REPORT

Distribution, abundance and diversity of crustose coralline algae on the Great Barrier Reef

Angela J. Dean · Robert S. Steneck · Danika Tager · John M. Pandolfi

Abstract The Great Barrier Reef (GBR) is the world's largest coral reef ecosystem. Crustose coralline algae (CCA) are important contributors to reef calcium carbonate and can facilitate coral recruitment. Despite the importance of CCA, little is known about species-level distribution, abundance, and diversity, and how these vary across the continental shelf and key habitat zones within the GBR. We quantified CCA species distributions using line transects ($n = 127$) at 17 sites in the northern and central regions of the GBR, distributed among inner-, mid-, and outer-shelf regions. At each site, we identified CCA along replicate transects in three habitat zones: reef flat, reef crest, and reef slope. Taxonomically, CCA species are challenging to identify (especially in the field), and there is considerable disagreement in approach. We used published, anatomically based taxonomic schemes for consistent identification. We identified 30 CCA species among 12 genera; the most abundant species were *Porolithon onkodes*, *Paragoniolithon conicum* (sensu Adey), *Neogoniolithon fosliei*, and *Hydrolithon reinboldii*. Significant cross-shelf differences were observed in CCA community structure and CCA abundance, with inner-shelf reefs exhibiting lower CCA abundance than outer-shelf reefs. Shelf position, habitat zone, latitude, depth, and the interaction of shelf position and habitat were all significantly associated with variation in composition of CCA communities. Collectively, shelf position, habitat, and their interaction contributed to 22.6 % of the variation in coralline communities. Compared to mid- and outer-shelf sites, inner-shelf sites exhibited lower relative abundances of *N. fosliei* and *Lithophyllum* species. Reef crest habitats exhibited greater abundance of *N. fosliei* than reef flat and reef slope habitats. Reef slope habitats exhibited lower abundance of *P. onkodes*, but greater abundance of *Neogoniolithon clavycymosum* than reef crest and reef slope habitats. These findings provide important data on CCA distribution within the GBR and reinforce the fundamental role of cross-shelf variation and diverse habitat zones as contributors to the biodiversity of the GBR.

Keywords Coralline algae · Great Barrier Reef · Continental shelf · Benthic community structure · Biodiversity · Coral reefs

A. J. Dean · D. Tager · J. M. Pandolfi
Centre for Marine Science, School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

A. J. Dean
CoralWatch, Queensland Brain Institute, The University of Queensland, St Lucia, QLD 4072, Australia

R. S. Steneck
School of Marine Sciences, Darling Marine Center, University of Maine, Walpole, ME, USA

J. M. Pandolfi
Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies, The University of Queensland, St Lucia, QLD 4072, Australia

J. M. Pandolfi (✉)
Gehrmann Laboratories 60, School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia
e-mail: j.pandolfi@uq.edu.au

Introduction

Spanning a length of 2,300 km across 14° of latitude and containing almost 3,000 distinct reefs (Great Barrier Reef Marine Park Authority 2009), the Great Barrier Reef

(GBR) is the world's largest coral reef ecosystem. Reefs of the GBR vary longitudinally across the continental shelf—inshore and fringing reefs, mid-shelf reefs, and outer-shelf reefs—each comprising a variety of habitats and depths. Differences in oceanographic and environmental conditions across the continental shelf create substantial diversity in reef habitats. This diversity and complexity contributes to the outstanding value and importance of the GBR (Lucas et al. 1997).

Although coral reef ecosystems possess the highest phyletic diversity of any ecosystem (Connell 1978), they are also among the world's most vulnerable to environmental change (Pandolfi et al. 2011), and threats of species extinction are unusually high (Carpenter et al. 2008). In the last 27 yr, the GBR has lost 25–50 % of its coral cover (Bruno and Selig 2007; De'ath et al. 2012). There are many threats to coral reefs operating at local and global scales (Burke et al. 2011). The two predominant calcifying groups on coral reefs are hard corals and non-geniculate crustose coralline algae (CCA) (Adey and Macintyre 1973), both of which are sensitive to increasing sea temperatures and ocean acidification (Kleypas et al. 1999; Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011; Kroeker et al. 2013). While numerous studies have detailed the distribution and abundance of hard corals at the species level across the GBR (e.g., Done 1982), no such study has done this for CCA.

CCA are among the most abundant organisms to occupy hard substrates within the marine photic zone. They are distributed worldwide, from the high arctic through the tropics and from the intertidal zone to the deepest depths recorded for any attached autotroph (Littler et al. 1985; Steneck 1986). The distribution of particular genera or species is influenced by environmental factors such as depth, water motion, light intensity, and temperature (Steneck and Adey 1976; Adey et al. 1982; Steneck 1986; Lund et al. 2000). In tropical regions, CCA build algal ridges (Steneck et al. 1997) and can contribute to primary productivity on reefs (Chisholm 2003). Certain species of CCA induce metamorphosis and settlement of reef corals (Harrington et al. 2004), while other species can inhibit coral settlement (Ritson-Williams et al. 2009a). As a group, CCA have an excellent geological record because they readily colonize dead corals and become fossilized into reef rock. This allows palaeontologists to better interpret past marine environments (e.g., Macintyre et al. 2001; Pandolfi et al. 2006). Certain CCA species are excellent indicators of sea level at wave exposed sites (Steneck and Adey 1976) or indicate specific cryptic environments of the past that no longer persist due to human activities (Macintyre et al. 2001).

Coralline algae taxonomy is in a state of flux, and this impedes progress in ecological studies. Earlier estimates of 31–34 genera, incorporating 500 species (Steneck 1986), have changed and will continue to change in the light of rapidly evolving phylogenetic schemes based on molecular genetics (Bittner et al. 2011; Kato et al. 2011). Field identification of CCA species is especially difficult because it requires knowing specialized anatomical and morphological characteristics; these are also sources of debate among taxonomists. As a result, few studies have described this group's ecology or community structure at the species level for coral reef ecosystems in general, and the GBR in particular (Steneck 1986; Daume et al. 1999; but see Ringeltaube and Harvey 2000 for Heron Island on the GBR).

Most ecological studies to date simply pool CCA as a functional group. However, many CCA species differ with respect to their ecosystem function and their sensitivity to environmental gradients. For example, while the species *Titanoderma prototypum* facilitates both coral settlement and recruitment (Harrington et al. 2004), the far more abundant species, *Porolithon onkodes*, inhibits both (Price 2010). Examining composition of coralline communities not only informs our understanding of CCA ecology in the GBR, but it also allows us to detect important community shifts that may not be observed examining CCA per cent cover alone.

Despite their high diversity and importance to coral reefs, little is known about the spatial distribution of CCA within reef ecosystems, and how their community structure changes among coral reef habitats. The GBR offers a broad palette to study CCA within a reef ecosystem by providing substantial gradients in depth, latitude, and position along the continental shelf. The primary aim of this study was to quantify abundance and distribution of CCA species and morphological groups across the northern and central GBR. Secondary aims were to identify how shelf position and other available environmental factors (latitude, longitude, depth, and habitat zone) influence abundance, richness, diversity, and per cent cover of CCA and to examine differences in community structure across shelf position and other environmental gradients.

Methods

Study sites

Surveys were conducted at 17 sites across the northern (14.68–13.48°S) and central (18.81–18.25°S) regions of the GBR. These sites were selected from the sites of the Australian Institute of Marine Science Monitoring Program. Seven inner-shelf sites (Hannah, Hay, Heath, Mac-Donald, and Pandora reefs, and two sites at Wilke Reef), six mid-shelf sites (Britomart, Ogilvie, John Brewer, and
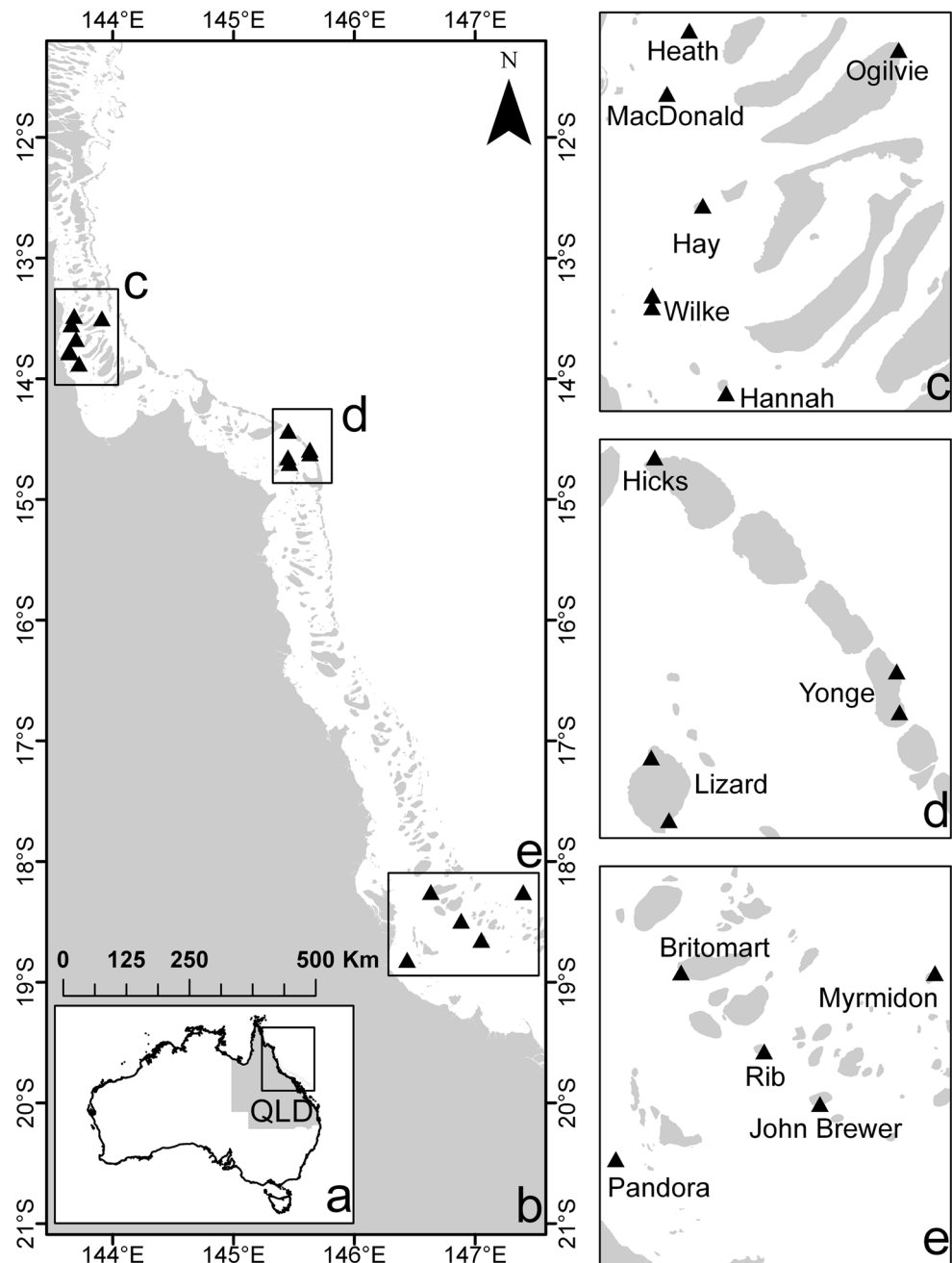
Rib reefs, and two sites at Lizard Island), and four outer-shelf sites (Hicks reef, Myrmidon reef, and two sites at Yonge reef) were surveyed (Fig. 1).

Survey methods

For each site, quantitative surveys were taken using in situ transects that were placed in three habitat zones: reef flat, reef crest, and reef slope. Reef flat and reef crest sites were sampled on their seaward edge. CCA can be patchily distributed along transects; as a result, point-intercept methods could under-sample, especially the more rare species (Dethier et al. 1993). Therefore, we used line-intercept transect methods, modified after Benayahu and Loya (1981). Specifically, 10-m transects were replicated parallel to depth contours and stretched taut across the reef surface. This method quantifies all CCA organisms living on hard surfaces. When individual organisms overlapped, the portion of each individual exposed along the transect length was counted. CCA were provisionally identified to species level in situ, collected, and identified or verified to species level in the laboratory. Only conspicuous and

Fig. 1 Map of survey sites in the northern and central regions of the Great Barrier Reef, Queensland, Australia

unmistakable species were not collected upon each encounter (e.g., *Neogoniolithon fosliei*, *P. onkodes,* and *Lithothamnion prolifer*). Due to logistical challenges emerging in the field, not all sites contributed data from the full range of habitat zones (Table 1). Data were collected from a total of 127 transects.

Rationale for taxonomic scheme

In this study, we use a conservative taxonomic approach. CCA taxonomy has been in flux since the late nineteenth century. Since the 1970s, two schools developed, with very different taxonomic schemes. By the 1980s, several abundant CCA genera had been determined to be synonymous with other genera, only to have those generic combinations later reversed. For example, the anatomically and morphologically distinctive genus *Porolithon* was considered the most abundant CCA on Indo-Pacific reefs where it dominated shallow zones and built algal-ridge bioherms (e.g., Littler and Doty 1975). Species of *Porolithon* commonly inhibit coral recruitment. In contrast, the rhodolith-forming and deep-water genus *Hydrolithon* (Adey et al. 1982) facilitates coral settlement (Ritson-Williams et al. 2009b). Despite anatomical, morphological, ecological, and geological differences, those two genera were once combined into a third genus *Spongites* (Penrose and Woelkerling 1988). A subsequent reassessment determined

that *Spongites* was distinct from *Hydrolithon,* which still included *Porolithon* (Penrose and Woelkerling 1992). More recent molecular studies determined that *Porolithon* and *Hydrolithon* are distinct 'unrelated' genera (Bittner et al. 2011). A result of these polyphyletic combinations, from the late 1980s to until very recently, is the loss of resolution among studies that identified CCA taxa only to genus (e.g., *Hydrolithon* sp.) in those years.

Another synonymy involved the abundant species *Paragoniolithon conicum* (sensu Adey et al. 1982). This thick species possesses a massive coaxial hypothallus. However, *P. conicum* was combined into the genus *Pneophyllum* (Keats et al. 1997). Diagnostic generic characters of *Pneophyllum* are that they are very thin (fewer than 50 cells thick) and never possess a coaxial hypothallus (Penrose and Woelkerling 1991). Because of this, we prefer to retain the combination for *Paragoniolithon* proposed by Adey et al. (1982).

It was originally thought that anatomical features called trichocytes (large hair cells) possessed no taxonomic value (Penrose and Woelkerling 1988); this contributed to the synonymy of *Porolition* and *Paragoniolithon*. However, studies found that genetically distinct genera corresponded well with these anatomical characteristics. The tight cluster of trichocytes within fields clearly differentiated the genus *Porolithon* (Kato et al. 2011); the widely scattered trichocytes of *Hydrolithon* are distinct from the loose trichocyte field of *Paragoniolithon* (Bittner et al. 2011).

Table 1 Surveys sites, number of transects, and depth range (m), within habitat zone

Shelf position	Site	Number of transects	Number of transects (depth range)			Per cent cover data available
			Reef flat	Reef crest	Reef slope	
Inner	Hay[a]	8	3 (0.61)	3 (1.22)	2 (5.49–8.84)	N
	Heath[a]	8	3 (1.83–2.44)	3 (3.66–5.49)	2 (10.1–11.0)	N
	Wilke1[a]	8	3 (0.61)	3 (1.22–2.13)	2 (4.88–7.01)	N
	Hannah	5	0	2 (1.52)	3 (6.10–8.23)	N
	MacDonald	6	0	3 (2.74–3.96)	3 (7.32–8.84)	N
	Pandora	6	0	3 (2.74–4.57)	3 (10.1–11.9)	Y
	Wilke2	7	3 (1.52)	3 (3.35–3.66)	1 (7.92)	N
Mid	John Brewer[a]	9	3 (1.83–2.44)	3 (4.57)	3 (12.8–14.0)	Y
	Lizard1[a]	10	3 (1.22–1.52)	3 (4.27)	4 (9.5–14.9)	Y
	Rib[a]	9	3 (1.52–1.83)	3 (4.27–4.88)	3 (14.0–14.9)	Y
	Britomart	7	NA	NA	NA	N
	Ogilvie	7	1 (1.83)	3 (2.74–3.35)	3 (11.6–14.9)	Y
	Lizard2	4	0	2 (3.05–3.96)	2 (10.4–10.7)	Y
Outer	Myrmidon[a]	10	3 (2.44–4.27)	4 (4.57–7.01)	3 (16.8–18.3)	Y
	Yonge2[a]	9	3 (1.22–1.83)	3 (3.96–4.57)	3 (30.2–30.5)	Y
	Hicks	6	0	3 (2.74–5.79)	3 (12.2–14.6)	Y
	Yonge1	3	0	1 (4.88)	2 (18.3–19.8)	Y

[a] Sites contributing to 'more balanced' data subset

Polyphyletic groupings are problematic for studying diversity. Nevertheless, there is a steady increase in reports revealing the existence of 'cryptic species'—distinct and reproductively isolated species that cannot be differentiated using conventional taxonomic methods (Bickford et al. 2007). This invariably results in local diversity being underestimated. Pooling unrelated genera exacerbates the problem by creating cryptic genera, and results in a scientific impasse (e.g., '*Hydrolithon* spp' in papers from the past decade could include ecologically and taxonomically distinct genera). Molecular genetic studies suggest that at least some of the recently abandoned anatomical characters do have taxonomic value. For this study, we chose to use taxonomic schemes that employed the greatest number of characters. For the Indo-Pacific region, two excellent and well-illustrated taxonomic treatments exist that used multiple, independent anatomical, and morphological taxonomic characteristics (e.g., Gordon et al. 1976; Adey et al. 1982). The flora we describe in this paper are consistent with these two approaches.

Importantly, in many older studies, anatomical and morphological characters were measured to determine quantitative differences between multiple characters (e.g., Steneck and Adey 1976; Adey et al. 1982). This results in replicable identifications. We expect scientific binomials will continue to change and more cryptic species found, but as long as standardized methods yield repeatable taxonomic entities, scientific studies can move forward.

To minimize including cryptic species, we followed Adey's taxonomic schemes (Adey 1970; Adey et al. 1982) and follow many of the original descriptions; these conform well to recent genetic studies (Bittner et al. 2011; Kato et al. 2011). Specifically, we used several undervalued characters recorded for taxonomic identification including gross morphology, surface texture, margin and branching characteristics, thallus thickness (hypothallus to epithallus), and the size (inside and outside dimensions), shape, and pore characteristics of conceptacles (including cystocarpic, spermatangial, or sporangial). Anatomical characteristics of the hypothallus, perithallus, and trichocytes (size, shape, and arrangement) were recorded. Each of the collected specimens was examined using a dissecting microscope. A few difficult taxa required analysis using a scanning electron microscope.

Convergent coralline morphologies are common (Steneck 1986). Although morphological groups can be finely divided, we used the most fundamental divisions of thick, branched, and thin thallus formation (Steneck 1986).

Data analysis

For each transect, the following univariate measures were calculated:

- Total Abundance: calculated as the total number of individual CCA present within a single transect.
- Relative abundance: calculated for each species, as the number of CCA from a particular species within a single transect, divided by Total Abundance for that transect.
- Richness: calculated as number of different CCA species present within a single transect.
- Species Diversity: calculated using the Shannon Diversity Index, $H' = -\Sigma \ [(pi)(\ln \ pi)]$ (Spellerberg and Fedor 2003).
- Per cent cover: calculated as the percentage of transect distance covered by a particular species, adjusted to correct for the proportion of hard substrate within each transect; values indicate the percentage cover of transect areas with hard substrate available. Per cent cover data were only available for 74 transects (58 %). We assessed whether there were any differences between transects where per cent cover data were collected and sites where per cent cover data were not collected. Using Chi-square tests for categorical variables such as shelf position, and t tests for continuous variables such as latitude, we identified that sites with per cent cover data available were of higher latitude, greater longitude, greater depth, and more likely to include outer-shelf sites (100 % included) compared to inner-shelf sites (only 11 % included; data not shown).

Two sets of analysis were conducted. Primary analysis was conducted on a subset of data that was identified as a 'more balanced' data set. This was defined as study sites that incorporated at least two transects from each habitat zone. This more balanced data set incorporated three sites from inner-shelf reefs (Hay, Heath, and Wilke), three sites from mid-shelf reefs (John Brewer, Lizard Island, and Rib), and two sites from outer-shelf reefs (Myrmidon and Yonge; Table 1). Secondary analysis was conducted on the full data set.

Predictors of coralline algae total abundance, diversity, richness, and per cent cover were identified using mixed effects models. Mixed effects models were selected because they are suitable for analysis of unbalanced data sets (SPSS® 2002; Hedeker and Gibbons 2006) and are able to control for the hierarchical nature of the data (i.e., data collected from transects at a particular site will exhibit more relatedness than transects from a different site; Zuur 2009). Each analysis started with the full model, using the following predictors as fixed effects: shelf position, habitat zone, latitude, longitude, depth, the interaction between shelf position and habitat zone, and the interaction between shelf position and depth. No other interactions were considered. Initial model selection sought to identify the most

suitable random effects structure and covariance structure, using restricted maximum likelihood estimation (REML). Based on this, a random intercept was included in each model. Study site was also included as a random effect to control for the clustering effect of study site (Zuur 2009). The next stage involved identifying the most optimal fixed structure. To achieve this, each model iteratively removed the least significant factor at each step, using the Akaike Information Criterion (Akaike 1974) and maximum likelihood estimation. The final model reported was refitted using REML (Zuur 2009). Normality was verified for each model by inspecting histograms of model residuals (Zuur 2009). All models reported met criteria for normality. Mixed effects models were conducted on both 'more balanced' and full data sets using SPSS (IMB Corp Released 2011, version 20.0). Results presented focus on findings from the 'more balanced' data set.

Taxonomic composition of coralline algal communities was visualized using non-metric multidimensional scaling (NMDS). Differences in community composition across key environmental gradients were assessed using permutational multivariate analysis of variance with distance matrices (ADONIS). This is similar to analysis of similarity (ANOSIM), but has been shown to be more robust (Anderson 2001; Oksanen et al. 2013). Key species contributing to differences in community composition were then identified using similarity of percentages (SIMPER) analysis. Species contributing to the first 50 % of differences were identified. To ensure that the species identified by SIMPER reflected true between-group differences (rather than within-group variation; Warton et al. 2012), between-group differences were confirmed with t-tests (Witt et al. 2012). All community analyses were based on fourth-root-transformed relative abundance data and Bray Curtis distance matrices and utilized the R statistical software ('vegan' Community Ecology Package). Community analyses were conducted on both 'more balanced' and full data sets. Results presented focus on findings from the 'more balanced' data set.

Results

Patterns of distribution and abundance

Overall, 30 species of CCA, representing 12 genera, were observed across 17 study sites. Twenty species were recorded in inner-shelf sites, 25 species in mid-shelf sites, and 20 species in outer-shelf sites (Table 2). The most abundant species was *P. onkodes*, which was present in 66.9 % of transects (mean relative abundance ± SD: 0.36 ± 0.32). The next most abundant species were *P. conicum* sensu Adey et al. 1982 (54.3 % of transects, mean

relative abundance 0.16 ± 0.21), *H. reinboldii* (36.0 % of transects, mean relative abundance 0.08 ± 0.20), and *N. fosliei* (28.3 % of transects, mean relative abundance 0.06 ± 0.12). Branching species exhibited the highest abundance at all shelf positions. Thin morphologies exhibited limited abundance at mid- and outer-shelf reefs, with the greatest abundance at inner reef sites (Fig. 2).

Predictors of abundance, diversity, richness, and per cent cover

Mixed effects models of the 'more balanced' data set indicated significant differences in CCA abundance across shelf position, with outer-shelf reefs exhibiting higher abundance than mid-shelf ($\beta = -222.0 \pm 43.7$) and inner-shelf ($\beta = -666.7 \pm 155.7$) reefs (Tables 3, 4). Reef slope communities exhibited lower abundance compared to reef crest habitats ($\beta = -52.6 \pm 17.8$; Fig. 3). High abundance was also associated with higher latitude ($\beta = -132.1 \pm 38.1$) and lower longitude ($\beta = -300.6 \pm 90.1$). When analysis was repeated on the full data set, these findings were retained. Analysis of the full data set also yielded a significant interaction between shelf position and habitat zone ($F = 6.89$, $p < 0.001$); in both mid- and outer-shelf reefs, highest abundance was found in reef crest habitats, whereas inner-shelf reefs exhibited no difference in abundance across habitat zones.

Within the 'more balanced' data subset, the interaction between shelf position and habitat zone was a significant predictor of CCA diversity (Table 4). Compared to diversity observed for outer-shelf reef crest habitats, significantly lower diversity was observed at all inner-shelf habitats (reef flat: $\beta = -0.65 \pm 0.22$, $p = 0.012$; reef crest: $\beta = -0.60 \pm 0.22$, $p = 0.019$; and reef slope: $\beta = -0.90 \pm 0.24$, $p = 0.002$; Fig. 3). A trend suggested lower diversity at mid-shelf reef flat habitats ($\beta = -0.45 \pm 0.22$, $p = 0.067$) compared to all outer-shelf habitats. When predictors of diversity were analysed on the full data set, this interaction remained significant. Additional predictors of higher diversity in the full data set were higher longitude ($\beta = -0.13 \pm 0.03$) and shelf position, where CCA diversity was significantly higher in outer-shelf reefs than mid-shelf ($\beta = -0.18 \pm 0.15$) and inner-shelf ($\beta = -0.19 \pm 0.15$) reefs.

Within the 'more balanced' subset of data, there were no significant predictors of CCA richness (Table 4). We found a potential interaction between shelf position and habitat zone ($F = 2.05$, $p = 0.092$; Fig. 3), driven by lower richness at inner-shelf reef slope habitats ($\beta = -3.06 \pm 1.20$, $p = 0.034$) and mid-shelf reef flat habitats ($\beta = -2.20 \pm 0.76$, $p = 0.009$) compared to outer-shelf reef crests. When analysing the full data set, this interaction remained; in addition, higher CCA richness was observed

Table 2 Total abundance (total number of CCA organisms per 10-m transect) and Relative abundance (number of specific CCA organisms per 10 m transect, divided by total number of CCA organisms per transect) of CCA species in each shelf position on the GBR

	Total Abundance			Relative Abundance		
	Inner	Mid	Outer	Inner	Mid	Outer
Lithophyllum insipidum	0	5.98 (2.82)	13.39 (4.94)	0	0.031 (0.012)	0.052 (0.015)
Lithophyllum moluccense	0	5.43 (1.06)	8.39 (3.28)	0	0.075 (0.016)	0.035 (0.013)
Lithophyllum kotschyanum	0.70 (0.31)	0.89 (0.56)	1.96 (0.87)	0.040 (0.017)	0.009 (0.004)	0.008 (0.003)
Titanoderma prototypum	0	0.04 (0.04)	0.21 (0.12)	0	0.0002 (0.0002)	0.002 (0.001)
Titanoderma tessellatum	0	0.26 (0.22)	0.54 (0.37)	0	0.004 (0.003)	0.006 (0.005)
Titanoderma sp.[a]	0	0.09 (0.05)	0.18 (0.18)	0	0.001 (0.001)	0.002 (0.002)
Hydrolithon reinboldiii	3.09 (1.15)	0.89 (0.35)	8.75 (4.41)	0.131 (0.035)	0.010 (0.005)	0.086 (0.049)
Hydrolithon breviclavium	0.47 (0.47)	0	0	0.009 (0.009)	0	0
Hydrolithon megacystum	0	0.43 (0.30)	1.89 (1.13)	0	0.006 (0.005)	0.016 (0.010)
Hydrolithon laeve	0	0.37 (0.33)	0	0	0.005 (0.004)	0
Hydrolithon sensu stricto[a]	0.11 (0.08)	0.15 (0.12)	0.36 (0.36)	0.028 (0.022)	0.001 (0.001)	0.002 (0.002)
Lithoporella melobesioides	0.42 (0.23)	0.48 (0.44)	0.18 (0.18)	0.039 (0.021)	0.009 (0.009)	0.001 (0.001)
Mastophora pacifica	5.09 (5.09)	0	0	0.018 (0.018)	0	0
Neogoniolithon frutescens	0.06 (0.06)	0.17 (0.13)	0	0.002 (0.002)	0.006 (0.004)	0
Neogoniolithon fosliei	0.19 (0.19)	4.72 (1.18)	20.36 (4.95)	0.010 (0.010)	0.062 (0.004)	0.124 (0.031)
Neogoniolithon clavycymosum	0.79 (0.34)	1.41 (0.79)	0.36 (0.25)	0.077 (0.033)	0.016 (0.009)	0.004 (0.003)
Neogoniolithon megalocystum	0	0.2 (0.20)	0	0	0.003 (0.003)	0
Neogoniolithon rufum	0.09 (0.09)	0.2 (0.12)	0.71 (0.50)	0.005 (0.005)	0.003 (0.002)	0.004 (0.003)
Neogoniolithon sp.[a]	0	0.59 (0.23)	1.43 (0.67)	0	0.013 (0.006)	0.007 (0.004)
Paragoniolithon conicum sensu Adey et al. (1982)	2.00 (0.55)	14.24 (2.06)	27.61 (4.97)	0.134 (0.035)	0.176 (0.029)	0.160 (0.031)
Paragoniolithon sp.[b]	0.42 (0.23)	1.96 (1.01)	11.25 (4.23)	0.046 (0.026)	0.011 (0.005)	0.051 (0.020)
Porolithon onkodes	7.06 (2.43)	62.33 (13.78)	98.5 (18.01)	0.229 (0.046)	0.456 (0.043)	0.388 (0.050)
Porolithon gardineri	0	0.11 (0.11)	3.43 (0.96)	0	0.002 (0.002)	0.017 (0.005)
Porolithon sp.[a]	0	0	0.18 (0.18)	0	0	0.001 (0.001)
Lithothamnium australe	0.75 (0.49)	1.00 (0.39)	0.36 (0.25)	0.023 (0.012)	0.015 (0.006)	0.005 (0.004)
Lithothamnium asperulum	0.15 (0.11)	0	0	0.023 (0.021)	0	0
Lithothamnium prolifer	0.09 (0.09)	0.83 (0.49)	0.18 (0.18)	0.005 (0.005)	0.011 (0.006)	0.002 (0.001)
Lithothamnium pulchrum	0	0.43 (0.44)	0	0	0.005 (0.005)	0
Mesophyllum madagascariense	0.57 (0.57)	2.65 (1.19)	0.46 (0.27)	0.002 (0.002)	0.042 (0.020)	0.002 (0.001)
Mesophyllum purpurescens, funifu	0.64 (0.31)	1.63 (0.85)	0	0.058 (0.031)	0.021 (0.011)	0
Mesophyllum fluatum	0.40 (0.22)	0	0	0.080 (0.036)	0	0
Sporolithon episporum	0	0	0.18 (0.18)	0	0	0.002 (0.002)
Sporolithon erythraeum	0.55 (0.31)	0.76 (0.35)	2.93 (1.37)	0.037 (0.023)	0.007 (0.003)	0.025 (0.013)
Undescribed leafy coralline[c]	0.06 (0.06)	0.04 (0.04)	0	0.008 (0.008)	0.001 (0.001)	0

Values presented are mean (SE)

[a] May comprise more than one taxa

[b] Single taxon not yet named

[c] Unidentified coralline resembling *Archaeolithophyllum* (Wray 1964)

in outer-shelf reefs compared with mid-shelf ($\beta = -1.22 \pm 0.55$) and inner-shelf ($\beta = -2.32 \pm 0.58$) reefs, and also in sites with greater longitude ($\beta = 0.13 \pm 0.03$).

Insufficient per cent cover data were available for analysis with the 'more balanced' data subset. However, per cent cover of CCA from the full data set was significantly greater in outer-shelf than in mid- and inner-shelf reefs ($F = 6.62$, $p < 0.01$), and significantly greater in reef crest habitats, compared to reef slope and reef flat zones ($F = 3.16$, $p < 0.05$).
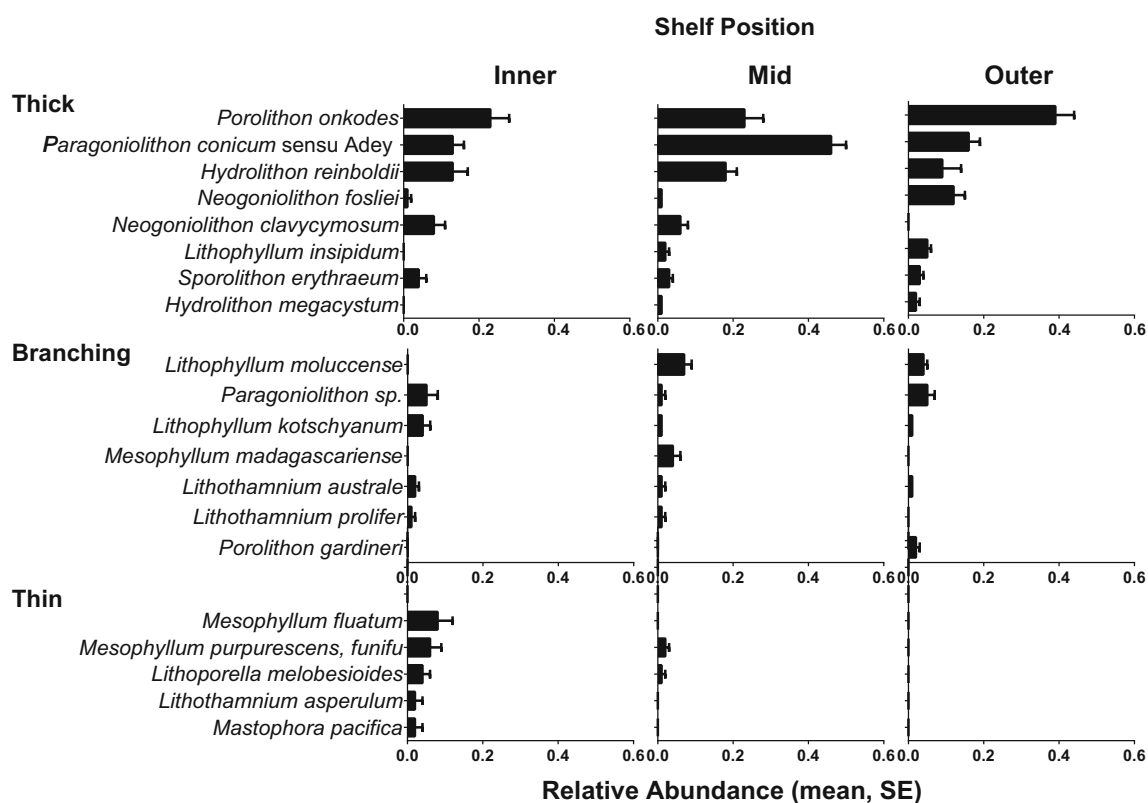
Fig. 2 Relative abundance of CCA species by shelf position and morphological groups ($n = 127$ transects) on the Great Barrier Reef, Queensland, Australia. *Error bars* indicate standard error

Table 3 Observed values of coralline abundance, richness, diversity, and per cent cover across GBR shelf position from all transects

	Inner-shelf	Mid-shelf	Outer-shelf
Total abundance	23.50 (43.42)	107.54 (103.44)	201.82 (111.32)
Diversity (Shannon)	0.53 (0.41)	1.03 (0.45)	1.14 (0.41)
Richness	1.87 (1.00)	4.17 (1.73)	5.29 (1.76)
Percent cover	9.97 % (11.00)	21.95 % (16.07)	30.67 % (15.68)

Values presented are mean (SE)

Table 4 Final models identifying predictors of abundance, diversity, and richness of coralline algae ('more balanced' subset of data)

Response variable	Predictors in final model	F	p	AIC (original model[a])	AIC (final model[b])
Abundance	Position	13.38	0.000	797.86	793.68
	Zone	4.42	0.016		
	Latitude	12.04	0.001		
	Longitude	11.14	0.001		
Diversity	Position × Zone	4.73	0.003	72.87	69.39
Richness	Longitude	3.77	0.119	275.07	271.31
	Position × Zone	2.05	0.092		

[a] Predictors in original model: shelf position, habitat zone, latitude, longitude, depth, the interaction between shelf position and habitat zone, and the interaction between shelf position and depth

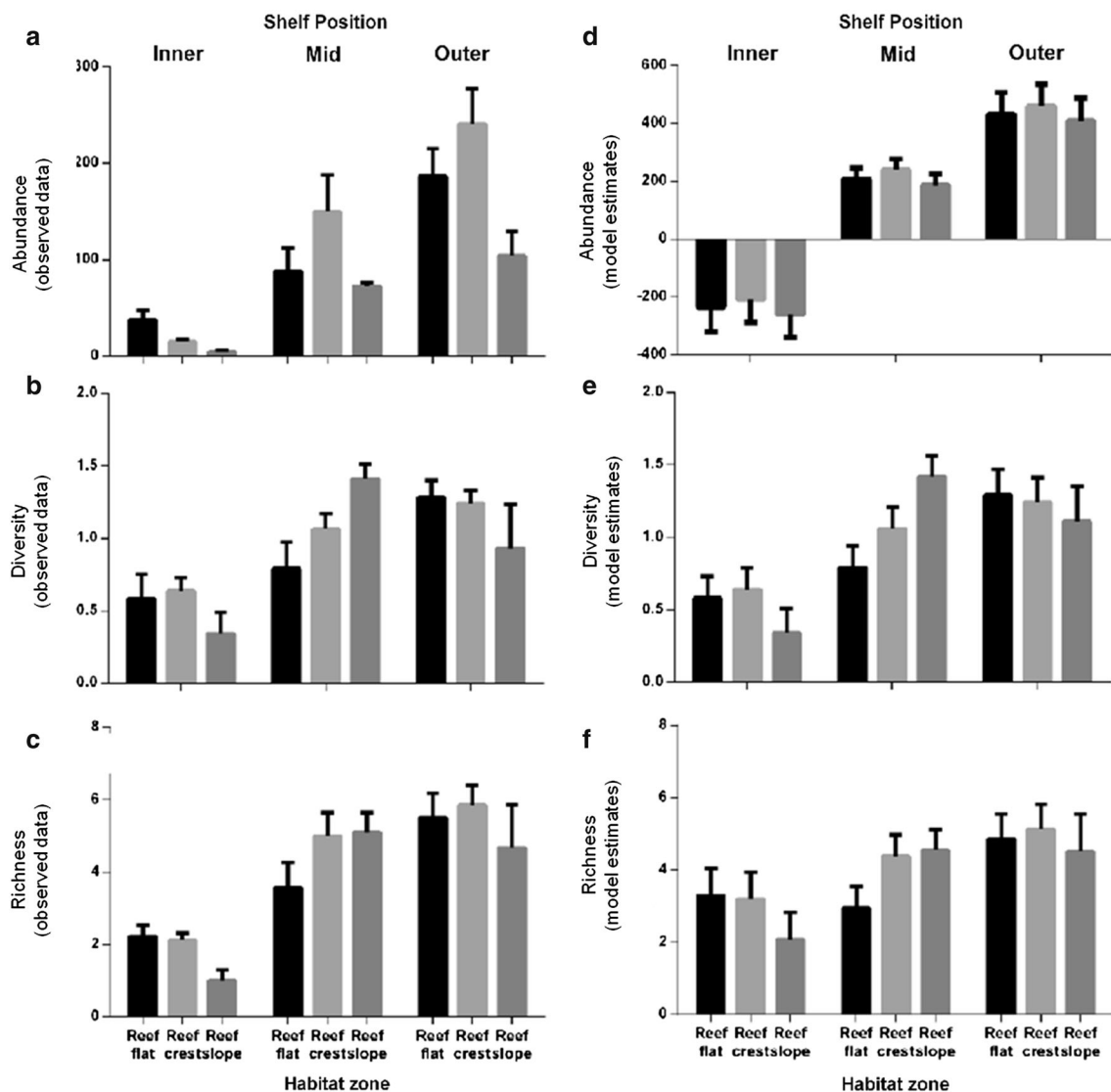[b] Predictors in final model: listed for each response variable

Fig. 3 CCA abundance (**a**, **d**), diversity (**b**, **e**), and richness (**c**, **f**) among habitat zones relative to GBR shelf position, for observed data (*left panels* **a**, **b** and **c**) and model estimates (*right panels* **d**, **e** and **f**). All panels are derived from the 'more balanced' subset of data. *Error bars* indicate standard error

Community analysis: patterns of community composition

Nonmetric multidimensional scaling ordination demonstrated some clustering of coralline communities across shelf position with corresponding distribution of environmental variables (Fig. 4). Within the 'more balanced' subset of data, latitude was the strongest contributor to variance in community composition, contributing to 21.3 % of variance (ADONIS: $F = 11.74$, $R^2 = 0.213$, $p = 0.001$). Shelf position explained 6.5 %, habitat zone explained 11.7 %, and the interaction between shelf position and habitat zone explained an additional 4.4 % of the variance in community composition (Table 5). Collectively, shelf position and

habitat zone (and their interaction) contributed to 22.6 % of the variance in coralline communities. Overall, all variables examined contributed to 46.3 % of variance in community composition (Table 5). When ADONIS analysis was conducted on the full data set, all predictors significantly contributed to variance in community composition, with the strongest factors being shelf position ($F = 8.47$, $R^2 = 0.103$, $p = 0.002$) and habitat zone ($F = 6.59$, $R^2 = 0.120$, $p = 0.001$).

SIMPER analysis of the 'more balanced' data subset identified key species contributing to differences between inner-shelf and mid-/outer-shelf areas. Inner-shelf sites exhibited lower relative abundances of *N. fosliei* and *L. moluccense* (Table 6). Reef crests had higher relative
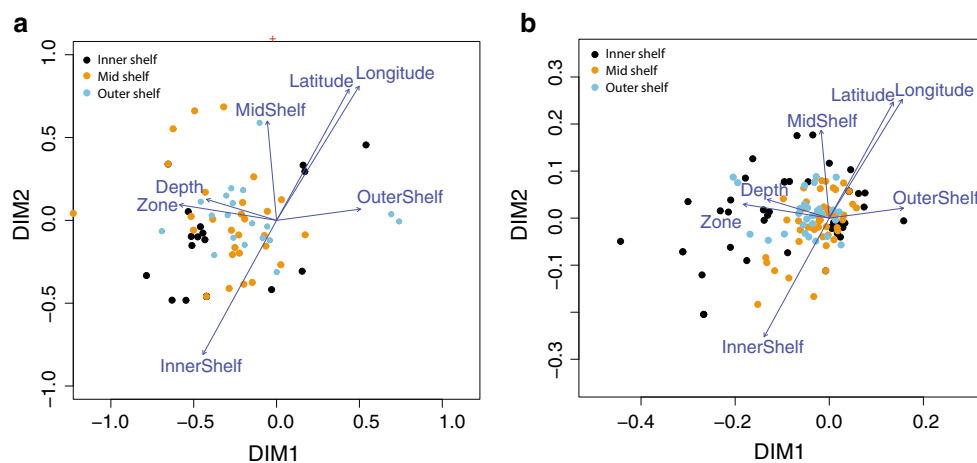
Fig. 4 Nonmetric multidimensional scaling (nMDS) ordination of **a** the 'more balanced' subset of data; and **b** all transects across the GBR. *Coloured circles* designate sample sites across shelf positions, and *vectors* represent the influence of environmental variables (Stress = 0.09)

Table 5 Results of analysis of variance using distance matrices (ADONIS), indicating strength of relationship between environmental variables and variance in structure of CCA communities (based on Bray Curtis distance matrices), using 'more balanced' subset of data

	F	*R*^{2}	*p*
Position	6.92	0.065	0.001
Zone	11.74	0.111	0.001
Latitude	3.25	0.214	0.001
Longitude	–	0	–
Depth	3.07	0.029	0.011
Position × Zone	4.68	0.044	0.002

abundance of *N. fosliei* than reef flats. Reef crests also had higher relative abundance of *P. onkodes and N. fosliei*, but lower relative abundance of *N. clavycymosum* than reef slope habitats. Reef flats had higher relative abundance of *P. onkodes* but lower relative abundance of *N. clavycymosum* compared with reef slope habitats. Higher latitude sites (also the high longitude sites) had higher relative abundance of *L. moluccense* and *N. fosliei*, but lower relative abundance of *H. reinboldii*. Shallower sites (<5 m) were more likely to contain *P. onkodes* (Table 6).

Discussion

This study provides the most geographically extensive assessment of the community structure of crustose coralline algae (CCA) on the Great Barrier Reef (GBR) and is the first to examine CCA distribution, abundance, and diversity across a range of regions and sites. We observed significant effects of cross-shelf position and habitat zone in abundance, diversity, and community composition—at the species level. These findings not only highlight the

diversity of CCA communities across the GBR, but also reinforce the importance of cross-shelf variation and diverse habitat zones in contributing to the diversity of the GBR.

Based on data from 17 sites in the northern and central GBR, we recorded 30 species of CCA, representing 12 genera, similar to previous work recording 29 species across northern, central, and southern sites (Steneck 1982). *Porolithon onkodes* was the most dominant species in all shelf positions. This is consistent with its dominance across the Pacific (Steneck 1986). *P. onkodes* forms unbranched, thick crusts. *P. onkodes* abundance was greater in shallower sites, and in reef crest and reef flat habitat zones, reflecting its tolerance to high wave energy and resistance to grazing (Littler and Doty 1975; Steneck 1986). Outer-shelf sites were dominated by thick CCA species with virtually no thin species present; this is likely to represent greater tolerance of thick CCA to grazing and herbivory. Habitat zone is a well-established predictor of community structure in benthic habitats (Hughes et al. 2012). We observed strong effects of habitat zone on CCA community structure, and interactions between habitat zone and shelf position, for CCA abundance, richness, and diversity. *N. fosliei*, also a dominant GBR species (Steneck 1982), was more abundant in mid- and outer-shelf sites than inshore regions, in reef crest areas compared to reef slope and reef flat habitats, and in higher latitudes.

The percentage cover we recorded for inshore sites (9.97 %) is substantially higher than other reports of CCA cover ranging between <1 and 4 % (Fabricius and De'ath 2001; Fabricius et al. 2005; Wismer et al. 2009). It is possible that, given that per cent cover data were only collected from 11 % of the inner-shelf reef transects, more depauperate inshore sites were not represented in our data. Alternatively, estimates of per cent cover of CCA reported

Table 6 Main contributors to differences in CCA community composition as identified by SIMPER analysis, using 'more balanced' subset of data

	Cumulative contribution (%)	t	p	Relative abundance	
				Inner-shelf	Mid/outer-shelfs
Paragoniolithon conicum	14.4	0.23	0.82	19.1	20.6
Porolithon onkodes	28.3	0.08	0.94	37.7	38.3
Neogoniolithon fosliei	37.2	4.27	0.00	0	8.29
Hydrolithon reinboldii	46.2	−0.69	0.50	9.29	5.90
Lithophyllum moluccesnse	54.9	4.71	0.00	0	6.98
				Reef crest	Reef flat
Paragoniolithon conicum	16.6	0.85	0.40	17.8	23.9
Neogoniolithon fosliei	29.6	−2.48	0.02	10.9	2.13
Porolithon onkodes	40.3	0.22	0.82	49.8	51.5
Lithophyllum insipidum	50.7	0.04	0.97	4.76	4.86
				Reef crest	Reef slope
Porolithon onkodes	17.0	6.36	0.00	49.8	10.2
Paragoniolithon conicum	27.9	−0.08	0.93	17.8	18.3
Neogoniolithon fosliei	36.6	2.22	0.03	10.9	2.99
Hydrolithon reinboldii	44.9	−1.57	0.12	3.30	14.1
Neogoniolithon clavycymosum	51.5	−2.32	0.04	0	12.0
				Reef flat	Reef slope
Porolithon onkodes	17.5	5.61	0.00	51.5	10.2
Paragoniolithon conicum	29.8	0.74	0.46	23.9	18.3
Hydrolithon reinboldii	38.8	−1.42	0.17	4.47	14.1
Lithophyllum moluccesnse	46.7	−0.77	0.44	4.93	7.37
Neogoniolithon clavycymosum	53.7	−2.32	0.04	0	12.0
				Higher latitude[a]	Lower latitude
Paragoniolithon conicum	14.7	−0.66	0.51	0.22	0.19
Porolithon onkodes	28.1	−0.97	0.34	0.42	0.35
Hydrolithon reinboldii	37.3	2.46	0.02	1.41	10.7
Lithophyllum moluccesnse	45.6	−3.11	0.00	8.93	1.81
Neogoniolithon fosliei	53.6	−2.36	0.02	9.36	2.97
				Deeper sites (>5 m)	Shallow sites (≤5 m)
Porolithon onkodes	13.5	5.92	0.00	14.0	51.2
Paragoniolithon conicum	26.5	−0.26	0.80	21.0	19.5
Hydrolithon reinboldii	35.5	−1.81	0.16	12.7	4.00
Neogoniolithon fosliei	44.3	−0.78	0.44	6.93	4.71
Lithophyllum moluccesnse	52.5	−1.10	0.28	6.49	3.60

[a] Split by median at −16.00°

from rapid ecological assessment may be lower than the estimates we obtained using more intensive techniques that quantify all CCA organisms. Across all offshore sites, mean CCA cover was 30.7 %, which is higher than the 20 % reported in one study (Fabricius and De'ath 2001), but similar to other studies across the Pacific Ocean (Adey et al. 1982; Iryu et al. 1995).

Inner-shelf reefs exhibited the lowest abundance and diversity of CCA. There was also significant cross-shelf variation in composition of coralline communities

identified by ADONIS analysis (Table 5). Our findings are consistent with studies indicating significant cross-shelf variation in per cent cover of CCA (Fabricius and De'ath 2001; Wismer et al. 2009). Such cross-shelf variation has also been documented for community composition of hard corals (Done 1982), parrotfish (Hoey and Bellwood 2008), and bacterial biofilms (Witt et al. 2012), population genetic structure of the coral *Acropora millepora* (van Oppen et al. 2011), and rates of bioerosion (Bellwood et al. 2003).

Why do these differences in CCA abundance and community structure between inshore and offshore reefs occur? It is unclear whether they reflect dispersal barriers between inshore reefs and mid- and outer-shelf reefs (van Oppen et al. 2011) or occur in response to recent declines in water quality. In general, inner-shelf reefs experience poorer water quality and are in poorer condition than outer-shelf reefs (Brodie and Waterhouse 2012). Human activities, such as land clearing, livestock grazing, and agricultural practices (Schaffelke et al. 2012), expose inner-shelf reefs to sediment, nutrients, and pollutants (McCulloch et al. 2003; Kroon et al. 2012), which may negatively affect CCA abundance (Fabricius and De'ath 2001; Harrington et al. 2005; Littler et al. 2010). It is possible that other factors, such as reduced biomass of herbivorous parrotfish in inshore areas (Hoey and Bellwood 2008), augment the effect of poor water quality (McCook 1996; Chisholm 2003; Wismer et al. 2009) on CCA community structure. Recent analysis of life, death, and fossil assemblages from sediment cores at the inshore Pelorus Reef in the central GBR indicates a major shift in coral assemblages over time, with a collapse of branching *Acropora* assemblages in the early to mid-twentieth century (Roff et al. 2013). Further analysis of reef matrix cores for historical abundances of CCA would shed light on the historical persistence of cross-shelf differences through time. Our study did not address causation of observed cross-shelf variation, and it is possible that *both* barriers to dispersal and more recent water quality gradients may have contributed to our observed patterns in CCA distribution.

It is important to note that, in total, the factors we examined only contributed to 46 % of variation in community structure. Habitat zone is a well-established predictor of community structure in benthic habitats (Hughes et al. 2012) and was the strongest contributor to variation in our findings. Many other factors not measured in the current study are known to vary across habitat zone and the continental shelf and may influence growth of coralline communities. For example, Bellwood and Wainwright (2001) report significant variation in fish assemblages across habitat zones and suggest that water movement influences patterns of distribution. They describe reef flat and crest sites in mid- and outer-shelf reefs as having the highest exposure to wave energy. Wave energy does influence growth of CCA, with thick, unbranched species dominating in areas of high wave energy (Steneck 1986). Ecosystem processes such as herbivory may also contribute to CCA abundance and diversity. Many CCA species require herbivory to minimize fouling by fleshy algae (Steneck 1986), and there is a well-established relationship between coralline-dominant communities and herbivore biomass (Steneck 1986). Greater biomass of herbivorous parrotfish in outer-reefs

(Hoey and Bellwood 2008) could shape the diversity or abundance of CCA in these areas. Sediment, nutrients, and light intensity may also influence CCA communities (Steneck 1986). The extent of unaccounted for variance in our findings highlights the importance of examining the role of such factors in future research.

This study has a number of limitations. Many CCA species are present on cryptic surfaces, which are difficult to detect using standard transect measures. Thus, it is possible that our findings may under-represent CCA abundance and diversity. Our sampling approach resulted in an unbalanced data set, with not all habitat zones or depths represented within each shelf position. This resulted in strong correlations between factors such as habitat and depth, or shelf position and longitude. *Mathematically*, mixed effects models are well suited to analyse unbalanced data sets and parse out the relative contribution of environmental factors to our outcomes. However, *ecologically*, this unbalanced design may limit the generalisability of our findings. Nonetheless, analyses of both the 'more balanced' subset of data, and the full unbalanced data set, indicate significant effects of shelf position and habitat zone on a range of CCA indices. Correlation between environmental variables may have diminished the observed contribution to variance in community composition; for example, it is well established that many coralline species or genera are depth stratified (Adey et al. 1982; Steneck 1982; Lund et al. 2000). However, we observed only a small effect of depth on composition of coralline communities and did not find a significant effect of depth on abundance, diversity, richness, or per cent cover. It is possible the effect of depth is partially driven by factors such as habitat zone, with shallow reef crests exhibiting higher abundance than deeper reef slopes. Moreover, we sampled across a limited depth range (>90 % of transects <15 m, maximum depth 30 m), which may have limited our capacity to assess variation across depth.

This study is one of the first that has examined abundance and diversity of CCA across the GBR. Our findings reinforce the influence of the continental shelf and habitat variation on benthic diversity of the GBR. Identifying spatial dynamics of CCA communities informs our understanding of the benthic structure of coral reefs. Our findings raise the possibility that, similar to hard corals, inshore CCA communities have become degraded in response to a series of anthropogenic influences. It is well known that successful recruitment and survival of hard corals may depend on certain CCA, but it is unclear the degree to which CCA may also rely on healthy hard coral communities. Documenting distribution of CCA provides a foundation for future work that seeks to identify determinants of benthic community structure and approaches to optimizing future health of reef ecosystems.

References

Adey WH (1970) A revision of the Foslie crustose coralline herbarium. Det Kongelige Danske Videnskabernes Selskabs Skrifter 1:1–46

Adey WH, Macintyre IG (1973) Crustose Coralline Algae–Re-Evaluation in Geological Sciences. Geol Soc Am Bull 84:883–904

Adey WH, Townsend RA, Boykins WT (1982) The crustose coralline algae (Rhodophyta: Corallinaceae) of the Hawaiian Islands. Smithsonian Contributions to the Marine Sciences, vol 15. Smithsonian Institution Press, Washington, D.C, pp 1–74

Akaike H (1974) New look at statistical-model identification. IEEE Trans Automat Contr 19:716–723

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs 20:139–150

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett 6:281–285

Benayahu Y, Loya Y (1981) Competition for space among coral-reef sessile organisms at Eilat, Red-Sea. Bull Mar Sci 31:514–522

Bickford D, Lohman DJ, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends Ecol Evol 22:148–155

Bittner L, Payri CE, Maneveldt GW, Couloux A, Cruaud C, de Reviers B, Le Gall L (2011) Evolutionary history of the Corallinales (Corallinophycidae, Rhodophyta) inferred from nuclear, plastidial and mitochonclrial genomes. Mol Phylogenet Evol 61:697–713

Brodie J, Waterhouse J (2012) A critical review of environmental management of the 'not so Great' Barrier Reef. Estuar Coast Shelf Sci 104:1–22

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS One 2:e711

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute, Washington, DC

Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, Devantier L, Edgar GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilan MC, Reboton C, Richards ZT, Rogers AD, Sanciangco J, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JE, Wallace C, Weil E, Wood E (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321:560–563

Chisholm JRM (2003) Primary productivity of reef-building crustose coralline algae. Limnol Oceanogr 48:1376–1387

Connell JH (1978) Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199:1302–1310

Daume S, Brand-Gardner S, Woelkerling WJ (1999) Community structure of nongeniculate coralline red algae (Corallinales, Rhodophyta) in three boulder habitats in southern Australia. Phycologia 38:138–148

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci USA 109:17995–17999

Dethier MN, Graham ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover estimations - objective Is not always better. Mar Ecol Prog Ser 96:93–100

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

Fabricius K, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. Coral Reefs 19:303–309

Fabricius K, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Mar Pollut Bull 51:384–398

Gordon GD, Masaki T, Akioka H (1976) Floristic and distributional account of the common crustose coralline algae on Guam. Micronesica 12:247–277

Great Barrier Reef Marine Park Authority (2009) Great Barrier Reef Outlook Report 2009. Great Barrier Reef Marine Park Authority, Townsville, Qld

Harrington L, Fabricius K, De'Ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. Ecology 85:3428–3437

Harrington L, Fabricius K, Eaglesham G, Negri A (2005) Synergistic effects of diuron and sedimentation on photosynthesis and survival of crustose coralline algae. Mar Pollut Bull 51:415–427

Hedeker D, Gibbons RD (2006) Longitudinal data analysis. J. Wiley, Hoboken, NJ

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. Science 318:1737–1742

Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs 27:37–47

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2012) Assembly rules of reef corals are flexible along a steep climatic gradient. Curr Biol 22:736–741

Iryu Y, Nakamori T, Matsuda S, Abe O (1995) Distribution of marine organisms and Its geological significance in the modern reef complex of the Ryukyu Islands. Sediment Geol 99:243–258

Kato A, Baba M, Suda S (2011) Revision of the Mastophoroideae (Corallinales, Rhodophyta) and polyphyly in nongeniculate species widely distributed on Pacific coral reefs. J Phycol 47:662–672

Keats DW, Chamberlain YM, Baba M (1997) *Pneophyllum conicum* (Dawson) comb nov (Rhodophyta, Corallinaceae), a widespread Indo-Pacific non-geniculate coralline alga that overgrows and kills live coral. Botanica Marina 40:263–279

Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284:118–120

Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, Singh GS, Duarte CM, Gattuso JP (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Glob Chang Biol 19:1884–1896

Kroon FJ, Kuhnert PM, Henderson BL, Wilkinson SN, Kinsey-Henderson A, Abbott B, Brodie JE, Turner RDR (2012) River loads of suspended solids, nitrogen, phosphorus and herbicides delivered to the Great Barrier Reef lagoon. Mar Pollut Bull 65:167–181

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

Littler MM, Littler DS, Brooks BL (2010) The effects of nitrogen and phosphorus enrichment on algal community development: Artificial mini-reefs on the Belize Barrier Reef sedimentary lagoon. Harmful Algae 9:255–263

Littler MM, Littler DS, Blair SM, Norris JN (1985) Deepest known plant life discovered on an uncharted seamount. Science 227:57–59

Lucas PHC, Webb T, Valentine PS, Marsh H (1997) The outstanding universal value of the Great Barrier Reef World Heritage Area. Great Barrier Reef Marine Park Authority, Townsville, Australia

Lund M, Davies PJ, Braga JC (2000) Coralline algal nodules off Fraser Island, eastern Australia. Facies 42:25–34

Macintyre IG, Glynn PW, Steneck RS (2001) A classic Caribbean algal ridge, Holandes Cays, Panama: an algal coated storm deposit. Coral Reefs 20:95–105

McCook LJ (1996) Effects of herbivores and water quality on *Sargassum* distribution on the central great barrier reef: Cross-shelf transplants. Mar Ecol Prog Ser 139:179–192

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421:727–730

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) Package 'vegan' Community Ecology Package, http://cran.r-project.org

Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Projecting coral reef futures under global warming and ocean acidification. Science 333:418–422

Pandolfi JM, Tudhope A, Burr G, Chappell J, Edinger E, Frey M, Steneck R, Sharma C, Yeates A, Jennions M, Lescinsky H, Newton A (2006) Mass mortality following disturbance in Holocene coral reefs from Papua New Guinea. Geology 34:949–952

Penrose D, Woelkerling WJ (1988) A taxonomic reassessment of *Hydrolithon foslie*, *Porolithon foslie* and *Pseudolithophyllum lemoine* emend - Adey (Corallinaceae, Rhodophyta) and their relationships to *Spongites* Kützing. Phycologia 27:159–176

Penrose D, Woelkerling WJ (1991) *Pneophyllum fragile* in southern Australia: implications for generic concepts in the Mastophoroideae (Corallinaceae, Rhodophyta). Phycologia 30:495–506

Penrose D, Woelkerling WJ (1992) A reappraisal of *Hydrolithon* and its relationship to Spongites (Corallinaceae, Rhodophyta). Phycologia 31:81–88

Price N (2010) Habitat selection, facilitation, and biotic settlement cues affect distribution and performance of coral recruits in French Polynesia. Oecologia 163:747–758

Ringeltaube P, Harvey A (2000) Non-geniculate coralline algae (Corallinales, Rhodophyta) on Heron Reef, Great Barrier Reef (Australia). Botanica Marina 43:431–454

Ritson-Williams R, Shjegstad SM, Paul VJ (2009a) Larval metamorphosis of *Phestilla* spp. in response to waterborne cues from corals. J Exp Mar Bio Ecol 375:84–88

Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermeij MJA, Paul VJ (2009b) New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithsonian Contrib Mar Sci 38:437–457

Roff G, Clark TR, Reymond CE, Zhao JX, Feng YX, McCook LJ, Done TJ, Pandolfi JM (2013) Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore Great Barrier Reef, following European settlement. Proc R Soc Lond B Biol Sci 280:20122100

Schaffelke B, Carleton J, Skuza M, Zagorskis I, Furnas MJ (2012) Water quality in the inshore Great Barrier Reef lagoon: Implications for long-term monitoring and management. Mar Pollut Bull 65:249–260

Spellerberg IF, Fedor PJ (2003) A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon-Wiener' Index. Glob Ecol Biogeogr 12:177–179

SPSS® (2002) Linear mixed effects modeling in SPSS® - an introduction to the MIXED procedure, Technical Report LMEMWP-1002

Steneck RS (1982) Adaptive trends in the ecology and evolution of crustose coralline algae (Rhodophyta, Corallinaceae). PhD Thesis. John Hopkins University, Baltimore, MD

Steneck RS (1986) The ecology of coralline algal crusts - convergent patterns and adaptative strategies. Annu Rev Ecol Syst 17:273–303

Steneck RS, Adey WH (1976) Role of environment in control of morphology in *Lithophyllum congestum*, a Caribbean algal ridge builder. Botanica Marina 19:197–215

Steneck RS, Macintyre IG, Reid RP (1997) A unique algal ridge system in the Exuma Cays, Bahamas. Coral Reefs 16:29–37

van Oppen MJH, Peplow LM, Kininmonth S, Berkelmans R (2011) Historical and contemporary factors shape the population genetic structure of the broadcast spawning coral, *Acropora millepora*, on the Great Barrier Reef. Mol Ecol 20:4899–4914

Warton DI, Wright ST, Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. Methods Ecol Evol 3:89–101

Wismer S, Hoey AS, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Mar Ecol Prog Ser 376:45–54

Witt V, Wild C, Uthicke S (2012) Terrestrial runoff controls the bacterial community composition of biofilms along a water quality gradient in the Great Barrier Reef. Appl Environ Microbiol 78:7786–7791

Wray JL (1964) *Archaeolithophyllum*, an abundant calcareous alga in limestones of the Lansing Group (Pennsylvanian), southeastern Kansas. Kansas Geological Survey Bulletin 170:1–13

Zuur AF (2009) Mixed effects models and extensions in ecology with R. Springer, New York/London