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Sublittoral seaweed communities on natural and artificial substrata in a high-latitude coral community in South Africa

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Abstract

Coral mortality may result in macroalgal proliferation or a phase shift into an alga dominated state. Subtidal, high-latitude western Indian Ocean coral communities at Sodwana Bay on the KwaZulu-Natal coast, South Africa, have experienced some mortality because of warm water anomalies, storms and other causes, but the response of the macroalgae is unknown. We investigated the abundance and diversity of benthic algae on different hard natural substrata (dead digitate, brain and plate corals and beach rock) on Two-Mile Reef, Sodwana Bay. We also compared algal communities colonising ceramic, marble and pretreated ceramic tiles placed on the reef for six months. We identified 95 algae (14 Chlorophyta, 11 Phaeophyceae, 69 Rhodophyta and one cyanobacterium). Assemblages on natural and artificial substrata were dominated by the brown alga *Lobophora variegata* (Lamouroux) Womersley ex Oliveira and non-geniculate corallines (Rhodophyta, Corallinaceae). Cluster and ordination analyses revealed that the algae showed no affinity for particular substrata, whether natural or artificial. Algal cover was occasionally higher on rougher tiles and crustose corallines were significantly more abundant on marble than ceramic tiles. Two-Mile Reef had 23.1% dead and 48.4% live scleractinian coral cover, where dead corals were colonised indiscriminately by many small algal species, but there was no evidence of algal proliferation. The results provide a baseline for monitoring this high-latitude reef system.

Introduction

Coral reefs are among the most ecologically heterogeneous and economically important ecosystems on Earth, but are under stress from a variety of anthropogenic factors, such as overfishing, pollution and sedimentation, as well as from climate change and natural disturbances (Hughes 1994; Wilkinson 2002; Hughes et al. 2003; Pandolfi et al. 2005). Algae are rapid and efficient primary colonisers of newly available substrata on almost any part of a coral reef that has been opened by disturbances (Diaz-Pulido and McCook 2002). Past studies have shown how hurricane damage on reefs can lead to rapid macroalgal proliferation (Hughes 1994; Fong and Lirman 1995; Rogers et al. 1997) and, in severe cases, cause extensive phase shifts from coral-dominance to dominance by benthic algae (McCook 1999; Hoegh-Guldberg et al. 2007), potentially contributing to long-term reef degradation (McCook 1999). Rising ocean temperatures have triggered mass bleaching episodes that have resulted in catastrophic loss of coral cover around the world (Glynn 1993; Hoegh-Guldberg et al.

2007). Many studies on coral bleaching describe the physiological and climatological causes of bleaching, behaviour of zooxanthellae and recovery of zooxanthellae after damage (e.g. Hoegh-Guldberg 1999). However, there has been little work focusing on algal recruitment on damaged corals that fail to recover their zooxanthellae. Work that has been conducted includes recruitment dynamics studies (Diaz-Pulido and McCook 2002; Titlyanov et al. 2008), which reported that dead coral skeletal tissue was colonised by diverse commu nities of macroalgae and concluded that macroalgae do not colonise healthy coral tissue and that algal colonisation was not the initial cause of coral tissue mortality. Successional patterns of tropical macroalgae rely upon vacant space, nutrient availability and grazing pressure. Various studies have reported the recovery of coral reef systems after a catastrophic event and the succession of algae during this process, along with succession on experimental settlement plates. In general, turf algae are among the first to colonise available space, followed by a dominance of thin and finely branched filamentous seaweeds, which at a later stage are replaced by dense growths of thick canopyforming seaweed (McManus and Polsenberg 2004; Mumby 2009). The 37-year history of the coral reef assemblages in Moorea, French Polynesia, represents one of the longestkept records of coral reef dynamics. Between 1991 and 1994, disturbances caused declines in coral cover, with consequent colonisation by algal turfs. However, Adjeroud et al. (2009) did not observe a successional sequence of algal growth, but instead the cover of turf algae decreased and returned to pre-disturbance levels within a decade. This result indicates that the availability of empty substratum is not sufficient to cause a persistent increase in algal cover and that other factors, such as an increase in nutrients or a reduction in grazing pressure, may be pertinent for a phase shift to macroalgal dominance (McManus and Polsenberg 2004; Mumby et al. 2005). A pattern of algal succession emerged from the extensive loss of coral cover on the Great Barrier Reef, Australia, following the massive bleaching event in 1998. Algal assemblages were initially dominated by blue-green photosynthetic bacteria, but rapidly shifted to an assemblage dominated by algal turfs, whereafter fleshy macroalgae and crustose coralline algae overgrew the turfs during later stages of the succession (Diaz-Pulido and McCook 2002). Fluctuating weather conditions throughout the year strongly affect the abundance of macroalgae in tropical regions; for example, lower temperatures during the rainy season can cause a significant increase of algal biomass. Ateweberhan et al. (2006) carried out an extensive overview of seasonality of four major functional groups of coral reef macroalgae (canopy, foliose, turf and crustose corallines) in the southern Red Sea. They observed strong seasonal shifts in macroalgal biomass, although seasonal variation differed among groups. Canopy and foliose macroalgae were highly seasonal, whereas turf and crustose coralline algae displayed much less seasonal variability. The settlement and recruitment of algal propagules onto reef communities require suitable hard substrata and the ability to compete with organisms already present (Worm and Chapman 1998). Surface texture, material and chemical composition have been shown to influence strongly the settlement and survival of algal recruits. Diaz-Pulido and McCook (2002) reported that algal colonisation on clay settlement tiles differed markedly from that on dead coral skeleton and their subsequent study (Diaz-Pulido and McCook 2004) found that natural substrata supported more mature assemblages than artificial substrata. In addition, the species composition of algal assemblages differed according to the severity of bleaching damage to

the corals: species composition on severely bleached corals was in a more developed successional stage than that on less-bleached corals. The inshore, high-latitude coral communities of southern Africa suffered negligible impacts during past mass bleaching events, but the most recent bleaching in 2005 in southern Africa, when a warm-water anomaly affected much of the southern Indian Ocean, resulted in more extensive damage to coral on South African reefs (McClanahan et al. 2007; Celliers and Schleyer 2008). Although some information on subtidal macroalgal turf communities in Sodwana Bay is available (Anderson et al. 2005), there is no information on the distribution ofmacroalgal assemblages on the different types of hard substrata, including dead corals. There is also no information on possible seasonal changes in algal community structure. Although anecdotal reports received from divers by RJA suggested extensive seaweed colonisation of dead coral on Two-Mile Reef, this has never been formally investigated. This study aimed to investigate algal colonisation on the different types of hard substrata (including different taxa of dead coral) that are present on the reefs. We also explored the relationship between abiotic properties of artificial substrata (i.e. surface texture and material) and algal recruitment. Three hypotheses were tested: (i) different natural hard substrata support different algal commu nities; (ii) communities colonising different types of artificial substrata (ceramic tiles, marble tiles and pretreated ceramic tiles) would differ; and (iii) algal communities differ between autumn and spring (seasonal differentiation).

Material and methods
Data collection
The study was carried out on Two-Mile Reef (27°31′29″ S, 32°40′37″ E), which is located in the central Maputaland reef complex at Sodwana Bay (KwaZulu-Natal, South Africa; Figure 1). Two-Mile Reef is a highly rugose patch-reef system, with reef ridges, reef slopes and gullies (Ramsay and Mason 1990; Jordan and Samways 2001). The reef, lying 1 km offshore, is approximately 1.8 km long and 900 m wide and is always submerged (Ramsay and Mason 1990; Celliers and Schleyer 2008). The water depth on the reef varies between 6 and 10 m on its shallowest pinnacles, to 14–19 m on extensive deep subtidal reef flats and 24–27 m at the edge of the fore-reef (Celliers and Schleyer 2002). Study sites were scattered on the reef at various depths ranging from 8 m to 19 m. Seawater tempera ture was measured with a Starmon Mini (Star-Oddi, Iceland) recorder at 12 m depth on the reef. All fieldwork was carried out on 1–4 March and 6–9 September 2010 by divers using SCUBA. Because algal communities were being studied, divers placed quadrats at least 1 m apart in a stratified random pattern (fortyfive 10 cm × 10 cm wire quadrats per sampling period) on substrata bearing seaweeds, rather than randomly over the whole substratum of the reef. The same sites (within approximately 50 m) were sampled in March and September. All the visible macroalgae within each quadrat, except highly adherent crustose forms, were scraped off the dead coral using a paint scraper and collected in fine-mesh bags. The substratum directly under each of the quadrats was then recorded and was visually classified into one of four categories: digitate coral, plate coral, brain coral and 'hard (bare) substratum'. In instances where it proved difficult or impossible to scrape the surface effectively, chunks of the substratum were broken off using a chisel and hammer and taken to the field laboratory. Estimates of the relative cover of different types of substrata were made using line-point

intercept (LPI) methods along 20-m transect lines, which were placed haphazardly at approximately right angles to the reef axis. A diver swam along the transect line and recorded the benthic category directly below the transect line at every 0.25-m interval (80 points/transect; four transects per sampling period). Benthic categories used were: live coral, dead coral, macroalgae (including non-geniculate coralline algae), sand, hard (bare) substratum and sponge.
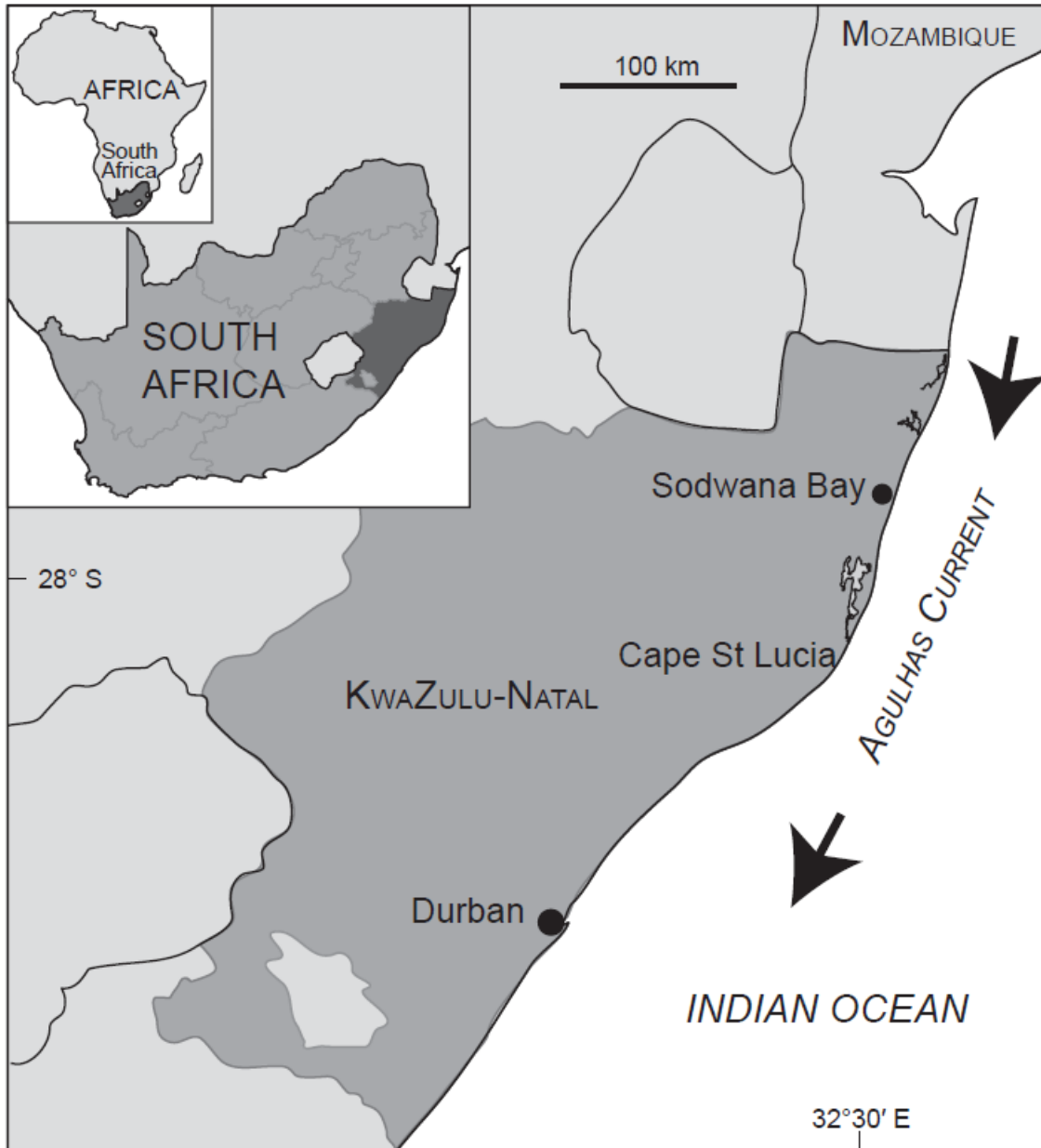

Figure 1: Map of KwaZulu-Natal, South Africa, showing the location of Sodwana Bay

In the field laboratory, each quadrat sample was placed in a sorting tray and covered with seawater. All macroalgae Dead coral was defined as a substratum that maintained the full structural integrity of coral, but had no live coral tissue, whereas bare consolidated surfaces on the reef that could from each sample (quadrat) were sorted into separate species or genera (provisional identifications) and an initial visual estimate of cover-abundance was made. A modified Braun-Blanquet scale (Lepš and Hadincová 1992) was used to assign a cover-abundance value to each species within each quadrat: 0 – no cover; 1 – rare (<5% cover); 2 – occasional (5–25% cover); 3 – common (25–50% cover); 4 – abundant (50–75% cover); and 5 – dominant (>75% cover). In cases where whole chunks of substratum were broken off, an initial estimate of cover was made, followed by subsequent sorting to species or generic level. Seaweeds were preserved in 5% formalin in seawater for subsequent identification, where possible to species level. When necessary, specimens were stained with fast green and mounted in corn syrup on microscope slides (Tsuda and Abbott 1985) for later identification and for cross-referencing during sorting of subsequent samples. Seaweeds were identified using morphological descriptions according to Jaasund (1976), Stegenga et al. (1997), De Clerck et al. (2005) and Oliveira et al. (2005) and/or compared to appropriate material and other published literature. Identification procedures for non-geniculate coralline algae followed Maneveldt and van der Merwe (2012).

Artificial settlement surfaces: *experimental design*
To test the hypothesis that seaweed recruitment would differ on different artificial settlement surfaces, we quantified algal colonisation on settlement tiles used by Hart (2012) to assess how coral settlement varies on different artificial settlement surfaces. Three replicate concrete Y-frames (Figure 2), with 15 settlement tiles attached to each, were positioned 5–15 m apart from each other on flat reef areas at three study sites on Two-Mile Reef (Figure 2).

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Figure 2: An example of a Y-frame to which the three types of tiles were attached and general appearance of the reef (photo: C Floros)

Each monitoring site was similar in depth and topography and was selected in a north–south direction on the reef. The northern site was the deepest (15–17 m), characterised by flat topography with few gullies. The central (12–15 m) and southern sites (9–12 m) were in an area of varied topography with sharp drop-offs into sand gullies. Three types of artificial substratum were used: unglazed ceramic tiles, marble tiles and ceramic tiles preconditioned with crustose coralline algae (ceramic tiles were preconditioned for two months in an aquarium where *Mesophyllum funafutiense* (Foslie) Verheij in Verheij & Prud'homme van Reine was prolific). All tiles were 9.7 cm × 9.7 cm × 1 cm and had a 6-mm hole drilled in their centre to enable horizontal attachment onto the frames. The weight of each frame (75 kg) and its flat, three-armed shape provided sufficient anchorage and stability for the settlement tiles during major turbulence on the reef. Five replicates of each tile type were anchored onto each Y-frame, in a stratified sampling design that mixed tile types on each arm. The tiles were left on the reef for six months (October 2009–April 2010), then retrieved and preserved in 4% formalin seawater solution for storage prior to examination in the laboratory. The upper surface of each tile was examined for fleshy algae and non-geniculate coralline algae using a Zeiss Stemi stereo dissection microscope at 10× magnification. The Braun-Blanquet scale was used to assign a cover-abundance value to the macroalgal recruits (including non geniculate coralline algae) on the tiles, using the same categories as for the algae on natural substrata. Subsequently, the macroalgae were scraped off the tile with a dull surgical blade; wherever possible, the algal material obtained was identified to species.

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Statistical analyses

Data were analysed using Community Analysis Package 4.0 (Pisces Conservation Limited). The seaweed community data were subjected to multivariate analysis (ordination by detrended correspondence analysis [DECORANA], using the option to downweight rare species) and cluster analysis (complete linkage, Bray–Curtis similarity coefficient), to show how substrata and seasons cluster with respect to their seaweed flora. To assess the adequacy of sampling, species accumulation curves were generated in PRIMER 6 (PRIMER-E Ltd), where a first-order jackknife (jackknife 1), a species richness estimator, was calculated. Using Statistica 11, a Kruskal–Wallis non-parametric test was used to detect significant differences in macroalgal abundance among different natural substrata (digitate coral, brain coral, plate coral and hard substratum) and likewise among the tile treatments (marble, ceramic and treated ceramic tiles). Differences among substrata/treatments were considered significant if $p < 0.05$. Where the results of Kruskal–Wallis tests were significant, pairwise Mann–Whitney tests between the substrata/treatments were performed with significance levels adjusted to account for multiple comparisons (Bonferroni correction, $\alpha = 0.017$).

Results

Sea temperature

Monthly mean temperature reached a maximum of 26–27 °C during the summer with a minimum monthly mean temperature of 22.4 °C in winter (Figure 3). The lowest temperature recorded was 20.2 °C on 2 August 2010 and the highest (27.8 °C) on 23 February 2010. There was a notable drop in temperature during February, to a minimum of 21.6 °C.

Composition of benthic categories

Benthic cover was dominated by live scleractinian corals, comprising 48.4% of the total cover. Dead corals occupied much less space (23.1% of total benthic cover), followed by hard (bare) substratum (20.9%). Non-geniculate coralline and fleshy macroalgae (5%) exceeded sponges and other invertebrate groups, the latter comprising <3% of the cover.

Species accumulation curves

On all four natural substratum types on which seaweeds were found, species richness increased as a function of sampling effort. Observed species accumulation and jackknife 1 estimated curves (not shown) did not plateau on any substratum type, indicating that the macroalgal species identified comprise only a portion of the total diversity occurring on the different substrata. Based on jackknife 1 estimates, the recorded vs expected numbers of species for the various substratum types were: brain coral = 28 vs 43, plate coral = 31 vs 51, digitate coral = 41 vs 65 and hard substrata = 54 vs 81. A further species accumulation curve (not shown), based on the cumulative number of species plotted against the overall number of samples collected, approached an asymptote, indicating that the macroalgae found on Two-Mile Reef were sufficiently well-sampled to capture most of the species diversity: the estimate curve predicted 123 species, whereas the observed curve recorded 95 species.
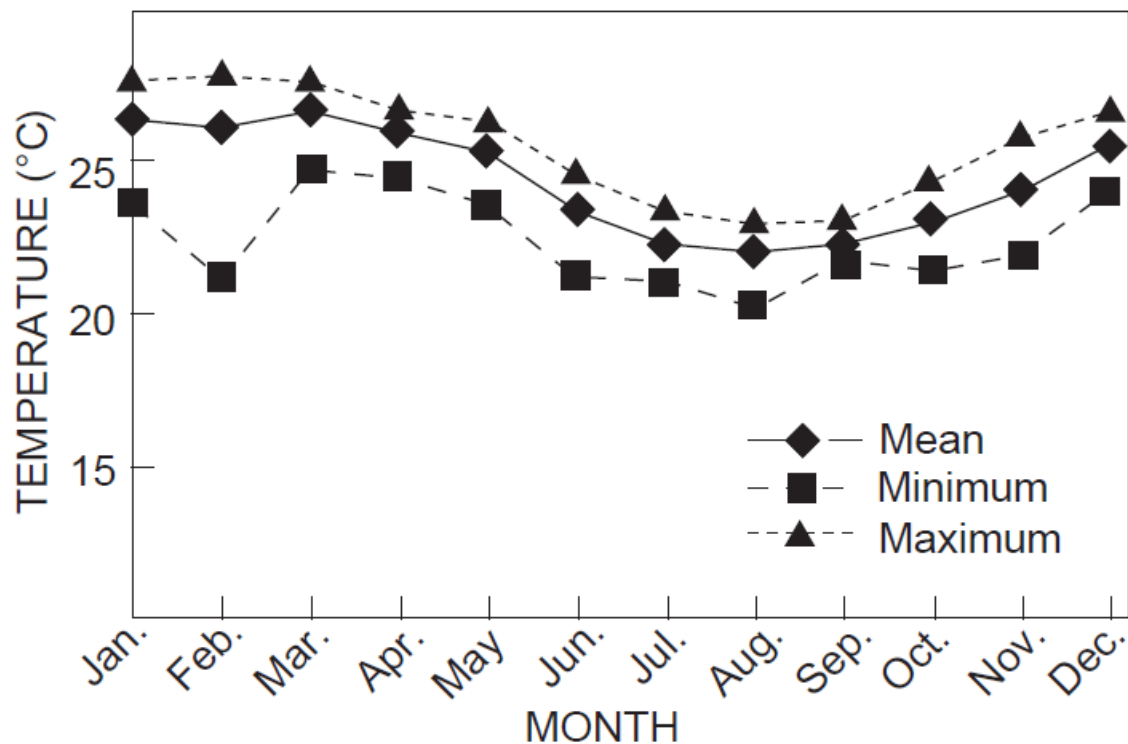
Figure 3: Seawater temperatures at 12-m depth on Two-Mile Reef, Sodwana Bay, January–December 2010. Solid line shows monthly mean temperature, broken lines show the highest and lowest absolute temperatures measured during each month

Algal colonisation on natural substrata

In total, 95 taxa of subtidal seaweeds were recorded in the 90 sample quadrats, including 14 Chlorophyta, 11 Phaeophyceae, 69 Rhodophyta and one cyanobacterium (Table 1). In all quadrats, the greatest number of species belonged to the red algae (Table 1) and these were mostly small turf-forming species. Rhodophyta that were present and relatively common in March and September were: *Hypnea spinella*, *Pterocladiella caerulescens* and *Herposiphonia tenella*. The brown alga *Lobophora variegata* was found throughout the sampling periods (66 out of 89 quadrats), either as a low turf component or with larger conspicuous blades. Three species were recorded for the first time in South African waters: *Codium dwarkense* (Chlorophyta, Codiaceae), *Lithophyllum cuneatum* and *Pneophyllum* sp. (both Rhodophyta, Corallinaceae) (Table 1).

Seasonal variability

Ordination of the species' Braun-Blanquet data in all 90 quadrats (correspondence analysis, not shown) produced a highly skewed pattern with Quadrat 43 (March) completely separate on the *x*-axis and forcing all of the 89 other quadrats into a small group. Quadrat 43 was very unusual in that it contained only one species of alga (*Champia* sp.). It was accordingly excluded from subsequent ordinations. The Bray–Curtis cluster analysis (not shown) of the 89 remaining quadrats revealed no seasonal clustering in the composition and abundance of

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algal communities. The results were similar for the ordination analysis where the DECORANA (Figure 4) failed to display any distinct pattern that related to seasonal change. As a result, data for the two sampling periods were combined for many of the subsequent analyses.

Overall patterns of algal communities

The brown foliose alga *Lobophora variegata* was the most common macroalga encountered in the quadrat surveys and was found in 73% of all the samples (Figure 5) from Two-Mile Reef. It was usually abundant across all substratum types in March and September and it had the highest mean Braun-Blanquet score (2.2) of any of the taxa (Figure 6). Of the other macroalgae, non-geniculate crustose coralline algae (as a combined form) were the next most common 'taxon,' occurring in 63% of all quadrats with a mean Braun-Blanquet score of 2.07. Overall among the algae, six species were present at a frequency >20% and a further two species >50% (Figure 5), whereas 67 species showed a frequency <5%. Several species were considered 'rare' according to their Braun-Blanquet cover score (<5% cover), including *Halymenia durvillei*, *Jania intermedia*, *Platysiphonia delicata*, *Turbinaria ornata*, *Wurdemannia miniata* and *Codium acuminatum*.

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Table 1: Seaweeds (including non-geniculate coralline algae) collected at Two-Mile Reef, Sodwana Bay. Species marked with an asterisk are new records for South Africa. 'March' and 'September' refer to natural substrata and 'Tiles' to artificial substrata. 1 = present, 0 = absent

Taxon	March	September	Tiles
Chlorophyta			
Caulerpa serrulata (Forsskål) J.Agardh	1	0	0
Caulerpa nummularia Harvey ex J.Agardh	1	1	0
Cladophora coelothrix Kützing	0	1	0
Cladophora sp.	0	1	1
Codium acuminatum O.Schmidt	0	1	0
Codium arabicum Kützing	0	1	1
Codium dwarkense Børgesen *	1	1	1
Codium geppii O.C.Schmidt	0	1	0
Codium pocockiae P.C.Silva	1	0	0
Derbesia sp.	0	1	0
Neomeris sp.	0	1	0
Neomeris van-bosseae M.A.Howe	0	0	1
Ulva sp.	1	0	0
Valonia macrophysa Kützing	0	1	0
Phaeophyceae			
Dictyopteris delicatula J.V.Lamouroux	1	1	1
Dictyota cervicornis Kützing	1	1	1
Dictyota humifusa Hörnig, Schnetter & Coppejans	1	0	0
Dictyota sp. 1	0	1	0
Dictyota sp. 2	0	0	1
Lobophora variegata (J.V.Lamouroux) Womersley ex E.C.Oliveira	1	1	1
Sargassum sp. 1	1	0	0
Sargassum sp. 2	1	0	1
Sargassum sp. 3	0	1	0
Sphacelaria novae-hollandiae Sonder	0	1	1
Turbinaria ornata (Turner) J.Agardh	1	0	0
Rhodophyta			
Acrosorium ciliolatum (Harvey) Kylin	0	1	0
Acrosorium sp.	1	0	0
Amansia rhodantha (Harvey) J.Agardh	0	1	0
Amphiroa sp.	1	0	0
Amphisbetema indica (J.Agardh) Weber-van Bosse	1	0	0
Anotrichium sp.	0	1	0
Apoglossum spathulatum (Sonder) Womersley & Shepley	1	1	0
Botryocladia leptopoda (J.Agardh) Kylin	1	0	0
Botryocladia sp.	0	1	0
Callophycus condominius R.E.Norris	0	1	0
Centroceras clavulatum (C.Agardh) Montagne	0	0	1
Centroceras sp.	0	1	0
Ceramium centroceratiforme Simons	0	1	0
Ceramium sp.	1	1	1
Champia compressa Harvey	0	1	0
Champia parvula (C.Agardh) Harvey	0	1	1
Champia sp.	1	0	0
Chondria collinsiana M.A.Howe	0	1	1
Chondria sp. 1	1	1	0
Chondria sp. 2	0	1	0
Crouania attenuata	0	1	0
Dasya baillouviana (S.G.Gmelin) Montagne	0	1	0
Dasya pedicellata (C.Agardh) C.Agardh	0	1	0
Dasya sp. 1	1	0	1
Dasya sp. 2	0	1	0
Dasya sp. 4	0	1	0
Dasya sp. 3	0	1	0
Eucheuma sp.	0	0	1
Gelidiella myriocladia (Børgesen) Feldmann & G.Hamel	1	1	1
Gelidiopsis repens (Kützing) Weber-van Bosse	1	1	0
Gelidiopsis variabilis (Greville ex J.Agardh) F.Schmitz	0	1	0
Gelidium reptans (Suhr) Kylin	1	1	0
Gloiocladia iyoensis (Okamura) R.E.Norris	1	1	0
Griffithsia sp.	0	1	0

Table 1: (cont.)

| Taxon	March	September	Tiles
Griffithsia weber-vanbosseae Børgesen	0	1	0
Halichrysis coalescens (Farlow) R.E.Norris & A.J.K.Millar	1	1	0
Halymenia durvillei Bory de Saint-Vincent	0	1	1
Herposiphonia tenella (C.Agardh) Ambronn	1	1	1
Heterosiphonia wurdemannii (J.Bailey ex Harvey) Falkenberg	1	1	0
Hydrolithon farinosum (J.V.Lamouroux) D.Penrose & Y.M.Chamberlain	0	1	0
Hydrolithon pellire Y.M.Chamberlain & R.E.Norris	1	0	0
Hypnea sp. 1	1	0	0
Hypnea sp. 2	1	0	0
Hypnea spinella (C.Agardh) Kützing	1	1	1
Jania intermedia (Kützing) P.C.Silva	0	1	0
Jania pumila J.V.Lamouroux	0	1	1
Jania sp.	1	0	0
Laurencia sp. 1	1	1	1
Laurencia sp. 2	0	1	0
Lithophyllum acrocamptum Heydrich	0	1	0
Lithophyllum cuneatum Keats *	1	1	0
Lithothamnion muelleri Lenormand ex Rosanoff	1	0	0
Martensia elegans Hering	0	1	0
Neogoniolithon brassica-florida (Harvey) Setchell & L.R.Mason	1	1	0
Platysiphonia delicata (Clemente) Cremades	1	0	0
Plocamium beckeri F.Schmitz ex Simons	0	1	0
Plocamium sp.	0	1	0
Pneophyllum sp.*	0	1	0
Porolithon onkodes (Heydrich) D.Penrose & Woelkerling	1	1	0
Polysiphonia coacta C.K.Tseng	0	1	1
Polysiphonia ferulacea Suhr ex J.Agardh	0	1	0
Pterocladiella caerulescens (Kützing) Santelices & Hommersand	1	1	1
Ptilothamnion cladophorae (Yamada & T.Tanaka) G.Feldmann-Mazoyer	0	1	0
Rhodymenia sp.	0	1	0
Spongites yendoi (Foslie) Y.M.Chamberlain	1	1	0
Tiffaniella sp.	0	1	0
Tolypiocladia calodictyon (Harvey ex Kützing) P.C.Silva	1	0	0
Wrangelia penicillata (C.Agardh) C.Agardh	1	0	0
Wurdemannia miniata (Sprengel) Feldmann & G.Hamel	0	1	0
Cyanophyceae			
Lyngbya sp.	1	0	1
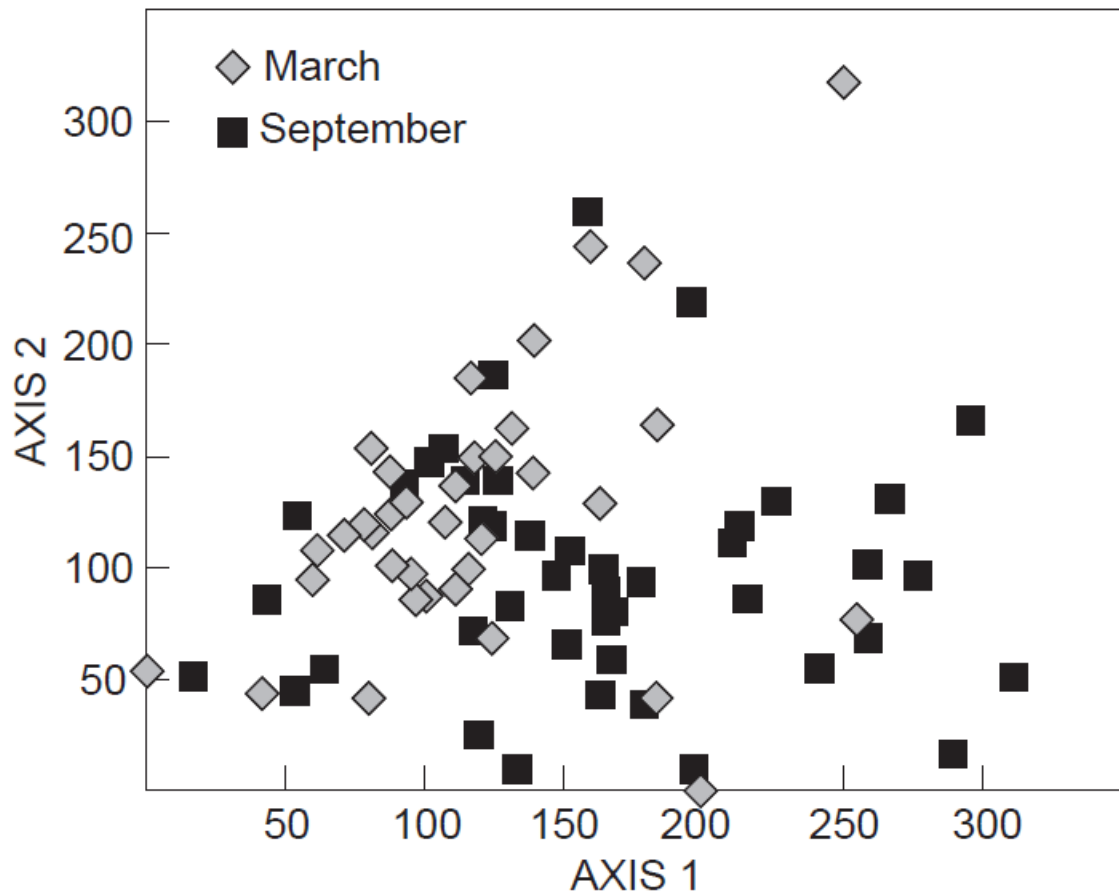
Figure 4: DECORANA analysis showing similarity between samples (quadrats), based on species' Braun-Blanquet cover values (excluding Quadrat 43) in March and September 2010. Each point represents a single quadrat (eigenvalues: Axis 1 = 0.344, Axis 2 = 0.294)

Community variation on different substrata

There was no detectable clustering of substratum types according to the cover abundance of community assemblages on them (Bray–Curtis analysis, not shown). This result was supported by the DECORANA ordination analysis (Figure 7) of the cover abundance of algal species. Crustose coralline algae and *L. variegata* comprised most of the macroalgal cover on each natural substratum type with other algae patchy, scattered or rare. *Lobophora variegata* was present in almost all the quadrats and had the highest frequency value of all the fleshy macroalgae (91.7%; Table 2). However, cover abundance of *L. variegate* showed no statistical difference among the substratum types (Kruskal–Wallis: H(3, n = 90) = 5.05; p = 0.14).
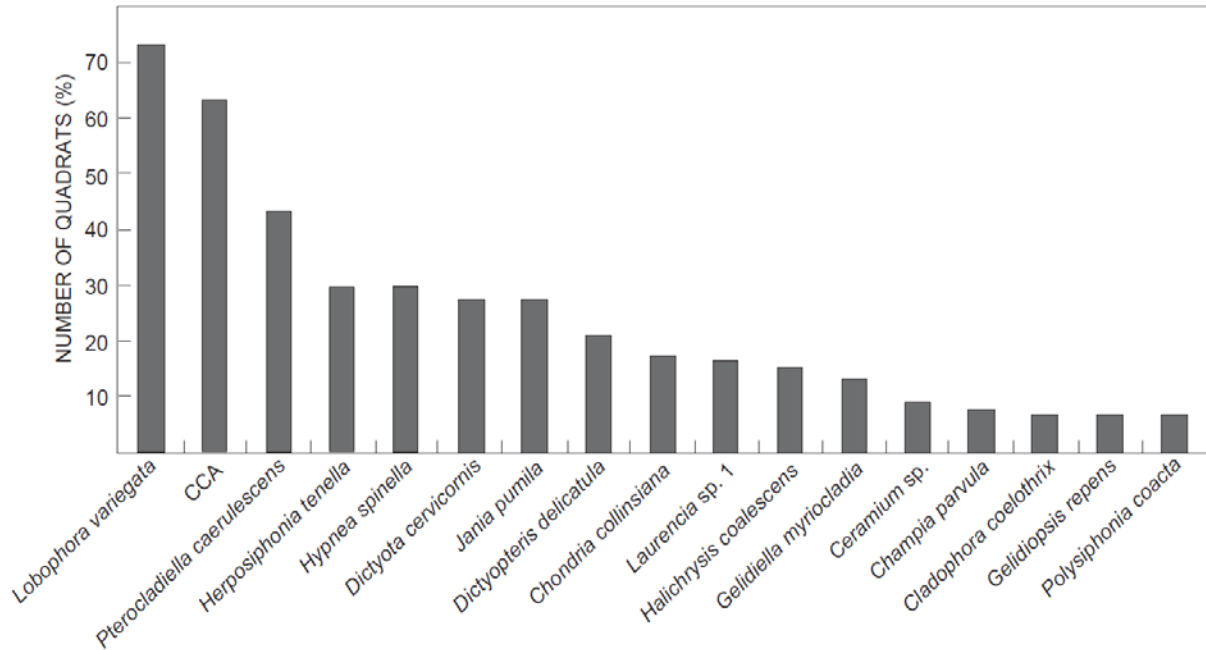
Figure 5: Overall percentage frequency for dominant taxa (mean cover >6%), including crustose coralline algae (CCA), in March and September 2010
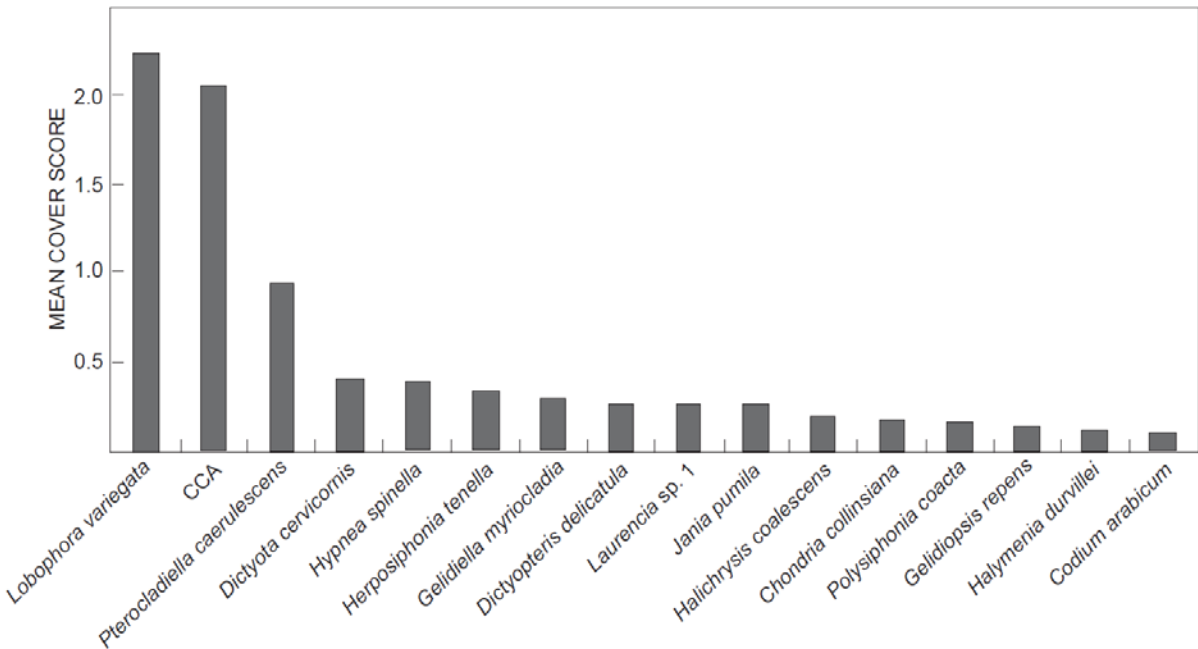

Figure 6: Overall mean Braun-Blanquet cover scores for dominant taxa (mean cover score >0.1), including crustose coralline algae (CCA), in March and September 2010
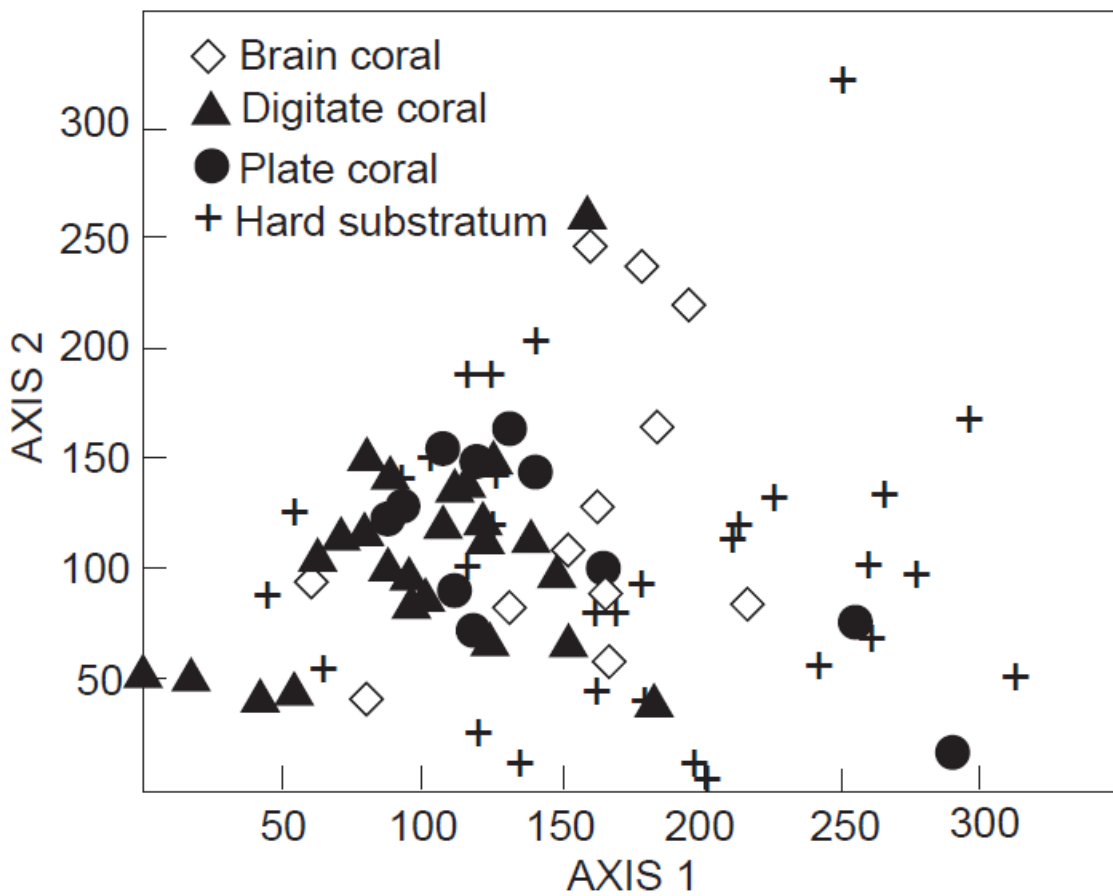
Figure 7: DECORANA analysis showing similarity between samples (quadrats) based on overall species' Braun-Blanquet cover values on different substrata (excluding Quadrat 43). Each point represents a single quadrat (eigenvalues: Axis 1 = 0.344, Axis 2 = 0.294)

Table 2: Percentage frequency of dominant macroalgal species collected on each substratum type (see Material and methods for details) for March and September 2010, combined

	Substratum type			
Algal taxon	Brain coral	Digitate coral	Plate coral	Hard substratum
Lobophora variegata	91.7	76.0	75.0	63.4
Crustose coralline algae	66.7	92.0	50.0	48.8
Pterocladiella caerulescens	66.7	24.0	25.0	56.1
Herposiphonia tenella	41.7	28.0	16.7	29.3
Hypnea spinella	41.7	16.0	25.0	31.7
Dictyota cervicornis	58.3	32.0	25.0	14.6
Jania pumila	33.3	12.0	8.3	36.6
Dictyopteris delicatula	16.7	36.0	16.7	14.6

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Pterocladiella caerulescens, a common turf alga, displayed the highest frequency of all turf taxa found on hard substratum (Table 2). There was a significant difference in *P. caerulescens* abundance between brain and digitate coral (Kruskal–Wallis: $H(3, n = 90) = 11.33$; $p = 0.01$; *post hoc* Mann–Whitney U-test: $U = 74$; $p < 0.01$), but it was most often observed distributed in small patches across the different substrata. Crustose coralline algae were the most abundant taxa on digitate coral, being recorded on 92% of these corals during the study (Table 2). Significant differences in cover were evident between digitate and plate corals ($H(3, n = 90) = 17.75$; $p < 0.001$; $U = 43.5$; $p < 0.001$) and between digitate coral and hard substratum ($H(3, n = 90) = 17.75$; $p < 0.001$; $U = 242.5$; $p < 0.001$). Macroalgae rarely had mean cover scores >2, indicating they rarely covered more than 25% of a quadrat, but occas ionally *L. variegata* or crustose coralline algae were found to cover most of a quadrat (Table 3). The high SD values indicate extreme patchiness in the distribution of almost all taxa.

Algal colonisation on artificial substrata

There was no detectable clustering of the macroalgal communities on the different tile types (Bray–Curtis analysis; results not shown). The results were similar for the ordination analysis where the DECORANA (Figure 8) failed to display any major separation between tile types based on their algal assemblages. In total, 24 taxa were identified growing on artificial settlement tiles, comprising 4 Chlorophyta, 6 Phaeophyceae and 14 Rhodophyta (Table 1). Crustose coralline algae were frequently found with high abundance across all tile types, with the highest mean Braun-Blanquet score (3.05) of any of the taxa (Table 4) and at least one species of this algal group on each tile (Figure 9). Among the other taxa, the brown seaweed *L. variegata* was the most common fleshy macroalga found on the tiles, occurring on 84% of the 135 tiles (Figure 9) with a mean Braun-Blanquet score of 2.25 (Table 4). Other species with less cover, but with relatively high frequency (>10%), were: *Dictyota* sp. 1, *Sphacelaria novae-hollandiae*, *H. tenella*, *H. spinella* and *Chondria collinsiana* (Figure 9; Table 4). Of the remaining macroalgal species in Table 4, most had low mean cover scores (seldom >1), indicating they rarely covered more than 5% of a tile, but frequently *L. variegata* and crustose coralline algae were observed to cover the majority of a tile. The overall macroalgal settlement on the tiles did not differ markedly among the three tile types. At the end of the 6-month experiment, crustose coralline algae were found to have settled on every tile tested, regardless of treatment or material (Figure 10). Additionally, all three tile types supported a high frequency and abundance of *L. variegata*: frequency ranged between 88.9% on treated tiles and 80% on marble tiles (Figure 10) and mean cover scores between 2.38 (SD 1.40) on treated tiles and 2.09 (SD 1.49) on marble tiles (Table 4). In contrast, *H. tenella*, *H. spinella* and *C. collinsiana* were most often distributed in small patches with low cover abundance scores (Table 4). Cover values were compared among the pretreated ceramic, marble and ceramic tiles. These data did not have homogeneous variances and were therefore analysed using Kruskal–Wallis tests. *Lobophora variegata* was observed overgrowing the majority of tiles during the study. There was no significant difference in the abundance of *L. variegate* among tiles types ($H(2, n = 135) = 1.05$; $p = 0.09$; Table 4). In contrast, there was a significant difference in crustose coralline abundance between ceramic and marble tile types ($H(2, n = 135) = 20.06$; $p < 0.001$; $U = 494.5$; $p < 0.001$).

Discussion
Sea temperature

Table 3: Mean Braun-Blanquet cover scores of dominant macroalgal species on each substratum type for March and September 2010 combined and significance of differences between substratum types

Algal taxon	Brain coral (SD)	Digitate coral (SD)	Plate coral (SD)	Hard substratum (SD)	Significance
Lobophora variegata	2.33 (1.07)	2.44 (1.73)	3.08 (2.07)	1.88 (1.79)	ns
Crustose coralline algae	2.33 (2.06)	3.28 (1.51)	1.08 (1.24)	1.54 (1.80)	*
Pterocladiella caerulescens	1.58 (1.62)	0.32 (0.63)	0.50 (1.00)	1.30 (1.65)	*
Herposiphonia tenella	0.58 (0.79)	0.28 (0.46)	0.17 (0.39)	0.33 (0.53)	ns
Hypnea spinella	0.50 (0.67)	0.32 (0.85)	0.25 (0.45)	0.45 (0.78)	ns
Dictyota cervicornis	0.67 (0.65)	0.68 (1.11)	0.33 (0.65)	0.18 (0.45)	ns
Jania pumila	0.33 (0.49)	0.12 (0.33)	0.08 (0.29)	0.38 (0.49)	ns
Dictyopteris delicatula	0.17 (0.39)	0.48 (0.77)	0.17 (0.39)	0.20 (0.56)	ns

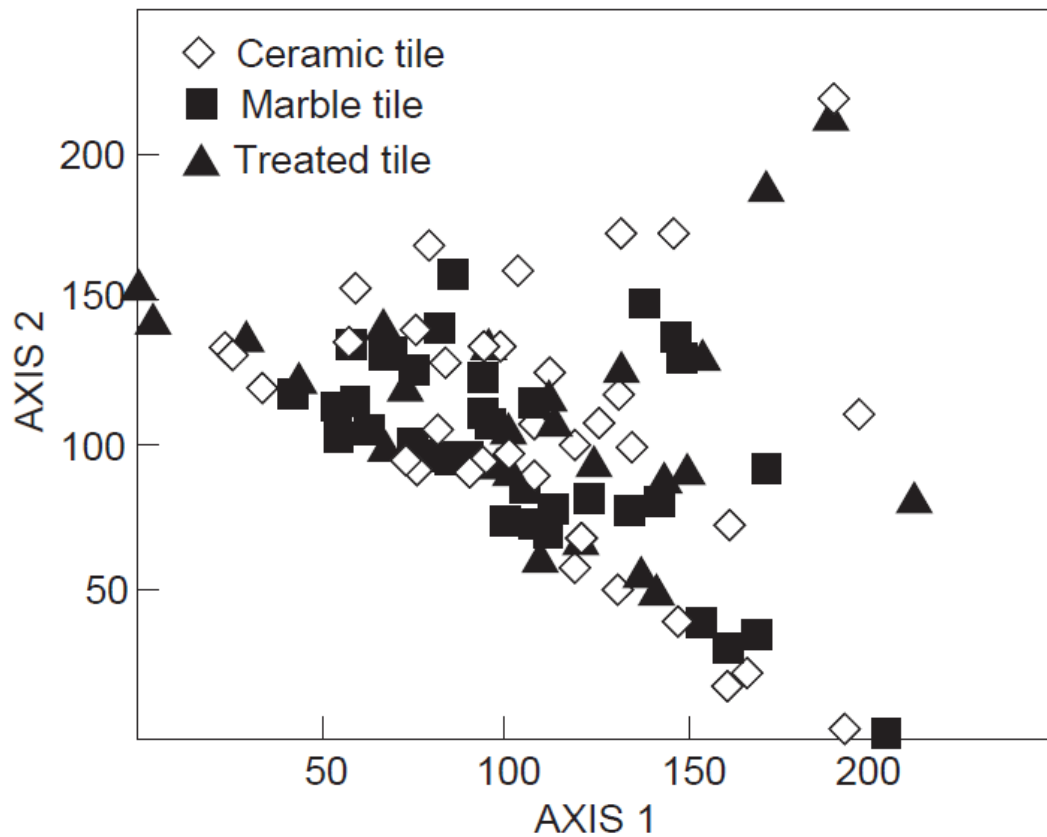$* = p < 0.001$; ns = not significant

Figure 8: DECORANA analysis of tile types (ceramic, marble and treated), based on the macroalgae that occurred on them (eigenvalues: Axis 1 = 0.239, Axis 2 = 0.178)

The measurements collected over a year in this study gave a seasonal temperature curve almost identical in shape to those of Schleyer (1999) and Anderson et al. (2005), including an annual cold event in February (the height of summer). This cold spike is attributed to small-scale localised upwelling of deep, cooler water (Ramsay et al. 1989), which is suggested to

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protect Sodwana Bay reefs to some extent from excessive temperatures and coral bleaching (Riegl and Piller 2003; Roberts et al. 2006). The minimum monthly mean seawater temperature is above the 20 °C minimum considered to indicate a tropical biogeographical region (Lüning 1990). The means of even the lowest temperatures recorded during each month never fell below 20 °C, indicating that there are possibly very few instances when cooler water might inhibit the growth or reproduction of tropical algal species. Previous studies of seaweed communities at Sodwana and in northern KwaZulu-Natal confirm the dominance of tropical elements in the flora (e.g. Bolton et al. 2004; Anderson et al. 2005).

Composition of hard substrata

High-latitude coral reefs are typically characterised by relatively low coral cover and high abundance of fleshy macroalgae (Harriott and Banks 2002; Vroom and Braun 2010). This study revealed that the live coral cover on Two-Mile Reef, one of Africa's southernmost coral communities, was higher (overall mean = 48.1%) than most other high-latitude reefs (c. 3.9 25.3%; Tribble and Randall 1986; Harriott and Banks 2002; Vroom and Braun 2010) and broadly comparable to lower latitude reefs of the Great Barrier Reef, where mean coral cover typically ranges from 18.3% to 27.0% on inshore reefs and from 30.7% to 33.6% on offshore reefs (Wismer et al. 2009; Emslie et al. 2010). Estimates of hard coral cover (as a percentage of total benthic cover) on Sodwana reefs vary considerably. Riegl et al. (1995) and Riegl and Riegl (1996) reported values around 22.5% for Two-Mile Reef, Schleyer et al. (2008) reported averages around 10–12% at Nine-Mile Reef and Celliers and Schleyer (2008) reported values of 29% for Two-Mile Reef. Our value of 48.4% is consequently very high, but similar to that of 48.8% reported for Four-Mile Reef by Celliers and Schleyer (2008). Although this might indicate that Two-Mile Reef was in good condition at the time we sampled, we suggest that such comparisons should be treated with caution, as differences between methods (point-intercept vs photographic quadrats), total area sampled and sampling site would all affect such data. Nevertheless, our results do indicate healthy populations of hard corals on Two-Mile Reef in 2010. This apparent stability of coral communities in Sodwana Bay may imply that they are relatively resilient, because these reefs have largely escaped the bleaching and disease that have caused marked declines in coral cover on tropical Indo-Pacific reefs over the same period (Bellwood et al. 2004; Schleyer et al. 2008). However, the most recent bleaching event in 2005 in southern Africa highlights that these high-latitude reefs are not immune, with extensive bleaching (up to 39% of colonies) in localised areas of the Maputaland coastline, northern KwaZulu-Natal, caused by fluctuating sea temperatures and solar radiation (Ruiz Sebastián et al. 2009), although there is no information on how much of the bleached coral died. The results of the current study were similar to those of Riegl et al. (1995) and Riegl and Riegl (1996), who reported that scleractinian corals occupied slightly more space than alcyonaceans (soft corals) and both exceeded sponges and other invertebrates. Macroalgae were not mentioned in their studies. Riegl and Riegl (1996) specifically reported that
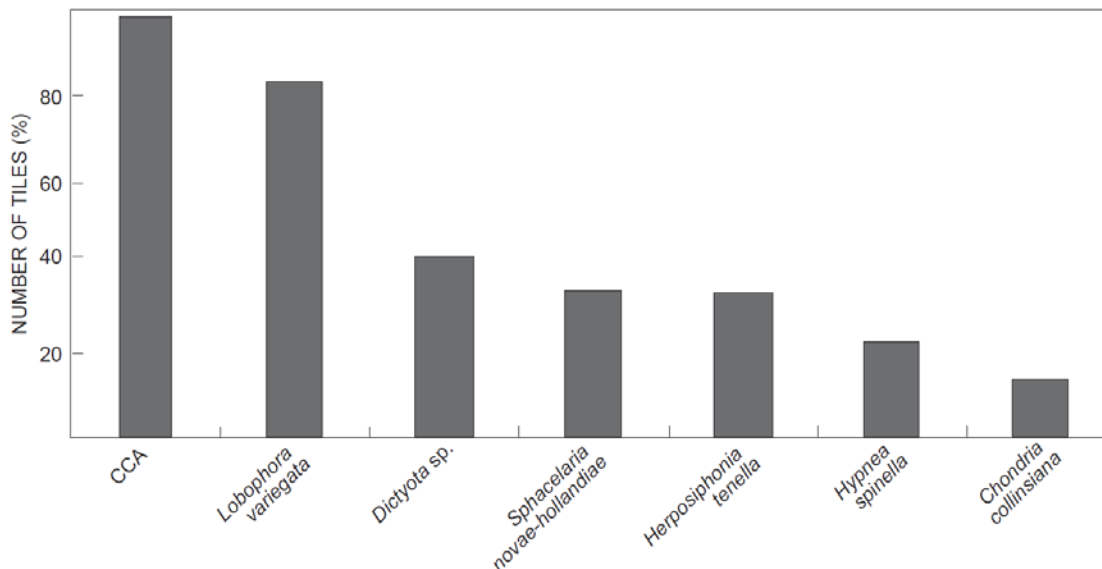
Figure 9: Overall percentage frequency for the seven most common macroalgal taxa (mean cover >10%), including crustose coralline algae (CCA), on all tile types

Table 4: Mean Braun-Blanquet cover scores for the seven most common macroalgal taxa, including crustose coralline algae, for each tile type and significance of the difference between tile types. Mean refers to cover scores over all tile types

Algal taxon	Treated (SD)	Marble (SD)	Ceramic (SD)	Significance	Mean
Crustose coralline algae	3.04 (0.98)	3.58 (1.05)	2.50 (0.97)	*	3.05
Lobophora variegata	2.38 (1.40)	2.09 (1.49)	2.29 (1.34)	ns	2.25
Dictyota sp.	0.73 (1.01)	0.87 (1.06)	0.69 (1.06)	ns	0.76
Sphacelaria novae-hollandiae	0.36 (0.65)	0.29 (0.46)	0.53 (0.73)	ns	0.62
Herposiphonia tenella	0.56 (0.92)	0.58 (1.06)	0.73 (1.07)	ns	0.39
Hypnea spinella	0.42 (1.08)	0.22 (0.42)	0.33 (0.67)	ns	0.33
Chondria collinsiana	0.07 (0.25)	0.13 (0.34)	0.20 (0.40)	ns	0.13

* = $p < 0.001$; ns = not significant

Two-Mile Reef was clearly dominated by soft corals and low-growing massive hard corals. During the 2005 warm-water anomaly in the southern Indian Ocean, coral bleaching reached unprecedented levels (McClanahan et al. 2007) and resulted in a significant shift in abundance of corals and benthic algae on the high-latitude reefs. The cover of dead corals found at our study site in 2010 was 23.1%, but there are no earlier data from which to infer a trend. As for causes of coral mortality, scleractinian taxa at Sodwana (the digitate coral *Stylophora* and the plate coral *Montipora*) are reported to be very susceptible to bleaching (Celliers and Schleyer 2002; Floros et al. 2004), but make up a small percentage of total coral cover (e.g. Schleyer et al. 2008). The important point is that our results showed that all dead corals were colonised by macroalgae. Rapid colonisation of corals by algae after environmental disturbances is a general phenomenon that has been documented following mechanical injuries (Glynn 1990) and bleaching events (Glynn 1993; Hoegh-Guldberg 1999).

Algal colonisation on natural substrata
This study provides the first quantitative description of the composition and abundance of species comprising the macroalgal community on digitate coral, brain coral, plate coral and hard substrata of Two-Mile Reef. The epilithic and epizoic algal communities were characterised by a high incidence of 'rare' species, as is common of tropical systems

elsewhere. Stuercke and McDermid (2004) found that 60% of the Hawaiian shallow subtidal turfs were rare taxa, based on methods that fundamentally measured cover. Scott and Russ (1987) considered 63% of the epilithic algal community of the central Great Barrier Reef to be rare species, individually comprising <7% of the canopy cover. On Two-Mile Reef, 91% of the species individually comprised <7% of the percentage cover. A considerable number of algal genera observed on the reef are common components of algal communities in tropical parts of the world. Of the 16 macroalgal genera described by Scott and Russ (1987) as being widespread across several coral reef areas, such as the Caribbean, the Great Barrier Reef, Hawaii and Guam, 12 were common at Two-Mile Reef.
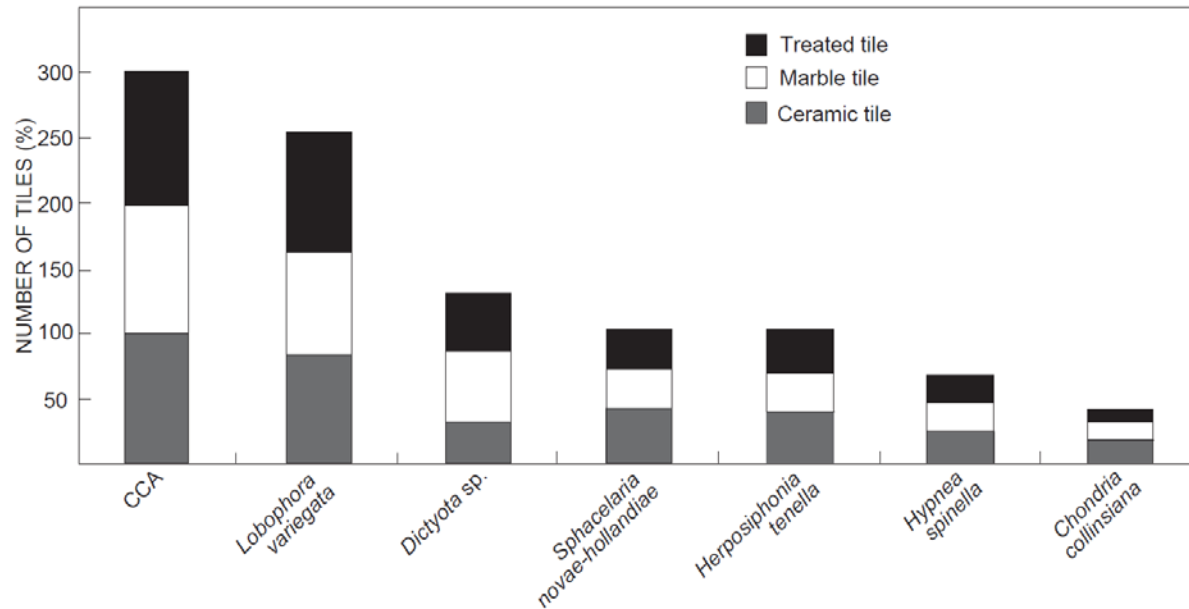
Figure 10: Cumulative percentage frequencies across tile types for the seven most common macroalgal taxa (mean >6%), including crustose coralline algae

These included *Centroceras, Ceramium, Gelidiella, Herposiphonia, Hypnea, Jania, Laurencia, Polysiphonia* (Rhodophyta), *Cladophora* (Chlorophyta), *Dictyota, Sphacelaria* (Phaeophyta) and *Lyngbya* (Cyanobacteria). Only six of the 95 taxa (including crustose coralline algae as a group) were classed as common, abundant or dominant regarding occurrence; two of these, the dictyotalean *L. variegata* and the non-geniculate corallines, accounted for most of the algal cover on all the different substrata.

Seasonal variability

The macroalgal communities of Two-Mile Reef showed no marked seasonal dynamics. Lüning (1990) and Ateweberhan et al. (2006) described temperature as one of the primary factors controlling macroalgal growth in high-latitude reefs, because algal growth was stimulated during low water temperatures in winter. Yet the current study could not identify significant seasonal changes in macroalgal communities on natural substrata, a finding that is inconsistent with previous studies. For example, studies on tropical Atlantic and Caribbean

macroalgae have found that different algal groups dominated their respect ive communities at distinct times of the year (Lirman and Biber 2000; Diaz-Pulido and Garzón-Ferreira 2002; Ferrari et al. 2012). In the Caribbean, the abundance of *Dictyota* spp. was positively correlated with water temperature and highest during the summer (Lirman and Biber 2000; Ferrari et al. 2012), whereas *L. variegata* was more abundant during winter (Ferrari et al. 2012). Similar seasonal changes in *L. variegata* have been observed on the Great Barrier Reef by Diaz-Pulido et al. (2009).

Community variation on different substrata

The fact that *L. variegata* is the dominant macroalgal low-growing species in the subtidal of Sodwana Bay is consistent with its known abundance worldwide in many tropical to warm-temperate areas (Womersley 1967; Littler and Littler 2000). The abundance of *L. variegata* along Two-Mile Reef fits with the expected pattern of dominance of dictyotalean assemblages along the Maputaland region (Bolton et al. 2004). The dominance of *L. variegata* may be partly explained by the algal defence mechanisms that contribute to their persistence against herbivory. Two common macroalgal defence mechanisms are escape and deterrence (Hay and Fenical 1988), which may be used by *L. variegata*. Diaz-Pulido et al. (2009) reported that *L. variegata* under normal or undisturbed conditions is not able to grow beyond the base of the branches, on account of competitive inhibition by the corals. However, we frequently observed *L. variegata* growing upwards from the base and between the branches of most digitate coral colonies on Two-Mile Reef. The high abundance of *L. variegata* on branching substrata suggests that it was released from space competition with the corals, because of the bleaching mortality on the reef. Additionally, the high cover of *L. variegata* further suggests that the branching coral framework provides an 'escape' from herbivores. The second mode of defence that may have contributed to the high cover of *L. variegata* is deterrence. The deterrence of herbivores by *L. variegata* is achieved primarily through the use of allelochemicals (Targett and Arnold 1998) and its exhibition of different morphological forms (ruffled, decumbent and encrusting; Coen and Tanner 1989). In the current study, encrusting and decumbent forms of *L. variegata* were commonly found along the reef. Coen and Tanner (1989) suggest that the decumbent form may be among the least palatable tropical algae for both crabs and fish, whereas the encrusting form appears to be less susceptible to grazing, because of its tightly adhering (encrusting) habit. There are no previous observations of such extensive growths of *Lobophora variegata*, or indeed any single species of fleshy macroalga, on Two-Mile Reef. Our data support the observations of Coen and Tanner (1989), Bennett et al. (2010) and Sangil et al. (2011) that *L. variegata* forms a dynamic component of many coral reef communities. However, it should be noted that *L. variegate* may in fact comprise more than one species, because molecular studies of New Caledonia *Lobophora* detected 31–39 species where only four were previously recognised (Vieira et al. 2014) and molecular evidence suggests the presence of several species in this complex in South Africa (C Vieira and O De Clerck, Ghent University, Belgium, pers. comm.). We noted some morphological variations among specimens on the reef (e.g. semi-creeping vs erect), but many individuals were intermediate between these forms and in the absence of better taxonomic information we regarded them all as one species. The similarity between seaweed species on the different types of substrata, including the types of

coral, indicates that seaweeds will recruit onto any hard substratum on these reefs. In a system like this, where there are many species present and scattered throughout the reef, with few dominants, this is perhaps not surprising. This patchy distribution pattern with numerous rare species (as found on Hawaiian reefs by Stuercke and McDermid 2004) suggests that opportunistic recruitment is the main determinant of community composition. There do not appear to be any other studies that have investigated algal growth on different morphological types of dead coral.

Algal colonisation of artificial substrata

The most important outcome of this aspect of the study was that the nature of the artificial substratum had little influence on the recruitment success of coral reef macroalgae on Two-Mile Reef. In general, variations in the abundance of non-crustose macroalgal recruits among tile types were not significant, notwithstanding significant differences in crustose coralline abundance between ceramic and marble tiles. Earlier researchers have generally found that some crustose coralline algae inhibit the recruitment of algal propagules, either by epithallial shedding or enhanced grazing on the surface of the crustose corallines (Keats et al. 1997; Littler and Littler 1997). These processes could explain the weak negative relationship between non-crustose macroalgal recruits and pretreated ceramic tiles. However, this contrasts markedly with the relatively high cover of *L. variegata* on the pretreated tiles. Santelices and Varela (1994) found that calcium carbonate facilitated rhizoidal attachment in fleshy macroalgae, perhaps explaining an apparent association between *L. variegate* and crustose coralline algae. At the end of our experiment, bare tile surfaces had developed epilithic algal communities dominated by filamentous algal turfs, non-geniculate (crustose) corallines and canopy-forming brown algae. The algal communities colonising the settlement tiles in this study showed a similar structure to those of previous studies in the western Indian Ocean (Uku et al. 2000) and Great Barrier Reef (McClanahan 1997). McClanahan (1997) reported that algal turf and coralline algae were dominant on all plates within 150 days following tile placement. He reported that the succession of algae was from algal turf to coralline algae, followed by an increase in calcareous algae and climaxing with an abundance of large canopy-forming brown algal genera, such as *Sargassum* and *Turbinaria*. The results of the current study suggest that the sequence of succession was similar, except that calcareous algae never developed greatly on most tiles, in the 6-month study period. Relatively large brown algae, such as *L. variegate* would appear to be the most abundant space-occupying species at the climax of succession. Fleshy algae, although common on Two-Mile Reef, did not grow to any size or abundance on the experimental tiles. This may be because of insufficient time, but is more likely because of the flat shape of the tiles. Flat tiles may not provide the rugosity and associated refuge that is necessary for the development of these species (McClanahan 1997). Rugose ceramic tiles have been suggested to protect algal recruits from dislodgement by herbivore activity and wave action and to increase the tile surface area available for settlement and recruitment (Amsler et al. 1992; Anderson and Underwood 1994). Diaz-Pulido and McCook (2004) found that ceramic tiles with rougher surfaces had significantly more algal recruits than those with smoother surfaces. Among the ceramic and pretreated ceramic tiles in the current study, there was a higher (although not significant) cover abundance of *L. variegata* compared to the smoother marble tiles. In

contrast, marble tiles had significantly higher cover of non-geniculate coralline algae. This may reflect the outcome of competition with other macroalgae, the adherence of which may have been weakened by the smooth marble surface. Although it is not possible to compare directly recruitment on natural substrata and artificial tiles in a factorial analysis, it is noteworthy that abundance of non-geniculate coralline algae was lower on natural substrata than on artificial substrata. Whether this resulted from physical or chemical differences in the substrata is unclear, although flat surfaces provide little refuge and are consequently more susceptible to grazing disturbance. Consequently, roaming herbivorous fish, like some surgeonfish and parrotfish, may promote coralline recruitment by cropping the easily accessible and nutritious turfs.The current study is the first to investigate macroalgal colonisation of dead corals and other substrata on these high-latitude eastern Indian Ocean coral reefs and demonstrates an essentially indiscriminate settlement of macroalgae on hard surfaces, including any types of dead coral. It also provides quantitative baseline information on algal diversity and substratum types that should be useful in future studies of these systems, particularly considering the increasing threats to coral systems worldwide.

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