

Macroalgal species richness and assemblage composition of the Great Barrier Reef seabed

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ABSTRACT: Understanding the drivers of broad-scale patterns of biodiversity is an overarching goal in ecology. We analysed environmental drivers of macroalgal species richness and composition on the continental shelf seabed of Australia's Great Barrier Reef (GBR), and mapped these patterns to show phylogenetically diverse and depauperate areas. Although shelf seabed habitats constitute ~61% of the GBR Marine Park area, previous floristic studies have been largely confined to intertidal and coral reef areas. Recognising the lack of knowledge of this habitat, the GBR Seabed Biodiversity Project (SBP) surveyed environmental variables and associated biodiversity across the shelf. We used SBP data for 1195 epibenthic sled sites, of which 639 sites recorded 370 macroalgal taxa, including 250 taxa not previously described in the GBR. Regression Random Forests were used to identify the environmental variables that most influence algal richness. Patterns of species composition, or assemblages, were investigated using partitioning around medoids (pam) clustering, and classification Random Forests identified the environmental variables most influential, and shapes of responses, for each assemblage. The 5 assemblages were distinguished based on taxonomy, dominant species, functional form or abundance and species richness. Overall, sediment grain size composition and light availability had the greatest influence on species richness and assemblages, with strong thresholds at 20% mud and at relative benthic irradiance of ~0.06 ($\equiv \text{PAR} \approx 120 \mu\text{mol m}^{-2} \text{s}^{-1}$). This study is the first systematic analysis of the macroalgal communities of the GBR shelf seabed, providing valuable information to stimulate future research on taxonomy, productivity and ecosystem services of this habitat.

KEY WORDS: Benthos · Biophysical · Threshold · Seaweed · Macroecology · Inter-reefal · Biodiversity · Seafloor

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INTRODUCTION

Broad-scale biodiversity patterns are a focus in ecology, with distinct distributional patterns observed in marine and terrestrial habitats (Hillebrand 2004, Tittensor et al. 2010). Within the marine environment, spatial patterns along environmental gradients or over space (e.g. terrestrial inputs or latitude) have been identified (Gaston 2000, Fabricius et al. 2005). It has long been established that coral reefs display the highest diversity in the tropics (Bellwood & Hughes 2001) and that coral species richness

increases away from the coast along a cross-shelf gradient (Fabricius et al. 2005). Other organisms follow these latitudinal and/or environmental gradients, some display opposing trends. Macroalgae generally have greater species richness in temperate regions (Kerswell 2006) and in inshore locations as opposed to continental shelf regions (De'ath & Fabricius 2010), but the forces driving these patterns of distribution of marine macroalgae are not always clear (Kerswell 2006). While temperature (Carballo et al. 2002), light (Irving & Connell 2002) and depth (Piazzi et al. 2002) are key broad-scale drivers of

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macroalgal distributions, these factors can be complicated at local scales by variables such as substrate type (Kautsky & Van der Maarel 1990), turbidity (Airoldi & Cinelli 1997, Balata et al. 2007), eutrophication (Korpinen et al. 2007) and species interactions (Davis & Fourqurean 2001).

The Great Barrier Reef (GBR) provides an ideal system to determine the role of latitudinal or cross-shelf gradients in macroalgal distributions. The GBR Marine Park stretches over 2000 km along Australia's northeast coastline and covers 348 000 km². The region contains a large number of interconnected ecosystems along a 'catchment-to-reef' continuum (Schaffelke et al. 2005) in which coral and macroalgal communities constitute the reef-building organisms (Goreau 1963). The continental shelf seabed constitutes 61% of the GBR Marine Park region (Wachenfeld et al. 1998). The shelf seabed forms an integral part of the network of habitats and is composed of 2 main zones: (1) lagoonal areas located between mainland and reef and (2) inter-reefal areas situated between reefs on the mid- and outer-shelf and edge of the continental shelf (Pitcher et al. 2008).

It is estimated that 400–500 species of macroalgae occur in the GBR (Schaffelke et al. 2005, Diaz-Pulido 2008), where they are important primary producers (Lobban & Harrison 1994), but comparatively few floristic studies have been performed (reviewed by McCook & Price 1997). Cowan (2006) reported approximately 630 species and varieties from published distributions of macroalgae within the GBR; however, collections mostly focused on easily accessible coastal regions and reefs around islands (Diaz-Pulido 2008). Diversity and taxonomy of Rhodophyta (Price & Scott 1992) and Phaeophyceae (Phillips & Price 1997) have been examined but habitats and distribution of macroalgae have not been comprehensively analysed. This is surprising given the importance of macroalgae for the formation and function of coral reefs and the role of macroalgae in providing habitat and food for fauna (Schaffelke et al. 2005).

Macroalgal occurrence and growth are determined by both abiotic (substratum, light, temperature, salinity, nutrient availability) and biotic factors (epiphytic loads, competition, herbivores) (de Guimaraens & Coutinho 1996, Schils & Coppejans 2003, Stuercke & Mcdermid 2004, Korpinen et al. 2007, Irving et al. 2009, Lefevre & Bellwood 2010). These variables can also play a role in macroalgal distributional patterns and can interact with other factors such as recruitment and dispersal and stress and disturbance regimes (McCook & Price 1997). Previous research has assessed the effects of water quality including

sediment load and nutrient availability as well as herbivory and recruitment on macroalgal distribution in the GBR (McCook & Price 1997). Studies focusing on the productivity and abundance of algal turfs on reefs in the GBR found that this functional group is influenced by herbivory (Hatcher & Larkum 1983, Wilkinson & Sammarco 1983, Klumpp & McKinnon 1992, Lefevre & Bellwood 2010), nutrient availability (Hatcher & Larkum 1983, Fabricius et al. 2005) and competition (Jompa & McCook 2002). Another study found correlations between macroalgal cover and wave energy, sedimentation and grazing intensity on GBR reefs (Wismer et al. 2009). The role of these and other factors in the distribution and abundance of macroalgae has not been examined for the continental shelf seabed of the GBR (Kerswell 2006).

The species composition of seabed habitats varies with structure and environmental conditions. Different geophysical and environmental attributes may influence the occurrence of biota at different levels of a hierarchical habitat classification. For example, substratum type is a major determinant of biotic composition because distinct communities inhabit consolidated and unconsolidated surfaces such as rocky surfaces and sand, respectively (Williams & Bax 2001). Within rocky habitats, areas characterised by greater vertical relief and complexity, compared with gentle slopes, can have higher fish species diversity (Ebeling et al. 1980) and a distinct assemblage of organisms (Harman et al. 2003). Habitats with unconsolidated substratum, distinguishable by sediment size composition and, at lower hierarchical levels, by presence or absence of vegetation cover and dominant algal species, will also host distinct assemblages of organisms. The ability to predict the presence of organisms based on geophysical and other environmental attributes is useful for ecological assessments. Seabed habitat is often mapped to identify the distribution and structure of marine ecosystems and is used as a surrogate measure of biodiversity for marine protected area planning (Aswani & Lauer 2006). As faunal diversity can be higher in macroalgal habitats (Levin & Hay 1996, Pitcher et al. 2007) than un-vegetated substrate, an understanding of the distributional patterns of the floral community complements information on abiotic variables and provides insight into resources, habitats and ecosystem function.

The habitats and associated biodiversity of the GBR's 210 000 km² continental shelf were sampled and mapped in 2003–2006 by the GBR Seabed Biodiversity Project (GBR SBP; Pitcher et al. 2007) to provide information to assist conservation planning and

fisheries management. This study uses data extracted from the GBR SBP's epibenthic sled sample database to test the hypotheses that macroalgal diversity and community structure vary in relation to environmental variables and habitat suitability rather than as a simple function of latitude and cross-shelf distance.

MATERIALS AND METHODS

Sampling seabed communities

The GBR SBP sampled almost 1400 sites during 10 one-month-long voyages on 2 vessels. Data were collected and processed from towed video and digital stills, baited remote underwater video stations, digital echograms, an epibenthic sled and a research trawl (Pitcher et al. 2007). Here, we analyse the data for the macroalgal samples collected by the epibenthic sled, which was 1.5 m wide, with a 25 mm stretched mesh net attached, and towed for ~200 m at each site (a sample area of 300 m² of sea floor). The sled was dragged over the seabed, primarily on unconsolidated sediments (mud, silt, sand, gravel, cobbles) but also on some harder, low-rugosity substrata (i.e. low-profile bedrock, small rocks) and sampled both sessile and mobile benthic organisms on or just above the substrate. In total, 1195 sites were sampled between 6 and 126 m depth by the sled, of which 639 contained macroalgae.

The marine plant samples were identified, using available algal guides (Skelton & South 2002, South & Skelton 2003) and the online database 'AlgaeBase', by Dr P. A. Skelton with support from Professor G. R. South, both experienced algal taxonomists with over 2 dozen publications on Pacific macroalgae (e.g. South 1992, South et al. 2001, South & Skelton 2003). Samples were weighed and representative voucher specimens were preserved in formalin and later transferred to ethanol and catalogued with the Queensland Department of Primary Industries, Townsville. Herbarium sheets were also prepared for each voucher specimen. Specimens were identified to known named species where possible, otherwise to nearest comparable known species (cf.) or—in cases of suspected new taxa—to alpha species level (i.e. sp. #). Some specimens (10.8%) could not be identified to species-equivalent level; in most cases these were identified to genus level—only 1.8% were limited to family or order level.

The GBR SBP collated data layers for the major environmental variables that may influence the distribution and abundance of the seabed habitats and

assemblages in the GBR, including: bathymetry (depth, slope, aspect); sediment grain size (% mud [$<63 \mu\text{m}$], sand [$63 \mu\text{m}$ – 2mm] and gravel [$>2 \text{mm}$]); force of water currents (seabed shear stress; a function of the current speed and the friction due to seabed rugosity); chlorophyll, light attenuation and benthic irradiance (relative to sea surface at equator, annual average); and bottom water attributes (temperature, salinity, dissolved O₂, NO₃, PO₄, Si) (Pitcher et al. 2007).

Data analysis

The algal species richness, calculated simply as the number of taxa sampled by the sled at each site, was mapped to show diverse and depauperate areas of the GBR. Richness was analysed against the 25 environmental data layers to identify those variables that were most influential for predicting the richness of algal assemblages, using the ensemble tree method Random Forests (Breiman 2001), as implemented in the R package 'randomForest' (Liaw & Wiener 2002). Each tree in a 'forest' (of 500 trees) is fitted to a random sample (0.632, on average) of the observations (the 'in-bag'), each branch split is selected from a different random subset of one-third of the predictors, and the performance of each tree is cross-validated against the remaining 'out-of-bag' observations. The overall fit over the forest and the predictive performance was indicated by the average proportion of out-of-bag variance explained (R²). This cross-validated R² is more conservative than explained variation of fit to in-bag samples, and is a more robust estimate of prediction error. The marginal importance of each variable was assessed by random permutation of the variable and calculating the degradation in fit. The partial dependence of species richness on each variable was plotted for each value of the variables in the data set by averaging the forests' prediction for all other values of all other variables in the data set. This provides a graphical representation of the marginal response of species richness along the gradient of each variable.

Patterns of species composition, or 'assemblages', were investigated using the clustering method 'partitioning around medoids' (pam) (Kaufman & Rousseeuw 1990), as implemented in the function pam in the R package 'cluster'. First, a Bray-Curtis dissimilarity matrix was calculated from the log_n(biomass + 1) transformed site-by-species matrix. The data set had substantial compositional variation; however, there was little evidence of distinct clustering from

the pam diagnostics over a wide number of clusters ('silhouette width'; Kaufman & Rousseeuw 1990). Consequently, multivariate regression trees (De'ath 2002; R package 'mvpart') were used to indicate how many assemblages may be predictable from the environmental variables. Over several randomizations, the best performing cross-validated trees indicated that 4–6 terminal nodes (clusters) were predictable from the environmental variables; hence, 5 clusters were chosen for the pam clustering of the dissimilarity matrix. The 5 pam clusters were mapped, and for additional presentation and interpretation purposes a 2-dimensional non-metric multidimensional scaling (MDS) of the Bray-Curtis dissimilarities between sites was also plotted, along with a spanning tree to indicate similarities between the cluster medoids. For comparison, the Bray-Curtis dissimilarities between medoids were also plotted as a simple dendrogram using the function `hclust` in the R package 'stats'.

To identify the environmental variables that were most influential for each of the algal assemblages, classification Random Forests were used to predict the 5 pam clusters and the predictor importance diagnostics and partial response plots for each cluster were examined. The algae that typified each cluster were also identified: those taxa that were dominant with respect to biomass in clusters were listed from the top 2.5th percentile of $\log_n(\text{biomass})$ and those taxa having greatest fidelity and relative abundance in clusters were listed from the top 5th percentile of the Dufrene-Legendre indicator (DLI) (Dufrene & Legendre 1997; function 'indval', R package 'labdsv'). All analyses were conducted in the R statistical computing environment (R Development Core Team 2009).

RESULTS

Species richness

A total of 367 macroalgal taxa, representing a variety of functional forms and attachment types, were collected and identified during the GBR SBP (Table S1 in the Supplement at www.int-res.com/articles/suppl/m492p069_supp.pdf). Red algae constituted the most diverse phylum with 193 taxa (53%), green algae were second (131 taxa, 36%), while brown algae were represented by 43 taxa (11%). *Gracilaria* sp. 2 (a likely new species of Rhodophyta; P. Skelton pers. comm.), a cartilaginous strap-like species, was the most commonly occurring single taxon (collected at 240 out of a total of 639 sites

with algae) followed by *Udotea orientalis* (Chlorophyta) (collected at 204 sites). Eighty-eight algal taxa (24%) were sampled at only one site in the GBR shelf seabed.

No simple cross-shelf or latitudinal gradients in GBR macroalgal species richness were observed. The richness of seabed macroalgal species assemblages varied greatly across the locations sampled and ranged from no alga collected up to 76 taxa per sled tow (termed 'per site' in the following) (Fig. 1). Highest species richness (>15 taxa per site) was observed in the southern GBR off the coast of Gladstone and Rockhampton and in the central area of the GBR off the coast of Townsville. Offshore *Halimeda* banks (large elevated areas of 15–20 m thick sediment banks situated between the reefs and reaching to within 20 m of the surface with extensive macroalgal meadows dominated by *Halimeda*; Drew 2001) north of ~15°S also displayed relatively high species richness with an average of 10–12 taxa per site. The lowest species richness of 1–5 algal taxa per site was observed in Shoalwater Bay in the southern area and many inshore sites in the northern half of the GBR. No algae were detected in sled samples in a large area of the Capricorn Channel representing over 130 sites and a sampled area of ~40 000 km². Similarly, 9 sites from smaller areas in Princess Charlotte Bay, representing a sampled area of ~3000 km², did not contain algae (Fig. 1). Only 4 sites deeper than 80 m had algae present, with the majority of sites containing algae found between 10 and 65 m depths.

Percent mud and benthic irradiance were the most important predictors for algal species richness in Random Forest models (Fig. 2). Sites with a low percentage of mud in the seafloor substratum and high benthic irradiance had the greatest species richness. The lowest species richness was observed at sites with a high percentage of mud in the sediment and low irradiance. Other important predictors for species richness were % gravel, % carbonate, average salinity, % sand, bottom stress and salinity standard deviation. The cross-validated R² was 48%, indicating that the environmental variables could predict substantial variation in the species richness of out-of-bag samples (by comparison, explained R² was ~91%).

The shape of the relationships between algal species richness and the top 8 environmental predictors are shown in a series of 'partial response plots' (Fig. 3). The plots display how richness changes along each gradient, averaged over all values of all other variables in the data set. Species richness changed very steeply at certain points along these

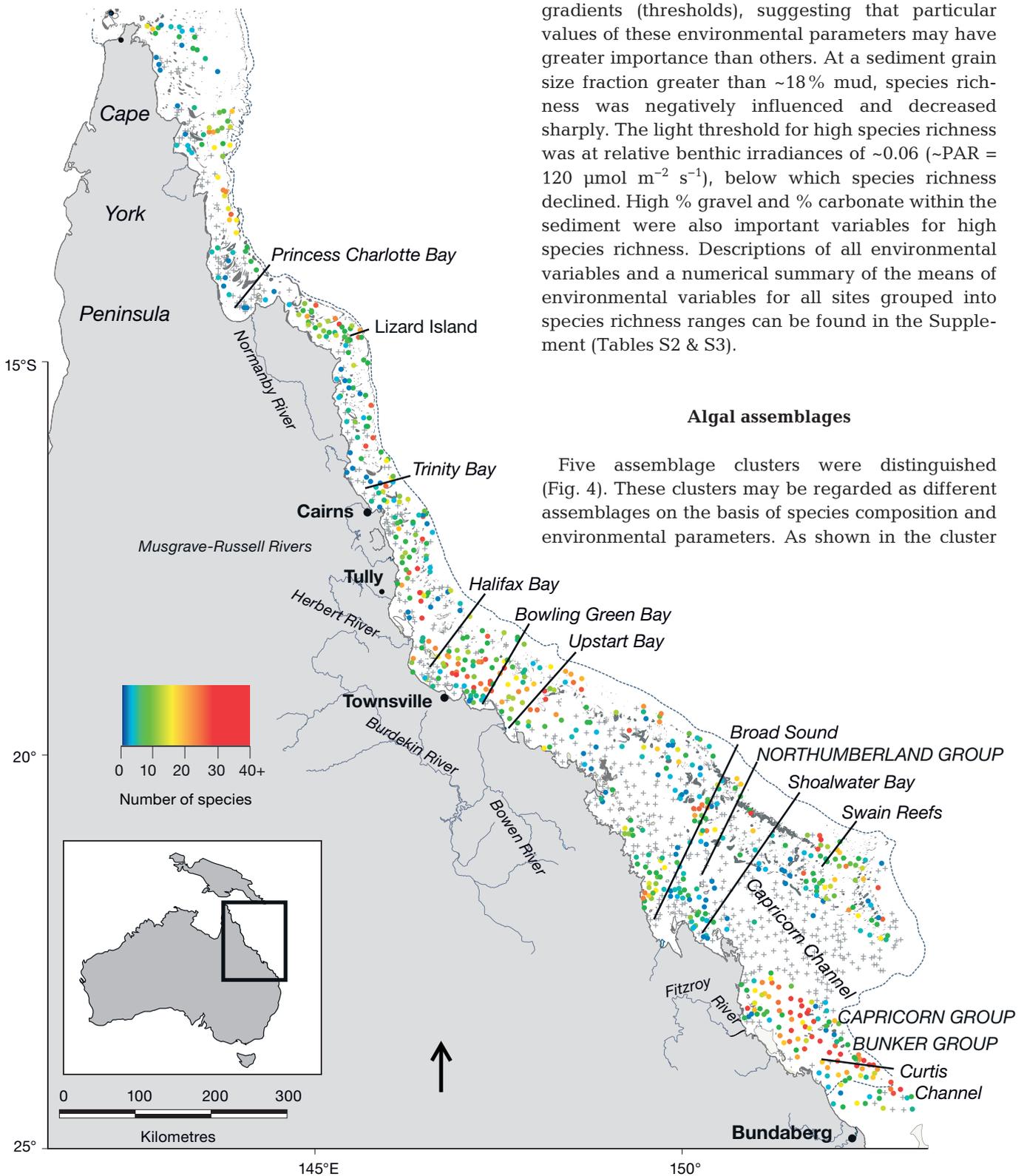


Fig. 1. Algal species richness on the Great Barrier Reef continental shelf seabed showing areas of high richness, which tended to be associated with sandy or gravelly sediments and adequate light, and areas of low richness, which tended to be associated with muddy sediments and low light. Grey '+' symbols mark sites with no algae

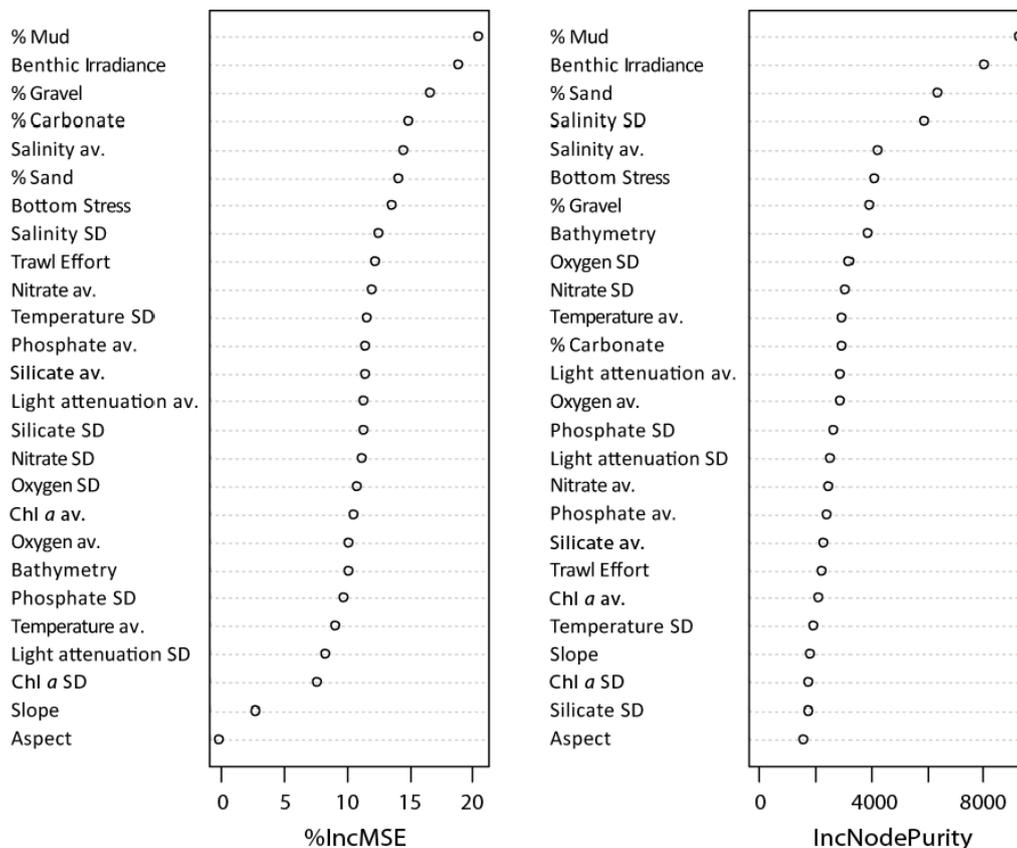


Fig. 2. Predictor importance plots for algal species richness on the GBR seabed. %IncMSE is the mean decrease accuracy; a higher %IncMSE value represents higher variable importance. IncNodePurity is the total decrease in node impurities from splitting on the variable, averaged over all trees. For regression, it is measured by residual sum of squares. Higher values indicate higher variable importance. Overall, the environmental variables explained ~91% of the variation in species richness and predicted 48% of variation in cross-validation sets

dendrogram, assemblages 2 and 3 were the most similar, followed by assemblages 1 and 4, which were clustered with assemblage 5. The MDS plot shows the degree of similarity between the assemblages for individual sites. Each cluster medoid was relatively distinct, although some sites overlapped between assemblage clusters. Assemblage 1 was the least distinct and overlapped with assemblages 2 and 5. The high stress value of the MDS plot indicates that the variation in composition was not well represented in 2 dimensions (extending the MDS to 3 dimensions reduced the stress). This suggests that the compositional patterns were complex, with diverse distributional patterns of many species at numerous sites. Information about the composition of the assemblages and corresponding environmental characteristics is presented in Table 1 and additional attributes are contained in Table 2. The DLI values indicate 'representative' taxa; i.e. those taxa with the highest DLI have the strongest affinity and fidelity to the assemblage. The partial response plots for the 4 most important en-

vironmental variables for each assemblage are included in Fig. 5. All partial response plots for each assemblage along 25 environmental gradients and a numerical summary of the means and SDs of environmental variables for all sites grouped into assemblages can be found in the Supplement (Figs. S1–S6, Table S4).

The first assemblage (referred to here as the '*Hali-medea gracilis* assemblage') was characterised by a single taxon, *H. gracilis*, with a DLI of >0.44, the highest fidelity of any taxa in the identified assemblages (Table 1). This was the least common of the identified assemblages occurring at 62 (9.7%) out of a total of 639 sites containing algae (Table 2) and was low in biomass and species richness. It occurred in small geographical clusters scattered throughout the seabed of the GBR (Fig. 4). The environmental variables contributing most to the prediction of this assemblage were high standard deviation of chlorophyll *a* content of seawater (mean \pm SD: 0.69 ± 0.76), low average silicate content of seawater ($1.74 \pm 1.22 \mu\text{M}$) and high average nitrate content of sea-

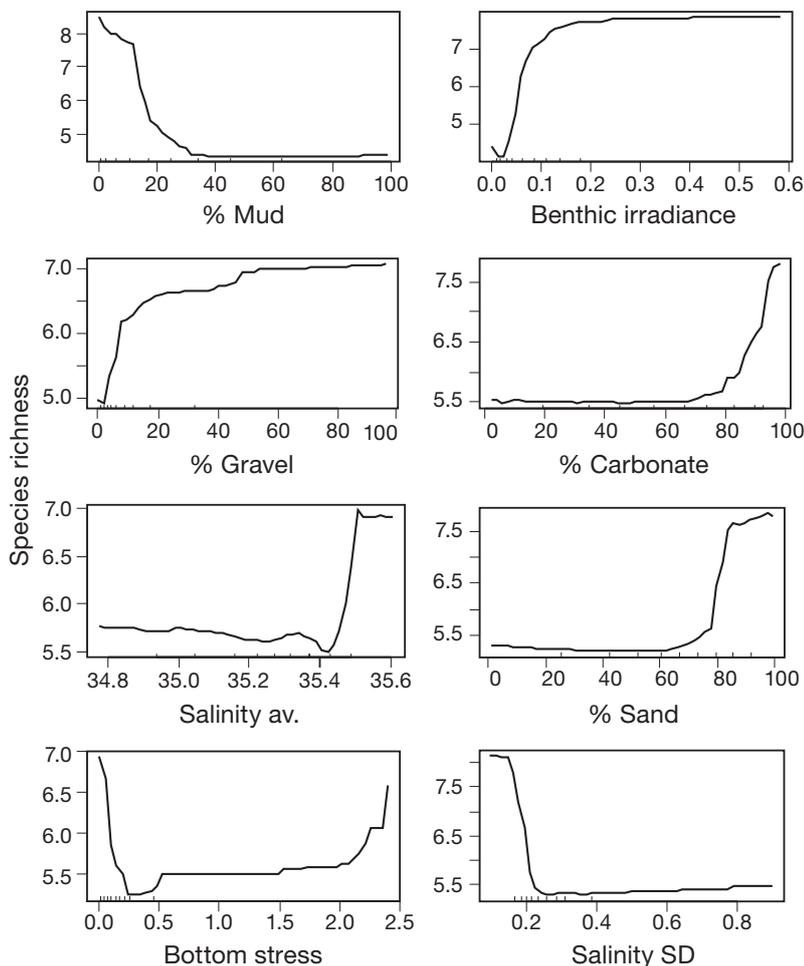


Fig. 3. Partial response plots for algal species richness along gradients of the top 8 most important environmental variables in the GBR seabed. The plots display how species richness changes along each gradient, averaged over all values of all other variables in the data set

water ($0.95 \pm 1.67 \mu\text{M}$). Overall, the occurrence of this assemblage was the most difficult to predict (class prediction error = 0.89).

Assemblage 2 (the 'Bryopsidales assemblage') was characterised by siphonous (Vroom & Smith 2001) calcareous green algae from the order Bryopsidales including *Udotea orientalis*, *Halimeda gigas* and *H. opuntia*, with a DLI > 0.30 (Table 1). Other taxa, also from the Bryopsidales, somewhat less characteristic of this assemblage included *H. borneensis*, *Caulerpa taxifolia* and *C. sertularioides* (DLI > 0.20). Many of these taxa are psammophytic (sand-dwelling) species. This assemblage occurred at 17.2% of sites where algae were recorded (Table 2). North of 15°S , species of *Halimeda* indicative of this assemblage formed the northern GBR *Halimeda* banks, while around the northern/outer Swains reef complex, dense, non-bank forming communities of taxa from

assemblage 2 commonly occurred (Fig. 4). The environmental variables contributing most to the prediction of this assemblage were high relative benthic irradiance (mean \pm SD: 0.14 ± 0.08), low % mud ($12.13 \pm 14.41\%$) and high % gravel ($17.02 \pm 21.6\%$); class prediction error = 0.46.

Assemblage 3 (the '*Lobophora*-turf assemblage') was characterised by the brown alga *Lobophora variegata* and a mixture of unidentified red turf algae (DLI > 0.30; Table 1). This highly diverse assemblage possessed an average of 19 taxa per site with representatives from 3 phyla. It was also the most common assemblage in our analysis, occurring in 31.8% of sampled sites that contained algae (Table 2). Distribution was concentrated in 2 main areas: the Capricorn Bunker area and Central GBR off Townsville (Fig. 4), mostly in combination with dense seagrass beds. The environmental variables contributing most to the prediction of this assemblage were low standard deviation of salinity (mean \pm SD: 0.21 ± 0.08), high relative benthic irradiance (0.11 ± 0.06) and low % mud ($10.35 \pm 14.77\%$); this was the best-predicted assemblage (class prediction error = 0.35).

The fourth assemblage (the 'red foliose assemblage') was dominated by larger red algae, primarily *Aneuri-anna lorentzii* (DLI > 0.32) with *Gracilaria* sp. 2 and *Osmundaria fimbriata* showing only slightly lower fidelity (DLI > 0.20; Table 1). These 3 species all belong to the same subclass (Rhodymeniophycidae), while *A. lorentzii* and *O. fimbriata* are both within the Amansieae tribe. The assemblage occurred at 20.3% of algae-containing sites clustered around the Northumberland Island group in the southern GBR and also in small clusters in the Cairns/Cooktown area (Fig. 4). The environmental variables contributing most to the prediction of this assemblage were low % mud (mean \pm SD: $19.53 \pm 21\%$), high bottom stress ($0.35 \pm 0.42 \text{ Nm}^{-2}$) and high % gravel ($17.83 \pm 18.46\%$); class prediction error = 0.68.

The fifth assemblage (the 'marginal assemblage') did not contain taxa with strong DLI in the top 5th percentile (Table 1). The assemblage was very sparse in algal abundance, had low species richness (aver-

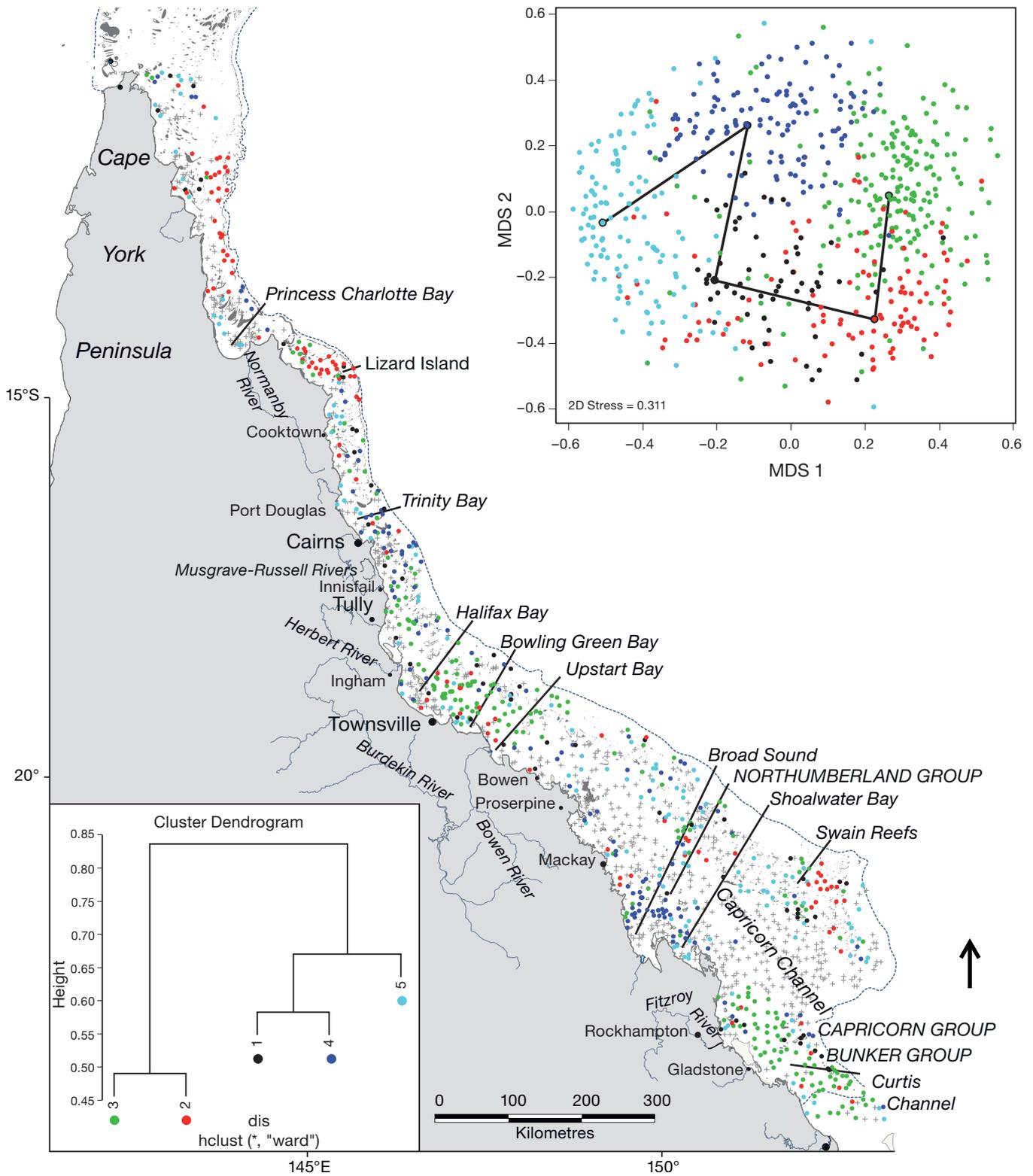


Fig. 4. Distributions of GBR seabed algal assemblages: (1-black) *Halimeda gracilis* assemblage; (2-red) Bryopsidales assemblage; (3-green) *Lobophora*-turf assemblage; (4-blue) red foliose assemblage; and (5-cyan) marginal assemblage (for details on assemblages, see Table 1). Grey '+' symbols mark sites with no algae. Insets show a dendrogram and a 2D multi-dimensional scaling (MDS) plot of the 5 pam (partitioning around medoids) clusters, with medoids connected by a minimum spanning tree. Sites with no algae are not shown in the ordination

Table 1. Description and composition of the 5 algal assemblages. The Dufrene-Legendre indicator (DLI) shows 'representative' species; those species with the highest DLI of fidelity have the strongest affinity or loyalty to the assemblage. N/A: not applicable

Assemblage	Species with high fidelity	DLI	Description of algae
1 <i>Halimeda gracilis</i> assemblage	<i>H. gracilis</i>	0.44	A generally deep-growing calcareous alga
2 Bryopsidales assemblage	<i>Udotea orientalis</i>	0.36	A mixture of siphonous green algae, some calcareous
	<i>Halimeda gigas</i>	0.33	
	<i>H. opuntia</i>	0.3	
	<i>H. borneensis</i>	0.23	
	<i>Caulerpa taxifolia</i>	0.22	
	<i>C. sertularioides</i>	0.2	
3 <i>Lobophora</i> -turf assemblage	<i>Lobophora variegata</i>	0.37	A mixture of mostly red species, some turfs, with some green algae. Often found in association with seagrass beds
	Florideophyceae sp. 3	0.3	
	<i>Gracilaria</i> sp. 2	0.28	
	<i>U. argentea</i>	0.23	
	<i>Haloplegma duperreyi</i>	0.23	
	<i>Distromium flabellatum</i>	0.22	
4 Red foliose assemblage	<i>Aneurianna lorentzii</i>	0.33	A red foliose mixture
	<i>Gracilaria</i> sp. 2	0.25	
	<i>Osmundaria fimbriata</i>	0.21	
5 Marginal assemblage	No individual species with high fidelity	N/A	N/A

age only 2 taxa per site; Table 2) and occurred at 21 % of algae-containing sites. This assemblage was not strongly clustered in any area and overlapped with the distribution of the red foliose assemblage in a number of areas. The environmental variables contributing most to the prediction of this assemblage were low relative benthic irradiance (mean \pm SD: 0.08 ± 0.09), high % mud ($22.53 \pm 23.46\%$) and low average phosphate ($0.15 \pm 0.05 \mu\text{M}$); class prediction error = 0.85.

No algae were found at 556 sites (46.4%) of the 1195 sampled sites. Sites where no algae were found were clustered in the Capricorn Channel and other muddy areas along the coast and elsewhere; as well as the turbid, high-current Broad Sound (Fig. 4). The environmental variables contributing most to the prediction of sites with no algae were high % mud (mean \pm SD: $35.25 \pm 26.47\%$), low relative benthic

irradiance (0.06 ± 0.07), <80 % sand ($54.94 \pm 23.89\%$) and high standard deviation of temperature (1.57 ± 0.4). Sites without algae were readily described by the predictors (class prediction error = 0.12).

DISCUSSION

Species richness

This study presents the first analysis of diversity and distribution of continental shelf seabed algal communities of the GBR, and was based on the 370 macroalgal taxa sampled and identified at 639 of 1195 sites by the SBP (Pitcher et al. 2007). We show that seabed macroalgae cluster into 5 assemblages that occur in regions of the GBR characterised by distinct environmental variables rather than simple

Table 2. Details of sample composition for each assemblage showing biomass, frequency of occurrence, and species richness. The '*Lobophora*-turf assemblage' is the most species-rich and most common assemblage, while the 'Bryopsidales assemblage' had the greatest biomass

Assemblage	Total biomass (kg), sampled sites scaled to 1 ha	Number of sites of this assemblage	Average biomass per site (kg ha ⁻¹)	Number of species in assemblage	Average number of species per site
1 <i>H. gracilis</i>	1915	62	30.9	119	5.8
2 Bryopsidales	31 218	110	283.8	178	10.6
3 <i>Lobophora</i> -turf	20 985	203	103.4	331	19.5
4 Red foliose	2315	130	17.8	167	6.6
5 Marginal	393	134	2.9	143	2.4

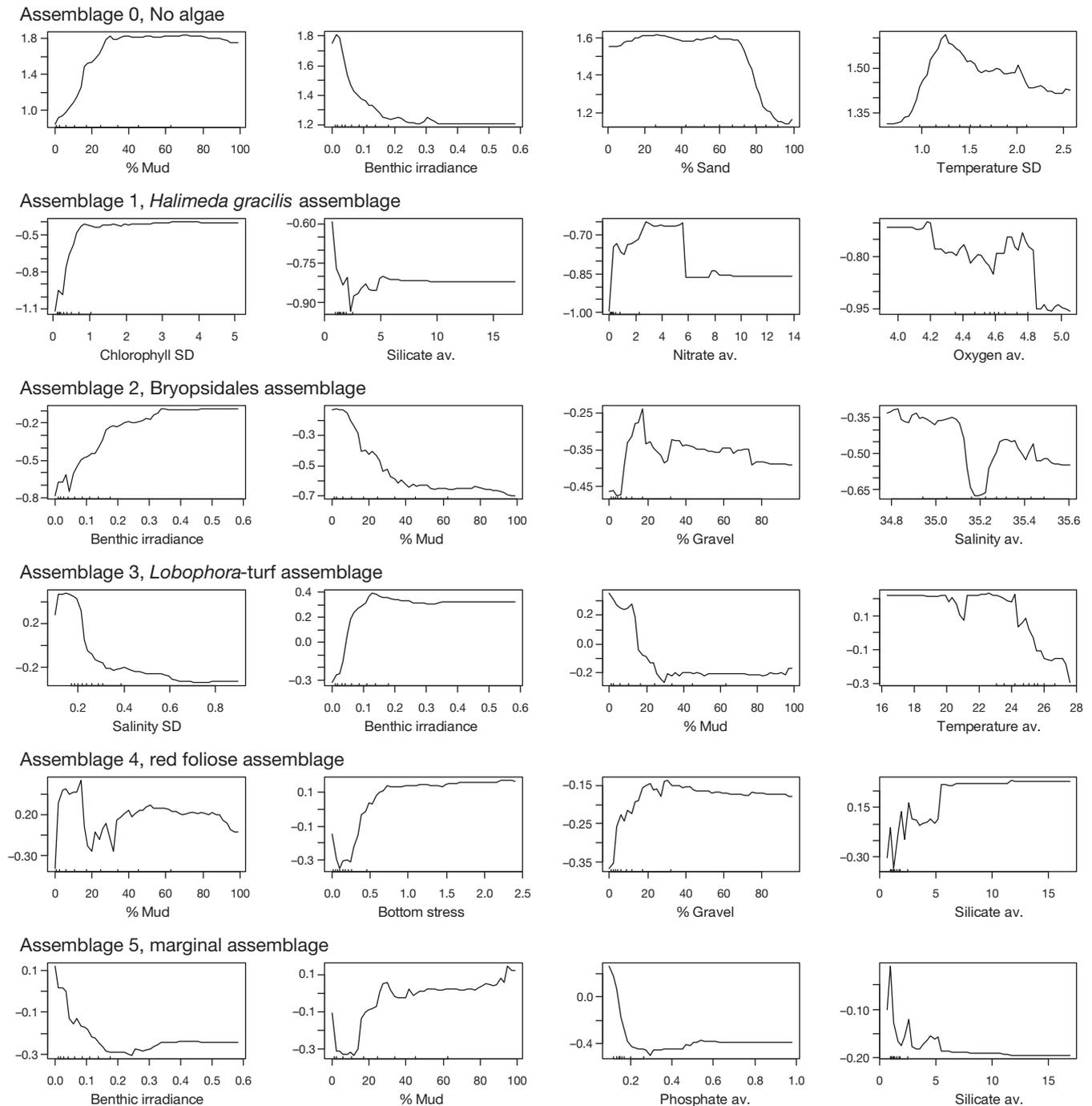


Fig. 5. Partial response plots indicating the probability (logit y-axis scale) of each algal assemblage (including sites without algae as 'assemblage 0') along gradients of the top 4 most important environmental variables (averaged over all values of all other variables in the dataset)

cross-shelf or latitudinal gradients. Approximately 630 species and varieties of macroalgae were recorded previously within the GBR (Cowan 2006). This estimate is based on collections focused on reefal and intertidal regions (Diaz-Pulido 2008) and largely excluded the shelf seabed. Approximately

250 taxa occurred in the GBR SBP samples that were not listed by Cowan (2006), giving a revised total species estimate of ~880 taxa. This demonstrates that although there is some overlap between reefal and seabed species, there are many macroalgal species that are found on the shelf seabed but not on coral

reefs, and vice versa. While the taxonomy of numerous species remains unresolved, the presence of previously unrecorded taxa indicates that overall species richness of GBR macroalgae is ~30 % higher than previously estimated.

The lack of previous algal sampling of the GBR shelf seabed, rather than GBR reefs, precludes comparison of our seabed-specific findings with others. Shelf seabed algae have mostly been studied in temperate zones (e.g. Bax & Williams 2001), with comparatively few studies in the tropics and subtropics. In addition, most studies involving mapping algal distributions usually are focused on limited regional habitats such as bays (e.g. Jervis Bay, Barrett et al. 2008) or around islands (e.g. Kent Group of Islands, Jordan et al. 2005). Our study examined algal assemblage patterns over a wide geographical range and diverse habitat types including lagoonal, shelf-edge, inter-reefal and deeper channel areas ranging to ~100 m depth. This study demonstrates that algae form a very extensive and important, formerly unknown, shelf habitat covering about 25 000–30 000 km² (cover data from towed video transects; Pitcher et al. 2007). To date, no reports of extensive cover of shelf seabed algae to this scale have been published.

Within Australia, the GBR region contains ~60 % of the total species found within the well-studied, and phylogenetically species-rich, southern temperate region (Womersley 1981, Phillips 2001; ~1150 spp.; Kerswell 2006). High phylogenetic diversity has been linked to high productivity (Bruno et al. 2005). Over large geographic scales it is highly likely that variation in diversity is associated with variation in productivity (Chase & Leibold 2002, Chase 2010), suggesting that the GBR seabed has higher productivity per unit area than many other tropical sites, but lower productivity than Australia's temperate waters. However, the disparate size and research intensity of northern and southern continental shelf regions make comparisons difficult.

This study identified 'thresholds' of certain environmental variables for species richness, the 2 most important of these being light availability and % mud. As macroalgal communities require suitable substrata and light is often a limiting resource, it is not surprising that variability in these factors influences the structure of most macroalgal communities (Luning 1990). Our study highlights that particular levels of these environmental parameters may have greater importance than others, with strong changes in species richness at 'thresholds' in available light and % mud. Luning (1990) proposes that high-light-

adapted macroalgae are light saturated at ~500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ whereas shade-adapted macroalgae are saturated at 60–150 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Another study observed changes in the macroalgal and cyanobacterial species present between low (150 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and high (500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) light (Fong & Zedler 1993). Our study found steep declines in species richness at sites with benthic irradiances below PAR $\approx 120 \mu\text{mol m}^{-2} \text{ s}^{-1}$. While no previous studies were found that propose thresholds in sediment grain size, our study found that species richness decreased sharply at a sediment grain size fraction greater than ~18 % mud. Species richness increased at sediment grain size fractions greater than ~10 % gravel and ~80 % sand. On the GBR seabed, we identified that the most species-rich areas were characterised by sand or gravel sediments, which generally have less turbid water and higher light penetration due to lower availability of fine particles for re-suspension by waves and tidal currents. These included areas offshore (up to 80 km) from Curtis Channel in the Capricorn Bunker lagoon, and in the inner mid-shelf lagoon offshore from Townsville. Areas with coarse sand, such as offshore regions around Lizard Island in the north and the Swain Reefs in the south, provide suitable substratum for species in the genus *Udotea* and psammophytic species of *Halimeda*, which form rhizoidal masses, allowing anchorage in the sediment (Littler & Littler 1990). When growing in sufficient densities, these algae create a baffling effect that reduces current strength at the sediment–water interface and may benefit other species, resulting in increased species diversity (Scoffin 1970).

Conversely, species richness was low (1–3 species) in areas characterised by low light (relative benthic irradiance mean \pm SD: 0.08 \pm 0.08) and high mud (mean \pm SD: 24.72 \pm 24.41 %) conditions. This low light/high mud pattern was also observed by Kuenen & Debrot (1995) in the Netherlands Antilles, where algal communities with the lowest species richness were typically associated with low light intensities or mud-rich substrates. Mud provides a poor substratum for algal attachment, and fine particles in suspension reduce light availability (Devlinny & Volse 1978). Fine sediment grain size negatively impacts algae by smothering adult thalli and reducing settlement success (Devlinny & Volse 1978), and may reduce recruitment, growth, survival and regeneration (Umar et al. 1998, Chapman & Fletcher 2002, Schiel et al. 2006, Irving et al. 2009). We show that the majority of algal species were found in the 10 to 65 m depth range. These results are similar to previous findings (Doty et

al. 1974) from the seaward edge of the Hawaiian algal ridge, where a depth range from 10 to 165 m was surveyed and the majority of the algae were found between 20 and 60 m. Algae were absent from deeper areas of the GBR, such as the Capricorn Channel, which can reach depths in excess of 80 m, where light availability is low due to depth of the seabed and/or high turbidity (Pitcher et al. 2007).

The GBR is linked to large and diverse river catchments, and riverine sediments influence the GBR ecosystems directly and indirectly. Direct influences occur through enhanced turbidity, sedimentation and changes in substratum; indirect impact occurs by facilitating nutrient transport from terrestrial sources (Neil et al. 2002). No algae were present in shallower areas of the GBR characterised by high turbidity and high mud content, indicating that inshore species richness is limited by sediment loads carried from river catchments that create areas that are too muddy and turbid to support diverse algal assemblages. Macroalgal responses to sediment run-off vary with species and functional form but can include die-back, reductions in recruitment, competitive shifts and loss of diversity (reviewed in Diaz-Pulido 2008).

Nitrate and phosphate were only moderately important predictors of species richness in this study. These results give weight to the relatively recent paradigm shift, suggesting that nutrients may not be the primary limiting factor in many algal communities (reviewed in McCook 1999). Nutrients can contribute to productivity and composition of these communities, but the effects of nutrient enrichment have to be considered in the context of other environmental factors, especially light availability and substratum type. Additionally, the form of nutrients is likely to play a role in these communities. Nitrate was the sole nitrogen form available for analysis; however, other forms of nitrogen (ammonium, organic nitrogen) may dominate in terrestrial runoff or upwelling events (Fabricius et al. 2005) and these nitrogen sources can stimulate growth of some macroalgal species (Campbell 2001, Tyler et al. 2005, Lovelock et al. 2008). We cannot exclude the possibility that nitrogen forms other than nitrate influence the algal communities studied here.

Algal assemblages

There have been few studies globally that have assessed the distribution of shelf seabed algal assemblages. Most seabed studies have focused on large-scale mapping of habitats using methods such as a digital acoustic seabed classification system on a

large scale (Anderson et al. 2002) and autonomous underwater vehicles on a smaller scale (Armstrong et al. 2006). The taxonomic resolution resulting from the use of these methods is usually low, often only identifying algae to approximate groups. The GBR SBP study identified algae to fine-scale taxonomic levels and enabled a better understanding of macroalgal biology. Determining which different species aggregate into assemblages presents an opportunity to study community structure and monitor change, and provides a benchmark of the current status of the GBR seabed. This study described 5 macroalgal assemblages within the GBR seabed region. While some assemblages overlapped spatially, clear patterns were observed in a number of locations. Two of the assemblages were characterised taxonomically ('Bryopsidales assemblage') or by a single dominant species ('*Halimeda gracilis* assemblage') and 2 were characterised by functional form ('red foliose assemblage' and '*Lobophora*-turf assemblage'). The 'marginal assemblage' was not characterised by any recurrent species or functional form.

Our results challenge previous studies suggesting that inshore areas of the GBR are generally dominated by leafy brown algae such as *Sargassum* (McCook 1996, Diaz-Pulido 2008). Rather, our study contradicts simplified patterns of inshore dominance by foliose species. Distributional patterns in inshore areas, as in mid- and outer-shelf areas, were highly varied, with each of the 5 assemblages occurring in multiple locations, both inshore and offshore. These findings highlight the variability of the inshore areas of the GBR that are subject to a diverse range of coastal inputs and substratum types, creating different habitats that cannot be summarised simply as 'inshore'. The presence of cross-shelf and latitudinal gradients in GBR macroalgal communities has been discussed (e.g. Wismer et al. 2009), but the patterns observed in our study suggest greater complexity. All assemblages occurred in multiple locations ranging from the far northern to the southern GBR and across the shelf. From our results it appears that physical environmental drivers and location of particular environmental combinations play a far greater role in distributional patterns than cross-shelf or latitudinal spatial patterns alone.

The identified 'threshold' values in our analysis provide useful information for management decisions and potential benchmarks for use in other comparable ecosystems. Knowledge of key environmental drivers of assemblage structure provides a tool to monitor or predict shifts in species presence. While projections of future changes in rainfall and river

flow for most tropical locations are not well defined, there is agreement that the intensity of extreme flood and drought events is likely to increase (Meehl et al. 2007). Larger flood events have the potential to increase mud and turbidity of the GBR. The richer assemblages, with a strong affinity to high-light and low-mud environments, such as the 'Bryopsidales assemblage' and the '*Lobophora*-turf assemblage', may shift their range or be reduced in extent or lost from these areas. A reduction in the distribution of the largely calcareous 'Bryopsidales assemblage', the assemblage with the highest biomass and containing species that contribute large quantities of biogenic carbon to the GBR, could impact sediment production and carbon sequestration (Doney 2010). This assemblage, in contrast to assemblages with non-calcifying species, may also be negatively affected by ocean acidification, as lower calcification rates have been observed for component species under elevated CO₂ conditions (Borowitzka & Larkum 1986). Furthermore, this assemblage, which includes the Northern *Halimeda* banks, may rely on upwelling of oceanic nutrients (Drew 1983) that may change in frequency and magnitude in the future (Bakun 1990, Roemmich & McGowan 1995). Reductions in the extent of the most common assemblage, the '*Lobophora*-turf assemblage', through changes in light availability due to increased turbidity, may impact higher trophic levels through a loss of habitats for crustaceans and other fauna (Choat & Ayling 1987, Briones-Fourzán & Lozano-Álvarez 2001, Parker et al. 2001, McAbendroth et al. 2005).

Taken together, the results of our study highlight that variation in algal assemblages and species richness of the GBR seabed is linked to variation in the physical environment of the seabed. There is a known relationship between biodiversity and ecosystem function (Loreau 2000), and macroalgal species richness and identity can have striking effects on productivity (Bruno et al. 2005). Thus, changes in marine biodiversity will affect community properties and ecosystem processes including nutrient use and cycling, productivity, stability and trophic transfers (Stachowicz et al. 2007). Our results provide a baseline for future studies on the ecosystem services and productivity of the GBR shelf seabed macroalgae community.

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