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REPORT

Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef, Australia

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Abstract Mesophotic coral reefs in the Indo-West Pacific, the most diverse coral reef region on earth, are among the least documented. This study provides the first detailed investigation of the diversity of Scleractinia and Octocorallia of the mesophotic Great Barrier Reef (GBR). Specimens were collected by 100-m rock dredge tows at 47–163 m depth on 23 sites in four regions (15.3°–19.7° latitude South). Twenty-nine hard coral species from 19 families were recorded, with the greatest diversity found at <60 m depth, and no specimen was found >102 m. Many of these species are also commonly observed at shallower depths, particularly in inshore areas. Twenty-seven octocoral genera were collected, 25 of which represented azooxanthellate genera. Generic richness of octocorals was highest at depths >60 m. Sixteen of the 25 azooxanthellate genera were either absent or very rare at <18 m, and only five azooxanthellate genera were common on both shallow and mesophotic reefs. Species-area models indicated that the total diversity of hard corals on the deep mesophotic reefs sampled during this study was ∼84 species while octocorals were represented by ∼37 genera; however, the wide 95% confidence limits indicates that more intensive sampling effort is required to improve the accuracy of these estimates. Nonetheless, these results show that the taxonomic richness, particularly of hard corals, on mesophotic reefs may be much higher than previously thought, a finding that has implications for the comprehensive and adequate protection of the full range of biodiversity of the GBR.

Keywords Mesophotic · Diversity · Scleractinia · Octocorallia · Great Barrier Reef

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Introduction

Tropical coral reefs contain greater biodiversity than any other marine ecosystem on earth (Veron 1995; Bellwood and Hughes 2001). Although shallow-water coral reefs are relatively well known, deeper reef habitats (>30 m) represent a significant gap in coral reef science. The occurrence of hermatypic corals on deep-water reefs has been known for some time: Darwin (1842) reported collecting corals to 128 m depth, while substantial deep-water collections were made on Indo-Pacific atolls by Gardiner (1903) and Vaughan (1907). The advent of SCUBA as the primary means of collecting data on coral reefs, however, has resulted in deeper reef habitats (below the depth limit of traditional SCUBA) being largely neglected by both scientists and management agencies in recent decades.

The term mesophotic coral ecosystem (MCE) is used to define reef communities that occur in the middle to lower photic zone but which still contain phototrophic taxa, particularly zooxanthellate Scleractinia (Kahng et al. 2010). Early studies were conducted on a limited number of Indo-Pacific MCEs using manned submersibles (Maragos and Jokiel 1986; Colin 1986; Colin et al. 1986). Recent technological advances such as autonomous underwater vehicles (AUVs), remotely operated vehicles (ROVs) and closed-circuit rebreather diving have enabled the investigation of MCEs in American Samoa (Bare et al. 2010), Hawaii (Kahng and Kelley 2007), the Coral Sea (Bongaerts et al. 2011) and the Great Barrier Reef (GBR) (Williams et al. 2010; Bridge et al. 2011a, b). All have shown mesophotic reef habitats to contain diverse benthic communities, including unique depth-endemic species (e.g., Pyle et al. 2008). They may also provide refugia to shallow-water coral reef species from the environmental stress such light-enhanced warm water bleaching and severe tropical cyclones (Glynn 1996; Riegl and Piller 2003; Bongaerts et al. 2010). These studies have also shown that, not surprisingly, MCE communities can vary considerably among sites. Due to this diversity and data scarcity, few generalisations can be made regarding the composition of MCE communities in the Indo-Pacific (Kahng et al. 2010).

Benthic habitat models combining multibeam bathymetry and backscatter reflectivity data with optical imagery have become a popular tool for characterising the seafloor, particularly in deep or remote habitats and/or over large geographical scales (e.g., Kostylev et al. 2001; Hewitt et al. 2004). Remotely sensed data collected by ROV (Kahng and Kelley 2007), AUV (Armstrong et al. 2006; Bridge et al. 2011a, b) and towed video camera (Bare et al. 2010) have all proved successful in providing optical imagery for classifying MCE communities. However, detailed identification of many sessile benthic megafaunal taxa such as corals and octocorals is often only possible using skeletal features or genetics, and therefore, requires extractive sampling. Many MCE taxa are either undescribed or rare in shallow water, further complicating accurate identification of remotely sensed images. Therefore, many studies of MCE community ecology (particularly in species-rich or poorly described regions such as the Indo-West Pacific) lack detailed taxonomy. The specific aims of this study are to provide (1) the first detailed taxonomic survey of the most common groups of macrobenthos, Scleractinia and Octocorallia (hard corals and octocorals hereafter), on mesophotic reefs in the Great Barrier Reef World Heritage Area (GBRWHA); (2) a comparison of diversity of mesophotic reefs in the GBRWHA with previously studied shallow-water reefs; and, (3) a reference for future studies on MCEs in the poorly described but species-rich Indo-West Pacific.

Materials and methods

Sampling took place in four regions along a 750 km section of the GBR outer shelf (~15°–20°S) during September–October 2007 (Fig. 1). Specimens were collected using a standard rock dredge from 48 to 163 m depth. Twenty-three sites were sampled in total: three from the Ribbon Reefs, seven from Noggin Pass, eight from Viper Reef and five from Hydrographers Passage (Table 1). Detailed bathymetric and AUV surveys provided targeted site locations in each area (Webster et al. 2008). Dredges were towed along the seafloor for 100 m parallel to depth contours.

For hard corals, taxonomic identification was conducted by microscopic inspection of bleached skeletons, referenced to specimens from Veron and Pichon (1976, 1980, 1982), Veron et al. (1977), Veron and Wallace (1984), Wallace (1999) and Veron (2000), housed in the Museum of Tropical Queensland, Townsville, Australia. Location data were referenced to known species ranges in Veron (2000). The maximum depth at which coral species were observed was compared with the maximum depth limit reported by Carpenter et al. (2008) (Electronic Supplemental Material, ESM). Hard corals were identified to species level where possible; however, in some cases, identification was only possible to genus level; these corals may represent new undescribed species or known species that appear substantially different at mesophotic depths than in shallower environments. Without collection of further specimens, it was not possible to assign these specimens (recorded as "sp.1") to described species. Octocorals were identified by detailed examination of sclerites and colony morphology referenced to Fabricius and Alderslade (2001). Octocorals were identified to genus level because the majority of Indo-Pacific octocoral species are not yet described (Fabricius and De'ath 2008). Mesophotic diversity, as species or generic richness, respectively, was compared to that of the shallow-water GBR reefs (<18 m depth) using data presented in DeVantier et al. (2006) for hard corals and Fabricius and De'ath (2008) for octocorals.

Species-area curves were generated to estimate total species richness of hard corals and generic richness of octocorals on the mesophotic GBR. Richness was estimated using the Chao 2 richness estimator, which estimates the true number of species in an assemblage based on the number of rare species in the sample (Colwell and Coddington 1994) with corresponding log-linear 95% confidence intervals in the statistical program EstimateS v8.2.0 (Colwell 2006) using 500 random iterations. The Chao 2 index was used because of its suitability for small sample sizes and requirement of only presence/absence data (Colwell and Coddington 1994), which are all that are obtainable from dredged fragments. For hard corals,

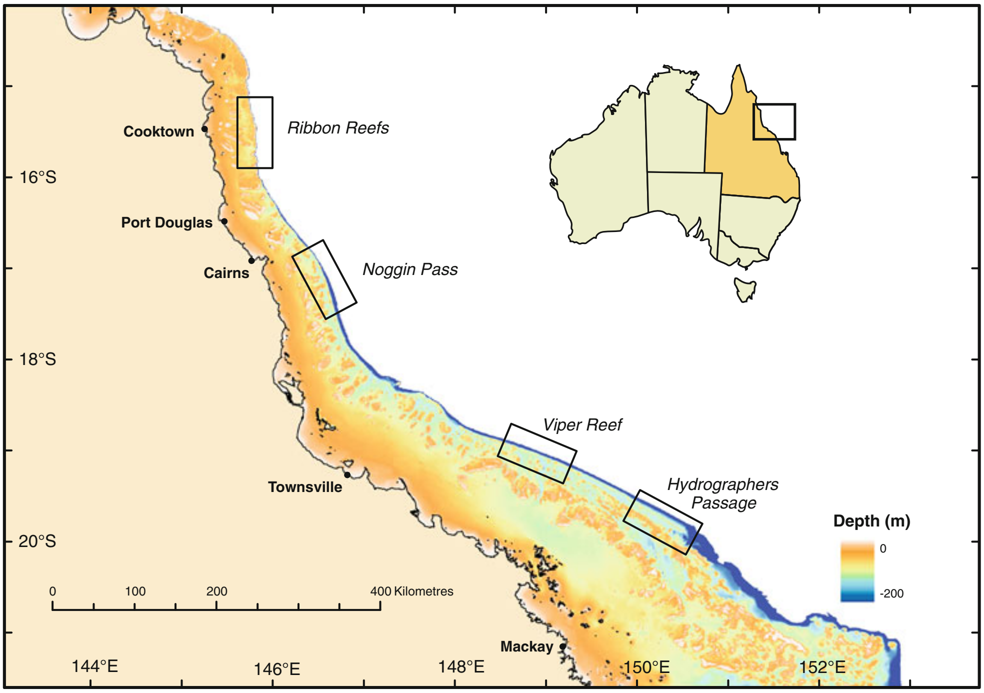

Fig. 1 Location of study sites. *White boxes* indicate extent of area mapped during surveys. Dredge locations (Table 1) were chosen based on bathymetry

Table 1 Location of dredge sites (sorted by depth for each site), and number of scleractinian and octocoral taxa retrieved

Dredge_#	Latitude	Longitude	Area	Mean depth (m)	No. of scleractinian species	No. of octocoral genera
4	−15.49	145.82	Ribbon Reefs	47	4	1
2	−15.38	145.80	Ribbon Reefs	55	6	1
3	−15.38	145.80	Ribbon Reefs	70	4	10
9	−17.09	146.57	Noggin Pass	58	3	4
8	−17.10	146.57	Noggin Pass	60	1	3
6	−17.13	146.59	Noggin Pass	90	0	0
5	−17.13	146.59	Noggin Pass	101	0	1
7	−17.10	146.58	Noggin Pass	108	0	0
11	−17.09	146.57	Noggin Pass	109	0	7
10	−17.02	146.54	Noggin Pass	112	0	1
18	−18.88	148.44	Viper Reef	61	1	1
17	−18.88	148.45	Viper Reef	72	0	0
15	−18.88	148.45	Viper Reef	99	1	1
16	−18.88	148.45	Viper Reef	99	2	3
20	−18.89	148.49	Viper Reef	102	2	6
19	−18.88	148.49	Viper Reef	114	0	8
13	−18.78	148.20	Viper Reef	159	0	1
14	−18.78	148.20	Viper Reef	163	0	0
21	−19.69	150.23	Hydrographer Pass	55	18	9
22	−19.68	150.24	Hydrographer Pass	90	1	8
26	−19.79	150.46	Hydrographer Pass	104	0	7
25	−19.78	150.46	Hydrographer Pass	129	0	0
D24	−19.73	150.36	Hydrographer Pass	130	0	2

species-area curves were calculated using the Classic Chao 2 equation (Colwell 2009, ESM Appendix 2)

$$\hat{S}_{\text{Chao 2}} = S_{\text{obs}} + \frac{Q_1^2}{2Q_2}$$

where S_{obs} is the observed number of hard coral species, Q_1 is the number of species found in only one dredge, and Q_2 is the number of species found in two dredges. This is the prescribed index when the estimated incidence distribution CV is >0.5 (0.551 in the case of hard corals).

For octocorals (CV <0.5 in this case), the bias-corrected Chao 2 equation was used:

$$\hat{S}_{\text{Chao 2}} = S_{\text{obs}} + \left(\frac{m-1}{m}\right)\left(\frac{Q_1(Q_1-1)}{2(Q_2+1)}\right)$$

where m is the total number of samples.

Confidence limits were obtained using the equations:

$$\text{Lower 95\% bound} = S_{\text{obs}} + \frac{T}{K}$$

$$\text{Upper 95\% bound} = S_{\text{obs}} + TK$$

where $T = \hat{S}_{\text{Chao 2}} - S_{\text{obs}}$, and

$$K = \exp\left\{1.96\left[\log\left(1 + \frac{\hat{\text{var}}(\hat{S}_{\text{Chao 2}})}{T^2}\right)\right]^{1/2}\right\}$$

Multidimensional scaling (MDS) was used to explore associations of corals, octocorals or both groups combined, associated with particular regions, environmental properties or depth zones. The following environmental variables of each dredge site were included: *latitude* (recorded as 15°, 17°, 19° or 20°S for each of the four regions); *depth* (derived from multibeam bathymetry), *optical water clarity* (Secchi disk) and *water column chlorophyll* (as proxy for productivity). The latter two variables were estimated for each site using data from the AIMS e-atlas (http://e-atlas.org.au/geoserver/wms, accessed 7 December 2010; De'ath 2007). Normalised environmental variables were analysed using the BIOENV function in PRIMER v 6 (Clarke and Gorley 2006) to reveal potential correlations with the distribution patterns of hard corals, octocorals and both assemblages combined. Similarity Percentages (SIMPER) analysis was conducted to identify the primary taxa responsible for the variation between sites and depths.

Insight into bottom temperature at each site was obtained using conductivity–temperature–depth (CTD) casts taken during International Ocean Drilling Program (IODP) Expedition 325 to drill the submerged reefs of the GBR outer shelf in Expedition 325 Scientists (2010). Data were collected from 11 separate CTD casts (four from Hydrographers Passage from 3 to 6 March 2010, two from the Ribbon Reefs on 22 March and five from Noggin Pass from 29 to 31 March) to a depth of ~100 m (Webster et al. 2011).

Results

Hard corals were recorded at 11 of 23 sites at depths of 47–102 m, representing 29 species from 19 genera (Table 2). Although dredges were conducted to 163 m depth, no hard corals were collected deeper than 102 m. Hard coral specimens have been assigned to 21 described species, of which three—*Acropora elegans*, *Leptoseris striata* and *Pocillopora molokensis*—represent the first recorded occurrence of these species on the GBR according to the distribution maps presented in Veron (2000) and Wallace (1999). Most hard corals recorded in this study were from <70 m depth, with only two genera, *Leptoseris* and *Echinophyllia*, occurring deeper. Species-area modelling predicted that total species richness in the four regions is ~84 species (Fig. 2a). The wide range of 95% confidence limits (46–213) indicates that an accurate estimate of total richness requires further sampling effort.

Octocorals were collected in 19 of 23 dredges at depths ranging from 47 to 159 m (Table 3). Of the 27 octocoral genera collected, only two were obligate phototrophs (zooxanthellate) (*Lobophytum* and *Cespitularia*). Both were collected in a single dredge at Hydrographers Passage from 55 m depth. A third genus, *Junceella*, has been shown to contain both zooxanthellate and azooxanthellate species (van Oppen et al. 2005). However, zooxanthellate colonies are beige in colour while azooxanthellate ones are brightly coloured. Both colonies of *Junceella* recorded in this study were bright red, suggesting that they likely represent azooxanthellate species despite occurring in shallower dredges (55–70 m depth). The other 24 genera were obligate heterotrophs (azooxanthellate) from 12 families. At least five genera (*Callogorgia*, *Heliania*, *Paracis*, *Pteronisis* and *Pterostenella*) represent the first records from the GBR.

Octocoral richness was the highest at 60–120 m depth, peaking at 100–120 m and dropping substantially below 120 m. Hydrographers Passage was the richest site (20 genera), although all sites contained at least 11 genera. Three genera (*Viminella*, *Siphonogorgia* and *Keroeides*) were recorded in all four regions, while a further eight were recorded from three regions. Species-area modelling (Fig. 2b) estimated that total generic richness of octocorals on mesophotic reefs on the GBR is ~37 genera (95% confidence intervals: 30–69 genera).

Multidimensional scaling (Fig. 3) indicated that the composition of dredge samples showed some relationship with depth when placed into three broad depth bins: <60, 60–120 and >120 m. Dredges <60 m depth contained the highest diversity of hard corals, ranging from four species in dredges 4 and 9, up to 18 species in dredge 21, as well as the two obligate zooxanthellate octocorals. No dredges deeper than ≥60 m contained more than four hard coral

Table 2 List of Scleractinia. Also indicated is the depth range recorded in this study

Family	Identification	Depth range (m)
Acroporidae	*Acropora cardenae*	55
Acroporidae	*Acropora elegans*[a]	47–55
Acroporidae	*Acropora* sp. 1	55
Acroporidae	*Montipora foliosa*	47
Acroporidae	*Montipora millepora*	55–70
Acroporidae	*Montipora* cf. *tuberculosa*	55
Acroporidae	*Montipora* sp. 1	55
Agariciidae	*Leptoseris striata*[a]	55–102
Agariciidae	*Leptoseris hawaiiensis*	60–102
Agariciidae	*Leptoseris papyracea*	55
Agariciidae	*Leptoseris scabra*	70–99
Agariciidae	*Pachyseris speciosa*	55–60
Agariciidae	*Pavona minuta*	55
Faviidae	*Cyphastrea* sp. 1	55
Faviidae	*Favites halicora*	55
Fungiidae	*Diaseris distorta*	55
Fungiidae	*Fungia* cf. *danae*	55
Merulinidae	*Hydnophora exesa*	55
Mussidae	*Cynarina* sp. 1	70
Oculinidae	*Galaxea astreata*	55
Pectiniidae	*Echinophyllia aspera*	55–90
Pocilloporidae	*Pocillopora damicornis*	55
Pocilloporidae	*Pocillopora molokensis*[a]	55
Pocilloporidae	*Seriatopora hystrix*	55
Pocilloporidae	*Stylophora pistillata*	55
Poritidae	*Goniopora djboutiensis*	58
Poritidae	*Porites* cf. *lutea*	55–70
Poritidae	*Porites* cf. *myrmidonensis*	47–55
Siderasteridae	*Coscinarea wellsi*	58

[a] New record for the GBR

species but instead yielded a range of azooxanthellate octocoral genera. SIMPER analysis indicated the key contributors to the shallow group to be *Acropora elegans*, *Porites* cf. *lutea* and *Pachyseris speciosa*, which together accounted for 63% of the similarity within the group. For the 60–120 m group, *Siphonogorgia*, *Keroeides*, *Leptoseris striata*, *Ellisella* and *Viminella* contributed 60% of the similarity within the group. However, similarity within each of the two groups was low (16.5% for the <60 m group and 15.5% for the 60–120 m group). Octocorals were collected in only two of the four dredges from >120 m, with no similarities within this group. The BIO-ENV procedure indicated that the environmental variables *latitude*, *depth*, *water clarity* and *chlorophyll* could not sufficiently explain the observed distribution of hard coral and octocoral taxa, although *depth* alone was the most predictive combination of variables (0.235, $P = 0.12$).

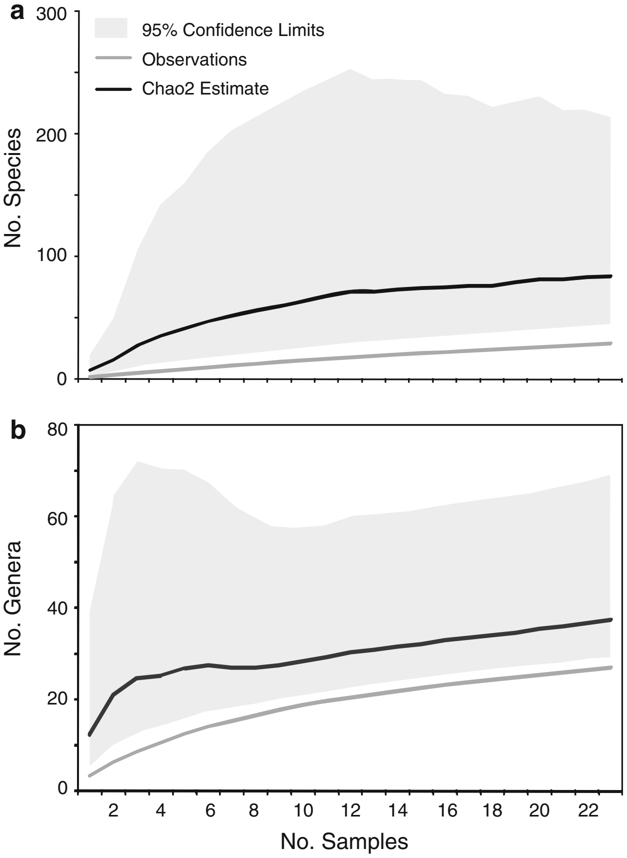

Fig. 2 Species-area curves showing the observed number of species (observations, *grey line*) and the estimated Chao 2 projection of total species richness (*black line*) for hard corals (**a**) and generic richness for octocorals (**b**) across all 23 sites using 500 random iterations. *Grey* areas indicate 95% confidence limits

Discussion

This study demonstrates that mesophotic reefs in the GBR region contain diverse benthic megafaunal communities, including several taxa previously not recorded from the region. The data also suggest that other taxa considered to be rare may be widespread at mesophotic depths. Zooxanthellate hard corals were diverse and common above 60 m depth, while deeper reefs were dominated by azooxanthellate suspension-feeding octocorals. The inability of the environmental variables to explain the observed distribution is likely due to a combination of lack of replication of regions and sites, the inherent limitations of dredge surveys, which are often biased towards species that are easily broken off by the rock dredge, and a lack of long-term environmental data from mesophotic reef

Table 3 List of octocoral genera

Family	Genus	A/Z	Depth range (m)
Acanthogorgiidae	*Acanthogorgia*	A	102–115
Acanthogorgiidae	*Muricella*[a]	A	57–70
Alcyoniidae	*Eleutherobia*[b]	A	129–130
Alcyoniidae	*Lobophytum*	Z	55
Clavulariidae	*Carijoa*[b]	A	90
Ellisellidae	*Dichotella*[b]	A	102
Ellisellidae	*Ellisella*	A	55–113
Ellisellidae	*Heliania*[a, c]	A	104
Ellisellidae	*Junceella*	Z/A	55–70
Ellisellidae	*Nicella*[a]	A	70–101
Ellisellidae	*Verrucella*[b]	A	70–109
Ellisellidae	*Viminella*	A	55–113
Isididae	*Pteronisis*[a, c]	A	104
Keroeididae	*Keroeides*[a]	A	70–112
Melithaeidae	*Acabaria*	A	47
Nephtheidae	*Dendronephthya*	A	55–130
Nidaliidae	*Chironephthya*[b]	A	104
Nidaliidae	*Siphonogorgia*	A	55–113
Parisidae	*Parisis*[a]	A	114
Plexauridae	*Astrogorgia*	A	55–113
Plexauridae	*Echinogorgia*	A	55–159
Plexauridae	*Paracis*[a, c]	A	70–113
Plexauridae	*Villogorgia*[b]	A	90–99
Primnoidae	Callogorgia[a, c]	A	102-113
Primnoidae	Pterostenella[a, c]	A	114
Subergorgiidae	*Annella*	A	54–105
Xeniidae	*Cespitularia*	Z	55

A azooxanthellate, *Z* zooxanthellate genus. Also indicated is the depth range recorded in this study

[a] Absent from shallow-water surveys reported in Fabricius and De'ath (2008)

[b] Rare: <20 specimens recorded in shallow-water surveys

[c] New record for GBR

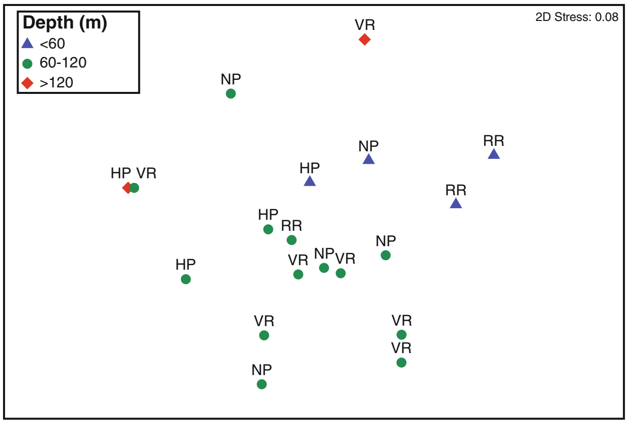

Fig. 3 Multidimensional scaling plot based on the composition of hard corals and octocorals recovered in each dredge. *Letters* represent dredge location: *RR* Ribbon Reefs, *NP* Noggin Pass, *VR* Viper Reef, *HP* Hydrographers Passage. *Blue triangles* indicate dredges with mean depth <60 m deep, *green circles* 60–120 m and *red diamonds* >120 m

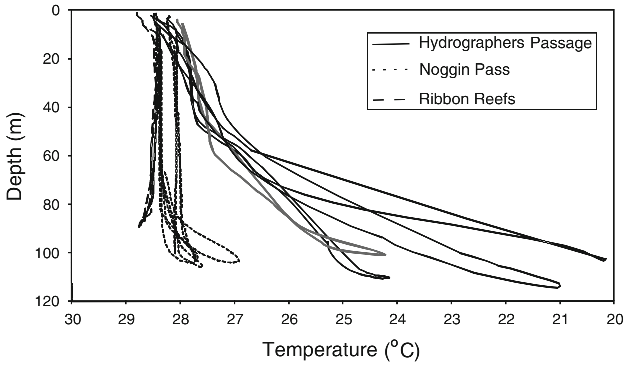

Fig. 4 Temperature versus depth plots for three of the four sites sampled during the present study. Temperature data were collected on a separate expedition to the shelf-edge reefs in March 2010

habitats. Nonetheless, this study does provide the first detailed information on coral and octocoral richness in a largely unexplored coral reef habitat of the GBRWHA.

Given the latitudinal range of the study sites and the depth range of the sampling, it is possible that temperature may be an important determinant of species distributions. Unfortunately, long-term temperature records do not exist; however, some temperature data were collected by CTD casts IODP Expedition 325 (Webster et al. 2011) and indicate a strong thermocline occurring at depths >60 m at Hydrographers Passage (Fig. 4). These data only represent a "snapshot" and therefore no conclusions can be drawn regarding the role of temperature in determining community composition at the present time; however, it is possible that upwelling of cold, nutrient-rich water may be an important environmental control on some deeper mesophotic reefs (Leichter and Genovese 2006).

Scleractinia

Richness predictions in the present study (84 species) suggest that the richness estimates of Carpenter et al. (2008), without the benefit of many depth distribution data, are likely to be much too low. Maximum depth limits of hard coral species presented in that study suggested only 30 coral species occur at ≥50 m depth and only 12 at ≥60 m. Of those species, only one (*Acropora elegans*) was observed in this study. This information suggests that hard coral diversity on mesophotic reefs may be significantly greater than previously reported, a finding that has

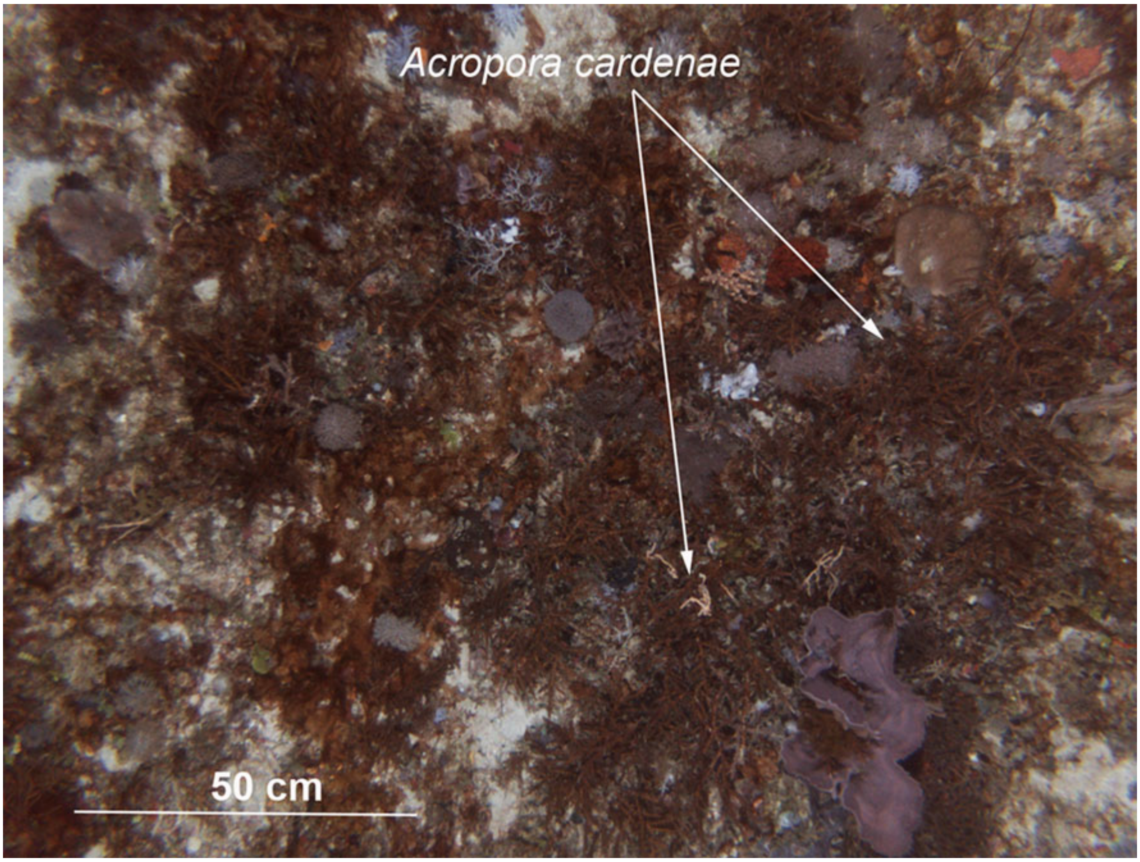

Fig. 5 In-situ photograph of *Acropora cardenae* taken by autonomous underwater vehicle at a depth of ∼50 m at Hydrographers Passage

implications for the comprehensive and adequate protection of the full range of biodiversity on the GBR.

The lack of knowledge of deeper reefs is highlighted by the *Acropora* specimens collected during this study. Despite the small sampling effort and paucity of specimens, this study found large range extensions and one heretofore extremely rare species. These include the first Australian record of *Acropora elegans*, previously recorded from reef wall habitats of central Indonesia (Wallace 1999; Veron 2000; and Museum of Tropical Queensland collections). Collecting this species at 47–55 m depth in a mesophotic reef slope habitat represents a large increase in the species' known geographic, depth and habitat ranges and suggests that poor representation of *A. elegans* is due to the depth limitations of SCUBA collections as well as limited sampling effort in mesophotic habitats. This study also presents the first specimen-confirmed record of *Acropora cardenae* in Australia since its description by Wells (1985) from samples dredged from mesophotic depths in the GBR lagoon. Figure 5 shows *A. cardenae* occurring as a dominant species in parts of the sampled region (Hydrographers Passage) and provides the first in situ photograph of the species from the GBR and possibly the world, since the only other published field photograph (Veron 2000, p. 419, from the Philippines) is not confirmed by a specimen.

The maximum lower depth limit of zooxanthellate corals is influenced to a large extent by optical water clarity (Done 1983, 2011), while slope has also been shown to affect coral community composition in deeper waters (e.g., Ohlhorst and Liddell 1988). Corals that can exist in low light habitats may do so by means of efficient photoacclimation (Fricke et al. 1987; Mass et al. 2007, 2010) and/or increased reliance on heterotrophy (e.g., Muscatine et al. 1989; Anthony and Fabricius 2000). Species of *Leptoseris* have been reported as common inhabitants of MCEs in the Indo-Pacific to over 100 m depth (Wells 1954; Colin et al. 1986; Kahng and Kelley 2007), a finding that is supported by this study and one of the few consistent patterns recorded to date among MCE communities in the Indo-Pacific region (Kahng et al. 2010). Clearly, *Leptoseris* spp. possess morphological characteristics and physiological mechanisms allowing them to exist in low light environments, although these remain poorly understood.

There is some evidence that some coral species may increase their reliance on heterotrophy to provide a greater proportion of nutritional requirements at mesophotic depths (Leichter and Genovese 2006; Mass et al. 2007), although the evidence for this is inconsistent (Alamaru et al. 2009; Einbender et al. 2009). DeVantier et al. (2006) suggest that heterotrophy may be an important characteristic of corals, which dominate turbid inshore reefs; indeed, many of these taxa (e.g., poritids, faviids and fungiids) were recorded in the present study. A high heterotrophic capacity in some coral species (e.g., *Favia favus*, Alamaru et al. 2009) may therefore make them better able to survive at mesophotic depths. Although modelled data for optical water clarity and chlorophyll indicate the outer shelf contains clear, oligotrophic water, upwelling may result in elevated nutrient levels on mesophotic reefs in the GBR (Wolanski and Pickard 1983). Furnas and Mitchell (1996) observed significant upwelling events near Myrmidon Reef in the central GBR, whereas Drew and Abel (1988) attribute extensive meadows of the calcareous algae *Halimeda* in the same region to localised nutrient upwelling. Similar upwelling events in other locations along the GBR shelf (e.g., Hydrographers Passage) may provide an important source of nutrients for corals in such light-limited environments.

DeVantier et al. (2006) examined diversity and composition of hard coral communities at 135 mainly inner-shelf and mid-shelf reefs in the GBR, which provides an interesting comparison with the present study. They recorded a total of 362 coral species; however, the vast majority were classed as rare or uncommon. Therefore, many of these would be unlikely to have been collected in the present study due to the low number of samples. Moreover, DeVantier et al. (2006) reported the highest coral diversity in the far northern GBR, including many species that were rare or absent in surveys further to the south. The far northern GBR was not sampled in the present study, and further sampling effort on mesophotic reefs in that region may lead to higher estimates of total hard coral diversity on the GBR.

Octocorallia

Patterns of octocoral diversity observed in this study are substantially different from those reported in an extensive study of ~150 shallow-water GBR reefs by Fabricius and De'ath (2008). Data in that study were collected along SCUBA transects that were roughly equivalent to those sampled by the rock dredge (~100 m in both cases). Only 30 genera of heterotrophic octocorals were recorded in 1,257 shallow ($\leq$18 m) transects, whereas it took only 23 dredges in this survey to yield 25 genera. Richness of heterotrophic octocorals on the shallow GBR is highly variable but generally low in most areas: only 11% of the 1,257 shallow-water surveys recorded more than six genera of heterotrophic octocorals and 48% recorded none at all. In contrast, 30% of the deep dredges contained at least six heterotrophic octocoral genera, and only 17% of dredges recovered no octocorals.

Fabricius and De'ath (2008) also conclude that heterotrophic octocorals in shallow environments appear to have relatively homogeneous habitat requirements. However, the turnover of heterotrophic octocoral genera in this study suggests that many mesophotic taxa likely possess different habitat requirements to those commonly encountered in shallow water. For example, only five obligate heterotrophic genera collected in the dredges are also common (i.e., occur in >100 transects in Fabricius and De'ath 2008) on shallow-water reefs: *Annella*, *Astrogorgia*, *Ellisella*, *Dendronephthya* and *Viminella*, in addition to *Junceella,* which contains both heterotrophic and phototrophic species. All of these genera were recorded at multiple sites and to depths over 100 m, suggesting they have broad ecological niches enabling them to survive in a wide range of habitats. Similarly, some of the most common heterotrophic taxa in shallow water (e.g., *Subergorgia*) were not recorded in this study. Nine genera (*Callogorgia*, *Heliania*, *Keroeides*, *Muricella*, *Nicella*, *Paracis*, *Parisis*, *Pteronisis* and *Pterostenella*) identified in this study were not recorded in the shallow transects, while a further six (*Eleutherobia*, *Carijoa*, *Dichotella*, *Verrucella*, *Chironephthya* and *Villogorgia*) were recorded on <20 of 1,257 shallow transects.

In contrast to the limited geographic ranges of many heterotrophic octocoral genera in shallow waters (Fabricius and De'ath 2008), most genera in this study were widespread, with 17 of 25 genera occurring at two or more sites. Heterotrophic octocoral richness on shallow-water reefs is highest in the far northern GBR in inshore regions with high water column productivity and is strongly correlated to depth and water flow but negatively correlated with wave energy (Fabricius and De'ath 2008). Only in the far northern GBR region are rich communities of heterotrophic octocorals found on shallow offshore reefs. These results suggest that the occurrence of heterotrophic octocorals in shallow waters is strongly influenced by temperature, wave energy and exposure to cyclones. Only in the far north, where temperatures are warm and cyclones are rare, can rich communities of heterotrophic octocorals occur on offshore reefs in shallow waters. However, in this study, heterotrophic octocoral richness was still high at the most southerly site, with 20 genera recorded at Hydrographers Passage. The depth of the mesophotic reefs likely provides protection from storms, creating an ideal habitat for heterotrophic octocorals and explaining their widespread distribution in deeper waters. In addition, GBR MCEs may experience strong currents resulting from a combination of low-frequency longshore and semidiurnal tidal components (Wolanski and Pickard 1983). Particularly strong currents were observed both at the surface and near the seabed at Hydrographers Passage during the offshore drilling phase of the International Ocean Drilling Program Exp. 325 to the GBR, although quantitative data were not collected (Expedition 325 Scientists 2010). Such strong currents promote suspension feeding and are associated with fast growth rates in heterotrophic octocorals (Fabricius et al. 1995a, b) and likely contribute to their high diversity sites such as at Hydrographers Passage.

Significance of mesophotic reefs

This study reveals information about mesophotic reefs that is important for understanding of coral reef ecosystems as a whole. Firstly, mesophotic reefs do support coral species that are rare or absent in shallow waters, adding to the total species pool represented in the GBR. Secondly, mesophotic reefs extend the range of species that also occur on shallower reefs and may therefore provide refugia from environmental disturbances that affect shallow reefs. Although very little is known about vertical connectivity of corals (Bongaerts et al. 2010), there is some evidence indicating that deep reef habitats may, in some cases, provide a source of colonists to replenish shallow-water reef habitats after depletion by disturbance events (van Oppen et al. 2011). Many species recorded from > 50 m depth in this study (e.g., *Seriatopora hystrix*, *Echinophyllia aspera*, *Favites halicora*, *Montipora foliosa* and *Galaxea astreata*) are common over a wide variety of reef habitats and depth ranges (Veron 2000) and as such represent "depth-generalist" species. Based on their distribution patterns alone, this would make them suitable candidates to recolonise reefs that have suffered coral mortality from disturbances such as bleaching and cyclones. The upper mesophotic zone (30–60 m) was only partially sampled in this study (four dredges at 47–60 m), but likely supports an even greater range of hard coral species. Further studies of both coral species diversity and vertical connectivity of coral populations are required before the question of refugia can be accurately addressed; however, the results of this study suggest that MCEs should be given greater consideration by both scientists and managers examining connectivity and resilience in the GBR ecosystem.

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