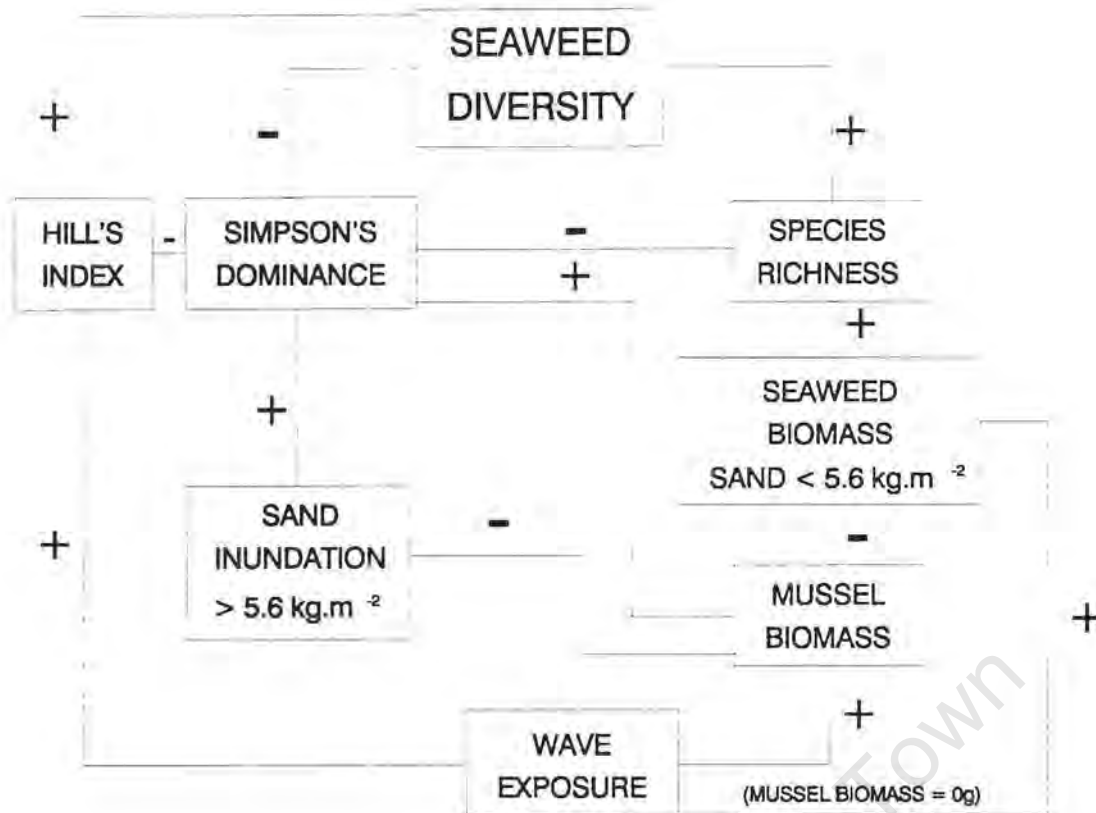


Fig. 5.3: Model representing significant correlations between various factors and seaweed diversity.

(+ and - : represent positive and negative correlations respectively)

There would therefore appear to be a system of interacting factors that affect seaweed species diversity (Fig. 5.3). Species diversity on the Namibian coast is primarily affected by sand inundation (with degree of wave exposure as a secondary co-factor), in areas where sand was over 5.6 kg.m^{-2} , via a process of seaweed dominance. At sand levels less than 5.6 kg.m^{-2} , mussel biomass becomes the single most important factor affecting seaweed diversity. Mussel biomass is however determined by the degree of wave exposure (i.e. the latter has an indirect control on seaweed diversity). In areas where mussels are absent, degree of wave exposure has a direct positive effect on seaweed species richness / diversity via seaweed biomass and equitability. Sand inundation, the degree of wave exposure and mussel biomass appear to be the three most important factors in determining seaweed diversity in the lower eulittoral zone on the Namibian coast. These findings are in agreement with Littler and Littler's (1981) hypothesis that biological interactions increase as physical gradients become less harsh.

In conclusion, this method of data analysis provides a framework for more defined experimental studies which test the various hypotheses proposed. The degree of variation explained in the data at this level of study is relatively small, but it does, however, give insight into more broad scale processes taking place over a large area. To obtain more a comprehensive account of the factors controlling seaweed diversity, a closer look at specific interactions between intertidal organisms and their physical environment is required. This study has also highlighted the importance of lower limits of various factors on seaweed diversity on this coast e.g. degree of sand inundation, below which there is little or no effect. A correlation type analysis can only point to possible cause and effect relationships, and therefore experimental testing is required to gain confirmation of these findings.

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Intertidal Zonation Patterns on the Namibian Coast

Introduction

One of the most striking features of any intertidal shore around the coastlines of the world are the banding patterns formed by intertidal organisms. This banding pattern has been referred to as zonation or vertical distribution (South & Whittick, 1987; Russell, 1991). A fair amount of similarity in the pattern of zonation has been observed by various authors. As a result various systems have been developed to describe these zonation patterns, Stephenson & Stephenson (1949, 1972) and Lewis (1961, 1964) being the first notable researchers in this field. As Lewis (1961) points out, rocky shore zonation patterns are a biological phenomenon despite any underlying physical factors responsible for them. Lewis and the Stephensons divided the rocky shore intertidal into three principal zones based on the presence of particular kinds of organisms, and once a zone was identified the species present were simply recorded. The biggest problem with this method is that it is subjective and largely descriptive (Russell, 1991; Field & Griffiths, 1991), and the shores are forced into a zonation structure. Russell (1991) alludes to the fact that this method of zone determination is predominantly two dimensional in that it focuses on the uppermost layer of organisms zonation pattern, thus other zonation patterns that are present go undetected. Russell (1991) illustrates this point using a zonation study by Den Hartog (1959), on a dyke in the Netherlands, which comprised three layers of organisms each with their own zonation pattern. The three-dimensional aspect of the shore is therefore lost in the Lewis and Stephenson & Stephenson method.

The system followed in this study of marine benthic organisms zonation is outlined in Russell (1991). This scheme makes use of three primary zones, viz. the supralittoral, the eulittoral and the sublittoral. They may be defined as follows:

- (1) Supralittoral - the upper boundary of this zone is the point where sea spray ceases to have an effect on community structure. The upper reaches of this zone is predominantly terrestrial in nature while the lower reaches are more marine. The lower limit is usually characterized by the presence of lichens or cyanobacteria.
- (2) Eulittoral - this is the area of the shore that is periodically totally immersed in seawater. The lower boundary of this zone is set at the mean low water mark of spring tides, while the upper limits are raised by increasing wave action. The upper limit on the southwestern African coast

may be seen as the upper extent of *Nodilittorina* snails and/or *Porphyra* spp.. This zone is usually divisible into three sub-zones based on biological entities, but as Russell (1991) states, the structural and environmental complexity of this zone are too complex to come to a consistent global pattern.

(3) Sublittoral - this zone is constantly immersed by seawater.

Each of these zones may be further subdivided into the communities that form the observed banding patterns on rocky shores. This is done by means of more quantitative analysis where samples are taken randomly or in some set format, the results are then analysed and an objective zonation pattern is deduced (Russell, 1991). The advantage of such a system is increased objectivity, but it is also a more time consuming exercise.

Literature on the intertidal zonation patterns on the Namibian coast comprises the publications of Penrith and Kensley (1970 a, b), Kensley and Penrith (1980), and Lawson *et al.* (1990). Only the latter paper deals with the algae in any degree of detail. The papers of Penrith and Kensley focus predominantly on the fauna found in and around Lüderitz, Rocky Point and False Cape Fria. These studies contain a subjective, descriptive account of the shores, lacking a quantitative element. This chapter will summarize the generalized vertical zonation patterns observed within the eulittoral zone (as described above) on the Namibian coast, based on more objective data.

As was noted in Chapter 3, Namibia has a similar flora to that found on the west coast of South Africa. The latter area has been relatively well researched and documented with respect to vertical zonation on the various shores (Isaac, 1937; Stephenson, 1939, 1943, 1944; Stephenson & Stephenson, 1972; Lüning, 1990; Bolton & Anderson, 1997; Stegenga *et al.* 1997). As the west coast of southern Africa is relatively straight, a "typical" shore on this coast is exposed to a relatively high degree of wave exposure (Field & Griffiths, 1991). These shores usually have a zone of *Littorina* spp. and blue-green filamentous algae (*Lyngbya* sp. & *Calothrix* sp.) on the lower supralittoral zone (Stegenga *et al.*, 1997). Moving down the shore, this zone usually gives rise to a zone containing *Porphyra* spp., which often extends down into the mid-eulittoral (Stegenga *et al.* 1997). This genus is, however, patchy in its vertical distribution and may be seasonal depending on the location (N.Griffin, pers. comm.). Lower down the shore is a zone relatively devoid of macroscopic plant material. *Patella granularis* is the most noticeable organism within this zone, but the seaweeds (*Nothogenia ovalis* & *N.erinacea*), trochid (*Oxystele variegata*), limpet (*Helcion pectunculus*), and barnacles (*Octomeris angulosa*, *Chthamalus dentatus*, & *Tetraclita serrata*) may also be present (McQuaid *et al.* 1985; Branch & Griffiths, 1988; Lüning, 1990; Field & Griffiths, 1991). The latter organisms are more abundant on the south coast, but seem to decrease in number

and biomass as one moves north (Branch & Griffiths, 1988). Tufts of *Chordariopsis capensis*, which are restricted to shallows pools, depressions and crevices, may also be found in this region. In the lower part of this zone patches of *Aeodes orbitosa* and *Splachnidium rugosum* (Stegenga *et al.*, 1997; Bolton & Anderson, 1997) are present, with the limpet *Patella granatina* becoming more abundant (Field & Griffiths, 1991). In areas where sand inundation occurs, *Mazzaella capensis* replaces *Aeodes orbitosa* as the dominant seaweed in this zone (R.J. Anderson, pers. comm.). At the lower end of this zone on some shores the polychaete tube worm *Gunnerea capensis* forms extensive beds, these may stretch all the way down to the lower limit of the eulittoral zone (Field & Griffiths, 1991). This *Patella* zone then gives way to a mussel zone, which may also extend all the way down to the spring low water mark if wave exposure is extreme. The dominant species are the ribbed mussel (*Aulacomya ater*), the black mussel (*Choromytilus meridionalis*), and the introduced black mussel (*Mytilus galloprovincialis*) (Field & Griffiths, 1991). The density and extent of mussels is positively related to the degree of wave exposure (McQuaid *et al.*, 1985; McQuaid & Branch, 1985). The following zone comprises two abundant species, the pear-shaped limpet *Patella cochlear* and the crustose coralline alga *Spongites yendoi* (Stegenga *et al.*, 1997). This lower eulittoral zone is more prominent in the south and decreases as one moves further north. This rapidly becomes a mixed algae dominated zone, with *Champia lumbricalis*, *Plocamium cornutum*, *Sarcothalia stiriata*, *Bifurcaria brassicaeformis* and articulated coralline species dominating (McQuaid *et al.* 1985; Bolton & Anderson, 1997; Stegenga *et al.*, 1997). The dominant animals in this zone are *Patella argenvillei*, sea anemones and mussels. In more sheltered areas *Sarcothalia stiriata* is replaced by *Gigartina polycarpa* (Bolton & Anderson, 1997; Stegenga *et al.* 1997). This zone extends to the intertidal fringe, where the first kelp plants are encountered, *Ecklonia maxima*, *Laminaria pallida* (southern Benguela marine province) and *Laminaria schinzii* (replaces *L. pallida* from Ysterfontein northwards as the dominant species) (Stegenga *et al.*, 1997).

On the south coast, and west / south coast overlap, *Patella cochlear* replaces *Patella argenvillei* as the dominant low intertidal animal (Branch & Griffiths, 1988; Jackelman *et al.*, 1991). This species together with *Spongites yendoi*, forms a distinctive zone in the lower intertidal region. There is also an increase in turf-forming species e.g. *Caulacanthus ustulatus*, *Centroceras clavulatum* and *Gelidium pristoides* on these shores. The dominant mussel on these shores is *Perna perna*, which is described as a circum-tropical species by Penrith & Kensley (1970b).

As was mentioned above, this chapter will look at the intertidal zonation patterns observed on the Namibian coast, using abundance data. Those organisms which are the most abundant within the various regions will be discussed.

Methods

The raw data used in this analysis comprise the biomass data collected in 1990 and 1992, as well as data from the NamDeb offshore island's survey in 1995. The latter data are in the form of percentage cover, and therefore biomass values are not available (see Chapter 2 - General Methods). Also, the sampling method differed in that quadrats were taken within subjectively chosen zones. As a result the zones indicated do not represent height above spring low water mark (SLWM), but bands of transition as one moves from the SLWM to SHWM (spring high water mark). The reason for incorporating these data is the lack of sheltered and sand inundated shores in the Lüderitz area. Two sites from the 1995 data set were used, comprising six transects at each site. The data are from the sheltered side of Possession Island, and the partially sand inundated (only lower intertidal reaches) semi-exposed site of Pomona Island (no measure of degree of inundation was taken).

To establish relation between sites an average biomass of each of the species was taken for each shore. This was done by adding the biomass values (wet weight) of each species and dividing this by the number of quadrats. The data was then subjected to a detrended correspondence analysis (DCA) to reveal site similarity. This data differs from previous DCA analyses in that it takes the actual biomass values of the respective species into consideration.

General zonation patterns of dominant species of fauna and flora were objectively established using the following method. The total biomass for each quadrat was calculated and the percentage representation of each species in the quadrat ascertained. Species with a representation of greater than or equal to 10% were considered to constitute a dominant / abundant species. This percentage was arbitrarily chosen, but it is believed to be a fair and useful assumption. Those species that met the criteria were extracted together with their biomass value. Each species was assigned a height value corresponding to its quadrat height. This data was then sorted according to site and species, and plotted on area kite diagrams, with the Y-axis representing relative abundance, and the X-axis height above spring low water mark (SLWM), for each site. A scale bar, in g / quadrat, is given for the regions and sites of the biomass data.

It was noted that the various sites in southern and central Namibia had much in common with each other, so a composite shore diagram of the basic zonation pattern was done for these two areas. Only those species which were representative of 40% or more of the sites were considered in the area kite diagrams of vertical zonation patterns. The remaining species were tabulated. Information included in the tables about the various species are as follows:

- (1) **% Sites present** - the percentage of sites where the species occurred;
- (2) **Range** - its minimum and maximum height above SLWM;
- (3) **g / Quadrat** - the range in weight found in the various quadrats (a single value indicates that it was found in a single quadrat);
- (4) **Site** - the sites which contained the specific species.

Northern Namibia however seemed to be too variable from site to site, and as a result three representative shores were chosen to represent the area: Toscanini, Torra Bay and Möwe Bay.

To see whether there is was any relationship between functional form and the three regions under investigation, a DCA analysis was performed on the biomass data. All the species present in the biomass data were classified into one of ten functional forms outlined in Table 6.1 (below). The algal functional forms were based on Littler *et al.* (1983), with the addition of a "Turf" category. The animals were divided into three functional trophic groups, viz. grazers, filter-feeders and carnivores. The biomass for each functional group within each quadrat was recalculated and a DCA analysis run on all the quadrats, i.e. for all the zones and sites on the Namibian coast.

Table 6.1 : Functional form groups for algae and trophic groups for animals.

Functional Form	Morphology	Examples
Unbranched	Thin sheet-like blades	<i>Enteromorpha, Pugetia, Petalonia, Porphyra, Ulva</i>
Branched	Branched flaccid foliose species	<i>Neuroglossum, Microcladia, Plocamium, Rhodophyllis, Delesseria, Fauchea</i>
Fine Filaments	Filamentous algae which have a delicate structure	<i>Griffithsia, Herposiphonia, Ectocarpus, Erythrotrichia, Euptilota, Polysiphonia, Pleonosporium, Streblocladia, Ulothrix</i>
Terete	Terete algae which have a coarse / robust form	<i>Hypnea, Gymnogongrus, Ahnfeldtiopsis, Gracilariopsis, Chondria, Champia</i>
Cartilaginous	Tough, thick algal blades - may be branched or simple blades	<i>Epymenia, Gigartina, Sarcothalia, Plocamium, Aeodes, Botryocarpa, Rhodymenia, Mazzaella, Leathesia, Nothogenia, Pachymenia</i>
Coralline	Articulate coralline species	<i>Arthrocardia, Corallina</i>
Turfs	Species that have a turf-forming habit or have been recorded as sand binding	<i>Chylocladia, Ophidocladus, Cladophora, Ahnfeltiopsis, Caulacanthus, Polysiphonia, Tayloriella</i>
Grazers	Herbivores	<i>Patella, Siphonaria, Oxystele, Helcion, Gibbula, Fissurella</i>
Filter Feeders	Mussels, barnacles, sea anemones, sea cucumbers	<i>Choromytilus, Mytilus, Aulacomya, Perna, Semimytilus, Chthamalus, Bunodactis, Roweia</i>
Carnivores	Whelks	<i>Burnupena, Nucella</i>

Results

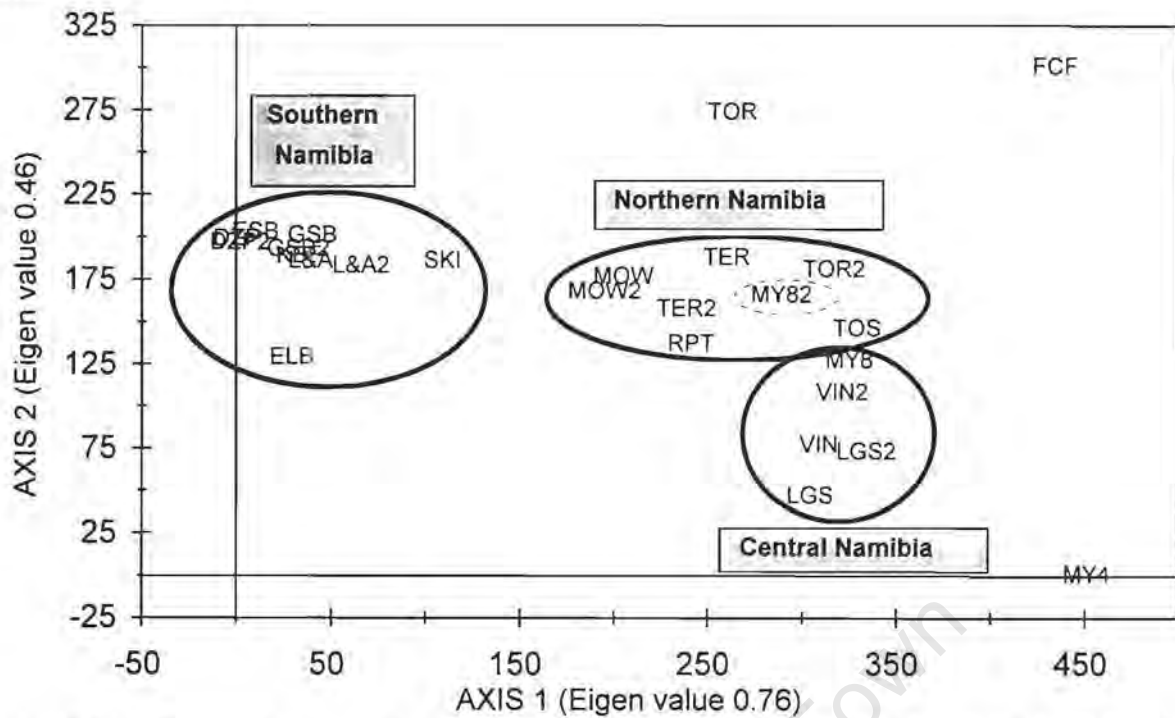


Fig. 6.1: DCA of average biomass for the various sites sampled during 1990 and 1992. A key for the various sites are given below.

KEY			
DZP	Diaz Point	MOW	Möwe Bay
ELB	Elizabeth Bay	MY4	Myl 4
ESB	Essy Bay	MY8	Myl 8
FCF	False Cape Fria	RPT	Rocky Point
GSB	Grossebucht	SKI	Shark Island
KBF	Kleinbogenfels	TER	Terrace Bay
L&A	Rocks near Agate Beach	TOR	Torra Bay
LGS	Langstrand	TOS	Toscanini
		VIN	Vineta Beach

(If the three letter abbreviation is followed by the number "2" it refers to the samples collected in March / April 1992, otherwise the samples are from September - December 1990).

As can be seen from Fig. 6.1, the Namibian shores separate out into the three main regions defined. The southern Namibian sites show a close affinity for one another, with the exception of Elizabeth Bay. The sites in this area are spread along Axis 1, showing that they possibly lie on some gradient. The central Namibian sites come out as almost a cohesive group, with Myl 8 (1992) sample forming part of northern Namibia. The only other outlier is Myl 4 which closely aligns with False Cape Fria on the Axis 1, although they are widely separated on Axis 2. The central Namibian sites show very little difference with respect to the primary axis (i.e. Axis 1), but separate on Axis 2. The northern Namibian sites are more spread out and diverse, as was seen in the previous chapter. Toscanini on the northern Namibian coast has a high degree of similarity with Myl 8 from central Namibia.

Most of the sites that were sampled in both years show very little difference between them, with the exception of Torra Bay. The northern Namibian coast is spread out on both axes.

In the following area diagrams, animals are represented by means of diagonal line shading, whereas the algae have solid shading. It should also be noticed that the Y-axis represents relative abundance of the various organisms on the shore; a scale representing actual biomass is given in the bottom right-hand corner of each diagram. A general pattern that emerges from the diagrams below is the decrease in biomass as one moves from the bottom of the shore to the top. This is a world wide phenomenon in intertidal communities, but is once again high-lighted in this study. The results are arranged according to the three main regions.

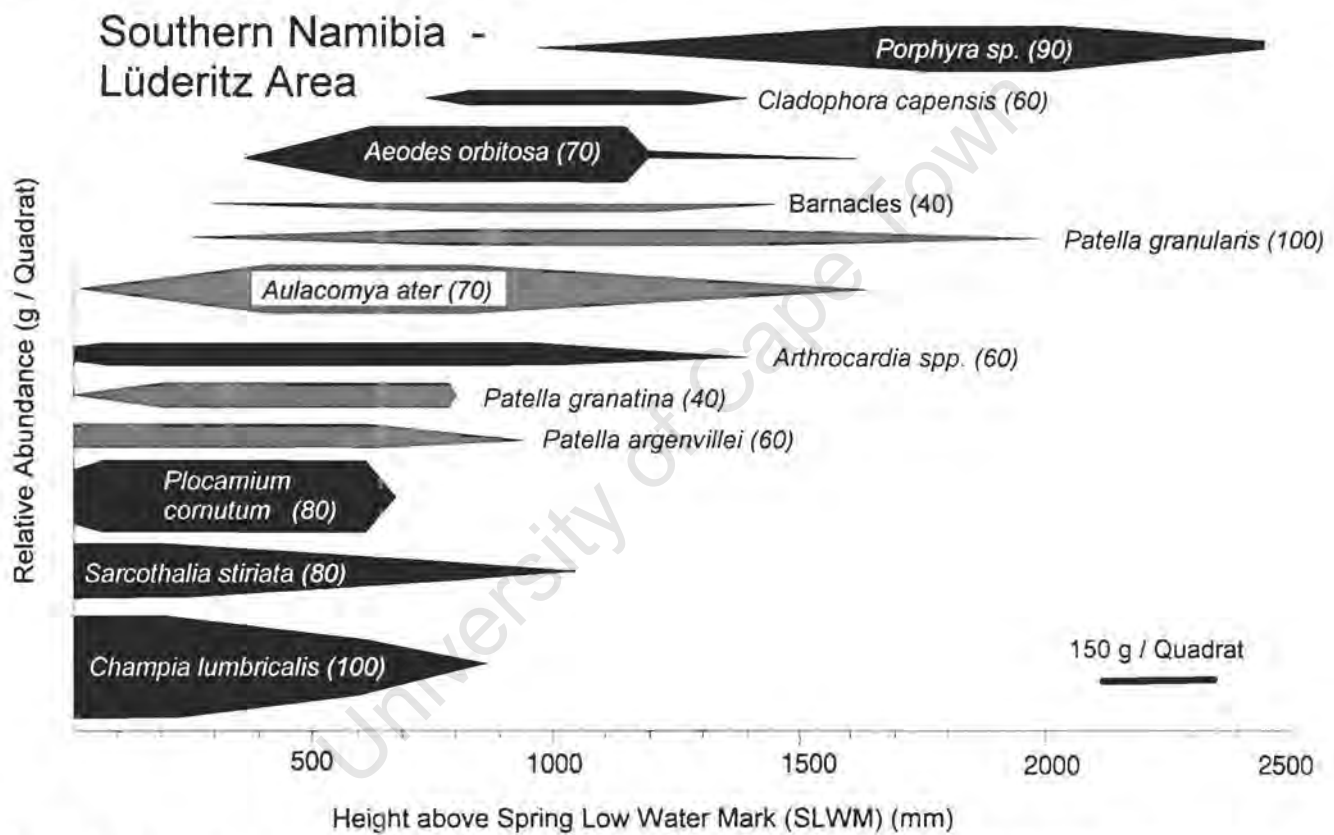


Fig. 6.2: Generalized schematic representation of relative abundance of species that constitute $\geq 10\%$ of biomass / quadrat as one moves up the shore. The value in parentheses represents the percentage of sites in which the species occurred within the southern Namibia region. (The latter applies to the area graphs below).

As can be seen from Fig. 6.2 the lower end of these shores, 0 - 600mm, is dominated by the seaweeds *Champia lumbricalis*, *Sarcothalia stiriata*, and *Plocamium cornutum*; *Arthrocardia spp.* are also found in this area in slightly lower amounts. The dominant animals, in this mixed seaweed zone, are the limpets *Patella argenvillei* and *P. granatina*, with the mussel *Aulacomya ater*

increasing in abundance from about 400mm above SLWM. This zone merges into a zone of *Aeodes orbitosa*, *Aulacomya ater* and *Patella granularis*. Other organisms which constitute a dominant component are the filamentous green seaweed *Cladophora capensis* and the barnacles, *Chthamalus dentatus* and *Notomegabalanus algicola*. The following zone is a transition area between the *Aeodes / Patella granularis* zone and *Porphyra* zone higher up. This transition area may be characterised by having *Patella granularis* and the occasional *Porphyra* plant. As can be seen from the diagram, however, *P. granularis* has a wide distribution range over these shores, stretching from 300 - 2000 mm above SLWM. The upper shore is dominated by *Porphyra* spp.

Table 6.2: Species found in southern Namibian (Lüderitz area) with biomass values greater than or equal to 10% of the quadrat biomass, but found in less than 40% of the sites in the region. Animals indicated by means of “*”. The table is arranged according to degree of exposure, going from exposed to semi-exposed / semi-sheltered (Shaded area). Wave exposure as per *General Methods* chapter 2. Range - Height above SLWM (mm). Parentheses in the “g / quadrat” column indicate values which are unusually low, and they correspond to the areas in parentheses in the “sites” column.

SPECIES	% OF SITE PRESENT	RANGE		g / Quadrat	SITE
		MIN	MAX		
* <i>Helcion dunkeri</i>	10	1081		30	GSB
<i>Mazzaella capensis</i>	10	2057		4 - 10	GSB
* <i>Patella miniata</i>	20	200	464	28 - 30	GSB, DZP
<i>Corallina</i> spp.	20	100	378	20 - 59	GSB, ESB
<i>Splachnidium rugosum</i>	30	528	1182	(1-15) 21- 164	GSB2, (ESB, KBF)
*Sea anemone	20	302	598	41 - 90	GSB2, SKI
* <i>Perna perna</i>	30	577	849	(15) 81 - 184	(GSB2), SKI, L&A2
<i>Pachymenia carnosa</i>	20	0	217	164 - 193	GSB, KBF
<i>Bryopsis</i> spp.	20	468	1414	27 - 41	DZP, L&A
<i>Streblocladia camptoclada</i>	30	510	1322	(11) - 116	(DZP), SKI, KBF
<i>Herposiphonia heringii</i>	10	0		46	SKI
<i>Caulacanthus ustulatus</i>	10	1057		9	SKI
* <i>Choromytilus meridionalis</i>	20	0	434	(73) - 259	SKI, (ELB)
<i>Ceramium</i> spp.	20	185	845	10 - 51	SKI, ELB
<i>Centroceras clavulatum</i>	10	0		65	L&A
* <i>Pyura stolonifera</i>	10	0		136	L&A
<i>Polysiphonia urbana</i>	10	474		6	L&A
* <i>Siphonaria capensis</i>	10	970		4	L&A
<i>Hypnea spicifera</i>	10	0		65	L&A2
<i>Gigartina polycarpa</i>	30	89	801	(16) 34 - 317	L&A, (KBF), ELB
* <i>Burnupena</i> sp.	20	93	639	(15) 53 - 85	(L&A), ELB
<i>Plocamium rigidum</i>	10	391		174	KBF
<i>Chordariopsis capensis</i>	20	605	1641	15 - 58	KBF, ELB
<i>Codium isaacii</i>	10	0		365	ELB
<i>Enteromorpha atroviridis</i>	10	734		15	ELB

Table 6.2 represents the species that were found in less than 40% of the sites sampled. The table has been partitioned with respect to degree of wave exposure. The unshaded part of the table indicates areas that are mostly exposed, whereas the shaded area are those sites which are semi-exposed to semi-sheltered (i.e. those found in Lüderitzbucht and Elizabeth Bay). Within the low intertidal or mixed seaweed zone of the exposed areas, *Pachymenia carnosa*, *Corallina* spp. and *Streblocladia camptoclada* are encountered as the most abundant seaweeds, with *Patella miniata* and sea anemones (*Bunodactis reynaudi*, *Bunodosoma capensis*, & *Pseudactinia flagellifera*) as the dominant sessile fauna. *Streblocladia camptoclada* showed a gradient of increasing biomass with increasing degree of shelter. *Splachnidium rugosum*, *Bryopsis* spp. and *Mazzaella capensis* were found in the mid-eulittoral in the *Aeodes / Patella granularis* zone. The brown mussel, *Perna perna*, was found in the *Aeodes / Patella granularis* zone at three of the sites. Two of these sites, viz. Shark Island and Agate Beach, occur within Lüderitzbucht. The third site is Grossebucht, with a single quadrat containing an insignificant amount of *Perna perna* in the order of 10 times less biomass than those from the Lüderitzbucht. *Helcion dunkeri* is a low-mid shore limpet, which was only abundant at Grossebucht.

The horizontal gradient (Axis 1) observed in the southern Namibia cluster in Fig. 6.1 seems to represent the degree of exposure. The shaded half of Table 6.2 are those sites within Lüderitzbucht, Elizabeth Bay and Kleinbogenfels. All these areas are relatively sheltered when compared with the other sites in the Lüderitz area. Owing to the shallowness of these bays, I would predict slightly elevated temperatures within these areas, especially during the summer months. Within the algal zone there are a number of filamentous seaweeds that seem to be more prevalent, *Herposiphonia heringii*, *Ceramium* spp., *Centroceras clavulatum* and *Polysiphonia urbana*. Other species found in this region are *Hypnea spicifera* (which seems to be seasonal - as it is only observed during late summer and autumn), *Plocamium rigidum* and *Codium isaacii* (only in Elizabeth Bay). There are two abundant filter feeders recorded from this area, *Choromytilus meridionalis* (mussel) and *Pyura* sp. (tunicate). The former, however, is only present in a sizeable amount at Shark Island, whilst Elizabeth Bay has a small biomass representation. Also present in this zone is the whelk, *Burnupena* sp.. The following species are found in the lower *Aeodes / Patella granularis* zone, *Chordariopsis capensis* and *Enteromorpha atroviridis*; while *Caulacanthus ustulatus* and *Siphonaria capensis* are only present in the upper reaches of this zone.

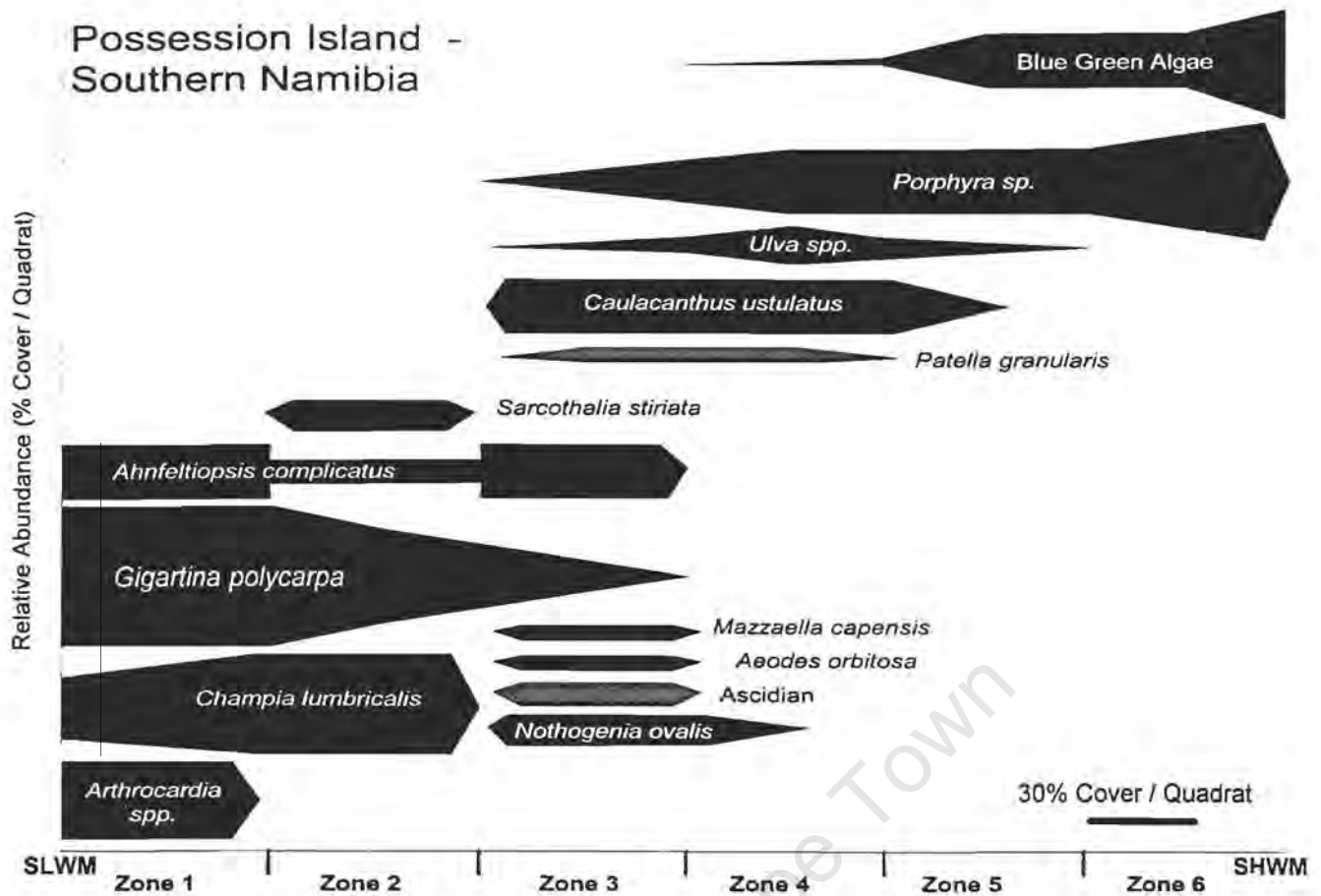


Fig. 6.3: Generalized schematic representation of relative abundance of species that constitute $\geq 10\%$ of % cover / Quadrat from various zones as one moves up the shore on the sheltered side of Possession Island. (No value is given in parenthesis since the data represent the whole site).

Fig. 6.3 represents the sheltered side of the offshore Possession Island, just outside Elizabeth Bay. As can be seen zones 1 and 2 represent the low eulittoral mixed seaweed zone as seen above. It differs from Fig. 6.2 in having *Gigartina polycarpa* as an abundant species, and *Ahnfeltiopsis complicata* making an appearance. Note that *Sarcothalia stiriata* has a relatively small representation and vertical distribution. There is also a lack of abundant animals in this zone. Zone 3 corresponds to the *Aeodes / Patella granularis* zone above, but there is also a significant representation of *Caulacanthus ustulatus*, *Nothogenia ovalis*, *Ulva* spp. and an ascidian. Zone 4 is the upper part of the *Patella granularis* zone, but as can be seen, seaweeds comprise the biggest component with respect to biomass. Zones 5 and 6 form the *Porphyra* zone, where filamentous blue-green algae make a significant contribution to the total area occupied in this region. It should be noted that the zones are less clearly defined than in Fig. 6.2, tending to merge into one another. This is interesting in that the zones were subjectively chosen in this study by means of the dominant organisms present.

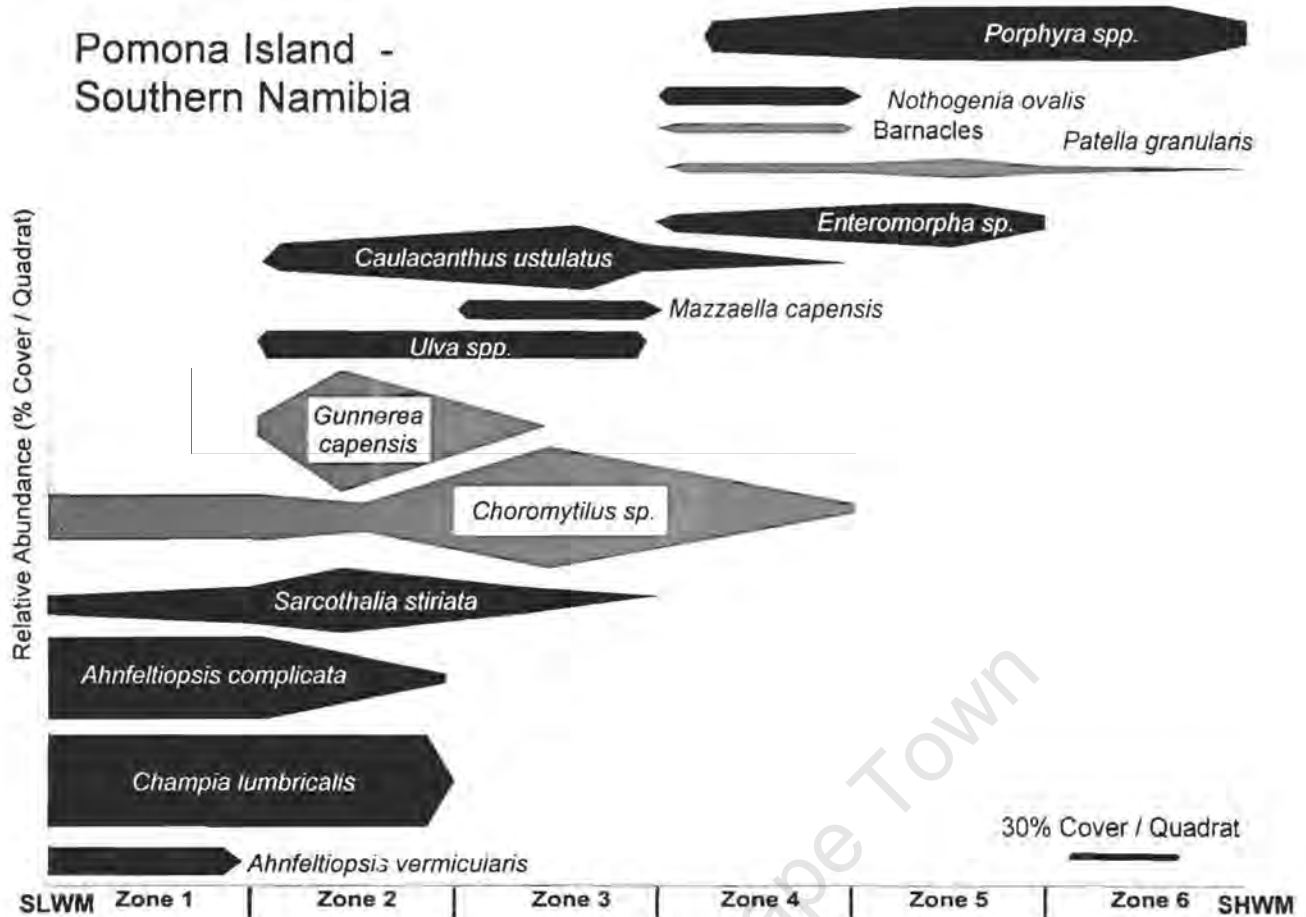


Fig. 6.4: Generalized schematic representation of relative abundance of species that constitute $\geq 10\%$ of % cover / quadrat from various zones as one moves up the shore at Pomona. (No value is given in parenthesis since the data represent the whole site).

Pomona (Fig.6.4) seems to have biota intermediate between the previous two sites in Fig.6.2 and Fig. 6.3. A significant difference is the high representation of *Ahnfeltiopsis* spp. in the lower eulittoral zone and *Caulacanthus ustulatus* in the low to mid-eulittoral zone. *Gunnerea capensis* and *Choromytilus meridionalis* also feature quite strongly in the low to mid-intertidal. Zone 1 is again the mixed seaweed zone, although there is a fair cover of mussels at this particular site. Zones 2 - 4 would best approximate the mid-eulittoral *Aeodes / Patella granularis* zone, although the zone may be further sub-divided into three, the first of the sub-divisions seeing the introduction of *Gunnerea capensis*, *Ulva* spp. and *Caulacanthus ustulatus*. Zone 3 is the middle sub-zone predominantly consisting of mussels but still containing most of the organisms from zone 2. Note that *Aeodes orbitosa* is not present here but is replaced by the seaweed *Mazzaella capensis*. Zone 4 is the upper sub-zone of the mid-eulittoral, although it is more of a transition zone between the *Aeodes / Patella granularis* and *Porphyra* zone. Zones 4 - 6 are dominated by *Patella granularis* and *Porphyra* spp., with *Nothogenia ovalis*, *Enteromorpha* sp. and barnacles forming a band in the lower regions of the zone.

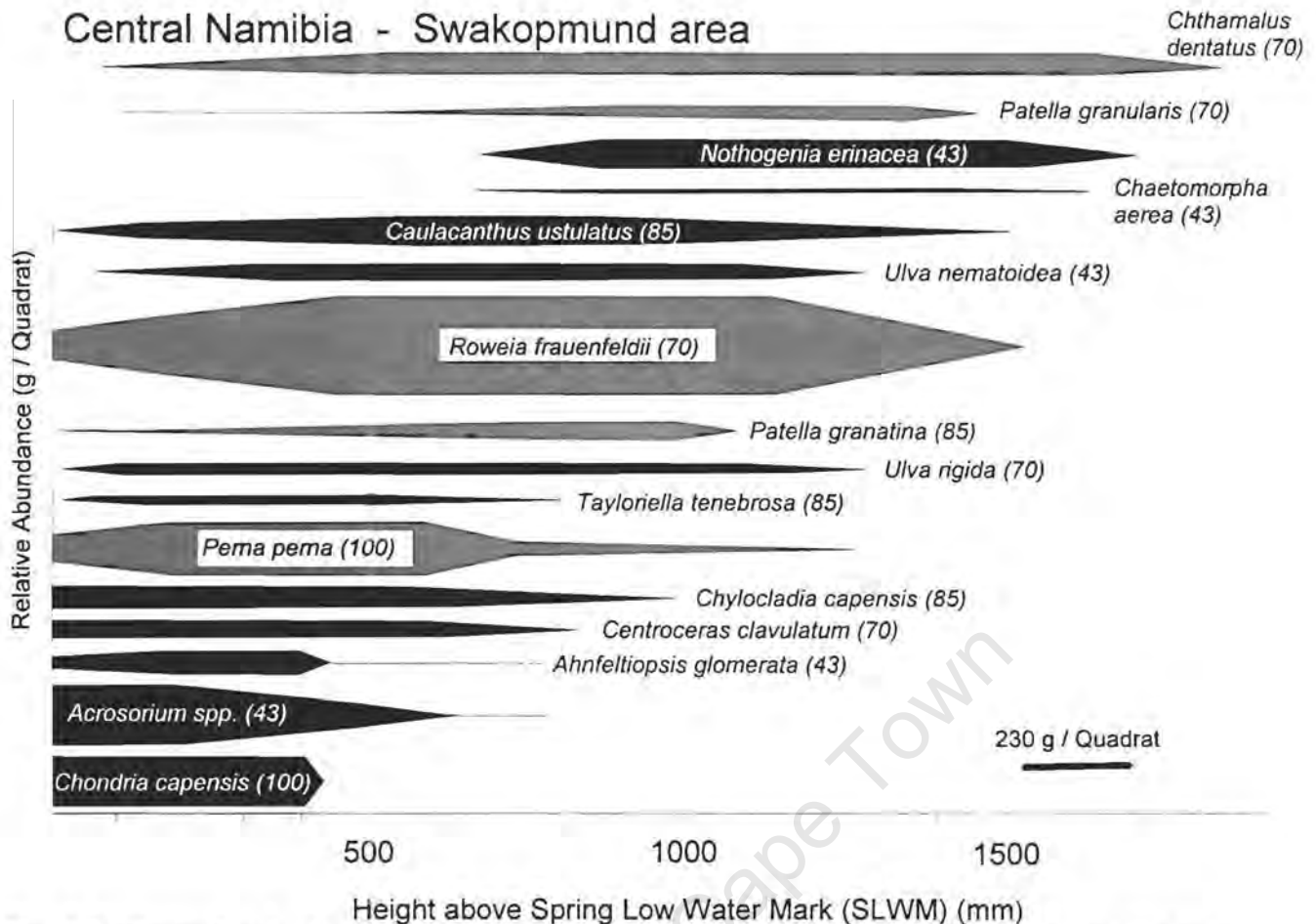


Fig. 6.5: Generalized schematic representation of relative abundance of species that constitute $\geq 10\%$ of Biomass / Quadrat as one moves up the shore. The value in parenthesis represents the percentage of sites in which the species occurred within central Namibia (Swakopmund area).

The vertical distribution of organisms within the intertidal region of central Namibia (Fig. 6.5) is anomalous to the previously discussed shores in that most of the species present have their origin in the lower intertidal and then extend up shore. Some species have a short distribution and remain within 500 mm above SLWM, whilst others extend well into the upper intertidal region (>1500 mm). There appears to be a break-down in zonation pattern on these shores. Zones can nevertheless be defined on the basis of species abundance or disappearance within a height range. There is a lower eulittoral zone of turf forming algae, viz. *Chondria capensis*, *Acrosorium* spp., *Ahnfeltiopsis glomerata*, *Centroceras clavulatum*, *Chylocladia capensis*, *Tayloriella tenebrosa*, and the brown mussel, *Perna perna*. The succeeding zone has its origins in the previous zone and comprises: *Caulacanthus ustulatus*, *Ulva* spp., *Patella granatina*, and sea cucumbers (*Roweia frauenfeldii*). The highest zone comprises *Nothogenia erinacea*, *Chaetomorpha aerea* and *Patella granularis*. *Chthamalus dentatus* (barnacle) seem to be evenly spread through all the zones.

Table 6.3: Species found in central Namibia (Swakopmund area) with biomass values $\geq 10\%$ of the quadrat biomass, but found in less than 40% of the sites in the region. “*” denotes animal species.

SPECIES	% OF SITE PRESENT	RANGE		g / Quadrat	SITE
		MIN	MAX		
<i>Pterosiphonia cloiophylla</i>	14	605		32	VIN
<i>Corallina</i> sp.	14	1090		12	LGS
<i>Porphyra</i> spp.	28	414	1374	5 - 52	LGS, MY4
Blue greens	14	0		8	LGS2
<i>Arthrocardia</i> spp.	14	0		222	LGS2
<i>Cladophora flagelliformis</i>	14	0		5 - 205	LGS2
<i>Mazzaella capensis</i>	14	415		40	LGS2
<i>Ophidocladus simpliciusculus</i>	14	807		14	LGS2
* <i>Siphonaria capensis</i>	14	1520	1737	1 - 26	LGS2
<i>Chondracanthus teedii</i>	28	978	1025	11 - 16	MY4, MY8
<i>Plocamium rigidum</i>	14	0		20	MY8
<i>Hypnea tenuis</i>	28	0	759	(7) - 22	MY8, (LGS2)
<i>Gymnogongrus dilatatus</i>	14	0		22	MY82
<i>Streblocladia camptoclada</i>	14	0	650	22	MY82
* <i>Semimytilus algosus</i>	14	213	795	4 - 95	MY82

The unshaded portion of Table 6.3, consists predominantly of species found at Langstrand. All the low-eulittoral algae are either turf-forming, filamentous, or have a crustose phase in the life history / portion of the thallus. In the mid-eulittoral one finds: *Mazzaella capensis*, which has a persistent basal portion; *Ophidocladus simpliciusculus*, a sand-binding turf; and *Porphyra* spp., whilst in the upper-eulittoral zone, only the pulmonate limpet *Siphonaria capensis* is present. The shaded part of Table 6.3, consists predominantly of Myl 8, which has been divided up with respect to the two seasons sampled. The first three species in this portion of the table are from spring, while the last three species were taken from the autumn collection.

Toscanini - Northern Namibia

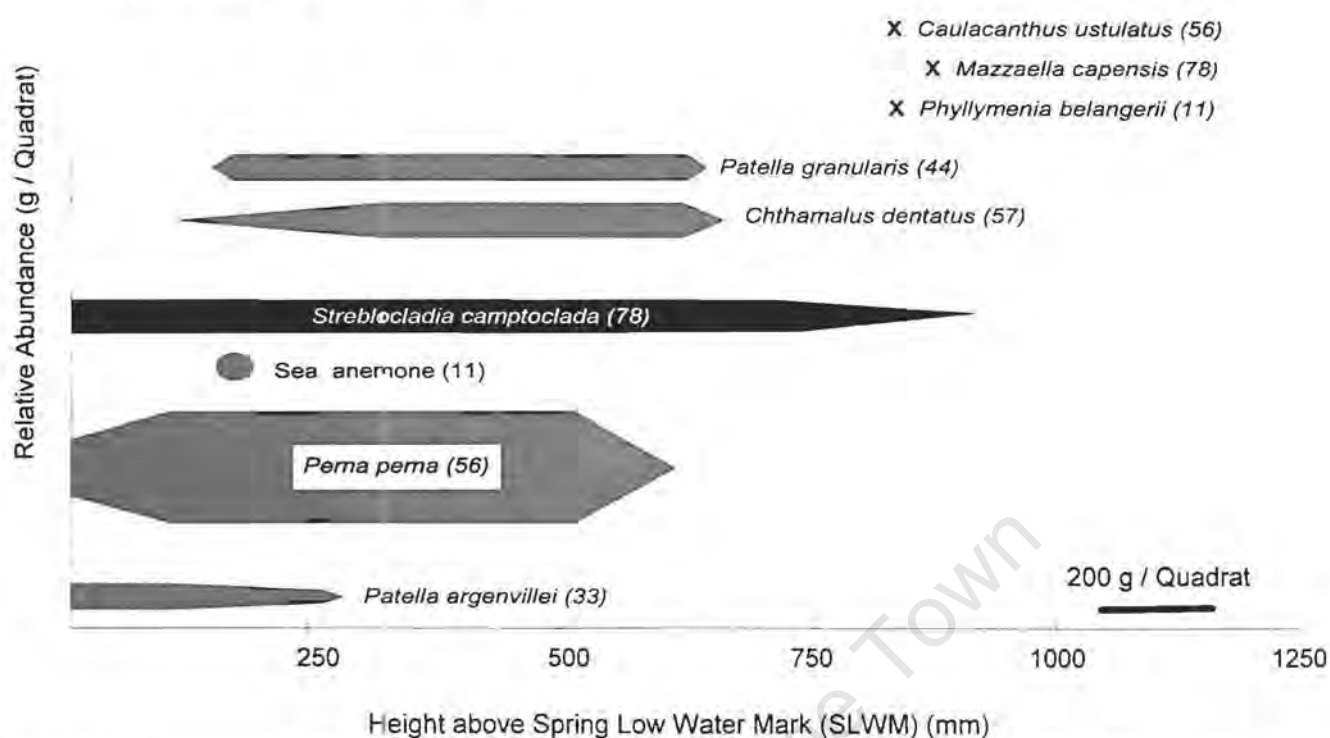


Fig. 6.6: Generalized schematic representation of relative abundance of species that constitute $\geq 10\%$ of Biomass / Quadrat as one moves up the shore at Toscanini. The value in parentheses represents the percentage of sites in which the species occurred within the northern Namibia region. X - Seaweeds, and • - Animals, that were only present in a single quadrat and in relatively small quantities.

Figs. 6.6 - 6.8 are shores which have been chosen as being representative of the intertidal in northern Namibia (Skeleton Coast Area). Fig. 6.6 is of Toscanini, a small rocky outcrop, flanked by sandy beaches on either side. There appear to be three zones on the shore, the lower two dominated by animals. The lower eulittoral zone is characterised by the presence of *Patella argenvillei* and the sea anemone *Bunodactis reynaudi*. The brown mussel, *Perna perna*, and filamentous red seaweed, *Streblocladia camptoclada*, are also found in this zone. The latter two species continue into the mid-eulittoral zone and are joined by *Patella granularis* and the barnacle *Chthamalus dentatus*. The upper eulittoral zone consists of three seaweed species in small amounts, viz. *Caulacanthus ustulatus*, *Mazzaella capensis*, and *Phyllymenia belangeri*, no animals are found in abundance in this region of the shore. As can be seen from the DCA in Fig. 6.1, this shore closely aligns itself with Myl 8 from central Namibia.

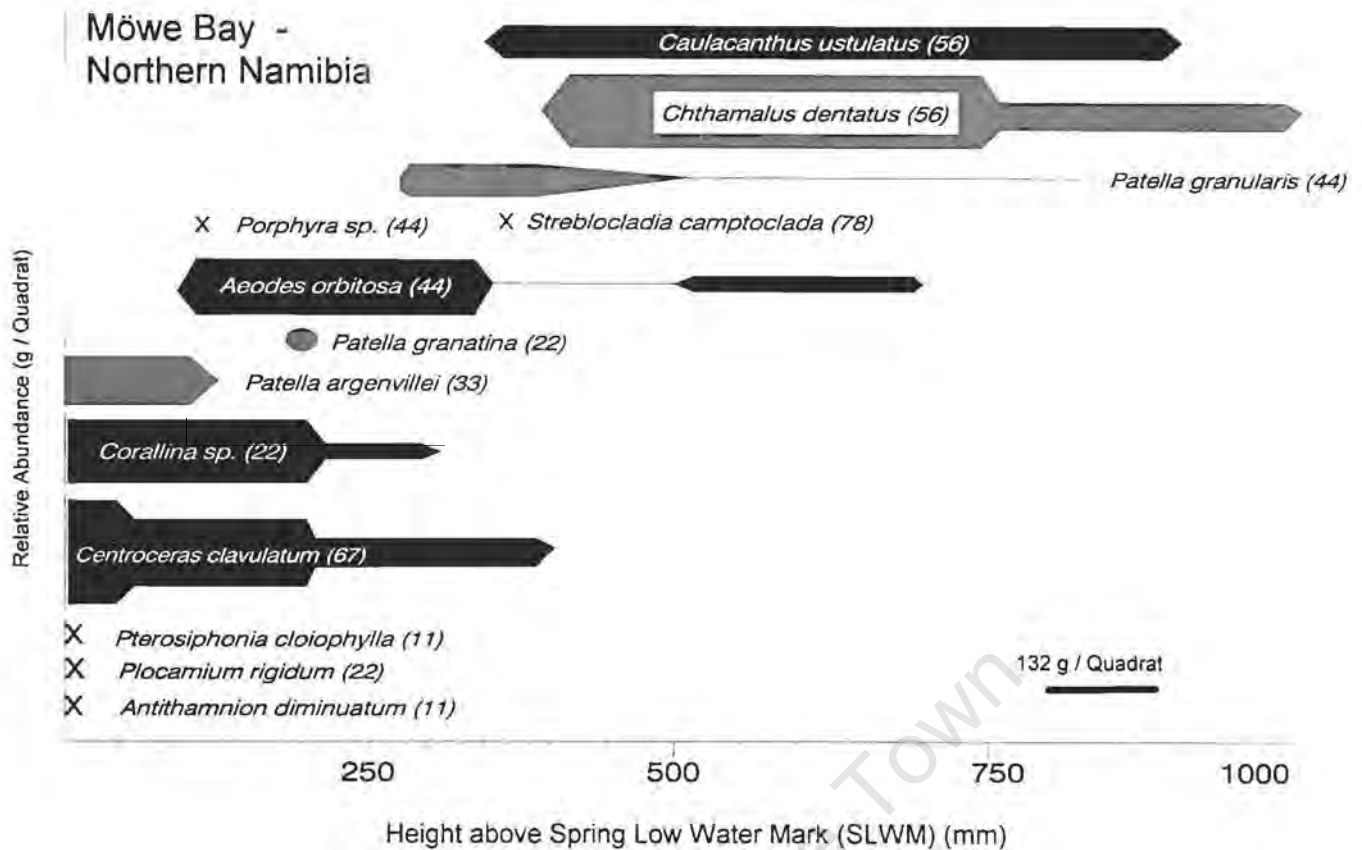


Fig. 6.7: Generalized schematic representation of relative abundance of species that constitute $\geq 10\%$ of Biomass / Quadrat as one moves up the shore at Möwe Bay. The value in parentheses represents the percentage of sites in which the species occurred within the northern Namibia region. x - Seaweeds, and ● - Animals, that were only present in a single quadrat and in relatively small quantities.

Fig. 6.7 represents Möwe Bay, sampled in both seasons. This shore has relatively low sand, Fig. 2.4, and it is the site, in northern Namibia, with greatest affinity to the southern Namibian sites (Fig. 6.1). The lower eulittoral is again dominated by algae, in particular *Centroceras clavulatum* and *Corallina sp.*. The most abundant animal here is *Patella argenvillei*. The algal species continue into the next zone where *Aeodes orbitosa* is the most abundant organism, with *Patella granatina* forming a relatively minor component. Note that a *Porphyra sp.* does occur here, but that this species is epiphytic on *Aeodes*, and it is undescribed at this stage (N.G.Griffin, pers.comm.). *Streblocladia camptoclada* is also present in relatively small quantities in the upper reaches of this zone. *Patella granularis* forms a relatively short zone, as compared with the previous shores, which rapidly gives rise to an upper *Chthamalus dentatus* - *Caulacanthus ustulatus* zone. Note that high intertidal *Porphyra spp.* are absent from Figs. 6.6 and 6.7. There are also a number of species here that have a relatively low representation on Skeleton Coast shores, *Pterosiphonia cloiophylla*, *Plocamium rigidum*, *Antithamnion diminuatum* and *Corallina sp.*. This shore is dominated equally by fauna or flora.

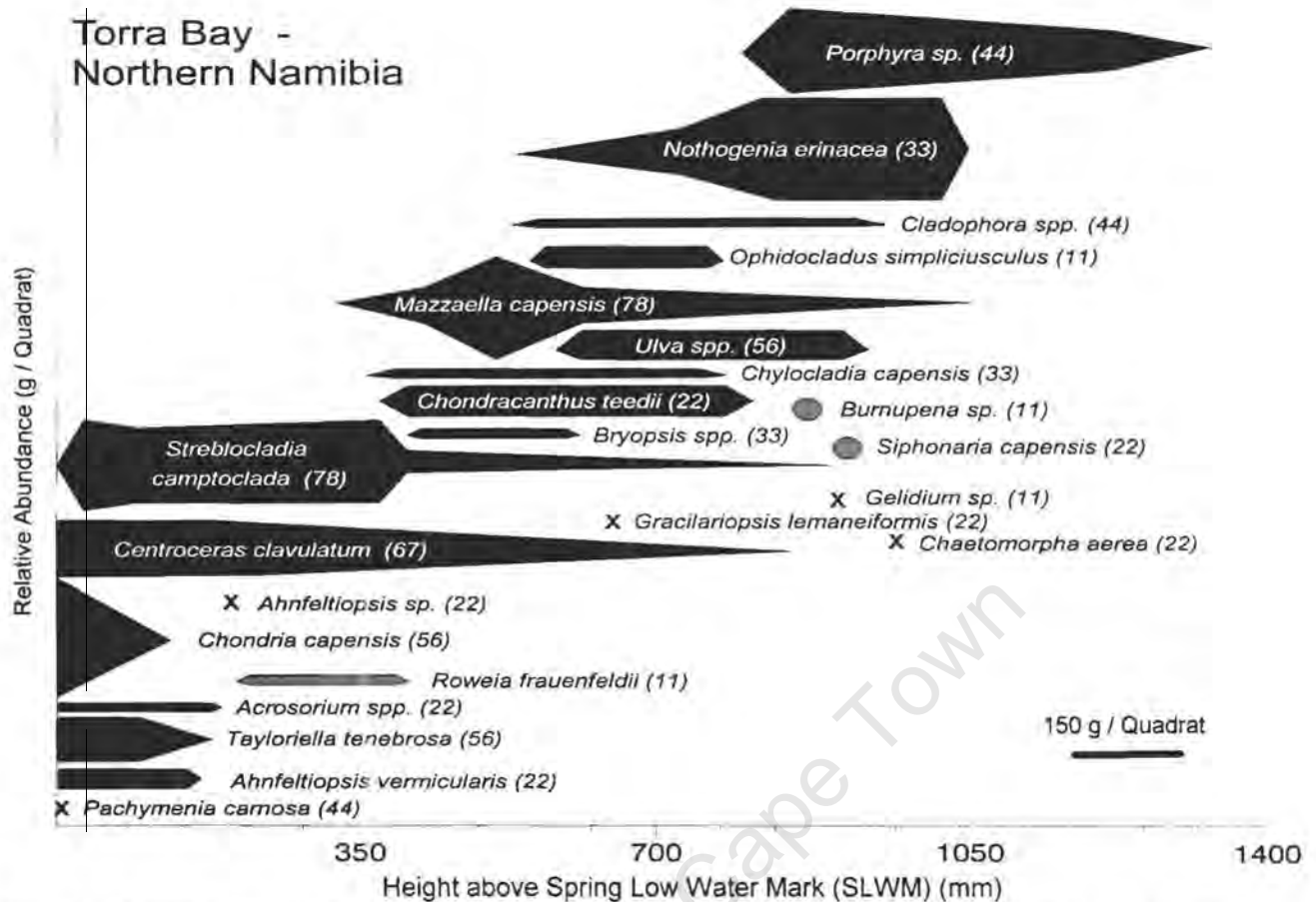


Fig. 6.8: Generalized schematic representation of relative abundance of species that constitute $\geq 10\%$ of Biomass / Quadrat as one moves up the shore at Torra Bay. The value in parentheses represents the percentage of sites in which the species occurred within the northern Namibia region. x - Seaweeds, and • - Animals, that were only present in a single quadrat and in relatively small quantities.

Fig. 6.8 represents Torra Bay, a heavily sand inundated site (Fig. 2.4), occurring geographically between Toscanini and Möwe bay. This site, as can be seen, is dominated by seaweed species which contribute to a five zone pattern. This shore contains many of the same species found within the central Namibian region, although the latter had more abundant animal species and fewer seaweed species. The lower eulittoral zone at Torra Bay is particularly high in turf-forming species, *Streblocladia camptoclada*, *Centroceras clavulatum*, *Acrosorium* spp., *Tayloriella tenebrosa* and *Ahnfeltiopsis* spp.. Two other species of note in this zone are *Pachymenia carnosa* and *Chondria capensis*. The following zone is characterised by having sea cucumbers, as well as the filamentous species *Streblocladia camptoclada* and *Centroceras clavulatum*. The mid-eulittoral zone comprises *Mazzaella capensis*, *Ulva* spp. and *Chondracanthus teedii*. Sand-binding turf and filamentous algae are also present here, viz. *Cladophora* spp., *Ophidocladus simpliciusculus*, *Chylocladia capensis*,

Bryopsis spp. and *Gracilariopsis lemaneiformis*. The lower upper-eulittoral zone comprises predominantly *Porphyra* sp. and *Nothogenia erinacea*, two gastropods, *Siphonaria capensis* and *Burnupena* sp., and two other seaweed species, *Gelidium* sp. and *Chaetomorpha aerea*. The upper eulittoral zone is a *Porphyra* sp. zone. Note the absence of *Caulacanthus ustulatus*, *Patella granatina*, *Perna perna* and *Chthamalus dentatus* from this site, as compared with central Namibia (Fig.6.5).

Table 6.4 represents those species found in northern Namibia with biomass values $\geq 10\%$ of the quadrat biomass, but not encountered in the above three sites. As can be seen, the actual amount of material present on these shores is relatively low and restricted to a narrow range on the shore. The only exceptions are the two ceramiaceous species, *Ceramium atrorubescens* and *Griffithsia confervoides*, found at Terrace Bay; and *Grateloupia longifolia*¹ found at False Cape Fria.

Table 6.4: Species found in northern Namibia with biomass values $\geq 10\%$ of the quadrat biomass, but not found in the three representative sites chosen.

SPECIES	% OF SITES PRESENT	RANGE		g / Quadrat	SITE
		MIN	MAX		
<i>Ceramium atrorubescens</i>	11	889		15	TER
<i>Griffithsia confervoides</i>	11	0		15	TER2
<i>Chordariopsis capensis</i>	11	556		3	TER2
<i>Oxystele</i> sp.	11	825		3	TER2
Colonial diatoms	22	0	959	2	TER2; RPT
<i>Polysiphonia scopulorum</i>	22	426	959	1 - 3	TER2; RPT
<i>Enteromorpha linearis</i>	11	959		1	RPT
<i>Grateloupia longifolia</i>	11	0		92	FCF

¹ The later species has been placed in *G. doryphora* by Stegenga *et al.* (1997) - the old name has been retained as the 'longifolia' form seems to have different ecological requirements.

Fig. 6.9A represents the DCA results for the ten functional form groups, while Fig. 6.9 B-D represents the quadrat ordination for the three regions (SNAM-NNAM). Fig. 6.9 was divided into three groups:

- (1) fine filaments, grazers and unbrached sheet-like algae;
- (2) carnivores and cartilaginous, coralline, terete, and branched algal categories; and
- (3) turf-forming algae and filter feeders.

Group 1 is common to all the regions (Fig. 6.9 B-D). Southern Namibia has its greatest concentration of functional forms in Group 2, as well as a number of quadrats in the filter feeder area, but shows a low affinity for turf forming algae. Central Namibia in contrast shows a strong affinity for turf forming algae and filter feeders (Group 3), whilst northern Namibia has a more even spread of functional groups over its sites, although it too has a slightly stronger leaning towards group 3.

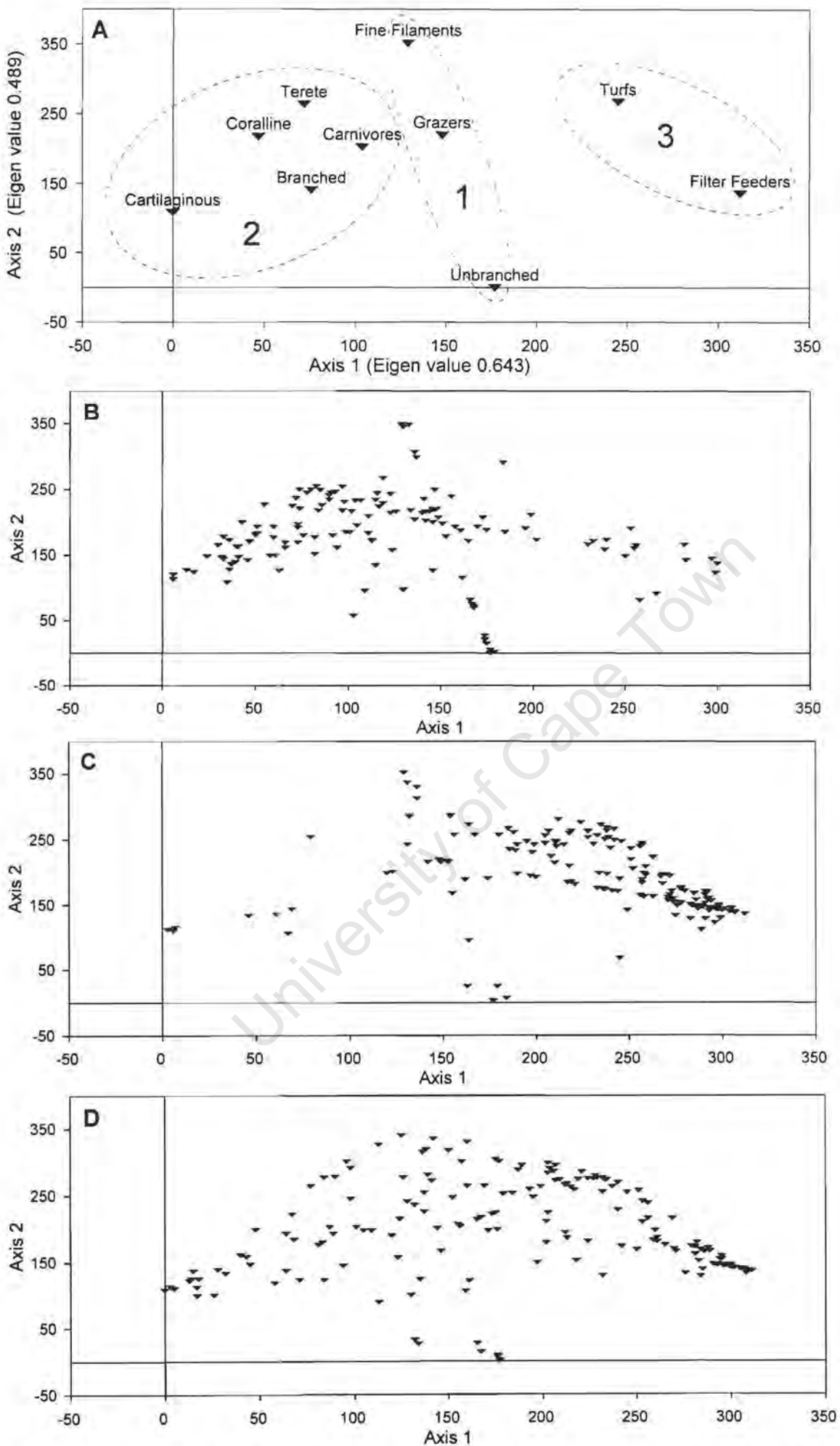


Fig. 6.9: DCA analysis of functional form data for the three regions sampled. **A** - Functional form category; **B - D** - Quadrat data for SNAM, CNAM, & NNAM respectively.

Discussion

Exposed shores in southern Namibia (Fig. 6.2) are similar to the general shore description of a 'typical' exposed South African west coast shore (described in the Introduction to the chapter). This is not surprising as many of the environmental conditions found in the two regions are similar. A low eulittoral mixed algae zone is largely composed of *Champia lumbricalis*, *Sarcothalia stiriata*, and *Plocamium cornutum*, with *Patella argenvillei* being the most abundant animal. The abundance of the three former seaweed species varies from between shores with one or two being particularly abundant. This zone then expands into a lower mid-eulittoral zone containing the cool temperate ribbed mussel, *Aulacomya ater* (Penrith & Kensley, 1970 b), and the seaweeds *Aeodes / Mazzaella*. It is also important to note that the limpet *Patella granularis* also features in this region of these shores. As has been mentioned, mussel abundance is dependant on degree of wave action (McQuaid & Branch, 1985), and therefore this component of these shores is variable. Likewise, *Aeodes orbitosa* is sand intolerant and shows seasonal fluctuation in biomass (Bolton & Levitt, 1992; Stegenga *et al.*, 1997, p. 33), while *Mazzaella capensis* has a strong preference for areas of sand inundation. As a result these three species do not necessarily make good candidates for defining a zone. *Patella granularis*, on the other hand, is common on most shores and the most conspicuous component by presence, as a result I have termed the zone the *Aeodes (Mazzaella) / Patella granularis* zone. This zone may be divided into two regions, a lower *Aeodes / Mazzaella* zone and an upper zone where these species are absent. Other species that are found in this zone include *Cladophora capensis* and barnacles. At the top of these shores *Porphyra* spp. are abundant, as on South African west coast shores. The blue green algae component mentioned in the Introduction seems to be restricted to the more sheltered areas of Lüderitz (with respect to abundance).

A species that is often noted as being a component of South African west coast intertidal communities is *Splachnidium rugosum* (Bolton & Anderson, 1997), which in the southern Namibia region is more seasonal and seems to favour more exposed sites (Table 6.2), and it is therefore not a ubiquitous species. Other seaweed species that constitute a noticeable portion of the flora when present are *Pachymenia carnosa* and articulated coralline algae.

The above describes the 'typical' exposed west coast shore. There are however other types of shores that occur along this coast. Under more sheltered conditions as are seen in Fig. 6.3 and semi-sheltered conditions (shaded portion of Table 6.2) similar species occur, but in different proportions.

There is however probably a temperature difference between the Possession Island sheltered site and the sites found within Lüderitzbucht and Elizabeth Bay. The reason is that Possession Island is a small offshore island surrounded by water of much the same temperature (it has an exposed and sheltered side); whereas the sites in Lüderitzbucht and Elizabeth Bay occur in shallow bays, which will be exposed to some degree of heating. It is therefore proposed that the species occurring within Lüderitzbucht are the product of temperature as well as a certain degree of shelter.

This idea of warmer water within Lüderitzbucht may be supported by the presence of known warmer water species e.g. *Hypnea spicifera* and *Perna perna*. *Perna perna* (Table 6.2), the brown mussel, is described by Penrith and Kensley (1970b) as being a circum-tropical species. As was noted in Table 6.2, this species is only abundant to any great extent in southern Namibia within Lüderitzbucht itself. The sites where it was found were also not very sheltered, which would explain the presence of a filter feeder (McQuaid & Branch, 1985). This species becomes the most abundant mussel further north in central and northern Namibian coastal regions. These regions are known to be warmer than the stretch from Lüderitz to Cape Point. McQuaid & Branch (1984, 1985) point out the primary importance of temperature in deciding what species are present within the marine provinces in southern Africa. They also place *Perna perna* as a species that prefers warm, wave exposed, water with strong east coast (i.e. South African) affinities. Two other species that occur in greater biomass in these sites are *Streblocladia camptoclada* and *Centroceras clavulatum*. These species form a dominant part of the shores in central and northern Namibia (Fig. 6.5 - 6.8). These species are found in both sand-inundated and sand-free sites (in the central and northern regions), as well as a range of exposures. It may therefore be concluded that the temperature difference accounts for the increase in biomass. *Centroceras clavulatum* has also been noted by Lawson and John (1987) as being one of the most common species in tropical west Africa. This could make abundance of these species indicators of locally increased temperatures on the South African west coast.

Gigartina polycarpa, appears to be the most abundant species in sheltered areas (Table 6.2; Fig. 6.3). This has also been noted by Bolton and Levitt (1992) and Levitt in Stegenga *et al.* (1997). Other species of note in the shaded part of Table 6.2 and Fig. 6.3 are: *Caulacanthus ustulatus*, *Centroceras clavulatum*, *Plocamium rigidum*, *Streblocladia camptoclada*, *Burnupena* sp. and *Siphonaria capensis*. This is not to say that these species do not occur on wave exposed shores, but that they are not an abundant component on these shores. *Choromytilus meridionalis* is also recorded from these semi-sheltered sites (Table 6.2; Fig.6.4). This species has been recorded as

only occurring on a sheltered shore of 'Q Bay' within the Lüderitz lagoon by Penrith and Kensley (1970a). Members of the Ulvaceae, *Ulva* spp. and *Enteromorpha* spp., also seem to be more dominant on more sheltered shores, especially within the upper mid-intertidal reaches of the shore (Fig. 6.3 & 6.4; Table 6.2).

As was seen in the previous chapter, a high degree of sand inundation seems to be an important factor on the central and northern Namibian coast. These type of shores are present in southern Namibia, but they are inaccessible to the general public owing to diamond mining in the area. The site Pomona has some sand inundation in its lower reaches, but this area is also only semi-exposed and not as exposed as the sites further north. It nevertheless gives an indication of a sandy/rocky shore in southern Namibia. Daly & Mathieson (1977) and Littler *et al.* (1983) point to a number of morphological and life history strategies found in algae which favour sand-stressed environments:

- (1) They are often tough and wiry;
- (2) Turf forming species, or those with basal stolons.
- (3) Opportunistic;
- (4) Regenerate upright fronds from their bases;
- (5) Have incomplete alternation of generations.

Ahnfeltiopsis spp. in the lower intertidal are often found in areas of sand inundation (Daly & Mathieson, 1977; Stegenga *et al.*, 1997). Many of the species belonging to this genus are not only tough and wiry, but also have a crustose phase in their life history (Bolton & Anderson, 1990 - as *Gymnogongrus* spp.). *Caulacanthus ustulatus* is a turf forming species; this functional form is often recorded as being dominant in areas where sand inundation occurs (Daly & Mathieson, 1977; Littler & Littler, 1981; Stewart, 1983). There are also opportunistic species such as *Ulva* spp., *Chaetomorpha* spp. and *Enteromorpha* spp. (Littler *et al.*, 1983), as well as those species with life history stages that can persist through sand inundation events (Littler *et al.*, 1983) e.g. *Mazzaella capensis* (Bolton & Joska, 1993; Stegenga *et al.* 1997). The presence of the polychaete *Gunnerea capensis*, which builds its tubes from sand, is another indicator that the area experiences some sand inundation. The presence of *Sarcothalia stiriata* and *Champia lumbricalis* point to the fact that this area is to some extent exposed.

The pattern for central Namibia is quite different to that found in southern Namibia. As was noted in the results, central Namibia seems to lack the clear zonation pattern observed further south. This could be attributed to the fact that, due to continued disturbance on these shores in the form of sand inundation, wave exposure and exposure to east wind conditions, these shores have not had the

opportunity to reach a final successional state. In support of the latter, Littler *et al.* (1983) found that “sand inundation resulted in subclimax and mature intertidal communities being intermingled in a mosaic-like pattern on San Nicolas Island”. Mathieson *et al.* (1991) also noted that ice-scouring in the northwest Atlantic limits the development of perennial zone-forming taxa, and sand inundation could be assumed to have a similar effect. The zones in central Namibia are, as a result, less clearly defined or more intermingled.

This region seems to be dominated by turf forming species (*Acrosorium* sp., *Centroceras clavulatum*, *Chylocladia capensis*, *Tayloriella tenebrosa*, *Caulacanthus ustulatus*, *Pterosiphonia cloiophylla*, *Ophidocladus simpliciusculus*, *Streblocladia camptoclada*), opportunistic species (*Ulva* spp.), and those with a crustose stage in the life history (*Nothogenia erinacea*, *Ahnfeltiopsis glomerata*, *Gymnogongrus dilatatus*, *Mazzaella capensis*, *Corallina* sp., *Arthrocardia* spp.; (Fig.6.5, Table 6.3). As was mentioned above, turf forming species are known to be particularly prevalent on sand inundated rocky shores. Opportunistic species can take advantage of areas cleared due to sand scouring, by their ability to grow fast and reproduce, while species with a crustose phase in the life history are able to survive burial, and ‘resprout’ once they are uncovered again.

The great abundance of the sea cucumber, *Roweia frauenfeldii*, is indicative of the high degree of sand inundation, since it is usually buried in sand (Day, 1974; Branch *et al.*, 1994). Conversely, the presence of *Patella* spp. and barnacles, which do not tolerate sand inundation very well, imply that the levels of sand are either not too high or that sand inundation is sufficiently patchy not to be a problem in certain regions of these shores. It was noticed that sand inundation is concentrated within the lower-mid eulittoral zone on many shores in central Namibia. When one considers Fig. 2.4, sand inundation in central Namibia is intermediate when compared to a site like Torra Bay in northern Namibia. The above explanation would seem to imply an intermediate disturbance phenomenon which should according to theory increase species diversity. Species richness at a site or transect levels, however, showed no significant difference between the three Namibian regions.

The other dominant animal in this region is the circum-tropical mussel, *Perna perna*, which replaces the more cool temperate *Aulacomya ater* found further south. The former species is largely absent from the South African west coast and only reappears on the South African south coast. It has also been noticed that there is a significant sea surface temperature increase from southern to northern Namibia (Fig. 2.3). The presence of species would seem to indicate this temperature increase. The

following abundant algal species have warmer water affinities: *Chondracanthus teedii*, *Plocamium rigidum*, and *Hypnea tenuis* (Table 6.3).

The degree to which a species is sand tolerant is species specific. For example, *Caulacanthus ustulatus* (Fig. 6.10) does not tolerate extremely high levels of sand inundation (despite being a turf-forming species), as are found in Torra bay, Myl 4, and Myl 8 (Fig. 2.4), and as a result is absent from these sites. The difference observed between the two seasons in Myl 8 may be attributed to the variability in sand inundation. As can be seen from Fig. 2.4 the sand present in spring was six times more than the sample collected in autumn. *Caulacanthus* is, however, most abundant at intermediate sand levels as is found in the central Namibian region. The reason for the latter could be that this species occurs within the same zone as *Patella granularis* (a grazer) which is intolerant of sand. By excluding the limpet or reducing its numbers, this seaweed would be able to proliferate and / or increase its biomass. There is, however, no significant correlation between *Patella granularis* and *Caulacanthus* biomass. Another reason for *Caulacanthus* not tolerating extremely high sand inundation is that it is unable to cope with sand burial, whereas at intermediate moderate levels the sand is trapped between its branched turf-like structure but a significant portion of the thallus is still projecting. Under this circumstance it is able to survive and escape its herbivore.

The sites in southern Namibia which have moderate to high levels of *Caulacanthus* are the more sheltered sites. As was pointed out above, this could be a temperature factor and not a shelter factor, especially since this species has greater biomass levels in central and northern Namibia. The one factor in favour of shelter, as opposed to temperature, is the dominance of *Caulacanthus* at the sheltered and semi-exposed sites of Possession Island and Pomona respectively. If *Caulacanthus* is favoured by a relatively lower degree of wave action, then maybe the exposure in the central and northern regions are not as high as has been calculated. Sand, nevertheless, seems to be an important factor affecting its abundance in this area.

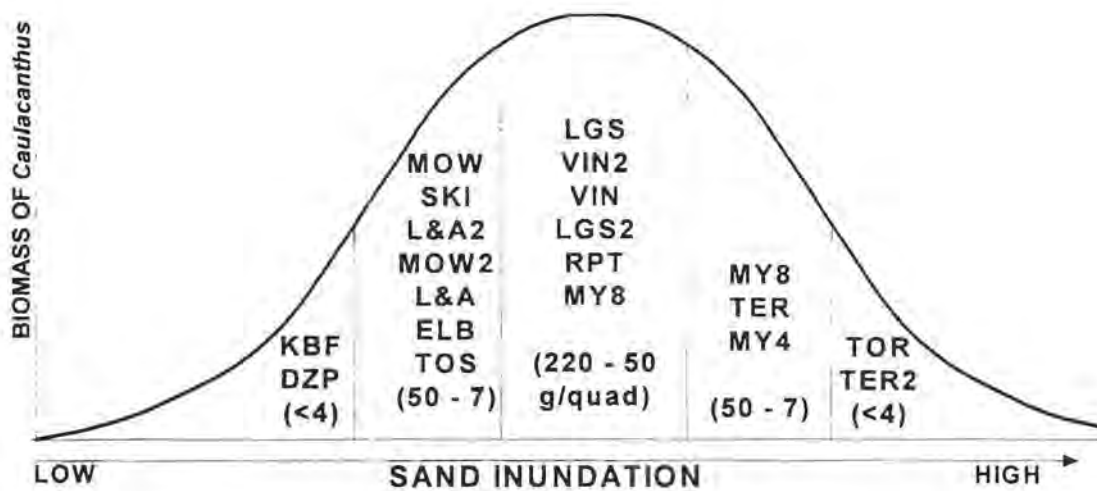


Fig. 6.10: A schematic representation of the abundance of *Caulacanthus ustulatus* with respect to sand inundation. Biomass value (wet weight) ranges are given in parentheses.

The northern Namibian coast represents a mixture of shores that range from sand-free rocky shores (Möwe Bay) to highly sand inundated shores (Torra Bay) (Fig. 2.4). The degree of wave exposure at most of the sites range from exposed to extremely exposed. The degree of exposure is however less than that found in southern Namibia (based on exposure measures in Chapter 2). The three sites chosen represent a range of the more extreme habitats encountered in the northern region. Toscanini is an animal dominated shore, largely dominated by the filter feeder (*Perna perna*), sea anemone (*Bunodactis reynaudi*) and barnacle (*Chthamalus dentatus*). This shore is representative of low lying, small rocky outcrops, flanked on either side by sandy beaches. As was seen in the DCA (Fig. 6.1), this site is closely aligned to Myl 8 from the Swakopmund area. It is proposed that these sites are exposed to sand scouring as opposed to sand inundation. Because of their size and low lying status, sand is easily moved onto and off the rocks by wave action. This would explain the existence of sand intolerant (in this case species that are intolerant of sand burial) species such as barnacles and *Patella* spp. being present. The only seaweeds to cope with these shores are *Mazzaella*, which has a crustose phase, and *Caulacanthus ustulatus* and *Streblocladia camptoclada*, which are turf forming seaweeds.

Möwe Bay on the other hand, forms part of an extensive rocky outcrop on an exposed coast, with little sand inundation. It is also the site which shows the strongest affinity to southern Namibian sites (Fig. 6.1), in particular those which are more sheltered. This is not to imply that Möwe Bay is sheltered, but that this could be a phenomenon of temperature rather than exposure. The abiotic

conditions on this shore are such that species found in the Lüderitz area should be able to survive here. There is, however, a four degree rise in average surface temperature. The three most abundant seaweed species found in the low intertidal reaches in southern Namibia, *Champia lumbricalis*, *Sarcothalia stiriata* and *Plocamium cornutum*, are absent further north, probably due to a temperature boundary. At Möwe Bay, *Centroceras clavulatum*, *Corallina* sp., *Plocamium rigidum*, *Pterosiphonia cloiophylla* and *Antithamnion diminuatum*, form the dominant species in this zone. The presence of *Aeodes orbitosa*, *Patella* spp. and high amounts of barnacles, support the idea of little sand inundation. It is therefore proposed that the above mentioned species are probably better adapted to warmer water conditions, or are able to compete more vigorously with other west coast species under warmer water conditions. The loss of *Champia lumbricalis*, *Sarcothalia stiriata* and *Plocamium cornutum*, also seems to be a function of temperature as opposed to sand inundation, as Möwe Bay makes an otherwise ideal site for their establishment.

The last shore looked at in this region was Torra Bay. This site showed the highest degree of sand inundation of all the sites. The most noticeable feature of Fig. 6.8, is the degree to which algae dominate this shore. Most of the species that typify the central Namibian region (Fig. 6.5) are found here. The algal diversity of abundant intertidal species is higher here than that found in central Namibia, and the zonation is more clearly defined. This implies that the community is probably in a more stable state or final successional stage. Other species which occur here are *Pachymenia carnosa*, *Ahnfeltiopsis* spp., *Gracilariopsis lemaneiformis*, *Gelidium* sp., and *Burnupena* sp.. The composition of central Namibian sites and Torra bay do not differ radically, as is borne out by Fig. 6.1 (all these sites fall within a narrow range on Axis 1; the differences seem to arise on Axis 2). With respect to degree of exposure, it was noted in the shore description (Chapter 2), that this site was not visibly as exposed as the other northern Namibian coast sites. The presence of the whelk *Burnupena* sp., which has been found to inhabit sheltered shores on the west coast (Stephenson, 1948; & Table 6.2 - ELB, L&A), would seem to indicate a more sheltered shore. A factor that was not taken into account when calculating exposure was the gradient of the immediate off-shore subtidal bed. This would give an indication of the force with which a wave would impact. The more gradual the slope the less powerful the wave action. If the intertidal is an indication of the subtidal bed, then Torra Bay, which has a long intertidal region with a gradual slope, would experience a milder form of wave action, as opposed to Toscanini, which is a small rocky outcrop within a steep sandy beach.

As was seen in Fig. 6.9, group 1 was common to all the regions. This group comprised the fine filaments, grazers and the thin, unbranched blades. The fine filaments have the ability to live in interstitial spaces, and are therefore able to occur in a wide variety of habitats, while the grazers tend to be ubiquitous, especially within the mid-eulittoral zone. The thin sheet-like unbranched blades are either opportunistic species (e.g. *Ulva* and *Enteromorpha*) or the upper eulittoral *Porphyra* spp.. There did however appear to be an ecological shift in functional form type from southern to northern Namibia, with northern Namibia exhibiting a greater variety of functional form. Southern Namibia comprised functional forms from Group 2, and central Namibia, in contrast, showed a strong affinity for turf forming algae and filter feeders (Group 3). Northern Namibia had a more even spread of functional form groups over its sites, although it too had a slightly stronger leaning towards group 3. The latter emphasised the increased shift towards turf-forming algae and filter-feeders between southern and central Namibia. This shift in functional form between these regions can be attributed to presence of shores with and without sand inundation.

Conclusions

The vertical zonation patterns observed on the Namibian coast may be divided into two main areas:

- (1) A southern region, which is similar to communities of South African west coast shores; and
- (2) A central and northern region, showing a predominance of turf-forming, “resprouting” and opportunistic algal species.

This shift is an ecological shift, rather than a “floristic” one, driven by a change in temperature, increase in degree of sand inundation and possibly wave exposure. As a result, a number of species are excluded from the central and northern regions of Namibia on the basis of the rise in temperature. Other species are then able to become dominant because of one or more of the following:

- (1) they are now free from the dominant species / late successional species further south;
- (2) they are better adapted to the rise in temperature;
- (3) they are able to cope with a moderate to high degree of sand inundation on most shores.

The method for evaluating the degree of wave exposure needs to be revised. If some component of near subtidal gradient could be obtained, a more reliable index could be devised. Alternatively, regular measurements of water motion, e.g. clod cards or dynamometers (Jones & Demetropoulos, 1968; Palumbi, 1984), in various sites in the three main regions will give a more accurate idea of water motion activity along this coast-line. This will serve to establish whether some of the proposals, with respect to indicator species of degree of exposure, are valid or not.

A number of species have been implicated as being environmental indicators of various conditions along this coast. These ideas need to be tested to ascertain the validity of these statements, however, this did not fall within the ambit of this project.

β -Diversity and the Similarity between Transects, Sites, and Regions

Introduction

β -Diversity is the rate of species or habitat turnover between sites on an environmental gradient (Wilson & Shmida, 1984; Magurran, 1988). This chapter's aim is to look at the change in species turnover and try to establish an explanation for the observed patterns. β -diversity may be looked at, at various scales which would in turn determine the scale of interpretation. For example, β -diversity may be viewed at a site, local or regional level.

β -Diversity at a site level, for example, could be the comparison of transects within a "homogeneous" area. This is described by Whittaker (1972) as pattern diversity. This comparison could act as a measure of variability within the site. Factors that may be responsible for such changes in species composition are: patchiness of communities (and the concomitant factors responsible for this patchiness), microhabitat variability or simply colonization limitations (Currie, 1991; Tilman 1994). Colonization limitation is the ability of an organism to colonize a space. This is largely dependant on the reproductive strategy of the organism (including reproductive output, present size of local population relative to surrounding species, settlement potential, growth rates, etc.). If a seaweed species dominates an area on the shore and it has a high reproductive output, it is more likely to colonize a newly made space on the shore (at the same zone level) than another species, which is less common.

At a local level, β -diversity, such as comparison between various sites / shores within a biogeographically homogeneous region, would give an indication of variability within a region. The principal factor that may be responsible for such changes at this scale would be habitat heterogeneity. Assuming that most of the species are collected at each site, then it is reasonable to assume that a comparison between two sites with different species composition may be accounted for by a change in environmental factors. Alternatively, if the conditions (at the sites concerned) appear to be too similar, then maybe the environment is too stochastic or the environmental factors too disruptive to allow the community to come to an equilibrium status. The latter would result in a more random selection of species at any particular site depending on the availability of propagules

for settlement (colonization limitation) on the disturbed site, which would result in a concomitant degree of variability in β -values.

The last scale of β -diversity I will discuss has already been covered to some extent in Chapter 3 on the biogeography of the Namibian coast. Here the turn-over of species was examined between the various regions under investigation within the Benguela phytogeographical province. This served as a measure of species turn-over along a temperature gradient. All the species found in a particular region (both intertidal and subtidal species) were combined into a comprehensive species list and compared. It was found that there is low turnover of species between adjacent regions, supporting the idea of a single biogeographical province. This chapter will look at β -diversity at a finer resolution, by comparing individual sites within the intertidal zone of the Namibian sub-region. This allows one to compare sites with different environmental conditions, while at the same time maintaining phytogeographical integrity.

The formula used in this chapter to describe β -diversity is that of Wilson and Shmida (1984) (see Methods Chapter), where the values range from 0 - 1. A complete turnover of species is represented by the value 1, while 0 represents no change. This formula also represents the degree of dissimilarity in species composition between sites, in that it compares the sum of the number of species lost and gained divided by the mean sample richness between the sites. It therefore indicative of site relatedness, despite the sites not necessarily occurring along an environmental gradient *per se*. These comparisons are concerned with floristic turnover as opposed to community structure i.e. the relative abundance of the species is not taken into account.

This chapter will focus on the various scales outlined above and will be divided up as follows:

- (1) Species similarity between transects at the various sites, i.e. how similar are adjacent transects;
- (2) Average β -diversity within the sites of the three defined regions, viz. southern, central and northern Namibia. This is comparing the species turnover between sites within a homogenous / defined region;
- (3) Average β -diversity between the three defined regions, to see the extent of species change along the latitudinal / temperature gradient i.e. the difference between individual shores from different regions sampled;
- (4) β -turnover between specific sites, i.e. how each shore relates to every other shore sampled;
- (5) The use of species turnover as a tool for examining sampling method.

Method

The data used in this section is of a species presence / absence nature extracted from the biomass data set. To ascertain the relatedness of adjacent transects to each other within each site, a species list of each transect was established and the percentage similarity calculated using the formula in Chapter 3. The results were then displayed on a frequency histogram with a 5% interval.

For calculating β -values between sites the quadrats of all the transects found at a particular site were combined and a species list for each site compiled. Each species was assigned the value 1 to indicate its presence. Samples from different seasons were kept separate so as not to confuse any seasonal effects taking place. The sites were then compared with one another to establish site relatedness and the results recorded in data matrices.

The average β -value, standard deviation, minimum and maximum β -values were obtained for each season of the three main regions on the coast, southern Namibia (Lüderitz area), central Namibia (Swakopmund area) and northern Namibia (Skeleton Coast area) The following comparisons were made:

Southern Namibia vs Southern Namibia (SNAM);
Central Namibia vs Central Namibia (CNAM);
Northern Namibia vs Northern Namibia (NNAM);
Southern vs Central Namibia (SNAM vs CNAM);
Southern vs Northern Namibia (SNAM vs NNAM); and
Central vs Northern Namibia (CNAM vs NNAM).

Local species richness is either less than or equal to regional species richness. The species that occur on a local level are therefore drawn from the regional species pool. To test whether the results obtained from the above comparisons were the result of random assortment of species in the respective regions or due to specific species favouring a specific type of site, a number of hypothetical shores were created. This was done as follows:

(1) Distinguishing characteristics for the three main regions were determined and are included in the Table 7.1, below.

Table 7.1: Species numbers parameters for the three regions sampled. (For clarification of calculations see the worked example in Fig. 7.1 for SNAM)

	SNAM	CNAM	NNAM
Total # of Intertidal Spp.	84	69	84
Total # of Abundant Spp.	24	24	28
Average # Dom. Spp. > 66% of Sites	7	5	4
Average # Dom. Spp. > 33% of Sites	4	4	7
Average # Dom. Spp. < 33% of Sites	13	15	17
Average # Dom. Spp. / Site	7	11	11

(The above data are derived from the previous chapter on abundant intertidal species zonation patterns i.e. those species with average biomass values $\geq 10\%$ of the total quadrat biomass)

- (2) An average of 31 ± 9 species / site was found for all regions, and no significant difference was encountered between regions.
- (3) A model was designed to randomly select species from a data base, using the above parameters, to generate a hypothetical shore. (See Fig. 7.1)
- The data base consisted of the total number of species found in the region; this would account for the species variation that was found in the particular region concerned.
 - This data base was divided into two parts:
 - Abundant species: the reason for dividing the data set into abundant and non-abundant species is as follows. Biomass was taken to be an indirect measure of reproductive potential. Therefore, the more abundant a species is, the more likely it will be able to colonize a region.
 - This group was further subdivided into three groups based on the number of these species present at $>66\%$, $>33\%$, and $<33\%$ of the sites in the region (based on abundance data from previous chapter). Species were weighted 3, 2, and 1 times with respect to the above categories depending on the relative abundance. This would therefore increase the chances of these species being randomly selected from a group of species, thus imitating the natural occurrence of abundant species on the shore, yet still maintaining random assortment of these abundant species.

- Non-abundant species: the remainder of the species that were not classified as abundant were given equal weighting.
 - Species were then randomly selected from the two sub sets of species and gave rise to the desired number of species per sub set. This number varied slightly to give the average stated above of 31 species / site. (See Fig. 7.1 for clarification)
- (4) The average β -value, standard deviation, minimum and maximum β -values were obtained for each hypothetical region and displayed graphically.

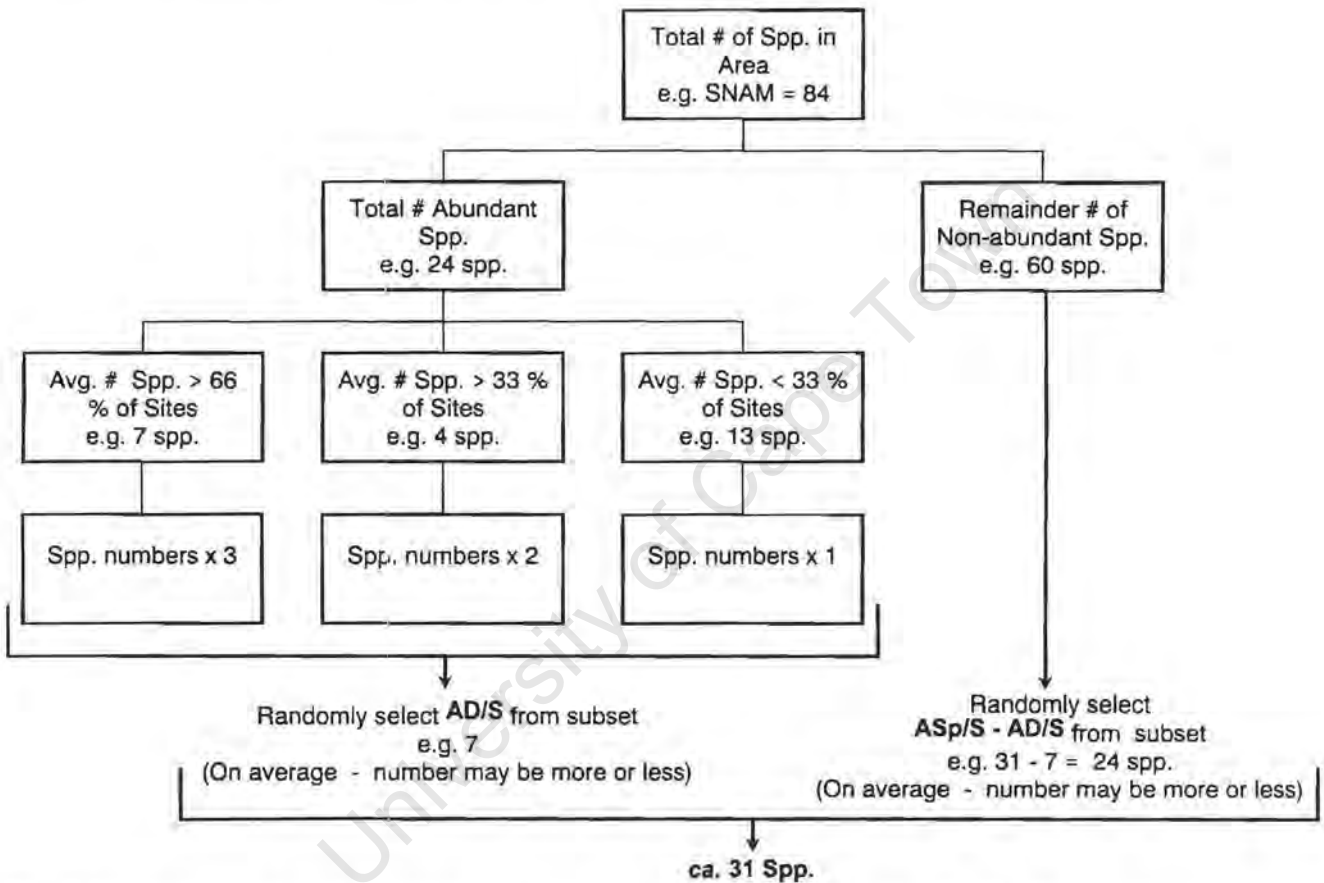


Fig. 7.1: Diagram of model used to construct hypothetical shores / sites for the three regions studied. (**AD/S** - Average # **A**bundant Species / Site; **ASp/S** - Average # **S**pecies / Site)

The averages for all the comparisons, i.e. within region (including model sites) and between region comparisons, were then subjected to a two-tailed student *t*-Test, where a significant result was set at $p < 0.05$, to establish if there were any significant differences between the various comparisons.

The implications of the model are as follows:

- (1) If the actual β -values are not significantly different from the model values, then the species arrangement within the various regions may be attributed to random assortment of species, with the condition that abundant species have a greater likelihood of occurrence by virtue of the fact that they have greater reproductive potential and therefore colonization potential.
- (2) If the actual β -values are significantly greater than the model values, then the species are more patchily distributed, with species showing a particular affinity to specific shores, thus giving rise to a high turnover between sites and concomitant high β -values.
- (3) If the actual β -values are significantly less than the model values, then there are more species in common between sites than would be predicted by random assortment. This would imply that some of the non-abundant species are more evenly spread amongst the various sites and that they have a sufficiently high reproductive potential to maintain a successful colonization.

For a more detailed view of how the sites compared to one another, the β -values obtained are displayed in a frequency matrix, and the various regions are separated by means of thickened lines.

Lastly, the rate of species accumulation in each region was ascertained as follows: transects for each region were randomly arranged using a random number table. The species richness for the first transect was established. The next transect was added and the species richness of the combined transects was then established, i.e. the addition of any new species encountered added to the previous species richness. Transects were added one by one until all the transects in a particular region had been sampled. The transects were then rearranged and the procedure repeated twice more, to obtain an average. The seasons were kept separate, but the species accumulated in spring (1990) formed the starting point for species accumulated in autumn (1992). These results are in the form of an accumulative line graph, which is separated into two halves based on season. The reason for this was to ascertain whether there is a difference in species composition between these two sampling periods. The transects for both seasons were then interspersed and randomly arranged, and the procedure repeated. This would serve as an indication of the minimum number of transects that would be needed to sample 85 and 90 % of the species found in the respective regions.

Three non-parametric methods of estimating species richness for a sampled region were employed to see how close the sampling was to 100 %. The three formulas used are described and discussed in Colwell and Coddington (1995). They are as follows:

Chao 2 Estimator

$$S = S_{\text{obs}} + (L^2 / 2M)$$

S - Estimated Species Richness

S_{obs} - Observed Species Richness

L - Number of Species that occur in only one sample (transect)

M - Number of Species that occur in exactly two samples (transects)

1st Order Jackknife Estimate

$$S = S_{\text{obs}} + L \left(\frac{n-1}{n} \right)$$

n - Number of samples

2nd Order Jackknife Estimate

$$S = S_{\text{obs}} + \left[\frac{L(2n-3)}{n} - \frac{M(n-2)^2}{n(n-1)} \right]$$

According to Colwell and Coddington (1995), these three species richness estimators provide the best estimate for small sample sizes with the least amount of bias. The Chao 2 estimate is particularly good for presence-absence data, as used in this chapter.

Results

Similarity between Transects

Fig. 7.2 represents a frequency histogram of number of sites with similar percentage similarity of transects i.e. with respect to species composition. As can be seen, most of the sites show a 75 - 80% similarity between adjacent transects. Only two sites had transects with less than 70% similarity, Agate Beach (64%) and Myl 4 (69%).

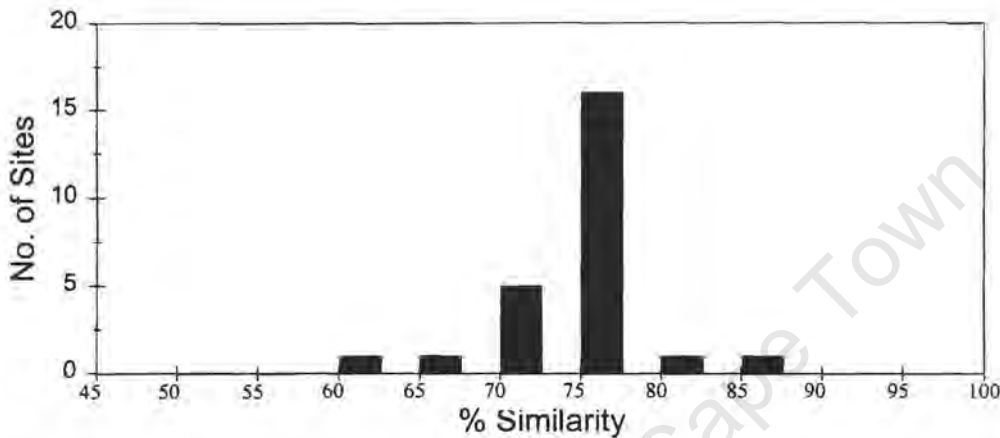


Fig. 7.2: Frequency histogram of the percentage similarity between adjacent transects at the various sites.

Within Region Comparisons

In the within region comparisons (Fig. 7.3), SNAM (spring) was not significantly different from CNAM (Spring), whereas there is a significant difference between these two regions in the autumn collection. NNAM was significantly different from both SNAM and CNAM for both seasons. There was no significant difference between seasons of respective regions. CNAM showed the least variation among its sites, while the greatest turnover on average was noted for NNAM. The standard deviation and range was greatest in NNAM, while for SNAM and CNAM these values were relatively small and similar. The minimum values in NNAM are also considerably higher than the averages in SNAM and CNAM for the spring samples, and on par with SNAM in the autumn samples (these values are still greater than CNAM's maximum value).

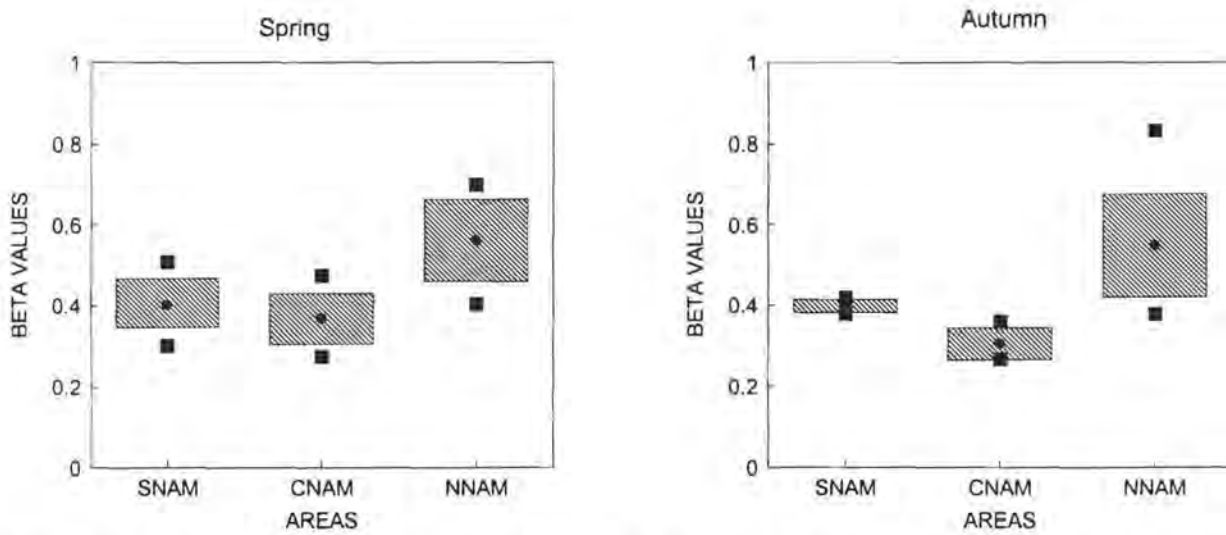


Fig. 7.3: Within region comparisons of average β -diversity values for the two seasons sampled. Dot - average; Hatched box - Standard deviation; and, Squares - Minimum & Maximum values.

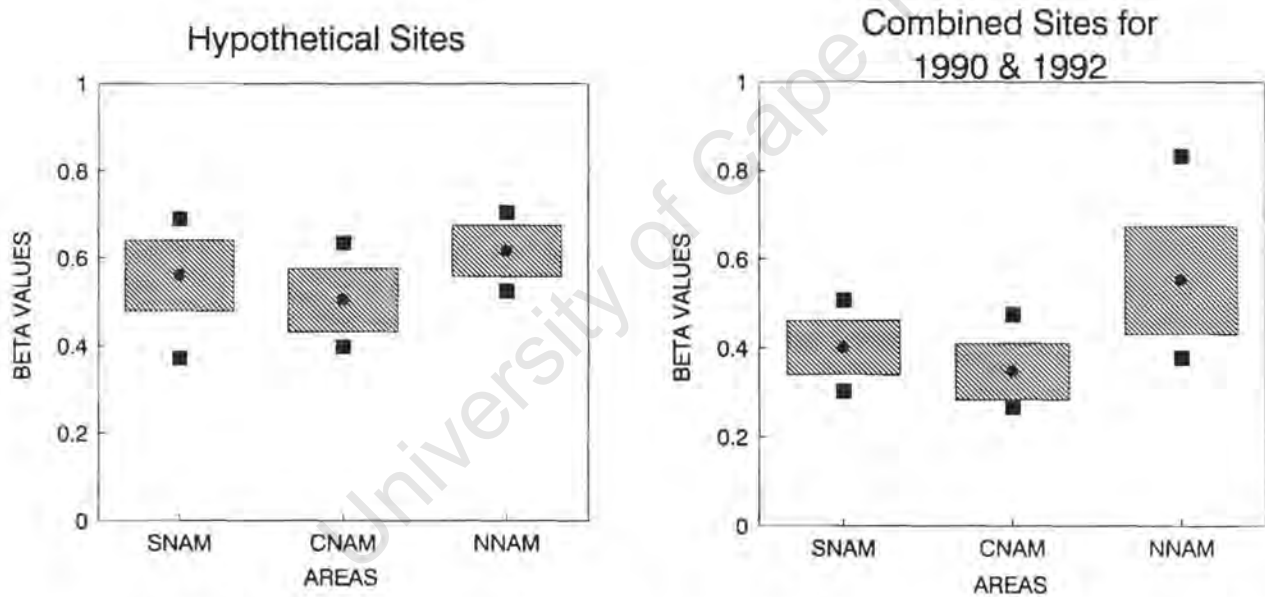


Fig. 7.4: Within region comparisons of average β -diversity values for the Hypothetical sites and the Combined 1990 & 1992 sites for the three regions. Dot - average; Hatched box - Standard deviation; and, Squares - Minimum & Maximum values.

Table 7.2a: *t*-Test for within site comparisons between hypothetical and actual data sets.

	SNAM	CNAM	NNAM
<i>t</i> -Statistic	5.540	5.013	1.937
D.F.	31	17	29
<i>p</i> <	0.001	0.001	0.1

Table 7.2b: Average species richness and standard deviation for sites for 1990 and 1992.

	SNAM	CNAM	NNAM
Average # of Species / Site	33	33	30
Standard Deviation	7.2	6.9	12.9

As can be seen from Fig. 7.4 and Table 7.2a there is a significant difference between the hypothetical and actual sites for SNAM and CNAM, but not for NNAM. Both SNAM and CNAM have lower β -values than would be expected by random assortment of species. It should also be noted that the variance for NNAM in the combined sites are substantially larger in the actual data set. This variation is also seen with respect to average species richness and standard deviation for the sites of the different regions (Table 7.2b). NNAM has almost double the standard deviation of SNAM and CNAM. The hypothetical data set had an average of 31 species and standard deviation of 2.15 for the three regions.

Between Regions Comparisons

Fig. 7.5 represents the average β -values for spring and autumn for the various regions. The means of SNAM vs CNAM and SNAM vs NNAM were found to be not significantly different for both seasons. Whereas CNAM vs NNAM was found to be highly significantly different ($p < 0.005$) from the other two comparisons, for both seasons ($p < 0.05$). There is a β turnover of approximately 0.7 on average for SNAM vs CNAM and SNAM vs NNAM, as opposed to a β turnover of 0.5 for CNAM vs NNAM. There is also no significant difference between CNAM vs NNAM β -values and NNAM within site values (Fig. 7.3 & 7.4). There is no significant difference between the two seasons.

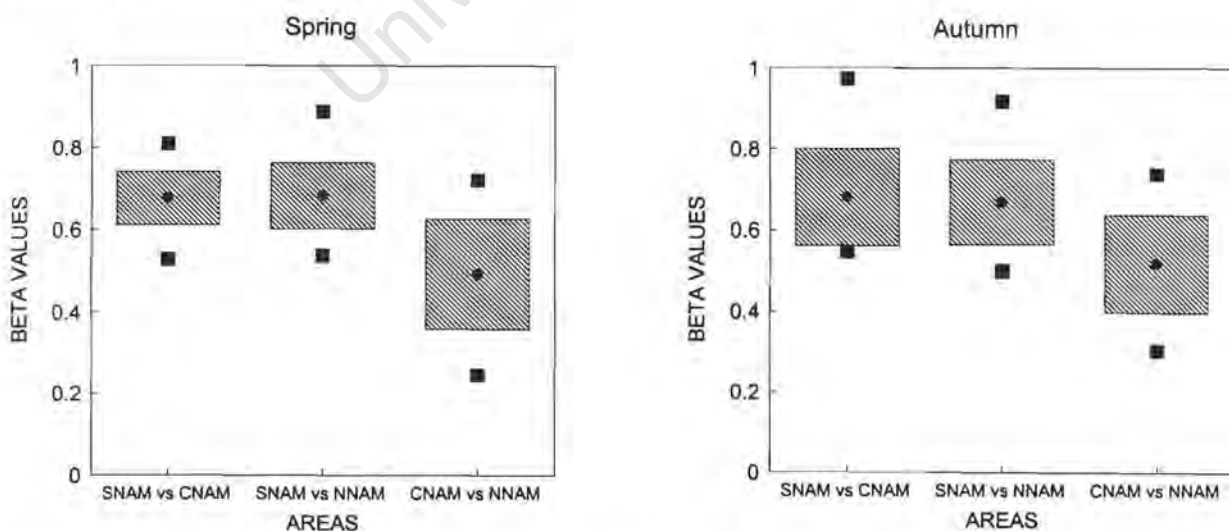


Fig.7.5: Between regions comparisons of average β -diversity values for the two seasons sampled. Dot - average; Hatched box - Standard deviation; and, Squares - Minimum & Maximum values.

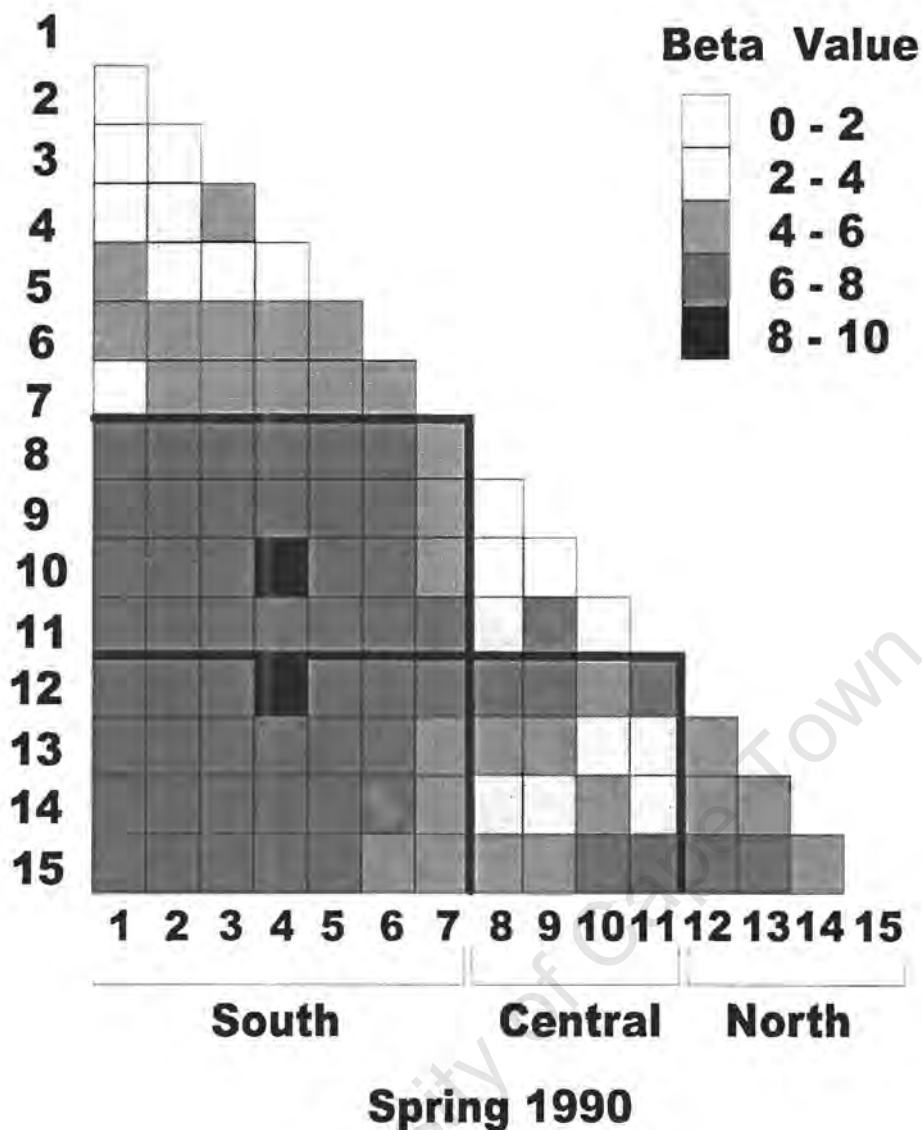
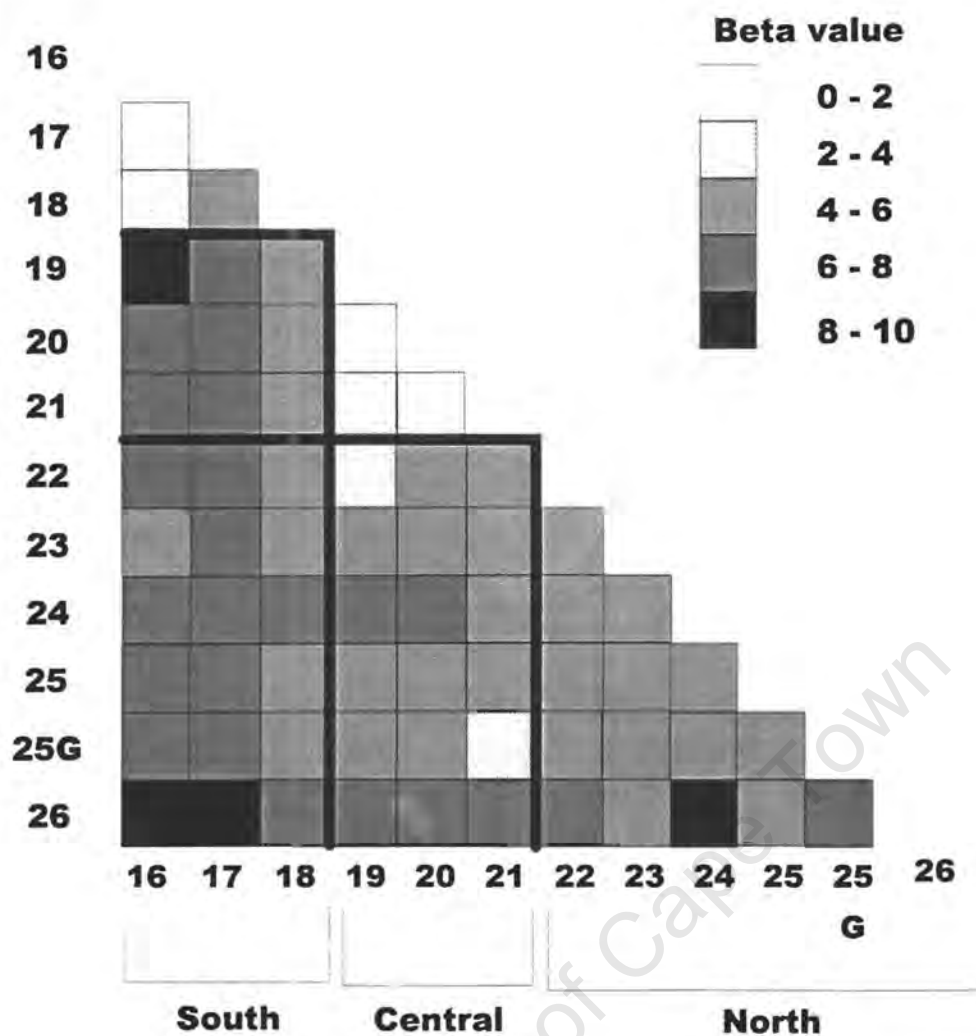


Fig. 7.6: β -values between the various sites sampled in spring 1990. The thickened lines divide the three regions under observation. (The β -values have been multiplied by a factor of 10).

Fig. 7.6 represents the β -values obtained between the various sites during the spring 1990 collection. The results displayed here represent a detailed picture of Figs. 7.3 and 7.5. Within the southern Namibian region sites 6 and 7 show the greatest degree of variation from the other sites in the region; whilst sites 1 and 2 show the least amount of turnover between sites. In the central Namibia region there is little variation between sites, with the exception of the turnover between sites 9 and 11 (Vineta Beach and Myl 8 respectively). The northern Namibia region has a high degree of variability, with Möwe Bay (site 15) showing the greatest difference. As seen above, in the between site comparisons, southern Namibia differed quite substantially from central and northern Namibia. Site 7 (Agate Beach), from southern Namibia, did show a greater affinity to these regions, likewise, the comparison 6 and 15 (Shark Island and Möwe Bay respectively). The difference between central and northern Namibia is very variable, β -values ranging from 0.2 - 0.8.



Autumn 1992

Fig. 7.7: β -values between the various sites sampled in autumn 1992. The thickened lines divide the three regions under observation. (The β -values have been multiplied by a factor of 10).

Fig. 7.7 is the same concept as Fig. 7.6 with season being the only difference between the two, i.e. autumn as opposed to spring. The same general patterns are observed within and between the various regions, southern Namibia being moderately variable, central Namibian being highly similar, and northern Namibia showing a high degree of variability. Agate Beach (site 18) again exhibits the greatest similarity to sites in central and northern Namibia, with site 26, False Cape Fria, showing the greatest difference from all other sites.

Evaluation of Sample number and Estimation of Regions Species Richness

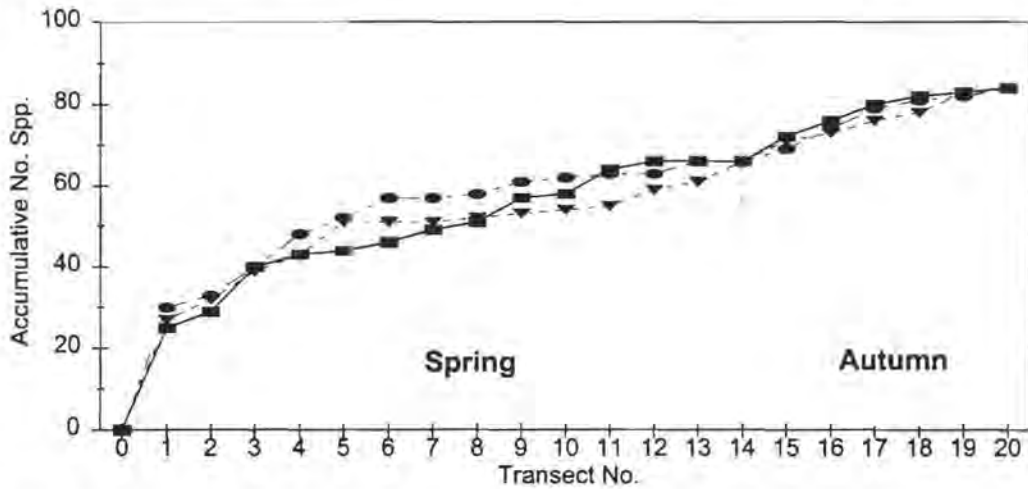


Fig. 7.8: Accumulative Species Richness with increasing number of transects for the southern Namibia region for three randomly selected transect orders. Dashed line represents the change from spring 1990 to autumn 1992 data sets.

Figs. 7.8 - 7.11 comprise a series of graphs which deal with the rate of species accrual with increasing transect number for the three regions. In Fig. 7.8 the species accumulation appears to be tailing off towards transect 12 of summer, and transect 19 of autumn. The difference between the summer and autumn is 17 species. There were 66 species collected intertidally within each season, and a combined species richness of 84 species.

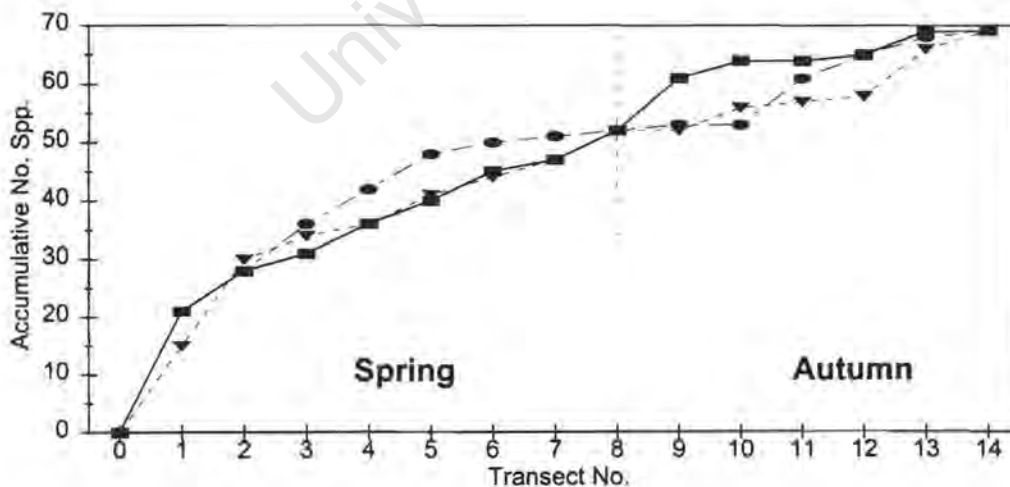


Fig. 7.9: Accumulative Species Richness with increasing number of transects for the central Namibia region, for three randomly selected transect orders. Dashed line represents the change from spring 1990 to autumn 1992 data sets.

In Fig. 7.9 the graph does not appear to tail off (for all three curves) towards the end of spring, but does appear to start to tail off at transect 13 in autumn. There is a difference of 14 species between these two seasons (see Table 7.3 below). The spring sample had 55 species, as opposed to the autumn collection of 60 species, with a total species richness of 69.

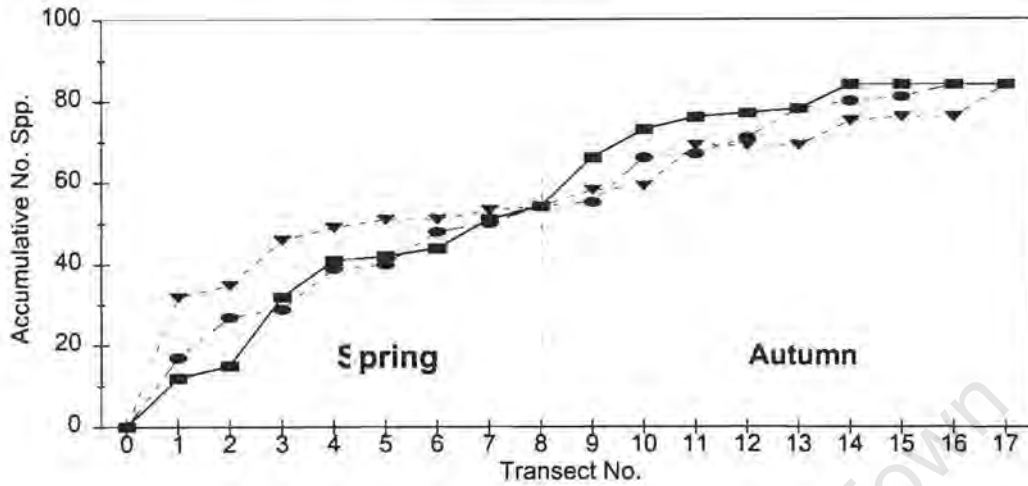


Fig. 7.10: Accumulative Species Richness with increasing number of transects for the northern Namibia region, for three randomly selected transect orders. Dashed line represents the change from spring 1990 to autumn 1992 data sets.

Fig. 7.10 appears to start tailing off at transect 7 (spring) and 14 (autumn). There was an increase of 28 species between seasons, but this could largely be attributed to the addition of two sites found further north, viz. Rocky Point and False Cape Fria. There was a total species richness of 84 species, and 56 and 76 species for spring and autumn respectively.

Table 7.3 represents the number of species that were not present in each season and the possible explanation for their absence in the alternate season. The reasons for the categories chosen are as follows:

- (1) Annual species: the species are either winter or summer annuals and therefore either appear or disappear from the intertidal during the change of seasons.
- (2) Subtidal species: these are species that are almost exclusively subtidal, but are occasionally able to survive the low shore conditions; they therefore do not constitute 'real' intertidal species, and tend to be uncommon in the data set.
- (3) Rare species: these species are not very abundant on the rocky shore and therefore the probability of them not being sampled is quite high.
- (4) Warm water species and / or low sand: these are species that tend to favour slightly warmer water temperatures or low sand levels. With respect to temperature, since the samples are taken

at the turn of the seasons, the abundance of these species could be affected as follows: at the onset of spring they would start to increase in biomass / abundance; or, by the start of autumn the water has not become sufficiently cold for a reduction in the biomass accumulated during summer.

- (5) Moderate sand species: these are species that seem to require a moderate degree of sand inundation to be present in sufficient quantity, since sand levels fluctuate on an irregular basis, so would the presence of these species.
- (6) No Explanation?: These are species for which no explanation could be found for the presence or absence in the opposing seasons.

Table 7.3: Several categories for explaining the number of species not accounted for in the alternate season for the three regions.

	Southern Namibia		Central Namibia		Northern Namibia	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Annual species	2	1	0	0	1	0
Subtidal species	4	9	1	5	2	4
Rare species	8	1	6	4	4	13
Warm water spp. and/or low sand	2	5	1	1	0	0
Moderate Sand	1	0	1	1	0	2
No Explanation ?	0	1	0	3	1	9

As can be seen from Table 7.3 very few annual species are responsible for the difference in species numbers between seasons. Most of these differences are due to Subtidal or Rare species. In southern Namibia the warmer water and low sand tolerance species appear to be important - these species were found only in Elizabeth Bay and Lüderitzbucht (mostly the Agate Beach site). Within central and northern Namibia there seemed to be a number of species that defied explanation, particular those species found in the latter region. These species included: *Ceramium planum*, *Enteromorpha compressa*, *Enteromorpha prolifera*, *Grateloupia longifolia*, *Gymnogongrus dilatatus*, *Polysiphonia urbana*, and *Ulva capensis*. The increase in species richness between spring and autumn for northern Namibia, as was noted earlier, is partly due to the addition of Rocky Point, in particular, to the data set in 1992.

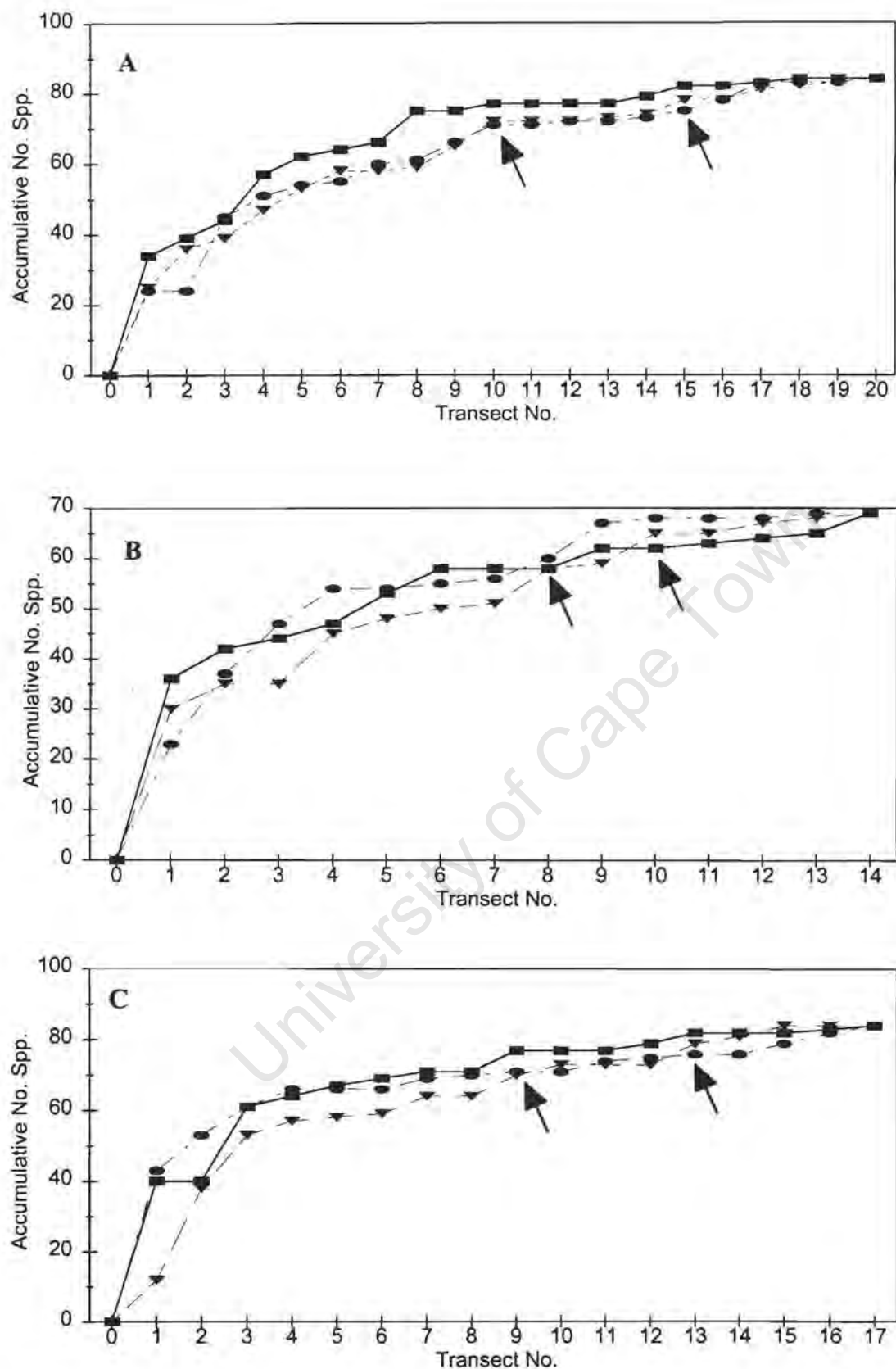


Fig. 7.11: Three randomly selected accumulative transect sequences from both the 1990 and 1992 data set, A - Southern Namibia; B - Central Namibia; C - Northern Namibia.

↖ - minimum of 85% of total number of species for the respective region; ↗ minimum of 90% of total number of species for the respective region.

Fig. 7.11 represents species accumulation over a random selection of habitats and seasons. Thus, if one wanted to know what was the minimum number of transects to run within these regions and still include 85 - 90 % of the species, it could be ascertained. These graphs also give an indication of how varied the region is. Southern Namibia requires a minimum of 10 transects to obtain 85 % of the species and 15 transects for 90 %. The graph does appear to be tailing off with an indication that there may be only a few more species to be found so that the species richness for the region is close to the absolute value. For central Namibia fewer transects are needed to obtain 85% and 90% total species richness for the region, namely 8 and 11 transects respectively. This region would also appear to be close to its regional species richness. Lastly, northern Namibia seems to be somewhere in between, with 9 transects for 85%, and 13 transects for 90% of the total region richness. It too shows a final species richness which is probably close to absolute species richness for the region.

Table 7.4: Observed and estimated Species Richness values for the three regions. The percentage of the Observed / Estimated Species Richness is adjacent the Estimated value.

Region	Total # Spp. Observed	Chiao 2 Estimate (S1)		1 st Order Jackknife Estimate (S2)		2 nd Order Jackknife Estimate (S3)	
		# Spp.	%	# Spp.	%	# Spp.	%
SNAM	84	104	81	105	80	115	73
CNAM	69	97	71	89	78	100	69
NNAM	84	113	74	106	79	119	71

As can be seen in Table 7.4 the observed species richness would seem to be somewhere between 70 - 80% of the estimated species richness for the various areas. Out of the three regions SNAM is the most thoroughly sampled.

Discussion

Similarity Between Transects

Looking at the degree of similarity between adjacent transects is *sensu stricto* not β -diversity as it does not occur along an environmental gradient. As Magurran (1988) points out, β -diversity at a pattern diversity level is an alternative to similarity co-efficients. This measure however, could serve as an indication of patchiness within a community. If there is a high degree of similarity between transects then the community / site being sampled can be assumed to be homogeneous, with respect to species composition. Conversely, if there is a low degree of similarity, then the community being sampled is either heterogeneous or highly patchy in construction within the site. The latter suggests that not all the species are included in the sampling.

There is no apparent difference between the three regions with respect to percentage similarity of adjacent transects for the different sites. Most, as was noted, showed a species composition similarity of 70-75 % similarity (alternatively, a 25-30 % dissimilarity) (Fig.7.2). This degree of dissimilarity is considerably high considering, as was noted above, that the transects occurred on the same shore in relatively close proximity to one another. If one is to assume that the difference in microhabitat is negligible, and that it is these microhabitats that are responsible for species composition, then there should be little difference between adjacent transects. It should theoretically be borne in mind that each transect comprises a number of quadrats within each zone, hence this should reduce the probability of differences between transects. It was noted in a previous chapter that there are definite zonation patterns within the various regions, and that the most abundant species on the various shores are quite consistent (with the exception of northern Namibia). There would therefore appear to be a certain degree of patchiness on any particular shore with respect to species composition, even though the composition of the most abundant species may not differ considerably.

Patchiness within communities is not so much due to local biotic interactions or microhabitat variation, but colonization limitation (Connell, 1972; Paine, 1974; Menge & Sutherland, 1987; Tilman, 1994). As was seen previously (Chapter 6), equitability in the lower reaches of the shore was relatively low, particularly in southern Namibia. These parts of the shore were therefore dominated by a few species, while remaining species (being of substantially less biomass) occupied the remaining space. The bulk of the species in this zone are therefore present in relatively small

amounts. It is therefore highly likely that the arrangement of these species on the shore are due to random assortment, thus giving rise to the relatively high dissimilarity values. As a result hypothetical shores for each of the regions was established to test this idea of random assortment.

Within Region Comparisons

As was seen in Fig. 7.3 there was little difference between the β -values for SNAM and CNAM. Both these regions are on average 40% dissimilar, and the range around these means are also relatively small. This indicates that the differences found between any two shores in these regions are relatively consistent and therefore predictable. A 40 % turnover of species between any two sites may be considered to be high; but, as was found with the hypothetical shores, an average β -value of 50-55% could be attributed to random assortment of species in both these regions.

According to the hypothetical model data there are more species in common between sites than could be explained by random assortment of species. A number of non-abundant species were found to be present in > 33% of the sites (Table 7.5, below). These species constitute characteristic species of these shores even though they do not form part of the criteria for dominance. Many are small, filamentous and occupy interstitial spaces between more abundant species. Others, like species of *Grateloupia* and *Gymnogongrus / Ahnfeltiopsis*, have a persistent basal crust, and often go undetected in samples as they are only visible or collected when the upright portions of the thallus are present. *Laminaria schinzii*, *Rhodomenia* sp., and *Cladophora mirabilis* are predominantly subtidal species, but may occur on the sublittoral fringes. Their presence would therefore be dependant on the subtidal community and not on the intertidal community. *Ulva rigida* is usually a notable opportunistic species and one of the primary succession species. There is therefore more than 'apparent' dominance to determining species composition. Rarer species may be significantly represented dependent on niche space occupied, growth habits, and reproductive strategies. Coexistence of rare species within more abundant species stands may be made possible by regular spaces/patches becoming available within communities.

Table 7.5: Non-Abundant spp. with site distributions > 33 % for southern and central Namibia.

SNAM		CNAM	
Species	% of Sites	Species	% of Site
<i>Platysiphonia intermedia</i>	36	<i>Grateloupia doryphora</i>	43
<i>Pleonosporium harveyanum</i>	36	<i>Grateloupia filicina</i>	43
<i>Arthrocardia</i> sp.	45	<i>Laminaria schinzii</i>	43
<i>Ahnfeltiopsis vermicularis</i>	45	<i>Pleonosporium filicinum</i>	43
<i>Leathesia difformis</i>	45	<i>Ceramium planum</i>	57
<i>Ulva rigida</i>	45	<i>Cladophora capensis</i>	57
<i>Cladophora</i> sp.	55	<i>Cladophora mirabilis</i>	57
<i>Gymnogongrus dilatatus</i>	55	<i>Rhodymenia</i> sp.	57
<i>Laminaria schinzii</i>	55	<i>Aristothamnion collabens</i>	71
<i>Tayloriella tenebrosa</i>	64	<i>Gracilariopsis</i> sp.	71
<i>Pterosiphonia cloiophylla</i>	73	<i>Streblocladia corymbifera</i>	86
<i>Aristothamnion collabens</i>	82	<i>Bryopsis</i> spp.	100
<i>Delesseria papenfussii</i>	82		

These sites occur within a "homogeneous" biogeographic region, and where the dominant physical factor of wave exposure was, *sensu lato*, kept relatively similar (i.e. no sheltered areas sampled in southern Namibia as there are no such sites further north). Habitat heterogeneity of the various sites may be used to explain these differences, but this measure alone is not sufficient to speculate as to the degree of habitat heterogeneity. Again the above argument of colonization limitation may be invoked as an explanation, but on a larger scale. These meta-communities, as they are often referred to, are also often sensitive to initial conditions. The initial species settlement and resultant succession after stochastic events will often determine the final succession (Wilson, 1992). The range in β -values observed may be an indication of degree of local environmental perturbation. The more stable an environment the more the community will approach a stable state, and abundant species will under these conditions gradually displace less abundant species. While an increase in perturbation or stochastic events will result in a number of alternate stable states, these will allow non-abundant species to coexist.

Northern Namibia had high β -values on average, ranging from 40 - 80% turnover (Fig. 7.3). The standard deviation of the β -values was also much larger than for SNAM and CNAM. This would seem to imply a highly heterogeneous habitat or a high degree of stochastic events to account for this high turnover. It was also noticed that NNAM had the greatest variation with respect to species richness in each transect. According to Magurran (1988), the Wilson and Shmida formula for β -diversity is independent of α diversity. Therefore this wide range of β -values is not due to differences in species richness but probably habitat heterogeneity.

From a descriptive point of view, it may be seen from the site and region descriptions, that the northern Namibia region comprises sites and environments which run from heavily sand inundated low lying rocky outcrops through to sand-free exposed/semi-sheltered extensive rocky outcrops. Each rocky shore on this part of the coast is therefore mostly substantially different from any other shore. This idea is supported by the minimum β -values from this region which are almost as great as the maximum values for the other regions (Fig. 7.4). This covers the habitat heterogeneity aspect of this part of the coast, but there is also considerable environmental perturbation in the form of sand inundation. As has been pointed out previously, some shores experience periodic movement of sand. This will make space for colonization by sessile organisms, the composition of which will be dependant on propagule availability when the sand is removed. Since habitat availability on this coast is not as extensive as southern Namibia, the source of propagules is largely restricted to those species that survive the stochastic events, as there are large distances between adjacent rocky shores. Shores with permanent sand inundation or sand free reach different stable states, and are themselves subject to initial recruitment and colonization limitation factors.

Between Regions Comparisons

Southern Namibia, as was seen earlier (Chapter 3), is significantly different from central and northern Namibia (Table 7.3). There is a minimum of a 50 % turnover of species between sites in southern Namibia versus central and northern Namibia. The marked change in temperature, as one moves north, was previously considered the dominant physical factor. This temperature differential results in a different suite of species, abundant and/or ubiquitous non-abundant, representing the average shore in these regions. As a result, the species that are most likely to occur in southern Namibia are not necessarily going to occur with the same regularity in central or northern Namibia. This site-on-site comparison, however, does not impact the region-on-region comparisons, as was reported in Chapter 3, where a low β turnover was noted between SNAM and CNAM.

The difference between central and northern Namibia is a 50% species turnover on average. As the standard deviation indicates, however, the range of variation between these two regions is relatively large (β -values between 0.25 - 0.74). The low β -values may be attributed to the fact that the typical central Namibian shore is also encountered further north; whereas such sites are not found in southern Namibia. The northern region is more variable than the central region (as was seen above) which would account for the wider range of β -values. As these two regions comprise the same biogeographic sub-province, they have similar temperature conditions, and central Namibia's habitat heterogeneity forms a subset of northern Namibia's habitat ranges.

Figs. 7.6 and 7.7 show the details of Figs. 7.3 to 7.5. Here the specific relationships between sites could be observed, as opposed to general trends. It was noted that sites 6 and 7 (Shark Island & Agate Beach, respectively) were most different from the other sites. Both these sites occur within Lüderitzbucht, and has been noted in previous chapters, they are only semi-exposed, occur in a shallow bay, and are exposed to westerly, north westerly and north winds. Being situated in a shallow bay in a slightly sheltered area would result in slightly higher temperatures than those areas on the exposed coastline. It was also noted that the Agate Beach site showed greatest affinity to the central and northern region sites. There are two main possible factors responsible for this, viz. temperature increase or reduced wave exposure north of Lüderitz. There is still a large difference between this site and the central and northern Namibian sites, but this can be accounted for by the high level of sand inundation in the latter regions. Elizabeth Bay (1 - southern Namibia) may also be expected to have slightly warmer water because it is also a semi-exposed shallow bay, however, this site is south facing and therefore exposed to south and south easterly winds which are the dominant and upwelling winds on this coast. The water at this site is therefore probably well mixed and close to the temperature of open coastline sites.

As was seen in Figs. 7.3 and 7.5 there is little variation in central Namibia and a high degree of variation in northern Namibia. This gave rise to moderate to high variation in β -values in the comparison between these two regions (Fig. 7.6 & 7.7). False Cape Fria (Fig. 7.7) emerges as the site most different from every other site. This shore was completely animal dominated, exposed, and is situated alongside a cape fur seal colony, therefore exposed to a high degree of perturbation. Most of the other sites have relatively high species richness, however, this site has a particularly low species richness. The above method enables one to quickly assess the variation within a region, as well as highlighting areas which are particularly different or similar.

Evaluation of Sample number and Estimation of Regions Species Richness

One factor that is particularly noticeable in Table 7.3 is the high number (10-20 % of total species richness) of rare species that were not found in the two seasons / years sampled. This is not an altogether unexpected result, as Lande (1996) comments "...rare species often will be absent even in large samples or exhaustive surveys." This factor must be borne in mind if the reason for the survey or data collection is for the purposes of biodiversity and / or reserve allocation. Annual species, on the other hand, accounted for a negligible portion of the observed 'seasonal' variation.

Northern Namibia had also a large number of species whose presence / absence could not be explained. This may be due to the extremely unpredictable nature of many of these shores with respect to disturbance (viz. sand inundation). In this study the data are in the form of a snap shot of the results of preceding events. Many of the shores are constantly sand inundated, while others are periodically or stochastically covered by sand. The sand data used in the preceding analyses represent the shores as they were encountered. As a result, the shores may have harboured somewhat different communities days, weeks or months before sampling. To a large extent it is these factors that are responsible for generating the observed communities.

β values give an indication of turnover between sites, whereas the rate of species accumulation gives an idea of how many transects it would take before all (or nearly all) the species in a region were sampled. Looking at the combination of these two measures one can get an idea of how variable the environment is.

Table 7.6: Comparing various measures of region diversity.

<i>Region</i>	<i>Regional Species Richness</i>	<i>Average β-value</i>	<i>Minimum No. of Transects to Achieve</i>	
			<i>85%</i>	<i>90%</i>
SNAM	84	0.401	10	15
CNAM	69	0.347	8	10
NNAM	84	0.553	9	13

(Bold indicates no significant difference between regions)

As was seen above in Table 7.6, southern Namibia required more transects to reach 85 - 90% of the total species richness of the region. The reason was that the difference in species composition between the various shores are relatively high, this is seen in the β -values (approx. 40% dissimilarity). The first transect will account for approximately 30 % of the total species (Fig. 7.11), after which the successive transects increase at a rate of 5% on average until transect 10, thereafter accumulation of species is relatively slow (1% / transect). Conversely, central Namibia approaches 85-90% at a much faster rate. Despite the similar β -values between southern and central Namibia, the latter reaches equilibrium faster. This implies that the variability in shores is greater in southern Namibia than in central Namibia. This may however be explained by the fact that southern Namibia has a greater regional species richness than central Namibia, but that both have a similar species richness per site. Therefore, the number of species in southern Namibia that may randomly occupy a shore is greater than central Namibia.

Northern Namibia, on the other hand, has the same regional species richness as southern Namibia, but its β -values are far higher than southern Namibia. The shores in northern Namibia are so different from one another that the full complement of species is reached more rapidly than southern Namibia. The implication here is, that whereas the species recorded from central and northern Namibia may be close to their absolute intertidal species richness, southern Namibia may still under sampled.

Paradoxically, as was seen in Table 7.4, in all three species richness estimates, NNAM and CNAM are the most under-collected regions, although the differences seem insignificant for the three regions when all the estimates are considered. What is clear is that 20 - 30% of the intertidal flora is still outstanding in the various regions. Also, that a sample size of 10 randomly sampled transects will only result in a 60-70 % representation of the species in a region.

Intertidally, southern and northern Namibia have the same species richness (using the biomass data); but whereas northern Namibia includes most of the habitats, sites chosen in southern Namibia were more restricted owing to the sampling procedure. In central and northern Namibia, sampling sites were chosen, to a large extent, on availability, whereas in southern Namibia, a more selective approach could be adopted for consistency with regions further north. As there is more rocky shore to choose from and wave exposure was deemed as being of primary importance, sites were chosen to minimize this variable. However, the problem in the south is that more sand

inundated sites occurred within the restricted diamond areas and could not be sampled. I was able on other occasions to go into some of these areas, but no removal sampling was allowed, which makes the data not strictly comparable. Most of the "habitats" were sampled in the central and northern reaches of Namibia (all being on a relatively wave exposed coast), whereas, only a fraction of the available habitats were biomass-sampled in southern Namibia. It is believed that by sampling these habitats a greater species richness will be realized as well as a clearer understanding of the relationship between the south and northern parts of Namibia.

In conclusion, there is considerable variation between transects and sites within homogeneous areas, as well as between regions of large geographical distance in a homogeneous biogeographic province. There would appear to be a carrying capacity for each region and a carrying capacity for a transect. The species present from the latter are then drawn from the former. In NNAM this pattern of species determination is largely due to abundant species effect on colonization and random assortment of non-abundant species, whereas for SNAM and CNAM this variation is less than would be expected from random assortment. Here the environments are more predictable and a number of non-abundant species occur more evenly spread over all the sites.

Site variation seems to be greatest in NNAM, moderate in SNAM, and least in CNAM, remembering that site selection was limited in SNAM. Sites in SNAM that showed greatest affinity to CNAM and NNAM are those whose conditions are more sheltered and probably have slightly higher temperatures.

With respect to the number of transects sampled, it would appear that 70 - 80 % of the intertidal species have been collected within each region. A random sample of 10 transects would result in a 60-70 % species richness for any of the regions sampled. This sample size would result in maximum information per unit effort.

Chapter 8

Conclusions

Biogeographically the Namibian seaweed flora forms part of the Benguela marine province. This province stretches from Cape Point, South Africa, to southern Angola, with a Benguela-Agulhas transition zone from Cape Point to Cape Agulhas. The Province may be divided into two regions, a southern Namaqua and a northern Namib sub-province. The difference between these two sub-provinces is a decrease in species richness. This decrease was noted in all three seaweed divisions, but particularly in the Phaeophyta and Rhodophyta. This decrease may be attributed to several factors:

- Temperature effects:
 - A 'cool' temperate flora abutting a sub-tropical flora on its northern boundary;
 - A 3-4°C rise in mean monthly sea surface temperatures between southern and central Namibia;
 - Stochastic warm water events due to El Niño and counter-currents from Angola;
 - Unpredictable, non-seasonal upwelling occurs north of the southwestern Cape region.
- Habitat availability and heterogeneity:
 - There is a general decrease in habitat availability and heterogeneity as one moves north;
 - These are particularly lacking in central Namibia, which comprises few small rocky outcrops that are low-lying and often sand inundated.
- Local Factors:
 - Sand inundation, which is particularly prevalent in central and northern Namibia, limits the species that are able to survive these conditions;
 - East wind events on the Namibian coast that coincide with low tide have a desiccating effect on seaweeds, possibly resulting in local extinction.

The principle factor affecting seaweed diversity in the lower eulittoral zone on Namibian shores was the degree of sand-inundation. The latter however, only has a negative effect of species richness at levels greater than 5.6 kg.m^{-2} . Mussel biomass was found to be positively related to degree of wave exposure, and negatively to seaweed diversity. As a result, areas with extreme wave actions are dominated by mussels. The effects of herbivores and whelks in the lower eulittoral seemed to be negligible on the Namibian coast.

Sand inundation also has an effect on vertical zonation patterns observed on the Namibian coast. Many of the most abundant seaweed species found in central and northern Namibia comprised sand tolerant species, as opposed to the southern region, which has similar communities to South African west coast shores. The moderate to high degree of sand inundation in central Namibia seemed to cause a breakdown in intertidal zonation patterns, indicating a system in a state of perturbation. The northern region had greater habitat heterogeneity and the zonation patterns were more varied. The central and northern regions of Namibia, which constitute the Namib sub-province, not only have less species than are found further south but also a different set of species that are abundant intertidally. There is thus an ecological shift as well as a "floristic" attenuation dividing these two sub-provinces.

The abundance of certain species in the intertidal zonation pattern study seemed to indicate that some sites were less exposed than calculated. The method for evaluating the degree of wave exposure therefore needs to be revised. As was pointed out in the methods section (p.8), incorporating the slope of the immediate subtidal would improve the reliability of the wave exposure index, but this information was unavailable.

The different transects and sites within biogeographically homogeneous areas were found to be considerable. In northern Namibia the pattern of species present on a shore relative to regional richness is largely determined by the effect of abundant species on colonization and random assortment of non-abundant species. In southern and central Namibia this variation is less than would be expected from random assortment. The environments in the latter regions are more predictable and a number of non-abundant species occurs more evenly spread over all the sites.

It was estimated that approximately 20-30% of the intertidal species have still to be collected. It was also noted that only the exposed and semi-exposed sites were sampled in this study. The sheltered sites of southern Namibia would therefore probably add a number of species to the intertidal species list. Northern Namibia, as was implied in Chapter 6, had some sites which appeared to be more sheltered than calculated. Regional species richness for this region is therefore probably close to its upper limit. The use of genera and/or families as a surrogate measure for species richness seemed to be too inaccurate for determining species richness, but could be utilized if a vague approximation was required. Another concept arising out of Chapter 2, was the generalised family structure of a flora. This poses some interesting evolutionary questions that require further investigation.

This thesis has generated a number of ideas as to the factors controlling the biogeography and diversity of the Namibian intertidal seaweed communities. Many of these ideas, however, need to be tested. As was pointed out above, the more sheltered and sand inundated shores of southern Namibia still need to be studied in detail. Another potentially interesting area of research is the restricted stretch of coast between Lüderitz and Walvis Bay. The transition between the two sub-provinces occurs along this part of the coast. Many of the near offshore islands in southern and central Namibia make ideal subjects for studying the effect of wave exposure along this coast, having both sheltered and exposed sides. Subtidal studies need to be done along this coast but, owing to the generally rough seas and the high turbidity, subtidal work is difficult at best. There is still much work that can be done on this coast concerning rocky shore ecology and this thesis may serve as a reference point for future research.

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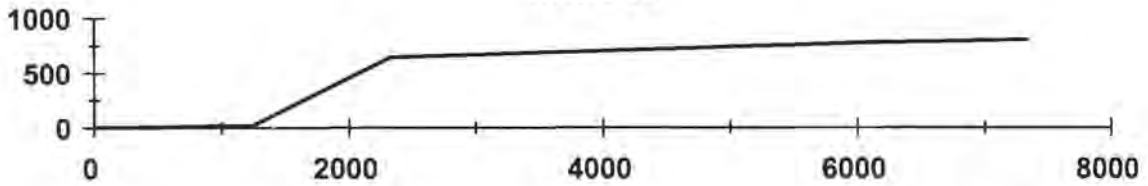
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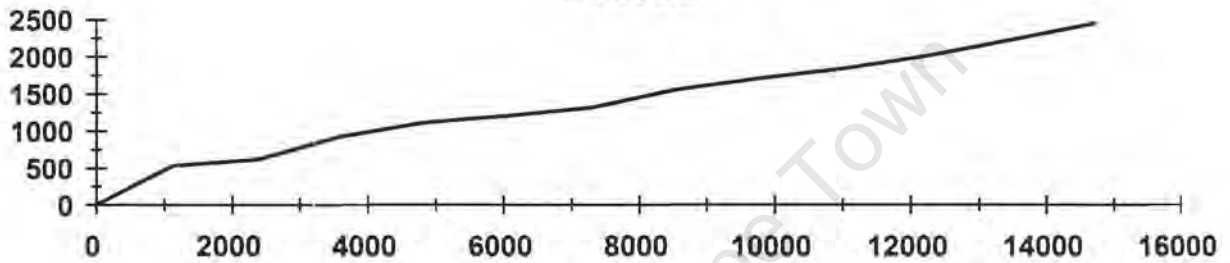
Appendix A

Shore profiles of the various sites sampled. The horizontal axis represents distance from SLWM (mm), while the vertical axis represents height above SLWM (mm). Note that the scale varies for each site / transect, but that the X and Y - Axes are in a 1:1 proportion. The angle of exposure and dominant on-shore winds are given in the Table at the end of this appendix.

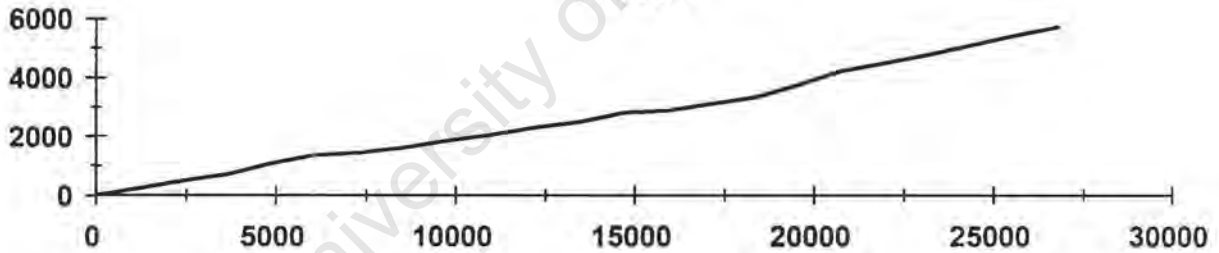
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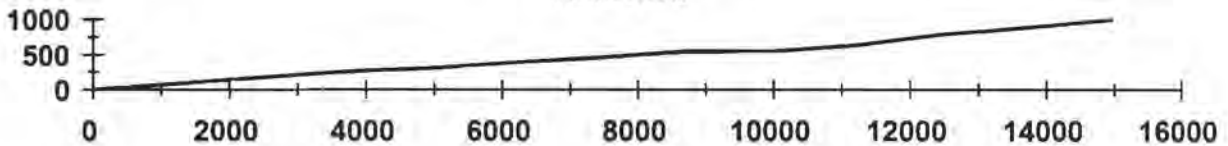
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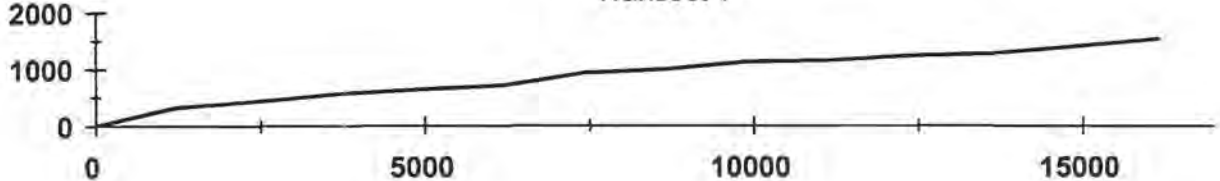
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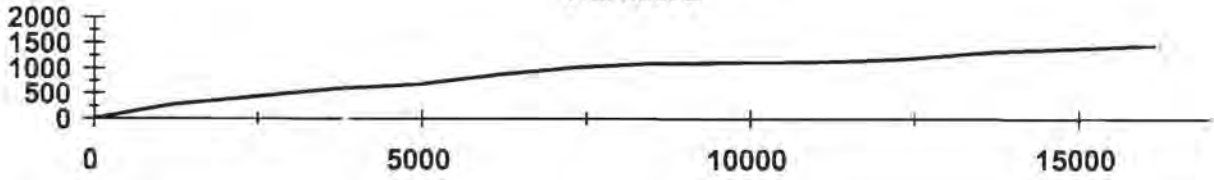
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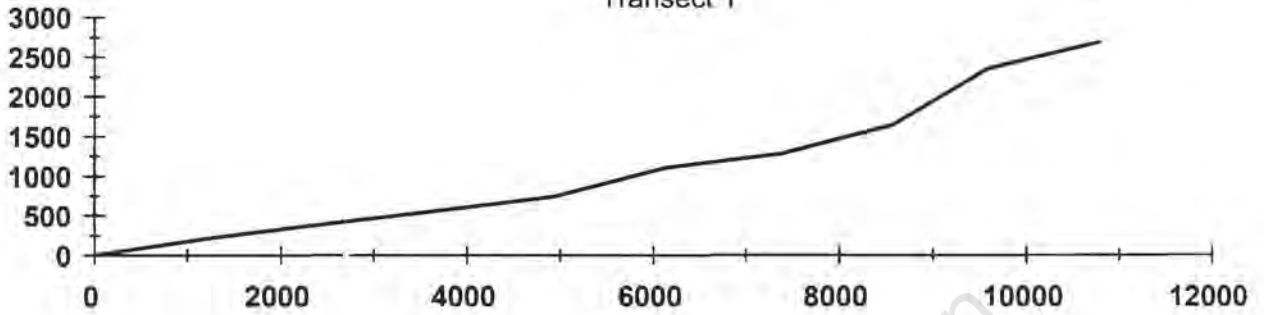
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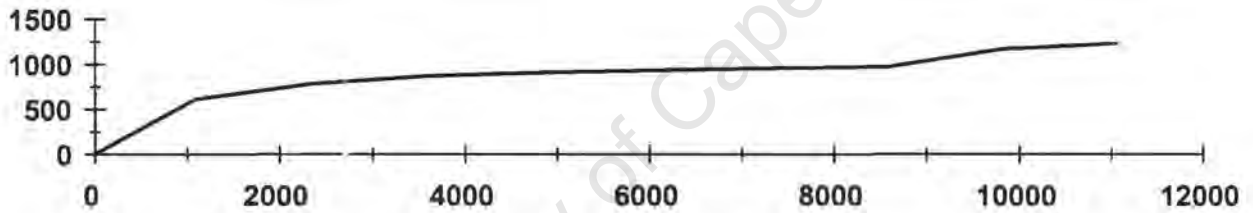
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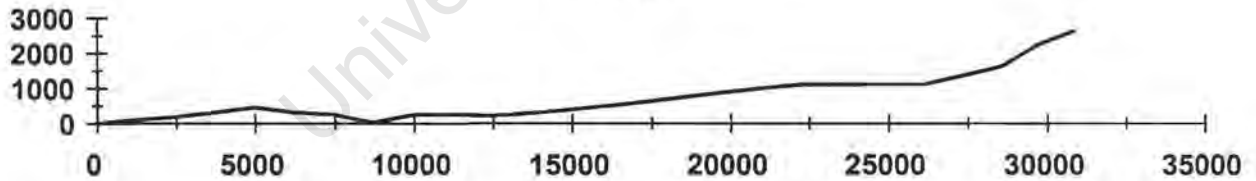
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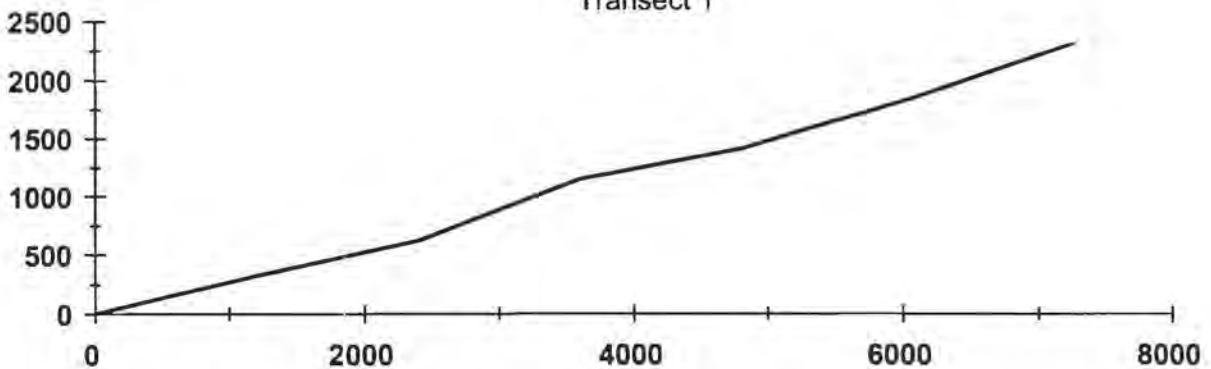
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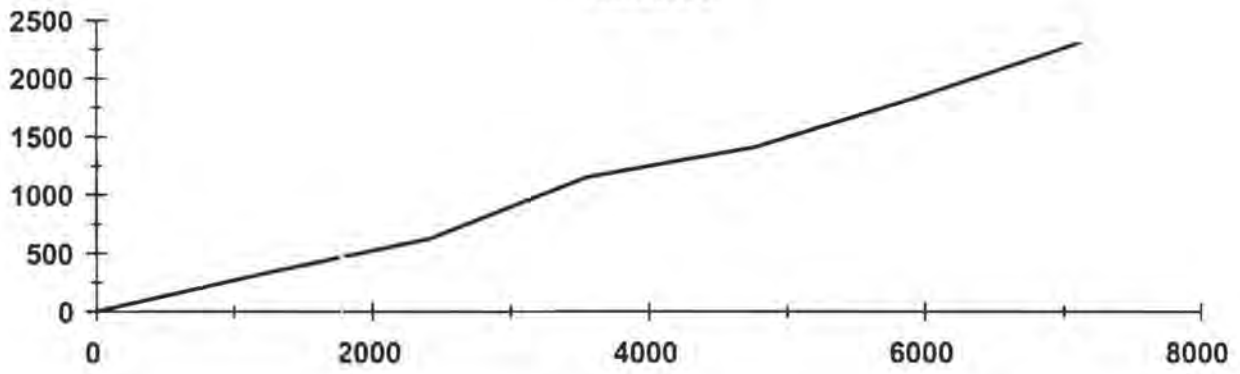
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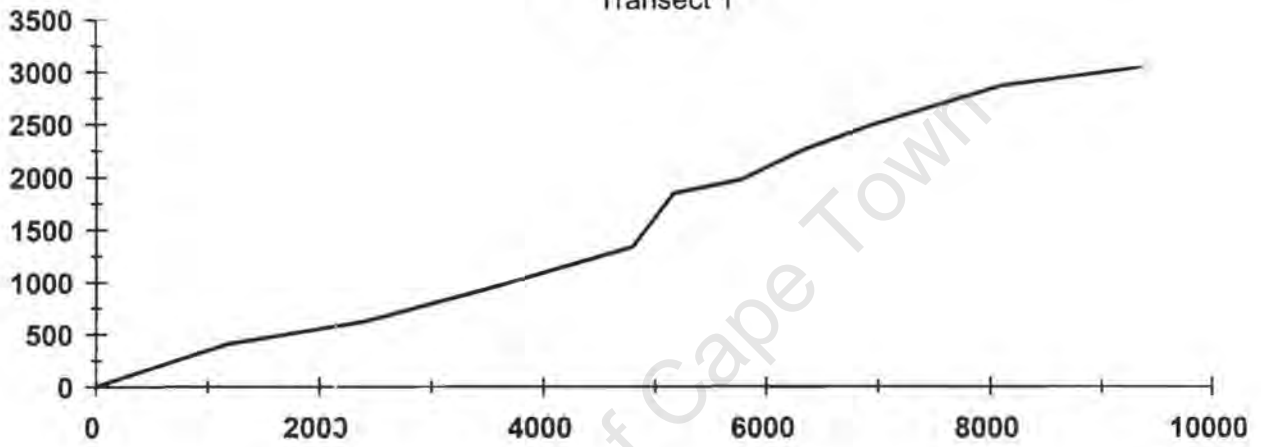
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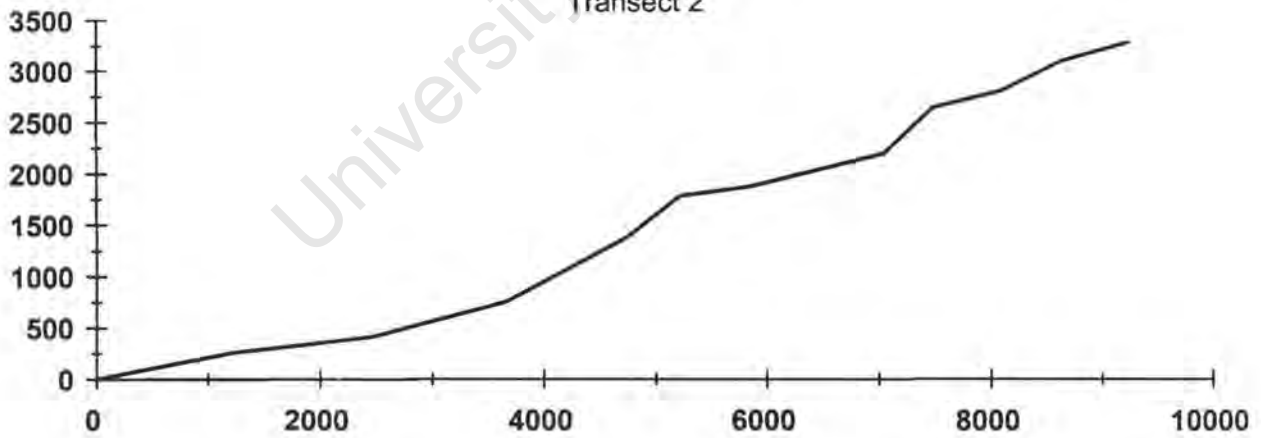
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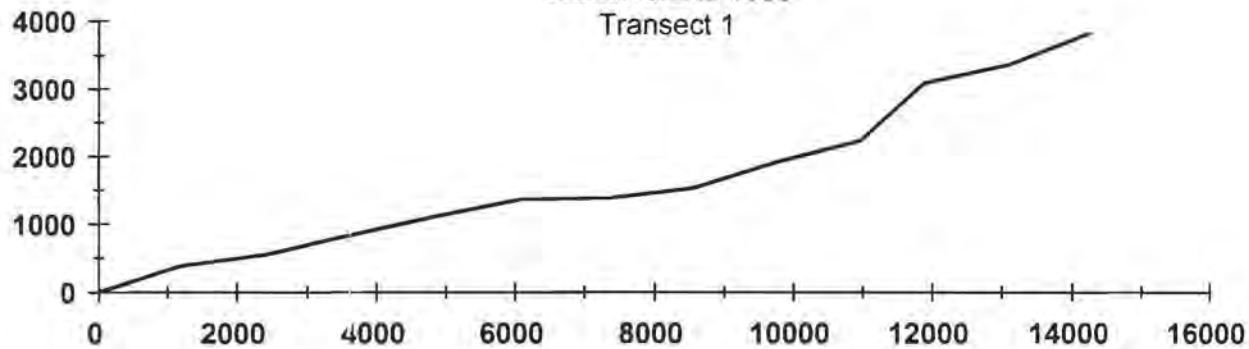
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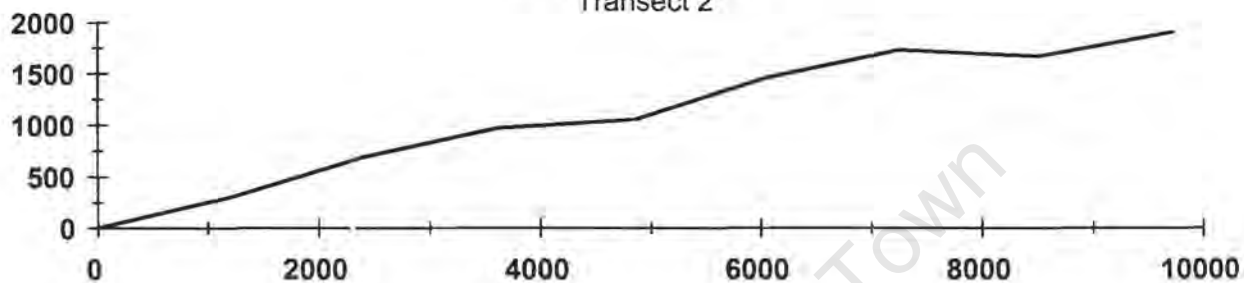
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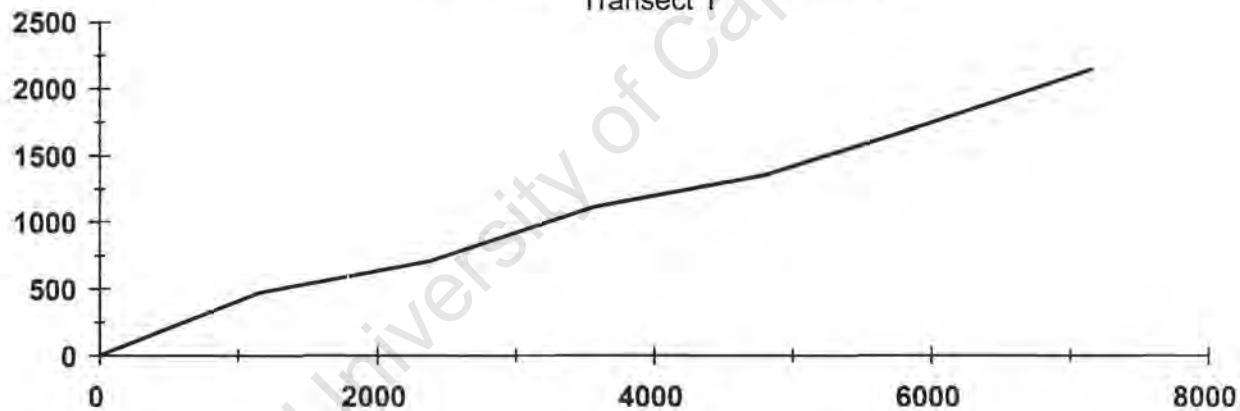
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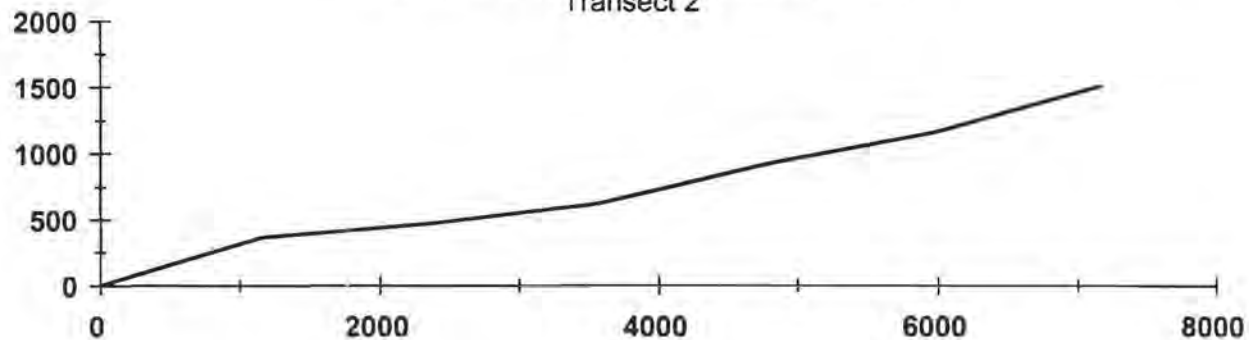
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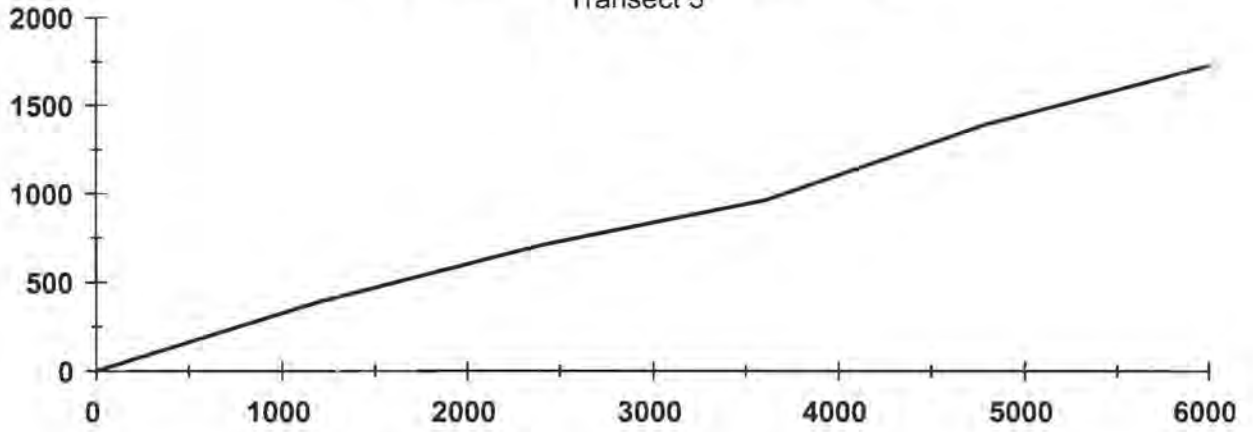
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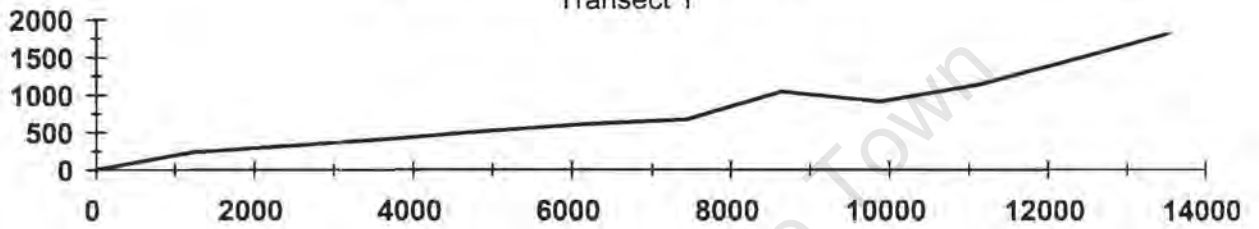
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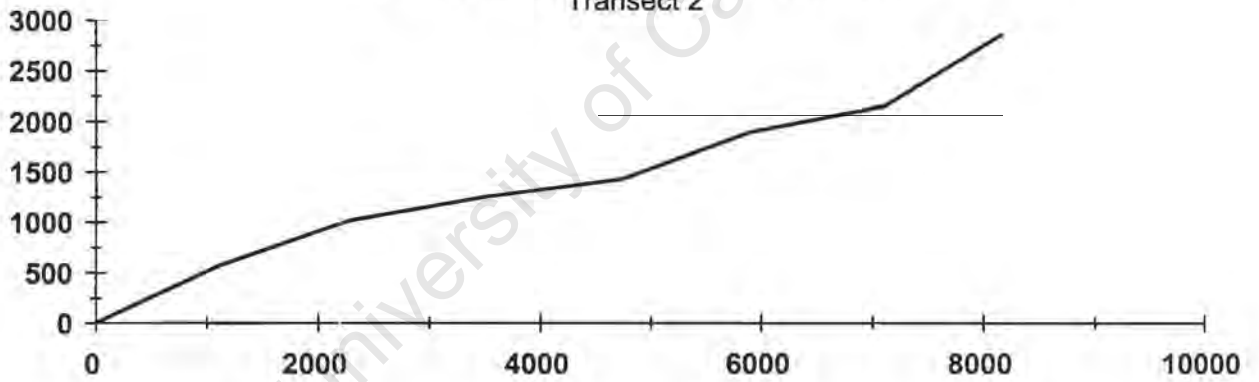
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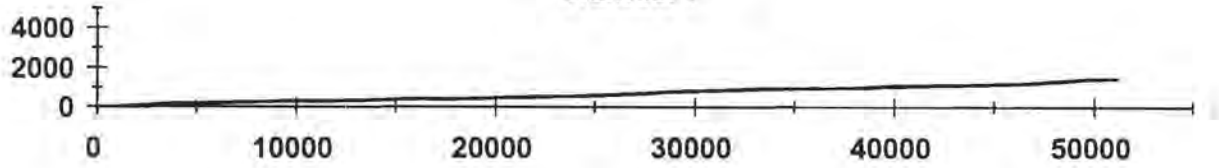
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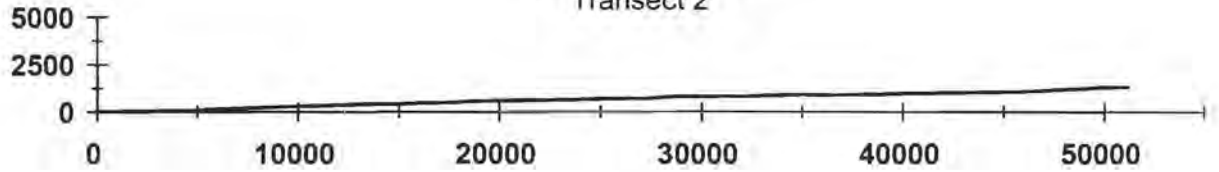
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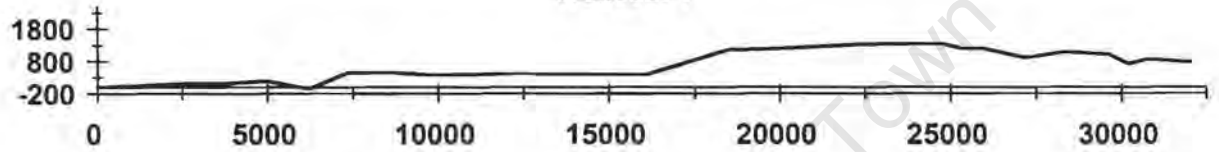
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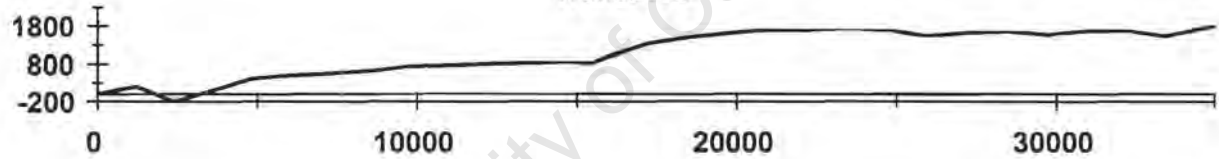
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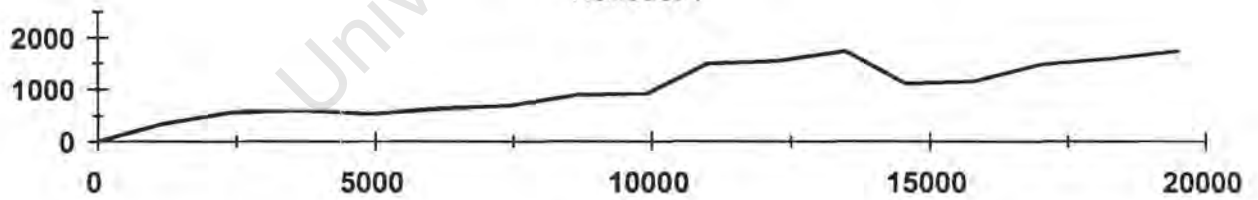
Langstrand 1992
Transect 1



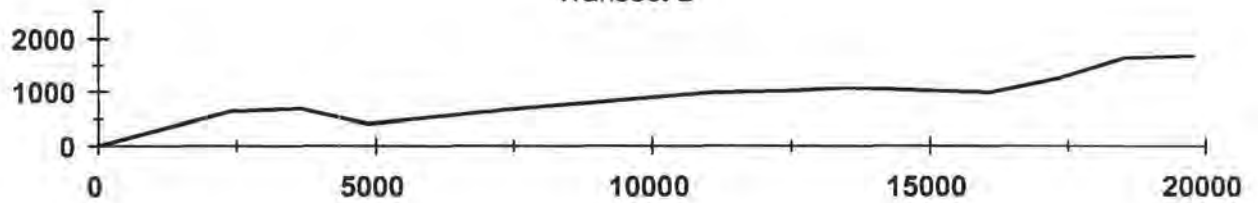
Langstrand 1992
Transect 2



Vineta Beach 1990
Transect 1

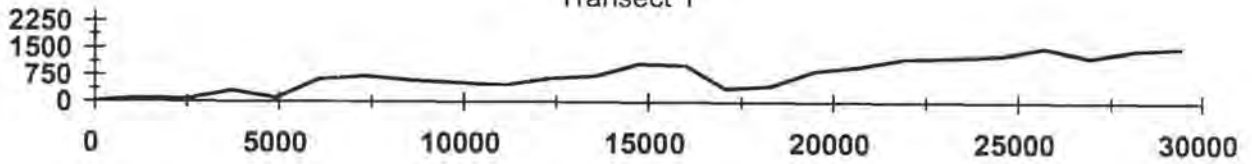


Vineta Beach 1990
Transect 2



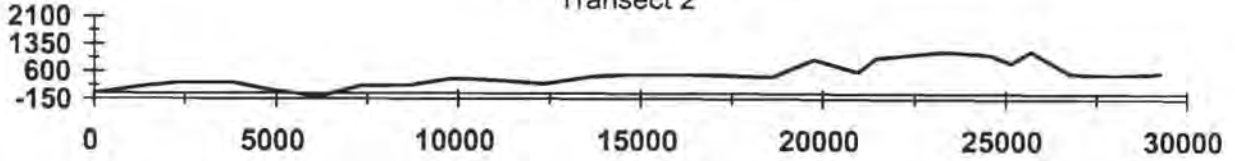
Vineta Beach 1992

Transect 1



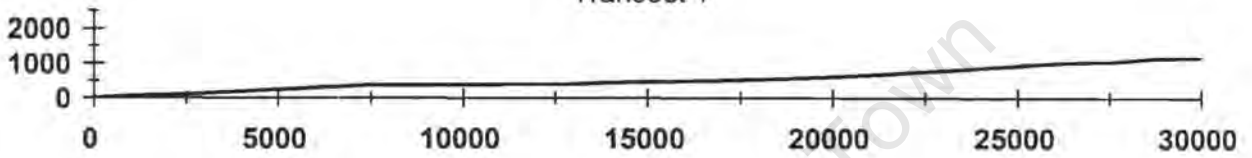
Vineta Beach 1992

Transect 2



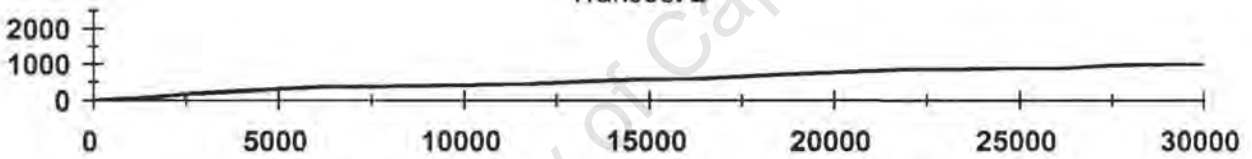
Myl 4 1990

Transect 1



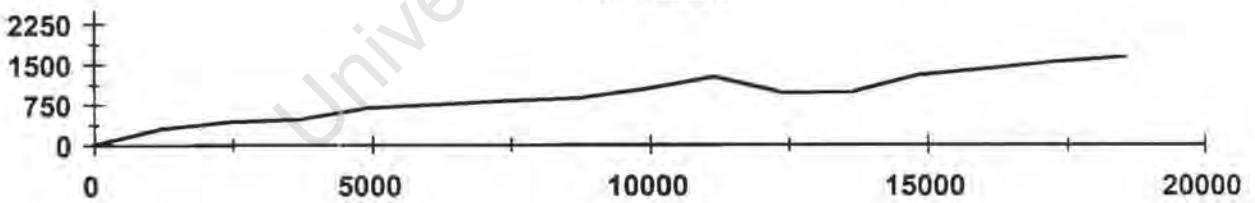
Myl 4 1990

Transect 2



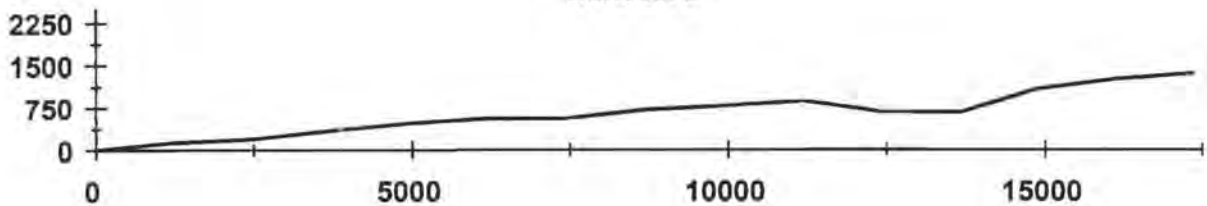
Myl 8 1990

Transect 1

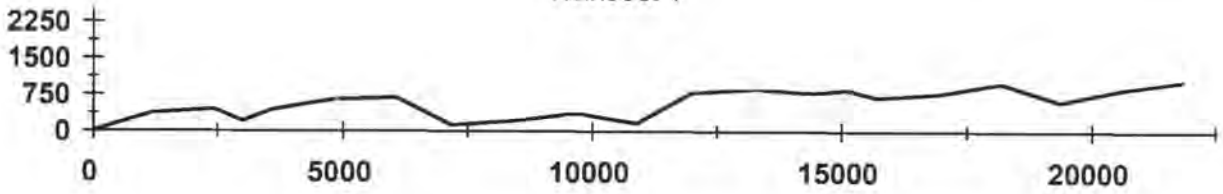


Myl 8 1990

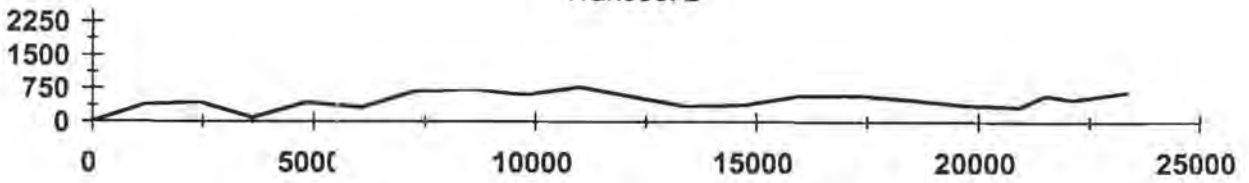
Transect 2



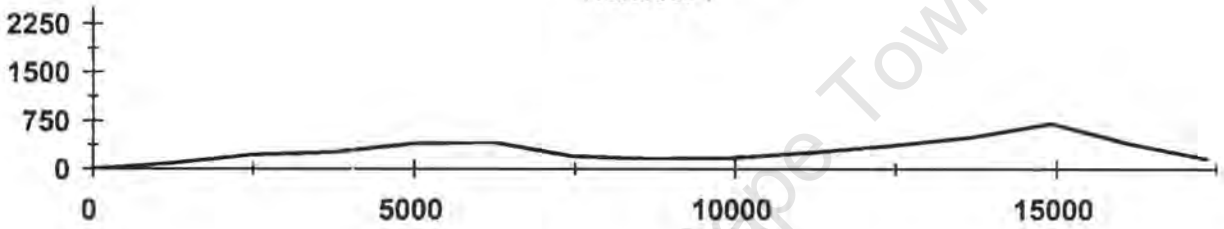
Myl 8 1992
Transect 1



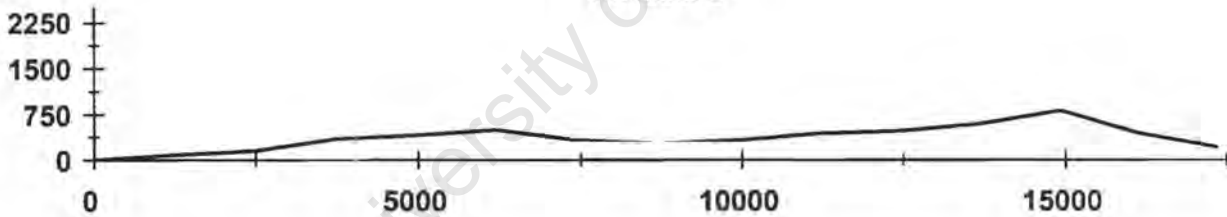
Myl 8 1992
Transect 2



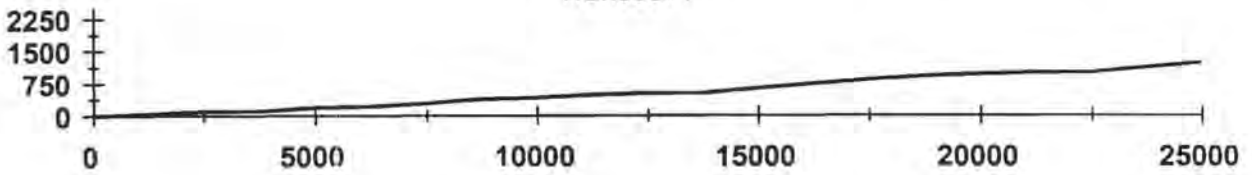
Toscanini 1990
Transect 1



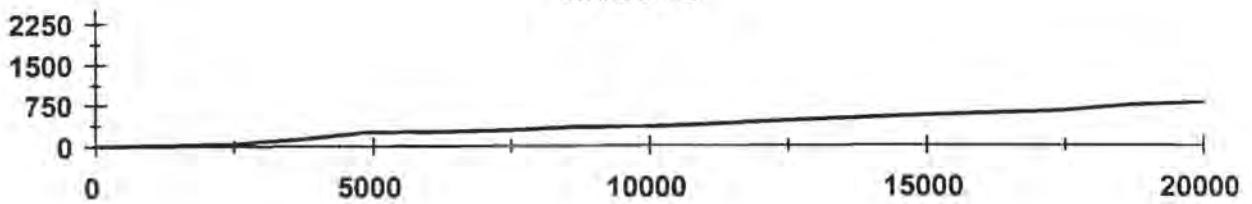
Toscanini 1990
Transect 2



Torra Bay 1990
Transect 1

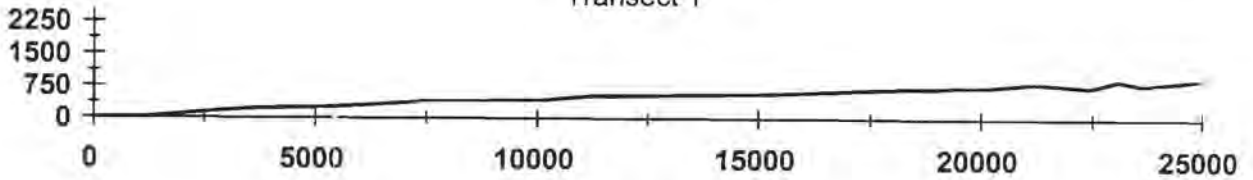


Torra Bay 1990
Transect 2



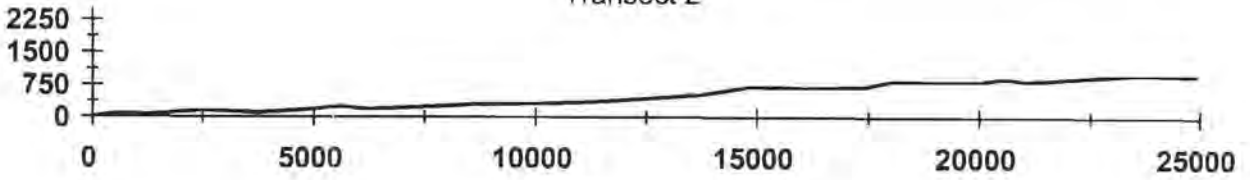
Torra Bay 1992

Transect 1



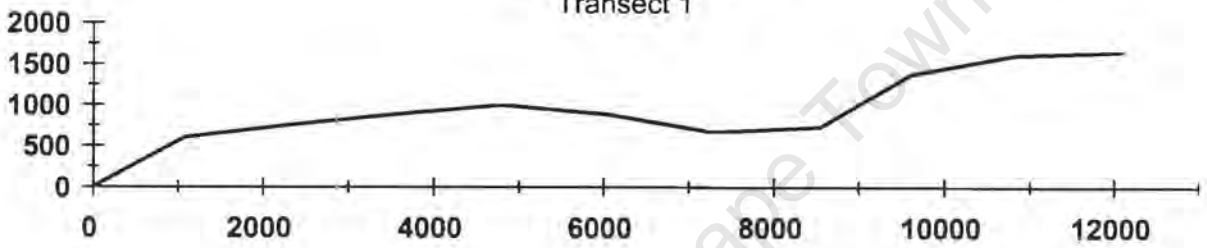
Torra Bay 1992

Transect 2



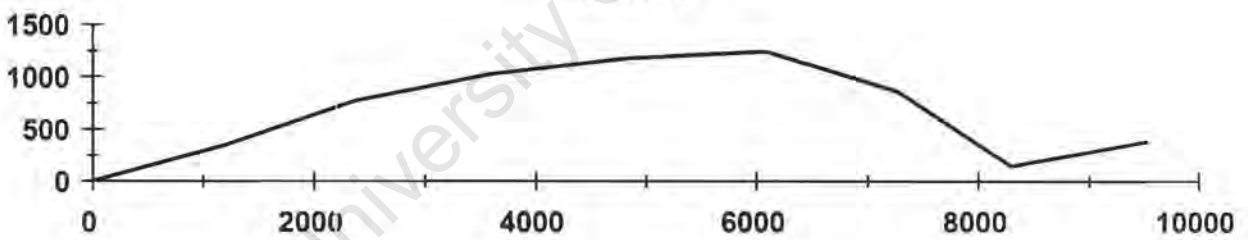
Terrace Bay 1990

Transect 1



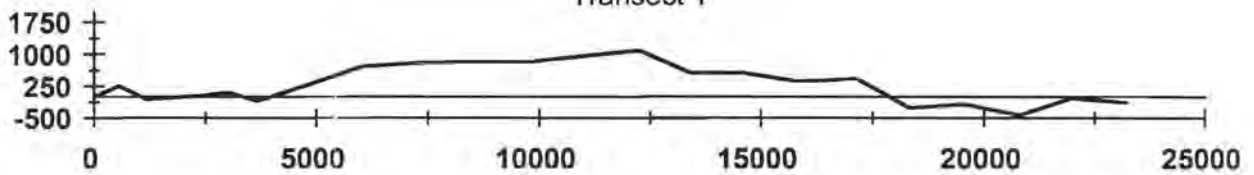
Terrace Bay 1990

Transect 2



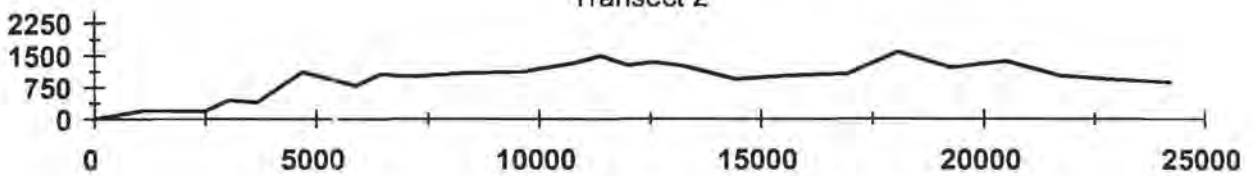
Terrace Bay 1992

Transect 1



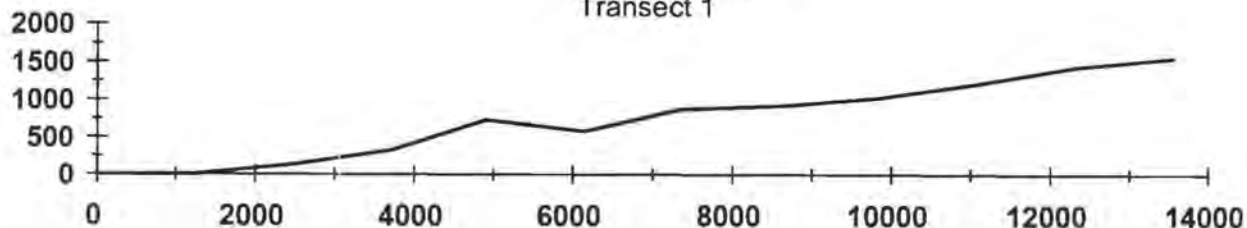
Terrace Bay 1992

Transect 2



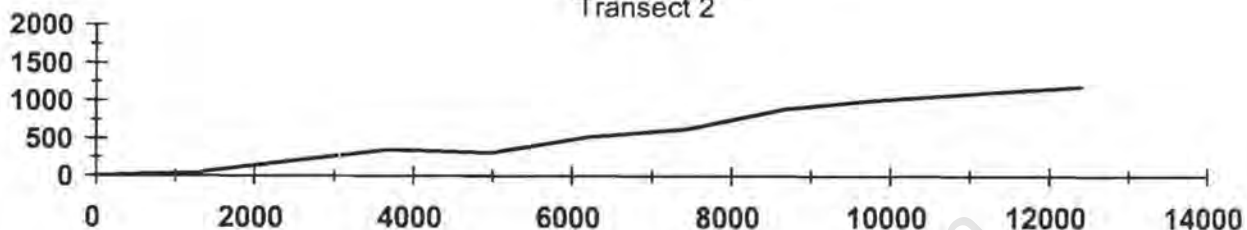
Möwe Bay 1990

Transect 1



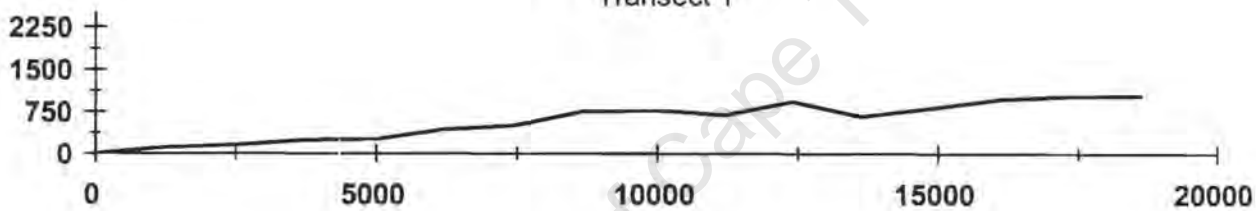
Möwe Bay 1990

Transect 2



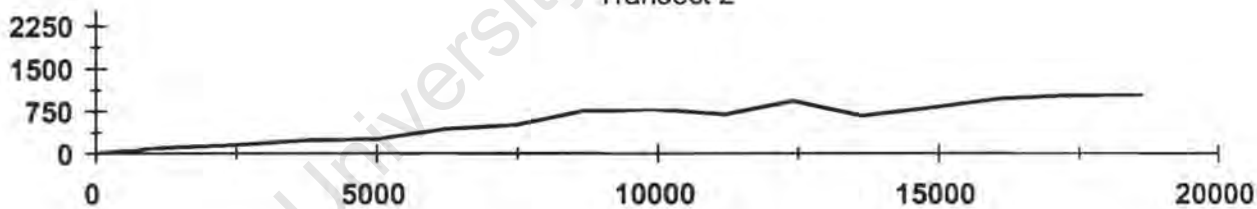
Möwe Bay 1992

Transect 1



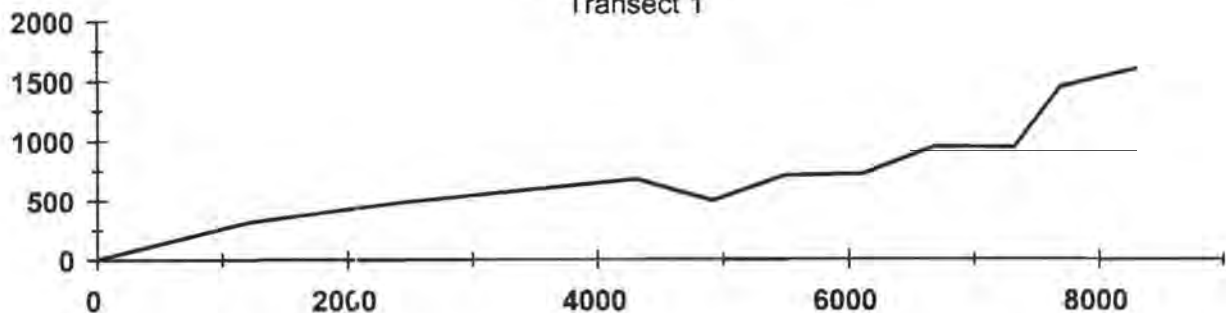
Möwe Bay 1992

Transect 2



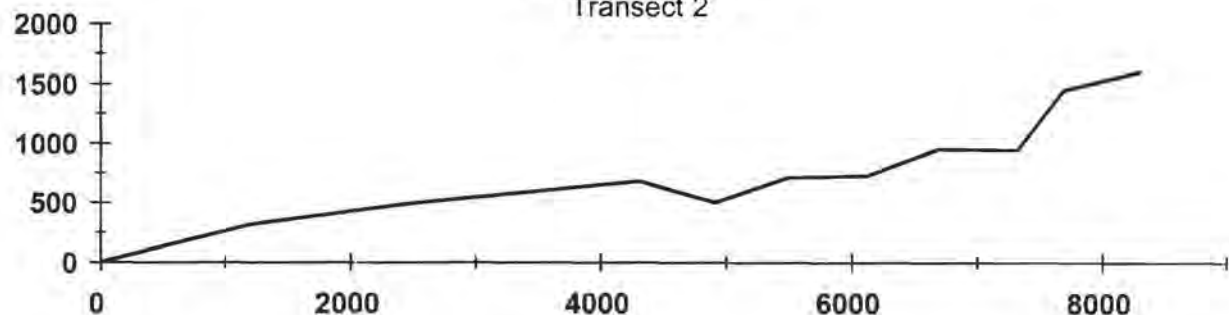
Rocky Point 1992

Transect 1



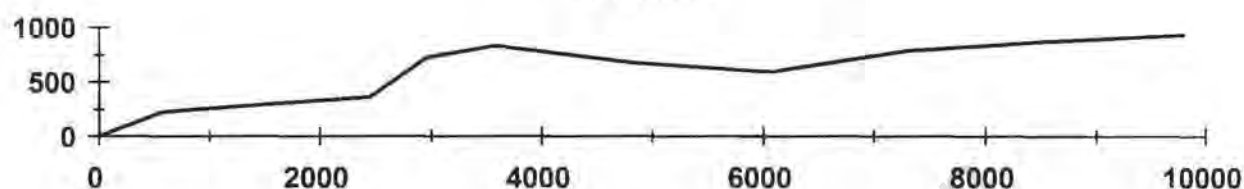
Rocky Point 1992

Transect 2



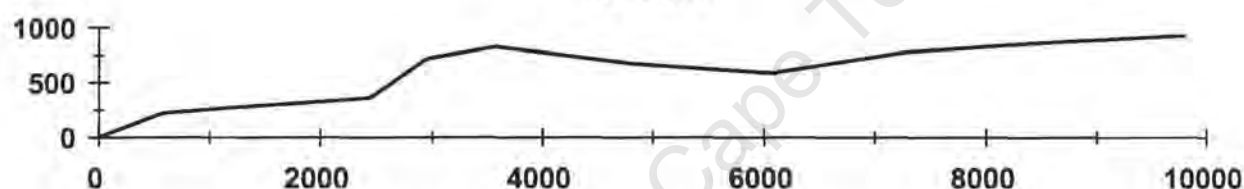
False Cape Fria 1992

Transect 1



False Cape Fria 1992

Transect 2



Site	Angle of Exposure	Dominant Onshore Winds
Southern Namibia		
Elizabeth Bay	160°-210°	S
Grossebucht	135°-305°	SE, S, SW, W
Kleinbogenfels	200°-345°	SW, W, NW
Essy Bay	200°-290°	SW, W
Diaz Point	230°-340°	SW, W, NW
Shark Island	260°-10°	W, NW, N
Agate Beach	265°-330°	W, NW
Central Namibia		
Langstrand	190°-350°	S, SW, W, NW, N
Vineta Beach	200°-340°	SW, W, NW
Myl 4	190°-340°	S, SW, W, NW
Myl 8	160°-330°	S, SW, W, NW
Northern Namibia		
Toscanini	170°-350°	S, SW, W, NW, N
Torra Bay	200°-320°	SW, W, NW
Terrace Bay	210°-330°	SW, W, NW
Möwe Bay	265°-340°	W, NW
Rocky Point	270°-50°	W, NW, N, NE
False Cape Fria	170°-320°	S, SW, W, NW

Appendix B

Species list for the eight defined areas in the Benguela marine province. "1" represents the presence of the species with the specific area.

SPECIES	FAMILY	ANG	CNAM		NWC	FB		
		NNAM	SNAM	SWC	SFB			
Chlorophyta								
<i>Urospora media</i> Levring	Acrosiphoniaceae				1	1		
<i>Bryopsis africana</i> Aresch.	Bryopsidaceae			1			1	
<i>Bryopsis balbisi</i> Lam. & C. Ag.	Bryopsidaceae	1						
<i>Bryopsis caespitosa</i> Suhr ex Kütz.	Bryopsidaceae		1	1	1	1	1	1
<i>Bryopsis corymbosa</i> J. Ag.	Bryopsidaceae	1						
<i>Bryopsis plumosa</i> (Hudson) C. Ag.	Bryopsidaceae	1	1	1	1	1	1	1
<i>Bryopsis tenuis</i> Levring	Bryopsidaceae				1	1		
<i>Derbesia hollenbergii</i> Taylor	Bryopsidaceae							1
<i>Derbesia lamourouxii</i> (J.Ag.) Solier.	Bryopsidaceae				1			
<i>Derbesia marina</i> (Lyngbye) Solier	Bryopsidaceae							1
<i>Caulerpa bartoniae</i> G. Murray	Caulerpaceae							1
<i>Caulerpa filiformis</i> (Suhr) Hering	Caulerpaceae							1 1
<i>Caulerpa holmesiana</i> G. Murray	Caulerpaceae							1
<i>Sporoclopsis novae-zelandiae</i> Chapman	Chroolepidaceae						1	1 1
<i>Chaetomorpha aerea</i> (Dillw.) Kütz.	Cladophoraceae	1	1	1	1	1	1	1
<i>Chaetomorpha antennina</i> (Bory) Kütz.	Cladophoraceae	1						
<i>Chaetomorpha capillaris</i> (Kütz.) Boergesen	Cladophoraceae							
<i>Chaetomorpha robusta</i> (Aresch.) Papenfuss	Cladophoraceae	1	1		1	1	1	1
<i>Chloropelta caespitosa</i> Tanner	Cladophoraceae							1
<i>Cladophora albida</i> (Fox) John	Cladophoraceae	1						
<i>Cladophora capensis</i> (C. Ag.) De Toni	Cladophoraceae		1	1	1	1	1	1
<i>Cladophora contexta</i> Levring	Cladophoraceae		1	1	1	1	1	
<i>Cladophora dalmatica</i> Kütz.	Cladophoraceae				1			1
<i>Cladophora flagelliformis</i> (Suhr) Kütz.	Cladophoraceae	1	1	1	1	1	1	1
<i>Cladophora isaacii</i> Simons	Cladophoraceae			1		1	1	1
<i>Cladophora mirabilis</i> (C. Ag.) Rabenhorst	Cladophoraceae		1	1	1	1	1	1
<i>Cladophora radiosa</i> (Suhr) Kütz.	Cladophoraceae						1	1
<i>Rhizoclonium africanum</i> Kütz.	Cladophoraceae	1						
<i>Rhizoclonium implexum</i> (Dillw.) Kütz.	Cladophoraceae	1						
<i>Rhizoclonium lubricum</i> Setchell & Gardner	Cladophoraceae	1						
<i>Rhizoclonium riparium</i> (Roth) Harvey	Cladophoraceae	1	1		1			
<i>Codium decortatum</i> (Woodward) Howard	Codiaceae	1	1	1				
<i>Codium duthieae</i> Silva	Codiaceae		1	1	1			1 1
<i>Codium extricata</i> Silva	Codiaceae							1
<i>Codium fragile</i> spp. <i>capense</i> (Sur.) spp Silva	Codiaceae		1	1	1	1	1	1
<i>Codium guineunse</i> Silva (Lawson & John)	Codiaceae	1						
<i>Codium isaacii</i> Silva	Codiaceae			1	1	1	1	
<i>Codium lucasii</i> spp. <i>capense</i> Setchell spp Silva	Codiaceae							1 1
<i>Codium papenfussii</i> Silva	Codiaceae							1 1
<i>Codium platylobium</i> Aresch.	Codiaceae							1
<i>Codium stephensiae</i> Dickinson	Codiaceae						1	1 1
<i>Halimeda tuna</i> (Ellis & Solander) Lam.	Halimedaceae	1						
<i>Percursaria percurta</i> (C. Ag.) Rosenvinge	Percursariaceae						1	1
<i>Boodlea composita</i> (Harvey) Brand	Siphonocladaceae	1						
<i>Chlorodesmis</i> sp.	Udoteaceae						1	
<i>Ulothrix flacca</i> (Dillw.) Thuret	Ulotrichaceae						1	1

SPECIES	FAMILY	ANG	CNAM		NWC		FB		
		NNAM		SNAM	SWC	SFB			
<i>Ulothrix speciosa</i> (Carmichael) Kütz.	Ulotrichaceae			1				1	
<i>Blidingia marginata</i> Kylin	Ulvaceae								
<i>Blidingia minima</i> (Naegeli ex Kütz.) Kylin	Ulvaceae							1	
<i>Enteromorpha atro-viridis</i> (Levring) Wynne	Ulvaceae			1	1	1	1		
<i>Enteromorpha bulbosa</i> (Suhr) Kütz.	Ulvaceae			1	1	1	1		
<i>Enteromorpha compressa</i> (L.) Grev.	Ulvaceae	1	1	1	1	1	1	1	
<i>Enteromorpha flexuosa</i> (Wulfen) J. Ag.	Ulvaceae	1						1	
<i>Enteromorpha intestinalis</i> (L.) Link	Ulvaceae	1				1	1	1	
<i>Enteromorpha lingulata</i> J. Ag.	Ulvaceae	1							
<i>Enteromorpha linza</i> (L.) J. Ag.	Ulvaceae	1	1	1	1	1	1	1	
<i>Enteromorpha prolifera</i> (O. Mueller) J. Ag.	Ulvaceae	1	1	1	1	1	1	1	
<i>Enteromorpha tubulosa</i> Kütz.	Ulvaceae	1	1						
<i>Ulva capensis</i> Aresch.	Ulvaceae		1	1	1	1	1	1	
<i>Ulva fasciata</i> Delile	Ulvaceae	1	1	1				1	
<i>Ulva lactuca</i> L.	Ulvaceae	1	1	1	1	1	1	1	
<i>Ulva nematoidea</i> Bory	Ulvaceae		1	1	1				
<i>Ulva rhacodes</i> (Holmes) Papenfuss	Ulvaceae		1	1	1			1	
<i>Ulva rigida</i> C. Ag.	Ulvaceae	1	1	1	1	1	1	1	
<i>Entocladia vagans</i> (Boergesen) W.R. Taylor	Ulvellaceae				1				
<i>Entocladia viridis</i> Reinke	Ulvellaceae				1	1	1	1	
<i>Stromatella monostromatica</i> (Dang.) Kornmann	Ulvellaceae				1	1	1		
<i>Ulvella</i> sp.	Ulvellaceae			1	1	1	1		
Phaeophyta									
<i>Ecklonia maxima</i> (Osbeck) Papenfuss	Alariaceae				1	1	1	1	
<i>Ecklonia radiata</i> (C. Ag.) J. Ag.	Alariaceae							1	
<i>Myriocladia capensis</i> J. Ag.	Chordariaceae						1	1	
<i>Myriogloea papenfussii</i> Kylin	Chordariaceae			1	1	1	1	1	
<i>Papenfussiella gracilis</i> Kylin	Chordariaceae			1	1	1	1		
<i>Chordariopsis capensis</i> (C. Ag.) Kylin	Chordariopsidaceae		1	1	1	1	1	1	
<i>Leathesia difformis</i> (L.) Aresch.	Corynophlaeaceae				1	1	1	1	
<i>Aglaozonia</i> sp.	Cutleriaceae							1	
<i>Bifurcaria brassicaeformis</i> (Kütz.) Barton	Cystoseiraceae						1	1	
<i>Bifurcariopsis capensis</i> (Aresch.) Papenfuss	Cystoseiraceae						1	1	
<i>Cystophora fibrosa</i> Simons	Cystoseiraceae							1	
<i>Desmarestia firma</i> (C. Ag.) Skottsberg	Desmarestiaceae			1	1	1	1	1	
<i>Dictyopteris longifolia</i> (Suhr) Schmidt	Dictyotaceae							1	
<i>Dictyota cervicornis</i> Kütz.	Dictyotaceae	1							
<i>Dictyota dichotoma</i> (Hudson) Lam.	Dictyotaceae	1						1	
<i>Dictyota dichotoma</i> var. <i>intricata</i> (C. Ag.) Grev.	Dictyotaceae							1	
<i>Dictyota liturata</i> J. Ag.	Dictyotaceae							1	
<i>Dictyota naevosa</i> (Suhr) J. Ag.	Dictyotaceae							1	
<i>Lobophora variegata</i> (Lam.) Womersley ex Oliveira	Dictyotaceae	1							
<i>Padina australis</i> Hauck	Dictyotaceae	1							
<i>Padina tetrastromatica</i> Hauck	Dictyotaceae	1							
<i>Padina vickersiae</i> Hoyt	Dictyotaceae	1							
<i>Zonaria harveyana</i> (Pappe ex Kütz.) Aresch.	Dictyotaceae							1	
<i>Zonaria subarticulata</i> (Lam.) Papenfuss	Dictyotaceae							1	
<i>Zonaria tempta</i> ? (in Lawson et al., 1990)	Dictyotaceae		1						
<i>Acinetospora crinita</i> (Carmichael) Kornm.	Ectocarpaceae							1	

SPECIES	FAMILY	ANG	CNAM		NWC		FB		
		NNAM	SNAM	SWC	SFB				
<i>Ectocarpus acutus</i> Setchell et Gardner	Ectocarpaceae			1	1	1			
<i>Ectocarpus fasciculatus</i> Harvey	Ectocarpaceae			1	1	1	1	1	
<i>Ectocarpus rhodochortonoides</i> Boergesen	Ectocarpaceae			1	1				
<i>Ectocarpus siliculosus</i> (Dillw.) Lyngbye	Ectocarpaceae		1	1	1	1	1		
<i>Feldmannia irregularis</i> (Kütz.) Hamel	Ectocarpaceae						1	1	
<i>Hincksia granulosa</i> (Smith) Silva et al.	Ectocarpaceae	1	1	1	1	1	1	1	
<i>Hincksia rallsiae</i> (Vick)	Ectocarpaceae	1							
<i>Streblonema codii</i> Barton	Ectocarpaceae							1	
<i>Streblonema nemastomae</i> Baardseth	Ectocarpaceae					1			
<i>Streblonema transfixum</i> Setchell & Gardner	Ectocarpaceae					1	1		
<i>cf. Microsyphar porphyrae</i> (Stegenga's Priv. Coll.)	Ectocarpaceae					1			
<i>Laminaria pallida</i> Grev. ex J. Ag.	Laminariaceae					1	1	1	
<i>Laminaria schinzii</i> Foslie	Laminariaceae	1	1	1	1				
<i>Macrocystis angustifolia</i> Bory	Lessoniaceae						1	1	
<i>Compsonea cf. sessile</i> Setchell & Gardner	Myrionemataceae						1		
<i>Myrionema magnusii</i> (Sauvageau) Loiseaux	Myrionemataceae							1	
<i>Bachelotia antillarum</i> (Grunow) Gerloff	Pilayellaceae	1						1	
<i>Pilayella littoralis</i> (L.) Kjellm.	Pilayellaceae	1						1	
<i>Basispora africana</i> John & Lawson	Ralfsiaceae	1	1						
<i>Endopleura</i> sp.	Ralfsiaceae		1						
<i>Ralfsia verrucosa</i> (Aresch.) J. Ag.	Ralfsiaceae	1	1	1	1	1	1	1	
<i>Zeacarpa leiomorpha</i> Anderson et al.	Ralfsiaceae						1		
<i>Anthophycus longifolius</i> (Turner) Kütz.	Sargassaceae							1	
<i>Sargassum elegans</i> Suhr	Sargassaceae							1	
<i>Sargassum heterophyllum</i> (Turner) C. Ag.	Sargassaceae							1	
<i>Sargassum vulgare</i> C. Ag.	Sargassaceae	1							
<i>Colpomenia sinuosa</i> (Mert.) Derbes & Solier	Scytosiphonaceae	1			1	1	1	1	
<i>Compsonea cf. sessile</i> Setchell & Gardner	Scytosiphonaceae						1		
<i>Endarachne binghamiae</i> J. Ag.	Scytosiphonaceae		1					1	
<i>Iyengaria stellata</i> (Boergesen) Boergesen	Scytosiphonaceae						1	1	
<i>Petalonia fascia</i> (O.F. Mueller) Kuntze	Scytosiphonaceae		1	1	1	1	1		
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	Scytosiphonaceae				1	1	1	1	
<i>Axillariella constricta</i> (J. Ag.) Silva	Seirococcaceae						1		
<i>Sphacelaria brachygonia</i> Montagne	Sphacelariaceae							1	
<i>Sphacelaria rigidula</i> Kütz.	Sphacelariaceae	1						1	
<i>Splachnidium rugosum</i> (L.) Greville	Splachnidiaceae				1	1	1	1	
<i>Carpomitra filiformis</i> (Stackhouse) Batters	Sporochneaceae							1	
<i>Sporochneus pedunculus</i> (Hudson) C. Ag.	Sporochneaceae							1	
<i>Phloiocaulon squamulosum</i> (Suhr) Geyler	Stypocaulaceae							1	
<i>Stypocaulon funiculare</i> (Montagne) Kütz. in Reike	Stypocaulaceae				1	1	1	1	
Rhodophyta									
<i>Acrochaetium catenulatum</i> Howe	Acrochaetiaceae			1	1	1	1	1	
<i>Acrochaetium moniliforme</i> (Rosenv.) Boerg.	Acrochaetiaceae		1					1	
<i>Acrochaetium reductum</i> (Rosenvin.) Hamel	Acrochaetiaceae		1	1				1	
<i>Acrochaetium secundatum</i> (Lyng.) Naegeli	Acrochaetiaceae		1	1	1	1	1	1	
<i>Acrochaetium tenuissimum</i> (Collins) Pape.	Acrochaetiaceae							1	
<i>Audouinella balliae</i> Stegenga	Acrochaetiaceae					1	1		
<i>Audouinella desmarestiae</i> (Kyllin) Garbary et al.	Acrochaetiaceae					1			
<i>Audouinella endophytica</i> (Batters) Dixon	Acrochaetiaceae			1				1	
<i>Audouinella endozoica</i> (Darbishire) Dixon	Acrochaetiaceae							1	

SPECIES	FAMILY	ANG	CNAM		NWC	FB	
			NNAM	SNAM	SWC	SFB	
<i>Audouinella hypneae</i> Boergesen	Acrochaetiaceae	1	1	1			
<i>Audouinella pectinata</i> (Kyllin) Papenfuss	Acrochaetiaceae					1	
<i>Audouinella spongicola</i> (Weber-v.B.) Stegenga	Acrochaetiaceae					1	1
<i>Colaçonema caespitosa</i> (J. Ag.) Jackelman <i>et al.</i>	Acrochaetiaceae						1
<i>Colaçonema codicolum</i> (Boerg.) Stegenga <i>et al.</i>	Acrochaetiaceae						
<i>Colaçonema daviesii</i> (Dillw.) Stegenga	Acrochaetiaceae			1	1	1	1 1
<i>Colaçonema monorhiza</i> Stegenga	Acrochaetiaceae					1	
<i>Colaçonema nemalione</i> (De Notaris) Stegenga	Acrochaetiaceae				1	1	1 1
<i>Colaçonema plumosum</i> (Drew) Woelkerling	Acrochaetiaceae			1	1	1	
<i>Rhodothamniella floridula</i> (Dillw.) Feldmann	Acrochaetiaceae					1	1 1
<i>Bangia atropurpurea</i> (Roth) C.Ag.	Bangiaceae						
<i>Porphyra</i> spp.	Bangiaceae	1	1	1	1	1	1 1
<i>Asparagopsis armata</i> Harvey	Bonnemaisoniaceae						1 1
<i>Bonnemaisonia hamifera</i> Hariot	Bonnemaisoniaceae						1
<i>Delisea flaccida</i> (Suhr) Papenfuss	Bonnemaisoniaceae					1	
<i>Caulacanthus ustulatus</i> (Turner) Kütz.	Caulacanthaceae	1	1	1	1	1	1 1
<i>Heringia mirabilis</i> (C. Ag.) J. Ag.	Caulacanthaceae		1	1	1	1	1
<i>Anotrichium furcellatum</i> (J. Ag.) Baldock	Ceramiaceae						1
<i>Anotrichium tenue</i> (C. Ag.) Naegeli	Ceramiaceae	1			1	1	1
<i>Antithamnion diminuatum</i> Wollaston	Ceramiaceae		1			1	1
<i>Antithamnion eliseae</i> Norris	Ceramiaceae		1				
<i>Antithamnion leptocladum</i> (Mont.) Wynne	Ceramiaceae			1			
<i>Antithamnion pseudoarmatum</i> Stegenga	Ceramiaceae					1	1
<i>Antithamnionella australis</i> Baardseth	Ceramiaceae		1		1		1 1
<i>Antithamnionella elegans</i> (Berth.) Price & John	Ceramiaceae	1					
<i>Antithamnionella spirographidis</i> (Schiff.) Wollaston	Ceramiaceae						
<i>Antithamnionella tormentosa</i> Stegenga	Ceramiaceae					1	
<i>Antithamnionella verticillata</i> (Suhr)Lyle	Ceramiaceae						1 1
<i>Aristothamnion collabens</i> (Rudolph.)Papen.	Ceramiaceae	1	1	1	1	1	1 1
<i>Ballia callitricha</i> (C. Ag.) Kütz.	Ceramiaceae					1	
<i>Ballia sertularoides</i> (Suhr) Papenfuss	Ceramiaceae				1	1	
<i>Bornetia repens</i> Stegenga	Ceramiaceae		1				1
<i>Callithamniella capensis</i> Simons	Ceramiaceae						1 1
<i>Callithamnion cordatum</i> Boergesen	Ceramiaceae						1
<i>Callithamnion decompositum</i> (Grat.)J. Ag.	Ceramiaceae	1					
<i>Callithamnion hookeri</i> (Dillw.)S.F. Gray	Ceramiaceae	1			1	1	
<i>Callithamnion stuposum</i> Suhr	Ceramiaceae						1
<i>Callithamnion tripinnatum</i> C. Ag.	Ceramiaceae						1
<i>Carpoblepharis flaccida</i> (C. Ag.) Kütz.	Ceramiaceae			1	1	1	1 1
<i>Carpoblepharis minima</i> Barton	Ceramiaceae		1	1	1	1	1
<i>Centroceras clavulatum</i> (C. Ag.)Montagne	Ceramiaceae	1	1	1	1	1	1 1
<i>Centroceras distichum</i> Okamura	Ceramiaceae						1
<i>Ceramium arenarium</i> Simons	Ceramiaceae		1	1	1	1	1
<i>Ceramium atrorubescens</i> Kylin	Ceramiaceae		1	1	1	1	
<i>Ceramium camouii</i> Dawson	Ceramiaceae						1
<i>Ceramium capense</i> Kütz.	Ceramiaceae		1		1	1	
<i>Ceramium centroceratiforme</i> Simons	Ceramiaceae						1 1
<i>Ceramium diaphanum</i> (Roth) Aresch.	Ceramiaceae	1	1	1	1		
<i>Ceramium glanduliferum</i> Kylin	Ceramiaceae					1	1 1
<i>Ceramium gracillimum</i> (Ktz.) Griff. &Harv.	Ceramiaceae	1					

SPECIES	FAMILY	ANG	CNAM		NWC		FB	
		NNAM	SNAM	SWC	SFB			
<i>Ceramium gracillimum</i> (Ktz.) Griff. & Harv. <i>var. byssoideum</i> (Harv.) Mazoyer	Ceramiaceae	1						
<i>Ceramium mazatalense</i> Dawson	Ceramiaceae	1						
<i>Ceramium obsoletum</i> C. Ag.	Ceramiaceae			1	1	1	1	
<i>Ceramium papenfussianum</i> Simons	Ceramiaceae	1	1	1	1	1	1	1
<i>Ceramium planum complex</i> Kütz.	Ceramiaceae		1	1	1	1	1	
<i>Ceramium tenerrimum</i> (Martens) Okamura	Ceramiaceae					1		1
<i>Ceramium tenuissimum</i> (Roth) Aresch.	Ceramiaceae	1						
<i>Composhamnionella sciadophila</i> Stegenga	Ceramiaceae							1
<i>Crouania attenuata</i> (C. Ag.) J. Ag.	Ceramiaceae							1
<i>Crouania franciscii</i> Corma., Furn. & Scam.	Ceramiaceae							1
<i>Euptilota pappeana</i> Kütz.	Ceramiaceae				1	1	1	1
<i>Griffithsia confervoides</i> Suhr	Ceramiaceae		1	1	1	1	1	1
<i>Griffithsia opuntiodes</i> J. Ag.	Ceramiaceae	1						
<i>Griffithsia subbiconica</i> Stegenga	Ceramiaceae							1
<i>Gymnothamnion elegans</i> (Schousboe ex C. Ag.) J. Ag.	Ceramiaceae							1
<i>Laurenciophila minima</i> Stegenga	Ceramiaceae							1
<i>Lomathamnion capense</i> Stegenga	Ceramiaceae							1
<i>Lomathamnion humile</i> (Kütz.) Stegenga	Ceramiaceae		1	1	1	1	1	1
<i>Microcladia gloria-spei</i> Stegenga	Ceramiaceae		1		1	1	1	1
<i>Platythamnion capense</i> Stegenga	Ceramiaceae						1	
<i>Platythamnion recurvatum</i> Wollaston	Ceramiaceae						1	1
<i>Pleonosporium caribaeum</i> (Boerg.) R. Norris	Ceramiaceae							1
<i>Pleonosporium filicinum</i> (Harv. ex J. Ag.) De Toni	Ceramiaceae		1	1				1
<i>Pleonosporium harveyanum</i> (J. Ag.) De Toni	Ceramiaceae		1	1	1	1	1	1
<i>Pleonosporium paternoster</i> Stegenga	Ceramiaceae						1	
<i>Pleonosporium ramulosum</i> (J. Ag.) De Toni	Ceramiaceae					1	1	
<i>Pleonosporium</i> sp.	Ceramiaceae	1						
<i>Spermothamnion</i> sp.	Ceramiaceae	1						
<i>Spyridia clavulata</i> Kütz.	Ceramiaceae	1						
<i>Spyridia filamentosa</i> (Wulfen) Harv. in Hook.	Ceramiaceae							1
<i>Spyridia plumosa</i> Schmitz ex J. Ag.	Ceramiaceae						1	
<i>Tiffaniella schmitziana</i> (Bart.) Bolt. & Steg.	Ceramiaceae							1
<i>Wrangelia purpurifera</i> (Harvey) J. Ag.	Ceramiaceae							1
<i>Nothogenia erinacea</i> (Turner) Parkinson	Chaetangiaceae							1
<i>Nothogenia ovalis</i> (Suhr) Parkinson	Chaetangiaceae							1
<i>Scinaia capensis</i> (Setchell) Huisman	Chaetangiaceae							1
<i>Scinaia salicornioides</i> (Kütz.) J. Ag.	Chaetangiaceae						1	1
<i>Champia compressa</i> Harvey	Champiaceae							1
<i>Champia lumbricalis</i> (L.) Desveaux	Champiaceae				1	1	1	1
<i>Champia parvula</i> (C. Ag.) Harv.	Champiaceae	1						
<i>Chylocladia capensis</i> Harvey	Champiaceae		1	1	1	1	1	1
<i>Amphiroa beauvoisii</i> Lam.	Corallinaceae	1						1
<i>Amphiroa capensis</i> Aresch. in J. Ag.	Corallinaceae							1
<i>Amphiroa ephedraea</i> (Lamarck) Decaisne	Corallinaceae							1
<i>Arthrocardia</i> spp. Decaisne	Corallinaceae	1	1	1	1	1	1	1
<i>Cheilosporum cultratum</i> (Harv.) Aresch. in J. Ag.	Corallinaceae							1
<i>Cheilosporum sagittatum</i> (Lam.) Aresch. in J. Ag.	Corallinaceae							1
<i>Corallina</i> spp. Linnaeus	Corallinaceae	1	1	1	1	1	1	1
<i>Jania adhaerens</i> Lam.	Corallinaceae							1
<i>Jania capillacea</i> Harv.	Corallinaceae							1

SPECIES	FAMILY	ANG	CNAM	NWC	FB	
		NNAM	SNAM	SWC	SFB	
<i>Jania crassa</i> Lam.	Corallinaceae	1				1
<i>Jania fastigiata</i> Harv.	Corallinaceae	1				
<i>Jania verrucosa</i> Lam.	Corallinaceae				1	1 1
<i>Rhodophyllis reptans</i> Kütz.	Cystocloniaceae		1	1	1	1
<i>Dasya scoparia</i> Harvey ex J.Ag.	Dasyaceae			1	1	1 1
<i>Heterosiphonia arenaria</i> Kylin	Dasyaceae					1 1
<i>Heterosiphonia crispera</i> (Suhr) Falkenberg	Dasyaceae		1	1	1	1 1 1
<i>Heterosiphonia dubia</i> (Suhr) Falkenberg	Dasyaceae		1	1		1 1 1
<i>Heterosiphonia pellucida</i> (Harvey) Falkenberg	Dasyaceae			1	1	1
<i>Heterosiphonia wurdemanni</i> (Bailey ex Harv.) Falk.	Dasyaceae	1				
<i>Acrosorium acrospermum</i> (J.Ag.) Kylin	Delesseriaceae		1	1	1	1 1 1
<i>Acrosorium cincinnatum</i> Wynne	Delesseriaceae		1	1		
<i>Acrosorium maculatum</i> (Kütz.) Pappen.	Delesseriaceae	1	1	1	1	1 1 1
<i>Acrosorium venulosum</i> ((Zanardini) Kylin	Delesseriaceae					1 1
<i>Apoglossum ruscifolium</i> (Turner) J.Ag.	Delesseriaceae					1 1
<i>Bartoniella crenata</i> Kylin	Delesseriaceae					1
<i>Botryocarpa prolifera</i> Greville	Delesseriaceae			1	1	1
<i>Botryoglossum platycarpum</i> (Turner) Kütz.	Delesseriaceae			1	1	1 1
<i>Caloglossa leprieurii</i> (Mont.) J.Ag.	Delesseriaceae					1
<i>Cryptopleura calophylloides</i> (J.Ag.) Wynne	Delesseriaceae	1	1			
<i>Delesseria papenfussii</i> Wynne	Delesseriaceae			1	1	1 1 1
<i>Delesseria</i> sp.	Delesseriaceae	1				
<i>Erythrogloum</i> sp.	Delesseriaceae					1 1
<i>Gonimophyllum africanum</i> Martin & Pocock	Delesseriaceae					1 1
<i>Haraldiophyllum bonnemaisonii</i> (Grev.) Zinova	Delesseriaceae		1			1 1
<i>Holmesia capensis</i> J.Ag.	Delesseriaceae					1
<i>Hymenena venosa</i> (L.) Kylin	Delesseriaceae			1	1	1 1
<i>Hypoglossum abyssicolum</i> Taylor	Delesseriaceae	1				
<i>Hypoglossum</i> sp.	Delesseriaceae		1			
<i>Myriogramme livida</i> (Hooker & Harv.) Kylin	Delesseriaceae		1	1		1
<i>Myriogramme eckloniae</i> Stegenga <i>et al.</i>	Delesseriaceae					1
<i>Neuroglossum binderianum</i> Kütz.	Delesseriaceae			1	1	1 1
<i>Nienburgia serrata</i> (Suhr) Papenfuss	Delesseriaceae					1
<i>Nitophyllum</i> sp.	Delesseriaceae	1				
<i>Platyclinia</i> sp.	Delesseriaceae					1
<i>Platysiphonia intermedia</i> (Grunow) Wynne	Delesseriaceae		1	1	1	1 1
<i>Pollexfenia laciniata</i> Harv.	Delesseriaceae					1 1
<i>Pollexfenia minuta</i> (Kylin) Papenfuss	Delesseriaceae					1 1
<i>Taenioma perpusillum</i> (J.Ag.) J.Ag.	Delesseriaceae					
<i>Erythrocladia polystromatica</i> Dangeard	Erythropeltidaceae			1		1
<i>Erythrotrichia boryana</i> (Mont.) Berthold	Erythropeltidaceae		1	1		1 1
<i>Erythrotrichia carnea</i> (Dillwyn) J.Ag.	Erythropeltidaceae					1
<i>Erythrotrichia welwitschii</i> (Ruprecht) Batters	Erythropeltidaceae					1 1 1
<i>Membranella africana</i> Stegenga <i>et al.</i>	Erythropeltidaceae					1 1
<i>Sahlingia subintegra</i> Korumann	Erythropeltidaceae		1	1	1	1 1 1
<i>Gelidiopsis variabilis</i> (J.Ag.) Schm.	Gelidiaceae	1				
<i>Gelidium abbottiorum</i> R.E.Norris	Gelidiaceae					1
<i>Gelidium applanatum</i> Stegenga <i>et al.</i>	Gelidiaceae					1 1
<i>Gelidium capense</i> (Gmelin) Silva	Gelidiaceae			1		1 1 1
<i>Gelidium corneum</i> Boergesen	Gelidiaceae	1				
<i>Gelidium micropterum</i> Kütz.	Gelidiaceae			1	1	1 1

SPECIES	FAMILY	ANG		CNAM		NWC		FB	
			NNAM		SNAM		SWC	SFC	SFB
<i>Gelidium pristoides</i> (Turner) Kütz.	Gelidiaceae				1			1	1
<i>Gelidium pteridifolium</i> Norris <i>et al.</i>	Gelidiaceae								
<i>Gelidium pusillum</i> (Stackh.) Le Jolis	Gelidiaceae	1	1	1					
<i>Gelidium reptans</i> (Suhr) Kylin	Gelidiaceae		1					1	1
<i>Gelidium versicolor</i> (Gmel.) Lam.	Gelidiaceae	1							
<i>Gelidium cf. latifolium</i> Grev.) Bornet <i>et Thur.</i>	Gelidiaceae		1					1	
<i>Suhria vittata</i> (L.) J.Ag.	Gelidiaceae		1	1	1	1	1	1	1
<i>Chondracantus teedii</i> (Roth) Kütz.	Gigartinaeae	1	1	1					
<i>Gigartina clathrata</i> (Decaisne) Rabenhorst in Hommersand <i>et al.</i>	Gigartinaeae			1	1	1	1	1	
<i>Gigartina insignis</i> (Endlicher & Diesing) Schmitz in Barton	Gigartinaeae								1
<i>Gigartina pistillata</i> (Gmelin) Stackhouse	Gigartinaeae							1	1
<i>Gigartina polycarpa</i> (Kütz.) Setchell & Gardner	Gigartinaeae				1	1	1	1	1
<i>Mazzaella capensis</i> (J.Ag.) Frederiq.	Gigartinaeae		1	1	1	1	1	1	
<i>Mazzaella convoluta</i> (Aresch. ex J.Ag.) Hommersand	Gigartinaeae							1	1
<i>Rhodoglossum</i> sp.	Gigartinaeae							1	
<i>Sarcothalia scutellata</i> (Hering) Leister	Gigartinaeae	1			1	1	1	1	
<i>Sarcothalia stiriata</i> (Turner) Leister	Gigartinaeae				1	1	1	1	1
<i>Gracilaria dentata</i> J.Ag.	Gracilariaceae	1							
<i>Gracilaria gracilis</i> Steentoft <i>et al.</i>	Gracilariaceae				1			1	
<i>Gracilariopsis lemaneiformis</i> (Bory) Dawson	Gracilariaceae	1	1	1					
<i>Haematocelis</i> sp.	Gymnophloeaceae							1	
<i>Nemastoma lanceolatum</i> J.Ag.	Gymnophloeaceae					1	1	1	
<i>Nemastoma pulchrum</i> Baardseth	Gymnophloeaceae							1	
<i>Schizymenia obovata</i> (J.Ag.) J.Ag.	Gymnophloeaceae		1		1	1	1	1	
<i>Aeodes orbitosa</i> (Suhr) Schmitz	Halymeniaceae		1	1	1	1	1	1	1
<i>Cryptonemia hibernica</i> Guiry & Irvine	Halymeniaceae			1					
<i>Cryptonemia luxurians</i> C.Ag.	Halymeniaceae	1							
<i>Grateloupia doryphora</i> (Mont.) Howe	Halymeniaceae	1	1	1	1	1	1	1	1
<i>Grateloupia filicina</i> (Lam.) C.Ag.	Halymeniaceae		1	1	1	1	1	1	1
<i>Grateloupia longifolia</i> Kylin	Halymeniaceae		1	1	1	1	1	1	1
<i>Pachymenia carnosa</i> (J.Ag.) J.Ag.	Halymeniaceae		1	1	1	1	1	1	1
<i>Pachymenia cornea</i> ((Kütz.) Chiang	Halymeniaceae			1	1	1	1	1	1
<i>Phyllymenia belangeri</i> (Bory) Setchell & Gardner	Halymeniaceae		1	1	1	1	1	1	1
<i>Polyopes constrictus</i> ((Turner) J.Ag.	Halymeniaceae				1	1	1	1	
<i>Helminthocladia papenfussii</i> Kylin	Helminthocladaceae							1	1
<i>Helminthora furcellata</i> (Reinbold in Tyson) Martin	Helminthocladaceae							1	1
<i>Hildenbrandia lecanellierii</i> Hariot	Hildenbrandiaceae	1	?	?	1	1	1	1	1
<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini	Hildenbrandiaceae	1	1	1	1	1	1	1	1
<i>Hypnea benguelensis</i> ?	Hypneaceae	1							
<i>Hypnea ecklonii</i> Suhr	Hypneaceae				1	1	1	1	
<i>Hypnea rosea</i> Papenfuss	Hypneaceae							1	1
<i>Hypnea spicifera</i> (Suhr) Harvey in J.Ag.	Hypneaceae		1		1	1	1	1	1
<i>Hypnea spinella</i> (C.Ag.) Kütz.	Hypneaceae	1							
<i>Hypnea tenuis</i> Kylin	Hypneaceae	1	1	1	1			1	1
<i>Kallymenia agardhii</i> Norris	Kallymeniaceae				1	1	1	1	1
<i>Kallymenia schizophylla</i> J.Ag.	Kallymeniaceae		1	1	1	1	1	1	
<i>Pugetia harveyana</i> (J.Ag.) Norris	Kallymeniaceae				1	1	1	1	
<i>Thamnophyllis discigera</i> Norris	Kallymeniaceae			1	1	1	1	1	
<i>Thamnophyllis pocockiae</i> Norris	Kallymeniaceae				1		1	1	1

SPECIES	FAMILY	ANG	CNAM		NWC		FB	
		NNAM	SNAM	SWC	SFB			
<i>Lomentaria patens</i> Kütz.	Lomentariaceae			1				
<i>Lomentaria</i> sp.	Lomentariaceae						1	1
<i>Peyssonnelia atropurpurea</i> Crouan & Crouan	Peyssonneliaceae				1	1	1	1
<i>Peyssonnelia capensis</i> Mont.	Peyssonneliaceae	1					1	1
<i>Peyssonnelia inamoena</i> Pilger	Peyssonneliaceae	1						
<i>Neevea repens</i> Batters	Phragmonemataceae						1	
<i>Ahnfeltiopsis complicata</i> (Kütz.) Silva & De Cew	Phylloporaceae		1	1	1	1		
<i>Ahnfeltiopsis glomerata</i> (J.Ag.) Silva & De Cew	Phylloporaceae		1	1	1	1	1	1
<i>Ahnfeltiopsis intermedius</i> (Kylin) Stegenga <i>et al.</i>	Phylloporaceae						1	1
<i>Gymnogongrus dilatatus</i> (Turner) J.Ag.	Phylloporaceae		1	1	1	1	1	1
<i>Gymnogongrus nigrans</i> P.Dang.	Phylloporaceae	1						
<i>Gymnogongrus tenuis</i> (J.Ag.) J.Ag.	Phylloporaceae	1						
<i>Schottera nicaeensis</i> (Lam. ex Duby) Guiry & Hollenberg	Phylloporaceae			1				
<i>Plocamiocolax papenfussiana</i> Martin & Pocock	Plocamiaceae							1
<i>Plocamium beckerii</i> Simons	Plocamiaceae	1	1	1	1	1	1	1
<i>Plocamium corallorhiza</i> (Turner) Harv. in Hooker & Harv.	Plocamiaceae	1	1				1	1
<i>Plocamium cornutum</i> (Turner) Harv.	Plocamiaceae		1		1	1	1	1
<i>Plocamium glomeratum</i> J.Ag.	Plocamiaceae			1				1
<i>Plocamium maxillosum</i> (Poiet) Lam.	Plocamiaceae			1	1	1	1	1
<i>Plocamium rigidum</i> Bory in Belanger	Plocamiaceae		1	1	1	1	1	1
<i>Plocamium suhrii</i> Kütz.	Plocamiaceae	1	1	1				1
<i>Plocamium vulgare</i> Lam.	Plocamiaceae	1	1					
<i>Stylonema alsidii</i> Reinsch	Porphyridiaceae	1		1				1
<i>Gelidiocolax suhriae</i> (Martin in Pocock) Fan & Papenfuss	Pterocladophilaceae						1	
<i>Portieria hornemannii</i> (Lynbye) Silva in Silva <i>et al.</i>	Rhizophyllidaceae						1	1
<i>Acanthophora muscoides</i> (L.) Bory	Rhodomelaceae	1						
<i>Aphanocladia cf. skottsbergii</i> (Levr.) Andre	Rhodomelaceae							1
<i>Bostrychia intricata</i> (Bory) Mont.	Rhodomelaceae						1	1
<i>Bostrychia moritziana</i> (Sonder in Kütz.) J.Ag.	Rhodomelaceae							
<i>Bostrychia scorpioides</i> (Hudson) Mont. ex Kütz.	Rhodomelaceae							
<i>Bostrychia tenella</i> (Vahl) J.Ag.	Rhodomelaceae	1						
<i>Chondria capensis</i> (Harvey) Falkenberg	Rhodomelaceae	1	1	1	1	1	1	1
<i>Falkenbergiella capensis</i> Kylin	Rhodomelaceae							1
<i>Herposiphonia didymosporangia</i> Stegenga & Kemperman	Rhodomelaceae				1	1	1	1
<i>Herposiphonia falcata</i> (Kütz.) De Toni	Rhodomelaceae				1			1
<i>Herposiphonia heringii</i> (Harv.) Falkenberg	Rhodomelaceae				1	1	1	1
<i>Herposiphonia prorepens</i> (Harv.) Schmitz in Engler	Rhodomelaceae							1
<i>Herposiphonia secunda</i> (C.Ag.) Falkenberg <i>f. tenella</i> (C.Ag.) Wynne	Rhodomelaceae	1			1			1
<i>Janczewskia meridionalis</i> Solms Laubach	Rhodomelaceae							1
<i>Laurencia flexuosa</i> Kütz.	Rhodomelaceae							1
<i>Laurencia glomerata</i> Kütz.	Rhodomelaceae					1	1	1
<i>Laurencia natalensis</i> Kylin	Rhodomelaceae							1
<i>Laurencia obtusa</i> (Hudson) Lam.	Rhodomelaceae							1
<i>Laurencia peninsularis</i> Stegenga <i>et al.</i>	Rhodomelaceae							1
<i>Lophosiphonia reptabunda</i> Kütz.) Kylin	Rhodomelaceae	1						
<i>Ophidocladus simpliciusculus</i> (Crouan & Crouan) Falkenberg in Engler & Prantl	Rhodomelaceae		1	1	1	1	1	1
<i>Murrayella pericladus</i> (C.Ag.) Schm.	Rhodomelaceae	1						

SPECIES	FAMILY	ANG	CNAM		NWC		FB	
		NNAM		SNAM		SWC	SFB	
<i>Pachychaeta cryptoclada</i> Falkenberg	Rhodomelaceae			1			1	1
<i>Placophora binderi</i> (J.Ag.) J.Ag.	Rhodomelaceae					1	1	1
<i>Placophora monocarpa</i> (Mont.) Papenfuss	Rhodomelaceae			1	1	1	1	
<i>Polysiphonia cf. tepida</i> Hollenberg	Rhodomelaceae						1	
<i>Polysiphonia denudata</i> (Dillw.) Kütz.	Rhodomelaceae	1						
<i>Polysiphonia incompta</i> Harv.	Rhodomelaceae			1	1	1	1	1
<i>Polysiphonia kowiensis</i> Stegenga <i>et al.</i>	Rhodomelaceae					1		
<i>Polysiphonia namibensis</i> Stegenga & Engledow in Stegenga <i>et al.</i>	Rhodomelaceae		1	1	1	1	1	1
<i>Polysiphonia scopulorum</i> Harv.	Rhodomelaceae		1				1	1
<i>Polysiphonia subtilissima</i> Mont.	Rhodomelaceae	1						
<i>Polysiphonia urbana</i> Harv.	Rhodomelaceae			1	1	1	1	1
<i>Polysiphonia virgata</i> Harv.	Rhodomelaceae		1	1	1	1	1	1
<i>Pterosiphonia cloiophylla</i> (C.Ag.) Falkenberg in Schmitz	Rhodomelaceae		1	1	1	1	1	1
<i>Pterosiphonia parasitica</i> (Hudson) Falkenberg	Rhodomelaceae	1	1					
<i>Pterosiphonia pennata</i> (Roth.) Falkenberg	Rhodomelaceae	1						
<i>Pterosiphonia spinifera</i> (Kütz.) Norris & Aken	Rhodomelaceae							1
<i>Pterosiphonia stangerii</i> (J.Ag.) Falkenberg	Rhodomelaceae							1
<i>Rhodomelopsis africana</i> Pocock	Rhodomelaceae							1
<i>Streblocladia camptoclada</i> (Mont.) Falkenberg	Rhodomelaceae		1	1	1	1	1	1
<i>Streblocladia corymbifera</i> (C.Ag.) Kylin	Rhodomelaceae		1	1	1	1	1	1
<i>Stromatocarpus parasiticus</i> Falkenberg in Engler & Prantl	Rhodomelaceae						1	1
<i>Symphocladia marchantioides</i> (Harv. in Hooker) Falkenberg	Rhodomelaceae							1
<i>Tayloriella tenebrosa</i> (Harv.) Kylin	Rhodomelaceae		1	1	1	1	1	1
<i>Rhodophysemata africana</i> John & Lawson	Rhodophysemataceae	1						
<i>Rhodophysemata feldmannii</i> Cabioch	Rhodophysemataceae							1
<i>Botryocladia thyrigerata</i> (C.Ag.) Schm.	Rhodymeniaceae	1						
<i>Botryocladia</i> sp.	Rhodymeniaceae	1					1	
<i>Chrysomenia</i> sp.	Rhodymeniaceae							1
<i>Epymenia capensis</i> (J.Ag.) Papenfuss	Rhodymeniaceae			1	1	1	1	1
<i>Epymenia obtusa</i> (Grev.) Kütz.	Rhodymeniaceae		1	1	1	1	1	1
<i>Faucheia</i> sp.	Rhodymeniaceae		1					
<i>Rhodymenia holmesii</i> Ardissonne	Rhodymeniaceae						1	
<i>Rhodymenia natalensis</i> Kylin	Rhodymeniaceae			1	1	1	1	1
<i>Rhodymenia pseudopalmata</i> (Lam.) Silva	Rhodymeniaceae			1	1	1	1	1
<i>Sarcodia dentata</i> (Suhr) Norris	Sarcodiaceae							1
<i>Trematocarpus flabellatus</i> (J.Ag.) De Toni	Sarcodiaceae			1	1	1	1	1
<i>Trematocarpus fragilis</i> (C.Ag.) De Toni	Sarcodiaceae			1	1	1	1	1
<i>Callophycus densus</i> (Sonder) Kraft	Solieraceae						1	
<i>Flauhaltia appendiculata</i> Bornet	Solieraceae	1						

Appendix C

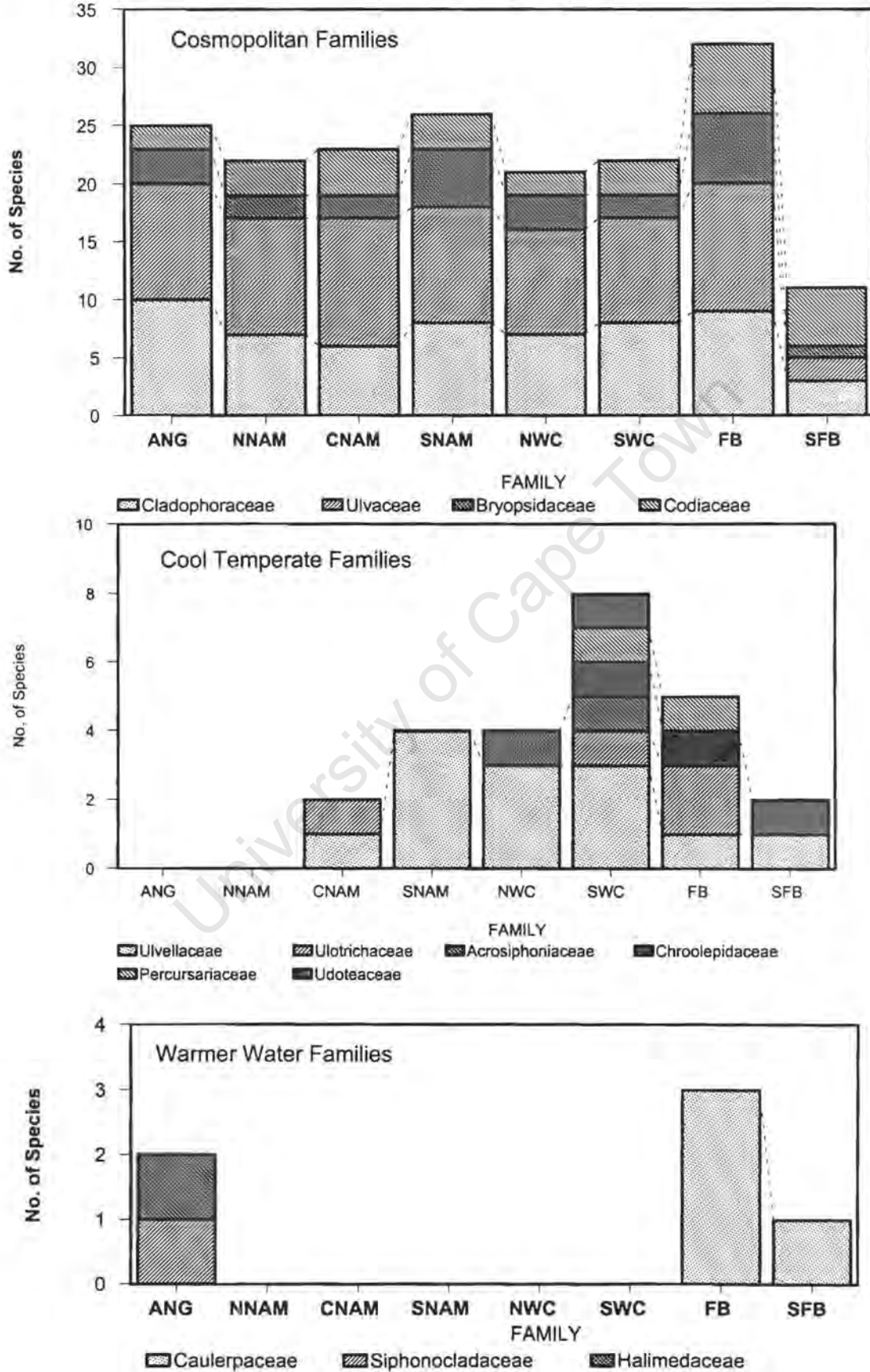
Sessile invertebrates species collected during survey of the Namibia intertidal.

Phylum / Class	Species
Porifera	<i>Hymeniacedon perlevis</i> (Montagu)
Cnidaria - Anemones	<i>Bunodactis reynaudi</i> (Milne Edwards) <i>Bunodosoma capensis</i> (Lessing) <i>Pseudactinia varia</i> Carlgren
Polychaeta	<i>Gunnarea capensis</i> (Schmarda)
Crustacea - Cirripedia	<i>Chthamalus dentatus</i> Krauss <i>Octomeris angulosa</i> Sowerby <i>Tetraclita serrata</i> Darwin
Brachiopoda	<i>Discinisca tenuis</i> (Sowerby)
Mollusca - Bivalvia	<i>Aulacomya ater</i> (Molina) <i>Choromytilus meridionalis</i> (Krauss) <i>Mytilus galloprovincialis</i> Lamarck <i>Perna perna</i> (L.) <i>Semimytilus algosus</i> (Gould)
Polyplacophora -	<i>Ischnochitan</i> sp.
Gastropoda - Periwinkles & Winkles	<i>Gibbula capensis</i> (Gmelin) <i>Nodilittorina africana</i> (Philippi) <i>Oxysteles variegata</i> (Anton) <i>Tricolia capensis</i> (Dunker)
Welks	<i>Burnupena catarrachta</i> (Gmelin) <i>Burnupena cincta</i> (Bolten) <i>Burnupena limbosa</i> (Lamarck) <i>Fasciolaria</i> sp. <i>Nucella cingulata</i> (L.) <i>Nucella dubia</i> (Krauss) <i>Nucella squamosa</i> (Lamarck) <i>Pyrene</i> sp.
Limpets	<i>Helcion dunkeri</i> (Krauss) <i>Helcion pectunculus</i> (Gmelin) <i>Crepidula porcellana</i> Lamarck <i>Fissurella mutabilis</i> (Sowerby) <i>Patella argenvillei</i> Krauss <i>Patella barbara</i> L. <i>Patella cochlear</i> Born <i>Patella granatina</i> L. <i>Patella granularis</i> L. <i>Patella miniata</i> Born <i>Patella safiana</i> Lamarck <i>Siphonaria capensis</i> Quoy & Gaimard
Echinodermata - Holothuroidea	<i>Roweia frauenfeldii</i> (Ludwig)
Tunicata	<i>Pyura stolonifera</i> (Heller)

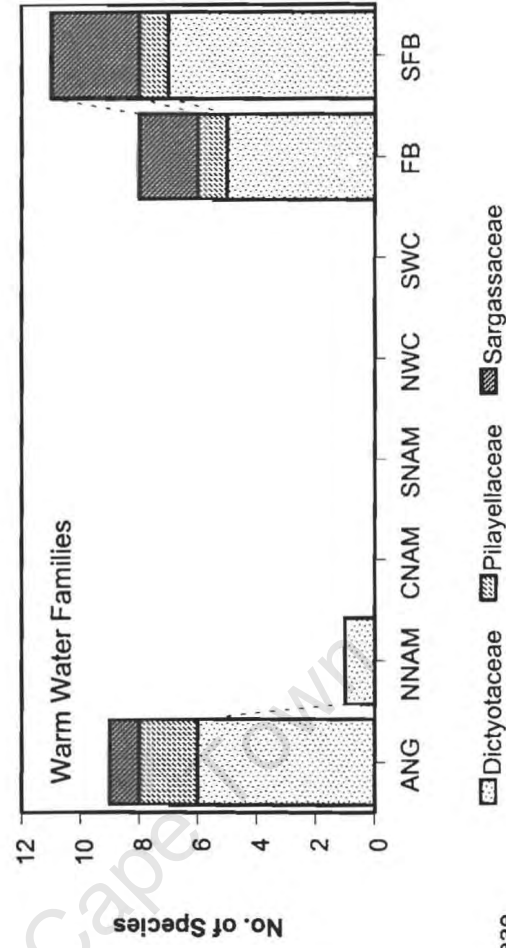
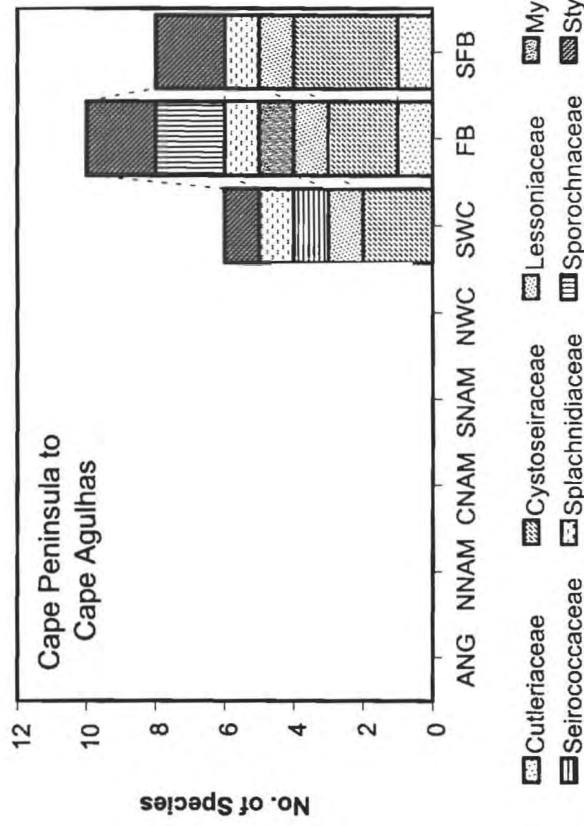
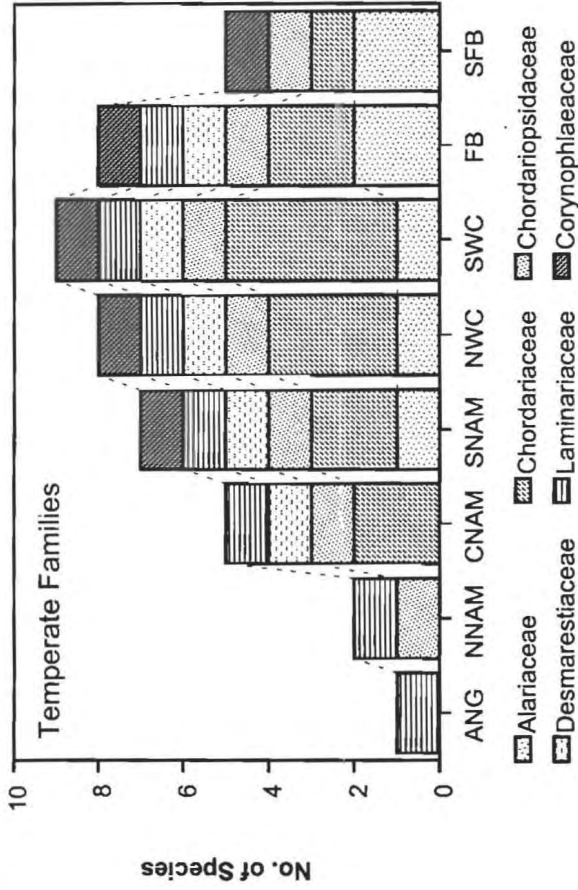
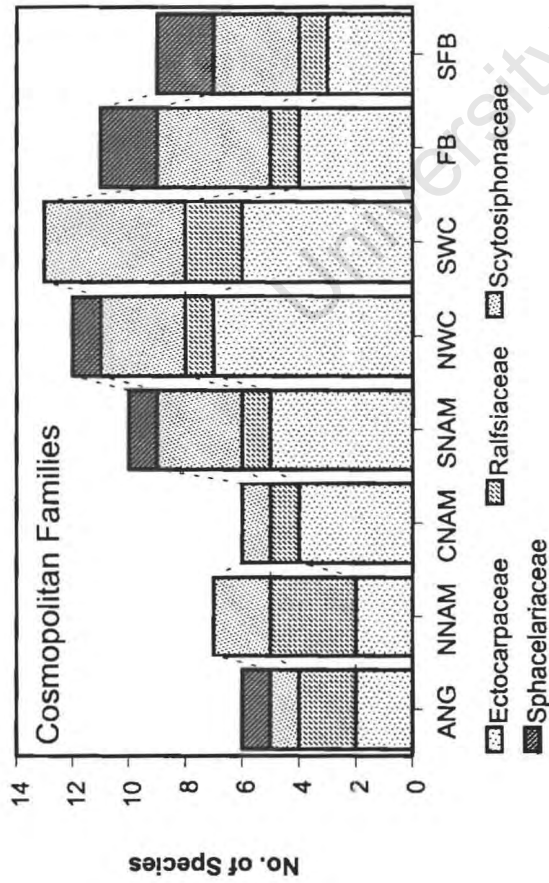
Appendix D

Family composition of the three seaweed divisions for the eight defined regions. Each division has been further divided into sub groups to aid visual presentation.

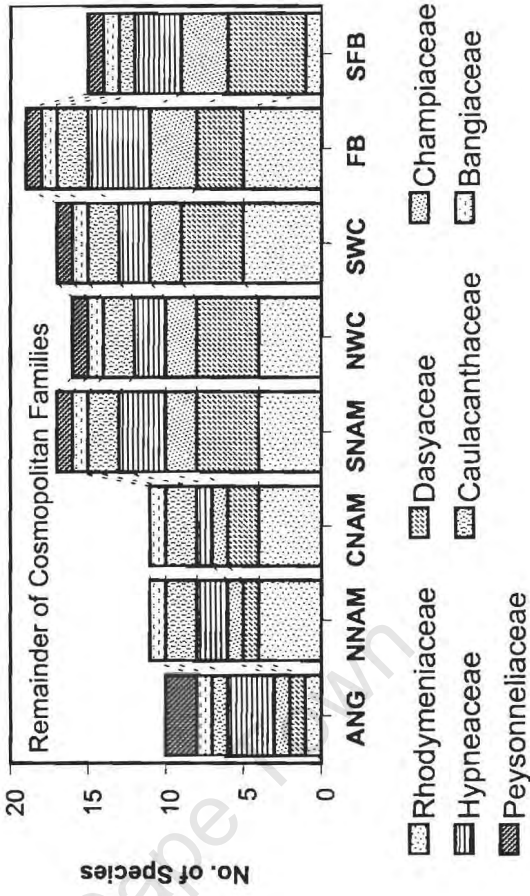
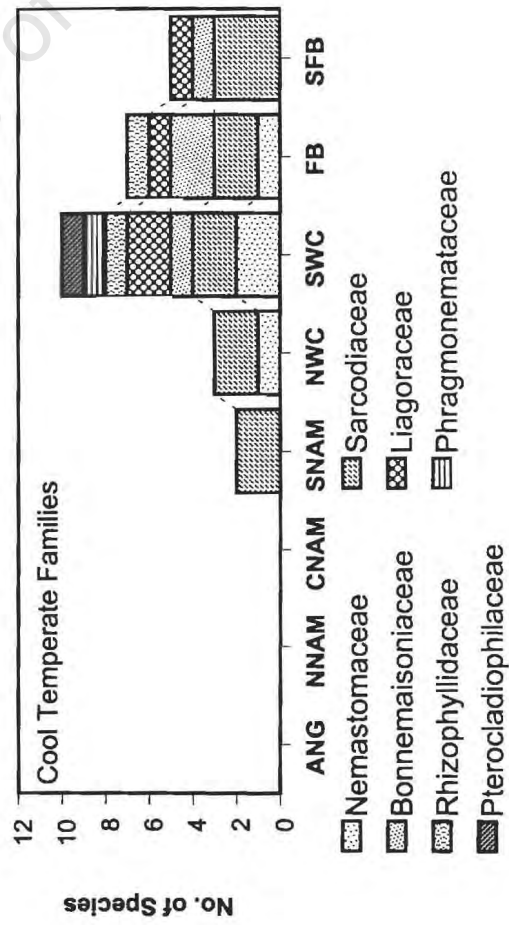
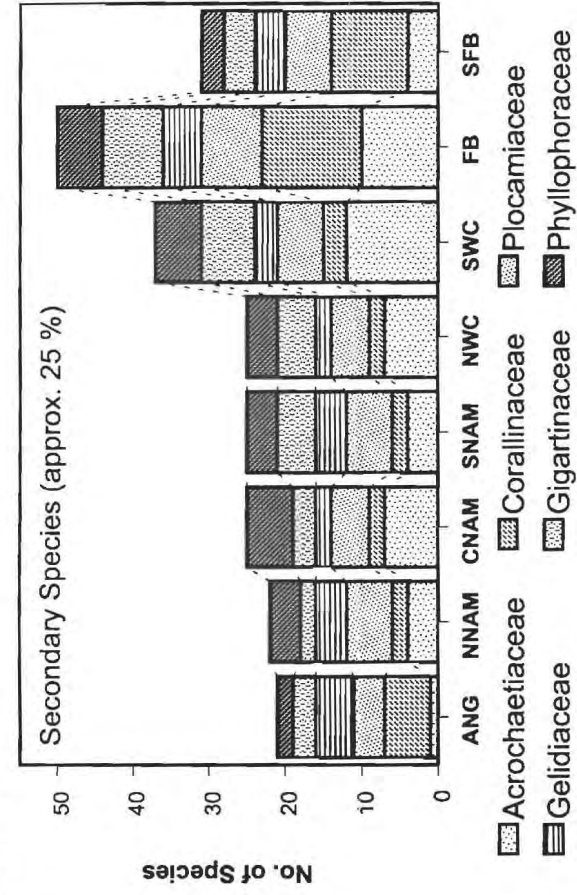
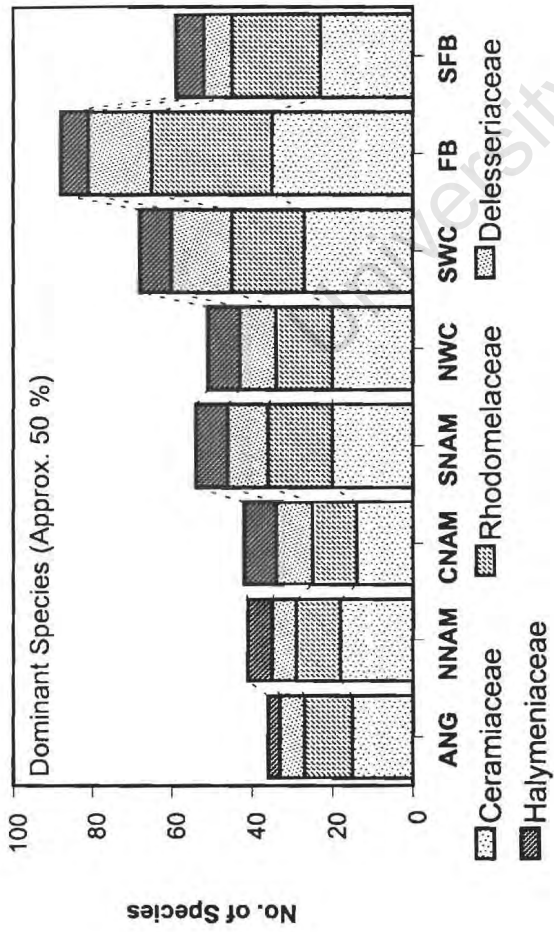
Chlorophyta



Phaeophyta



RHODOPHYTA



Appendix E

Additions to the Namibian Flora

The list below comprises some of the additions that have been made to the Namibian flora. Extensive comments have been made on select species, while others only have specimen details.

Sites

DZP - Diaz Point	M14 - Myl 14
ELB - Elizabeth Bay	MOW - Möwe Bay
ESB - Essy Bay	MY4 - Myl 4
FJD - Fjord	MY8 - Myl 8
GSB - Grossebucht	RPT - Rocky Point
GUA - Guano Bay	SHN - Saddle Hill North
HAL - Halifax Bay	SWA - Swakopmund
HOT - Hottentot's Bay	TER - Terrace Bay
KBF - Kleinbogenfels	TOR - Torra Bay
LGS - Langstrand	TOS - Toscanini
LUD - Luderitz Bucht	WZB - Wlotzka's Baken

BS., SS. - Microscope slides Reference Number.

S., C., V. - Preserved Specimen's Reference Number.

H. - Herbarium Sheet Reference Number.

Species Name

Reference used for ID

Location on Shore

Permanent Specimens

Comments

CHAETOPHORACEAE

Entocladia vagans Reinke

Lawson & John (1987)

Low Eulittoral

SS.156, 190, 192, 350, 351

Endophytic in cell walls of *Herposiphonia heringii* (Harvey) Falkenberg & *Anotrichium tenue* (C.Ag) Nägeli. The vegetative cells were 3-6µm x 5-26µm, with a single pyrenoid (5-8µm).

Entocladia viridis Reinke

Lawson & John (1987)

Low Eulittoral

SS.156, 190, 192, 350, 351

Endophytic in cell walls of *Herposiphonia heringii* (Harvey) Falkenberg & *Anotrichium tenue* (C.Ag) Nägeli. The vegetative cells 10-13 x 10-15µm(40), with 1-2 pyrenoids (2.5µm (-4µm)). Cell division was by means of transverse and vertical cross walls. Branching was irregular. No lenticular cells with acicular bodies found.

Stromatella cf. monostromata Kornmann & Sahling
Kornmann & Sahling (1983)
Mid Eulittoral
SS.181
Epiphytic on *Aeodes orbitosa* (Suhr) Schmitz

Ulvella sp.
Abbott & Hollenberg (1976), Kornmann & Sahling (1983)
Infratidal Fringe
SS.98
Epiphytic on *Epymenia obtusa* (Greville) Kützing

CLADOPHORACEAE

Cladophora cf. dalmatica Kütz.
Stegenga *et al.* (1997)
Upper Eulittoral
SS.459
Epilithic

Cladophora cf. sericea (Hudson) Kütz.
Stegenga *et al.* (1997)
Mid Eulittoral
SS.415
S.195
Epilithic

ULVACEAE

Ulva rhacodes (Holmes) Greville
Greville (1894)
Upper-Low to Mid Eulittoral
SS.244, 245, 249
S.102
H.55
Epiphytic on *Ophidocladus simpliciusculus* (Crouan) Falkenberg & *Chaetomorpha linum* (O.F.Mueller) Kützing

ECTOCARPACEAE

Ectocarpus cf. acutus Setchell & Gardner
Stegenga *et al.* (1997)
Drift
SS.621
Epiphytic on *Desmarestia firma*.

Ectocarpus cf. rhodoortonoides Børgesen

Lawson & John (1987)

SS.137

Epiphytic on *Laminaria schinzii* Foslie (stipe)

Ectocarpus siliculosus (Dillwyn) Lyngbye

Womersley (1987)

Low Eulittoral

SS.121, 137, 207, 334

C.1

Epiphytic on *Hincksia granulosa* (Smith) Silva & *Laminaria schinzii* (stipe)

RALFSIACEAE

Basispora africana John & Lawson

John & Lawson (1974)

Low to Mid Eulittoral

SS.195, 199, 341

S.130, 133

Epilithic

STYPOCAULACEAE

Stypocaulon funiculare (Montagne) Kützing in Reike

Papenfuss (1956), Stegenga *et al.* (1997)

Gulley

SS.325

S.80

Mid to Upper-Eulittoral, and in gulleys. One of the sites was relatively sand inundated.

ERYTHROPELTIDACEAE

Erythrocladia cf. polystromatica Dangeard

Wæm (1952)

Low Eulittoral

SS.192

Epiphytic on *Anotrichium tenue* (C.Ag) Nägeli. A 3-Dimensional cushion stage (ca. 30µm thick), except in young individuals which are flat. There was not dichotomous branching of the thalli. Monosporangia were cut-off obliquely, with a cell diameter of 6-8µm.

Erythrocladia subintegra Rosenvinge

Abbott & Hollenberg (1976), (See Kornmann 1989 - Sahlingia)

Infratidal Fringe & Low Eulittoral

SS.104, 113, 194, 277

C.11

Epiphytic on *Polysiphonia scopulorum* Harvey, *Codium isaacii* Silva, *Hypnea tenuis* Kylin & *Streblocladia camptoclada* (Montagne) Falkenberg. Peripheral cells displaying a forked (dichotomy) pattern, the dimensions of these cells are 5-9 x 13-18µm. The central cells are 10-15µm. Appears to radiate from a central portion - it differs from *E.polystromatica* in that the latter's cells divide intercalary or within the disc.

Erythrotrichia boryana (Montagne) Berthold

Garbary (1980)

Low Intertidal

SS.255

Epiphytic on *Gymnogongrus* sp.. A monostromatic disc 150-600µm in diameter. Uniseriate portion of thallus (8-)10-13 (-24)µm. Multiseriate portion of thallus 2-6 cells wide, 20-50µm diameter, cell shape quadrate to rectangular, cell size 2-5 x 4-16 (-25)µm. The chloroplast was stellate with a single central pyrenoid.

ACROCHAETIACEAE

Acrochaetium catalatum Howe

Stegenga (1985)

Low Eulittoral - Sublittoral fringe

SS.652

S.201

Epiphytic on *Chondria capensis*

Acrochaetium densum (Drew) Papenfuss

Stegenga (1985)

Low Eulittoral

SS.183, 194, 121

Epiphytic on *Codium isaacii* & *Griffithsia confervoides*

Acrochaetium moniliforme (Rosenvinge) Børgesen

Stegenga (1985)

Low to Mid Eulittoral

SS.242, 243, 247

Epiphytic on *Ceramium atrorubescens* Kylin

Acrochaetium reductum (Rosenvinge) Papenfuss

Stegenga (1985)

Low Eulittoral

SS.107, 113, 122, 138, 231

C.9, 11, 17

Epiphytic on *Ophidocladus simpliciusculus*, *Gynogongrus* sp., *Streblocladia corymbifera* (C.Ag.)

Kylin, *Cladophora* sp.

Acrochaetium secundatum (Lyngbye) Nägeli

Stegenga (1985)

SS.30, 183, 245, 260

Epiphytic on *Streblocladia camptoclada*, *Codium isaacii*, *Cladophora* sp., *Chaetomorpha linum*
(O.F.Müller) Kützing

Audouinella endophytica (Batters) Dixon

Jackelman et al.(1992)

Low Eulittoral

SS.338

S.142

Endophytic on *Pleonosporium filicinum* (Harv. ex J.Ag.) De Toni

Colaconema daviesii (Dillwyn) Stegenga

See Stegenga (1985)

SS.138

Epiphytic on *Ophidocladus simpliciusculus*

Colaconema plumosum (Drew) Woelkerling

See Stegenga (1985)

Drift & Infratidal Fringe (Mostly Submerged)

SS.117, 118, 137

Epiphytic on *Laminaria schinzii* (stipe)

University of Cape Town

GELIDIACEAE

The only species belonging to the Gelidiaceae to have been recorded from Namibia are: *Gelidium capense* (Gmelin) Silva, *G. pristoides* (Turner) Kütz., *G. micropterum* Kütz., *G. pusillum* (Stackhouse) Le Jolis, and *Suhria vittata* (L.) J.Ag.. The first three species have only been recorded for southern Namibia; whilst *Suhria* has been found in central and southern Namibia. *G. pusillum* was recorded, by Lawson *et al.* (1990), as occurring in central Namibia by citing Price *et al.* (1988). Unfortunately, Price *et al.* cited Lawson *et al.* (Unpubl. Manuscript), thus making the reference circular. This species has not been recorded or collected in this region by the above author, and therefore the record can not be validated.

Fertile female material is required for an accurate identification for the various genera and species within the Gelidiaceae. However, as noted by Dixon & Irvine (1977), Rodriguez & Santelice (1988), etc., the lack of fertile sexual material *in situ* makes identification an onerous task. Practically, one has to resort to external form and internal structure for separation into the various taxa.

Three species belonging to the Gelidiaceae were found at Rocky Point (northern Namibia) on the 15 April 1992. The collected species are called *Gelidium sp.1* - 3. Numbers occurring within parentheses represent values at the extremes of the range.

Gelidium sp.1

Hatta & Prud'Homme van Reine, 1991; Dixon & Irvine, 1977

Sublittoral fringe to Lower Eulittoral.

SS. 638, 644

H.263, 655

S.208

This species was found near the spring low water mark and the subtidal fringe, growing epizooically on the shells of *Patella safiana*. It is dark red - black/brown in colour. Only tetrasporic material was available.

Gelidium micropterum, *G. latifolium*, and *Gelidium sp.1* are all morphologically quite similar. Table 1, both quantitatively and qualitatively, shows similarity between *Gelidium sp.1* and the other two species. There does, however, seem to be a greater similarity with *G. latifolium*. A fundamental difference between *Gelidium sp.1* and *G. micropterum* is that the latter has bisporangia as opposed to tetrasporangia.

Two other species which are similar to *Gelidium sp.1* is *G. corneum sensu* Borgesen and *G. regulare* Baardseth. The former species is recorded from Angola (Price *et al.* 1988), and in Lawson & John (1987) relatively thin description, seems to be quite similar. It was however pointed out by Dixon (1967) that this name is illegitimate, and that the epithet at this stage is "completely confused" (Price *et al.*, 1988). The Baardseth species, *G. regulare* from Tristan da Cunha, is also quite a close match; but as Baardseth (1941) points out:

"It is difficult to establish if this species should be referred to one of the rather many forms of *G. latifolium* (Grev.) Thuret et Bornet or if it should be considered a separate species."

The reasons for establishing a new species are not convincing. I have therefore decided to place *Gelidium sp.1* under the epithet *G. latifolium*.

Table 1: Comparing *Gelidium sp.1* with *G. micropterum* Kütz. And *G. latifolium* (Grev.) Bornet et Thur.

	<i>Gelidium micropterum</i> Kütz. (After Stegenga <i>et al.</i> 1997)	<i>Gelidium sp.1</i>	<i>Gelidium latifolium</i> (Grev.) Bornet <i>et</i> Thur. (After Hatta & Prud'Homme van Reine, 1991; Dixon & Irvine, 1977)
Gross Morphology			
Main Axis - Height	50 mm	30mm	30 - 35mm (-90)
- Width	upto 1.2mm	upto 2mm	1.1mm (-5)
- Thickness	150µm	138µm (non-fertile) 175µm (tetrasporic) upto 195µm	160 - 200µm
Erect portion of thallus	Complanate	Complanate	Compressed distally, terete near the base.
Prostrate portion of thallus	Terete	Terete	Terete
Branching of erect thallus			
- No. of Orders	2 (-3)	1 - 2	1 - 3 (4)
- Branching pattern of erect portion	Pinnately Branched	Mostly pinnate - sub-opposite	Pinnate, opposite or alternate
Anatomy			
Apical Cell Arrangement (Rodríguez & Santelice, 1988)	Apical initial at the base of apical depression	Apical initial at the base of apical depression.	Apical initial at the base of apical depression.
Cortex			
- Outer layer(s)	1	1	1
- Shape	Quadrangular, anticlinally elongated	Quadrangular, anticlinally elongated	Subquadrangular, anticlinally elongated
- Dimensions	4 - 8µm x 2 - 5µm	7 - 10µm x 3.5 - 5µm	4 - 6µm (rounded) (6 - 17µm x 2 - 5µm - forma <i>elongatum</i>)
- Ratio of length : breadth	2:1	2:1	2:1 - 3:1
- Inner layer(s)	2-3	2 - 3	3 - 5
- Shape	Cuboidal	Spherical - cuboidal	Subquadrangular -ovate
- Dimensions	5 - 8µm	4.5 - 7.5µm	6 - 17µm
Medulla			
- Diameter in T/S	10µm	(7-) 9µm (-12)	(Ovate) 16 - 22µm x 8 - 10µm
Rhizines	Narrow strip in central medulla.	Numerous and situated predominantly below at the base of the cortex.	Numerous within inner cortex, occasionally small bundles in the medulla.
Tetrasporangia			
- Arrangement	No Tetrasporangia, only Bisporangia. These occur in the ultimate and penultimate branchlets. Transversely divided.	In distinct sori in spatulate branches, including tips of main axis.	Irregularly arranged on spatulate terminal branches.
Tetraspores			
- Shape	Roundish to ellipsoidal	Ovoid, Cruciate (Only see 2 divisions from surface view)	Ovoid
- Dimensions	40µm x 30µm	42µm (-48) x 24µm (-34)	20 - 30µm

Gelidium sp.2

Womersley, 1994; Dixon & Irvine, 1977

Low to Mid-eulittoral, High shore rock-pool

BS.10

H.651, 652

This species was found growing epilithic in rock pools and at the subtidal fringe within a sand covered area. The colour is dark brown/black; and only tetrasporic material was present. As can be seen from table 2 this species compares favourably with *Gelidium pusillum* (Stackhouse) Le Jolis. This species however does represent a rather diverse range of morphs, and many species have been sunk or misidentified into this "complex". This species has a cosmopolitan distribution in temperate and warmer waters of the world. It has been recorded from Angola and west Africa (Lawson & John, 1987), but is absent south of northern Namibia into South Africa.

Table 2: Comparing *Gelidium sp.2* with *G. pusillum* (Stackhouse) Le Jolis


	<i>Gelidium pusillum</i> (Stackhouse) Le Jolis (After Womersley, 1994; Dixon & Irvine, 1977)	<i>Gelidium sp.2</i>
Gross Morphology		
Main Axis - Height	(2-) 5 - 20µm (-25)	25mm (- 35mm)
- Width	0.2 - 1mm	upto 0.75mm
- Thickness	50 - 100µm	130µm (- 146)
Erect portion of thallus	Complanate	Complanate
Prostrate portion of thallus	Terete	Terete
Branching of erect thallus		
- No. of Orders	1 - 3	1 - 3 (- 4)
- Branching pattern of erect portion	Subdistichous	Irregular; however all material has subdistichous to pinnate branching in distal parts.
Anatomy		
Apical Cell Arrangement (Rodríguez & Santelice, 1988)	Apical cell at the apex or rounded end of branch	Apical cell at the apex
Cortex		
- Outer layer(s)	1	1
- Shape	Cuboidal	Subquadrangular, anticlinally elongated
- Dimensions	3 - 5µm	9 - 12µm x 3.5 - 5µm
- Ratio of length:breadth (l:b)	1:1	2:1
- Inner layer(s)	3	1 - 2
- Shape	Ovate - cuboidal	Ovate - cuboidal
- Dimensions	ca. 8 - 12µm (based on drawing)	10µm (-17)
Medulla		
- Diameter in T/S	12µm approx. (based on drawing)	12µm (-15)
Rhizines	Throughout the medulla, and towards the outer medulla in older parts. Also, the rhizines are restricted to edges in tetrasporangial branchlets.	Predominantly in the edge of thallus
		 T/S Through Erect Portion of Thallus
Tetrasporangia		
- Arrangement	In sori at the upper parts of erect blades and laterals.	In side branches; around the regions of branching; Sori not always clearly defined.
Tetraspores		
- Shape	Ovoid, Cruciate	Globose - spherical
- Dimensions	20 - 35µm	18µm (-25µm).

Table 3: Comparing *Gelidium sp.3* with *G. reptans* (Suhr) Kylin

	<i>Gelidium reptans</i> (Suhr) Kylin (After Norris, 1992)	<i>Gelidium sp. 3</i>
Gross Morphology		
General Shape	Turf forming	Turf forming
Main Axis - Height	25mm	40mm
- Width	1mm	upto 1.2mm
- Thickness	125 μ m (Based on diagram)	150 μ m (-255)
Erect portion of thallus	Complanate	Complanate - terete at base
Prostrate portion of thallus	Terete	Terete
Branching of erect thallus		
- No. of Orders	? 2 (From diagram)	? 2 (Main axis obscure)
- Branching pattern of erect portion	Irregularly pinnate in older plants; branching often occurring after injuries.	Irregular; often pseudo-dichotomous, while occasionally opposite in distal parts. Proliferations seem to take place where the thallus has been damaged, & predominantly in the upper 2/3 of thallus. Constrictions at the point of branching.
Anatomy		
Apical Cell Arrangement (Rodríguez & Santelice: Fig. ??)	Apical initial at the apex of the axes	Apical initial at the apex of the axes
Cortex		
- Outer layer(s)	1	1
- Shape		Cuboidal
- Dimensions		4.8 - 7.2 μ m
- Ratio of length:breadth (l:b)		1:1
- Inner layer(s)	1 - 2	2
- Shape	Ovoid - spherical	Ovoid - spherical
- Dimensions	7 μ m (Based on diagram)	8.5 - 12 μ m
Medulla		
- Diameter in T/S	(7-) 14 μ m (-22)(Based on diagram) Medulla comprising large thick cell wall cells.	(6-) 10 μ m (-32) Medulla containing numerous large cells with thick cell walls.
Rhizines	Numerous and found throughout the medulla.	Numerous and found throughout the medulla, esp: the central regions
Surface arrangement of Cortical cells		
- Apex	?	Mostly pairs & occasionally tetrads but rapidly becoming irregular
- Middle		
Tetrasporangia		
- Arrangement	Ill-defined sori in primary blades, but more distinct in older side branches.	Irregularly scattered in central region of distal parts of the plant.
Tetraspores		
- Shape	?	Ovoid - spherical
- Dimensions	?	18 - 24 μ m x 10 - 20 μ m
Sexual Reproductive structures	?	Male material: Spermatangia is a single layer of quadrangular, anticlinally elongated cells 9.5 - 14.5 μ m x 2.4 - 3.6 μ m 4:1 (l : b ratio)

Gelidium sp.3

After Norris, 1992

Low to Mid-eulittoral

SS.635

BS.11, 17

H.653, 654

This species occurred in the lower eulittoral in an area with a high degree of sand inundation. The colour range from a light green-brown to yellow-brown. Male and tetrasporic plants were found.

The species which was found to be closest to *Gelidium sp.3* was *G. reptans* (Suhr) Kylin (Table 3). There is, however, not complete agreement with respect to this species. The gross morphology is not that closely aligned, the sori not as well defined, and rhizines not as numerate as those found in *G. reptans*. Also, the description of *G. reptans* as found in Stegenga *et al.* (1997) is a very different plant. It is not only smaller and of different form, but rhizines are scarce and the tetrasporangia are situated in the apices of the erect branches. This species has tentatively been placed in *G. reptans*, but more material is needed in order to make a more accurate identification as well as studying the type material of *G. reptans*.

G. reptans is recorded from False Bay (south-western South Africa), and then has a disjunct distribution from Port Elizabeth (east coast South Africa) to Mozambique. This would seem to indicate a species with warmer water requirements.

Of the three *Gelidium* species above, from northern Namibia, two have affinities with species identified from further north in Angola and tropical west Africa, whilst the third has been placed in *Gelidium reptans* (Suhr) Kylin, representing a disjunction in distribution between False Bay and northern Namibia. This distribution would make sense in the light of increase sea surface temperatures in northern Namibia.

PEYSSONNELIACEAE

Peyssonnelia atropurpurea Crouan et Crouan

Irvine & Maggs in Irvine (1983)

Mid Eulittoral

SS.166

HALYMENIACEAE

Grateloupia doryphora (Montagne) Howe

Howe, M.A. 1914 - Mem. Torrey Bot. Club 15:1-185.

Mid Eulittoral & Rock Pools in Mid Eulittoral

SS.236

H.53, ?

Grateloupia longifolia Kylin

Papenfuss (1968)

Drift, Low to Lower-Mid Eulittoral

SS.6, 8, 92, 102, 111, 112, 178, 344

C.5 ; S.8, 35, 36, 41, 108, 115

H.4, 5, 45, 57

Epilithic

Note: Many of the specimens had a pronounced undulating margin. It has been regarded by some as a synonym, but I have chosen to keep it separate due to its divergent form and ecology.

Pachymenia cornea (Kützting) Chiang

Stegenga *et al.* (1997)

High Eulittoral

SS.128, 129

C.25, 26

KALLYMENIACEAE

Kallymenia agardhii Norris

Norris (1964)

Drift

SS.32, 81, 85

S.37, 84

H.18, 20, 21, 25, 26

Pugetia harveyana (J.Agardh) Norris

Norris (1964)

Low Eulittoral, Infratidal Fringe, Lighter (Barge) & Drift

SS.82, 83, 168, 134, 252

C.28

H.19

Thamnophyllis discigera (J.Agardh) Norris

Norris, R. - Bot.Mar. 7:110.

Drift

SS.3, 7, 9, 76, 77, 78, 79, 80, 322

S.21, 36, 83

H.2, 6, 16, 17

PLOCAMIACEAE

Plocamium maxillosum (Poiret) Lamouroux

Simons (1964), Papenfuss (1968)

Drift

S.75, V.30

HYPNEACEAE

Hypnea tenuis Kylin

Kylin (1938)

Low to Mid Eulittoral (Including Rock pools)

SS.101, 185, 268, 287

C.4, 38 S.144

Epilithic & attached to other algae (e.g. *Gracilariopsis* sp.)

SARCODIACEAE

Trematocarpus fragilis (C.Agardh) De Toni

De Toni(1900), Searles (1965), Simons (1983)

Low Eulittoral & Drift

SS.41

S.6, 70; V.9

H.9, 10

RHODYMENIACEAE

Rhodymenia cf. holmesii A-dissone

Irvine (1983)

Mid Eulittoral

SS.211

Rhodymenia pseudopalmata (Lamouroux) P.C.Silva

Irvine (1983)

Drift

S.31

CERAMIACEAE

Anotrichium tenue C.Agardh) Nägeli

Stegenga (1986)

Low to Mid Eulittoral

SS.2, 190, 192

S.19, 25, 147

Epilithic

No reproductive material was available, but the general morphological features are in agreement with Stegenga (1986).

Antithamnion eliseae Norris

Norris (1987)

Subtidal to Mid Eulittoral

SS.196, 200, 202, 203, 206, 296

Epiphytic on *Arthrocardia* sp., *Laminaria schinzii* (stipe), *Caulacanthus ustulatus* (Turner) Kützing

The specimens were in agreement with Norris' description, however the diameter of mature axis cells were wider on average, ranging from 70 - 100µm.

Antithamnionella australis Baardseth

Baardseth (1941)

Low Eulittoral

SS.228

Only a small male fragment of the thallus was found, hence not all the measurement could be made.

Character	Specimen	Baardseth	Wollaston
Whorl branchlets	2-3	2-4	3-4
Unilaterally branched on upper side	100µm	150-400µm	200-250µm
Axial cells	45-55 x 25-30µm	100-200 x 20-60µm	100-200 x 30-60µm
Gland cells	18-23µm	?	12-18µm
Branching	Whorl-branchlets & ocellate branch tips	?	Whorl-branchlets & ocellate branch tips
Mature whorl-branches	8-11 cells	?	10-12
Spermatangia - mother cells	2-5µm	?	2-5µm
- branches	1-5 cells		1-5 cells

This specimen is also similar to Wollaston (1968) description of *A. tamanica* Wollaston, it is therefore possible that the latter is a synonym.

Antithamnionella verticillata (Suhr) Lyle

Stegenga *et al.* (1997)

Upper Eulittoral

SS.443 (2)

Ballia sertularioides (Suhr) Papenfuss

Stegenga (1986)

Drift, Low Eulittoral

SS.502, 516 (2), 535 (3)

Epilithic

Bornetia repens Thuret

Stegenga (1986)

Drift

SS.414

S.184

Bostrychia scorpioides (Hudson) Mont. Ex Kütz.

Stegenga *et al.* (1997)

Rock Pools Drift, Upper Eulittoral

SS.461

Epilithic

Euptilota pappeana Kützling

Stegenga (1986)

Drift, Low Eulittoral

SS.49, 501(3)

V.24

H.546

Epilithic

Lomathamnion humile (Kützing) Stegenga
Stegenga (1989)
Drift & Low to Lower-Mid Eulittoral
SS.50, 167, 237
Semi-endophytic on *Phyllymenia belangeri* (Bory) Setchell et Gardner

Pleonosporium filicinum (Harvey ex J.Ag.) De Toni
Stegenga (1986)
Low to Lower Mid-Eulittoral
SS.273, 274, 290, 310, 338
S.142

DELESSERIACEAE

Platysiphonia intermedia (Grunow) Silva et Cleary
Silva & Cleary (1954)
Rock pools & Low to Lower-Mid Eulittoral
SS.52, 180, 225, 262, 270
S.59, 77
Epilithic; Turf forming. Main axis diameter (350-) 400-600 μ m, 1:1 diameter: length ratio of segments. Spermatangia: central cell diameter 35-45 μ m, flanking cells 20-24 μ m, ratio of cell dimensions 1:3 \rightarrow 3.5.

Myriogramme livida (Hooker et Harvey) Kylin
Ricker (1987)
Lighter (Barge)
SS.131,132
C.15, 27
Identification by M.Wynne.

DASYACEAE

Dasya scoparia Harvey ex J.Agardh
Agardh (1841)
Low Eulittoral
SS.265

Heterosiphonia crista (Suhr) Falkenberg
Papenfuss (1968)
Low to Mid Eulittoral
SS.197, 201, 203, 317, 357, 475, 485, 488, 509, 526
C.44

Heterosiphonia pellucida (Harvey) Falkenberg
Harvey (1847)
Low Eulittoral
SS.280
6 Pericentral cells. Main axis: 20-42 x 23-65 μ m, 1:1 \rightarrow 1:2 segment width:length ratio.

RHODOMELACEAE

Herposiphonia didymosporangia Stegenga et Kemperman

Stegenga & Kemperman (1987)

Low Eulittoral

SS.139, 339, 356, 633(2)

C.37

Epilithic

Placophora monocarpa (Montagne) Papenfuss

Papenfuss (1956)

Drift

SS.117

Epiphytic on *Laminaria schinzii* (stipe)

Polysiphonia incompta Harvey

Harvey (1847)

Rock Pool

SS.140

C.40

Polysiphonia namibiensis Stegenga & Engledow

In: Stegenga *et al.* 1997 - (see for Diagrams)

Low to Mid Eulittoral, Infratidal Fringe & Rock Pools

SS.34, 65

S.57, V.11, 19, 25

Plants dark red to almost black, caespitose upto 20 mm tall. Main axes prostrate, apices ascending. Axes attached by unicellular digitate haptera continuous with the pericentral cells. Laterals of exogenous origin, spirally arranged, issued at intervals of two to several segments. Vegetative trichoblasts virtually absent. Majority of the laterals determinate, unbranched, upto ? long, with blunt apex when mature. Determinate laterals repeating the branching scheme of the main axis. Segments with four pericentral cells, without cortication; segments in all parts of the thallus are shorter than broad, much shorter in apical portions. Width of the central cell about 1/5 to 1/4 of the filament diameter. Diameter of prostrate filaments 160-220µm, erect filaments 64-88µm, determinate laterals 64-160µm.

Tetrasporangia in long orthostichous series in the determinate laterals, in all but the proximal three or four segments. Sporangia globose, upto 68µm in diameter, fertile pericentral cells giving rise to two long and one short cover cell. Spermatangial stichidia developing on the apical parts of the indeterminate branches; male trichoblasts rarely with vegetative parts; stichidia cylindro-conical, upto 50 x 210µm. Female trichoblasts on the apical portions of indeterminate axes, sterile parts well developed and upto three times bifurcate; mature cystocarps globose, ca. 400µm diameter, with a narrow ostiole.

HOLOTYPE in BOLUS HERBARIUM: Engledow v.11; ISOYTYPES: Engledow v.19, s.57 and slide 34, (BOL), Hottentots Bay, Namibia; Leg. H.Engledow, 7 June 1990.

Stegenga's Collections:

R.S.A. : Lamberts Bay, 8 March 1985, male - slide 806

Clovelly (Flase Bay), 13 October 1988, slide 1097

Cape Agulhas, 12 November 1989, male - slide 1240

Koppie Alleen (De Hoop Nature Reserve), 23 September 1984, female - slide 605

This species is reminiscent of the genus *Orcasia* Kylin: the virtual absence of vegetative trichoblasts and the possession of determinate laterals are in close agreement with that genus (although relevant details on the origin of laterals are not observed in our material - cf. Kylin 1956). It is therefore logical to make a comparison with *O. pulla* Simmons, described from Namibia (Simons 1970); Wynne (1986), however, states that "*O. pulla* appears indistinguishable from *Streblocladia camptoclada* (Mont.) Falk.", and he places the two in synonymy; a subsequent check of the type of *O. pulla* has proved this to be correct. On a more general note, the genus *Orcasia* is now considered to be obsolete, and the species have been returned to *Polysiphonia* (e.g. Kudo & Masuda 1981). In the meantime, Wynne's (1986, p. 322) description of an unidentified *Polysiphonia* sp. might well concern *P. namibensis*. Our species should also be compared with *P. boergesenii* Baardseth 1941, described from Tristan da Cunha; the latter has, however, abundant vegetative trichoblasts and urceolate rather than globose cystocarps - material of similar morphology has been found on the western side of the Cape Peninsula (Stegenga - unpubl. obs.).

***Polysiphonia scopulorum* Harvey**

Womersley (1979), Pocock (1953)

Upper Mid Eulittoral

SS.104, 146, 271

S.143

SYSTEMATIC POSITION UNCERTAIN

***Aiolocolax pulchella* Pocock**

Pocock (1956)

High Eulittoral

SS.104, 271

Parasitic on *Polysiphonia scopulorum* Harvey

Examiners Reports

All comments, questions and suggestions, made by the various examiners, have been addressed in the thesis. The points not covered in the thesis are given below:

W.F. Farnham

- 9 - Information was gleaned from a brochure by the Namibian department of Nature Conservation - No Author given.
- 11 - The scale on this map is too small to indicate these sites adequately as they are relatively close to one another, the coordinates have been given in the Methods chapter..
- 12 - The two Islands are arrowed as they were sites that were also sampled but, during an environmental impact assessment contract. The data obtained from these sites are used in Chapter 6 on zonation.
- 13 - Yes it is true that the point at which kelp starts may be shifted by wave action, but this appeared to be the best biological indicator between subtidal and intertidal samples.
- 14 - None of the crustose coralline seaweeds were measured - this was largely due to practical constraints (e.g. they are relatively difficult to remove from the substrate and at the time of the study little was known about the taxonomy of the southern African species). They are also seldom included in this sort of study.
- 20 - General photographs of these shores are uninformative and would therefore add nothing to the general understanding of the thesis. They have therefore been omitted.
- 23 - The reason for not using Sorenson's coefficient is that it is the number of species in common divided by the average species richness of the two site. Th reason for developing the formula used is outlined on page 40).
- 29 - The authors are listed in order of publication - this is an acceptable format.
- 32 - I have commented on the vagueness of family taxonomy within the algae, but not on the phenotypic plasticity of genera. The reason being that I do not believe that it is relevant to this section or the argument.
- 33 - See pp. 52-53.
- 38 - As is seem in the zonation patterns and beta diversity chapters, there is circumstantial evidence that would seem to imply that the system is quite dynamic, in particular within central Namibia (appears to be in a state of constant perturbation). The high beta diversity values between any two shores within the same shore / area / region also indicates a dynamic system. The stability is therefore a relative concept. In Chapter 5

- only the lower eulittoral zone was looked at, and it would appear that limpet do not appear to have dominant effect of seaweed diversity within this zone of the shore.
- 46 - As was stated in the methods section (p. 94) the data is derived from two different sources. The one data set was a measure of biomass whilst the other was percentage cover.
- 47 - Yes zone 4 does seem to be more characterised by *Nothogenia* and barnacles, however, it appears to be a subset of a greater zone, namely that of *Porphyra* and *Patella granularis*.
- 48 - *Semimytilus* is not an annual, however, as Myl 8 (p.25) is a small rocky outcrop, flanked by sandy beaches and relatively exposed, this shore probably experiences periodic sand burial. As a result it is not unlikely that the mussel population is quite dynamic. The mussels were also very small and numerous, which may indicate a relatively recent recruitment to the area.
- 49 - The zones in Fig. 6.4 were subjectively chosen zones (p.94) and therefore represent named zones, the 'zones' in the biomass data are objectively derived and have therefore been left out as not to bias or obscure the data.
- 50 - I agree that species reproductive output and strategies vary, however, in this simplified model I do not believe that it is unacceptable to assume that the more abundant a species is in both biomass and distribution is an indication of its success and colonisation ability.
- 52 - This could be the explanation, but I think it is unlikely, as these species listed tend to be more predictable / consistent in other areas.

M.W. Hawkes

- 1 - How do you think your results would look if you had been able to sample subtidally?
Would the same patterns emerge or would they be different?

This question can not be answered with any degree of accuracy as no subtidal work was done on this coast. But judging from the material collected in beach cast samples the subtidal communities southern Namibia are probably similar to those found on the South African west coast. As for the central and northern regions of Namibia no comment can be delivered as the drift material collected here was not as diverse and contained some species that were not found as in southern Namibia.

- 2 - How much of a role have historical factors played in determining the Namibian seaweed flora? Are there endemics? Major disjunctions (e.g. *Membranella*)? Among the disjuncts, are they ancient vicariants or is there evidence for recent introductions?

Historical factors are very important when determining what species are present in a flora. They form the potential species pool from which the present flora is derived, however, I believe that the species surviving at present are determined by ecological factors. The origin of the South African Rhodophyta are discussed in Hommersand (1986). As has been mentioned in Chapter 3 the Namibian flora is very depauperate when compared to the South African west coast. There are at this stage no species which are endemic to this area. There are a number of disjunctions, with species occurring in central and northern Namibia, but most of these species reappear further south in Langebaan Lagoon, False Bay and on the South African south coast. This is a temperature disjunction with the two boundaries of the flora being warmer. With respect to introduced species, there does not appear to be any evidence for this, although this is difficult to ascertain. A lot of work is still needed on this coast to determine many of the above questions.

- 3 - The species list for False Bay formed part of Dr Herra Stegenga personal collections, he is the present world authority on the South African west coast taxonomy. As a result I have no problem with the identification.

- 4 - No data exists on this issue, however, the central and northern parts of Namibia are well known for their angling. As many of these fish are herbivorous it is not unlikely that herbivory plays a bigger role in these parts.

- 5 - The species that form part of a local community are a subset of the regional pool. Understanding what factors are affecting the local population may help to explain the broader regional diversity. For example, if an region comprises numerous ecologically diverse shores it is likely to have a greater regional diversity than an area with fewer ecological habitats.

- 6 - Wave action has a positive affect on seaweed diversity via biomass and dominance. This is only up to the point where the wave action does not physically remove the seaweed from the shore .

- 7 - Some species for *Polysiphonia* and *Tayloriella* do form turfs on the South African and Namibia coast e.g. *Polysiphonia scopulorum*, *Tayloriella tenebrosa*.

- 8 - At this stage it is not clear if *Porphyra* are present. This genus is presently being revised for the South African species by Mr N. Griffin. Traditionally all *Porphyra* spp. have been referred to as *P. capensis* - this does not appear to be correct, therefore this genus has been left with the epithet *Porphyra* spp..
- 9 - Yes, this would imply clonal material - but as this did not form part of the current research, it is a hypothesis that may be investigated in the future.
- 10 - The species composition in the central and northern regions of Namibia form a subset of the flora found further south. The ecological structure of the shores in the former regions are however, very different from those further south. The change is therefore ecological and not floristic.
- 11 - Rare species were those that only occurred in a single quadrat within the defined region.

E.C. Oliveira

- 1 - All the subtidal material was either collected from beach cast material or in intertidal rock-pools.
- 2 - The problem of quantifying habitat heterogeneity is indeed a large one. I have thought about this in depth and have a number of ideas - but this subject is a PhD in itself. The most difficult aspect is determining the relative importance or weight of the various factors, e.g. how does the general contour of the coast rank against wave action. I will address this issue in another study.
- 3 - Only the leafy phase of *Porphyra* was looked at during this study largely due to pragmatic reasons, and as this is being studied by a colleague. While the reason for looking at *Gelidium* in such detail is that it formed part of a study in an exchange programme with Belgium.

EXAMINER'S RECOMMENDATION FORM

RECOMMENDATION ON EXAMINATION OF PhD THESIS SUBMITTED BY UNIVERSITY OF CAPE TOWN CANDIDATE

STRICTLY CONFIDENTIAL

To: THE DOCTORAL DEGREES BOARD
University of Cape Town
Private Bag, RONDEBOSCH
7701 South Africa

FROM: Dr William F Farnham
Dept Marine Sciences
University of Portsmouth
Eastney, Portsmouth
Hants PO4 9LY
UK

PHD CANDIDATE: H R ENGLEADOW

THESIS TITLE: The biogeography and biodiversity of the Namibian Intertidal Seaweed Flora.

I have examined this thesis and recommend (please tick the appropriate box) that:

- a) the candidate should be awarded the degree and no corrections need be made to the thesis.
- b) the candidate should be awarded the degree, but minor corrections, (e.g. spelling, typing references) should be made to the thesis to the satisfaction of the Doctoral Degrees Board.
- c) the candidate should be awarded the degree subject to a number of substantive and specified changes being made to the thesis to the satisfaction of the Doctoral Degrees Board.
- d) although the thesis does not meet the required standard, the candidate should be invited to do further work if necessary, revise and resubmit for re-examination.
- e) the degree should not be awarded to the candidate

I AGREE TO DISCLOSURE OF MY NAME TO THE CANDIDATE

I OBJECT TO DISCLOSURE OF MY NAME TO THE CANDIDATE

I ENCLOSE A REPORT ON THE THESIS

H R ENGLEADOW PhD thesis, UCT "The biogeography & biodiversity of the Namibian intertidal seaweed flora" 1998
Report (revised) by Dr W F Farnham, Univ. of Portsmouth, UK 14/01/99

I am happy to recommend this thesis for PhD (subject to corrections). It is original work which has succeeded in its objectives, as succinctly outlined in the introduction, of describing the Namibian algal flora in relation to its biogeography and biodiversity. Much work has been accomplished, and the candidate has applied and developed various techniques to analyse his field data. The methods were clearly explained, with their theoretical basis, in Chapter 2. Chapter 3 on biogeography presents an overview of the changes along the Namibian coastline, and the relationships of its flora with that of Angola to the north and S. Africa in the south.

One important criterion for a doctoral thesis is the formulation of testable hypotheses and this was achieved in Chapter 4 in predicting the diversity of species in a given region. This required Engledow to analyse additional data from floristic accounts elsewhere to result in an interesting concept of "flora family structure". This could be tested for other regions.

Another requirement is the publishability of the work, which is exemplified by Chapter 5 dealing with the factors affecting seaweed diversity. However, I would have welcomed suggestions for the testing of the model proposed in Fig. 5.4, such as monitoring the biotic effects of clearance and selective removal of key species.

The various diagrams and graphs throughout the thesis, presenting his concepts and results, were informative and well presented, as in Chapter 6 showing the different zonation patterns. The bibliography is extensive to cover adequately the topics investigated.

Although the basic science in this thesis is fine and represents original contributions to our knowledge of the Namibian marine flora and its affinities, the final presentation is disappointing. I was surprised that there are no photographic plates showing the study sites and their communities or biotopes, with examples of key species or functional types (e.g. turf, crustose), etc. These would assist any future worker to relocate his transects, which could provide a baseline for monitoring if their precise locations were stated.

SIGNED: *W F Farnham* DATE: 11/01/99

Notwithstanding his acknowledgments to his proof-readers, I must have annotated almost every other page if only for rather trivial, but irritating, errors and inconsistencies, such as use of italics, upper/lower case, etc.

Although I have no major criticisms of the work, I have pencilled numbers in the LH margins of the thesis to which the following comments/questions apply. I do not suggest that the candidate alters the text in response to all these (which would have been the basis for discussion topics in a viva), but he may care to consider them, perhaps before any papers are produced from the thesis.

I have already returned my copy with its annotations to assist the candidate in producing a final, corrected version, which I look forward to receiving in due course.

- 1 What does this “%” mean?
- 2 What depended i.e to what does “This” refer ??
- 3 Why not? (explained later in the text but an abstract has to stand by itself).
- 4 Briefly, say what kind of data.
- 5 A phylum has no ability to determine anything!
- 6 C or Kunene?
- 7 Protected from what - pollution, collecting?
- 8 Reference for productive system (Field?)
- 9 Reference required
- 10 Not all these refs. are in the Bibliography.
- 11 Fig 2.1 does not show CNAM in detail.
- 12 Some sites in Table 2.1 are not in Figs 2.1 & 2.8. Why are the two islands arrowed?
- 13 The upper limit of the kelp bed as = SLWM may be erroneous if the kelp zone is being uplifted by wave action, see 51.
- 14 Was the “lithothamnion” recorded for % cover? What about other crustose algae?
- 15 Why was this quadrat size chosen; were species/area curves determined?
- 16 It would be helpful to give refs. for the identifications as to which keys & handbooks were used.
- 17 (p17) Incomplete sentence!
- 18 Better to say that s decreases as m increases.
- 19 How were the quadrats randomly selected?
- 20 I would have expected photographs of the sites surveyed & habit shots of biotopes and organisms *in situ*.
- 21 Why not provide more detailed maps for CNAM & NNAM?

22 When was *Semimytilus* introduced to become dominant? Give reference.
22A (p29) A more detailed evaluation of previous biogeographic schemes, together with a critique of the different approaches & methodologies employed, is required. Discuss how provinces are delineated. I suggest a map of the Atlantic or Africa showing the extent of the Benguela marine province & neighbouring ones.

- 23 Why did you not use Sorenson's coefficient of similarity?
- 24 Are these temperatures for inshore/coastal waters? Offshore seawater may be much cooler.
- 25 Reword? “way that the high species richness of this region would not affect the resulting value”.
- 25A Explain why you suggest that *L. pallida* has evolved into *L. schinzii*.
- 26 Give some examples of Namibian endemic species.
- 27 I think that Humm (Phycologia 1969 7:) also commented that an extensive sandy shoreline acted as a biogeographic barrier along the Atlantic coast of the USA.
- 28 Give some examples of sand-tolerant (*Ahnfeltiopsis* & *Gymnogongrus* spp?) & sand-intolerant species, also turf-formers for those unacquainted with the flora.
- 29 Helpful to the reader in referring to the bibliography to list multiple refs. in alphabetical order.
- 30 I dislike these “compound noun formations” or should I say “formation of compound nouns” - just a personal preference.
- 31 Explain that this formula was derived from Feldman (no C) & has been used to assess the floristic affinities of regions over the world.
- 32 (p65) I think this is a significant point. Perhaps genera are more useful taxonomic units than species. Comment briefly on vagaries & problems of algal taxonomy, such as phenotypic plasticity, changes in circumscription of families, etc.
- 33 What might determine these upper limits?
- 34 (p82) Competition for space between mussels & limpets? -ve correlation stated on p83.
- 35 Presumably tough thalli are resistant to abrasion by sand grains e.g. *Ahnfeltiopsis*.
- 36 But algae could grow on mussels or between them.
- 37 How patchy are the mussels in their distribution in comparison with the size of quadrats used (25x25cm).
- 38 How stable are these communities likely to be over long periods of time? Consider Hawkin's work on long-term cyclical changes in limpet, barnacle & *Fucus* populations on English rocky shores.

whether these species represent significant range extensions, e.g. *Cryptonemia hibernica* (in App B), previously only known from Ireland, or changes in the composition of the province.

- 39 What is the upper limit of the eulittoral zone? Usually top of barnacles in quantity.
- 40 Your methods (p6) suggest that both wet & dry weights are going to be used. When you write biomass, do you mean dry weight?
- 41 (p98) There would appear to be two critical levels in Fig 6.2 at c600 & 1200mm. Is there any significance to this in relation to the tidal regime -neap heights?
- 42 Fig 6.2 does not indicate your "transition" zone to me - *P. granularis* is widely distributed on the shore.
- 43 *Gigartina polycarpa* (also in App B) = *G. radula*?
- 44 But your zone 4 does not contain *Aeodes*!
- 45 How were the zones recognised - presumably dominant species?
- 46 Why did you plot biomass in Figs 6.2 7 6.5, and % cover in Figs. 6.3 & 6.4?
- 47 The main biological feature of Zone 4 are the barnacles & *Nothogenia*. *Patella* is sub-dominant to other species.
- 48 Is *Semimytilus* not perennial i.e. should be present in both seasons?
- 49 I find it helpful when you indicate the zonation the X axis (as in Fig 6.4), in addition to vertical height.
- 50 (p123) But you might have the situation between two species of similar biomass, where one species consists of one large plant per sample, while the other consists of many more smaller plants. Are their reproductive potentials necessarily similar?
- 51 (p133) Did your transects include rock pools which often contain sublittoral species demonstrating zonation "uplift" e.g. *Laminaria*?
- 52 The three green algae, at least, are opportunist species which are likely to be sporadic in their occurrence and may reflect very localised conditions of disturbance.
- 53 Some comment could be made that Fig. 7.11 represents modified species/area curves - see Coppejans (1980) Shore Symposium.
- 54 Possibly the incursion of subtidal species into the intertidal is dependant on local climatic conditions (not too hot & dry?).
- 55 (p145) P49- Three sub-provinces proposed, not two.
- 56 What are the characteristic features of the Benguela province & its component sub-provinces? Tabulate? Would knowledge of the sublittoral flora be likely to change your biogeographical concepts?

There seems to be some information in the appendices not referred to in the main text, for example, App. E on new Namibian records, (with some of its references not cited in the bibliography). Comments could be made as to

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REPORT ON THE PH.D. THESIS OF MR H. R. ENGLEDDOW

Mr. Engledow is to be commended for his work on the Namibian intertidal seaweed flora. His collections along this little-studied and remote shoreline have added greatly to our knowledge of benthic marine algal biodiversity in the region. Mr. Engledow's innovative use of various methods of data analysis to get at the underlying causes for the biogeographic patterns has proven fruitful. The hypotheses he has generated can be subjected to experimental testing by future workers in the field.

Mr. Engledow has set an excellent foundation for further descriptive, quantitative, and experimental studies of the Namibian seaweed flora.

General Questions for the Candidate:

1. How do you think your results would look if you had been able to sample subtidally? Would the same patterns emerge or would they be different?
2. How much of a role have historical factors played in determining the Namibian seaweed flora? Are there endemics? Major disjuncts (e.g. *Membranella*)? Among the disjuncts, are they ancient vicariants or is there evidence for recent introductions?

General Editorial Comments:

1. Please add a list of Figures & a List of Tables at the beginning of the thesis.
2. A summary table listing % endemics, % rare, % tropical, etc would be helpful. Also, some comment on the disjuncts would be appropriate.
3. Formally state the hypotheses proposed (see my comments under Chap. 5, p. 89)

Specific Comments or Queries:

Abstract

- p. II: Since the Tokyo version of the I.C.B.N. Phylum is used instead of Division
p. II: It has recently been proposed to use Heterokontophyta instead of Phaeophyta
p. II: 2nd paragraph, "Each division's ability to determine its species richness from the genus and family richness,...." Meaning unclear.

Chapter 1

Please proof-read again; a number of minor errors

Chapter 3

- 3 p. 36 *Membranella africana* represents a major disjunction for this genus (type locality California), are you certain of the I.D.?
p. 37 & Appendix B, xvii: *Erythrocladia subintegra*. Is there a reason you have not treated this taxon under the genus *Sahlvingia*?

- 4 p. 48: 2nd para. "This, together with increased temperature conditions and possible related increases in herbivory, could account for the predominance of turf-forming seaweeds... What evidence do you have for long term herbivory in the area?"
p. 50: The factors you invoke to explain the biogeographic patterns are essentially ecological. What role have historical factors played in determining the flora?

Chapter 4

p. 67: last paragraph to top of p. 68. See some of Peter Stevens (Harvard Univ.) work on classification schemes, e.g. Stevens, P. F. 1994. *The Development of Biological Systematics: Antoine-Laurent de Jussieu, Nature and the Natural System*. Pp. xxiii + 616. New York: Columbia Univ. Press.

Chapter 5

- p. 74: 2nd para. Seems out of place here?
- p. 74: 3rd para. "Understanding diversity at a more local level may help us to understand the patterns at larger scales." It is unclear to me how this could be so. I associate local scale with 'Ecological Biogeography' and larger scale with 'Historical Biogeography' in terms of seeking an explanation for the patterns. Please comment.
- p. 81: Table 5.4. "sand quantities >5.6 kg.m²". Shouldn't this be <350 g?
- p. 87: 1st para. "As long as the wave action remains non-deleterious in the force it exerts i.e. intermediate disturbance hypothesis...." Please explain what you mean by this. If there is a disturbance then it must be deleterious to some of the algae concerned.
- p. 89: What happened to Fig. 5.3?
- p. 89: last line "....which test the various hypotheses proposes." Perhaps you should formally state the various hypotheses.

Chapter 6

- p. 91: You should cite M. Doty for his work on critical tide factors and their effect on intertidal zonation. Ref.: Doty, M.S. 1946. *Critical tidal factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast*. Ecology 27: 315-338.
- p. 91: line 12, "Russell (1991) eludes...." I think you mean alludes.
- p. 96: Table 6.1. Do *Polysiphonia* and *Tayloriella* really belong with these other 'turf-forming' taxa?
- p. 99: 1st para, last sentence, "The upper shore is dominated by *Porphyra* spp." Table 6.2 says sp., which is it?
- p. 113: 2nd para, point 5 "Have incomplete alternation of generations." Are you implying they are clonal? How good is the evidence that this is what is happening?
- p. 119: 1st para. "The shift is an ecological shift, rather than a "floristic" one,...." Please clarify this statement.

Chapter 7

- p. 134: Table 7.3. # of rare species given. Please name these and comment on what makes them rare. What criteria did you use for determining rarity?
- p. 137: last para. "Patchiness within communities is not so much due to local biotic interactions or microhabitat variation, but colonization limitation..." Don't biotic interactions and microhabitat variation limit colonization?

- p. 139: 1st para, last line, "While an increase in perturbation or stochastic events will result in a number of alternate stable states, these will allow non-abundant species to coexist."
Isn't this re-stating the Intermediate Disturbance Hypothesis?
- p. 142: 1st & 2nd lines. What Table 1. are you referring to? And, if species were not found in the two seasons/years sampled why does this make them rare?
- p. 143: end of 4th line. What Fig. 11?

Appendix B

- p. xiv: *Macrocystis angustifolia* should be *M. angustifolia*. Also, isn't this a subtidal species?
- p. xv: *Asparagopsis armata*, *Bonnemaisonia hamifera*, & *Delisea flaccida*; aren't these all subtidal species?
- p. xvii: *Heraldiophyllum* should be *Heraldiophyllum*
- p. xix: *Plocamiacolex* should be *Plocamiacolex*

Appendix D

- p. xxiv: Rhodophyta, Cool Temperate Families. Is Liagoraceae really cool temperate?

**PhD Thesis: THE BIOGEOGRAPHY AND BIODIVERSITY OF THE NAMIBIAN
INTERTIDAL SEAWEED FLORA**

Candidate: H. R. ENGLEADOW

Presented to: UNIVERSITY OF CAPE TOWN

Date: OCTOBER 1998

General Comments

I enjoyed reading this thesis. It is clearly written and well illustrated. Besides the hard data presented it also includes the personal view of the author on the concepts and methodology he utilized, instead of just referring to the methods in the classical literature. Therefore this thesis will work not only as a valuable reference to the objectives that it addresses to, but also as a sort of guide or manual to other students that intends to do the same sort of research in other regions.

It includes an amazing amount of primary data as can be seen in the appendices. Although the discussion could be richer, the methodology is adequate and the literature is extensive and up-to-date.

Relevance

The subject of research is relevant because it addresses an important aspect of seaweed distribution, horizontally as well as vertically. Although it is not firsthand, for it has been dealt with in the past, the approach utilized is by far much more detailed. Therefore it resulted in a substantial progress towards the knowledge of seaweed distribution in the Namibian coast and a sound contribution to the biogeography and biodiversity of the southwest coast of Africa.

Suggestions and other comments on specific points

I appreciated the data on sand inundation for this has been neglected in most ecologic studies with seaweeds. Some figures are really nice and innovative, e. g., Figs 3.10, and 5.4.

A list of figures and tables in the beginning of the text would help the reader to quickly locate particular illustrations.

There are not many people, like myself, that are familiar with the geography of Namibia. There are three maps in the thesis, but none of them very precise and with a good definition. The general one (p. 5) could have a better definition, including more coordinates. A general map of the region showing the prevailing currents, isobaths (7 lines of equal depths) and isotherms (summer and winter) would help.

The study is so detailed that it would be nice to have a very precise location of the transects (by GPS) so that others could repeat this work in the future for comparison and temporal variation assessment.

1 In some places subtidal species are mentioned, but I did not find information how often, and where, they were collected, and up to which depth.

It is a pity that sheltered places were not included in the surveys. I wonder if they could not alter some

of the conclusions.

2 Habitat heterogeneity is duly recognized as important in biodiversity. In fact, in my opinion it is a key factor. The problem is how to measure it objectively. I would like to see more discussion about this in the thesis.

Temperature another key factor in seaweed distribution. Although Fig. 2.3 gives an idea of T variation in the regions, nevertheless higher temperatures in some bays and collecting sites are more guessed than measured, what weakened some of the hypothesis (e. g., see 1st par. p. 112). But I assume that real data are scarce and the study visits limited.

Perhaps you could find some interesting data on temperature tolerance of the African species of *Laminaria* in Mar. Biol. 115: 151-160. 1993.

Check Stephenson on p. 29 (twice); Bonaerense or Bonaerense? The flora of Uruguay will be published in the March issue of Botanica Marina, in case you want to check Lawson's hypothesis.

I could not find an explanation for your concept of primary and secondary species in Tables 3.3.

p. 30 - did you actually studied the collections of all the authors mentioned on p. 30, as can be understood in the text, or you just saw the publications?

p. 39 - entering False Bay coming from where?

p. 46 - 2nd and 3rd pars = too much speculations on temperature influence. Physiological ecotypes? Good hypothesis to be tested *in vitro* and through transplantation.

It would be worthwhile to exploit the hypothesis of sand-burying as an strategy to avoid herbivory. How long sand burying species can withstand buried; what happen with photosynthesis and storage products, general metabolism?

p. 70, 1st par. - what Currie, 1991 says is not the opposite?, i. e., a certain number of niches to fill, therefore a limit to species richness?

It is not clear what is meant by structure of the flora (2nd par.)?

The way wave exposure was estimated is only indicative of prevailing trends. As this is a very important issue in your thesis, direct measurements on the sampling spots would be necessary. It is surprising to see how we make wrong assumptions on wave forces when we compare direct measures with some sort of dynamometers to indirect methods.

3 When you mentioned *Porphyra* I assume you mean the leafy phase. This detail can be relevant because the filamentous phase follows a completely different pattern of distribution in time and space. I was curious why you gave so much detail in the species of *Gelidium* and do not give any clue for the *Porphyra* ones.

In the diagrams presented in chapter 6 (e.g. Fig. 6.3 et seq.) it is not clear in which season the data where obtained. Dates of sampling should be included to avoid confusion due to seasonal variation.

Appendix B has a tremendous amount of information and work. A large amount of work and expertise is needed to put names in more than 400 species, including 58 new references (!). For many of them this implies in literature search, preparation of microscopic slides, sectioning, staining and measurements. A work that cannot be underestimated.

Based on which authority were the species grouped into families? This is an important information for

there are discrepancies among some authors.

The list of species needs a good revision for uniformization of format and correction of names. In a quick look into it I spotted mistakes in quite a few names.

The names that follow have problems in their spelling, authorities or others:

1. when you refer to a genus with an unknown species, no authorities should be included. Viz. *Chlorodesmis* sp. Harvey & Bailey; *Aglaozonia* sp., etc.;
2. *Enteromorpha flexuosa* (Wulfen);
3. Børgesen (correct spelling) appears as Borg., Boergesen;
4. for some spp authors initial are given, but most of the time it is not. In some cases they are mandatory, in some others they are facultative, but uniformity should be kept. E. g. *Entocladia vagans* (Børgesen) W. R. Taylor (recommendable because other Taylor's published in the field);
5. ideally one should not abbreviate authorities – in some cases they are misleading, e. g. Lam. (Lamouroux or Lamarck?);
6. *Stromatiella monostromatica* – the author is Kormann or Korum.;
7. *Myriogloea abbreviata* (Kyllin); *Hincksia rallsiae* (Vick.), etc.;
8. *Lobophora variegata* (Lam.) Womersley ex Oliveira – correct name;
9. *Macrocystis angustifolia*;
10. *Sphaecularia furcigera* – wrong authors;
11. do not use Steg. et al. (e. g. *Colaconema codicolum*, etc.);
12. corrections for spelling, e. g. *Taenioma perpusillum*, *Jania adhaerens*, *Tayloriella*, etc, etc.;
13. ex and not Ex – e. g. *Mazaella convoluta*, ...;
14. Nomenclatural problems – see Silva, Basson & Moe, 1996, (Catalogue of the Benthic Marine Algae of the Indian Ocean) in what concerns some names, such as *Achrochaetium* versus *Audouinella*, *Erythrocladia subintegra* x *Sahlingia*, etc.

Some people will consider the above mistakes as irrelevant, specially because the thesis is not addressed specifically to floristics. But, on a nomenclatural point of view, they are very important, and the floristic information is the basis of all work presented. A revision of all the list is advisable, specially if the papers are submitted for publication.

Appendix D – who said Udoteaceae is a cool Temperate family ?

Appendix E

needs revision on spelling (e. g. *Bostrichia* sic !) and incomplete information; specimens on drift should be looked with suspicion in what concerns new references; it would be very helpful in this part if you could include the usual area of occurrence for the new references; some species could come from a neighbor area with the usual area of occurrence for the new

what is a significant difference,

I was surprised to know that *Polysiphonia namibensis* (or *namibiensis*?) is a addition to the flora of Namibia.

In conclusion, I find a tremendous wealth of information in this thesis and the opening of ground to experimentally test several hypotheses. Therefore I congratulate the candidate, as well as his supervisor for such valuable piece of work and recommend the approval of the thesis with minor amendments.

I appologize for my limitations in the English language.

1. I put an X on alternative b) of the examiners form.
2. I agree to disclosure my name to the candidate.

December 07 1998

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