An analysis of subtidal seaweed communities on a depth gradient at Sodwana Bay, on the KwaZulu-Natal coast, South Africa

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Abstract

The subtidal seaweed communities of the KwaZulu-Natal coast are poorly understood. A recent collaborative research project between Belgian and South African phycologists, however, is currently investigating the diversity and biogeographical affinities of the marine benthic algal flora of this region. The newest leg of the project is focusing on correlating biogeographic patterns with abiotic factors in the area between the St. Lucia estuary and Sodwana Bay, where it has become evident that there is a huge turnover in species composition. The present study examines seaweed community change along a depth gradient (1-30 m depth) at Sodwana Bay on the KwaZulu-Natal (KZN) coast, South Africa. All seaweed cover within 25 x 25 cm quadrats was collected, identified and weighed. The environmental variables, depth and % sand cover, were also measured. Both biomass and presence/absence data were ordinated to show community differentiation related to the environmental variables. The seaweed communities are largely red turfs, with a total of 82 Rhodophyte, 14 Chlorophyte, and 8 Phaeophyte taxa recorded. These turf communities showed exceptional diversity with 105 taxa (>25 % of recorded KZN flora) occurring in the total sample area of 1.56 m^2. Seaweed communities clearly change with depth, but the biggest change occurs between the shallow subtidal zone (approx 1 m depth) and deeper waters (>5 m depth), mostly likely due to the effects of wave action; thereafter communities do change with depth, but the effects are less pronounced. Biomass (p=0.049, significant) and seaweed diversity (p=0.078, not significant) were both shown to decrease, and % bare (seaweed-free) cover (p=0.002, significant) increased, with increasing depth. It is likely that these changes with increased depth can be attributed to the effects of increased light attenuation on ecological functioning in the subtidal communities. Sand inundation patterns are shown to be important in determining seaweed community structure, but do not appear to be predictable along a depth gradient (p=0.544, not significant).

Introduction

The popular misconception about coral reefs is that they are animal dominated systems, displaying vast populations of corals, fish and other animals, whilst the algal population is largely inconspicuous (Price and Scott, 1992). Work by Odum and Odum (1955), however, clarified that coral reef systems have a trophic structure that is dominated by the primary production of plants. Research to date has focused on the importance of encrusting corallines in providing the primary cement for the reef matrix, and on the important role of symbiotic dinoflagellates (Price and Scott, 1992). It has been commonly noted that there is a lack of visual dominance of large seaweeds on coral reefs. Research over the past twenty years has begun to highlight the importance of the inconspicuous turf algae in the reef trophic structure (Adey and Goertemiller, 1987; Klumpp and McKinnon, 1989; Price and Scott, 1992). The turfs generally dominate the coral reef plant communities, in terms of primary production (Adey and Goertemiller, 1987), and previous field observations have indicated that the same is true of sites in the extreme northeast of South Africa, such as at Sodwana Bay.

The turf algae contribute significantly to reef structure, providing the major source of fixed carbon and nitrogen to nonsymbiotic consumers (Adey and Goertemiller, 1987; Klumpp and McKinnon, 1989). The algal turfs may provide up to 70-80% of total primary productivity on coral reefs (Hackney *et* al, 1989). These algal communities are characterised by a low standing crop (Rogers and Salesky, 1981), and an exceptionally rapid growth rate that leads to a biomass turnover once every 4-12 days (Klumpp and McKinnon, 1989). This rapid growth rate is an adaptation to intensive grazing by fishes and invertebrates, which consume nearly all of the algal production (Hay, 1981; Klumpp and Polunin, 1989). Turf species are thus able to persist in zones of intense grazing, whereas large seaweed adaptations to grazing are mainly through avoidance, competing successfully in grazing refugia (Hackney *et* al, 1989).

In coral reef environments turfs are generally promoted by high levels of disturbance (Cheroske *et* al, 2000). These include the effects of grazing, and abrasion and light reduction through rubble tumbling and sand inundation. Research by Cheroske *et* al (2000) showed that increased disturbance reduced algal biomass and canopy heights, but promoted highly productive, disturbance-tolerant turf algal forms. Despite the ability of turfs to persist and thrive through intensive grazing, it has been suggested that intensive browsing activity by herbivores is the main environmental factor responsible for the inconspicuousness of epilithic algal growth on coral reefs (van den Hoek *et* al, 1978). In the tropics, sea/urchin and fish grazing is common in the shallow subtidal zone, which experiences higher light levels and a higher diversity of taxa than the deep subtidal (Abbott, 1999). In support of this, van den Hoek *et* al (1978) found, along a transect from shallow subtidal to 40 m depth at Curacao, Netherlands Antilles, that larger algae were only common in deeper waters below 27 m, where grazing intensities were lowest. Additionally, the turf community reached its lower limit between 50 and 65 m, where radiation was approximately 1% of the surface radiation, often considered to be the lower limit of the euphotic zone. Hatcher and Larkum (1983) studied the effects of grazing on algal turf communities at the Great Barrier Reef and found grazing pressure to be significantly higher in shallower rather than deeper habitats. There was, however, no significant correlation between the grazing pressure and the turf algal standing crop across major habitat types. It was concluded that only within limited temporal and spatial scales is grazing intensity alone an adequate predictor of benthic algal standing crop. In a study of the responses of turf algae to sediment deposition, Airoldi and Virgilio (1998) found that large-scale variations in sedimentation had no clear effect on turf distributions, but, on a scale of centimetres, the biomass of the turfs became less variable with high sedimentation rates. No effects were observed on the cover of the filamentous algae. Similarly to the findings of Hatcher and Larkum (1983) regarding grazing disturbance, Airoldi and Virgilio (1998) concluded that turf responses to sedimentation varied at different spatial scales and were dependant on the concomitant action of other physical and biological factors. It is evident through the studies mentioned in this paragraph, that turfs are ~~e~~affected, and seemingly favoured, by disturbance, however the effects of different disturbance mechanisms on turf populations are not clearly predictable.

Light is also considered to have important consequences for coral reef algal communities. In the Hawaiian Islands, for instance, where there is a much clearer water column in the northern islands than in the south, light is able to penetrate deeper in the water column. Algae at 30 m depth in the north are often taller than 15cm, whilst in the south they are generally shorter than 2 cm. It has been suggested that these differences in algal growth are as a consequence of the decreased light attenuation in the clearer water (Abbott, 1999).

Taxonomically, the turfs are diverse, forming intermixed, multispecies communities. They represent four algal divisions, the Rhodophyta, Phaeophyta, Chlorophyta and Cyanophyta, of which the Rhodophyta dominate. Within turf communities, juvenile or suppressed larger seaweed species often occur, sometimes forming a major part of a community (Price and Scott, 1992). Encrusting algae, as well as microscopic epiphytic algae, often grow in close association with turf species.

Turf algal communities generally display high species richness and a large proportion of 'rare' species. For instance, in a study of the species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef, 63% of the species found were 'rare' (accounting for <7% of the canopy) (Scott and Russ, 1987). A variety of species have been recorded for tropical reef algal communities, but a large number of genera are common components of several coral 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, Enteromorpha* (Chlorophyta), *Dictyota, Giffordia, Sphacelaria* (Phaeophyta), *Calothrix* and *Lyngbya* (Cyanophyta) (Scott and Russ, 1987).

Morphologically, the turfs are small, generally less than 3 mm in height with slender branches of less than 1 mm width. Their thallus is frequently differentiated into a prostrate axis, attaching to the substrate at different points and giving rise to erect branches, resulting in a spreading turf-like habit (Price and Scott, 1992). Branches, which are generally cylindrical, but sometime flattened, are mostly not calcified.

Because of their small size and relatively simple morphology, identification of turf algal species is particularly difficult, and nearly impossible in the field. Due to the difficulties in studying this diverse group of minute algae, taxonomic knowledge is poor relative to other reef organisms, such as nongeniculate coralline algae, corals and fishes (Price and Scott, 1992). Detailed research on the biology and ecology of the turfs has, in turn, been restricted by the lack of a detailed turf algal flora.

The subtidal seaweed communities of the KwaZulu-Natal coast remain almost completely unknown (Bolton and Anderson, 1997; Leliaert *et* al, 2001). However, a recent collaborative research project between Belgian and South African phycologists is currently investigating the diversity and biogeographical affinities of the marine benthic algal flora of this region. Through the aforementioned study, it has become evident that there is a huge turnover in species composition in the area between the St. Lucia estuary in the south and Sodwana Bay in the north (Fig. 1; Leliaert *et* al, 2001). The transition between the tropical Indian Ocean and cool warm temperate south coast of South Africa along the rest of the KwaZulu-Natal coast is much more gradual. The new leg of the collaborative project will now concentrate on the St. Lucia-Sodwana Bay area, correlating biogeographic patterns with abiotic factors.

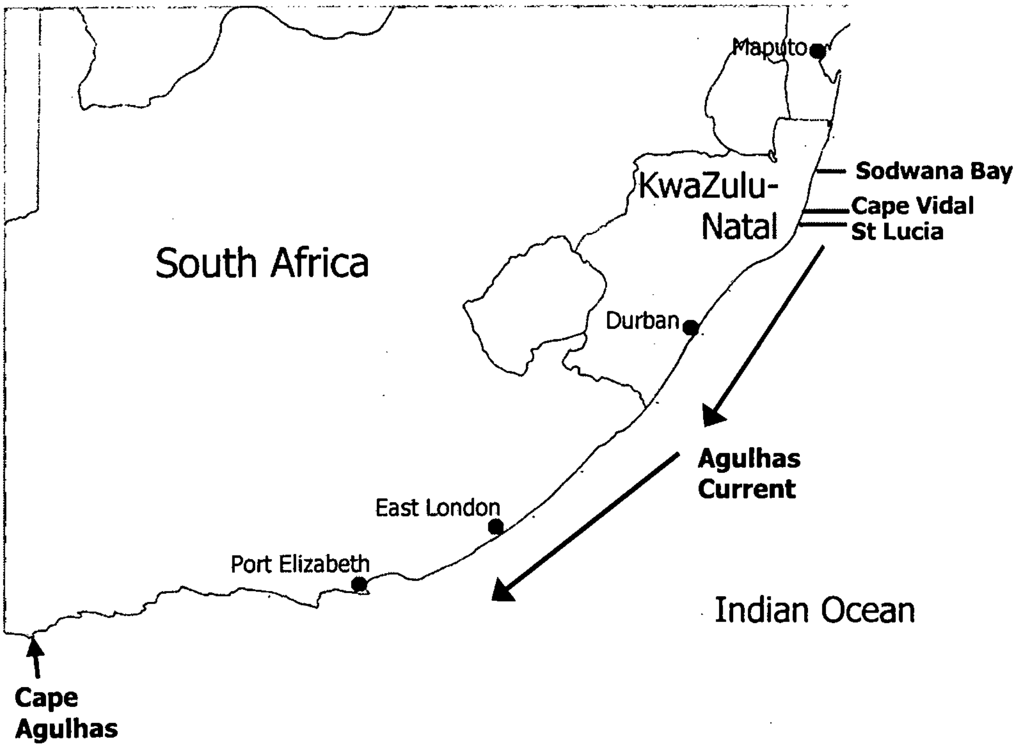

Figure 1. Map showing the south and east coasts of South Africa

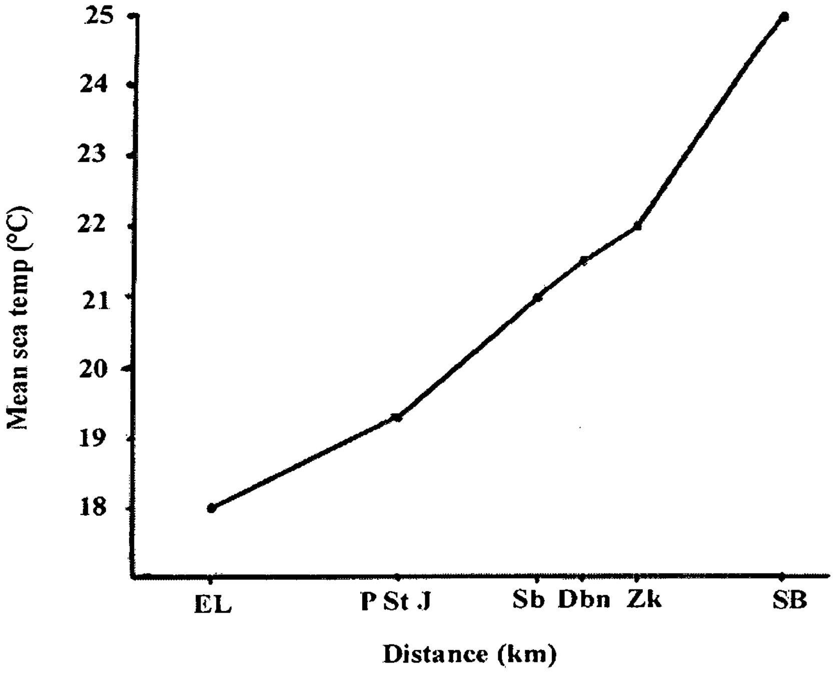

Figure 2. Change in mean sea surface temperatures, recorded between 10 and 20 m depth, along the South African coastline from East London (EL) through Port St. Johns (P St J), Scottburgh (Sb), Durban (Dbn), Zinkwazi (Zk) and Sodwana Bay (SB) (MCM environmental data: www.oceanafrica.com).

Temperature recorders are currently being placed at various sites along this stretch of coast, and at sites to the north and south, and this data is not yet available. Communities of algae will be studied at these sites, recording presence/absence data, abundance data and abiotic factors. Detailed distribution data will then be incorporated into a GIS-database in cooperation with the KwaZulu-Natal Nature Conservation Services (KZNNCS) and the Flanders Marine Institute and analysed in relation to the abiotic factors.

The South African coastline is considered to have three marine provinces: a cool temperate west coast (Benguela Marine Province), a warm temperate south coast (Agulhas Marine Province), and an east coast flora (Indo-West Pacific Marine Province) (Bolton and Anderson, 1997; Leliaert *et* al, 2001). Stephenson (1948) noted the 'Eastern Overlap', the poorly defined boundary that occurs between the east coast and south coast provinces, which he considered to occur between Port Elizabeth and Port Edward (southern KwaZulu-Natal border). Corresponding to this is a gradual rise in temperatures across the same region (Fig. 2). Stephenson (1948) designated the intertidal biota on the coast of KwaZulu-Natal as the 'sub-tropical East Coast'. Seaweed biogeographers do not, however, unanimously accept the sub-tropical affinities of the east coast flora. It has been alternatively suggested that the east coast of South Africa is an overlap region including the westernmost extension of the large Indo-West Pacific tropical region, rather than having a distinct sub-tropical flora (Bolton and Anderson, 1997; Leliaert *et* al, 2001). Many KwaZulu-Natal seaweeds also occur in the Agulhas Province, but there is an increase in tropical elements further northwards (Bolton and Anderson, 1997). Similarly the seawater temperatures are tropical from central Natal Northwards, defined as having monthly means always above 20^0C (Lüning 1990, Fig. 3). Preliminary biogeographical studies on the east coast, by the Belgian and South African collaboration, indicates that seaweed species turnover rate, moving northwards, is low (Leliaert *et* al, 2001). In the area between the St. Lucia estuary and Sodwana Bay, however, a major transition occurs from the typical warm temperate KwaZulu-Natal flora to one with predominantly tropical affinities. At this stage it appears is if an 'Eastern Overlap' occurs between the Agulhas and Indo-West Pacific Marine Provinces along the coast from East London to the St. Lucia-Cape Vidal area, and flora with tropical Indo-West Pacific Marine Province affinities occurs to the north of this area (Bolton and Anderson, 1997; Leliaert *et* al, 2001).

The marine floristic provinces, as they are described above, can be closely correlated to oceanographic conditions in the region. The warm Agulhas Current, flowing from the tropics, is the dominant large-scale oceanographic feature in the area (Schumann, 1988). The

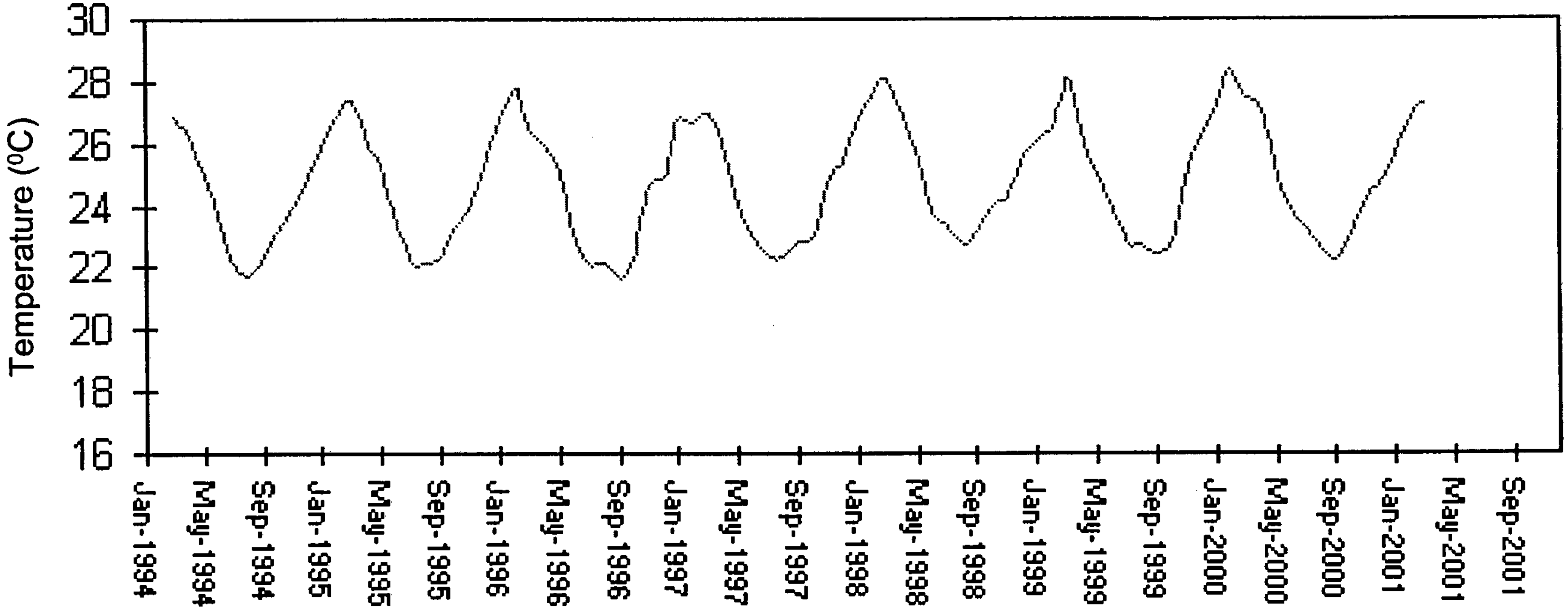

Figure 3. Averaged mean monthly sea-surface temperatures (^{0}C) recorded at Sodwana Bay (18m) between January 1994 and May 2001 (MCM environmental data: www.oceanafrica.com.

confluence of waters following complex paths in the Mozambique Channel and areas south of Madagascar form the western boundary of this current off the northern KwaZulu-Natal/Mozambique coast (Ramsay, 1994). The Agulhas current, flowing polewards, generally has its core just offshore of the shelf break and thus markedly affects the waters of the continental shelf (Schumann, 1988). The continental shelf in the study area is very narrow, with a width of approximately 3 km, and the Agulhas Current thus flows close inshore, attaining a maximum speed of up to 3 m/s (Ramsay, 1994). The effect of the warm Agulhas Current has thus allowed coastal seawater temperatures to be tropical, *sensu* Lüning (1990), from central KwaZulu-Natal northwards. To the south of St Lucia, a coastal bight causes the warm Agulhas Current to move offshore (Fig. 4, Schumann 1988), where there is an increased continental shelf width of up to 45 km, thus reducing the tropical effects of the current. Hence the gradual ? temperature rise from around East London to northern KwaZulu-Natal.

The maximum tidal range in the area averages 2 m and the coast is thus high microtidal or low mesotidal (Ramsay, 1994). Persistent high-energy waves and prevailing large-amplitude swells from the southeast dominate the coast for 40% of the year, while northeasterly to easterly onshore swells prevail for another 40% of the time (Ramsay, 1994).

Lowered sea levels (up to 130 m lower than present level), during the late Pleistocene glacial maximum of 18 000 BP, allowed for dune formation and later calcareous cementation to form aeolianites and beachrock (Ramsay, 1994). These formations were submerged during the Flandrian transgression and formed the base of modern coral reef structures off the northern KwaZulu-Natal/Mozambique coast. Present sea-level conditions allowed for the formation of a series of broad, marine, intertidal beachrock platforms that are completely exposed during spring low tides, displaying horizontal surfaces covered with marine organisms (Ramsay, 1994). The beachrock/aeolianite outcrops account for 20% of the shelf surface, and have been colonised by a thin veneer of Indo-Pacific type coral reefs at depths typically less than 25 m, the lower limit for coral growth being between 35 and 40 m (Riegl, 1993). These southeast African coral communities are not considered 'true coral reefs' mainly due to the absence of any noticeable reef accretion (Riegl, 1993). None of the typical geomorphological reef-zones such as lagoons, reef crests or reef slopes are developed. This lack of topographical differentiation has led to an absence of ecological differentiation, and hence a very uniform coral community structure. The coastal shelf to the north of Jesser Point (Fig. 5) has a series of coast-parallel oriented patch coral reefs varying in depth from 9 m to 35 m (Ramsay, 1994). The coral reefs of the northern KwaZulu-Natal shelf are the most

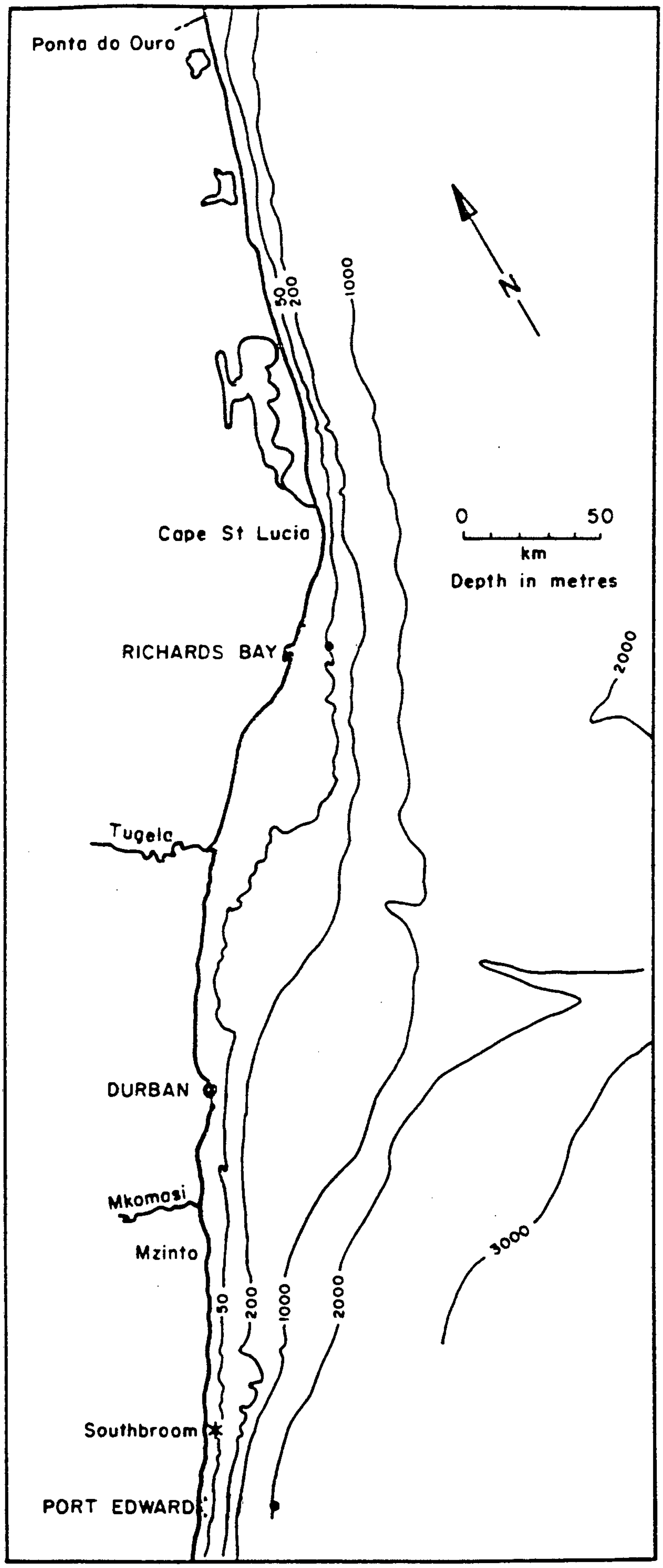

Figure 4. Coastal bathymetry off KwaZulu-Natal, showing the narrow continental shelf north of St. Lucia, and the coastal bight to the south (modified from Schumann, 1988)

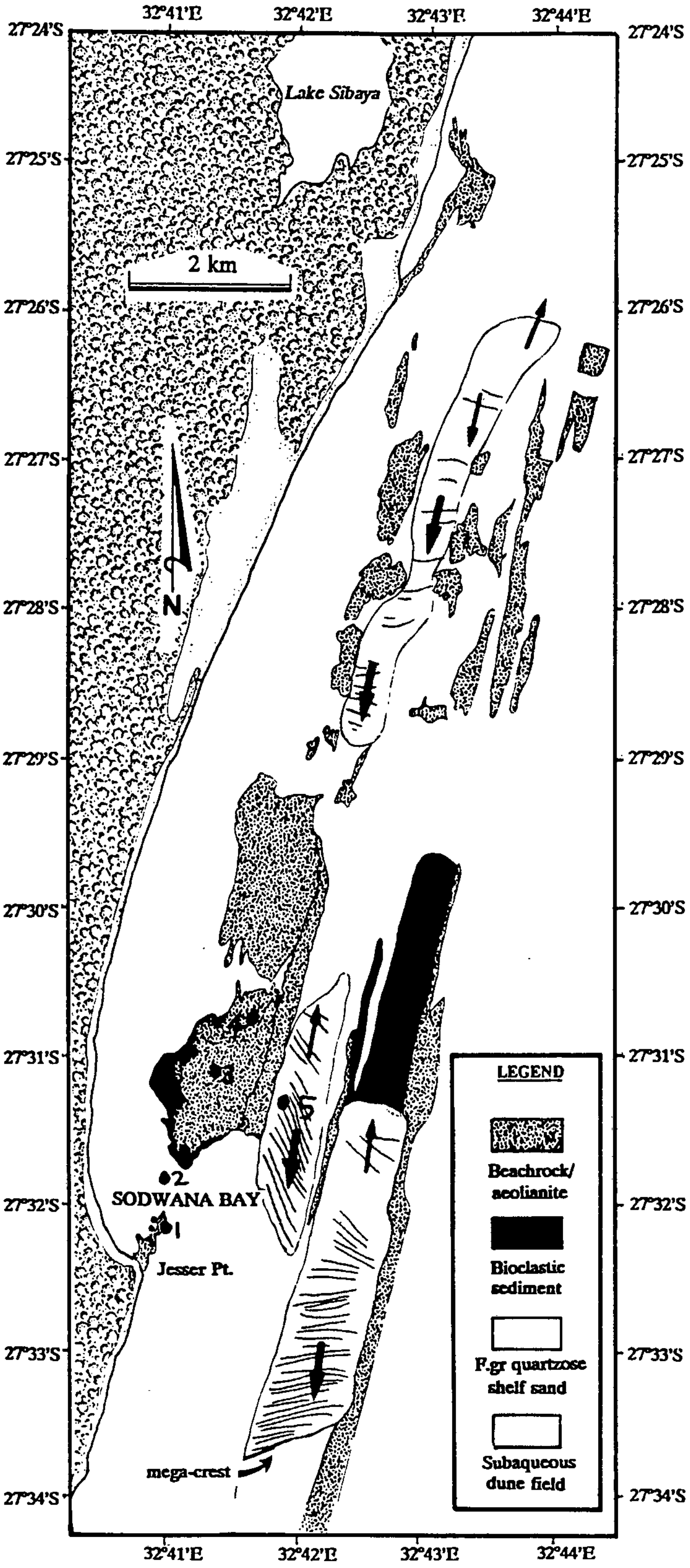

Figure 5. Sedimentology of the Sodwana Bay continental shelf interpreted from side-scan sonar imagery. Sites 1-5 are shown by dots and labelled by the relevant number (modified from Ramsay, 1994).

southerly coral reefs in Africa, and are sustained by the clear subtropical water of the warm Agulhas Current that passes close inshore. The reef fauna of the fossil sand dunes and shallow beachrock is dominated by alcyonarian (soft) corals, which constitute 60-70% of the total coral fauna. Hard corals dominate the deeper sandstone outcrops, and the deepest outcrops are dominated by a deep sponge community (Riegl, 1993).

The present study is the first of the new leg of the collaborative project between the Belgian and South African phycologists, which aims to analyse communities of algae at northern KwaZulu-Natal sites, recording presence/absence data, abundance data and abiotic factors. The present study aims to analyse marine benthic algal community change along a depth gradient at Sodwana Bay, serving as a pilot study. As light intensity is reduced with increasing depth due to the effects of attenuation, thus affecting general ecosystem productivity, an initial hypothesis is that the algal community will change from shallow water to deeper water. Secondly, in the shallow subtidal tropical waters it is generally expected that due to higher light levels, a greater diversity of algal taxa will be supported. Abbott (1999) maintained that clearer water would support a higher algal biomass. The shallow sites are expected to experience less light attenuation than the deep sites, however, due to the added effect of postulated higher grazing levels in the shallow water, a third hypothesis is that biomass will be similarly low in both the highly grazed shallow, and in the darker deep sites. Fourthly, the effects of sand inundation are not expected to be predictable in affecting algal communities as changes may vary according to changes in spatial scale and may be dependant on the concomitant action of other physical and biological factors (Airoldi and Virgilio, 1998).

Methods

Study area

Sodwana Bay is located approximately 300km north-northeast of Durban, South Africa (Fig 1). The area falls within the St Lucia Marine Reserve and is a protected natural area administered by the Ezemvelo KwaZulu-Natal Wildlife Authority. The present study analyses seaweed communities at five different subtidal sites at Sodwana Bay.

Site 1 was in a sheltered rocky cove on the seaward side of Jesser Point (Fig. 5). The rock cove was formed from the erosion of horizontal intertidal beachrock platforms. Disturbance and abrasion from wave action were high in the cove. Sand cover on the floor at this site was extremely high, with low exposure of rocky substrate, except on the beachrock walls. The occurrence of corals was low. The sandy substrate was interspersed with occasional boulders. Isolated patches of seagrass, including a variety of other algal species, and sand binding turfs were the dominant seaweeds at the site.

Site 2 was at Quarter Mile Reef (Koornhof, 1995) situated approximately 400 m north of Jesser Point (Fig. 5). The sample site had an average depth of 6.8 m. No bare substrate occurred at this site, which was largely covered with uniform turfs, interspersed with a few foliose and coralline specimens. Sponges were also common at this site, and the tunicate *Pyura stolonifera*, which dominated pinnacles. Coral cover was low.

Site 3 was at Pinnacles, on Two-Mile Reef (Koornhof, 1995, Fig. 5), having an average depth of 10.6 m. The substrate was largely bioclastic sediments with a high areal cover of large live corals and sponges. Algal communities were turf dominated and interspersed by a few foliose specimens. There was a high occurrence of sea urchins and grazing fish.

Site 4 was at Four Buoy, on Two-Mile Reef (Koornhof, 1995, Fig. 5), in an area with an average depth of 14.5 m. The reef at this site was of the typical aeolianite rock type with additional bioclastic sediments being common. Much of the underlying sediment was bare, and the biotic cover was dominated by turfs and a smaller areal live coral component. Sand cover was low.

Site 5 was at Sponge Reef, on Two-Mile Reef (Koornhof, 1995, Fig. 5), which had an average depth of 27 m. This was a low-lying reef of bioclastic sediments that gently sloped from a sandy bottom. Coral cover was intermediate to high, interspersed by turf algae, isolated foliose algae and bare substrate.

Sampling technique

Sampling was carried out between 30 March and 3 April 2002, at the five described sites at Sodwana Bay, by divers using SCUBA, except at Site 1 where snorkeling apparatus was used. At each site, five 25 cm X 25 cm wire quadrats were haphazardly placed in algal beds. The quadrats at each site were labeled 1-5 from the shallowest to the deepest, thus the shallowest quadrat at site 2 was labeled 21, and the second shallowest 22, and so forth. Large portions of reef surface at all sites were covered by corals, sand or exposed substrate, without any algal cover. As this study is examining algal community composition, divers placed the quadrats subjectively, but haphazardly, in typical algal beds, rather than randomly or systematically over the substratum, in order that the algal communities could be accurately represented. Within each quadrat the depth, the % areal cover of sand inundation, % cover of encrusting corallines, and the % cover of bare substrate (rock or dead coral), was measured. In addition to these, if the seagrass, *Thallassodendron ciliatum* was found in a quadrat, it was scraped off the substrate using a paint scraper, and its wet-weight was later recorded. These factors were considered as potentially having direct effects on the algal community.

All the visible algae within each quadrat, excluding crustose forms, were scraped off the substratum, using a paint-scraper, and collected in numbered fine-mesh bags. On land very abundant plants were identified, wet-weighed and discarded, whilst the remainder of each sample was preserved in 5% formalin/seawater for subsequent sorting. Samples were identified, sorted and weighed to an accuracy of 0.05 g in the laboratory. Specimens that were present in a sample, but weighed less than 0.1 g, were recorded as present and later assigned a nominal weight of 0.01 g for the purpose of analysing the data quantitatively. In the analysis, the small size of the turfs, and the fact that many were infertile and hence lacked diagnostic features, led to them being very difficult, and sometimes impossible to accurately identify. Many specimens could not be accurately identified to species, and the generic accuracy was sometimes uncertain. Pressed and slide mounted specimens of all taxa, however, were prepared so that taxa could be compared and cross-referenced during sorting and analysis. Species were identified by J.J. Bolton and R.J. Anderson, with the assistance of O. de Clerck and H.E. Engledow (University of Gent). A number of new records for South Africa occur in the samples.

A light/depth profile was measured down to a depth of 27 m at 13:30 on the sunny afternoon of 3 April 2002. For this a Li-cor light meter was used. The weighted spherical quantum sensor was lowered in an upright position, on a graded line, from a boat, in deep water at Sodwana Bay. Underwater photosynthetically active radiation values were recorded at regular intervals.

Analysis

The data set consists of 25 samples and 106 taxa. Correlations of the relationships between depth and % sand cover, % bare substrate, species number and biomass, were plotted. P-values and correlation co-efficients (r) for each relationship were also calculated.

For the ordination the FORTRAN program CANOCO (Ter Braak, 1988) was used. Ordinations were performed using both species biomass, and presence/absence data. For both datasets a correspondence analysis (CA) was performed. A CA is an indirect gradient analysis technique that searches for major gradients in the species data, irrespective of environmental variables, which are later used to interpret the species data. A canonical correspondence analysis (CCA) was also used as an ordination method for both datasets. A CCA is a multivariate direct gradient analysis technique that displays an ordination whereby the axes are constrained by linear combinations of environmental variables. The CCA thus detects patterns of variation in species data that can be best explained by observed environmental variables, expressing a pattern of variation in species composition, and the main relations between species and each environmental variable. CANOCO assigns eigenvalues to the first four axes of variation. Eigenvalues indicate the strength of each axis, thus an axis with an eigenvalue of 1 explains 100% of the variation in that direction (Ter Braak, 1988).

Results

The light readings taken at 13:30 on 3 April 2002 at Sodwana Bay clearly show the effects of light attenuation with increasing depth (Fig. 6). Light levels dropped from 1510 μmol.cm^{-2}.s^{-1} at the surface to 116 μmol.cm^{-2}.s^{-1} at 27 m.

A correlation co-efficient (r) of –0.13 was found for the relationship between depth and % sand cover within each quadrat (Fig. 7). This correlation was, however, insignificant ($p=0.544$).

A significant correlation ($p=0.002$) of the relationship between depth and % bare substrate, within each quadrat, had an r-value of 0.60 (Fig. 8). This result indicates that the quadrats sampled in deeper water had a significantly higher percentage of exposed substrate than the shallower sample sites.

The turf communities of Sodwana Bay show a remarkable diversity in that, of a total sample area of only 1.56 m^2, 105 taxa were found. This represents more than 25% of the recorded seaweed flora of KwaZulu-Natal. The turfs and semi-prostrate species collected in this study formed a low cover of approximately 1-2 cm, with occasional, isolated, large upright individuals of certain taxa, including: *Halymenia durvillei* and *Titanophora* (not present in sample collections), and *Tricleocarpa* and *Halimeda.*

Quadrats 14 and 15 were the only samples that included a population of the seagrass *Thallassodendron* sp., which had a biomass of 502 and 180 g respectively (Table 1). The

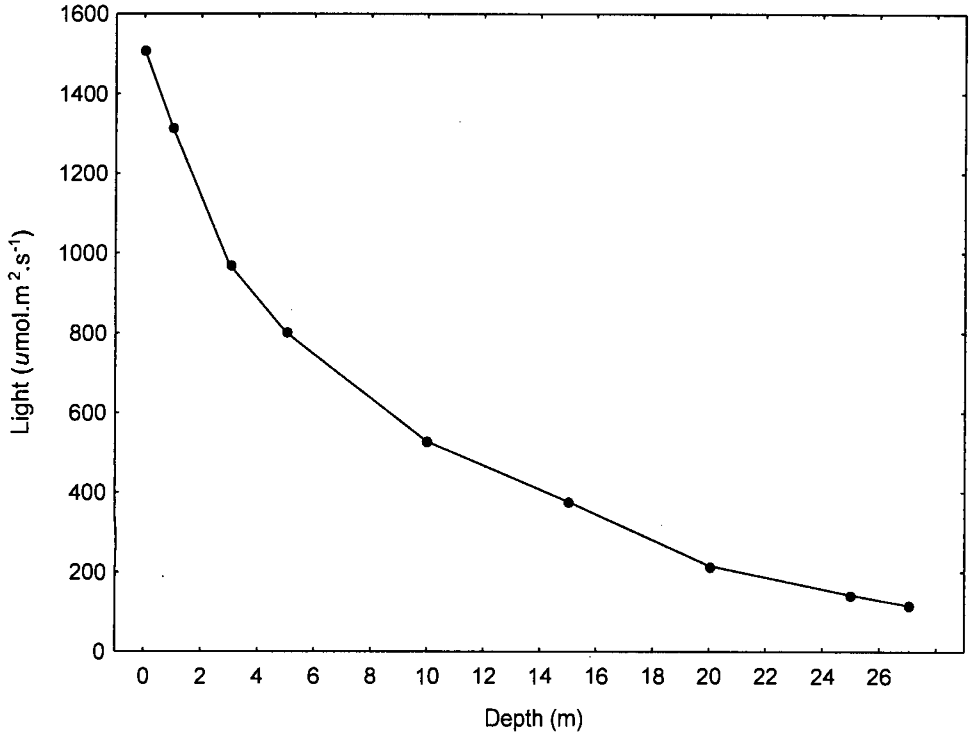

Figure 6. A light.depth profile, measuring photosynthetically active radiation ($u$mol.cm^{-2}.s^{-1}) at 13:30 on 3 April 2002 (fine weather) at Sodwana Bay, South Africa.

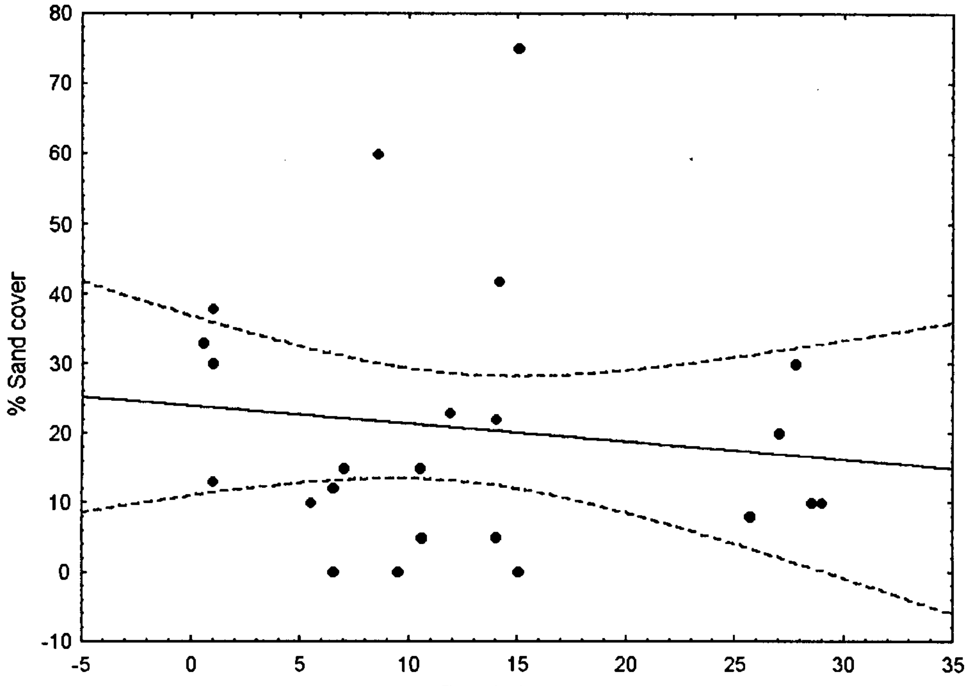

Figure 7. A regression fit (r= -0.13; p= 0.54, thus not significant) of the relationship between % sand cover and depth (m), as measured in 25 cm x 25 cm quadrats at Sodwana Bay, South Africa. Dashed lines indicate 95 % confidence limits.

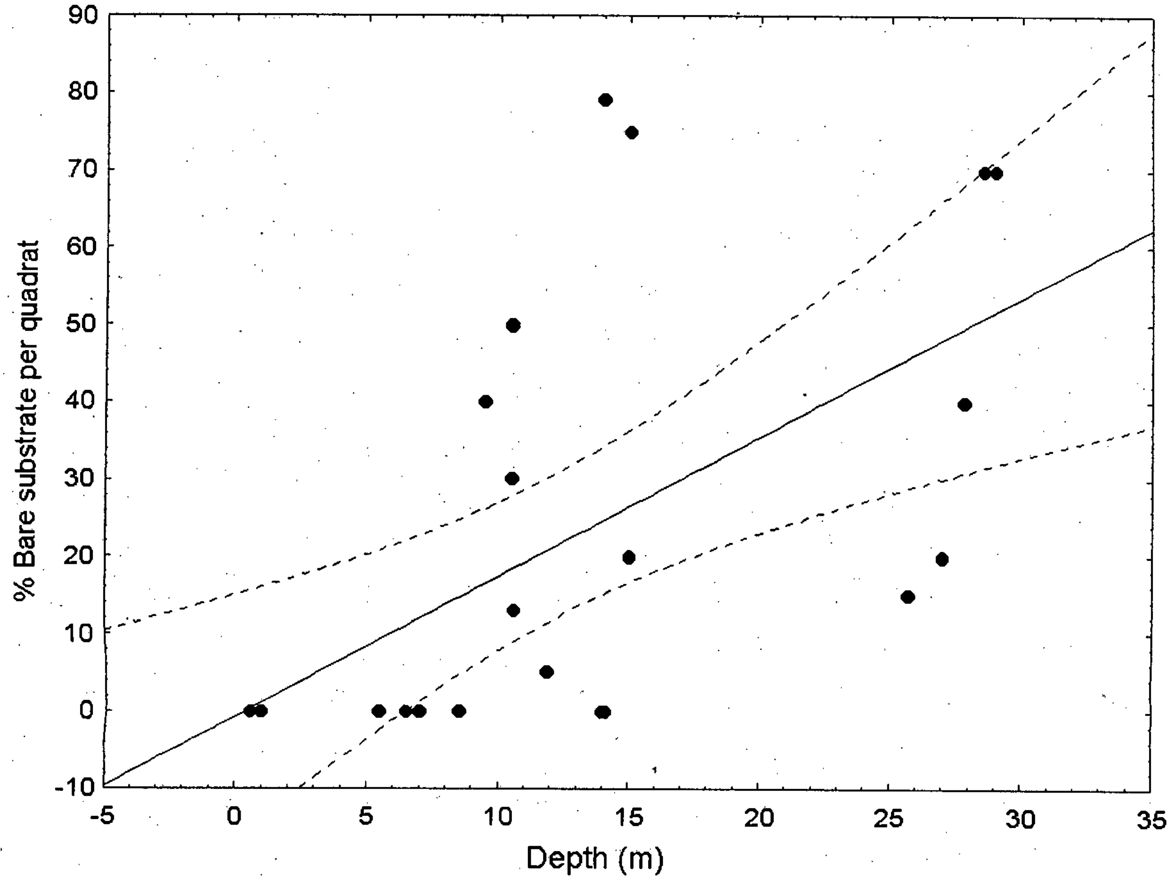

Figure 8. A regression fit (r= 0.6; p< 0.05, thus significant) of the relationship between % bare substrate and depth (m), as measured within 25 cm x 25 cm quadrats at Sodwana Bay, South Africa. Dashed lines indicate 95 % confidence limits.

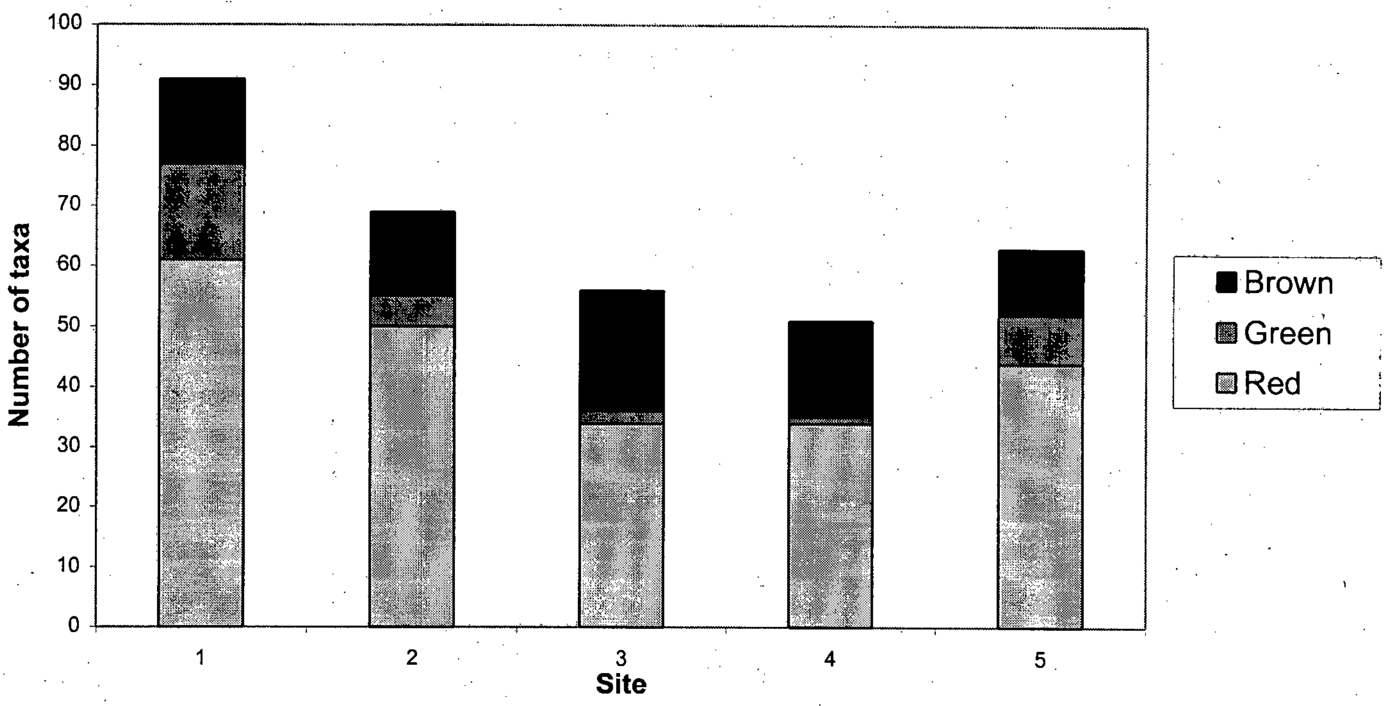

Figure 9. Total number of seaweed taxa per site at Sodwana Bay, as indicated by the numbers at the top of each column. Each column is further divided into numbers of brown, red and green seaweeds, as indicated by the grey scale.

Table 1. List of algae and seagrass (*Thallassodendron ciliatum*) biomass higher than 0.01 g (a nominal value) collected at Sodwana Bay. Depths (m) are also given for each sample. Samples from a particular site are numbered from 1-5, followed by the number of sample quadrat (ie. 11-55). Values in columns are taxa biomasses found in each sample.

Sample	11	12	13	14	15	21	22	23	24	25	31	32	33	34	35	41	42	43	44	45	51	52	53	54	55
Depth (m)	*0.5*	*1*	*1*	*1*	*1*	*5.5*	*6.5*	*6.5*	*7*	*8.5*	*9.5*	*10.5*	*10.5*	*10.6*	*11.9*	*14*	*14*	*14.1*	*15*	*15*	*25.7*	*27*	*27.8*	*28.5*	*29*
T. ciliatum weight (g)				*502*	*180*																				
Rhodophyta																									
Amphiroa beauvoisii						6.3	0.3																		
Amphiroa rigida	6.6	8			0.01				0.01								0.01	0.01		0.01					
Carpopeltis sp.													0.1												
Ceramiaceae indet. 1										11.4															
Champia compressa							0.1	0.01			0.01	0.01						0.01			0.01	0.01	0.01		0.01
Champia parvula						0.1																			
Champia sp. 1								1.3																0.01	
Chondria armata	1.1																								
Chondria cf. *dasyphylla*						0.4		0.01																	
Chondria simpliciuscula				0.1			0.01				0.01	0.01	0.01		0.01					0.01		0.01	0.01	0.01	0.01
Chondria sp. 1				0.3			0.01				1.2			4.6			0.01								
Delessariaceae indet.			1.1																						
Eucheuma cf. *odontophorum*																				0.3					
Galaxaura marginata				1																			0.3		
Gelidiopsis repens												0.2			0.01		0.01								
Gelidiopsis sp.	0.2																								
Gelidium reptans	0.1	0.2	0.01				0.01	1.6		0.01	0.4										0.2		0.2		0.2
Gelidium sp. undescribed												1.2	3.3	2.1	7.9	0.01	0.6	0.2	0.2	0.01	0.1				
Gracilaria cf. *canaliculata*					0.1																				
Gracilaria millardetii					2.4																				
Haliptilon subulatum	0.2			44.8	0.01																				
Hypnea spinella	0.01	0.2	0.01	0.01	0.01	6.3	2.4	0.01	0.2	0.7	0.01	0.01			4		0.02	0.01		0.01	0.01	0.01	0.01	0.01	0.01
Jania ungulata f. *brevior*	0.3		0.01		0.1	0.1	0.01	3.1		0.01	0.01	0.5	0.01	0.01	0.1		0.01	0.01	0.01	0.01			0.01		0.01
Laurencia brongniartii																					0.6				
Laurencia natalensis						1.5																			

Table 1. Continued

Sample	11	12	13	14	15	21	22	23	24	25	31	32	33	34	35	41	42	43	44	45	51	52	53	54	55
Leptofauchea anastomosans						0.01							0.01				0.01			0.01	0.1				
Peysonnelia capensis																						0.1			
Plocamium sp. 2																								0.01	0.1
Plocamium sp. 3				0.1																					
Plocamium sp. 4					0.1																				
Prostrate red																						0.1			
Pterocladiella caerulescens complex				0.1	0.01																				
Pterocladiella sp.				0.01		0.1									0.01										
Tricleocarpa cylindrica						76.7														17.8					
Chlorophyta																									
Bryopsis sp. 1							0.01																		
Caulerpa racemosa	0.01		0.7																						
Caulerpa scalpelliformis			0.01		0.5																				
Codium incognitum							21.5																5.6	0.2	
Halimeda cuneata		7.2	5.5	0.01																					
Pseudocodium de-vriessi			1.2	0.01																	0.2	0.1	0.01	0.01	0.01
Udotea indica		1.8		0.01																					
Phaeophyta																									
Dictyopteris delicatula	0.01			0.01		6.3	0.1			0.9		0.01	0.01	0.01	0.01		0.01	0.01	0.2	0.01		0.01			0.01
Dictyota cervicornis			0.01			0.1												0.01							
Dictyota ceylanica				0.01	0.01			2.1		0.01	0.01		0.01	0.3	0.1								0.01	0.01	0.01
Dictyota sp.	6.6				0.01		0.2			0.2	0.01	0.1		0.6	0.1					0.2	0.01	0.01		0.01	
Lobophora variegata	3.1	3.4	2.1	0.2	2.4	0.5	0.2	5.9		0.2	4.8	9.3	14.5	1.8	0.1	9.3	14.6	1.4	0.1	3		0.2		3.2	5.8
Sargassum sp. 1 (teeth)			1.9								0.6	2	0.1				0.01	0.01		0.6					
Sphacelaria rigidula			0.2					0.01					0.01						0.01	0.01					

epiphytic coralline *Haliptilon subulatum* was found, by observation, to be strongly associated with the *Thallassodendron ciliatum* bed of quadrat 14, having a high biomass of 44.8 g.

In the 25 sample quadrats, a total of 105 seaweed taxa were recorded (82 Rhodophyta, 14 Chlorophyta and 8 Phaeophyta; Table 2, Appendix). The most prominent and typical taxa in all sites, by biomass and species number, are the turf forming red algae (Fig. 9). The most prominent red taxa included *Hypnea spinella* (represented in 21 quadrats and at all sites), *Jania ungulata* f. *brevior* 1 (represented in 18 quadrats and at all sites), and *Gelidium* cf. *caerulescens* (only represented in 10 quadrats and at sites 3, 4 and 5, but at high biomass). The large red *Tricleocarpa* was atypical, found only in quadrats 15 and 45, but due it's large size it formed a major portion of the sample biomass. The Phaeophyta were represented at *all five* sites, the dominant taxon being *Lobophora variegata* that was present with a high biomass in all quadrats at all sites excluding quadrats 24, 51 and 53. Other dominant brown seaweeds include *Dictyopteris deliculata, Dictyota ceylanica* and *Dictyota* sp. Chlorophyta were less common, and were represented in significant biomass at only sites 1, 2 and 5. *Codium incognitum* was another atypical taxon, forming a large portion of the biomass of quadrat 22 due its large size.

An r-value of –0.36 was found for the relationship between depth and numbers of species per quadrat (Fig. 10). This correlation was, however, insignificant (p=0.078).

A significant correlation (p=0.049) of the relationship between depth and biomass, within each quadrat, had an r-value of –0.4 (Fig. 11). This result indicates that the quadrats sampled in deeper water had a significantly lower seaweed biomass than shallower sample sites.

For the purpose of the CCA ordinations, the only environmental variables used to constrain the axes were depth and % cover of sand. The effect of these environmental variables was also depicted in the unconstrained CA ordinations. The other environmental variables (% cover of encrusting corallines, % cover of live coral and % bare substrate) were considered to be co-dependants of the seaweeds as they inherently excluded seaweed growth, and thus directly influenced their presence and abundance. These latter environmental variables were thus excluded from all ordinations, as was *Thallassodendron ciliatum* biomass, which was only present in two quadrats and had a disproportionate effect on the ordinations.

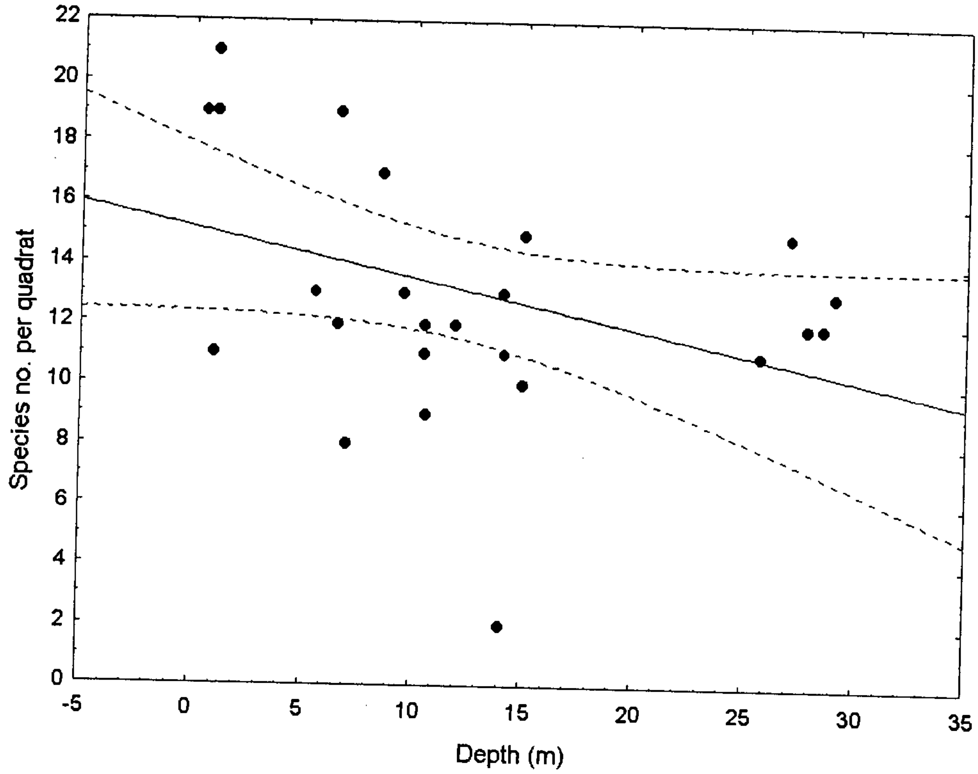

Figure 10. A regression fit (r= -0.36; p= 0.08, thus not significant) of the relationship between number of seaweed taxa and depth (m), as counted within 25 cm x 25 cm quadrats at Sodwana Bay, South Africa. Dashed lines indicate 95 % confidence limits.

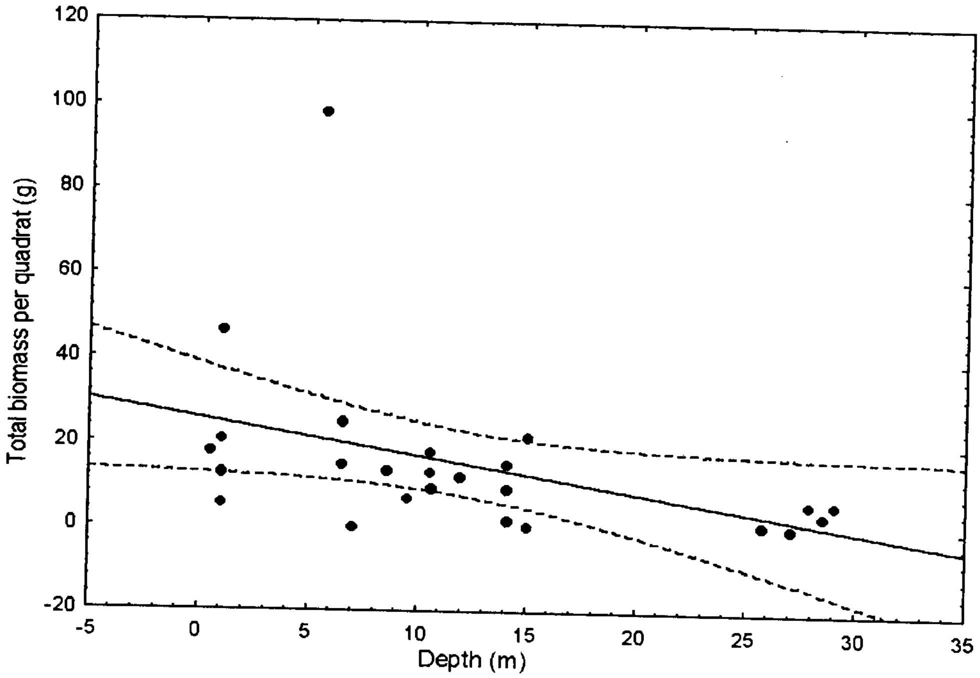

Figure 11. A regression fit (r= -0.4; p= 0.04, thus significant) of the relationship between seaweed biomass and depth (m), as measured within 25 cm x 25 cm quadrats at Sodwana Bay, South Africa. Dashed lines indicate 95 % confidence limits.

The results of an ordination, using species biomass data, and including all 25 quadrats, can be seen in the CA-diagram (Fig. 12) (eigenvalues of the first two axes: 0.975 and 0.910 respectively). This diagram depicts two groups separated along the first axis, the first including only Quadrat 14, and the second including all the other quadrats. This disproportionate separation was caused by the high biomass of the seagrass epiphyte *Haliptilon subulatam*, which had a biomass of 44.8 g in Quadrat 14, and no more than 0.2 in any other sites (Table 1). This ordination is most probably a skewed representation of the seaweed communities, and Quadrat 14 was thus excluded for the remaining ordinations.

A similar ordination to that described above (Fig. 12), excluding Quadrat 14, is shown in the CA-diagram (Fig. 13) (eigenvalues of the first two axes: 0.913 and 0.884 respectively). This diagram depicts a minor separation along the first axis, that does not show any patterns that obviously relate to the environmental variables. Quadrats 22 and 53 form a group that has been separated along the first, and more noticeably along the second axis. These quadrats are characterised by high biomasses (21.5 g and 5.6 g respectively, Table 1) of the green seaweed *Codium incognitum*. Another noticeable group has separated along the first and second axes that includes Quadrats 21, 25 and 45. Of this group, Quadrats 21 and 45 have high biomasses (76.7 g and 17.8 g respectively, Table 1) of the red foliose seaweed *Tricleocarpa* sp., Quadrats 21 and 25 have fairly high biomasses (6.3 g and 0.9 g respectively, Table 1) of the brown seaweed *Dictyopteris delicatula*, and Quadrats 25 and 45 both have a high % areal cover of sand (60% and 75% respectively). Excluding the separation of Quadrats 25 and 45 according to high sand cover, this ordination does not clearly depict any seaweed community separation according to known environmental variables. Any separation that does occur between quadrats is most probably due to the disproportionate effect of uncommon large seaweeds, such as *Codium incognitum*, *Tricleocarpa* and *Dictyopteris delicatula*, which have much higher biomasses than the surrounding turf communities.

Due to the disproportionate effects of uncommon large seaweeds, an indirect CA ordination was performed that used taxon presence/absence data (Fig. 14) (eigenvalues of the first two axes: 0.615 and 0.520 respectively). This ordination is consistent with preliminary observations, made during the sorting process of this study, that the seaweed species composition changed very little from Site 2 to Site 5, but the shallow Site 1 consisted of a markedly different seaweed species composition. This ordination shows a separation along the first axis into a first group including only Site 1, and second group including Sites 2, 3, 4 and 5. This separation appears to be correlated with depth and inversely with sand cover, and similarly, within the second group the deep Site 5 has separated to one end. Within the second group it is difficult see a pattern separating Sites 2, 3 and 4. There is a vast separation along the second axis within the Site 1 group, and this seems to indicate that the Quadrats of Site 1 each had markedly different seaweed species compositions. There is little second axis differentiation within the second group, indicating that the seaweed communities of these four sites were relatively similar.

Direct gradient analyses (CCA ordinations) of both species biomass and presence/absence data were performed, using depth and % sand cover to constrain the axes. These ordinations were used to attempt to explain remaining variation within the species data that was not obvious on axes 1 or 2, and hence provided an insight into the variation occurring within the second group depicted in Figure 14. Figure 15 and Figure 16 show the CCA-diagrams of the ordinations using biomass and presence absence data respectively. Except that the sites from the biomass data are separated slightly further apart in Figure 15, both ordinations are similar, and will thus be discussed as one. Site 1 still forms a group that is separated according to depth, as does Site 5. The remaining sites are separated from shallowest (Site 2) to deepest (Site 4), however a more noticeable separation has occurred in these sites according to sand cover, whereby Quadrats 25 and 45 (60 and 75% sand cover respectively), and Quadrat 43 (42% cover) to a certain extent, have become separated from the other groups of Site 2, 3 and 4. In the CCA-diagram (Figure 15) where biomass data was used, it is notable that the constraining effects of the environmental variables have overridden the high biomass effects of *Codium incognitum*, *Tricleocarpa* and *Dictyopteris delicatula*, which caused a noticeable separation of Quadrats 21, 25 and 45 in the CA ordination diagram (biomass data).

Discussion

The dominance of seaweed turfs is characteristic of tropical waters where grazing levels are high. This was also found to be true for the subtidal seaweed communities at Sodwana Bay that are dominated by turf-forming Rhodophyta. The occurrence of isolated, large, upright species can be explained through their having chemical defenses. Scott and Russ (1987) found 63 % of the central Great Barrier Reef species were 'rare', occurring at less than 7 % of the canopy cover. In comparison, the present study found an even higher percentage of rarity with 95 % of the taxa occurring at less than 7 % of the total biomass. 54 % of the taxa occur at masses of less than 0.01 g. Of the 14 macroalgal genera described by Scott and Russ (1987) as being common to several coral reef areas such as the Great Barrier Reef, the Caribbean, Hawaii and Guam, 10 were

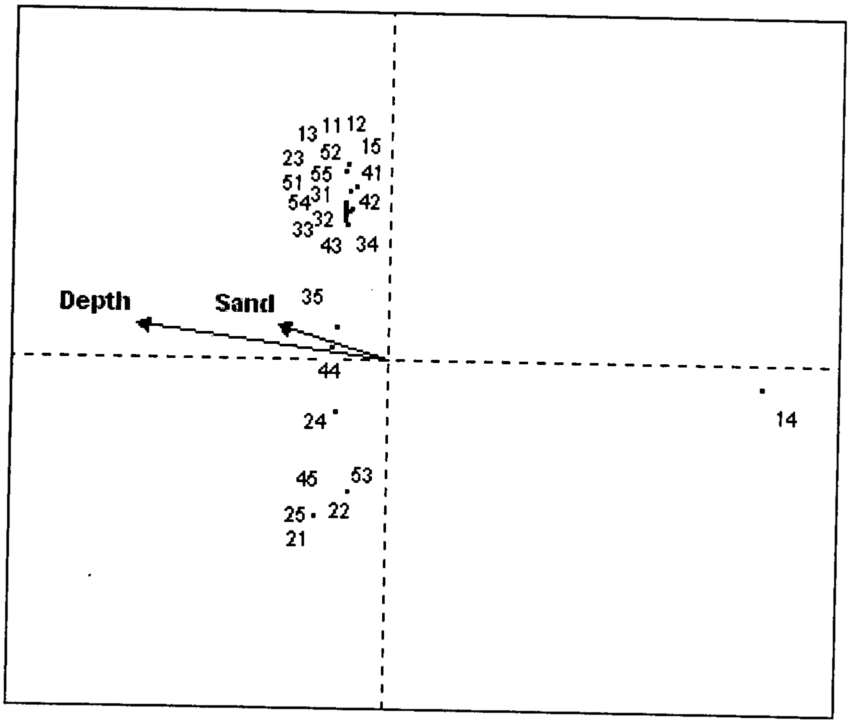

Figure 12. Correspondence analysis ordination (CANOCO; ter Braak, 1988) showing similarity between all 25 samples, based on taxon biomass data. Sites are spread according to arbitrary x and y axes with eigenvalues of 0.975 and 0.910 respectively. The unconstrained effects of depth (m) and % sand cover are shown by the two arrows.

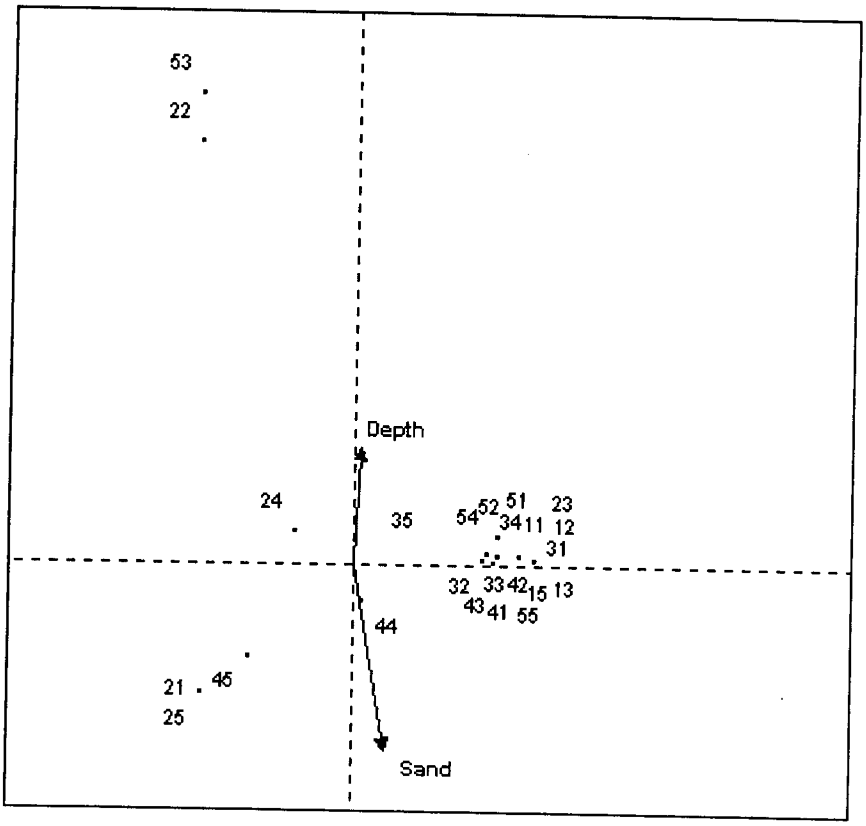

Figure 13. As in Figure 12, but sample 14 has been excluded. Eigenvalues for x and y axis: 0.913 and 0.884.

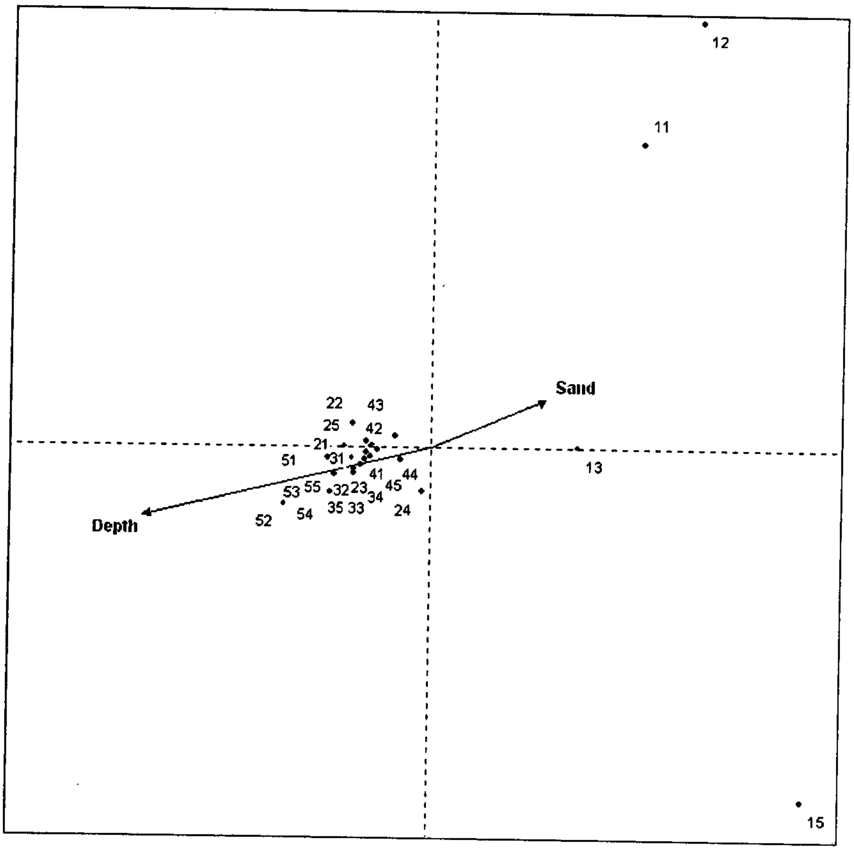

Figure 14. As in Figure 13, but based on taxon presence or absence data. Eigenvalues for x and y axis: 0.615 and 0.520.

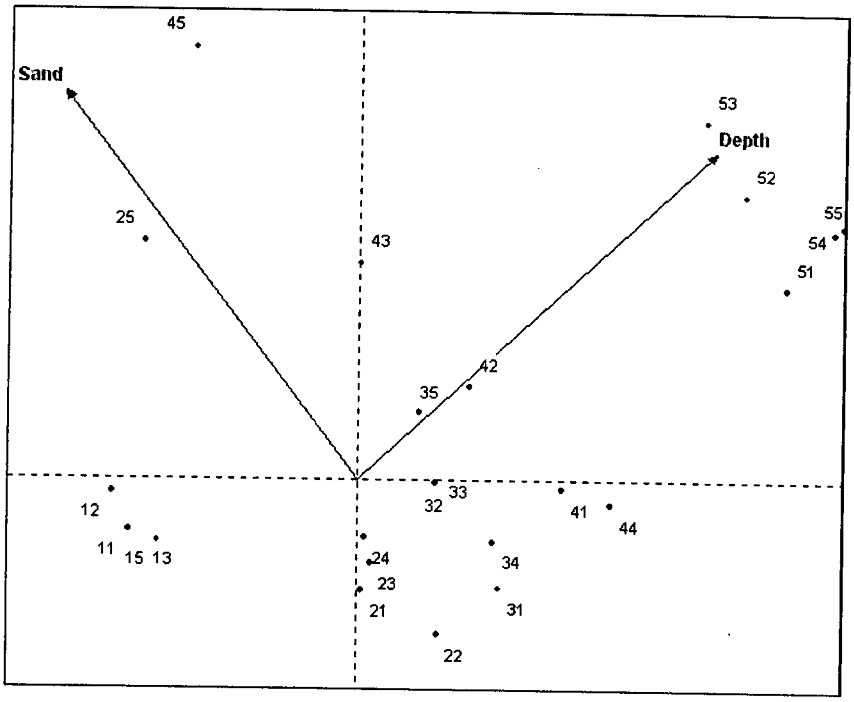

Figure 15. Canonical correspondence analysis ordination (CANOCO; ter Braak, 1988) showing similarity between all samples, excluding sample 14, based on taxon biomass data. Eigenvalues for x and y axis: 0.510 and 0.153. The constrained effects of depth (m) and % sand cover are shown by the two arrows.

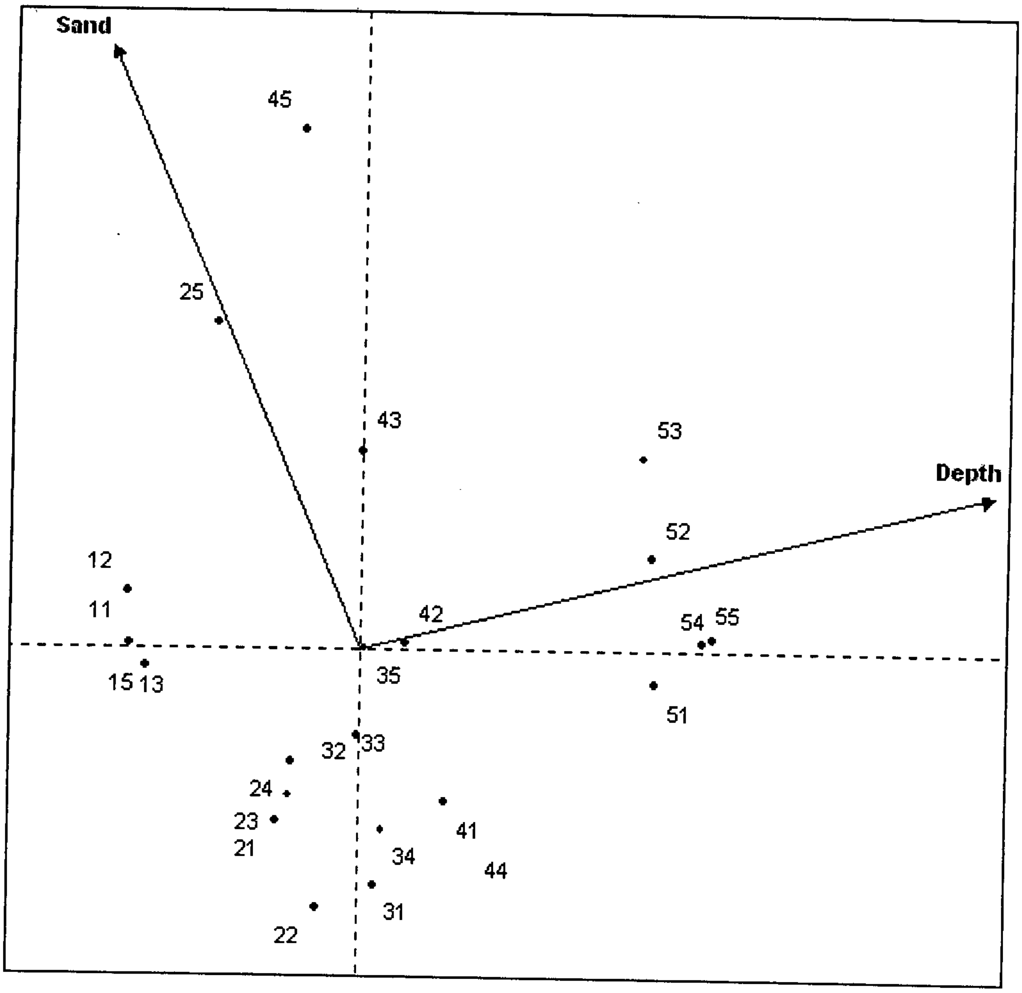

Figure 16. As in Figure 15, but based on taxon presence or absence data. Eigenvalues for x and y axis: 0.491 and 0.233.

commonly found in this study at Sodwana Bay: *Ceramium, Gelidiella, Herposiphonia, Hypnea, Jania, Laurencia, Polysiphonia* (Rhodophyta), *Cladophora* (Chlorophyta), *Dictyota, and Sphacelaria* (Phaeophyta). Thus the Sodwana Bay subtidal seaweed community can be considered as being relatively typical of a tropical reef assemblage. The exceptional diversity found in a small sampling area size at Sodwana Bay is particularly notable.

The results of this study have shown, in accordance with the initial hypothesis, that a change in epilithic seaweed communities occurs along a depth gradient at Sodwana Bay. Depth does not directly cause biological changes within communities and individual plants, but is rather a surrogate measure, primarily of light. As is well known (Abbott, 1999; Cheroske *et* al, 2000; van den Hoek *et* al, 1978), and as has been shown in this study, light intensity decreases logarithmically with depth due to the effects of light attenuation. In shallow or particularly clear water, where light intensities are greater, photosynthesis by algae is generally able to occur more efficiently, and a higher diversity of taxa can be supported by an ecosystem. This system is likely to be more productive than a system of similar environmental conditions, but with lower light intensities and hence lower levels of photosynthesis. These basic differences in, for instance, a shallow benthic community and a deep benthic community, will lead to two communities that are controlled by different interspecies interactions such as predation, herbivory, competition and mutualisms, as well as supporting different species assemblages that have different light and food requirements. In the present study it was shown that % bare substrate increased with depth, in other words, at the deeper sites larger patches occurred that had not been colonised by seaweeds, corals or encrusting corallines. This result is likely to be due to the decreased light levels that cause the community to support a lower biomass. The effect of animal grazing is more pronounced as primary production is not as high. This is speculation however, and further studies might reveal a different mechanism that would allow for larger areas of exposed substrate, as well as a lower biomass, in deeper benthic communities at Sodwana Bay.

Another factor that may be correlated with depth, affecting seaweed communities, is the effect of wave action. Shallower communities will experience greater wave action and water movement due to the closer proximity of the seafloor to the sea surface. This proximity allows the benthic community an increased contact with the oscillating motion of the swells, as well as increasing the effects of breaking waves on the community. This water motion is likely to impose greater stress on the seaweeds, as well as exposing them to higher levels of sand abrasion. A possible positive effect of the water motion is that of increased nutrient cycling, which will be experienced by the shallower benthic communities. Wave action may also have secondary effects on seaweeds through its effects on grazers and on the benthic animals with which they compete for space.

The deeper water communities of Sites 2 to 5 show a small amount of differentiation that is primarily related to depth. The shallow (<1 m depth) Site 1 seaweeds are separated from the afore-mentioned deeper seaweed community, also according to depth, however there is high differentiation within this community. Higher levels of disturbance are likely to be found in the shallow subtidal Site 1 from the effects of wave action, sand abrasion and higher levels of grazing. Grazing is expected to be higher at this depth due to higher levels of overall ecosystem productivity and diversity of taxa due to higher light levels (Abbott, 1999). A large and diverse fish community assemblage was in fact observed whilst sampling at this site. Turf-forming seaweed communities, which are able to maintain high diversity in disturbance prone environments (Cheroske *et* al, 2000), and are dominant throughout the Sodwana Bay seaweed community, are well suited to survive the shallow disturbed conditions of Site 1. The turf dominated Rhodophyta were, in fact, higher in species diversity at Site 1, and secondarily at Site 2, than in all the deeper sites. These high levels of disturbance are likely to promote this high community differentiation. It was unfortunately, however, not within the scope of this study to quantify the effects of disturbance factors such as grazing, wave-action and sand abrasion, so it is not possible to properly analyse their effects, which are likely to be complex.

The second hypothesis, predicting higher levels of seaweed diversity at the shallower sites, was true, however the regression was not statistically significant. Average species diversity was highest in the shallow subtidal Site 1. The lack of a significant depth/species diversity regression may be due to the patchy nature of the sites. In terms of environmental variables and seaweed communities, more samples needed to be collected to accurately represent this community.

Biomass was found to decrease significantly with depth. This result confounds the third hypothesis that biomass may be low in the shallow water due to higher levels of grazing, and be similarly low in the deeper water, but due to the lower light levels. This finding is contrary to those of Cheroske *et* al (2000), who found biomass to be reduced in areas of high disturbance, and van den Hoek *et* al (1978), who only found significant seaweed populations at depths below 27 m at Curacao, Netherlands Antilles. Hatcher and Larkum's results (1983) were similar to those of the present study. They found, despite significantly higher levels of grazing in shallow waters, no significant correlation between the grazing pressure and the turf algal standing crop, concluding that grazing intensity is only an adequate predictor of benthic algal standing crop within limited temporal and spatial scales. Light levels did indeed decrease rapidly from the surface to 27 m, indicating that the effects of light attenuation on the epilithic seaweed community biomass may be more important than the effects of grazing at Sodwana Bay. When considering biomass change with depth, however, it should be remembered that this data does not represent the true biomass at the sample sites, but rather subjectively selected portions of the algal community.

The fourth hypothesis of the present study is that the effects of sand inundation would not be predictable in determining seaweed communities. Airoldi and Virgilio (1998) showed that turf responses to sedimentation vary at different spatial scales and depend on the concomitant action of other physical and biological factors. Other factors that may be important in determining the levels of sand inundation in a community might include the proximity of the community to large sand patches, the effects of wave action, microcurrents and macrocurrents, and hence the effects of seafloor topography. Supporting this hypothesis, an insignificant correlation was found between % sand cover and depth, and those quadrats that were particularly inundated with sand (Quadrats 45, 25, 43 and 12, at 75, 60, 42 and 38 % cover respectively) showed only slight affinities in the ordination. The effects of wave action, light, animal grazing and competition, all of which change with depth, are evidently more important in determining seaweed community composition. The insignificant correlation between % sand cover and depth could also be a collecting artifact, as quadrats were subjectively sampled, and the proximity of sites to sandy patches would most likely have been random. Although the effects of sand inundation were not shown to be predictable, they are evidently important, because within the deeper water communities of Sites 2-5 a community separation occurred according to the % cover of sand, over and above a clear separation that was closely linked with depth.

This study found the Sodwana Bay seaweed flora to be typical of a tropical coral reef, and it showed tremendous levels of α-diversity. Seaweed communities clearly change with depth, but the biggest change occurs between the shallow subtidal zone (approx 1 m depth) and deeper waters (>5 m depth), mostly likely due to the effects of wave action; thereafter communities do change with depth, but the effects are less pronounced. It seems as though light attenuation with depth is crucial in determining seaweed communities and % seaweed cover, biomass and diversity are all highest in shallower waters. Sand inundation patterns, although important in determining seaweed community structure, do not appear to be predictable.

Further sampling by the Belgian-South African phycologist collaboration in the St. Lucia-Sodwana Bay area of KwaZulu-Natal is currently underway. This study will analyse how seaweed communities change with depth at other locations besides Sodwana Bay, and will then compare the results with those of the present study, thus contributing towards a more complete understanding of the poorly understood KwaZulu-Natal subtidal flora.

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Appendix

Table 2. List of algae collected at Sodwana Bay. Values in columns are numbers of plots in which each species was found, at each locality

Site	**1**	**2**	**3**	**4**	**5**
Rhodophyta					
Acanthophora cf. *spicifera*					1
Acrosorium cf. *acrospermum*	2				
Amphiroa beauvoisii		2		1	
Amphiroa rigida	3	1		3	
Amphiroa sp. 1	1				
Apoglossum cf. *spathulatum*				1	
Botryocladia skottsbergii					2
Carpopeltis phyllophora					1
Carpopeltis sp.			1		
Ceramiaceae indet. 1 ("Asp.")		1			
Ceramiaceae indet. 2	1				
Ceramium cf. *codii*		1			
Ceramium sp. 5/2			1		
cf. *Jania* sp.	1				
Chamaebotrys boergesenii					1
Champia compressa		2	2	1	5
Champia parvula		1			
Champia sp. 1		1			
Cheilosporum sagittatum	2				
Chondria armata	1				
Chondria cf. *collinsiana*	1				
Chondria cf. *dasyphylla*		2			
Chondria cf. *minitula*				1	
Chondria dangeardii		1		1	
Chondria simpliciuscula	1	1	4	1	4
Chondria sp.	1	1	2	1	
Crouania franciscoi		3			1
Dasya flagellifera Boergesen	2	2			
Dasya sp. nov.		1			
Delesseriaceae indet.	1				
Delesseriaceae sp. 2					1
Delesseriaceae sp. 3					1
Eucheuma cf. *odontophorum* (Norris 1992)				1	
Falkenbergia				1	
Galaxaura marginata	1				1
Gelidiella sp.	1	1	1		
Gelidiopsis repens			2	1	
Gelidiopsis sp. 1	1				
Gelidiopsis sp. 2	1				
Gelidium cf. *caespitosum*	1			1	
Gelidium lubrica		1			
Gelidium reptans	3	3	1		3
Gelidium sp. C			1		
Gelidium sp. Undescribed			4	5	1
Gloiocladia iyoensis		1		1	2
Gracilaria cf. *canaliculata*	1				
Gracilaria millardetii	1				
Griffithsia cf. *rhizophora*	1				
Griffithsia japonica	3	1			
Griffithsia sp. 1	1				
Haliptilon cubense	1				
Haliptilon subulatum	3				
Herposiphonia insidiosa			1		
Herposiphonia secunda	2			1	
Herposiphonia sp		1	2		1

Table 2. Continued

Site	**1**	**2**	**3**	**4**	**5**
Heterosiphonia arenaria	1				
Heterosiphonia cf. *crispella*		1		1	
Hypnea spinella	5	5	3	3	5
Hypneoid sp. 1	1				
Hypoglossum sp.				1	1
Jania ungulata f. *brevior*	3	4	5	4	2
Laurencia brongniartii		1			1
Laurencia natalensis		1			
Leptofauchea anastomosans		1	1	2	1
Lophocladia lallemandii		2		1	2
Martensia fragilis		3	4		
Peysonnelia capensis					1
Plocamium sp. 1				2	3
Plocamium sp. 2					1
Plocamium sp. 3	1				
Plocamium sp. 4	1				
Polysiphonia cf. *urbana*	2				
Polysiphonia flora		1			
Polysiphonia sp. 2	1				
Portieria hornemannii	1				1
Pterocladiella caerulescens complex	2				
Pterocladiella sp.	1	1	1		
Rhodophyta indet.		1	1	1	
Rhodymeniaceae sp. Indet.		1			
Spyridea filamentosa	2				
Symphocladia marchantioides	2				
Tricleocarpa cylindrica		1		1	
Chlorophyta					
Bryopsis sp. 1		1			
Boodleopsis pusilla	1				
Caulerpa racemosa	2				
Caulerpa scalpelliformis	2				
Caulerpa sp. 1		1			
Chamaedoris delphinii	2				
Cladophora sp.	1				
Cladophora vagabunda		1	1	1	
Codium incognitum		1			2
Dasycladus ramosus	1				
Halimeda cuneata	3				
Microdictyon kraussii					1
Pseudocodium de-vriessii	2				5
Udotea indica	2				
Ulva sp.		1	1		
Phaeophyta					
Dictyopteris delicatula	2	3	4	4	2
Dictyota cervicornis	1	1		1	
Dictyota ceylanica	2	2	4		3
Dictyota humifusa		2			
Dictyota sp.	2	2	4	1	3
Lobophora variegata	5	4	5	5	2
Sargassum sp. 1 (teeth)	1		3	3	
Sphacelaria rigidula	1	1	1	2	
Zonaria subarticulata					1