# An investigation into the ecology and biogeography of subtidal seaweed communities of KwaZulu-Natal.

by

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### **Declaration:**

I declare that this thesis is my own work. All work discussed in this thesis was carried out under the supervision of Prof. J. J. Bolton of the Department of Botany and Dr. R. J. Anderson of the seaweed unit, Marine and Coastal Management.

Material presented here is all original work by the author and has not been submitted in this or any other form to another university. Where use has been made of research of others, it has been duly acknowledged in the text.

Signed by candidate

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### Abstract:

This study is the first to investigate the ecology and biogeography of subtidal seaweed communities along the coast of the province of KwaZulu-Natal, on the east coast of South Africa. Intertidal studies have found a biogeographical break in the region of Cape St. Lucia and it was hypothesized that subtidal communities would mirror these trends. North of Cape St. Lucia, the continental shelf is narrow and the warm Agulhas current brings warm tropical waters onto the coast. South of St. Lucia, the continental shelf widens into the Natal Bight which extends for 160 km to Durban. Topographically-induced upwelling brings cooler nutrient-rich waters onto the Bight which is often discoloured by run-off from rivers like the Tugela. The Bight is influenced by wind driven currents and water is retained for extended periods. The high sedimentation and poor light conditions make this region poor for algal growth.

A total of 15 samples were obtained from 10 sites along the coast between 1 and 30 m deep. Each sample comprised a number of 25 x 25 cm quadrats [usually five] that were scraped off hard substrata. A number of easily measured environmental variables were recorded for each quadrat. These were correlated against the biological findings to investigate the effects on algal communities. Temperature recorders were placed at 15 m at Sodwana, Aliwal and Ballito. A year's temperature data was recorded and monthly means calculated. Biogeography was assessed using ordinations [Detrended Correspondence Analysis] and hierarchical clustering analyses [TWINSPAN].

A remarkable species richness [294 species] was recorded in 71 quadrats [a total sampling area of 4.44 m<sup>2</sup>], with a maximum of 40 species being recorded in a single quadrat. Crustose corallines and blue-green algae were not included in this analysis. The species were dominated by the Rhodophyta [77.9% of total species] with the remainder of the species from the Phaeophyta [9.9%] and Chlorophyta [12.2%]. The total biomass of 2420.8 g was more evenly distributed, with Rhodophyta [39.6% of total biomass] and Phaeophyta [35.2%] contributing similar amounts and the remainder coming from the Chlorophyta [25.2%]. The Phaeophyta included a number of genera [e.g. *Zonaria, Dictyota, Padina and Lobophora*] that are known to be

chemically defended against herbivory and able to attain larger sizes. The Chlorophyta also contribute a higher percentage of biomass than species numbers and this is mainly due to the large sand-binding species, *Caulerpa filiformis*, which dominated the heavily sand-affected Zinkwazi site.

The samples were dominated by algal turfs, with a few larger algae interspersed. Algal turfs [interwoven species forming mats less than 3 cm high] are common throughout the world and dominate algal communities in the tropics. They are morphologically similar but taxonomically diverse as can be seen by the high species richness found. There was a high percentage of rare species with 76.5% of the species being recorded in less than 7% of the quadrats and 64.6% of the species having a total biomass of less than 1 g.

Similarity calculations showed low average values between quadrats of the same sample [30-50%] indicating extremely high spatial variability in communities and a need for more extensive sampling. However due to the difficulties of collecting, sorting and identifying turf algae this was logistically impossible in this study, and is the main reason why turf algae are often ignored or simply lumped as a form group in many studies. This study shows that in KwaZulu-Natal these turfs are species-rich and highly diverse and their floristic identities cannot be ignored in any meaningful ecological study.

Depth was found [using regression analyses] to be the most important factor affecting the seaweed communities with species number and biomass declining significantly with depth. This is directly attributed to the decrease in light availability at deeper depths. Species composition and biomass were found to be highly variable in the first 5 m and generally with higher biomass and species number than the deeper samples. The percentage of calcified species' biomass also decreased with increasing depth. This is attributed to the combination of increased water motion from wave action increasing nutrient availability but causing mechanical damage. This results in a highly heterogeneous zone [< 5 m] that favours highly productive and fast growing species.

A species number and biomass regression revealed no pattern. A small amount of biomass in the form of turf algae could result in many species and larger species contributing high amounts of biomass did not exclude turfs through shading or mechanical damage. The crustose corallines did not increase with depth in response to the reduced algal cover with depth. The crusts require high levels of herbivory to create a habitat, but still require sufficient light and are particularly susceptible to shading from larger species. Distance to sand did not have an effect on the species composition or richness. This measurement was used to assess the effects of sand scour but the mechanisms for this are more complex and intricate than just distance to sand.

North of the Natal Bight, the temperature of Sodwana and Leadsman were highly similar for the entire year with annual mean temperatures of 24.2 °C and 24.1 °C, respectively. These sites are tropical by definition with the mean monthly average never below 20 °C. Ballito situated in the centre of the Natal Bight had temperatures of approximately 2 - 3 °C lower than north of the bight and an annual mean temperature of 22.2 ° C. The monthly temperature did drop below 20 °C for August and is therefore not tropical by definition. As temperature is the most important factor controlling global phytogeographic provinces, these data support the intertidal findings of a biogeographic break in the region of St. Lucia

Seaweed biogeographic patterns are generally based on the distribution of species along a coastline on the basis of presence-absence data of the total species composition. Thus the sampling method used in this study is not ideal for biogeographic analysis, but was necessary due to the turf algal component; however some inferences can still be made. The ordinations [CCA] and hierarchical clustering [TWINSPAN] analyses grouped the quadrats from sites north of the Bight closely together and separate from the sites in and south of the Bight. Thus there are good indications that the biogeography of some of the subtidal seaweeds of KwaZulu-Natal shows a similar pattern to the intertidal seaweeds: the species in the sites north of St. Lucia coming from the southern extension of the large Indo-West Pacific flora and thus being grouped together due to the similar species compositions; and the species in southern sites occurred in an area where a rapid change of species turnover is occurring and is often placed in two separate groups by the analyses.

### **Chapter 1: Introduction**

This study was conducted along the KwaZulu-Natal province on the east coast of South Africa [Fig 1.1]. Seaweed ecology in this region has generally been poorly studied, particularly in the subtidal. The aims of the study are to investigate the ecology of the seaweed communities along the coast and determine which factors are important in shaping the composition. A biogeographical break has been identified in the intertidal biota in the region of Cape St. Lucia [Sink 2001, Bolton et al. 2004] and this study will try to determine if the subtidal seaweeds follow this discontinuity. The introduction will introduce some concepts that are important to understanding the outcomes and outline some important features of the coast and seaweed biology. Firstly the concept of biogeography will be introduced outlining the main factors controlling it. A general description of the marine biogeography of the entire South African coast and main factors affecting patterns will be described, as well as a history of the studies conducted in KwaZulu-Natal. Factors that affect algal communities locally will be discussed, as well as algal responses. Algal turfs, a common growth form particularly important in the tropics, will be discussed in detail. The prevailing marine environmental conditions along the KwaZulu-Natal coast will be described in detail. Marine conservation measures [particularly the positions of existing Marine Protected Areas] along the KwaZulu-Natal coast will be described. The introduction will conclude by clarifying the aims of this study.



**Fig 1.1** Map of Southern Africa showing position of the KwaZulu-Natal province in South Africa. With important centres along the coast labelled.

### **General Biogeography:**

Biogeography is the study of the distribution, both past and present, and of related patterns of variation over the earth, in the numbers and kinds of living things [Brown & Lomolino 1998]. Van den Hoek & Donze [1967] described an algal biogeographic province as a part of the coast characterised by a more or less homogeneous flora separated from other such parts by comparatively small stretches of coast with a rapidly changing flora. Seven groups of biogeographical regions in the world's seas are recognised by modern marine zoogeographers and marine phytogeographers [Table 1.1, Lüning 1990]. The boundaries of these regions follow certain surface seawater isotherms [mean water temperature averaged over a number of years for a particular month], due to water temperature being the main factor governing the geographical distribution of seaweed species [Lüning 1990]. Temperature affects the absolute range of species by controlling the lethal limits high or low, limiting growth, inhibiting the formation of reproductive structures or one phase of the life cycle [Bolton 1983, Lüning 1990]. The sea temperature in a region is mostly influenced by

ocean currents and factors like wind which can cause upwelling events. Unlike many organisms that have an increase in diversity towards the tropics there is no peak in species number of macro algae in the tropical latitudes [Bolton 1994]. Macro-algal diversity is higher in the temperate latitudes rather than the tropics and lowest at the poles [Silva 1992].

**Table 1.1** Table showing the main biogeographical groups in the world's seas and the number of different regions within each groups. Alongside are the seawater isotherms that bound each group.

Biogeographical group	Seawater Isotherms
1] Arctic group [1 region]	Below 0 °C winter isotherm
2] Cold temperate group, Northern	Between a 0 °C winter isotherm and a 10
Hemisphere [3 regions]	°C summer isotherm
3] Warm temperate group, Northern	Between a 10 °C winter isotherm and a
Hemisphere [4 regions]	25 °C summer isotherm
4] Tropical group, [4 regions]	Above a 20 °C winter isotherm
5] Warm temperate group, Southern	Between a 10 °C winter isotherm and a
Hemisphere [5 regions]	25 °C summer isotherm
6] Cold temperate group, Southern	Between a 0 °C winter isotherm and a 10
Hemisphere[ 5 regions]	°C summer isotherm
7] Antarctic group [1 region]	Below 0 °C winter isotherm

The primary factor that determines the composition of a flora is the stock that is available to a region from historical time [Lüning 1990]. During the break up of Gondwanaland, the Mozambique Channel was opened to the Tethys sea [120 million years ago] and was more or less continuous with the Australian coastline to the south east [Hommersand 1986]. It is likely that a tropical Tethyan marine algal flora has persisted on the Southern African coast ever since the rifting of Gondwanaland [Hommersand 1986]. As such, the east and south coasts received taxa primarily from the Tethys Sea and its associated shores [e.g. Australia]. The Tethys Sea girdled the world as an uninterrupted warm-water belt since its formation [Lüning 1990]. Approximately 38 million years ago, cooling and thermal stratification occurred exposing the southern and western portions of Southern Africa to cooler waters which led to consequent changes in the remnants of the Tethys flora [Hommersand 1986]. These changes led to a decrease in similarity between once similar regions, and the appearance of endemics, especially on the south coast [Hommersand 1986, Lüning 1990]. The Indian Ocean is the largest remnant of the Tethys sea [Norris & Aken 1985, Lüning 1990] resulting in a high similarity around the entire large Indo-West Pacific flora. The subsequent arrival of taxa as epiphytes, via surface currents from Japan and Australia [e.g. the North Equatorial Current], is also a possibility of subsequent dispersal [Hommersand 1986].

### **Biogeography of South Africa:**

Phycological studies along the KwaZulu-Natal coast began with collections on early scientific expeditions by a number of collectors, most importantly C. L. P. Zeyher, C. F. Ecklon, J. F. Drege, F. Krauss & W. Gueinzius. Following these collections, the first major studies on biogeography of rocky intertidal organisms was by Stephenson & co-workers from the 1930's to the 1940's. A series of publications entitled 'The South African intertidal zone and its relation to ocean currents' studied the zonation scheme of southern African shores and the distribution of marine organisms [Stephenson *et al.* 1937, Bright 1938a, 1938b, Stephenson *et al.* 1938, Eyre & Stephenson 1938, Eyre *et al.* 1938, Eyre 1939; Stephenson *et al.* 1940]. From these studies Stephenson identified three biogeographical marine regions, a west coast cold temperate, a south coast warm temperate and an east coast sub-tropical province [Stephenson 1939, 1944, 1948]. The association between these biogeographic areas and ocean currents has long been noted [Isaac 1937, 1938, Stephenson 1948].



Fig 1.2 Map showing the oceanic current that flow around southern Africa [Walker 1989].

The west coast is influenced by the cool Benguela current which originates at the subtropical convergence from the Atlantic Central waters [Fig 1.2] [Shannon 1985]. It is influenced by the Antarctic West Wind Drift making it a cool current [Brown & Jarman 1978]. The prevailing southerly winds blowing along the coast force water to move away westerly from the coast due to Coriolis forces [Andrews & Hutchings 1980]. This generates coastal upwellings of cold nutrient rich waters which can result in as much as a 6° C drop in temperature [15 °C to 9° C recorded at Oudekraal on the Cape Penninsula] in a matter of days [Anderson & Bolton 1985].

The east coast is influenced by the Agulhas current which has its origins in the South Equatorial current of the Indian Ocean [Fig 1.2] [Schumann 1988]. This current cools as it moves southwards along the coast but still retains a core temperature of 25 °C which facilitates the spread of tropical marine organisms further to the south [Brown & Jarman 1978]. The east coast has a narrow continental shelf: generally only 10-20 km, and 50 km at its widest [Lutjeharms *et al.* 2000], allowing the warm tropical

current to influence the coast. The coastal sea surface temperatures reflect the drop in temperature of the Agulhas current by decreasing southwards [Fig 1.3]. In the graph below only sites 3 to 6 are situated in the KwaZulu-Natal province. Site 6 [Sodwana] is the only subtidal reading while the remainder are shallow recordings supplied by the Maritime Weather office.



**Fig 1.3** Sea water temperatures along the coast at East London [1], Port St. Johns [2], Southbroom [3], Durban [4], Zinkwazi [5] and Sodwana Bay [6]. The middle line is the annual mean with the upper line being the mean for the warmest month and lower line the mean for the coldest month of each year. The x-axis represents the distance along the coast from East London. [Anderson & Bolton 2005]

The south coast has a well-defined continental shelf that can be separated into two parts. A steep narrow shelf [30 km wide] northeast of Cape Padrone [80 km east of Port Elizabeth] and a wider gentle sloping shelf west of Cape Padrone, which forms the broad Agulhas bank up to 200 km wide [see Fig 1.4] [Brown & Jarman 1978, Lutjeharms 1998]. This extension of the shelf forces the core of the Agulhas current to flow further away from the shore. Where the fast flowing Agulhas current passes from a narrow shelf to a much wider shelf, deeper colder water is lifted onto the shelf [Lutjeharms 1998]. Once this water has been lifted onto the shelf it moves



Fig 1.4 Map of Southern Africa clearly showing the continental shelf with the Agulhas bank and Natal Bight [Lombard 2004].

parallel to the Agulhas current over the Agulhas bank. The winds along this coastline blow mainly in two directions, north-easterly and south-westerly. A strong and persistent north-east wind forces the sun-warmed surface layer [50 m] to move offshore and brings the colder upwelled water inshore [Lutjeharms 1998]. Winds from the south-west force a layer of warm water from the Agulhas current onshore to cover the colder upwelled water [Lutjeharms 1998]. These factors result in the large temperature fluctuations found in this region.

The marine regions proposed by Stephenson were widely accepted for a number of years [e.g. Brown & Jarman 1978]. However, a number of scientists considered the west coast to be warm temperate [Ekman 1953, Briggs 1974, Bolton 1986, Lüning 1990]. The two regions have similar mean temperature values but differ largely in the ranges of monthly mean temperatures. The west coast has an annual mean sea water temperature of 12 °C to 16 °C with an average mean warmest month between 13-19 °C and average mean coldest month between 11-14 °C, while the south coast has a slightly warmer mean temperature of 17 °C to 19 °C with the mean in the warmest month between 19-21°C and the average mean coldest month between 13-17 °C [Bolton 1986, Bolton & Anderson 1997, Lüning 1990]. This results in two distinct warm temperate regions, sensu Lüning 1990, with the west coast being dominated by large kelp beds [Bolton 1986]. Because the west coast monthly means are seldom above 15 °C, some authors have preferred to call this region cool temperate [Emanuel et al. 1992, Bolton & Anderson 1997]. There is a clear disjunction between the temperate regions of the West coast and South coast flora due to the influence of the cold Benguela and warm Agulhas currents. Thus there is a relatively short overlap region whose borders are generally agreed by scientists. The region of overlap is found between Cape Point and Cape Agulhas [Bolton & Anderson 1997]. In contrast, the change in temperature over the east coast is gradual with no clear disjunction, resulting in a large overlap region that is unclear and differs for different groups of organisms.

The overlap between the south coast and east coast region was considered by Stephenson [1948] to be the region between Cape Padrone and Port Edward [see Fig 1.1] based on intertidal organisms, while a study of the marine algae of Hluleka placed this transition between the Kei River and Hluleka [Bolton & Stegenga 1987]. A review of marine vegetation [Bolton & Anderson 1997] argued against the existence of a sub-tropical east coast flora, but considered the east coast to be a large overlap between the warm temperate south coast and the large tropical Indo-West Pacific flora. This overlap was considered to lie between East London and Durban. The water temperature of the northern KwaZulu-Natal coast is by definition tropical, having a mean monthly temperature above 20 °C for the entire year [Lüning 1990]. This results in the occurrence of coral reefs to as far south as Leadsman shoal, at 27° 50' S, and the corals which dominate these communities are mostly typical Indo-West Pacific coral reef taxa [Riegl 1993]. Other support for northern KwaZulu-Natal being the southern extension of the tropical Indo-West Pacific biota has been found in many different groups of organisms along this coastline having high affinities with the flora, including decapod crustacea [65%], fish [73.8%] [Schumann 1988] and echinoderms [73%] [Bolton et al. 2004]. The Indo-West Pacific region is one of the largest biogeographical regions and reaches from East Africa to the Pacific Islands covering the coasts of the Indian and western Pacific Oceans, including Indonesia and northern Australia, and the Pacific archipelagos of Micronesia, Melanesia, Hawai'i, and Polynesia [Lüning 1990]. Thus spreading over half the globe and 60° of latitude and is the richest marine flora [Lüning 1990].

A recent collaborative research project has been conducted between South African and Belgian phycologists investigating the diversity and biogeographical affinities of the marine benthic algal flora of the KwaZulu-Natal coast [Bolton *et al.* 2001]. They concluded using Beta Diversity indices, Detrended Correspondence Analysis [DCA], Two-Way-Indicator-Species-Analysis [TWINSPAN] cluster analysis, together with an observed lack of endemic species that, while the northern KwaZulu-Natal coast is essentially tropical, the southern and central areas of KwaZulu-Natal are a true overlap region and not a sub-tropical marine province. Also the change-over occurs most rapidly in the vicinity of St. Lucia [Bolton *et al.* 2004]. These results support the conclusions of Bolton & Anderson [1997], and thus the current understanding of phytogeographic marine provinces of southern Africa is shown in Fig 1.5.



**Figure 1.5** Map of Southern Africa showing the current understanding of the marine phytogeographic provinces [Bolton & Anderson 1997].

### Factors affecting algal communities:

Within a geographical area, many factors affect the structure and composition of communities both vertically and spatially. Light is one of the most important factors controlling the vertical distribution of seaweeds. As algae are photosynthetic organisms the ability to function and metabolise is dependent on receiving sufficient light of the required wavelength. Light is mainly affected by depth, as light is reflected and refracted with less light reaching deeper areas and longer wave lengths being absorbed first. For example in the Hawaiian Islands the water column is much clearer in the north-western Hawaiian Islands than in the southern Islands, thus light is able to penetrate further in the north-western Islands. The algae at 30 m deep are often taller than 15 cm in the north-west while generally shorter than 2 cm in the south, which has been attributed to the differing light attenuation [Abbott 1999]. All three algal phyla [Rhodophyta, Chlorophyta and Phaeophyta] are able to absorb the prevailing light found at great depth in clear oceanic waters due to the presence of chlorophyll a [Lüning 1990]. The algal phyla differ in the possession of varying accessory pigments that absorb light left in the green window not absorbed by

chlorophyll a, of which the Rhodophyta is particularly effective [Lüning 1990]. This can result in a displacement of algal phyla down a depth gradient. In a study in the Bahamas, red algae were able to grow at the deepest depths followed by green algae and then brown algae [Littler & Littler 1988]. However this is unlikely to be seen in the depths sampled during this study.

Other physical and chemical factors that affect seaweed distributions are salinity, turbidity, sedimentation and nutrient availability. Topographically or wind-induced upwelling results in cooler nutrient-rich waters, this can result in proliferation of phytoplankton which can increase turbidity. Runoff from inflowing rivers that add fresh water can increase turbidity, sedimentation and nutrients, especially when rivers travel through agricultural lands that contain high levels of sediments. In this study I refer to sediment as fine silt ['sludge-like'], while sand comprises larger, coarse particles. High depositions of sediments have been found to reduce the biomass of turf-forming algae, as well as their overall richness and diversity [Airoldi & Virgilio 1998]. These high silt loads have also been implicated in reducing coral growth south of St. Lucia [Sink 2001]. Sand directly affects algal biomass through burial, light reduction and abrasion [Cheroske et al. 2000]. Sand scouring could possibly promote certain forms of algae like calcified species, while Sink [2001] found heavily sandinundated intertidal shores in KwaZulu-Natal had higher covers of turf algae. A study in False Bay [Brown et al. 1991] found that sand discouraged many grazers and benefited some algae, but overall species diversity was lower on sand-inundated shores.

Algae absorb nutrients through their thallus from the surrounding water which in the tropics is generally nutrient-poor, but events like upwelling can result in large increases in nutrient levels. To simply absorb the nutrients from the water column does pose some problems. The diffusion rate of gases is as much as 10 000 times lower in water than in air [Lüning 1990]. Seaweeds are surrounded by a boundary layer which is a layer of slow moving water through which substances must diffuse to reach the plant from the solution [Koehl 1982]. The thickness of this boundary layer is dependent upon turbulent mixing and water flow around the plant [Lüning 1990]. Thus wave action which increases water motion has a marked effect on increasing the nutrient available to the algae. Wave action can also be a factor by clearing sediment

and causing sand abrasion and inundation. The effects of wave action decrease rapidly with depth. In tropical shallow water communities, it was hypothesised that in nutrient-poor waters corals, crustose algae and turf algae would dominate. As nutrients increase, benthic macro-algae will become more important and overgrow the other species, and when nutrient levels become very high, phytoplankton will reach high densities reducing the light levels and as a result suspension feeding animals like bivalves, barnacles, sponges and ascidians would dominate [Taylor 1997]. However on the temperate south coast of Australia turf-forming algae increased while canopy-forming algae was reduced in the areas close to urban regions due to the increase of nutrients and sediments [Gorgula & Connell 2004].

Biological factors are also important in shaping algal communities. Grazing is high in the shallow waters around the coastline from both invertebrates and fish. High levels of grazing have been indicated as one of the main factors responsible for algal turfs [van den Hoek et al. 1978, Hatcher & Larkum 1983]. However algae get protection in very shallow water [1 to 3 m] from increased water motion due to wave action, which reduces herbivore activity [Littler & Littler1988]. Grazing could possibly be higher in the warmer water of KwaZulu-Natal compared to the South Coast due to fish species diversity increasing northwards, and many of these are grazers or omnivores [Turpie et al. 2000]. Some algae gain protection from grazing by calcification of the thallus, which can also protection them from sand scour, wave shock and fouling epiphytes [Littler 1976]. For these reasons coralline red algae thrive in high wave environments [Lewis 1981]. Other algae use chemical compounds for defence [e.g. Halimeda, Stypopodium, Dictyota: Norris & Fenical 1982]. However these defences are metabolically expensive and algal turfs overcome high levels of grazing by allocating more materials to photosynthetic tissue than structural tissue [Littler & Littler 1988]. Generally as grazing intensity increases communities shift from macro-algae to fast growing turfs and eventually herbivore resistant algal crusts [Cheroske et al. 2000]. Littler & Littler [1988] proposed a combined effect of nutrients and herbivory for tropical waters but considered herbivory to be more important. If nutrients and herbivory are high, then the community will be dominated by coralline algal crusts. If herbivory is low but nutrients high, then frondose macro-algae will dominate. If herbivory is high and nutrients low, then corals will dominate and if both factors are

low, then microfilamentous algae will dominate. Competition for suitable hard substrate is high between algae, corals and sedentary animals.

### Algal turfs:

Algae turfs are common in intertidal and subtidal zones throughout the world [Stuercke & McDermid 2004], and dominate algal communities in tropical regions. Turf algae form uniform mats and the individual species in the turfs have often been overlooked or ignored. A popular misconception is that coral reefs are animaldominated systems displaying vast populations of corals, fish and invertebrates, while the algal population being largely inconspicuous, is species poor and unimportant [Price & Scott 1992]. However the trophic structure of coral reef systems has been shown to be dominated by the primary production of algae, which can be as much as 70-80% of local production on reefs [Odum & Odum 1955, Adey & Steneck 1985, Scott & Russ 1987, Hackney et al. 1989]. Turfs are promoted by large levels of disturbance, biological or physical, which reduces algal biomass and canopy heights but promotes highly productive algae [Cheroske et al. 2000]. A main driving force forming these turfs is grazing by herbivores [van den Hoek et al. 1978, Hatcher & Larkum 1983] with larger frondose macro-algae able to dominate in grazing refugia [Hackney et al. 1989]. Grazer exclusion experiments have shown the algal standing crop to increase by up to 15 times [Hatcher & Larkum 1983], and have shifted the community to be dominated by a few species of frondose macro-algae. Despite their small size the turfs have been shown to provide the major source of fixed carbon and nitrogen to non-symbiotic consumers [Adey & Goertemiller 1987]. In response to high levels of herbivory they have rapid growth rates that lead to a biomass turnover once every 4-12 days [Klumpp & McKinnon 1989].

Globally, turfs from a morphologically similar mat, generally less than 3 cm in height with slender branches less than 3 mm thick. The thalli of turf algae are frequently differentiated into a prostrate axis, attached to the substrate at a number of points with erect branches spread along the axis resulting in a spreading turf-like habit [Price & Scott 1992]. The branches are either cylindrical or flattened and usually not calcified, although articulated coralline genera, e.g. *Jania* may be locally abundant. Encrusting and epiphytic algae are often found in close association with turf species. The turfs

include juvenile or suppressed individuals of larger seaweed species that can sometimes form a major part of the community [Price & Scott 1992].

Algal turfs, although morphologically similar, are taxonomically diverse and speciesrich communities. Turfs are comprised of four algal divisions, the Rhodophyta, Phaeophyta, Chlorophyta and Cyanophyta, of which the Rhodophyta dominate [Scott & Russ 1987, Stuercke & McDermid 2004]. Turfs have a high incidence of 'rare' species, being found in low frequencies [Scott & Russ 1987, Stuercke & McDermid 2004]. There are a large number of genera that are common components of a number of tropical reef areas such as the Great Barrier Reef, the Caribbean, Hawaii and Guam. These genera include *Centroceras, Ceramium, Gelidiella, Herposiphonia, Hypnea, Jania, Laurencia, Polysiphonia, Taenioma* [Rhodophyta], *Cladophora, Ulva* [Chlorophyta], *Dictyota, Giffordia, Sphacelaria* [Phaeophyta], *Calothrix* and *Lyngbya* [Cyanophyta] [Scott & Russ 1987].

### The KwaZulu-Natal Coast:

The Agulhas current is the most important oceanographic feature along the coast of KwaZulu-Natal [Fig 1.6], [Schumann 1988]. It is a western boundary current that forms off northern KwaZulu-Natal/Mozambique coast from a confluence of waters, which flow from the Mozambique Channel and south of Madagascar [Ramsay 1994]. It is a globally significant current and flows southwards with its core generally just offshore the shelf break. The Agulhas current, approximately 100 km wide and 1 km deep, cools gradually as it travels south [Schumann 1998]. This results in a gradual temperature change along the east coast of South Africa. [Fig 1.3].



Figure 1.6 Satellite image of sea water temperatures showing the Agulhas current flowing along the coast.

The continental shelf of the KwaZulu-Natal coast is very narrow in comparison with the global average of 75 km and ranges from 2 to 50 km wide [Ramsay 1994, Lutjeharms *et al.* 2000]. The shelf off the KwaZulu-Natal coast can be divided into four sections [Schumann 1988]. The northern section has a narrow shelf less than 10

km wide in places. There is a well-formed shelf break and the Agulhas current generally flows just offshore of this break having a dominant influence in this area [Schumann 1988]. Just south of St. Lucia the shelf widens due to a gentle bight in the coastline. The Natal Bight [Fig 1.7] stretches for 160 km from Cape St. Lucia to Durban and reaches its widest point off the mouth of the Tugela River where it is around 50 km offshore [Lutjeharms et al. 2000]. The shelf break is still relatively steep but not as much as to the north or south of here, and the Agulhas current follows this break closely, thus enclosing the shelf waters of the Bight [Lutjeharms et al. 2000]. At the northern end of the Bight there is a topographically-induced upwelling cell which brings colder, saltier and nutrient-rich waters onto the shelf and most likely supplies the bottom water for the whole Bight [Lutjeharms et al. 2000]. Just south of the Bight is the Durban shelf which is an ill defined region extending from just north of Durban, to just south of Mzinto where the Agulhas current again flows close to the coast. The Durban shelf has been thought of as a transition between the winddominated shelf over the bight and the Agulhas current-dominated shelf to the south. The Southern region becomes increasingly under the influence of the Agulhas current as it moves closer inshore past the Bight [Schumann 1988].

On land, the KwaZulu-Natal coast has a humid sub-tropical climate with a warm summer [November to March]. The region is situated in a summer rainfall region and the annual mean precipitation varies between 1000 mm and 1100 mm over the coast [Schumann 1988]. It is important to note that the Tugela is the second largest river in South Africa in terms of outflow [Schumann 1988], and flows directly into the Natal Bight.

The tidal range is on average 2 m making it high microtidal or low mesotidal [Ramsay 1994]. The coast is characterised by persistent high-energy waves and prevailing large amplitude swells which dominate from the southeast for 40% of the year, and north-easterly to easterly for another 40% [Ramsay 1994]. The shelf is too narrow to have a marked influence on this amplitude and tidal currents are generally small [Schumann 1988]. The most common hard substratum along the KwaZulu-Natal coast is beachrock and aeolianite sequences of which linear aeolianite shoals are most common [Ramsay 1994].



Fig 1.7 Map showing the bathymetry of the Natal Bight and adjacent coastline [Schumann 1988].

### **Marine Protected Areas:**

The marine reserves are focused mainly in the northern parts of KwaZulu-Natal with the large Greater St. Lucia Wetlands Park stretching from Cape Vidal to the border of Mozambique. This park includes St Lucia Marine Protected Area and the Maputaland Marine Protected Area [Attwood *et al.* 1997]. The area around Aliwal Shoal has recently been named a Marine Protected Area and along with Trafalgar Marine Protected Area are the only reserves on the southern portion of KwaZulu-Natal [Fig 1.8]. Thus the marine reserves are focused in the northern parts with few in southern KwaZulu-Natal and none over the Natal Bight.



Fig 1.8 Coastline of KwaZulu-Natal showing the positioning of the Marine Protected Areas.

#### Aims:

Until recently most biogeographical work was conducted in, or focussed on, the two temperate provinces with some studies having limited numbers of sites along the KwaZulu-Natal coast [Isaac 1937, 1949, Bright 1938a; 1938b, Stephenson 1939; 1944; 1948, Eyre *et al.* 1938, Bolton 1986, Bolton & Stegenga 1987, Jackelman *et al.* 1991]. Only recently have there been specific seaweed studies [excluding taxonomic descriptions] on the east coast [KwaZulu-Natal] of South Africa [Farrell *et al.* 1993; 1994, Bolton *et al.* 2001; 2004] and all these studies have focused on the intertidal and shallow subtidal zones. A review on marine vegetation [Bolton & Anderson 1997] stated that the authors were unable to find a single published description of subtidal seaweed vegetation of KwaZulu-Natal, Bolton & Stegenga [2002] reiterated the need for studies on subtidal seaweeds in this province.

Algae are useful organisms for the study of marine biogeography. Bolton *et al.* [2004] stated "Seaweeds are ideal organisms for the study of biogeographic patterns on shallow, marine rocky shores. They are ubiquitous primary producers in these habitats, attached and non-motile, and easy to collect and preserve". Also they have similar species numbers in any one large region from temperate to tropical regions [Bolton 1994] unlike many other organisms. Therefore this study has been set out to investigate the subtidal marine algae flora of KwaZulu-Natal, focusing on the biogeography and ecology of the communities. It is important to gain knowledge on these communities to assess the functioning of current marine reserves and in setting up possible new reserves [See review of reserves later]. As KwaZulu-Natal is an overlap region it is useful to gain a base for monitoring events which may be caused by global warming, such as range extensions of seaweeds [Breeman 1990, Lüning 1990] and a recent coral bleaching event at Sodwana [Celliers & Schleyer 2002]. Also it is important to understand how the community functions ecologically to assess possible anthropogenic influences from increased pollution and invasive species.

The thesis is divided into three main sections. The first section is temperature and a continuous subtidal temperature record for the region will be studied. The second section's aim is to identify and describe the subtidal seaweed communities. The third aim is to test the hypothesis that the subtidal seaweed flora shows the same pattern as

the intertidal flora. This study is focused on subtidal algal communities of the KwaZulu-Natal coast particularly the St. Lucia region where the biogeographic changeover is reported to happen the most rapidly. The main hypotheses are highlighted in the next few sections.

### Temperature data:

There is a lack of subtidal temperature data for the coast of KwaZulu-Natal, with long term records only available from shallow depths. The aim is to present a continuous temperature regime for an entire year [February 2003 to January 2004] from the subtidal zone. The recorders were placed in and above the Natal Bight to detect any temperature changes around this region.

#### Ecological:

Due to the turf algae's small size, simple morphology and frequent lack of reproductive structures, identification is difficult and taxonomic knowledge of the algae is generally poor compared to other reef organisms like corals and fishes [Price & Scott 1992]. Therefore few studies have documented taxonomic identities of the individual algal species or acknowledged the variability in turf structure [Stuercke & McDermid 2004]. This study will describe the composition and diversity of the KwaZulu-Natal algal subtidal community including the taxonomic identities of the algal turfs.

Depth was the first factor investigated to assess its effect on the communities. Depth affects the light attenuation and could result in a vertical change of communities. The effect of depth on biomass and species richness was also investigated. Species richness and biomass are expected to decrease with depth as less light is available. As algae are photosynthetic organisms, low light conditions reduce their competitive abilities against heterotrophic organisms. However, depth could also reflect the fact that grazing intensity is greater in shallower depths with some larger algae able to grow in deeper water. The first ca. 5 metres could be highly variable due to the effect of wave action increasing nutrient flow, physical disturbance and providing some protection from grazers.

### The first hypothesis is that increasing depth will negatively affect algal biomass and species number per quadrat.

The effects of sand were investigated for both the presence of sand in a sampled quadrat and the distance to sand to determine the effects of sand inundation and scouring. High levels of sand scouring could possibly promote the abundance of some calcified species while sand inundation could promote turfs [Sink 2001] or large sand-binding species [e. g. *Caulerpa*].

### The second hypothesis investigates the effect of sand scour and states a decrease in distance to sand will promote the occurrence of calcified species.

The effects of biomass and diversity were investigated to test the hypothesis that they may have an inverse relationship, i.e. does a biomass increase result in a shift from a species-rich turf to a community dominated by a fewer larger macro-algae. The percentage cover of crustose corallines was also measured to investigate if they competed for space with the foliose algae, the hypothesis being the crustose corallines cover would increase with depth as foliose algae cover decreased.

The third hypothesis states that an increase in biomass per quadrat will result in a decrease in species numbers due to the presence of a few larger species. The fourth hypothesis looks at the competition between foliose algae and crustose algae stating that if the first hypothesis is correct then crustose algae will increase with depth as foliose algae decrease with depth.

Similarity among quadrats at each site was calculated to investigate the sampling intensity. High values will indicate that a few quadrats will sufficiently sample to sites community.

### Biogeography:

The final part of the study investigated the biogeography of the subtidal communities. There have been a few main methods for delineating marine provinces. The first uses endemism: if an area has a high percentage of endemic species [usually 10%] it is designated a separate province [Eckman 1953, Briggs 1974]. This is based on an arbitrary value and therefore not solely used but still a very good indicator. Some North Atlantic seaweed biologists used a system looking at the ratio of red and green algae divided by brown algae [Cheney 1977, Kapraun 1980]. A value of less than two was thought to characterise a cold temperate region, whereas a value greater than five indicated a tropical region. However Bolton [1986] found values above five for both the west and south coast. He argued that the brown taxa have not speciated in the southern hemisphere to the same extent as the northern hemisphere and thus this method does not work in the southern hemisphere. Most seaweed biologists follow van den Hoek & Donze [1967] who regarded a region to be a part of the coast characterised by a more or less homogenous flora and separated from other such parts by a comparatively small stretch of coast with a rapidly changing flora [Bolton 2004]. Using ordinations, Beta Diversity indices and Two-Way-Indicator-System [TWINSPAN], the biogeography of KwaZulu-Natal was investigated. Due to the gradual temperature change along the KwaZulu-Natal coast it is expected that the subtidal biogeography should mirror the patterns found from the inter-tidal biota [Sink 2001, Bolton et al. 2004]. However the temperature change along the coast could be more uniform at greater depth and this could result in a slightly different overlap.

The fifth hypothesis states that the biogeography of the KwaZulu-Natal coast will reflect the trends found from inter-tidal biota.

### **Chapter 2: Methods**

Sampling of seaweed communities took place at ten sites along approximately 450 km of the KwaZulu-Natal coastline, and where possible, at a range of depths. Sampling was carried out during the months of June to August to prevent any seasonal factors from skewing the community results. Quadrats were subjectively placed in seaweed-dominated patches as this is specifically a study on the biodiversity of seaweed communities rather than subtidal marine communities in general. Because of the biogeographic break in the intertidal seaweeds, in the Cape St. Lucia region, particular importance was placed at sites north and south of this locale. The temperature recorders were also placed to indicate the temperature variance around this region. At each site, samples were destructively sampled due to the difficulty of identification *in situ* and a number of environmental measurements were made. There were few large benthic grazers, and fish were assumed to be the main grazers for the reefs sampled. Difficulties during the collection of samples were mainly from bad weather preventing diving, poor diving conditions, a lack of reefs and difficulties in finding reefs, particularly in the Natal Bight.

### **Study sites:**



Fig 2.1 shows the sampling sites, number of quadrats, and depths sampled.

**Figure 2.1** East coast of South Africa showing relative positions of the sites along the coast. The values shown in brackets are the number of samples collected from a site and the number of quadrats per sample followed by the average depth of the sample. The stars indicate where temperature recorders were placed. The Ballito recorder is situated just south of Zinkwazi.

### Rocktail Bay [E]

The northernmost site in the study is situated at 27° 12' S, 32° 48' E. A sample of four quadrats was collected on Elusive Reef at an average depth of 16.5 m.

### Lala Nek [La]

This site is situated just south of Rocktail Bay at 27° 14' S, 32° 47' E. Five quadrats were collected by snorkel. Lala Nek has a sandy beach with a rocky outcrop on the southern end which extends into the sea. The samples were taken on pieces of broken reef between the depths of 1 and 2 m. The site was sheltered by a ledge breaking the swell at low spring tide but there was still good water motion.

Sodwana Bay [S]

This popular diving spot was extensively studied during a previous smaller [Honourslevel] project by Craig McKune [see Anderson *et al.* in press.], and the raw data reanalysed in this study. The site is situated at 27° 33' S, 32° 41' E. Five samples of five quadrats each were collected here along a depth gradient.

The first sample [S 1] was shallow [0.5-1 m] and collected off Jesser Point in a sheltered rocky cove. The site is on the seaward side and exposed to a high disturbance from wave action and abrasion from sand. The substrate was sandy, interspersed with occasional boulders.

The second sample [S 2] was at Quarter Mile Reef [Koornhof 1995] 400 m north east of Jesser point. The site had an average depth of 6 m. There was no bare substrate at this sample, which was uniformly covered with turfs.

The third sample [S 3] was at Pinnacles on Two-Mile Reef [Koornhof 1995] at an average depth of around 10 m. There was a high cover of live corals and sponges with the substrate being largely bioclastic sediment.

The fourth sample [S 4] was at Four Buoy on Two-Mile Reef [Koornhof 1995] at an average depth of 14.5 m. There was an increased occurrence of bare substrate but sand cover was low.

The fifth sample [S 5] was at Sponge Reef, on Two-Mile Reef [Koornhof 1995] and is the deepest site at around 27 m. It is a low lying reef that gently slopes from a sandy bottom with a high occurrence of bare substrate.

Leadsman Shoal [L and Le]

Here two samples of 5 quadrats each were collected in close vicinity but at two depths. Leadsman Shoal is found at 27° 55' S, 32° 36' E. Both were collected on relatively flat reefs where corals were present. The first sample was collected at an average of 10 m [Le] and the second at an average of 17 m [L].

### Cape Vidal [V]

This site was snorkelled and all 5 quadrats were from 1 to 2 m deep. The quadrats were collected on the inside of the point and thus protected from waves at low tide but exposed at high tide. The site is just to the south of the boat launching site at 28° 08' S, 32° 34' E.

### Maphelane [M]

This site was snorkelled and all 4 quadrats were from 1 to 2 m deep. This sample was collected at Crayfish Point around 1.5 km south of Maphelane beach at 28° 25' S, 32° 25' E. They were collected on a shallow rocky gulley behind a ledge. Although the site is protected by the ledge there was a strong current flowing and only four quadrats could be collected before the incoming tide made the current too strong.

### Zinkwazi [Z]

This site was snorkelled at the point near Zinkwazi beach at 29° 17' S, 31° 26' E. The site was close to a sand patch and had a high percentage sand cover in the quadrats.

The site was dominated by sand-binding *Caulerpa filiformis*. Five quadrats were collected from 1 to 2 m.

### Umhlali [U]

This site occurs roughly in the centre of the Natal Bight at 29° 25' S, 31° 18' E. The site was collected at Prince Grant on broken patches of reef around 21 m deep. The site was covered with silt and a layer of sediment covered the sample area. The algal cover was low and visibility was poor. Six quadrats were scraped but one contained no turf or macro-algae and was thus excluded.

### Durban [D]

A single quadrat was collected at Blood Reef off the Bluff at 29° 53' S, 31° 03' E. The sample was collected at a depth of 17.4 m. Due to a strong surge and current only a single quadrat was collected before the dive was aborted.

### Aliwal Shoal [A]

Seven quadrats were collected from this large reef at depths of 17 to 23 m. The site is at 30° 17' S, 30° 48' E and was collected from an area known locally as Eel Skin Reef. The site was dominated by turf algae with interspersed larger seaweeds and a number of large sponges.

### Sampling methods:

Three Star-Odd ® temperature recorders were deployed at Sodwana Bay, Leadsman and Ballito [near Umhlali] all at a depth of 15 m. Temperatures were recorded from February 2003 to January 2004 at half hour intervals to an accuracy of 0.01 °C

Samples were collected using either snorkel or Scuba depending on the depth. A site refers to a specific area and a sample refers to a set of quadrats collected at a certain depth. For each sample it was aimed to collect five quadrats but due to diving conditions this was not always possible.

At each sample quadrats of 25 x 25 cm were placed haphazardly in algal stands. The area was scraped with a thin metal blade and all material placed into a fine mesh bag. Because the algae were usually small and unidentifiable *in situ*, the samples had to be collected destructively. For each quadrat, physical data was recorded onto a white slate using a pencil. Depth and distance to large areas of sand were recorded in metres. A large area of sand was considered to be a patch greater than 5 metres in diameter, both horizontal distance and vertical height above the sand was measured in order to get an absolute distance to the sand. The percentage cover of algae [excluding crustose algae], algal crusts and sand was estimated in each quadrat. The samples were preserved in a 5% formalin/seawater solution and stored in a bucket covered with a black plastic bag to reduce bleaching.

Each sample was later rinsed and placed into a large white sorting tray filled with water. The species were then separated and identified. Identification was done to species level where possible, otherwise to genus [Appendix I has a list of the 23 references used to aid in identification and Appendix II list of the species identified with authorities]. Each species was cleaned from sand and epiphytes, patted dry with paper towel and a wet weight recorded to an accuracy of 0.01g.

Voucher specimens of each species were preserved. Larger species were prepared as herbarium specimens and smaller species were mounted on microscope slides in a solution of corn syrup [Karo] and phenol to prevent fungal growths. If required the microscope specimens were stained with aniline blue to increase contrast. The voucher specimens have been placed in the Phycology Laboratory collection in the Botany Building at the University of Cape Town.

#### Analyses:

### Temperature:

Monthly averages were calculated by summing the half hourly values in each month divided by the number of recordings. The minimum and maximum temperature recorded for each month was noted. The mean monthly averages values were plotted
on a graph bounded by the minimum and maximum temperature for that month. Annual mean temperatures were calculated for each site by summing the monthly means and dividing this total by 12.

#### Ecological:

The data were compiled into Excel sheets for all biomass, presence/absence and environmental data. For each species the frequency [no. of quadrats recorded in] and total biomass for all sites was calculated. These were plotted on two separate graphs with each species represented by a number along the x-axis. Forty of the most abundant and frequent species for both data sets have been included in a table.

Using Statistica a number of statistical correlation analyses were done to investigate possible relationships between environmental and biological patterns. For each graph an r squared, r and p value was calculated.

The first physical factor to be investigated was depth, with biomass being plotted against depth. Species number, percentage algal cover, percentage sand cover and percentage algal crusts for all quadrats were also plotted against depth. Using biomass data, the percentage of upright calcified algae was calculated for each quadrat and this was then also plotted against depth. Percentage upright calcified algae included all species that calcify their thallus to some extent and not just articulated corallines. Crustose algae were not included in this analysis.

Using a simple hypotenuse formula the total distance to sand [for each quadrat] was calculated combining the vertical and horizontal distances measured.

Total distance = 
$$\sqrt{[V^2 + H^2]}$$

Where: V = vertical distance

H = horizontal distance

This was then plotted against species numbers, biomass per quadrat and percentage calcified erect algae to investigate the effects of sand.

The number of species per quadrat was then plotted against the biomass per quadrat to reveal any relationship between biomass and diversity.

Similarities between quadrats at the same sites were calculated by dividing the number of shared species by the number of species in the quadrat with fewest species [Schils *et al.* 2001]. A histogram was plotted of the similarity values between quadrats within each sample. A second histogram of the average similarity for each sample was also plotted.

The average number of species and biomass per quadrat was calculated for all sites. These have been placed in bar graphs to investigate the differences between deep and shallow sites along the coastline of KwaZulu-Natal. These graphs always show the northernmost sites on the left going south along the x-axis.

To compare the distribution of different algal phyla along the coast and at varying depth, the average number and biomass of green, brown and red algae were calculated. This was calculated as a percentage of the total number of species or biomass per quadrat per site. These values were placed in bar graphs with the shallow and deeper samples separated, but still arranged from north to south along the x-axis.

## **Biogeography:**

#### **Diversity:**

Beta Diversity was calculated using the formula of Wilson & Shmida [1984]. This formula calculates the degree of change in species composition along an environmental gradient, with a maximum of 1 indicating a complete species turnover.

$$\beta = [Gs + Ls]$$
2S

Where,

 $\beta$  = Beta Diversity;

Gs = Number of species gained along a gradient;

Ls = Number of species lost along a gradient;

S = Mean sample richness of both samples along the gradient.

Firstly the five samples from Sodwana were placed into a table to show the changeover in species composition along a depth gradient. At each depth all five quadrats were combined into a single list to calculate Beta Diversity. Then for the whole data set in this study, all the sites of similar depths were compared for shallow samples [<5 m] and deeper samples [15-20 m] to investigate the change in species composition along a latitudinal gradient along the coastline of KwaZulu-Natal within these depth classes. Quadrats were combined for each sample, but as some samples only had four quadrats, only the first four sampled were used from other sites with five quadrats.

## Detrended Correspondence Analysis [DCA]:

It is difficult to easily visualise the relationship between samples that have a number of species as it would require as many axes as there are species. DCA is an indirect ordination of the quadrats used to analyse the species data independently of the environmental factors. DCA examines the similarity or dissimilarity of the floristic composition of the quadrats. The DCA is displayed as a plot where each point represents a quadrat and the distance between the points reflects their degree of similarity or difference. The Community Analysis Package Ver. 2.0 [Pisces Conservation Ltd] was used to calculate these analyses: for further information on this method consult Kent & Coker [1992]. Two DCA plots were constructed, one using biomass data and the other presence-absence data for all quadrats.

#### Canonical Correspondence Analysis [CCA]:

CCA is an ordination technique that uses both the biological and environmental data to construct a plot. Thus CCA is a restricted correspondence analysis where the quadrat axis scores are constrained by the environmental variables [Kent & Coker, 1992]. The analyses were performed using the programme ECOM Ver. 1.3 [Pisces Conservation Ltd]. Each axis was given an eigen value and a Monte-Carlo randomization test with 1000 trials was undertaken to calculate the probability for an axis that the observed magnitude of the eigen value could occur by random chance: a standard 5 % confidence limit was used. The first CCA used the biomass data for all quadrats, with sites at species centroids being selected. The environmental data used were percentage cover of sand, algal cover and depth. The second analysis used the same biological data but used latitude in place of percentage sand. Latitude was used as a surrogate for the temperature gradient along the KwaZulu-Natal coast since temperature decreases from north to south [Fig 1.3]. These two analyses were repeated using presence-absence data for all quadrats.

#### **TWINSPAN** analysis:

TWINSPAN [Two Way Indicator Species Analysis] is a hierarchical clustering method used mainly for vegetation analysis to show the relationship between samples. The Community Analysis Package Ver. 2.0 [Pisces Conservation Ltd] was used to calculate these analyses. The TWINSPAN analysis used, ordinates the samples using reciprocal averaging [RA]. The first TWINSPAN was drawn using the biomass data with the frequency option being selected. A second TWINSPAN analysis used presence-absence data and the presence-absence option was selected; the other options were left as standard.

# Chapter 3: Results

The entire data base consisted of 71 quadrats covering a total area of  $4.44 \text{ m}^2$ . A total of 294 taxa were identified [of which 50 could not be identified to species level], dominated by the Rhodophyta [77.9%] with the remainder from the Chlorophyta [12.2%], Phaeophyta [9.9%] and a single angiosperm, the seagrass *Thalassodendron ciliatum*. A total biomass of 2420.8 g was recorded from all the quadrats. The biomass was more evenly distributed between the algal divisions, with Rhodophyta [39.6%] and Phaeophyta [35.2%] having similar amounts and Chlorophyta [25.2%] contributing the least of the total biomass. The majority of the quadrats were dominated by a short layer of interwoven turf algae with the occurrence of some large algae.

## **Temperature:**

The temperature data for Sodwana, Leadsman and Ballito are presented below. Samples were taken close to each of these recorders and they present a gradient around the St. Lucia region where a biogeographical pattern has been identified in intertidal species [Sink 2001, Bolton *et al.* 2004]. Ballito is the southernmost recorder and is found in the Natal Bight just south of the Umhlali site.

Temperatures at Sodwana and Leadsman were very similar for the entire year shown, with monthly means never dropping below 20 °C [Fig 3.1 and 3.2]. Sodwana had an annual average of 24.2 °C and Leadsman 24.1 °C. Sodwana ranged from a highest monthly mean temperature of 27.1 °C in March to 21.1 °C in September and Leadsman ranged from 27.2 °C in February to 21.2 °C in September. The range between minimum and maximum temperatures recorded per month was generally small. The most noticeable difference between these two sites is the large drop in minimum temperature in September at Sodwana and June at Leadsman. Ballito had an average annual temperature of 22.2 °C. This site showed an overall lower temperature compared to the first two sites for the entire year [Fig 3.3]. Ballito had a mean maximum of 25.3 °C in March and a minimum of 19.5 °C in August. The range

between minimum and maximum temperatures had a large variance from Jan to May with the largest range of 7 °C in March [27.5 °C to 20.5 °C].



**Fig 3.1** Monthly temperatures for Sodwana Bay [15 m deep] for the period beginning in February 2003 to January 2004. The middle line represents mean monthly average, the top line is the maximum temperature recorded for that month and the bottom line is the minimum temperature recorded for that month.



**Fig 3.2** Monthly temperatures for Leadsman Shoal [15 m deep] for the period beginning in February 2003 to January 2004. The middle line represents mean monthly average, the top line is the maximum temperature recorded for that month and the bottom line is the minimum temperature recorded for that month.



**Fig 3.3** Monthly temperatures for Ballito [15 m deep] for the period beginning in February 2003 to January 2004. The middle line represents mean monthly average, the top line is the maximum temperature recorded for that month and the bottom line is the minimum temperature recorded for that month.

#### **Ecological:**

Figure 3.4 shows that most species were only found in a few quadrats, with 251 species [85.4%] found in less than 10% [7] of the quadrats and 179 species [60.9%] found in less than 5 % [3] of the quadrats. Figure 3.5 illustrates a similar trend with only a few species contributing any significant amount of biomass, with 255 species [86.7%] contributing less than 10 g and 190 species [64.6%] contributing less than 1 g of biomass. Table 3.1 shows the 40 species with the highest frequency and the 40 species which contributed the greatest biomass. 16 species from Table 3.1 occurred in both columns [Table 3.2].



Figure 3.4 Frequency each species was recorded in the data set [n = 71].



Figure 3.5 Total biomass for each species recorded from all the quadrats sampled.

	Biomass		No. of
Species	[g]	Species	quadrats
Caulerpa filiformis	499.13	Lobophora variegata	40
Halimeda cuneata	247.26	Hypnea spinella	34
Zonaria subarticulata	178.01	Champia compressa	30
Lobophora variegata	145.84	Jania ungulata	30
Rhodymenia natalensis	98.50	Dictyopteris delicatula	26
Dictyopteris ligulata	96.26	Jania adherens	23
Tricleocarpa cylindrica	94.50	Halimeda cuneata	19
Arthrocardia carinata	60.46	Chondria simpliscula	17
Digeneopsis subopaca	56.42	Gelidium reptans	17
Jania adherens	54.23	Amphiroa rigida	15
Padina tetrastromatica	48.54	Heterosiphonia arenaria	15
Haliptilon subulatum	45.53	Cheilosporum sagittatum	14
Galaxaura obtusata	44.90	Dictyopteris ligulata	14
Jania intermedia	44.22	Arthrocardia carinata	13
Thalassodendron ciliatum [Seagrass]	37.00	Chondria dasyphylla	13
Codium incognitum	27.30	Dasya scoparia	13
Amphiroa ephedraea	26.41	Dictyota sp.	13
Feldmannia irregularis	24.94	Gloiocladia iyoensis	13
Peysonnelia capensis	24.62	Griffithsia confervoides	13
Amphiroa rigida	24.32	Pachychaeta cryptoclada	13
Dictyota humifusa	20.18	Pseudocodium de-vriesii	13
Galaxaura deisingiana	18.98	Heterosiphonia crispa	12
Callophycus densus	18.80	Dictyota ceylanica	11
Pachychaeta cryptoclada	18.79	Amphiroa bowerbankii	10
Hypnea specifera	18.75	Chondria sp 1.	10
Padina gymnospora	17.25	Gelidium sp 1.	10
Dictyopteris delicatula	17.10	Griffithsia japonica	10
Pseudocodium de-vriesii	17.07	Hypnea rosea	10
Hypnea musciformis	16.50	Pterosiphonia spinifera	10
Chondria sp 1.	15.64	Caulerpa scalpelliformis	9
Gelidium sp 1.	15.62	Ceramium arenarium	9
Osmundaria serrata	15.58	Herposiphonia secunda	9
Metamastophora flabellata	15.04	Hypnea tenuis	9
Hypnea spinella	14.11	Nienburgia serrata	9
Amphiroa bowerbankii	14.00	Acrosorium acrospermum	8
Amphiroa beauvoisii	13.64	Dasyclonium incisum	8
Rhodomelopsis africana	11.62	Haliptilon subulatum	8
Ceramiaceae indet	11.41	Herposiphonia falcata	8
Gracilaria corticata	11.29	Hypnea arenaria	8
Caulerpa scalpelliformis	8.74	Jania intermedia	8

**Table 3.1** The first 40 species from Fig 3.4 and Fig 3.5 recording high biomass values and occurring in more quadrats respectively.

Species:			
Amphiroa bowerbankii	Amphiroa rigida	Arthrocardia carinata	Caulerpa scalpelliformis
Chondria sp 1.	Dictyopteris delicatula	Dictyopteris ligulata	Gelidium sp 1.
Halimeda cuneata	Haliptilon subulatum	Hypnea spinella	Jania adherens
Jania intermedia	Lobophora variegata	Pachychaeta cryptoclada	Pseudocodium de-vriesii

Table 3.2 The species that were recorded for both biomass and frequency in Table 3.1.

Figure 3.6 shows a significant negative relationship between biomass and depth. There are however two noticeable outliers that could be skewing the graph. But even when these are removed a significant negative relationship is still found, with an improved probability level [Fig 3.7]. Both these graphs show a high variability in the first 5 m. Although highly variable for the first 5m, there is a significant linear decrease of species numbers with an increase in depth [Fig 3.8].







Depth [m] Figure 3.7 Modified graph of Figure 3.6 excluding outliers [ $r^2 = 0.25$ ; r = -0.50; p < 0.00001]. 95% confidence limits have been plotted with the dotted line.



The percentage algal cover recorded within each quadrat had a significant negative relationship with depth [Fig 3.9]. The percentage red algae biomass shows a slight increase with depth but is variable and therefore not significant [Fig 3.10]. The percentage sand cover and percentage of crustose algae was not influenced by depth [Fig 3.11 and Fig 3.12]. The percentage of erect calcified algal biomass decreases significantly with depth [Fig 3.13] but with the first 5 m being most variable.



**Figure 3.9** Visible algal cover of each quadrat versus depth  $[r^2 = 0.45; r = -0.67; p < 0.0001.]$ .



**Figure 3.10** Percentage red algal biomass per quadrat against depth  $[r^2 = 0.01; r = 0.12; p = 0.3336.]$ .



**Figure 3.11** Percentage sand cover within each quadrat versus depth  $[r^2 = 0.02; r = 0.12; p = 0.2994.]$ .



Figure 3.12 Percentage crustose algal cover within each quadrat versus depth  $[r^2 = 0.01; r = 0.02; p = 0.8997.]$ .



Figure 3.13 Percentage of erect calcified algae biomass per quadrat versus depth [ $r^2 = 0.09$ ; r = -0.29; p = 0.0141.].

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There is no relationship between the percentage of erect calcified algal biomass and the total distance to the nearest large area of sand [Fig 3.14]. The distance to sand does not affect the species number per quadrat [Fig 3.15] or the biomass per quadrat [Fig 3.16].



Figure 3.14 Percentage of calcified algal biomass within each quadrat versus distance to sand  $[r^2 = 0.01; r = -0.02; p = 0.8675.]$ .



**Figure 3.15** Species number per quadrat versus total distance to sand  $[r^2 = 0.01; r = -0.09; p = 0.4661.]$ .



Fig 3.17 shows no relationship between species number and biomass per quadrat.

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Species number **Figure 3.17** Relationship between species number [diversity] and biomass per quadrat [ $r^2 = 0.01$ ; r = 0.03; p = 0.8034.].



Figure 3.18 Frequency histogram showing the similarity between quadrats of the same sample, for all samples.





Both histograms [Fig. 3.18 and Fig. 3.19] show that the quadrats have a peak similarity between 30 -50%. Umhlali had the lowest average similarity of 22.6%, while the highest was found at Sodwana sample 3 and 4 with 62.2% and 71.6% respectively.

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**Figure 3.20** Average species numbers per quadrat for all the shallow samples [< 10 m] with standard deviation illustrated. The samples are arranged from north to south along the x-axis



**Figure 3.21** Average number of species per quadrat for all the sites deeper than 10 m with standard deviation illustrated. The sites are arranged from north to south along the x-axis.

The most species rich samples were Lala Nek [34.4 species per quadrat] and Maphelane [35 species per quadrat] from the shallow samples while both Leadsman samples [L 19.8 and Le 24.8 species per quadrat] samples and Aliwal [19.4 species per quadrat] were the richest in species from the deeper samples [Fig. 3.20 and 3.21]. Umhlali [7.6] averaged the least species per quadrat. The overall average for species numbers per quadrat was 17.8, while the average for the shallow samples was 21.6



and 15.2 for the deeper samples. In Fig 3.21 it is interesting to note that the three Sodwana samples [S 3, S 4 and S 5] have similar species numbers.

**Figure 3.22** Average biomass per quadrat for the shallow samples [<10m] with standard deviation illustrated. Samples arranged from north to south along the x-axis.



**Figure 3.23** Average biomass per quadrat for all samples deeper than 10m with standard deviation illustrated. The samples are arranged from north to south along x-axis.

In Fig 3.22 Zinkwazi is shown to have a much larger biomass compared to the other shallow sites. This was due to the presence of a high biomass of the large seaweed *Caulerpa filiformis*. Similarly in Fig 3.23 Aliwal had a larger biomass compared to the other deeper samples due to a high occurrence of *Zonaria subarticulata*. The overall average biomass per quadrat was 32.98 g, while the average was 61.24 g for the shallow samples and 14.14 g for the deeper samples.



**Figure 3.24** Percentage composition of red, green and brown algal species number per quadrat per sample. The samples are arranged from north to south with samples deeper than 10 m on the right.



**Figure 3.25** Percentage biomass for red, green and brown algae for each site per quadrat. The samples are arranged from north to south along the x-axis with samples having a depth greater than 10 m on the right.

All the samples were dominated by the proportion of red species found in the quadrats [Fig 3.24]. This trend did not show always with the percentage of biomass per quadrat [Fig 3.25]. Some of the deep sites [E, S3, S4, S5 and A] had a small percentage of brown species but these contributed a large amount of the total biomass. Zinkwazi only had a few species of green algae but this dominated the biomass due to the presence of *Caulerpa filiformis*. The graph also shows that there is almost no brown algae in the Bight [Zinkwazi, Umhlali and Durban].

#### **Biogeography:**

#### Beta Diversity:

The Beta Diversity values show that there is a change in species composition along a depth gradient [Table 3.3], with the largest change occurring between the shallowest sample [S 1] and the other depths.

Tables 3.4 and 3.5 show there is a consistent difference in species composition between samples with all the values being between 0.28 and 0.46. There is no discernable pattern in the variability of Beta Diversity along the coast.

	S1	S2	S3	S4	S5
S1					
S2	0.340				
S3	0.340	0.232			
S4	0.347	0.220	0.232		
S5	0.371	0.300	0.286	0.300	

**Table 3.3:** Beta Diversity calculated between the samples of different depths at Sodwana.

**Table 3.4:** Beta Diversity of samples with a depth of around 15 to 20m. In order of latitude with the northernmost sites first.

	E	S4	L	U	A	
E						
S4	0.422					
L	0.339	0.370				
U	0.425	0.439	0.431			
A	0.400	0.404	0.356	0.375		

	La	S1	V	М	Z
La					
S1	0.407				
V	0.363	0.400			
М	0.277	0.421	0.345		
Z	0.394	0.457	0.409	0.339	
			1		

**Table 3.5:** Beta diversity of shallow samples [<5m] arranged from northern most along the coast. The values were calculated using four quadrats, as Maphelane only had four quadrats.

## Detrended Correspondence Analysis:

The DCA using biomass [Fig 3.26] showed three rough groupings, indicated by the dotted lines. The central group is from mostly northern sites dominated by Sodwana quadrats with the exception of Zinkwazi and some southern Umhlali quadrats. The group on the right are deeper quadrats mainly from southern sites and dominated by the Aliwal quadrats. The third group on the left is a mixture of mainly shallow quadrats from the north, including samples from Vidal, Maphelane, Sodwana and Lala Nek.



**Figure 3.26** DCA plot using biomass data for all quadrats. The x-axis had a sample score of 0.93 and the y-axis had a sample score of 0.86.

The DCA using presence-absence data [Fig 3.27] shows roughly four groups, indicated by the dotted lines. The top group is from the southern sites Aliwal. The group on the right is a cluster from the Sodwana quadrats. The bottom grouping is a mixture of most of the Leadsman quadrats [L and Le]. The left group is composed from mainly the shallow sites [La, M, V and Z] excluding the Sodwana shallow quadrats.



**Figure 3.27** DCA plot using presence/absence data for all quadrats. The x-axis has a sample score of 0.66 and the y-axis had a sample score of 0.49.

#### Canonical Correspondence Analysis:

In Fig 3.28 the first CCA using biomass data suggests that depth is the strongest factor affecting the grouping of the quadrats, while percentage sand and algae separate the quadrats in opposite directions. In this graph the x-axis is representing a depth gradient while the y-axis is separating the quadrats in opposite directions by the percentage covers of algae and sand. The Monte Carlo randomization showed depth to be significant [p < 0.0001], while percentage sand and algae had p > 0.05. When percentage sand is replaced by latitude [Fig 3.29] it has a larger effect on the grouping than percentage sand but depth is still the strongest factor, and all three factors have a Monte Carlo p < 0.01. Again the x-axis is showing a depth gradient while the y-axis shows a latitudinal gradient.

When the presence-absence data is used for the CCA [Fig 3.30 and 3.31] the first noticeable difference is that the eigen values are much weaker than the values for the biomass data. Depth is still a strong factor but latitude is stronger when included in the analysis, but they do not separate the sites in opposite directions. In Fig 3.30 only the percentage sand had a p > 0.05. While in Fig 3.31 all three factors had p < 0.01. Fig 3.31 shows the southern samples [A, D, U and Z] being separated from the north sites.



**Figure 3.28** CCA for all sites biomass data using sites as species centroids. The environmental data used for this plot was depth, percentage algal cover and percentage sand cover per quadrat. The canonical eigen values were 0.88 for depth, 0.55 for percentage algae and 0.35 for percentage sand.



**Figure 3.29** CCA for all sites biomass data using sites at species centroids. The environmental factors used were depth, percentage algal cover and latitude. The canonical eigen values were 0.88 for depth, 0.84 for latitude and 0.50 for percentage algae.



**Figure 3.30** CCA for all sites using presence absence data and sites at species centroids. The environmental constraints used are percentage sand cover, percentage algal cover and depth. The canonical eigen values were 0.48 for depth, 0.30 for percentage algae and 0.19 for percentage sand.



**Figure 3.31** CCA using presence absence data and sites at species centroids. The environmental data used was percentage algal cover, latitude and depth. The canonical eigen values were 0.506 for latitude, 0.443 for depth and 0.2321 for percentage algae.

#### **TWINSPAN Analysis:**

Twinspan plots were drawn for both biomass and presence-absence data. Fig 3.32 using biomass data has all the Sodwana quadrats in group B, there is a close association between the shallowest quadrats [S11-15] and some of the deeper quadrats [S31, S53 and S55], with a another deep quadrat being linked to this group [S51]. All the intermediate depth Sodwana quadrats are linked in a large group, and associated with the remaining deep quadrats [S52 and S54].Both Leadsman samples [L and Le] and some Rocktail quadrats [E2 and E 4] were closely linked with Sodwana in group B. The shallow samples were all linked in group C [excluding S1], but with Zinkwazi separated out due to the presence of *Caulerpa filiformis*. The top group [A] was made up of quadrats south of St. Lucia with the exception of Le 3.

Fig 3.33 [using presence-absence data] again shows a close association of the Sodwana samples in group B. However the shallow and deep Sodwana quadrats are separated, with the remaining intermediate depths lumped into one group. Both Leadsman samples [L and Le] are closely associated with the Sodwana sites [Group C]. The remaining shallow samples form a group with some of the deeper Rocktail quadrats [E1, E3 and E 4]. Zinkwazi is again separated from this group due to the presence of *Caulerpa filiformis*. The remaining quadrats found in group A and group F are from samples south of the St. Lucia region.



**Figure 3.32** Twinspan analysis of all the quadrats using biomass data. The species indicated at each branch show the change to the bottom group with a positive sign indicating the addition of the species and a minus the loss of that species.



**Figure 3.33** Twinspan analysis of all the quadrats using presence-absence data. The species indicated at each branch show the change to the bottom group with a positive sign indicating the addition of the species and a minus the loss of that species.

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# **Chapter 4: Discussion**

#### **Temperature:**

The temperature data for Sodwana and Leadsman were highly similar for the entire year [Fig 3.1 and Fig. 3.2] with Sodwana having an annual mean of 24.2 °C and Leadsman 24.1 °C. The monthly means never fell below 20 °C and by Lüning's definition are tropical [Lüning 1990]. Ballito showed a decrease in temperature of between 2-3 °C with an annual average of 22.2 °C [Fig 3.3]. The monthly mean fell below 20 °C during August and was just above it for September and October, indicating that this site is by definition not tropical. The large difference between maximum and minimum recorded temperature is due to the topographically-induced upwelling over the Natal Bight [Lutjeharms *et al.* 2000]. The temperature data shown here indicate that there is a clear temperature disjunction around St. Lucia between the northern region with its narrow continental shelf and below where the Bight is influenced by upwelled cooler waters.

#### **Ecological:**

The subtidal algal communities in KwaZulu-Natal are dominated by turfs. These algal turfs are common components in intertidal and subtidal communities globally and are not characterised by defining diagnostic species but by their recognisable short, dense, tangled growth form [Stuercke & McDermid 2004]. The diversity found was extremely high with 294 species being recorded in a total area of less than 4.5m<sup>2</sup>. This is a high portion [57.9%] of the total species [508] currently recorded for KwaZulu-Natal [Anderson & Bolton 2005]. The number of species recorded in this study is greater than the entire recorded flora of many countries with long coastlines e.g. Namibia [196 species] [Lluch 2002].

Fig 3.4 and 3.5 showed that most of the species were found in a few quadrats and very few were found to contribute a significant biomass. This is characteristic of turf algae which have high proportions of rare species [Scott & Russ 1987, Stuercke & McDermid 2004]. Scott & Russ [1987] in a study on the Great Barrier Reef found

63% of their species to be rare, which they defined as occurring in less than five of the total 72 coral blocks sampled. In comparison 225 species [76.5%] were found in five or less quadrats and 207 species [70.4%] were found in four quadrats or less, indicating that the there is a higher incidence of rarity in the KwaZulu-Natal algae. The rarity was more pronounced in the biomass data [Fig 3.5] with 64.6% of the species contributing less than 1 g of wet weight from a total of 2420.8 g biomass. The slope of Fig 3.5 is most likely very characteristic of a community dominated by turf algae with a sharp decline in species contributing significant amounts of biomass and a long 'tail' of species with low biomass. The majority of species that contributed large amount of biomass are from genera that are calcified or have chemical defences against herbivory [e. g. *Halimeda, Zonaria, Lobophora, Arthrocardia and Jania*].

The quadrats were dominated by the red algae Rhodophyta species [77.9%] similar to other studies in tropical regions [Scott & Russ 1987, Stuercke & McDermid 2004], and generally made up of an interwoven mat of small filamentous or foliose algae with a few larger species interspersed. The distribution of the biomass among the algal phyla was more even, with Rhodophyta [39.6%] and Phaeophyta [35.2%] contributing near equal amounts. This is due to the red algae having a high proportion of small filamentous genera [e. g. *Ceramium, Dasya, Antithamnion, Griffithsia, Herposiphonia* and *Heterosiphonia*], and the Phaeophyta having a number of large genera with chemical defences against herbivory like *Dictyota, Lobophora, Padina* and *Zonaria.* 

Turfs generally are not calcified, but in Table 3.2, six of the species that were recorded in the top forty species for biomass and frequency are articulated corallines which indicates they can be locally important, particularly in the first 5 m of depth, due to their defence against herbivory and mechanical damage.

Among the environmental factors examined in this study, the most important and noticeable factor affecting the algal communities along the KwaZulu-Natal coast is depth. Increasing depth was shown to reduce biomass, species diversity and algal cover significantly [Fig 3.6, 3.7, 3.8 and 3.9]. This could be attributed to the decrease in light available to algae as depth increases. Light is plentiful is the shallower depths and thus photosynthesis and production will be high. Although at the deeper sites

there is still sufficient light for macro-algae to survive, production will decrease and may reduce the competitive ability of the algae leading to a decrease in algal cover. Due to competition with sessile animals that do not require light, and seaweeds having a lower tolerance to herbivory, there is often an increase in sedentary suspension feeding organisms like sponges.

# The first hypothesis is thus proved correct with both algal biomass and number of species per quadrat decreasing with depth.

In tropical areas, herbivory is considered to be greatest in the shallow subtidal [2 - 5 m] where the greatest bulk of herbivorous species are present [Abbott 1999]. It was hypothesised in the present study that larger algae would be more common outside these depths, but this trend was not found [Fig 3.6]. Although grazing is highest in the shallow subtidal there are still grazers present in the deeper waters and the decreased light availability prevents the growth of large macro-algae.

Fig. 3.10 showed no variation in the proportion of biomass made up by red algae as depth increased. The result was highly variable and the composition of the quadrats by algal phyla is independent of depth. If a trend of algal phyla dominance changing with depth is to be observed it is most likely to be seen in clear water at much greater depths than those sampled in this study.

Although the cover and biomass of upright algae decreased with depth, there was no corresponding increase in crustose coralline cover [Fig 3.12], indicating that this group were not exploiting this niche. Similar results obtained in Australia on the Great Barrier Reef, showed the importance of crustose corallines decreased with increasing depth [Klumpp & McKinnon 1989]. The percentage cover of crusts and sand within the quadrats was low [Fig 3.11 and 3.12]. This was most likely partly influenced by how the quadrats were placed in algal beds, implying a bias in not selecting areas with a high cover of crusts or sand. However, at all depths algal stands were selected so some comparison is valid. Depth did not have an influence over these variables and they are more likely controlled by other factors. Local conditions are more likely to influence sand cover like river inflow and water motion. High levels of herbivory can result in a shift from a turf community to one dominated by crusts, whose flat

structure provide protection from the scraping mode of grazing used by most herbivores [Littler & Littler 1988, Cheroske *et al.* 2000].

# The fourth hypothesis is shown to be incorrect with crustose algae not increasing with depth and indicating that the competition between crustose and foliose algae is more complicated.

Some algae calcify their thallus as a defence mechanism providing protection from mechanical damage like grazing, sand scour and wave shock. This results in a lower production rate and the calcified algae are generally abundant in shallow turbulent waters [Lewis 1981, Littler & Littler 1988]. The percentage of erect calcified algal biomass was investigated to see if these algae were more abundant in the shallow waters, where grazing is likely to be highest [Abbott 1990], or if distance to sand and subsequent sand scour promoted this growth form. Although highly variable in the first few meters the calcified forms did decrease significantly with depth [Fig 3.13]. A combination of water motion, herbivory and light all decreasing with depth contributing to this trend. Calcified algae invest much of their carbon uptake into physical protection and thus require high light and nutrient levels to be competitively strong. High water motion reduces the boundary layer making nutrients available to the calcified thallus while high herbivory favours this growth form. Distance to sand did not influence the calcified forms at all [Fig 3.14], or have any effect on species number and biomass [Fig 3.15 and 3.16]. It was thought that quadrats close to large areas of sand would be influenced by high levels of sand inundation and scour. However, this was not seen, possibly due to the actual mechanisms for sand inundation and scour being more complex. For example, water motion and dynamics are more likely to have a greater effect on sand motion, and sand is generally abundant and sufficiently close to most subtidal areas on this coast.

# The second hypothesis was shown to be incorrect. The distance to sand resulted in no significant finding and the effects of sand score are assumed to be more complex than a simple distance to sand measurement.

The effect of biomass and diversity was investigated in Fig 3.17. It was expected that at both low and high biomass the species richness would be low. At low biomass it

was expected there would simply be fewer species. At a large biomass a shift from a turf of intermixed species to one being dominated by a few larger algae was hypothesised, with larger species out-competing the smaller turfs through shading and mechanical damage, as has been shown by macro-algae reducing turf biomass by 28% [Cheroske et al. 2000]. However, there was no clear relationship, as most samples contained a high level of species richness even where low biomass was present. Umhlali was an exception but a high sediment load was apparently decreasing the diversity of both large and turf algae. Samples with low species numbers per quadrat were either deep or in the Natal Bight indicating that depth and sedimentation are the more important factors controlling species richness.

# The third hypothesis was shown to be incorrect. Biomass and species number did not have any significant effect on each other.

From all the data that included depth it is interesting to note that the first 5m, of the subtidal, is highly variable with higher biomass and species numbers than the deeper samples [Fig 3.20 and Fig 3.22]. The main reasons for this are thought to be the abundance of light and the increased water motion from wave action. High water motion reduces the effects of the boundary layer and allows more nutrients to pass over the algal thalli [Lüning 1990]. However, increased water motion can also increase mechanical damage and increase the effects of sand scour. Herbivory is also considered to be high at this depth [Abbott 1999]. The combination of these factors results in a highly variable and dynamic environment where turfs dominate. Turfs are promoted by large levels of disturbance, biological and physical, which reduce algal biomass and canopy heights but promote highly productive algae [Cheroske et al. 2000], but the effects are varying and not clearly predictable [Anderson et al. in press.]. Thus a highly productive and heterogeneous zone is formed, where competition is high amongst a number of sedentary animals and algae. I also think this zone is not stable, but is under constant change, where fast growing species are able to colonise new areas quickly and exploit different niches. A fast growth rate and high biomass turnover [Klumpp & McKinnon 1989] allows these species to persist despite the high levels of disturbance.

Quadrats at the same site were 30-50 % similar with respect to algal species [Fig 3.18 and 3.19]. This was calculated to see if the sampling intensity was sufficient. The low values indicates that sampling intensity was low. However to increase the number of quadrats is logistically not possible due to the turf component. The turfs are morphologically similar and time intensive to sort with most taxa only identifiable with a compound microscope. For these reasons few studies have documented taxonomic identities of the individual algal species or acknowledged the variability of the turf communities [Stuercke & McDermid 2004].

A comparison of the sites shows that the shallow samples had more species per quadrat [Fig 3.20 and 3.21] than deeper samples. Lala Nek [34.4 species per quadrat] and Maphelane [35 species per quadrat] were the most diverse shallow samples, while the Leadsman samples [19.8 and 24.8 species per quadrat] and Aliwal [19.4 species per quadrat] were the most diverse deeper samples. Umhlali [7.6 species per quadrat] was the least diverse site and is situated in the centre of the Natal Bight. Zinkwazi is also situated in the Bight but is not as adversely affected from high sedimentation rates. It is shallow so under the influence of wave motion and sufficient light countering some of the factors that make algal growth over the Bight poor [see next paragraph]. Zinkwazi had the highest biomass for the shallow sites due to the presence of Caulerpa filiformis. The site was very sandy and this sand binding species was able to dominate the site [Fig 3.22]. Aliwal had the highest biomass for the deeper samples [Fig 3.23]. Aliwal was dominated by Zonaria subarticulata a large Phaeophyta, but still retained an algal turf component. Fig 3.24 showed that the Chlorophyta were consistently found in shallow sites compared to deeper sites in terms of species numbers and that all sites were dominated by Rhodophyta species. The Chlorophyta possibly have high light requirements and occur in low frequencies in the shallow samples. In Fig. 3.25 is shown that the Phaeophyta contribute large amounts of biomass from a few species, these species are chemically defended from herbivory and thus able to grow into large macro-algae. It was expected that the green algae may increase towards the north as seen with intertidal species presence/absence data [Bolton et al. 2004] but this trend was not seen with the subtidal sites. Interestingly almost no brown algae were recorded in the Bight. The poor conditions over the Bight probably exclude them due to their greater demands to produce herbivory-resistant adaptations.

The region over the Bight is generally a poor area for algal growth, with a low average number of species [7.6 species] and biomass [2.19 g] per quadrat being recorded at Umhlali. A topographically-induced upwelling cell at the north end of the Bight forces cooler-nutrient rich waters onto the bight [Lutjeharms et al. 2000]. The widened shelf results in the waters on the shelf being retained by wind-driven currents for periods of time unlike further north where the Agulhas current washes the water southwards [Schumann 1988]. 99% mean annual simulated runoff for KwaZulu-Natal enters the sea below St. Lucia [2001] with the second largest river in South Africa, the Tugela, flowing directly onto the bight. The higher nutrient levels also result in planktonic growth which, combined with the runoff from rivers causes high sediment loads and turbid water. These factors tend to support a benthic community that is species-poor and adapted to these conditions [Anderson & Bolton 2005] These conditions are similar to the tropical West African Coast where the seabed is largely covered with sand, gravel or mud and poor light conditions create an environment that is not ideal for seaweeds [Lüning 1990]. This large area is also affected by large inflowing rivers during summer rainfall months and has a species-poor flora of around 300 species [Lüning1990].

#### **Biogeography:**

Beta diversity along a depth gradient at Sodwana showed an increase in change in species composition as depth difference increases [Table 3.3]. This again confirms the effects of depth on subtidal communities. The shallow sample [S 1] had a larger change in species composition compared to the other samples due to the high variability in the first 5 m. When comparing sites along the coast of similar depth the change in species composition does not increase as distance apart increases, contrary to what was expected. This was the same for both shallow and deeper samples [Table 3.4 and 3.5]. There is a consistent change in species composition between samples and Beta-Diversity was often above 0.4. This indicates that communities are highly localized and change rapidly over short distances. Beta diversity was lower between samples at one Sodwana site than those between sites indicating that there is a unique community composition at each site.
The DCA analysis showed the similarity between the shallow samples for both biomass and presence-absence data [Fig 3.26 and 3.27]. Both these graphs showed the association of the large number of Sodwana quadrats generally lumped together. The DCA using presence-absence data separated the groups out more clearly and the southern Aliwal quadrats formed a unique group that did not include any other sites [Fig 3.27]. Unlike the biomass data there was a close association between the two Leadsman samples which was expected, because they are only 7 m apart in depth and both were at intermediate depths.

The CCA analyses again showed depth to be an important factor controlling community structure. The shallow samples were separated out by the amount of algae and sand cover which are controlled by more localised factors. Latitude, which was used as a surrogate for the temperature gradient along the coast, also strongly influenced community structure. Therefore the main factors affecting subtidal seaweed community structure along the KwaZulu-Natal coast is depth [light] and sea water temperature regime [represented by latitude in this data set]. It is difficult to separate the effects of temperature and nutrients as they are closely linked along the South African coast [negatively correlated] making it difficult to analysis these factors separately. For both these graphs [Fig 3.28 and 3.29] the Zinkwazi and Aliwal samples formed unique groups site , which is due to the large biomass of *Caulerpa filiformis* at Zinkwazi while the large depths and high biomass of *Zonaria subarticulata* characterise the Aliwal samples. Fig 3.31 based on presence-absence data illustrates the separation of the southern samples from the northern samples indicating their biogeographical affinities.

When using biomass data the, Durban quadrat is often linked closely with the Umhlali and Aliwal sites [Fig 3.26, 3.28, 3.29 and 3.32]. Thus showing a close association of the sites south of the St. Lucia region. The one quadrat from Leadsman [Le 3] is an outlier from the other Leadsman quadrats and is often linked to the southern sites, Umhlali and Durban. This is due to the presence of *Amphiroa bowerbankii* and *Nienbergia serrata* from biomass data [Fig 3.32]. In Fig 3.33 the Aliwal quadrats and some of the Umhlali quadrats are linked due to the presence of *Zonaria subarticultata* and *Dasyclonium incisum*. These species are generally considered to be South Coast species. It is interesting to note in the TWINSPAN analyses the differences between the biomass data [fig 3.32] and the presence-absence data [Fig 3.33]. The biomass data shows the shallow Sodwana quadrats closely linked with the deepest Sodwana quadrats. Also the two Leadsman sites [L and Le] are very closely associated. The presence-absence data, however, shows the separation between the deep and shallow Sodwana quadrats, with the middle depths lumped together and the Leadsman sites [L and Le] closely associated as sister groups. I believe that often, due to the nature of the turf algae being highly diverse but markedly different with a few species having large relative biomasses, the presence-absence data gives a better indication of community structure than biomass data. The sampling method used in this study is not ideal for biogeographic analysis. A true biogeographic analysis looks at the total species present in an area compared to other areas. However due to the large turf component of the algal communities this sampling method was used and some inferences can be made from these.

The CCA and TWINSPAN analysis show the samples from the northern sites are closely linked and separated from the samples from the southern sites. The southern samples are not always placed together and sometimes placed in two groups [Fig 3. 29 and Fig 3.33]. This indicates the northern sites are floristically similar and most likely from the same biogeographical region, while the samples in the Bight and southwards are in an overlap area with a rapid turnover of species composition.

There is a general trend that the subtidal biota follows the general trend shown in the inter-tidal biota in that the northern regions have higher affinities to the Indo-West Pacific tropical region, and the southern regions have higher affinities to the South Coast flora, with the break occurring in the region of Cape St. Lucia. This is in agreement with the fifth hypothesis.

The study was limited in the amount of sites where samples were taken, the time intensive sorting and identification made it logistically difficult to add more samples. However a full sample at Durban would have improved the biogeographic analyses. In addition a shallow subtidal site in the region of Aliwal would have been good to include.

#### **Conclusion:**

This study provides the first description of the subtidal algal communities of KwaZulu-Natal and gives more insight into the poorly understood turf algal growth form. The seaweed communities of KwaZulu-Natal are extremely species rich. This richness is mainly attributed to the turf growth form that is morphologically similar but taxonomically diverse. The turfs are similar to those found in the tropics being dominated by red algal species and having a high proportion of rare species [Scott & Russ 1987, Stuercke & McDermid 2004].

Depth was found to be the most important factor affecting the algal communities as a direct result of light availability. Light has been found to decrease with depth at Sodwana in a separate study [Anderson *et al.* in press.]. The shallow subtidal was highly variable due to a number of disturbances acting on this zone. These disturbances favour the fast growing turfs but the effects are difficult to predict.

The temperature data indicate that the sites north of the Bight are tropical by definition. A drop of 2 - 3 °C on the Natal Bight results in some monthly means dropping below 20 °C and therefore not tropical by definition [Lüning 1990]. KwaZulu-Natal has been shown to be an overlap region from the temperate South coast to the Tropical Indo-West Pacific Flora from intertidal studies [Sink 2001, Bolton *et al.* 2004]. The Northern KwaZulu-Natal is the southern most extension of this tropical flora and is heavily under the influence of the warm Agulhas current. The CCA and TWINSPAN analyses showed the close association of the northern sites and supports the biogeography of the intertidal studies. The Natal Bight is a significant factor determining this biogeographic trend with a topographically-induced upwelling cell reducing the temperature with a rise in nutrients [Lutjeharms *et al.* 2000] as well as high sediments results in poor conditions for algal growth over the Bight.

Conservation often deals with the preservation of individual species or species-rich areas. If the turf component of the communities is not properly analysed it will lead to an underestimate of a regions diversity and conservation status. The Marine Protected Areas cover most of the KwaZulu-Natal coast but are focussed in the northern sections. The southern section being an overlap region should be monitored to assess changes caused by global warming and if more protected areas are planned then these should be placed in this area. The Bight has poor conditions for algal growth and a marine park is not necessary to preserve algal diversity. However further studies should monitor this region especially for anthropogenic effects. Turf algae are replacing canopy-forming algae along the Australian south coast due to increased nutrients and sediments from urban areas [Gorgula & Connell 2004], and similar effects could occur on the Bight where sedimentation is already high.

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## Appendix 1:

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# Appendix II:

## Angiosperms:

Thallassondendon ciliolatum [Forsskål.] den Hartog

## Chlorophyta:

Boodleopsis pusilla [Collins] W. R. Taylor, Joly & Bernatowicz Bryopsis plumosa [Hudson] C. Agardh Bryopsis africana Areschoug Bryopsis sp 1. Caulerpa brachypus Harvey Caulerpa cupressoides [Vahl] C. Agardh Caulerpa filiformis [Surh] Hering Caulerpa mexicana Sonder ex Kützing Caulerpa racemosa [Forsskål] J. Agardh Caulerpa scalpelliformis [R. Brown ex Turner] C. Agardh Caulerpa sp 1. Chamaedoris auriculata Børgesen Chamaedoris delphinii [Hariot] J. Feldmann & Børgesen Chlorodesmis hildebrandtii A. Gepp & E. Gepp Cladophora isaacii Simons Cladophora ordinata [Børgesen] van den Hoek Cladophora prolifera [Roth] Kützing Cladophora rugulosa G. Martens Cladophora sp 1. Cladophora vagabunda [Linnaeus] van den Hoek Codium extricatum P. Silva Codium incognitum P. Silva Codium mozambiquense P. Silva Codium pocockiae P. Silva Codium tenue [Kützing] Kützing

Dasycladus ramosous Chamberlain Gayralia oxysperma [Kützing] K. L. Vinogradova ex Scagel et al. Halimeda cuneata Hering Microdictyon krausii J. Gray Pseudocodium de-vriesii Weber-van Bosse Udotea indica A. Gepp & E. Gepp Udotea orientalis A. Gepp & E. Gepp Ulva flexuosa Wulfen Ulva sp 1. Valonia macrophysa Kützing

#### <u>Phaeophyta:</u>

Colpomenia sinuosa [Mertens ex Roth] Derbès & Solier

Dictyopteris australis [Sonder] Askenasy

Dictyopteris delicatula Lamouroux

Dictyopteris ligulata [Suhr] O. Schmidt

Dictyopteris serrata [Areschoug] Hoyt

Dictyota adnata Zanardini

Dictyota cervicornis Kützing

Dictyota ceylanica Kützing

Dictyota crispata Lamouroux

Dictyota dichotoma [Hudson] Lamouroux

Dictyota humifusa Hörning, Schuetter & Coppejans

Dictyota liturata J. Agardh

Dictyota sp 1.

Dictyota sp 2.

Dictyota stolonifera Dawson

Dictyota suhrii G. Murray

Feldmannia irregularis [Kützing] Sonder

Lobophora variegata [Lamouroux] Womersley ex Oliviera

Padina boryana Thivy

Padina gymnospora [Kützing] Sonder

Padina tetrastromatica Hauck Sargassum sp 1. Spatoglossum asperum J. Agardh Sphacelaria novae-hollandiae Sonder Sphacelaria rigidula Kützing Stoechospermum marginatum [C. Agardh] Kützing Stypopodium zonale [Lamouroux] Papenfuss Zonaria subarticulata [Lamouroux] Papenfuss Zonaria tournefortii [Lamouroux] Montagne

#### **Rhodophyta:**

Acanthophora sp 1. Acanthophora spicifera [Vahl] Børgesen Acrosorium acrospermum [J. Agardh] Kylin Acrosorium maculatum [Sonder ex Kützing] Papenfuss Acrosorium uncinatum [Agardh] Kylin Amansia loriformis R. Norris Amphiroa beauvoisii Lamouroux Amphiroa bowerbankii Harvey Amphiroa ephedrea [Lamarck] Pecaisne Amphiroa rigida Lamouroux Amphiroa sp 1. Antithamnion diminuatum Wollaston Antithamnion diminuatum Wollaston var. polyglandum Stegenga Antithamnion eliseae R. Norris Antithamnion hubbsii Dawson Antithamnion lherminieri [P. Crouan & H. Crouan] Bornet ex Nasr Antithamnion secunda Gardner Antithamnionella tasmanica Wollaston Apoglossum spathulatum [Sonder] Womersley & Shepley Aristothamnion callithamnioides Joly & Ugadim Arthrocardia carinata [Kützing] Johansen Arthrocardia corymbosa [Lamarck] Decaisne

Arthrocardia filicula [Lamarck] Johansen Arthrocardia flabellata [Kützing] Manza Arthrocardia sp 1. Balliella crouanioides [Itono] Itono & Tanaka Balliella sp 1. Botryocladia beckeriana [Holmes] Papenfuss Botryocladia skottsbergii [Børgesen] Levering Callithamnion hookeri [Dillwyn] S. F. Gray Callithamnion sp 1. Callithamnion sp 2. Callithamnion stuposum Suhr Callithamnion tripinnatum C. Agardh Callophycus densus [Sonder] Kraft Carpopeltis maillardii [Montagne & Millardet] Chiang Carpopeltis phyllophora [J. Hooker & Harvey] Schmitz Carpopeltis sp 1. Centroceras clavulatum [C. Agardh] Montagne Ceramium arenarium Simons Ceramium camouii Dawson Ceramium codii [Richards] Mazoyer Ceramium dawsonii Joly Ceramium glanduliferum Kylin Ceramium obsoletum C. Agardh Ceramium sp 1. *Ceramium* sp 2. Ceramium subdichotomum Weber-von Bosse Ceramium tenerrimum [G. Martens] Okamara Chamaebotrys boergesenii [Weber-van Bosse] Huisman Champia compressa Harvey Champia lumbricalis [Linnaeus] Desvaux Champia parvula [C. Agardh] Harvey Champia somalensis Hauck Champia sp 1. Chauviniella jadinii [Børgesen] Papenfuss

Cheilosporum cultratum [Harvey] Areschoug Cheilosporum multifidum [Kützing] Johansen Cheilosporum sagittatum [Lamouroux] Areschoug Chondria armata [Kützing] Okamura Chondria collinsiana Howe Chondria compressa Papenfuss Chondria dangeardii Dawson Chondria dasyphylla [Woodward] C. Agardh Chondria minutula Weber-van Bosse Chondria simpliciuscula Weber-van Bosse Chondria sp 1. Chondria sp 2. Corallina sp 1. Crouania attenuata [C. Agardh] J. Agardh Crouania francescoi Cormaci, Furnari & Scammacca Dasya baillouviana [S. Gmelin] Montagne Dasya echinata Stegenga, Bolton & Anderson Dasya flagellifera Børgesen Dasya scoparia Harvey Dasya sp 1. Dasya sp 2. Dasya stanleyi [Weber-van Bosse] Millar Dasyclonium incisum [J. Agardh] Kylin Dasysiphonia chejuensis I. K. Lee & J. A. West Delesseria sp 1. Delesseria sp 2. Delesseria sp 3. Delesseria sp 4. Digenia simplex [Wulfen] C. Agardh Diplothamnion gordoniae Huisman

Eucheuma denticulatum [Berman] Collins & Hervey

Eucheuma odontophorum Børgesen

Euptilota fergusonii Cotton

Falkenbergia hillebrandii [Bornet] Falkenberg

Galaxaura diesingiana Zanardini Galaxaura marginata [Ellis & Solander] Lamouroux Galaxaura obtusata [Ellis & Solander] Lamouroux Galaxaura sp 1. Gelidiella lubrica [Kützing] J. Feldmann & G. Hamel Gelidiella sp 1. Gelidiopsis repens [Kützing] Weber-van Bosse Gelidiopsis sp 1. Gelidiopsis sp 2. Gelidium caespitosum Kylin Gelidium reptans [Suhr] Kylin Gelidium sp 1. Gelidium sp 2. Gelidium sp 3. Gloiocladia ioyensis [Okamura] R. Norris Gracilaria canaliculata Sonder Gracilaria capensis Schmitz ex Mazza Gracilaria corticata [J. Agardh] J. Agardh Gracilaria denticulata Schmitz ex Mazza Gracilaria millardetii [Montagne] J. Agardh Gracilaria protea J. Agardh Griffithsia confervoides Suhr Griffithsia japonica Okamura Griffithsia rhizophora Grunow ex Weber-van Bosse Griffithsia schousboei Montagne Griffithsia sp 1. Griffithsia weberii Børgesen Halichrysis coalescens [Farlow] R. Norris & Millar Haliptilon cubense [Montagne ex Kützing] Garbery & Johansen Haliptilon subulatum [Ellis & Solander] Jahansen Halopithys subpaca [Simons] L. E. Phillips & De Clerck Haloplegma duperreyi Montagne Herposiphonia falcata [Kützing] De Toni Herposiphonia heringii [Harvey] Falkenberg

Herposiphonia insiduosa [Greville ex J. Agardh] Falkenberg Herposiphonia propens [Harvey] Schmitz Herposiphonia secunda [C. Agardh] Ambronn Herposiphonia sp 1. *Herposiphonia* sp 2. Herposiphonia tenella [C. Agardh] Ambronn Heterosiphonia arenaria Kylin Heterosiphonia crispa [Suhr] Falkenberg Heterosiphonia crispella [C. Agardh] Wynne Heterosiphonia dubia [Surh] Falkenberg Heterosiphonia pellucida [Harvey] Falkenberg Hypnea arenaria Kylin Hypnea ceramoides Kützing Hypnea intricata Kylin Hypnea musciformis [Wulfen] Lamouroux Hypnea rosea Papenfuss Hypnea sp 1. Hypnea spicifera [Suhr] Harvey Hypnea spinella [C. Agardh] Kützing Hypnea tenuis Kylin Hypnea viridis Papenfuss Hypoglossum androlamellere M. J. Wynne & De Clerck Hypoglossum minimum Yamada Hypoglossum sp 1. Inkyuleea beckeri [F. Schmitz ex Mazza] Choi, Kraft & Saunders Jania adherens Lamouroux Jania capillacea Harvey Jania crassa Lamouroux Jania intermedia [Kützing] P. Silva Jania sp 1. Jania ungulata [Yendo] Yendo Jania verrucosa Lamouroux Kuetzingia natalensis J. Agardh Laurencia brongniartii J. Agardh

Laurencia complanata [Suhr] Kützing Laurencia glomerata [Kützing] Kützing Laurencia natalensis Kylin Laurencia pumila [Grunow] Papenfuss Laurencia sp 1. Leptofauchea anastomosans [Weber-van Bosse] R. Norris & Aken Lophocladia lallemandii [Montagne] Schmitz Macrothamnion sp1. Martensia elegans Hering Martensia fragilis Harvey Melanamansia sp 1. Metamastophora flabellata [Sonder] Setchell Myriogramme marginifructa R. Norris & Wynne Nienburgia serrata [Suhr] Papenfuss Ophidocladus simpliciusculus [P. Crouan & H Crouan] Falkenberg Osmundaria oliveae R. Norris Osmundaria serrata [Suhr] R. Norris Pachychaeta brachyarthra [Kützing] Trevison Pachychaeta cryptoclada Falhenberg Peyssonnelia capensis Montagne Placophora binderi [J. Agardh] J. Agardh Platysiphonia miniata [C. Agardh] Børgesen Pleonosporium callicladum R. Norris Pleonosporium caribaeum [Børgesen] R. Norris Pleonosporium filicinum [Harvey ex J. Agardh] De Toni Pleonosporium harveyanum [J. Agardh] De Toni Plocamium beckeri Schmitz ex Simons *Plocamium corallorhiza* [Turner] J. Hooker & Harvey Plocamium rigidum Bory de Saint-Vincent *Plocamium* sp 1. Plocamium sp 2. Plocamium sp 3. Plocamium sp 4. Plocamium suhrii Kützing

Plocamium telfairiae [W. Hooker & Harvey] Harvey ex Kützing Pollexfenia minuta [Kylin] Papenfuss Polysiphonia ferulacea Suhr ex J. Agardh Polysiphonia incompta Harvey Polysiphonia scopulorum Harvey Polysiphonia sp 1. Polysiphonia sp 2. Polysiphonia sp 3. Polysiphonia tepida Hollenberg Polysiphonia urbana Harvey Polyzonia elegans Suhr Porteria hornemannii [Lyngbye] P. Silva Pterocladia caespitosa [Kylin] R. Norris Pterocladiella caerulescens [Kützing] Santelices & Hommersand Pterocladiella sp 1. Pterosiphonia parasitica [Hudson] Falkenberg Pterosiphonia spinifera [Kützing] Ardré Pterosiphonia stangeri [J. Agardh] Falkenberg Ptilothamnion polysporum Gordon-Mills & Womersley Rhodomelopsis africana Pocock Rhodymenia natalensis Kylin Rhodymenia sp 1. *Rhodophyta* sp 1. Schottera nicaeënsis [Lamouroux ex Duby] Guiry & Hollenberg Sciurothamnion stegengae De Cleck & Kraft Solieria robusta [Greville] Kylin Spirocladia barodensis Børgesen Spyridia filamentosa [Wulfen] Harvey Spyridia hypnoides [Bory de Saint-Vincent] Papenfuss Spyridia plumosa Schmitz ex J. Agardh Symphyocladia marchantioides [Harvey] Falkenberg Tolypiocladia glomerulata [C. Agardh] Schmitz Tricleocarpa cylindrica [Ellis & Solander] Huisman & Borowitzka *Tricleocarpa* sp 1.

Vickersia baccata [J. Agardh] Karsakoff Wrangelia argus [Montagne] Montagne Wrangelia purpurifera J. Agardh

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