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REPORT

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Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef

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Abstract Crustose coralline algae (CCA) fulfill two key functional roles in coral reef ecosystems: they contribute significantly to reef calcification, and they induce larval settlement of many benthic organisms. Percentage cover of CCA, and environmental conditions, were visually estimated on 144 reefs of the Great Barrier Reef between 10 and 24° latitude S. Reefs were located across the shelf and ranged from turbid near-shore reefs close to rivers to clean-water reefs hundreds of kilometers from coastal influences. On each reef, two sites were surveyed between 0.5 and 18 m depth. Strong cross-shelf trends occurred in cover of CCA, amount of sediment deposited, water clarity, and slope angle. Relative distance across the shelf and sedimentation jointly explained 84% of variation in CCA cover. Three regions running parallel to the shore were identified, with a mean CCA cover of $<1\%$ on the inner third of the shelf, and $>20\%$ cover on the outer half of the shelf, with a narrow transition region between the two. Within each region, the cover of CCA was unrelated to distance across the shelf, but was related to the sedimentary environment, being relatively higher on reefs with low sediment deposits. On the inner third of the shelf, the most sediment-exposed reefs were unsuitable habitats for CCA. The inverse relationship between CCA and sediment has implications for the recruitment of CCA-specialised organisms, and for rates of reef calcification.

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Introduction

Crustose coralline algae (CCA, non-geniculate, calcareous, red algae of the order Corallinales) serve two key functional roles in coral reef environments. The most obvious and prominent role is their significant contribution to limestone formation and cementation of the reef pavement (Barnes and Chalker 1990). The rock-hard encrustations of CCA reinforce the skeletal structures of dead corals, and fill cracks in the reef substratum, thereby maintaining topographic complexity and reducing reef erosion. The second key functional role of CCA is as settlement substratum for many types of reef benthos. Induction of larval settlement and metamorphosis of many sessile organisms, including some hard corals (Morse et al. 1988; Heyward and Negri 1999), octocorals (Benayahu et al. 1989; Lasker and Kim 1996), and the crown-of-thorns starfish *Acanthaster planci* (Johnson et al. 1991), depend on the presence of CCA and their associated bacteria films (Johnson and Sutton 1994; Johnson and Cartwright 1996; Heyward and Negri 1999). Due to these two critical roles, CCA may be considered as a key functional group in coral reef ecosystems.

CCA are multicellular, fundamentally filamentous algae. They are heavily calcified by calcite crystals embedded in the cell walls, which protect against grazing by herbivores and provide wave resistance. Individual species or genera cannot generally be distinguished in rapid ecological field assessments, since their morphology and coloration vary greatly, depending on light and wave exposure (Maudsley 1990). The investigation of species-specific features such as shape and number of epithallial cells, or interfilamentous cell connections, requires special staining and sectioning techniques, followed by light microscopy or scanning electron microscopy (Braga et al. 1993; Mendoza 1995). CCA are found in a wide range of temperatures, from tropical to polar, and in light environments ranging from those of shallow tropical intertidal reef flats to almost complete darkness. On coral reefs, temperature, light availability, and grazing intensity by herbivores are major factors influencing growth rates of CCA (Littler and Doty 1975; Littler and Littler 1984; Liddell and Ohlhorst 1987; Iryu and Matsuda 1988; Klumpp and McKinnon 1992). Despite the fundamental role of these algae in the ecology of coral reefs, effects of other environmental variables on life history parameters and abundances of tropical CCA are poorly understood.

On the Great Barrier Reef (GBR), CCA cover is high on clear-water outer-shelf reefs, but decreases towards the coast (Scott and Russ 1987; Fabricius 1997; Sweatman et al. 1997). Dead corals are colonised by filamentous turf algae within days in all reef environments; however, successions from turf to CCA assemblages occur within months where environmental conditions are suitable for CCA. Over 6–12 months, CCA covered around 35% of dead coral skeleton plates deployed on an outer-shelf reef flat on central GBR, 28% on the mid-shelf, and 8% close to the coast (Klumpp and McKinnon 1992). Conversely, turf algae were abundant on plates deployed on the coastal reef flat, but decreased towards the outer shelf. Thus, on coastal reefs, turf algae dominate the epilithic algal communities for extended periods of time, and calcification of the substrate by CCA is negligible.

Although CCA are associated with clean and clear off-shore waters, the effects of water quality on CCA abundances are little known. A field study demonstrated decreasing abundances of CCA towards a point source of urban sewage (Bjoerk et al. 1995). Laboratory experiments by these authors demonstrated that growth rates and rates of calcification were reduced by high concentrations of phosphate, but not by nitrate or ammonia. Maudsley (1990) also reported on degeneration of coralline algae in areas of phosphate loading and other pollution; however, no data were presented to substantiate the observations.

In this paper, we describe the spatial distribution of CCA over 144 reefs of the Great Barrier Reef. Surveys covered all types of reef environments, ranging from turbid near-shore reefs close to river estuaries, to clear water reefs hundreds of kilometers from coastal influences. We investigated relationships between CCA cover and water clarity, sedimentation, slope angle, and relative distance across and along the GBR. We identify which of the environmental variables considered best explain CCA cover, and determine environmental conditions unsuitable for survival of CCA.

Methods

Field methods

The data were obtained during rapid ecological assessments (REA: Done 1982; Fabricius and De'ath 1997; Devantier et al. 1998; Fabricius and De'ath 1999) of 144 reefs from latitude 10 to 24°S, conducted between May 1996 and September 1999. The REA estimated cover of the major benthic groups, and related environmental conditions, to obtain taxonomic inventories and information on the state of the GBR. On each reef, REA were typically carried out at two locations (windward and leeward) and at up to five pre-defined depth ranges (18–13, 13–8, 8–3, 3–1 m, and reef flat). Surveys were conducted by one observer (the first author) on scuba, starting deep and slowly ascending to the shallower ranges, typically covering 200–300 m (~300–1,200 m^2) within 10–15 min per depth range.

The following biotic and abiotic data were recorded at each depth range:

1. Visual estimates of percent total cover of hard corals, octocorals, CCA, turf algae, *Sargassum* and other macroalgae, and unconsolidated substratum (sand/sediment/mud, and rubble). Cover was estimated as none (0%), in 2.5% increments from >0–10%, in 5% increments from >10–30%, and in 10% increments for >30% cover.
2. Thickness of sediment deposit on the reef substratum (rated on a 4-point scale; 0 = none, 1 = thin layer, 2 = moderate layer, and 3 = thick deep layer).
3. Visibility (Secchi distance; in metres).
4. Slope angle (assigned to 5° categories with the assistance of a plumb bob and protractor; in degrees).

Two spatial variables, 'relative distance across' and 'relative distance along' the shelf, were calculated based on the latitude and longitude (recorded by GPS) of each survey site. Relative distance across the shelf is defined as the distance from the survey site to the nearest point on the coast, divided by the sum of distances to the coast and to the closest point on the outer edge of the GBR. Thus, relative cross-shelf distance takes the value 0° at the coast and 1 on the outer shelf. Similarly, relative distance along the shelf was calculated as distance to the northern end of the GBR, divided by the sum of distances to the northern and the southern ends of the GBR.

Statistical methods

Data from all sites and depth zones of each reef were averaged. CCA cover was square-root transformed to give constant variance of model residuals. The relationships between CCA and the physical and spatial variables were explored using scatter plots and cross-validated smoothing splines (Hastie and Tibshirani 1990). CCA cover was modelled using regression tree analysis (Breiman et al. 1984; De'ath and Fabricius 2000). Trees are ideally suited to the analysis of complex ecological–environmental data which involve interactions and non-linearities (De'ath and Fabricius 2000). Trees form groups of cases with similar response values by repeated binary splitting of the data. Each split maximises the sums of squares between the two resulting groups of response values, and is based on one of the explanatory variables. At the end of the procedure, each of the terminal groups is characterised by the mean value of the response variable, the number of cases in the group, the variables that formed the divisions leading to the group, and their values. The size of the tree (number of terminal groups) was selected by minimising the cross-validated estimate of error (Breiman et al. 1984; De'ath and Fabricius 2000). The statistical software S-Plus (Statistical Sciences 1999) was used for all data analyses, and included use of the tree software RPART (Therneau 1998).

Results

Exploratory spatial analysis

The spatial distribution of CCA, sediment, visibility, and slope showed systematic trends across, but not along, the GBR (Fig. 1). Cover of CCA ($R^2 = 80\%$) and sediment ($R^2 = 56\%$) changed in a non-linear fashion across the shelf (Fig. 2), with relatively constant levels in the inner and outer regions of the shelf. CCA averaged $< 1\%$ cover on the inner shelf and ~20% on the outer shelf. Visibility ($R^2 = 48\%$) and slope ($R^2 = 31\%$) both increased linearly across the shelf. In addition to the strong non-linear relationship with relative distance across the shelf, CCA also had non-linear relationships of varying strengths with sediment ($R^2 = 62\%$), visibility ($R^2 = 56\%$), and slope ($R^2 = 34\%$) (Fig. 3). CCA cover was highest for low values of sediment, and high values of visibility and slope. Sediment was lower on steep slopes than on gradual slopes ($R^2 = 18\%$) (Fig. 4), and visibility decreased non-linearly with increasing levels of sediment ($R^2 = 55\%$).

Modelling cover of CCA

Regression trees were used to model CCA cover. To assess the contributions of the physical and spatial variables, three models were used: (1) including both physical and spatial variables, (2) with only spatial

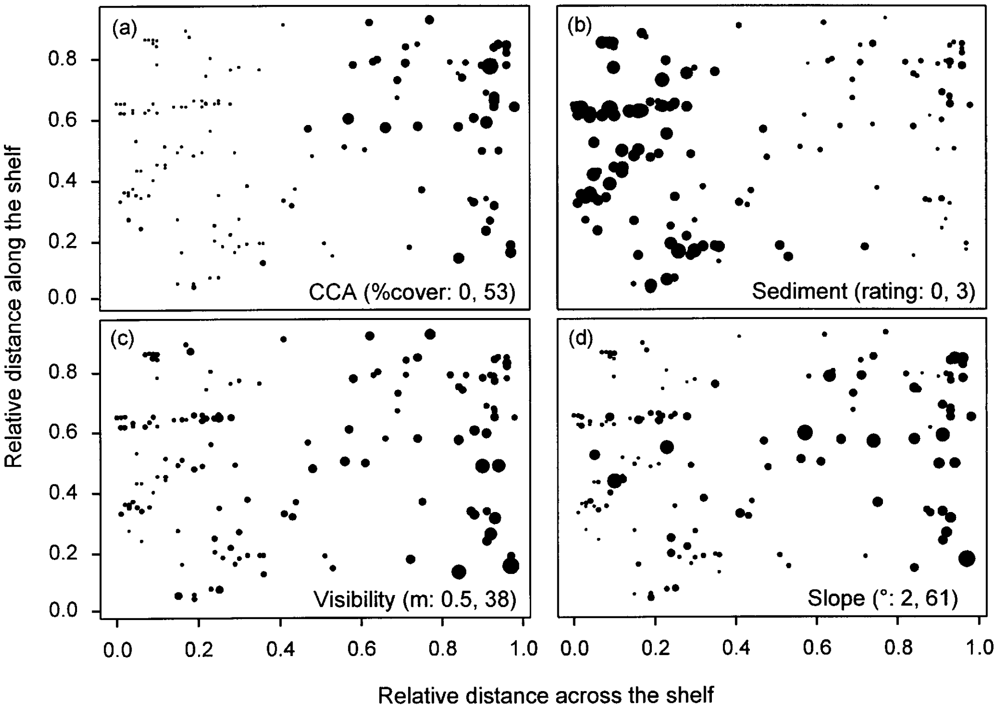

Fig. 1 Bubble plots showing variation of **a** crustose coralline algae cover, **b** sediment deposits, **c** visibility, and **d** slope angle with relative distance across and along the Great Barrier Reef. Sizes of bubbles are scaled linearly between minimum and maximum values (indicated in *parentheses*). Plots indicate strong cross-shelf trends for all variables, but there is no evidence of trends along the shelf

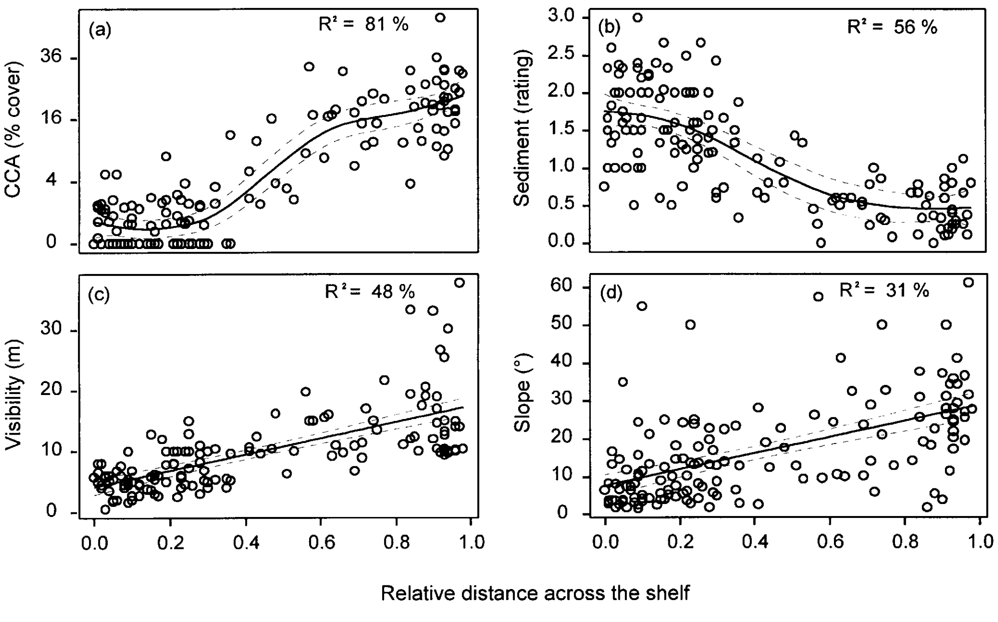

Fig. 2 Scatterplots showing cross-shelf trends in **a** crustose coralline algae cover, **b** sediment deposits, **c** visibility, and **d** slope angle. Cross-validated smoothing splines with 95% confidence intervals indicate strong, but highly non-linear, trends for crustose coralline algae and sediment. For visibility and slope angle, trends are linear, but weaker

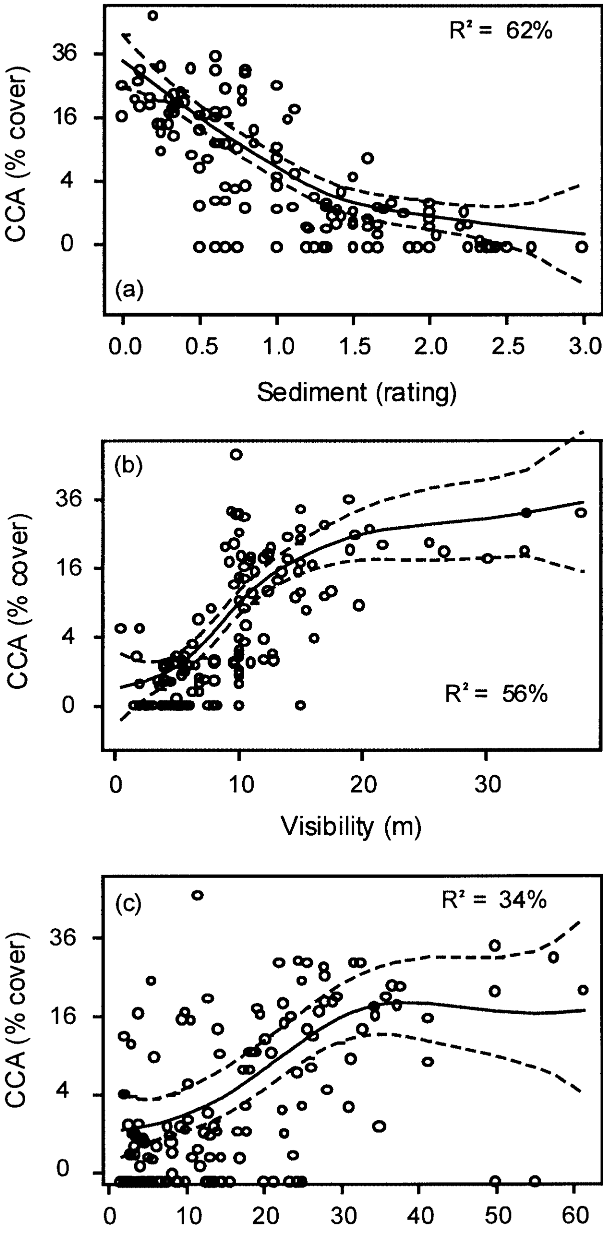

Fig. 3 Scatter plots showing trends in **a** crustose coralline algae cover with sediment deposits, **b** visibility, and **c** slope angle, and relationship between visibility and sediment. Cross-validated smoothing splines with 95% confidence intervals indicate strong, but non-linear, relationships between pairs of variables

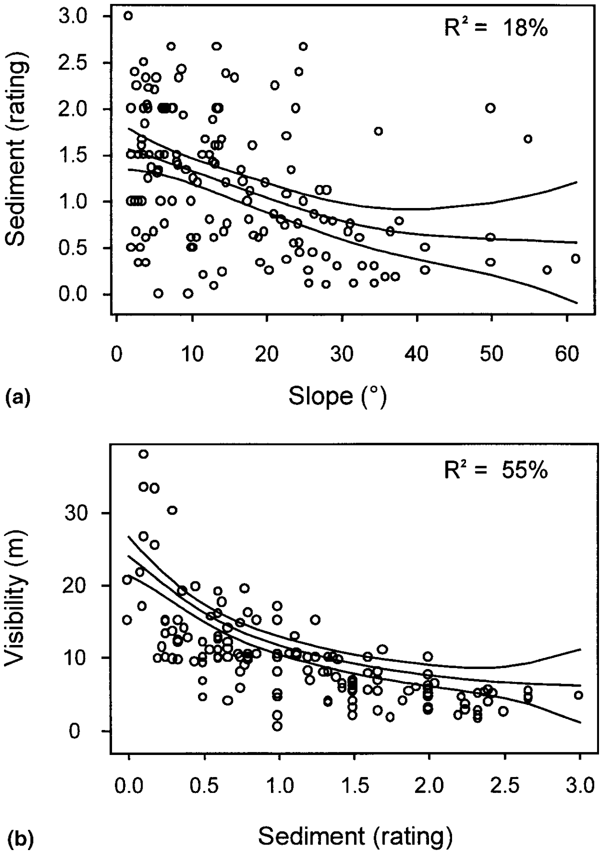

Fig. 4 Scatter plots showing relationship between **a** sediment and slope and **b** visibility and sediment. Cross-validated smoothing splines with 95% confidence intervals indicate strong, but non-linear, relationships between pairs of variables

variables, and (3) with only physical variables. In the model with both physical and spatial variables, only relative cross-shelf distance and sediment appeared in the model (Fig. 5), and the 6-leaf tree explained 85% of CCA variation. The tree defined three regions across the shelf (<0.36, 0.36–0.55, and >0.55), within each of which higher levels of sediments were related to lower levels of CCA. The effect of sediment varied across the three regions, being greatest on the outer shelf where lower sediment reefs had on average 9% greater cover of CCA. On the inner shelf, all reefs with high sediment had <0.5% CCA cover. Although CCA cover increased strongly across the whole shelf, there were no linear cross-shelf trends within any of the three cross-shelf regions defined by the tree ($P > 0.05$).

When only spatial variables were used to explain CCA cover, a three-leaf tree resulted. This was simply the 6-leaf tree of the physical and spatial model (Fig. 5), but without the three additional splits due to sediment. This tree explained 80% of CCA variation. The sediment effects of the six-leaf tree can thus be interpreted as explaining an additional 5% of CCA variation (or 25% of that unexplained by the three-leaf spatial model).

For the physical variable model, a five-leaf tree resulted (Fig. 6), with visibility, sediment, and slope all used in the model. The tree explained 79% of CCA variation, with highest CCA cover on reefs with high visibility (>8.5 m) and low sediment (<0.45). The models based on only physical or spatial variables were thus similar in terms of explained variation. A six-leaf tree based only on sediment explained 69% of CCA variation, with an identical first split to that of visibility in the physical variable model.

Jointly, these models suggest that: (1) relative cross-shelf distance is a strong surrogate for the physical

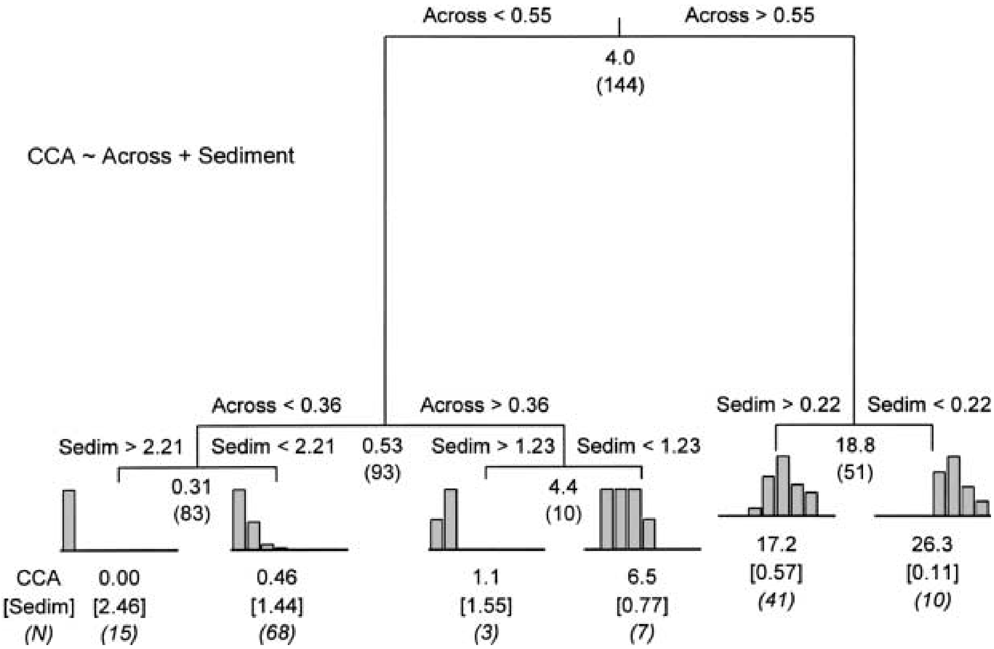

Fig. 5 Regression tree explaining crustose coralline algae (*CCA*) cover in terms of relative distance across shelf (*Across*) and sediment deposits (*Sedim*). For each of the six leaves of the tree, distribution of CCA cover (square-root transformed) is illustrated by a *histogram*, and mean values of CCA cover (back-transformed), sediment, and number of reefs are indicated. Lengths of vertical drops at each split are proportional to the variation it explains. Tree defines three regions across the shelf (< 0.36, 0.36–0.55, and > 0.55), within each of which higher levels of sediments are related to lower levels of CCA. Tree explains 85% of total CCA variation

factors that determine CCA cover, (2) sediment accounts for substantial local variation in CCA cover not explained by relative cross-shelf distance, and (3) sediment, slope, and visibility together account for most of the variation in CCA cover, but other unknown physical factors also determine CCA cover; for some of these unknown factors, relative cross-shelf distance is at least a partial surrogate.

Discussion

Cover of crustose coralline algae (CCA) on reefs of the Great Barrier Reef was strongly inversely related to relative cross-shelf distance and the sedimentary deposits on the reefs, and weakly related to water clarity (visibility) and the steepness of reef slopes. Three shore-parallel "CCA provinces" were identified, with transitions at 36 and 55% across the shelf. Within each of the three provinces, CCA cover was dependent on sedimentation and independent of distance across the shelf. The consistency of these three independent correlations may suggest a causal relationship between sedimentation and CCA cover. However, since causality cannot be established from observational data, controlled experiments will be necessary to identify whether and how sediments ultimately affect CCA life histories.

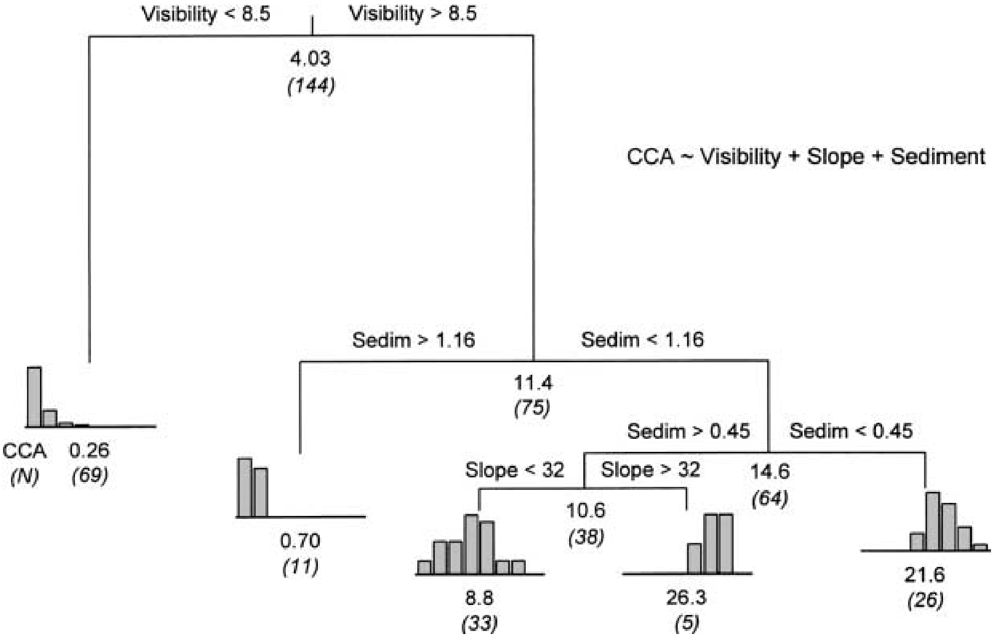

Fig. 6 Regression tree explaining crustose coralline algae cover in terms of visibility, sediment deposits, and slope. Tree explains 78% of total CCA variation. For explanation see legend of Fig. 5

Our visual estimates resulted in similar CCA estimates to those obtained from line intercept estimates on 14 front reefs of the central GBR (mean of 20 and 13% CCA cover at 10-m fore-reefs of outer- and mid-shelf reefs, respectively, recorded by the line intercept data: Fabricius 1997). However, both visual estimates and line intercept methods tend to miss undersides of ledges and dead corals which have more CCA than upper surfaces; thus both methods are likely to underestimate true CCA abundances. The absence of CCA under sediment was confirmed numerous times, by fanning off the sediment and closely inspecting the substrate underneath. Small CCA specks were occasionally found underneath thin to moderate sediment deposits. It was particularly sparse on horizontal sediment-covered surfaces, and where it occurred under the sediment (e.g., on sloping patches of substrate) it generally grew in small patches (up to a few centimetres squared). In contrast, turf algae were regularly found under thin to moderate sediments, apparently holding the sediment in place (Purcell 2000). Very little turf and crustose coralline algae were found underneath thick sediment deposits.

Relative cross-shelf distance acts as a proxy for a whole range of confounded environmental variables, and it was therefore the single variable that best explained variation in CCA cover. For example, sediments, visibility, and slope angles were all strongly related to relative cross-shelf distance. The same is true for large-scale variation in nutrient concentrations (Revelante and Gilmartin 1982) and grazing intensity by herbivores (Scott and Russ 1987; Williams 1991), both of which were referred to when explaining cross-shelf differences in epilithic and macroalgal abundances (reviewed in Szmant 1997; McCook 1999).

The inverse relationship between CCA cover and sedimentation has, to our knowledge, not been described before, and the mechanisms of how sediment deposits may affect CCA are unknown. CCA are able to survive long periods of burial under sediments, because the upper epithelial cell layers, which are killed by sedimentation, are sloughed off once the sediment is removed (Keats et al. 1997; Pueschel and Keats 1997). Sediment nevertheless appears to negatively affect their abundances, and although it may not kill the CCA, it is likely that it prevents CCA recruitment by blanketing suitable substrate for CCA settlement. Sedimentation is also likely to reduce photosynthesis by shading and by restriction of gas exchange (Klumpp and McKinnon 1989; Patterson et al. 1991); thus scope for growth and calcification may be diminished. Sediment also blankets surviving CCA as settlement substrate for other organisms from the system. Hence, CCA are less likely to fulfill their two key functional roles in coral reefs (calcification and settlement substrate for other organisms) whilst buried under sediment.

From a geological perspective, sediment does not accumulate on reefs, as the topography of reefs facilitates sediment transport downslope onto the sea floor (Larcombe and Woolfe 1999). Nevertheless, thick sediment deposits are regularly encountered on coastal reefs, with highest values found on the lower leeward sides of reefs. While relatively slow current speeds (< 3 cm s^{-1}) are sufficient to remove sediment from elevations and sloping surfaces (Rogers 1990), deposits on flat or concave surfaces are only shifted by rough seas. Sediment in synergy with elevated nutrients can form large and sticky aggregates which are more adhesive than sediments in oligotrophic conditions (Wolanksi and Gibbs 1995). Sedimentation of such sticky aggregates can detrimentally affect small reef organisms within hours to days (Fabricius and Wolanski 2000). While the potential effects of sedimentation of such nutrient-enriched particles on CCA are as yet unknown, they deserve attention, because the import of sediments and nutrients into the GBR lagoon during runoff events has increased several-fold due to expanding grazing and agricultural land use (Wolanski 1994; Larcombe et al. 1996).

The virtual absence of CCA in coastal areas of high sedimentation may have profound implications for the ecology of near-shore coral reefs. The formation of eroding rubble fields is a regular feature on near-shore reefs of the central GBR after coral die-off (Fabricius, personal observations). Caves and cavities below the surface, which are inhabited by diverse and trophically important communities (Wunsch and Richter 1998; Richter and Wunsch 1999), and organisms depending on surface complexity for protection disappear when the reef structure collapses (Szmant 1997). Those organisms with larvae specialised in settling on CCA are also excluded from areas that are unsuitable for the growth of CCA. The absence of CCA on sediment-rich near-shore reefs may partly explain why community composition and species abundances on reefs close to the coast are very different from those further offshore.

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References

Barnes DJ, Chalker BE (1990) Calcification and photosynthesis in reef-building corals and algae. In: Dubinsky Z (ed) Ecosystems of the world: coral reefs. Elsevier, Amsterdam, pp 109–131

Benayahu Y, Achituv Y, Berner T (1989) Metamorphosis of an octocoral primary polyp and its infection by algal symbiosis. Symbiosis 7:159–169

Bjoerk M, Mohammed SM, Bjoerklund M, Semesi A (1995) Coralline algae, important coral-reef builders threatened by pollution. Ambio 24:502–505

Braga JC, Bosence DWJ, Steneck RS (1993) New anatomical characters in fossil coralline algae and their taxonomic implications. Palaeontology 36:535–547

Breiman L, Friedman JH, Olshen RA, Stone CG (1984) Classification and regression trees. Wadsworth International Group, Belmont, California

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for the analysis of complex ecological data. Ecology 81(11) (in press)

Devantier LM, De'ath G, Done TJ, Turak E (1998) Ecological assessment of a complex natural system: a case study from the Great Barrier Reef. Ecol Appl 8:480–496

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1:95–107

Fabricius KE (1997) Soft coral abundance in the central Great Barrier Reef: effects of *Acanthaster planci*, space availability and aspects of the physical environment. Coral Reefs 16:159–167

Fabricius KE, De'ath G (1997) Habitat optima of soft corals on the central Great Barrier Reef: niche characterisation using regression tree analysis. In: Proc of The Great Barrier Reef, Science, Use and Management: A National Conference, vol 2. Great Barrier Reef Marine Park Authority, pp 167–174

Fabricius KE, De'ath G (1999) Effects of sediment and river proximity on coral reef communities. In: Heap AD (ed) North Queensland Sedimentologists' 1st Annual Workshop, Extended Abstracts, School of Earth Sciences, James Cook University, Townsville, pp 43–48

Fabricius KE, Wolanski E (2000) Rapid smothering of coral reef organisms by muddy marine snow. Estuarine Coastal Shelf Sci 50:150–120

Hastie TJ, Tibshirani RJ (1990) Generalized additive models. Chapman and Hall, London

Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. Coral Reefs 18:273–279

Iryu Y, Matsuda S (1988) Depth distribution, abundance and species assemblages of nonarticulated coralline algae in the Ryukyu Islands, southwestern Japan. In: Proc 6th Int Coral Reef Symp Publ 3, pp 101–106

Johnson CR, Sutton DC (1994) Bacteria on the surface of crustose coralline algae induce metamorphosis of the crown-of-thorns starfish *Acanthaster planci*. Mar Biol 120:305–310

Johnson CR, Sutton DC, Olson RR, Giddins R (1991) Settlement of crown-of-thorns starfish: role of bacteria on surfaces of coralline algae and a hypothesis for deepwater recruitment. Mar Ecol Prog Ser 71:143–162

Johnson LG, Cartwright CM (1996) Thyroxine-accelerated larval development in the crown-of-thorns starfish *Acanthaster planci*. Biol Bull Mar Biol Lab Woods Hole 190:299–301

Keats DW, Knight MA, Pueschel CM (1997) Antifouling effects of epithelial shedding in three crustose coralline algae (Rhodophyta, Corallinales) on a coral reef. J Exp Mar Biol Ecol 213:281–293

Klumpp DW, McKinnon AD (1989) Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. J Exp Mar Biol Ecol 131:1–22

Klumpp DW, McKinnon AD (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. Mar Ecol Prog Ser 86:77–89

Larcombe P, Woolfe KJ (1999) Increased sediment supply to the Great Barrier Reef will not increase sediment accumulation at most coral reefs. Coral Reefs 18:163–169

Larcombe P, et al. (1996) Terrigenous sediment fluxes and the central Great Barrier Reef shelf: the current state of knowledge. In: Larcombe P, Woolfe KJ, Purdon RG (eds) Great Barrier Reef: terrigenous sediment flux and human impacts, 2nd edn. CRC Reef Research Centre, Current Research, Townsville, 174 pp

Lasker HR, Kim K (1996) Larval development and settlement behavior of the gorgonian coral *Plexaura kuna* (Lasker, Kim and Coffroth). J Exp Mar Biol Ecol 207:161–175

Liddell WD, Ohlhorst SL (1987) Patterns of reef community structure, north Jamaica. Bull Mar Sci 40:311–329

Littler MM, Doty SD (1975) Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of Porolithon. J Ecol 63:117–129

Littler MM, Littler D (1984) Models of tropical reef biogenesis: the contribution of algae. In: Round FE, Chapman DJ (eds) Progress in phycological research, vol 3. Biopress, Bristol, pp 323–364

Maudsley B (1990) Defenders of the reef. New Sci 126:52–56

McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367

Mendoza ML (1995) The coralline algae (Rhodophyta). Taxonomic characters and methods for their structure study. Naturalia Patagonica Ciencias 3:175–189

Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agaricid corals. J Exp Mar Biol Ecol 116:193–217

Patterson MR, Sebens KP, Olson RR (1991) In situ measurements of flow effects on primary production and dark respiration in reef corals. Limnol Oceanogr 36:936–948

Pueschel CM, Keats DW (1997) Fine structure of deep-layer sloughing and epithallial regeneration in *Lithophyllum neoatalayense* (Corallinales, Rhodophyta). Phycol Res 45:1–8

Purcell SW (2000) Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. Bull Mar Sci 66:199–214

Revelante N, Gilmartin M (1982) Dynamics of phytoplankton in the Great Barrier Reef Lagoon. J Plankton Res 4:47–76

Richter C, Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs – a new link in reef trophodynamics. Mar Ecol Prog Ser 188:105–116

Rogers C (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202

Scott F, Russ GR (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar Ecol Prog Ser 39:293–304

Szmant AM (1997) Nutrient effects on coral reefs: a hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics. In: Proc 8th Int Coral Reef Symp Publ 2, pp 1527–1532

Statistical Sciences (1999) S-PLUS, Version 2000 for Windows. Statistical Sciences, a division of Mathsoft Inc., Seattle

Sweatman H, Ninio R, Osborne K, Ryan D (1997) Corals and sessile benthos. In: Long-term monitoring of the Great Barrier Reef. Status Report 2. Australian Institute of Marine Science, Townsville, pp 99–126

Therneau T (1998) RPART software from statlib@lib.stat-lib.cmu.edu

Williams DMcB (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 437–474

Wolanski E (1994) Physical oceanographic processes of the Great Barrier Reef. CRC Press, Boca Raton 194 pp

Wolanski E, Gibbs RJ (1995) Flocculation of suspended sediment in the Fly River Estuary, Papua New Guinea. J Coastal Res 11:754–762

Wunsch M, Richter C (1998) The CaveCam – an endoscopic underwater videosystem for the exploration of cryptic habitats. Mar Ecol Prog Ser 169:277–282