Patterns in subtidal seaweed communities on coral-dominated reefs at Sodwana Bay on the KwaZulu-Natal coast, South Africa

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Subtidal seaweed communities of the northern coast of KwaZulu-Natal (KZN) have not been studied before. At Sodwana Bay, we tested the hypotheses that the seaweed communities would (1) differ floristically with depth, (2) be more species-rich in shallower water, (3) show similar biomasses within the depth range sampled and (4) be affected (biomass and/or species composition) by sand. Samples were collected (using SCUBA) from reefs ('sites') at depths of about 1m, 7m, 10m, 15m and 26m. Each sample comprised all macroscopic (non-crustose) seaweeds within a 25cm x 25cm quadrat (five quadrats per depth). Environmental factors, including percentage sand cover and depth, were recorded. The seaweed communities were mainly compact turfs; a total of 82 Rhodophyta, 14 Chlorophyta and eight Phaeophyta were recorded. Ordination (canonical correspondence analysis) and classification (Twinspan) of the data showed clear differences in the floristic composition (either as species biomass or

presence/absence) with depth, mainly between shallow subtidal communities (0.5–1.0m depth) and those at intermediate depths (5.5-15.0m), followed by the deepest communities (25.7-29.0m) and those at intermediate depths. The shallow samples showed the greatest species diversity. Total seaweed biomass decreased significantly with depth and percentage bare (seaweed-free) substratum increased significantly with depth, possibly because of lower wave action, light penetration, or different grazing patterns. Sand (as percentage sand cover) also affected seaweed community composition, but this showed no pattern with depth. The algal communities on these reefs at Sodwana Bay showed exceptional α -diversity, with 104 taxa (>20% of the recorded KZN flora) occurring in the total sample area of only 1.56m². The seaweed communities of northern KZN are structurally and floristically similar to those of other tropical coral reefs around the world.

Keywords: coral reef algae, seaweed communities, seaweed diversity, Sodwana Bay, South Africa, turf algae

Introduction

It is now generally recognised that coral-dominated reef systems have a significant and functionally important algal component (Price and Scott 1992, Littler and Littler 1994). Odum and Odum (1955) pointed out that the trophic structure of coral reef systems is dominated by the primary production of plants, but most subsequent research has focussed on the encrusting corallines that often provide the primary cement for the reef matrix and on the role of symbiotic dinoflagellates (Price and Scott 1992). Large seaweeds are seldom conspicuous on coral reefs, but research has begun to demonstrate the importance of the inconspicuous turf algae in the trophic structure of many reefs (Adey and Goertemiller 1987, Klumpp and McKinnon 1989, Price and Scott 1992). Such turfs generally dominate primary production of coral reef plant communities (Adey and Goertemiller 1987, Hackney et al. 1989). Despite their low biomass (Rogers and Salesky 1981), their exceptionally

rapid growth rate leads to a biomass turnover once every 4–12 days (Klumpp and McKinnon 1989), and they may provide up to 70–80% of total primary productivity on coral reefs (Hackney *et al.* 1989).

These characteristics are considered to be adaptations to heavy grazing by fish and invertebrates, which consume nearly all of the algal production (Hay 1981, Klumpp and Polunin 1989). Turfs can therefore persist under intense grazing, whereas large seaweeds adapt to grazing mainly through avoidance in grazing refugia (Hackney *et al.* 1989) or the production of grazer-deterrent substances in the thallus (Paul and Hay 1986). Our previous diving observations suggested that seaweed turfs are abundant and ubiquitous on subtidal reefs in the extreme north-east of South Africa, such as at Sodwana Bay on the KwaZulu-Natal (KZN) coast.

Besides grazing, other factors are also considered to promote turfs, especially abrasion and light reduction caused

by sand (Airoldi and Virgilio 1998). Similar to the findings of Hatcher and Larkum (1983) regarding grazing disturbance, Airoldi and Virgilio (1998) concluded that turf responses to sedimentation varied with spatial scale and depended also on other physical and biological factors. Light is of course very important in the vertical distribution of algae, but generally the turf community can extend down to the accepted limit of the euphotic zone, where only 1% of surface radiation remains (e.g. 50–65m in the Netherlands Antilles; van den Hoek *et al.* 1978).

Taxonomically, tropical algal turfs are diverse, forming intermixed, multispecies communities that contain taxa of four algal divisions: the Rhodophyta (which tend to dominate), Phaeophyta, Chlorophyta and Cyanophyta. Juvenile or suppressed individuals of larger seaweed species often occur, sometimes forming a major part of a community (Price and Scott 1992), and encrusting and microscopic epiphytic algae often grow in close association with turf species. These algal turf communities are generally rich in species and contain a large proportion of 'rare' species. For instance, in a study on the central Great Barrier Reef, 63% of the algae found were 'rare' (accounting for <7% of the canopy, Scott and Russ 1987).

Morphologically, the turfs are small (usually <10mm high), with slender branches of <1mm width. Thalli frequently have a prostrate axis that attaches to the substrate at different points, giving rise to erect branches that result in a spreading turf-like habit (Price and Scott 1992). Branches are generally cylindrical but sometimes flattened, and usually not calcified.

Because turf algae are small, morphologically simple and frequently non-reproductive, they are difficult to identify in the laboratory and almost impossible to identify in the field. Worldwide taxonomic knowledge of this group is poor relative to many other reef organisms (Price and Scott 1992), which in turn restricts further research on their biology.

The subtidal seaweed communities of the KZN coast remain undescribed (Bolton and Anderson 1997, Leliaert *et al.* 2001). However, a recent South Africa/Flanders project has produced a number of taxonomic and biogeographic publications and has enabled initiation of ecological studies of KZN algal communities. Biogeographic analyses of intertidal collections show that there is an important turnover in species composition between the St Lucia Estuary in the south and Sodwana Bay in the north (Figure 1; Leliaert *et al.* 2001, Bolton *et al.* 2004), corresponding to the boundary between a tropical East African flora in the north and a warm-temperate flora to the south. The seaweed flora from Sodwana Bay northwards is predominantly composed of tropical Indo-West Pacific species.

These marine floristic provinces result from the environmental conditions in the region. The dominant oceanographic feature on the northern KZN coast is the Agulhas Current (Schumann 1988), which is formed by the confluence of tropical surface waters in the Moçambique Channel and areas south of Madagascar (Ramsay 1994). The continental shelf in northern KZN is very narrow, with a shelf break in many places only 2–4km from the shore. The Agulhas Current flows very close inshore, attaining a maximum speed of up to 3m s⁻¹ (Ramsay 1994), and bathing



Figure 1: Map of coastline of KwaZulu-Natal, South Africa, showing location of Sodwana Bay

these shores in warm, tropical water. To the south of Cape St Lucia, the continental shelf widens, forming the shallow Natal Bight, with a maximum width of about 45km, and causing the Agulhas Current to move offshore (Schumann 1988). Topographic upwelling of cooler subsurface water causes the temperatures over the bight to fall about 2°C below those of Agulhas-dominated areas to the north (Lutjeharms *et al.* 2000), resulting in the decline in tropical species and prevalence of warm temperate species over this area (Bolton *et al.* 2004).

The tidal range on the KZN coast averages 2m (high microtidal or low mesotidal) and large swells from the south-east reach the coast for 40% of the year, whereas smaller north-easterly to easterly swells prevail for another 40% of the time (Ramsay 1994).

Modern coral reefs off the northern KZN/Mocambigue coast grow on aeolianite and beachrock reefs, which were created by the submersion and calcareous cementation of beach dunes that formed when sea levels were up to 130m lower than present, during the Late Pleistocene glacial maximum of about 18 000 BP (Ramsay 1994). Subsequent rises in sea level have left a series of shoals extending down most of the KZN coast, and a series of broad, intertidal, aeolianite and beachrock marine platforms that are exposed at low tides (Ramsay 1994). The subtidal outcrops in northern KwaZulu-Natal account for 20% of the continental shelf surface, and have been colonised by a thin veneer of Indo-Pacific corals at depths typically <25m the depth limit for coral growth being between 35m and 40m (Riegl et al. 1995). These south-eastern African coral communities are sometimes not considered 'true' coral reefs because there is no noticeable reef accretion, no typical geomorphological zones such as lagoons, reef crests or reef slopes, and a very uniform coral community structure (Riegl et al. 1995). They are the most southerly



Figure 2: Map of Sodwana Bay showing aeolianite reefs (after Ramsay 1994), with positions of Sites 1–5 indicated

coral reefs in Africa, and are 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 accessible to SCUBA divers are dominated by sponges (Riegl *et al.* 1995).

The present study is the first to document the subtidal macroalgal communities of the tropical KZN coast, or in fact of any part of the KZN coast. It aims to analyse floristic and biomass changes in benthic algal communities along a depth gradient at Sodwana Bay. The first hypothesis was that the species composition of these (mainly turf) communities would change with depth. The second was that macroalgal diversity would be higher in shallow water, as maintained by Abbott (1999) for Hawaii, who explained the effect mainly in terms of higher light levels. The third, based on previous diving observations, was that macroalgal biomass would be similar throughout the depths that could be sampled (0-30m), possibly as a result of higher grazing in shallow water countering the stimulatory effects of higher light levels in shallow water. Finally, because the reefs vary in profile and tend to lack corals near their edges, it was hypothesised that the presence of sand should affect biomass and/or species diversity of the algal communities.

Material and Methods

Study area

Sodwana Bay is approximately 300km north-northeast of Durban, South Africa, and 70km south of Moçambique (Figure 1). It lies in a Marine Protected Area administered by Ezemvelo KwaZulu-Natal Wildlife. The bay is formed by Jesser Point, an aeolianite shelf that is exposed at low tide. Underwater, a series of aeolianite reefs runs north-east from Jesser Point, parallel to the coast and at depths from 5m to 35m (Figure 2). Seaweed communities at five subtidal sites were sampled, and all depths were corrected to below MLWS.

Site 1 was a semi-sheltered rocky cove eroded into the seaward side of Jesser Point. Sampling was done at depths from 0.5m to 1.0m. Wave and sand action are high because the site lies in the breaker-impact zone during high tides. Site 2 (mean depth 6.8m) was on Quarter-Mile Reef, situated approximately 400m north of Jesser Point. Site 3 (mean depth 10.6m) was at Pinnacles, on Two-Mile Reef. The substrate consisted largely of bioclastic sediments with a high areal cover of large live corals and sponges. Site 4 (mean depth 14.5m) was at Four Buoy, on Two-Mile Reef. The reef at this site was of the typical aeolianite rock type, with additional bioclastic sediments being common. Site 5 was at Sponge Reef (mean depth 27m), on Two-Mile Reef, a low-lying reef of bioclastic sediments that slopes up gently from a sandy bottom.

Water temperatures at Sodwana Bay were measured at 17m depth (Celliers and Schleyer 2002), using continuous underwater temperature recorders (UTRs) at Nine-Mile Reef, about 12km north of the study site. In order to obtain a quantitative measure of light attenuation with depth, a Li-Cor underwater Spherical Quantum Sensor and data logger (Lambda Instruments) were used to measure irradiance at intervals from the surface down to 27m at 13:00–13.30 on 3 April 2002, during sunny conditions.

Sampling technique

Sampling was carried out between 30 March and 3 April 2002 by divers using SCUBA, except at Site 1 where snorkelling was used. Because algal communities were being studied, divers placed the quadrats subjectively (five 25cm × 25cm wire quadrats at each site), but haphazardly, in typical algal beds, rather than randomly or systematically over the whole substratum. At all sites, large portions of reef were covered by corals, sand or exposed substrata without any algal cover; these areas were not sampled.

Within each quadrat, the depth and percentage cover of sand, cover of encrusting corallines, and percentage cover of bare substrata (rock or dead coral) were estimated and recorded on a slate. All the visible algae within each quadrat, excluding highly adherent crustose forms, were scraped off the substratum using a paint-scraper and collected in numbered, fine-mesh bags. The seagrass *Thallassodendron ciliatum* (Forsk.) den Hartog, and its epiphytes were also removed where they occurred in a quadrat.

On shore, very abundant algae (and Thalassodendron) were identified, mopped with paper towel, weighed fresh and all but a few voucher specimens discarded. The remainder of each sample was preserved in 5% formalin in seawater for subsequent sorting. Samples were identified, sorted and weighed to an accuracy of 0.05g (fresh weight) in the laboratory. Specimens that weighed <0.05g were recorded as present and later assigned a nominal weight of 0.01g for the purpose of analysing the data quantitatively. Identification was done to the level of species (where possible) or apparent species were assigned numbers; sub-specific taxa were not distinguished. It proved difficult, and in some cases impossible, to identify some of the small vegetative turf taxa to species level. Larger species were pressed and sectioned, and smaller species were stained with fast green or aniline blue and mounted in corn syrup on microscope slides for later identification and for cross-referencing during sorting of subsequent samples. Specimens were also compared with those collected during the concurrent South Africa/Flanders taxonomic studies along the KZN coast, which also benefited from several new records that were found during this study.

Analyses

Twenty-five quadrats and a total of 104 taxa were sampled. Correlations were plotted of the relationships between depth and percentage sand cover, depth and percentage bare substrate, depth and species number, and depth and biomass. P-values and correlation coefficients for each relationship were calculated using STATISTICA 5 for Windows (StatSoft).

The program CANOCO (ter Braak 1987) was used for the ordinations of both species biomass and presence/absence data with environmental data (as part of the ECOM package; Pisces Conservation Ltd, England). For both datasets, a correspondence analysis was performed. This is an indirect gradient analysis 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. This 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 best be 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 1987). The classification analysis TWINSPAN (Two-way-indicator-speciesanalysis; Hill 1979) was used as a Windows program (Pisces Conservation Ltd, England) to group sets of sites on the basis of their floristic composition (as presence/ absence data).

Results

Monthly mean temperatures were between 22°C and 26°C, whereas the lowest temperature recorded was 18°C and the highest just under 30°C (Figure 3). Minima occurred in winter and maxima in summer.

The light profile at 13:30 on a clear day in April (autumn) shows a typical attenuation with depth, from 1 510µmol photons $m^{-2} s^{-1}$ at the surface to 116µmol photons $m^{-2} s^{-1}$ at 27m (Figure 4). Under these conditions, 1% of surface light would be present at approximately 46m.

There was no significant correlation between depth and percentage sand cover within the 25 quadrats (r = -0.13, p = 0.544). Samples with a moderate (5–20%) sand cover were found at all sites; samples with particularly high values were found in Quadrats 45 (75%), 25 (60%), 43 (40%) and 12 (35%). There was no significant correlation between depth and number of species per quadrat (r = -0.36, p = 0.078). The relationship between depth and percentage bare substratum was significant (Figure 5; r = 0.60, p = 0.002), showing that there was a higher percentage of bare substratum in deeper water, at least in algal beds. The results indicated a trend of decreasing seaweed biomass with water depth (Figure 6; r = -0.4, p = 0.049).

Site 1 was dominated by sand-binding algal turfs, with only Quadrat 14 falling in a patch of seagrass. Sand cover on the substratum was moderately high, and there were only a few small scattered corals, none of which were within the quadrats. Site 2 had low coral cover, was largely covered with algal turf with scattered individuals of a few foliose species and articulated coralline species, and had no bare substrata. Sponges were common and the tunicate Pyura stolonifera Heller dominated pinnacles. The reef at Site 3 had a high coral cover with extensive patches of algal turfs and a few foliose species. Sea urchins and fish were numerous. At Site 4 the biotic cover was dominated by algal turfs, there were some sandy patches, some corals and a relatively high cover of bare aeolianite rock. The deepest Site (5) had a high coral cover, some bare substratum, and patches of turf algae interspersed with occasional foliose



Figure 3: Sea water temperatures at Sodwana Bay, 1995–2000. Mean monthly values are for the whole period, minima and maxima are means of the lowest and highest temperatures that were measured during each particular month

individuals. Sponges were more numerous than at the shallower sites.

A total of 104 seaweed taxa was recorded in the 25 sample quadrats. At all sites the greatest number of species belonged to the red algae (Figure 7), and were mostly small turf-forming species. Rhodophyta found at all sites were: Hypnea spinella (C. Agardh) Kützing (21 guadrats), Chondria simpliciuscula Weber van-Bosse (at least one quadrat at each site), and Jania ungulata (Yendo) Yendo (18 quadrats). Several brown algae that were present and relatively common at all sites were: Lobophora variegata (Lamouroux) Womersley ex Oliveira (either as a low turf component or with larger conspicuous blades), Dictyopteris delicatula (Lamouroux) Lamouroux, and Dictyota ceylanica Kützing. Several large seaweeds occurred as isolated or scattered individuals that contributed disproportionately to the biomass when they fell within quadrats, e.g. Tricleocarpa cylindrica (Ellis & Solander) Huisman & Borowitzka and Codium incognitum (P. Silva). Two occasional, conspicuous foliose species that were noticed at the deeper sites, but did not fall



Figure 4: Relationship between light and depth measured at 13:30 on a clear day in April, between the surface and 27m depth at Sodwana Bay



Figure 5: Relationship between percentage bare substratum and depth measured within quadrats at Sodwana Bay (r = 0.6, p = 0.05)

within quadrats, were *Halymenia durvillei* Bory de Saint-Vincent and *Titanophora pikeana* (Dickie) J. Feldmann.

Ordination of the species biomass data in all 25 quadrats (correspondence analysis, not shown) produced a highly skewed pattern with Quadrat 14 completely separate on the x-axis and forcing all 24 other quadrats into a small group. Quadrat 14 was very unusual in that it fell within a community completely dominated by the seagrass *Thalassodendron*, with a high biomass of epiphytic *Haliptilon subulatum* (Ellis & Solander) Johansen and small amounts of several other algae that appeared to be epiphytes on the seagrass. Quadrat 14 was therefore excluded from subsequent ordinations.

Correspondence analysis of the biomass of algal species in the remaining 24 quadrats (Figure 8) produced a minor separation along the first axis, which did not show any pattern that obviously relates to the environmental variables. However, groups of quadrats that separated out on account of disproportionately high biomasses of particular non-turf species were sometimes represented by only one or two



Figure 6: Relationship between seaweed biomass and depth measured within quadrats at Sodwana Bay (r = -0.4, p = 0.04)



Figure 7: Number of green, brown and red species of seaweed species per site at Sodwana Bay

12

11

Figure 8: Correspondence analysis (CANOCO) ordination showing similarity between samples (quadrats), based on species biomass (excluding Quadrat 14). Samples are arranged along arbitrary x- and y-axes with eigenvalues of 0.913 and 0.884 respectively. The unconstrained effects of depth and percentage sand cover are shown by arrows

43

35

• 24

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•23

32^{•33}

•22

42

• 34

•31

41 44 53•

, Depth 52

51

45

25

12

11° 1513

Sand

Figure 10: Canonical correspondence analysis (CANOCO) showing similarity between samples (quadrats), based on species biomass (excluding Quadrat 14). Eigenvalues for x-and y-axes are 0.510 and 0.153 respectively. The constrained effects of depth and percentage sand cover are shown by arrows



Figure 11: Canonical Correspondence Analysis (CANOCO) showing similarity between samples (quadrats), based on species presence/absence (excluding Quadrat 14). Eigenvalues for x-and y- axes are 0.491 and 0.233 respectively. The constrained effects of depth and percentage sand cover are shown by arrows







individuals per quadrat. For example, Quadrats 22 and 53 were characterised by high biomasses of *C. incognitum*, Quadrats 21 and 45 each contained one large individual of *T. cylindrica*, Quadrats 21 and 25 had high biomasses of *D. delicatula* Lamouroux, and Quadrats 25 and 45 had a high cover of sand (60% and 75% respectively).

In order to avoid the disproportionate effect of the biomass of occasional large seaweeds that occur among the mainly turf communities, only presence/absence data for the 24 quadrats were used, in an indirect ordination (Figure 9). Site 1 samples separated out from all the others on the first axis, which was related to sand cover and depth. This result was consistent with the observation during sorting of the samples, that seaweed species composition was similar among Sites 2–5, but that the shallow Site 1 was different. Site 1 samples also separated out widely from each other on the second axis, indicating that they differed markedly in species composition. There was relatively little axis-2 differentiation within the samples from Sites 2–5.

Direct gradient analyses (CCA ordinations) using both biomass (Figure 10) and presence/absence data (Figure 11), using the environmental variables of depth and percentage sand cover to constrain the axes, helped to show the remaining variation within the species data that was not obvious in the indirect analyses (Figures 8 and 9). The results of these direct gradient analyses were essentially similar to each other, so they are described together. Sites 1 and 5 form discrete groups at each end of the depth gradient. The remaining quadrats show some sorting along the depth gradient, but a more marked separation according to sand cover, particularly Quadrats 25 and 45 (60% and 75% sand cover respectively). Where the biomass data were used (Figure 10), the constraining effects of the environmental variables have over-ridden the effects of the high biomass of C. incognitum, Tricleocarpa and D. delicatula, which caused a noticeable separation of Quadrats 21, 25 and 45 in the (unconstrained) correspondence analysis (Figure 8).

Classification of the site data using TWINSPAN (Figure 12) supported the ordination results well, except that two intermediate-depth sites (23 and 44) were included with the deep group (Sites 51–55). Like the latter sites, both of these samples had relatively few species in them, but both contained an abundance of *D. delicatula* and *L. variegata*.

Species found only in shallow-site quadrats were the Rhodophyta Acrosorium acrospermum (J. Agardh) Kylin, Cheilosporum sagittatum (Lamouroux) Areschoug, Haliptilon subulatum, Polysiphonia urbana Harvey, Spyridia filamentosa (Wulfen) Harvey and Symphocladia marchantiodes (Harvey) Falkenberg, and the Chlorophyta Caulerpa racemosa (Forsskål) J. Agardh, Caulerpa scalpelliformis (R. Brown ex Turner) C. Agardh, Halimeda cuneata Hering and Udotea indica A. Gepp & E. Gepp. Three species of Rhodophyta were found only at the deepest site (5): Botryocladia skottsbergii (Børgesen) Levring, Carpopeltis phyllophora (J. Hooker & Harvey) Schmitz and Martensia fragilis Harvey. Species absent from the shallow site but found at all other sites were Gelidium reptans (Suhr) Kylin and Leptofauchea anastomosans (Weber van-Bosse) R. Norris & Aken.



Figure 12: Results of TWINSPAN classification of samples (quadrats). 'Indicator species' are shown on respective axes: these are the taxa that, within the data, create the most distinction in the classification

Discussion

The algal communities at Sodwana Bay were found to be dominated by turfs, comprising mainly small red algae, but also interspersed with isolated individuals of larger upright taxa, usually belonging to genera known to be protected from grazers by chemicals in the thallus (e.g. Laurencia, Halymenia) or carbonate-hardened thalli (e.g. Amphiroa) or both (e.g. Halimeda). The annual mean temperature is well above the 20°C considered to indicate a tropical biogeographical region (Lüning 1990). However, perhaps more importantly, means of even the lowest temperatures recorded during each month only fell below 20°C in September and October, indicating that there are probably very few occasions when cooler water might limit the growth or reproduction of tropical species. Furthermore, the Sodwana Bay samples had a high incidence of 'rare' species, as is typical of tropical systems in other parts of the world. Stuercke and McDermid (2004) considered 60% of the taxa in Hawaiian turfs to be 'rare', based on methods that essentially measured cover. Scott and Russ (1987) found that 63% of the central Great Barrier Reef species were 'rare', individually comprising <7% of the canopy cover. At Sodwana Bay, 95% of the taxa individually comprised <7% of the biomass (percentage cover of individual species was not measured). 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 common at Sodwana Bay: Ceramium, Gelidiella, Herposiphonia, Hypnea, Jania, Laurencia, Polysiphonia (Rhodophyta), Cladophora (Chlorophyta), Dictyota and Sphacelaria (Phaeophyta). Two of the most abundant species in Hawaiian turfs, Hypnea spinella and Dictyota ceylanica (Stuercke and McDermid 2004) were also common at Sodwana Bay. Although Sodwana Bay lies near the southern limit of the East African distribution of coral reefs, the subtidal seaweed community is therefore floristically similar to other tropical reef assemblages.

The results presented here support the hypothesis that seaweed communities at Sodwana Bay change floristically along a depth gradient. Although there was no correlation between depth and number of species per quadrat, the ordinations showed that communities in the shallow Site 1 (<1m) and deepest Site 5 (27m) were different (in terms of many of the actual species present) from those at all intermediate depths. Whereas depth itself is not expected to cause such changes, it is mainly a surrogate measure for other environmental variables such as irradiance and wave exposure, and probably factors such as herbivory, competition and epiphytism. It is well known that irradiance decreases logarithmically with depth (van den Hoek 1978, Abbott 1999, Cheroske et al. 2000), as is shown here. At Sodwana Bay >8% of surface irradiance reaches 27m, supplying sufficient light for algal growth. Absolute depth limits of multicellular algae are determined by light penetration and therefore by water clarity. However, seaweeds require at least 0.05–0.001% of surface illumination in order to survive (Lüning 1990). Extrapolation of the light curve to 50m indicates 0.6% of surface light on that day in autumn at Sodwana Bay. To establish the annual amount of light available would require frequent measurement over at least a year. However, it is perhaps not surprising that well developed beds of macroalgae have recently been found at Sodwana Bay at depths of 50m and more, on unstable substrata (K Sink, African Coelacanth Ecology Programme, pers. comm.).

In shallow water, higher photosynthesis and productivity would be expected, and perhaps the ability to exploit more niches, leading to a more diverse flora. However, shallow and deep communities will be controlled by different interspecies interactions such as predation, herbivory, competition and mutualisms, and would support species assemblages that have different light and nutrient requirements. The present quadrat data showed that bare substrata increased with depth, suggesting that there was a lower rate of colonisation by seaweeds, which may be a compound effect of reduced productivity and hence an amplified effect of animal grazing.

The shallow (Site 1) seaweed communities were floristically distinct from all other sites, and also the most diverse in terms of species, supporting the second hypothesis. According to Abbott (1999), the tropical, shallow subtidal zone is characterised by a higher diversity of taxa than the deep subtidal zone. Shallow communities undoubtedly experience more water motion, which increases nutrient exchange but also sand abrasion, and may have secondary effects by simultaneously influencing grazers and also sessile invertebrates with which seaweeds compete for space. Site 1 is in a zone of very high wave impact, and apparently subject to abrasion by suspended sand. There were many and varied fish, suggesting high grazing pressure. Turf-forming algae, which are able to maintain high diversity in disturbance-prone environments (Cheroske et al. 2000), are particularly well suited to survive in the relatively wave-disturbed conditions at Site 1. Although there was no statistical correlation between depth and number of species per guadrat, Figure 7 indicates relatively large total numbers of Rhodophyta and Chlorophyta at the shallowest site: a trend that would need to be confirmed by more sampling. However, the relative effects of factors such as grazing, wave action and sand abrasion are likely to be complex, and would require directed studies. Despite the higher diversity in the shallow samples, the prediction that seaweed species diversity would in general be inversely

related to depth was not supported over the range of our sampling.

Biomass was found to decrease significantly with depth, contradicting the third hypothesis. Cheroske et al. (2000) found lower biomass levels in areas of high disturbance, and van den Hoek et al. (1978) only found significant seaweed populations below 27m at Curacao, Netherlands Antilles, where grazing was reduced. However, Hatcher and Larkum (1983) found that, despite significantly more grazing in shallow water, there was no significant correlation between grazing pressure and standing crop of turf algae, and they concluded that grazing intensity is only an adequate predictor of benthic algal standing crop within limited temporal and spatial scales. Significantly, a large population of at least six species of foliose macroalgae was found at 55m at Sodwana Bay in April 2004, growing on coral fragments covered with a thin layer of sand (W Freshwater, University of North Carolina, Wilmington, USA, pers. comm.). This population was not near any hard reefs, and was probably only able to flourish in the absence of the normal grazers associated with hard reefs. It is therefore clear that generalisations about the effects of depth on seaweed biomass in these tropical systems must be treated with caution.

It was hypothesised that sand inundation (measured as percentage cover of sand) would affect the biomass or composition of seaweed communities at Sodwana Bay. Although there was no correlation between sand cover and depth, indicating no predictive relationship, direct ordinations of both biomass and presence/absence data did show some sand effects on algal communities. Among the samples from Sites 2–5 (depths from about 4m to 28m) some separation of communities occurred according to sand cover. Airoldi and Virgilio (1998) showed that responses of turfs to sedimentation vary at different spatial scales and depend on other physical and biological factors as well. Furthermore, sand moves, particularly in shallow water, and long-term effects are unlikely to be accurately measured by instantaneous percentage cover estimates. At Sodwana Bay, factors such as light, or other factors that were not measured, such as grazing and competition for space, may be more important in determining algal communities. Turfs are affected, and apparently favoured, by disturbance (Cheroske et al. 2000), but because of complex interactions, the effects of different disturbances are probably not clearly predictable.

This study shows that Sodwana Bay has a typical tropical coral reef flora, dominated by floristically diverse turfs, with occasional large, conspicuous foliose algae. The composition of communities changes somewhat with depth, but the shallow subtidal flora (0–1m) is the most diverse and differs most from communities down to at least 27m. The seaweed communities at Sodwana Bay show a remarkably high α -diversity, in that 104 taxa of Rhodophyta, Phaeophyta and Chlorophyta were recorded in a total sample area of 1.56m². This number represents >20% of the recorded seaweed flora of KwaZulu-Natal. Remarkably, this percentage is the same reported by Stuercke and McDermid (2004) in a recent study of turfs in Hawaii, where, in a total sampling area of only 1.13m², they found representatives of

20% of the known flora for the Hawaiian islands. Such studies clearly show that the algal components of such coral reefs may be exceptional, not only in terms of productivity, but also in terms of diversity.

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