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Habitats and Sessile Benthic Megafaunal Communities in the Mesophotic Zone of the Great Barrier Reef World Heritage Area, Australia

Thesis submitted by

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For the degree of Doctor of Philosophy

In the School of Earth and Environmental Sciences

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Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and la list of references is given.

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STATEMENT OF CONTENT

The body of this thesis is presented as four separate, self-contained works. Each chapter has been published, submitted, or will soon be submitted to journals of international significance in a similar format. Due to the completeness of each section, a small amount of repetition is unavoidable. The four data chapters are followed by a discussion of the findings of the research that places this work in reference to both the research aims outlined in the introduction and its place in the broader scheme of the scientific body of knowledge.

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ABSTRACT

The Great Barrier Reef (GBR) is the world’s largest coral reef ecosystem, extending for over 2300 km along Australia’s north-east coast. The Great Barrier Reef World Heritage Area (GBRWHA), one of the world’s largest Marine Protected Areas, covers a total area of ~348 000 km2, approximately 7% of which is currently classified as coral reef habitat. The vast majority of this habitat occurs in shallow waters <30 m depth. These iconic shallow-water reefs are well known, however a lesser-known but extensive series of submerged reefs also occurs on the shoulder of the continental shelf to depths of ~130 m. These reefs provide a vast potential habitat for mesophotic coral reef ecosystems (MCEs), tropical coral reef communities that occur in the middle to lower photic zone. Although there has been a significant increase in research interest on MCEs in recent years, very few studies have focused on the Indo-west Pacific region, the epicentre of coral reef biodiversity, and the ecology of MCEs in the GBR remains virtually unknown. This thesis provides the first quantitative analysis of the ecology of mesophotic coral reef ecosystems in the GBRWHA.

Data were collected on a 3-week expedition on board the RV *Southern Surveyor* in September-October 2007 at four sites along the GBR outer-shelf: the Ribbon Reefs (approximately 15˚S), Noggin Pass (17˚S), Viper Reef (19˚S) and Hydrographers Passage (20˚S). The surveys combined high-resolution multibeam bathymetry with over 57 000 Autonomous Underwater Vehicle (AUV) images, and samples collected by dredging from 50 to 150 m water depth. The specific scientific objectives of the study are to (1) examine the diversity of sessile benthic megafauna (SBM) occurring on MCEs in the GBRWHA and compare them to adjacent shallow-water reefs; (2) identify how SBM communities change along a depth gradient and to identify geophysical variables which explain the observed variation; (3) identify how SBM communities change along the length of the GBR outer-shelf in response to a range of environmental variables; and (4) to develop models to predict the distribution of SBM taxa and

communities and use them to estimate the total amount of mesophotic reef habitat in the GBRWHA.

In general, the diversity of phototrophic (zooxanthellate) taxa is highest in shallower waters <70 m depth, and diverse communities of heterotrophic taxa (particularly octocorals) occurs on deeper reef habitats from 90-120 m. Although some Scleractinia represent species only occurring in deep water, many species are also common inhabitants of shallow-water reef habitats. In contrast, many of the heterotrophic octocoral taxa occurring on mesophotic reefs are rare or absent from shallow-water habitats. Several Scleractinia and Octocoral taxa recovered during the expedition represent the first records from the GBR.

Vertical zonation of reef communities was clearly evident, with shallow areas (50-60 m depth) inhabited by a community comprised predominantly of phototrophic taxa, including zooxanthellate Scleractinia and Octocorallia and the phototrophic sponge *Carteriospongia*. Benthic communities below 75 m depth were comprised largely of heterotrophic suspension-feeders, primarily azooxanthellate octocorals but also containing sponges and black corals (order Antipatharia). There was also a transitional community comprising both phototrophic and heterotrophic taxa occurring in 60-75 m depth. The distribution of sessile benthic megafauna was strongly correlated to reef habitat, with sandy non-reef habitats exhibiting low abundance and diversity of megafauna.

Random sampling of images at a standardised depth (50-65 m) from Noggin Pass, Viper Reef and Hydrographers Passage revealed diverse communities of sessile benthic megafauna at all sites but significant variation in community composition both within and between each site. However, there were consistent patterns in the functional ecological groups occupying different finer-scale habitat types; in general, phototrophic taxa occupied the flatter tops of reefs while heterotrophic suspension-feeders occurred on steep walls of submerged reefs.

Reduced light irradiance on steeper slopes combined with low ambient light levels at mesophotic depths probably excludes phototrophic taxa from reef walls.

Predictive habitat suitability models indicate the GBR shelf contains over 10 000 km^2 of habitat which may potentially be inhabited by MCE communities. Habitat for phototrophic communities occur both on the submerged reefs of the outer-shelf and also on the deeper flanks of reefs inside the GBR lagoon, while heterotrophic communities are more confined to deeper reefs (90-120 m depth) along the outer-shelf. The models indicate that the outer-shelf of the GBR may be inhabited by extensive MCEs, and so including MCEs as “reef” habitats may increase the amount of reef habitat within the GBRWHA by ~40%.

This thesis provides the first quantitative study of MCEs in the GBR, indicates that MCEs in the GBR warrant further study, not only on their SBM but also on their fish and mobile invertebrate communities. In addition to containing unique ecological communities, MCEs may also provide important ecosystem services including sites for fish spawning aggregations and also by acting as refugia for corals and associated species from environmental stress, such as warm-water bleaching events and severe tropical storms. With shallow-water coral reefs predicted to be strongly affected by climate change in coming decades, MCEs should be given greater attention by both scientists and managers.

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Chapter 1

Introduction

Mesophotic coral reef ecosystems, or MCEs, are tropical coral reef communities which occur in the intermediate depths of the photic zone. MCEs are characterised by the presence of light-dependent corals and associated communities and are typically found at depths ranging from 30 to 40 m and extending to over 150 m (Hinderstein et al. 2010). They have been recorded in many parts of the world, including both the tropical western Atlantic (Armstrong et al. 2006; Smith et al. 2010) and Indo-Pacific (Colin et al. 1986; Kahng and Kelley 2007; Bare et al. 2010; Bongaerts et al. 2011). The existence of reef corals at mesophotic depths has been known for some time; indeed, Darwin (1842) reported collecting corals as deep as 128 m (Kahng et al. 2010). Australia’s vast and iconic Great Barrier Reef (GBR) contains an extensive series of submerged reefs which occur along the outer-shelf and would be expected to be occupied by MCEs. Anecdotal evidence suggests that these deep reefs support communities of sessile benthic megafauna (e.g. Scoffin and Tudhope 1985; Hopley et al. 2007), however, to date no systematic investigation of their ecology has been conducted. Therefore, this study aims to verify the existence of MCEs in such habitats along the GBR shelf-edge, and to characterise some of the biological and environmental variability among them. This chapter first provides a brief review of the history of the study of MCEs and their key biological characteristics and environmental drivers. Then it describes the potential habitats for MCEs on the GBR and, finally, it presents the specific aims of the present study to advance knowledge of this poorly known ecosystem.

Review of studies of MCEs

The earliest observations of MCEs were largely conducted using manned submersibles and focused primarily in the Caribbean (Fricke and Meischner 1985, Reed 1985; Ohlhorst and Liddell 1988; Macintyre et al. 1991), although some studies also occurred in the Indo-Pacific. Vertical zonation of benthic communities through the mesophotic zone to over 200 m depth was examined at Enewetak Atoll in the Marshall Islands (Colin 1986; Colin et al. 1986), Johnston Atoll, 1400 km west of the Hawaiian Islands (Maragos and Jokiel 1986), and also in the Red Sea (Fricke and Knauer 1986). All these studies reported diverse assemblages of benthic megafauna including scleractinian corals, octocorals and sponges. More recently, studies of MCEs using remotely sensed imaging techniques have been conducted in several locations in the Pacific including the Hawaiian Islands (Kahng and Kelley 2007; Rooney et al. 2010), American Samoa (Bare et al. 2010), and the western Coral Sea (Bongaerts et al. 2011). These studies have increased the scientific understanding of both the biodiversity of Indo-Pacific MCEs and the physical processes governing their community structure.

In the Caribbean, MCE coral assemblages appear to be quite similar between locations (Kahng et al. 2010). However, to date no such patterns have emerged from studies of MCEs in the Indo-Pacific, which contains ~75% of the world’s coral reefs and the vast majority of its marine biodiversity. Hard coral diversity in the Indo-Pacific is an order of magnitude greater than in the Caribbean (Veron 1995, 2000), and therefore it is expected that Indo-Pacific MCEs would contain significantly greater diversity than their Caribbean counterparts. An overview of studies conducted on Indo-Pacific MCEs are presented in Kahng et al. (2010). Although the authors do note some similarities between locations (e.g. the abundance of *Leptoseris* in the lower photic zone), they conclude that few generalisations can be made regarding community structure and distribution of Indo-Pacific MCEs. Detailed examination of MCEs in the Great Barrier Reef

(GBR), one of the world's largest coral reef ecosystems, would therefore provide valuable information on the ecology of Indo-Pacific MCEs.

The vast majority of research conducted on coral reefs has focused on shallow habitats <30 m deep. This is primarily due to the limitations imposed by traditional SCUBA diving technology, which has been the principal method used for surveying coral reefs. Similarly, research projects with sufficient funding to utilise technology such as submersibles have tended to explore the ocean depths, often venturing several kilometres beneath the surface (e.g. Le Pichon et al. 1987; Pautot et al. 1987; Desbruyeres et al. 2001). As a consequence, the intermediate depths between the easily-accessible surface waters and the deep ocean have remained largely unstudied. However, recent advances in SCUBA technology (e.g. closed-circuit rebreathers) and robotics, such as Remotely Operated Vehicles (ROVs) and Autonomous Underwater Vehicles (AUVs), combined with more widespread use of high-resolution multibeam mapping, have allowed scientists unprecedented access to these intermediate depths. Consequently, the last few years have seen an increased interest in MCEs from both scientists and managers due to an increasing awareness of both their unique ecological character and biodiversity (e.g. Pyle et al. 2008), and also for their potential importance as refugia for shallow-water coral reef species from environmental stresses, such as rising sea surface temperatures (Glynn 1996; Riegl and Piller 2003; Bongaerts et al. 2010). However, despite the potential importance of MCEs to the overall function of coral reef ecosystems, many aspects of MCE ecology remain unknown.

Physical controls on coral reef communities

Coral reef ecosystems contain greater biodiversity than any other marine ecosystem (Carpenter et al. 2008). Globally, the epicentre of coral reef diversity lies in the Indo-Australian Archipelago, a region often referred to as the Coral Triangle (Veron 2000; Bellwood et al. 2005). Diversity of hard corals decreases eastwards across the Pacific and westwards across the Indian Oceans, and also with latitude away from the equator (Veron 1995, 2000; Done 2011a). This has been attributed to a variety of factors including ocean circulation patterns over the last five million years (Veron 1995), mean annual ocean temperatures and energy availability (Fraser and Currie 1996), oceanic gyres in the Indian and Pacific Oceans (Connolly et al. 2003), geometric constraints on range locations (called the “mid-domain effect”, Bellwood et al. 2005) and the abundance and variety of reef habitats in the Indo-Australian Archipelago (Bellwood et al. 2005; Done 2011a). Although the GBR is located slightly to the south-east of the centre of diversity it is nonetheless a highly diverse ecosystem, supporting over 400 species of hard corals (Veron 2000). This is significantly higher than other regions (e.g. Hawaii) where MCEs have been studied in any detail. Therefore, it is quite likely that the unexplored mesophotic reefs of the GBR contain significantly higher diversity than other Indo-Pacific areas reported so far.

At local to regional scales, diversity and composition of reef communities varies significantly both within and between reefs in a coral reef ecosystem in response to a combination of physical controls and biological interactions (Done 1982; 1983; Dinesen 1982; Huston 1985; Wilkinson and Cheshire 1989; Cornell and Karlson 2000; DeVantier et al. 2006; Fabricius and De’ath 2008; Done 2011b). Water movement (including both waves and currents) and light irradiance have been recognised as the most important physical factors in determining the distribution of macrobenthos, although ecological interactions such as competition are also significant (Done 1983; Huston 1985).

Water movement

A large number of studies have examined the dynamics of wind-driven waves on coral reefs (summarised in Monismith 2007), with wave energy a significant component of reef zonation and coral community models for some time (Rosen 1975; Geister 1977; Pichon 1978; Dollar 1982; Done 1982). Although reef location and morphology cause some variation, the basic model shows surface-driven waves breaking on the reef crest and pushing water onto a reef flat and then into a lagoon (if there is one). Wave energy therefore dissipates with distance from the reef crest (both horizontally across the reef flat and also with depth). This results in a variety of microhabitats, evident in the clear zonation of dominant benthic species and growth forms. This zonation has been particularly well studied for corals (Huston 1985). For example, corals growing on reef crests are able to withstand high wave energy by being either compact and/or robust, aligned to minimise breaking forces, or by having other morphological traits to minimise drag. Although different coral species often exhibit different skeletal growth morphologies, some species also exhibit high phenotypic plasticity resulting in genetically similar or even identical colonies being able to adopt specific morphologies suited to a wide variety of coral reef environments (Todd 2008).

Comparatively little information is available on the influence of currents (other than those derived by surface-driven waves) on coral reef community composition. Fabricius and De'ath (2008) do note that the occurrence of heterotrophic octocorals on shallow-water reefs in the GBR is strongly correlated to current flow. In some locations, currents resulting from internal waves have been identified transporting cold, nutrient-rich water onto adjacent reefs, and likely affect the structure and composition of benthic communities (e.g. Leichter et al. 1996; Leichter et al. 2003). In Palau, daily temperature fluctuations up to 20 ˚C caused by internal waves are responsible for depauperate biological communities at mesophotic depths (Wolanski et al. 2004), while in the GBR internal waves have been identified as causing strong currents in the mesophotic zone near Myrmidon Reef (Wolanski and Pickard 1983), and vast meadows of the green calcareous algae *Halimeda to* depths of 96 m (Drew and Abel 1988). Because MCEs occur below the influence of high wave energy, currents may play a much more important role than wind-derived waves in determining the structure and composition of their benthic communities. This represents a significant difference between MCEs and shallow-water reefs, particularly on the GBR where the shallower community structure is strongly influenced by both fair weather wave-climate and periodic cyclones (Done 1983, 1992, 2011; Massel and Done 1993; Madin and Connolly 2006).

Light

Tropical reef-building corals all contain endosymbiotic dinoflagellates (zooxanthellae) that translocate fixed carbon produced by photosynthesis to the coral animal cells and enable coral reefs to survive in oligotrophic tropical waters (Chalker et al. 1983). However, zooxanthellate corals exist in a wide variety of reef environments in which light levels span over two orders of magnitude from ~0.5 to ~100% of surface intensity (Dubinksy and Falkowski 2011). Light required for photosynthesis (Photosynthetically Active Radiation; PAR) is in the spectral range of 400-700 nm, and mesophotic corals must adapt to both low overall light irradiance and also a much narrower light spectrum (~475 nm), with ultraviolet/blue and red wavelengths exhibiting the greatest decreases with increasing depth (Fricke et al. 1987; Mass et al. 2007; Lesser et al. 2009). Although most species are restricted to depths of <60 m, zooxanthellate corals have been reliably documented occurring as deep as 165 m (Maragos and Jokiel 1986) and therefore have clearly evolved methods of surviving in low-light habitats. Different coral species appear to adapt to low light in different ways, including both physiological and morphological photoadaptation (altering their structure and function in response to the characteristics of the light environment) and an increased reliance on heterotrophy. Photoadaptation has been observed in both the coral host and zooxanthellae (Kaiser et al. 1993).

Photoadaptation is known to occur in several species of zooxanthellate corals. The most abundant and widespread corals on mesophotic reefs in the Indo-Pacific belong to the genus *Leptoseris*, which are often observed growing at over 100 m depth (Kahng et al. 2010). Clearly, *Leptoseris* spp. have developed effective methods of dealing with the low ambient light. Somewhat surprisingly, colonies of *Leptoseris fragilis* occurring in deep waters of the Red Sea were found to have much lower zooxanthellae density than that reported for a range of species occurring in shallower water. Zooxanthellae density was further reduced by transplanting corals to even deeper water (from 116-160 m) (Kaiser et al. 1993). Schlicter and Fricke (1991) suggest that fluorescent proteins may enable *L. fragilis* to transform low wavelength light into longer wavelengths, however, Kahng et al. (2010) indicate that this is unlikely.

All members of the genus *Leptoseris* are generally most abundant in low-light environments, however, other coral species observed on MCEs also occur in a wide variety of other reef habitats including shallow areas with high ambient light. For example, *Stylophora pistillata* is common in a wide range of reef environments (Veron 2000), and shows both physiological and morphological variation across its bathymetric range of 0-70 m (Mass et al. 2007). Deep-water colonies contain increased photosynthetic pigments, rather than increased density of zooxanthellae (Falkowski and Dubinsky 1981; Mass et al. 2010). Stambler and Dubinsky (2005) reported similar increases in cellular chlorophyll concentrations in five common zooxanthellate coral taxa (*Acropora*, *Stylophora*, *Pocillopora*, *Favia*, and *Fungia* sp.) in low-light conditions. Corals occurring in low-light environments are generally more photosynthetically efficient than their shallow-water counterparts and reach their maximum rate of photosynthesis at lower irradiance levels (Chalker et al. 1983). Some coral species also show morphological adaptation to low light, including adopting flattened morphologies to maximise light capture (Jaubert 1977; Wallace 1978, Kuhlmann 1983; Anthony et al. 2005; Stambler and Dubinksy 2005). Most coral species possess the ability to feed heterotrophically on organisms ranging from bacteria to mesozooplankton (Houlbreque and Ferrier-Pages 2009), and this may play an important role in maintaining energy requirements in light-limited environments (Anthony and Fabricius 2000; Mass et al. 2007; Ferrier-Pages et al. 2011).

Light irradiance is also an important control on the distribution of other reef-associated taxa on the GBR, including octocorals and sponges. Fabricius and De'ath (2008) found a correlation between light irradiance and the range size and generic richness of both phototrophic and heterotrophic octocoral taxa. In general, phototrophic octocorals are most abundant at intermediate light levels. In contrast, suspension-feeding heterotrophic taxa are most common in low-light habitats with strong currents (Fabricius and De'ath 2008). Similar correlations have been demonstrated for hard corals (DeVantier et al. 2006) and phototrophic sponges (Wilkinson and Evans 1989), illustrating the importance of light irradiance to a range of unrelated benthic megafaunal taxa, and particularly those which contain both phototrophic and heterotrophic species (Fabricius and De'ath 2008).

Light irradiance on coral reefs is also affected by the amount of nutrients and suspended particles in the water column. In general, reef habitats with high rates of sedimentation contain lower coral cover (Fabricius 2005). On inshore reefs, terrestrial runoff not only reduces water clarity but also increases nutrient levels to the point where macroalgae may out-compete corals for available space (Fabricius 2005). Both eutrophication and downwelling of sediments would contribute to light limitation characteristic of some MCEs causing an upward shift in the distribution of phototrophic taxa, and in principle to the advantage to filter-feeding heterotrophs. Those mesophotic corals that exhibit two-dimensional plating or encrusting growth forms are highly susceptible to sedimentation in the absence of cleaning currents. High sedimentation may also limit the abundance of heterotrophic taxa, just as it does phototrophs, by restricting the ability of larvae to settle on sediment-covered reefs. For these reasons, the specific local sedimentation regime (grainsize and rates of settlement, accumulation and removal of sediments) is a key environmental driver of MCE presence and characteristics (Kahng et al. 2010).

Ecological controls on coral reef communities

Ecological interactions also play an important role in determining community structure and composition on coral reefs (Done 1983; Cornell and Karlson 2000). For many years, interspecific competition was presumed to be the principal driving factor of coral reef species richness (reviewed in Karlson and Cornell 1998). Biodiversity within habitats was assumed to be maintained near equilibrium, with high biodiversity being due to partitioning of a large number of microhabitats. Subsequently, non-equilibrium hypotheses (e.g. the Intermediate Disturbance Hypothesis, Connell 1978) have been put forward and argue that high biodiversity is maintained because the frequency of natural disturbances (e.g. cyclones) is greater than the rate of recovery. Under this hypothesis, coral communities are all works in progress – outcomes of inter-specific variation in response to a variety of biological and environmental drivers, such as competition (both among corals and between corals and other sessile benthos) or resistance to damage from storms (Done 2011b). The intermediate disturbance hypothesis posits that maximum diversity is reached at intermediate frequency and intensity of disturbance; areas of high disturbance are populated by fast-maturing taxa, while a lack of disturbance leads to domination by the most effective competitors. This is supported by long-term field observations such as by Wakeford et al. (2007), who conducted a long-term (23-year) study at Lizard Island in the northern GBR. They found that short intervals between disturbances led to a reduction in dominant hard coral groups and an increase in slow-growing but resilient soft corals, while long intervals led to monopolisation by the fast-growing plating hard coral *Acropora hyacinthus*.

Under the intermediate disturbance hypothesis, coral diversity is generally assumed to be highest at intermediate depths (Cornell and Karlson 2000), with shallower areas subjected to more frequent disturbance and light becoming limiting in deeper habitats. However, studies of depth zonation and community ecology on mesophotic reefs (e.g. Liddell and Avery 2000) have suggested a complex interplay of biotic and abiotic factors which may be inconsistent with the intermediate disturbance hypothesis (Kahng et al. 2010). Mesophotic reefs receive less energy input than their shallow-water counterparts, however, they are generally subject to less frequent disturbance events. This may lead to fast-growing species being unable to monopolise space as they do in undisturbed shallow-water habitats, and contribute to high diversity in deeper reef habitats (Rogers 1993; Avery and Liddell 1997).

Study area - Great Barrier Reef

Regional geomorphology

The Great Barrier Reef (GBR) extends along the continental shelf of north-eastern Australia for ~2600 km, covering 16° of latitude (Wolanski 1994). The Great Barrier Reef Marine World Heritage Area (GBRWHA) is the world's largest world heritage area, covering an area of 348 000 km^2 (Figure 1.1). The vast majority of scientific research on the GBR has focused on shallow-water coral reef habitats, although these account for only 7% of the area of the GBRWHA. The outer-shelf of the GBR contains an extensive series of submerged shelf-edge reefs (Hopley et al. 2007), which provides potential habitat for one of the largest mesophotic reef systems in the world. At present, many of these reefs are not classified as reef habitat by the Great Barrier Reef Marine Park Authority (GBRMPA), and their ecology remains virtually unknown.

The morphology of the GBR shelf changes significantly with latitude, being narrower and steeper in the north than in the south. This, in turn, affects the morphology of the reefs which occur on the outer-shelf, particularly those occurring in 50-100 m water depth (Hopley 2006). Six distinct modes of reef growth have been identified along the length of the GBR. The northernmost 800 km of the GBR is occupied by deltaic reefs (at the northern extremity) and ribbon reefs. Both these reef types occur on the shelf-edge and exhibit a steeply sloping drop-off on their eastern side. Further to the south, reefs are generally set back from the shelf-edge and this has allowed the development of submerged reefs on the shoulder of continental shelf.

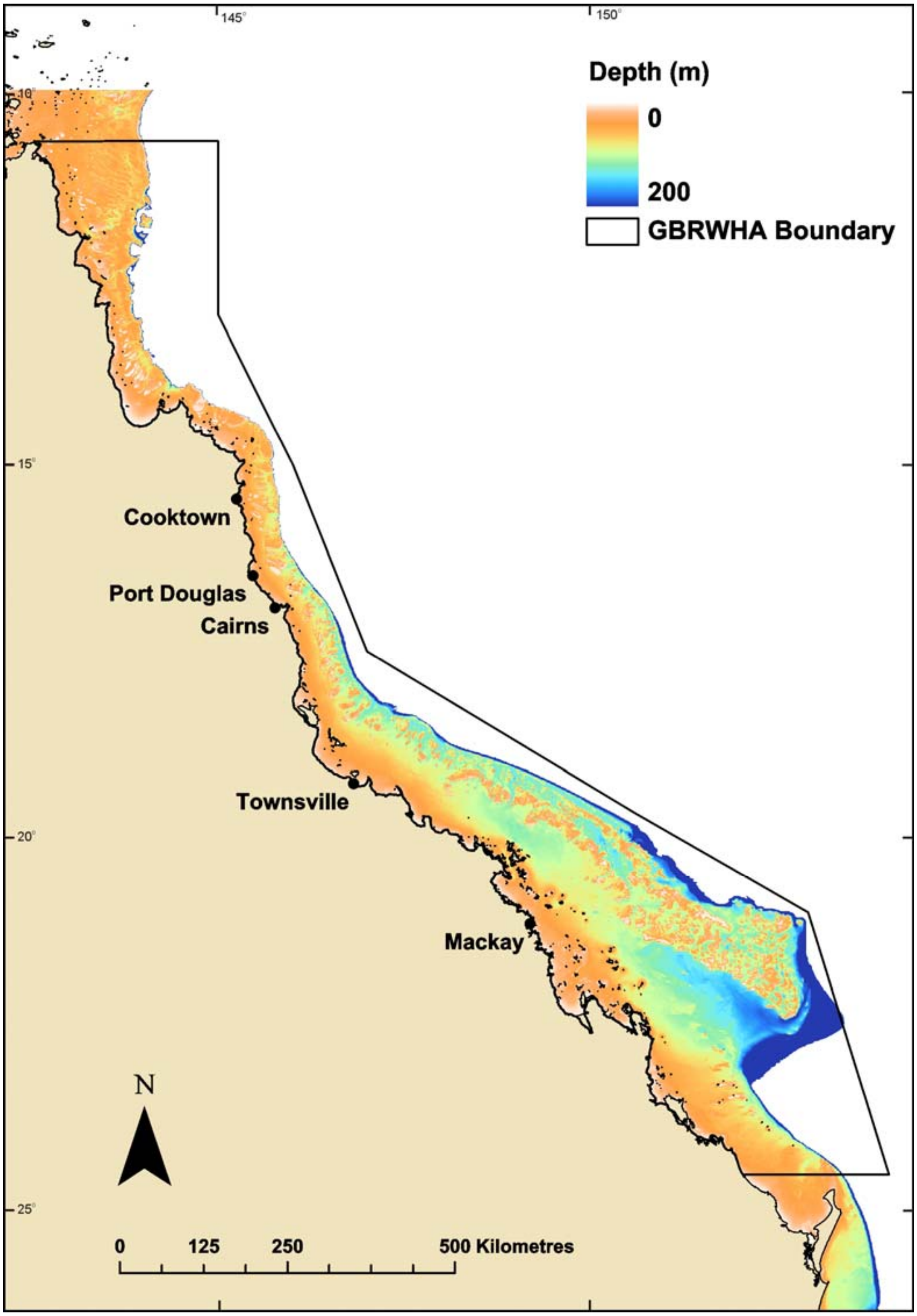

Figure 1.1: Map showing geomorphology of the Great Barrier Reef World Heritage Area to the 200 m depth contour.

Distribution and geomorphology of the submerged reefs

Submerged reefs (often referred to as “shoals”) coming close to the sea surface were first identified off Cairns by the Naval Surgeon Lieutenant WEJ Paradice in the 1920s (Hopley et al. 2007). Several of these shoals have been recorded in nautical charts, and some have been named (e.g. Marilyn Shoal and Blossom Bank in the central GBR). Deeper submerged linear shelf-edge reefs, with their bases in ~73 m water depth, were recorded by Hopley (1982) using echo-sounding profiles. In 1984, dives were conducted to over 200 m depth using the manned submersible *Platypus* on the front of Ribbon Reef No. 5 (described in Beaman et al. 2008) and Myrmidon Reef (Hopley et al. 2007). Despite the steeply sloping shelf-edge at Ribbon Reef No. 5, the submersible observed a submerged reef lying parallel to the shelf break in 45-50 m water depth. The shelf break occurs at approximately 70 m, and below this depth a vertical wall inhibited the development of any further reefs. Myrmidon Reef occurs on a more gently sloping shelf margin in the central GBR, and is the only emergent reef in this area located right on the shelf-edge (Hopley et al. 2007).

The first quantitative study of submerged shelf-edge reefs of the central GBR was conducted by Harris and Davies (1989). They identified a series of reefs between 15˚45’S and 21˚00’S off Cairns, Townsville and Hydrographers Passage. Hopley (2006) showed these features occur almost continuously for over 900 km along the central GBR margin, and they have been mapped as far south as the Swain Reefs (Tilbrook and Matear 2008). Most research conducted on these features has focused on their geomorphology (Harris and Davies 1989; Hopley 2006; Beaman et al. 2008; Webster et al. 2008; Abbey and Webster 2011), with little attention paid to the living benthos. However, the 1984 submersible observations indicated that these submerged reefs were occupied by diverse mesophotic coral reef communities. Although no living stony coral was reported as growing on the 50 m reef at Ribbon Reef No. 5, the reef was “densely covered in gorgonians, sea whips, ascidians, encrusting sponges and in places, luxuriant yellow soft corals” (Beaman et al. 2008). In contrast, Myrmidon Reef exhibited 100% cover of living scleractinian corals (*Leptoseris*, *Pachyseris* and *Endophyllia* spp.) from 60-80 m depth, and living coral growth to over 100 m (Hopley et al. 2007). More recently, Pitcher et al. (2007) examined biodiversity of inter-reefal seabed habitats within the GBRMP. Although some “shoals” were recognised in the study, little data were collected from the outer-shelf below 50 m depth. Consequently, the mesophotic communities associated with the submerged reefs of the GBR have remained virtually unknown.

Physical oceanography of the GBR outer-shelf

The physical properties of water in the GBR system, such as temperature, salinity, optical water quality and water column productivity vary considerably in space and time. Although there are some general latitudinal gradients (mean annual sea surface temperatures in the northern GBR are, on average, ~3 ˚C warmer than in the south), water properties exhibit greater variation across-shelf between coastal waters influenced by terrigenous sediments and the oceanic waters of the Coral Sea (Wolanski 1994). These variations are mirrored by changes in the ecology of coral reefs, which show significant across-shelf variation in a variety of taxa, including hard corals (Done 1982) and octocorals (Dinesen 1982; Fabricius and De’ath 2008). These patterns are generally explained by variations in physical variables such as wave energy and turbidity (hard corals and phototrophic octocorals) and water column productivity and current flow (heterotrophic octocorals). Because the submerged reefs are located far offshore on the shoulder of the continental shelf they are largely outside the influence of many of these factors identified as important determinants of community structure on shallow-water reefs in the GBR, and are predominantly influenced by the water from the Coral Sea.

The top 100 m of the Coral Sea is generally relatively homogeneous in salinity and temperature, although water column stratification may exist in summer during periods of low wind, and the mixed layer depth is much larger than the water depth over the continental shelf (Wolanski 1994). The South Equatorial Current flows westward across the Coral Sea to the GBR shelf, and bifurcates upon reaching the eastern Australian margin between 14˚S and 18˚S (Figure 1.2). The northward-flowing branch forms the Hiri Current, while the southward-flowing branch forms the East Australian Current (EAC). Fluctuations in the speed of the EAC on the continental slope, interpreted as internal waves, can cause variations in temperature and salinity along the GBR margin (Wolanski 1994; Brinkman et al. 2002). These waves result in episodic delivery of cold,

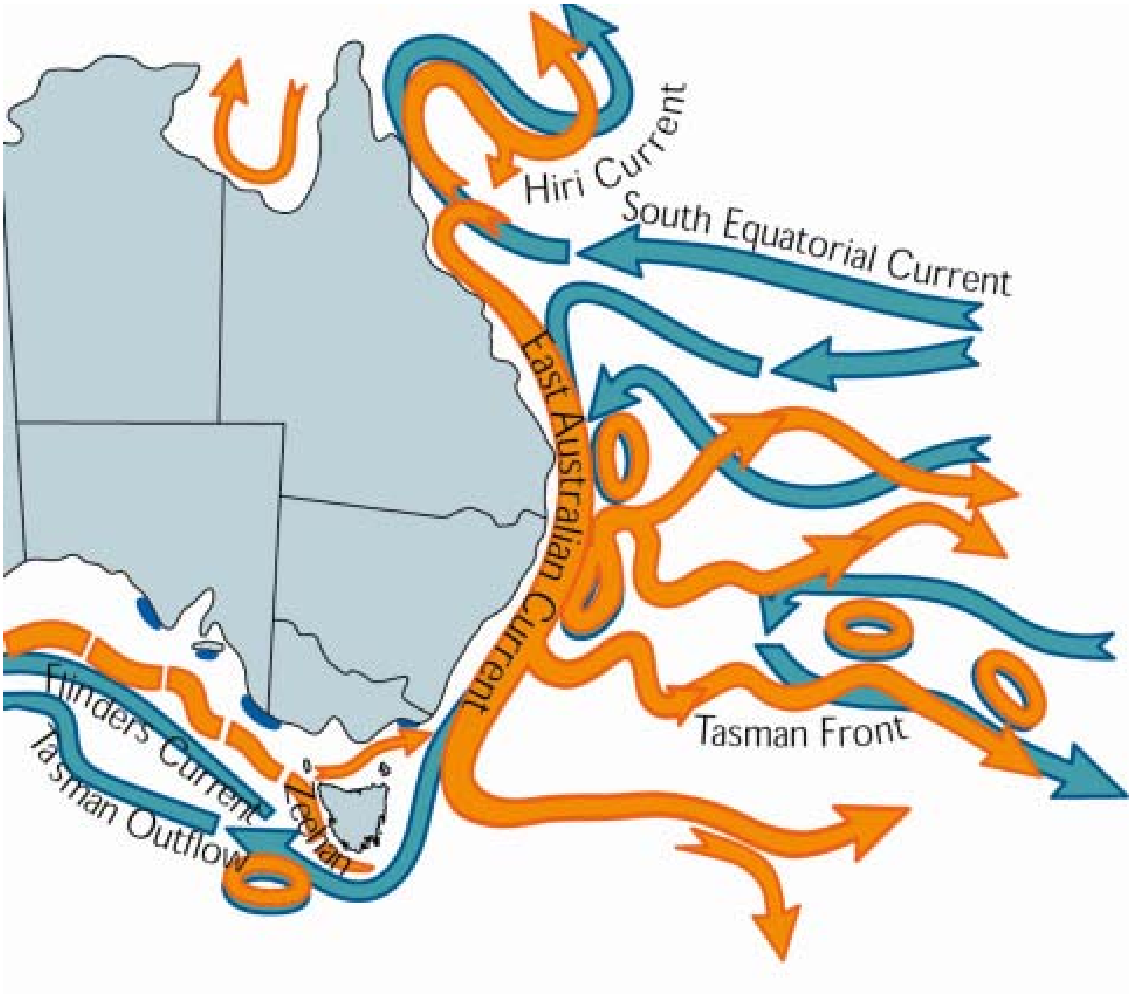

Figure 1.2: Ocean currents in the south-west Pacific and Coral Sea (from Ridgway and Hill 2009). Surface currents are shown in orange and subsurface currents in blue.

nutrient-rich waters onto the continental shelf; such waves have the potential to play an important role in the ecology of the GBR MCEs.

Study sites

This thesis focuses on four sites occurring along the GBR outer-shelf: Ribbon Reefs, Noggin Pass, Viper Reef and Hydrographers Passage (Figure 1.3). The sites span ~5° of latitude and 800 km of the GBR shelf-edge, ranging from the steeply sloping shelf-edge off the Ribbon Reefs (Figure 1.4a) to the gently sloping shelf at Hydrographers Passage in the central GBR (Fig 1.4b). Figure 1.4 clearly shows the effect of the shelf morphology on the development of shelf-edge reefs. The steep slopes in the north preclude reef development below 70 m depth (Fig 1.4a), while the more gently sloping seafloor in the south has allowed a series of parallel reefs to develop.

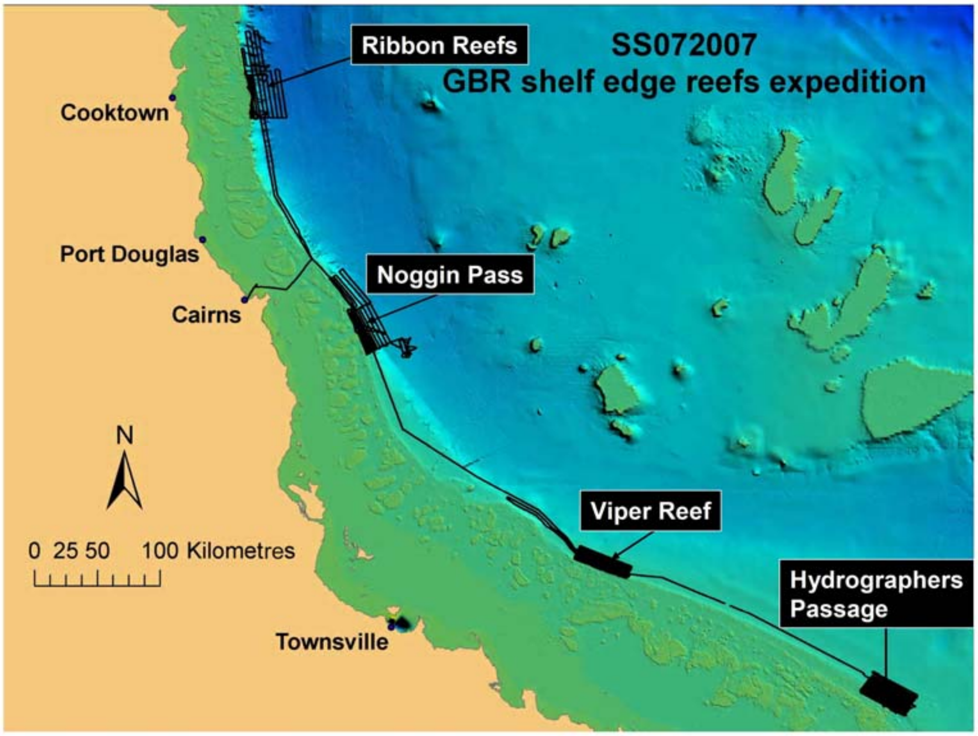

Figure 1.3: Location of study sites examined during the 2007 expedition to the GBR shelf-edge. Black line indicates the track of the RV *Southern Surveyor* during the expedition.

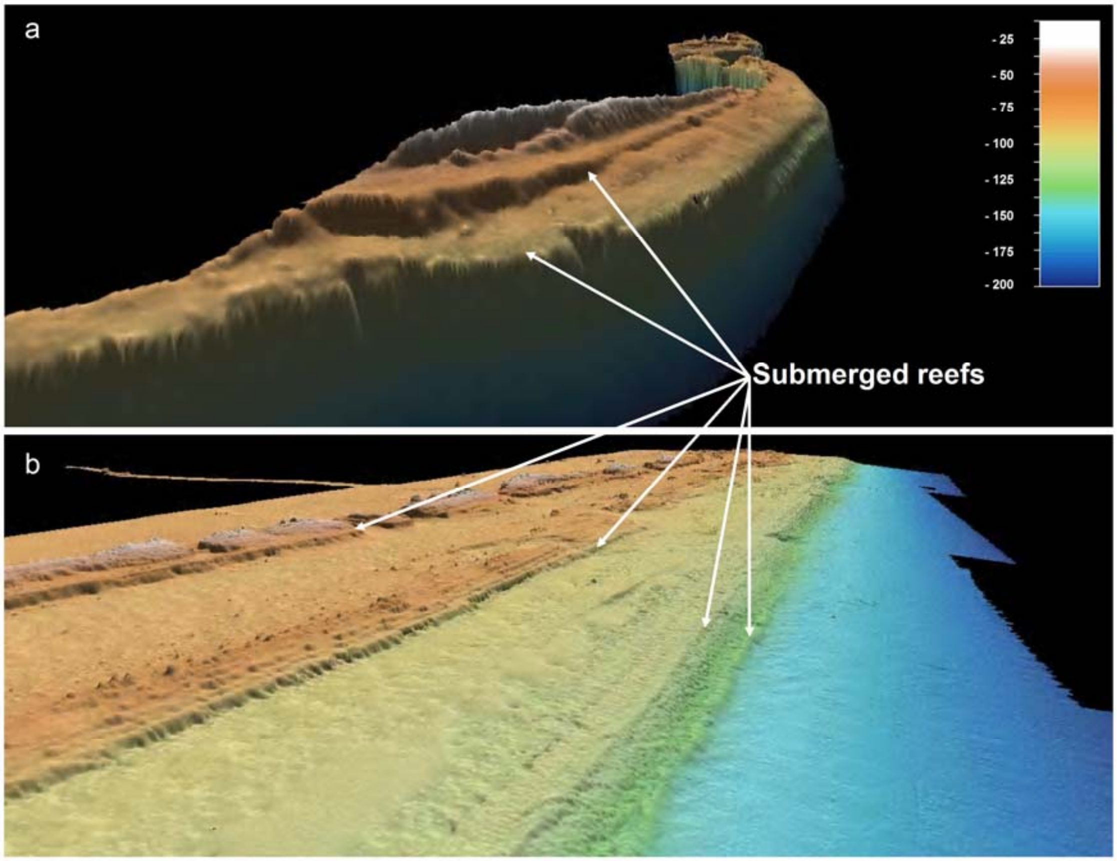

Figure 1.4: Bathymetric images of submerged reefs on the GBR shelf-edge at (a) Ribbon Reef No. 3 and (b) Hydrographers Passage.

Methods and data collection

Collecting specimens by dredge sampling has traditionally been the most common method of obtaining specimens from mesophotic reefs (e.g. Wells 1954), however, the rapid increase in Marine Protected Areas (MPAs) in recent years (e.g. Edgar et al. 2007) has restricted the use of extractive sampling techniques in many locations, including the GBR. Recent technological advances have allowed scientists unprecedented access to MCEs and other ecosystems occurring below the depths accessible by traditional SCUBA. New SCUBA technology such as closed-circuit rebreathers and trimix gases have been used to study MCEs in many parts of the world (Parrish and Pyle 2002; Mass et al. 2007; Pyle et al. 2008), however, Queensland and Australian scientific diving legislation does not currently allow the use of this technology. Remotely sensed optical imagery collected by AUV and ROV are therefore the most effective means of collecting non-extractive data on MCEs, and have been utilised on several MCEs around the world (e.g. Armstrong et al. 2006; Kahng and Kelley 2007; Bare et al. 2010; Rooney et al. 2010; Williams et al. 2010).

Mapping seafloor habitat is the fundamental first step for assessment of benthic habitats (Kostylev et al. 2001). Multibeam swath mapping employs an array of acoustic transducers to form beams of sound pointing over an arc (or swath) under the survey vessel, allowing the measurement of bathymetry and backscatter amplitude along a wide section of the seafloor (Courtney and Shaw 2000). Running parallel lines along a section of seafloor so that adjacent lines overlap allows the generation of digital elevation models. The amplitude of the backscatter signal can also be used to estimate the composition of the seafloor (i.e. soft or hard substrate). Combining broad-scale multibeam bathymetric data with fine-scale observations and ground-truthing, such as ROV and AUV images, can be used to create detailed benthic habitat maps and models. An early example of this approach was employed by Kostylev et al. (2001), who combined multibeam data with seafloor photographs and seafloor sediment samples to create benthic habitat maps of the Scotian Shelf, Canada. Similar approaches have subsequently been used to assess other marine habitats (e.g. Beaman and Harris 2007; Pitcher et al. 2007; McGonigle et al. 2009), and provides an ideal framework for habitat mapping of MCEs on the GBR.

The 2007 RV *Southern Surveyor* expedition collected three primary datasets; multibeam swath bathymetry, AUV imagery, and physical specimens collected using a rock dredge. Multibeam swath data were collected using a ship-mounted Kongsberg™ Simrad EM-300 multibeam swath mapping system, which operated at a frequency of 30 kHz and emitted a fanned arc of 135 beams per ping. All data were post-processed within Caris™ HIPS/SIPS software to remove erroneous depth values and to apply appropriate corrections (e.g. tides), and then gridded into a BASE (Bathymetry Associated with Statistical Error) surface at grid resolutions of 5 x 5 m. The total area mapped during the expedition was 4186 km^2.

AUV data were collected using the AUV *Sirius* from the Australian Centre for Field Robotics at Sydney University. *Sirius* collects a variety of environmental data including stereo imagery, multibeam sonar, conductivity-temperature-depth (CTD), chlorophyll and turbidity (Williams et al. 2010). The vehicle possesses a Prosilica 12-bit 1360 x 1024 stereo camera, which was programmed to collect images at a rate of 2 hZ while travelling at a speed of 1 knot. Nine AUV missions were conducted across all four sites (one from the Ribbon Reefs, two from Noggin Pass, and three from each of Viper Reef and Hydrographers Passage) yielding a total of ~57 000 image pairs in depths ranging from 15-150 m. Because many sessile benthic megafauna can only be accurately identified using skeletal features, it was also necessary to collect physical specimens to examine post-cruise. Specimens were collected using a rock dredge at 23 locations (three from Ribbon Reefs, seven from Noggin Pass, eight from Viper Reef and five from Hydrographers Passage) in depths ranging from 48 to 163 m.

Science objectives and thesis aims

This thesis provides the first quantitative analysis of MCEs within the GBRWHA, using a combination of high-resolution multibeam swath mapping, benthic sampling and high-resolution optical imagery collected using Autonomous Underwater Vehicle (AUV). The specific aims of this study are:

1. To identify sessile benthic megafauna occurring in the mesophotic zone of the GBRWHA and compare community composition on MCEs to adjacent shallow-water reef habitats;

2. To identify how the composition of sessile benthic megafaunal communities change in response to variations in topography and

substrata along a depth gradient through the mesophotic zone from 50-150 m water depth;

3. To identify how the composition of sessile benthic megafaunal communities changes across a standardised depth (50-65 m) along the GBR margin and to identify geophysical variables responsible for those changes; and

4. To examine whether predictive modelling techniques can be used to accurately predict the distribution of suitable habitat for sessile benthic megafauna and to estimate extent of mesophotic coral reef habitat in the GBRWHA.

The results of this thesis will provide a first look at an extensive but virtually unknown ecosystem within the GBRWHA. It will also provide important information required to fill knowledge gaps on the ecology of mesophotic coral ecosystems in the Indo-Pacific.

Thesis structure

Chapter 1 outlines the aims and objectives of the thesis and places this study in the context of the general field of coral reef science. It provides a review of the current state of knowledge on the ecology of mesophotic reefs around the world, and outlines the current ideas on environmental factors controlling coral reef community ecology, such as light and water movement. It also provides an overview of the study site, the Great Barrier Reef World Heritage Area (GBRWHA).

Chapter 2 examines the diversity and distribution patterns of two dominant habitat-forming taxa of sessile benthic megafauna: Scleractinia (hard corals) and Octocorallia (soft corals and gorgonians). Specimens collected on the 2007 RV *Southern Surveyor* expedition were examined using detailed skeletal features to identify colonies to species level (Scleractinia) and generic level (Octocorallia). Patterns of diversity on mesophotic reefs were compared to patterns observed on shallow-water reefs in the GBR. This chapter is presented in the format of a scientific research paper and is currently in review in the international peer-reviewed journal *Coral Reefs*.

Chapter 3 examines changes in substrata and the composition of sessile benthic megafaunal communities along a depth gradient from 50-150 m water depth at Hydrographers Passage in the central GBR. It uses high-resolution optical images collected by AUV along a 3.6 km transect to identify distinct communities of sessile benthic megafauna, and uses environmental variables collected using multibeam bathymetric maps and by AUV to explain the distribution of those communities. This chapter is presented in the form of a scientific paper and has been published in the international peer-reviewed journal *Coral Reefs* (Bridge et al. 2011a).

In Chapter 4, data from four separate AUV surveys are used to compare the composition and structure of benthic communities at a standardised depth (50-65 m) along a 500 km section of the GBR shelf-edge. The composition of benthic communities varied considerably both within and between sites, although there were consistent patterns in the functional ecological groups of taxa occupying particular habitat types. Flatter reef tops were dominated by phototrophic taxa, whereas steeper walls were dominated by heterotrophic suspension-feeders. Environmental variables including slope, rugosity, depth, water column productivity and water clarity are used to explain the distribution of sessile benthic megafaunal communities. This chapter is also presented in the form of a research paper and has been published in the international peer-reviewed journal *Marine Ecology Progress Series* (Bridge et al. 2011b).

Chapter 5 uses GBR-scale bathymetry-derived variables to create predictive habitat models of potential habitat for mesophotic coral reef ecosystems in the GBRWHA. AUV data is used to record the occurrence of mesophotic reef taxa and communities, and maximum entropy modelling techniques are then used to predict their distribution throughout the GBRWHA. The model indicates that the GBRWHA contains extensive mesophotic coral reef habitat, but that the vast majority is currently undocumented. This chapter is also presented in the format of a scientific research paper and will be submitted to the international peer-reviewed journal *Global Ecology and Biogeography*.

Chapter 6 discusses the major findings of the study and their implications for mesophotic reef research and wider coral reef science. It also suggests future research directions that would provide further insight into mesophotic coral reefs in the GBRWHA, their connectivity to shallower reef habitats and their role in the overall function of the GBR ecosystem.

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Chapter 2

Identification of sessile benthic megafauna occurring in the mesophotic zone of the Great Barrier Reef World Heritage Area

Specimens of Scleractinia and Octocorallia collected using rock dredges on the 2007 RV *Southern Surveyor* expedition were identified using skeletal features to examine composition and diversity of mesophotic communities in the GBRWHA. The diversity and composition of these two taxa were then compared to adjacent, shallow-water coral reef habitats. The research presented in this chapter primarily addresses research aim 1, although the results obtained were fundamental for addressing the more detailed ecological questions in research aims 2, 3 and 4.

This chapter is presented in the form of a research paper and has been accepted in the international journal *Coral Reefs*. The paper has six co-authors and their contributions are as follows:

- Dr Katharina Fabricius assisted with the identification of octocoral specimens and provided editorial support
- Dr Pim Bongaerts, Dr Carden Wallace and Dr Paul Muir assisted with the identification of scleractinian specimens and provided editorial support
- Dr Terry Done provided editorial assistance and guidance on the interpretations and ideas discussed within the paper
- Dr Jody Webster provided funding for the RV Southern Surveyor expedition

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 are the most diverse coral-reef region on earth and are amongst the least documented. This study provides the first detailed investigation of the diversity of Scleractinia and Octocorallia of the mesophotic Great Barrier Reef. Specimens were collected by 100-m rock dredge tows at 48–163 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-four octocoral genera were collected, 22 of which represented azooxanthellate genera. Generic richness of octocorals was highest at depths >60 m. Thirteen of the 22 azooxanthellate genera were either absent or very rare at <18 m, and only four 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 ~32 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 Great Barrier Reef.

Keywords: mesophotic; diversity; Scleractinia; Octocorallia; Great Barrier Reef

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 which 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 investigation of MCEs in American Samoa (Bare et al. 2010), Hawaii

(Kahng and Kelley 2007; Rooney et al. 2010), the Coral Sea (Bongaerts et al. 2011) and the Great Barrier Reef (GBR) (Williams et al. 2010; Bridge et al. 2011a, 2011b). 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 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; Bridge et al. 2011b) 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 GBR 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 at four regions along a 750 km section of the GBR outer-shelf (~15-20˚S) during September-October 2007 (Figure 2.1). Specimens were collected using a standard rock dredge from 48-163 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 2.1). 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.

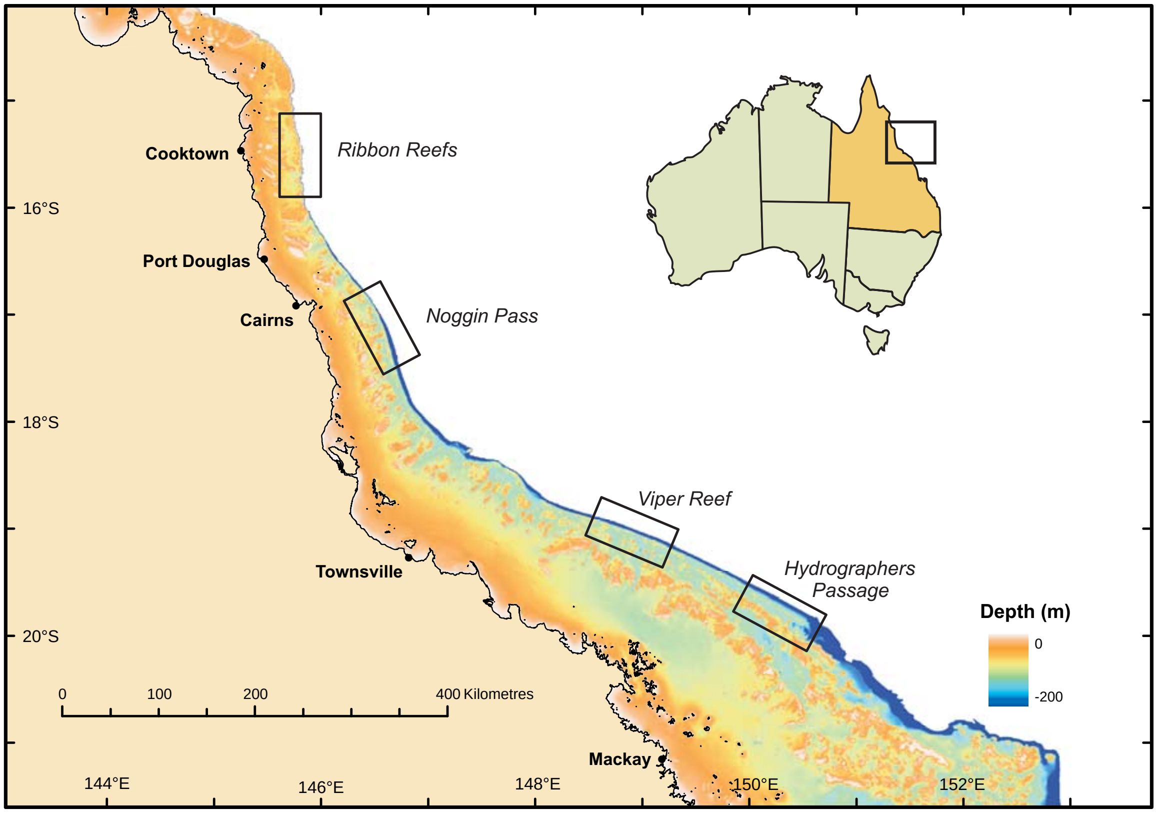

Figure 2.1: Location of study sites. White boxes indicate extent of area mapped during surveys. Dredge locations (Table 2.1) were chosen based on bathymetry.

Dredge No	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	5
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	8
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

Table 2.1: Location of dredge sites (sorted by depth for each site), and number of scleractinian and octocoral taxa retrieved.

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

$$\hat{S}_{Chao2} = S_{obs} + \frac{Q_1^{\,2}}{2Q_2}$$

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:

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

where m is the total number of samples.

Confidence limits were obtained using the equations:

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

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

where $T = \hat{S}_{Chao2} - S_{obs}$, and

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

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 variation between sites and depths.

Insight into bottom temperature at each site were 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 2010. Data were collected from 11 separate CTD casts (four from Hydrographers Passage from 3-6 March 2010, two from the Ribbon Reefs on 22 March, and five from Noggin Pass from 29-31 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 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 (Figure 2.2a). 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 18 of 23 dredges at depths ranging from 54 to 159 m (Table 3). Of the 24 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 21 genera were obligate heterotrophs (azooxanthellate) from 10 families. At least four of genera (*Heliania*, *Paracis*, *Callogorgia* and *Pteronisis*) represent the first records from the GBR.

Octocoral richness was 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 (Figure2.2b) estimated that total generic richness of octocorals on mesophotic reefs on the GBR is ~32 genera (95% confidence intervals: 26-57 genera).

Multidimensional scaling (Figure 3) indicated that the composition of dredge samples showed some relationship with depth when placed into three broad depth bins: <60 m, 60-120 m 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 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 BIOENV 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).

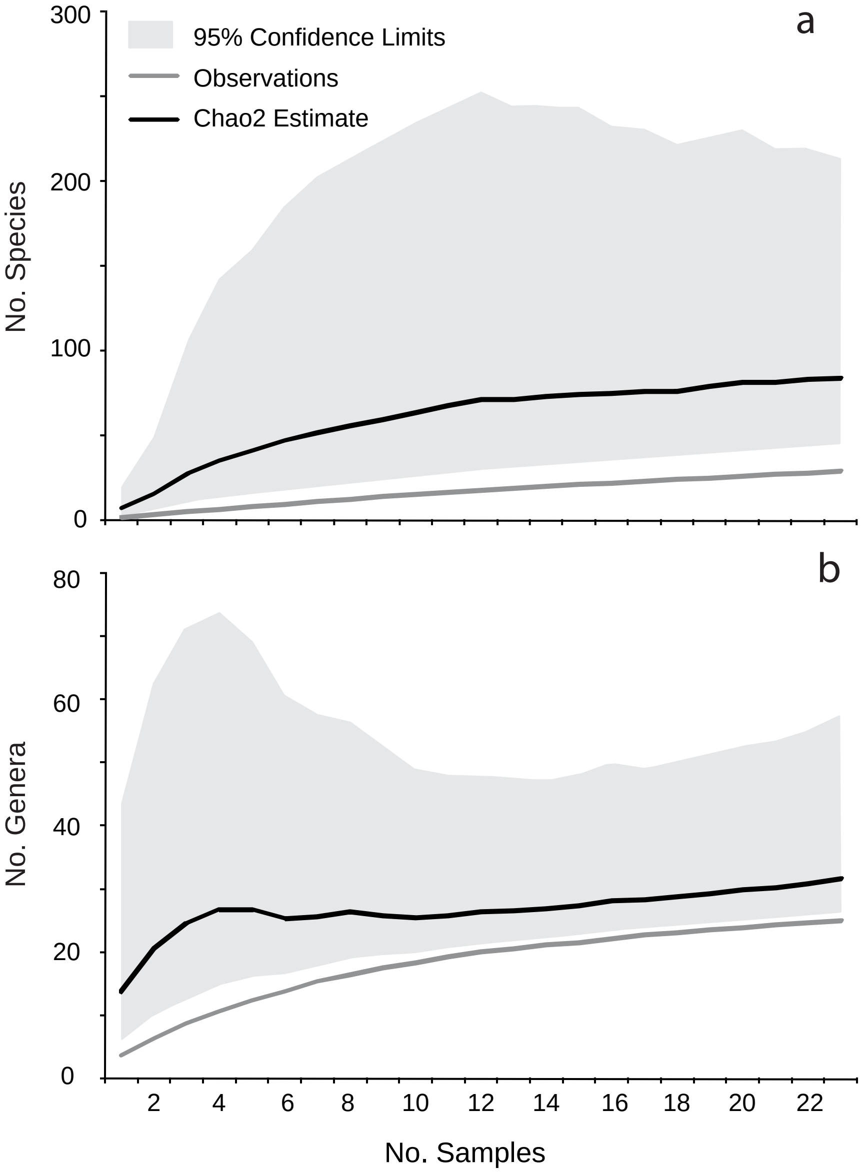

Figure 2.2: Species-area curves showing the observed number of species (observations, grey line) and the Chao 2 projection of total species richness (black line) for hard corals (a) and octocorals (b) across all 23 sites using 500 random iterations. Grey areas indicate 95% confidence limits.

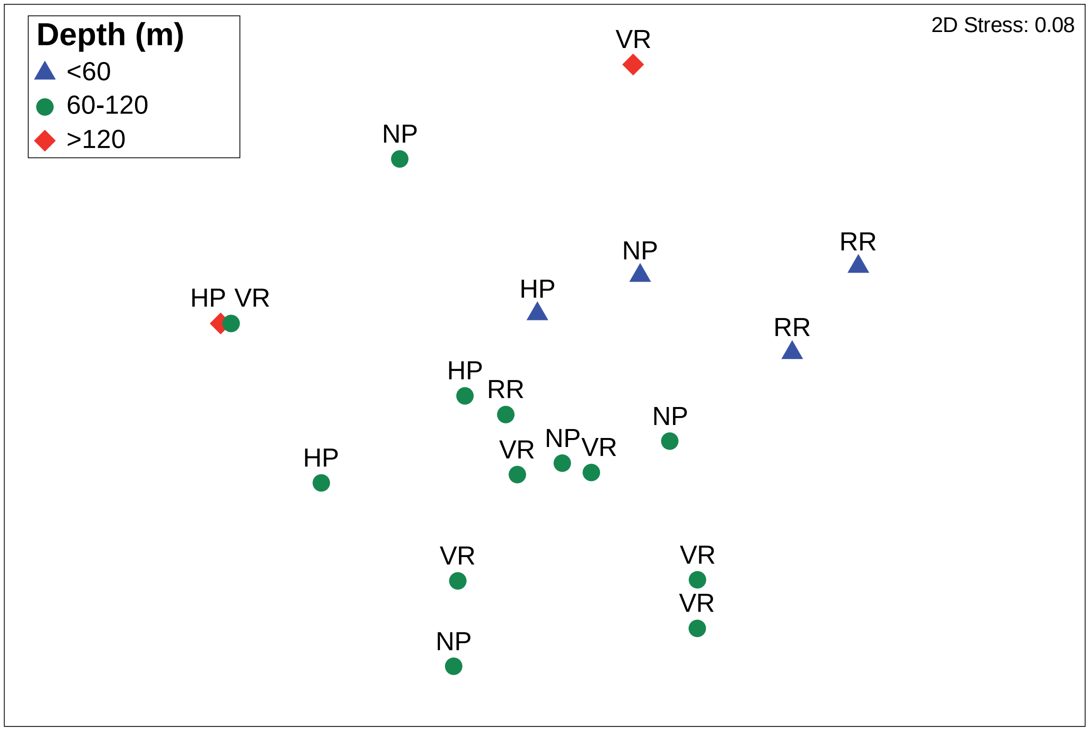

Figure 2.3: Multidimensional scaling plot based on the composition of hard corals and octocorals recovered in each dredge. Letters represent dredge location: RR – Ribbon Reefs, NP – Noggin Pass, VR – Viper Reef and HP – Hydrographers Passage. Blue triangles indicate dredges with mean depth <60 m deep, green circles 60-120 m, and red diamonds >120 m.

Family	**Identification**	**Depth range (m)**
Acroporidae	*Acropora cardenae*	55
Acroporidae	*Acropora elegans*	47-55
Acroporidae	*Acropora sp. 1*	55
Acroporidae	*Montipora foliosa*	47
Acroporidae	*Montipora millepora*	55
Acroporidae	*Montipora cf. tuberculosa*	55
Acroporidae	*Montipora sp. 1*	55
Agariciidae	*Leptoseris striata*	55-102
Agariciidae	*Leptoseris hawaiiensis*	60-102
Agariciidae	*Leptoseris papyracea*	55
Agariciidae	*Leptoseris scabra*	70-99
Agariciidae	*Pachyseris speciosa*	58-60
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*	55
Pocilloporidae	*Seriatopora hystrix*	55
Pocilloporidae	*Stylophora pistillata*	55
Poritidae	*Goniopora djboutiensis*	58
Poritidae	*Porites cf. lutea*	54
Poritidae	*Porites cf. myrmidonensis*	47-54
Siderasteridae	*Coscinarea wellsi*	58

Table 2.2: List of Scleractinia. Also indicated is the depth range recorded in this study.

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

Table 2.3: List of octocoral genera. A = azooxanthellate, Z = zooxanthellate genus. Also indicated is the depth range recorded in this study.

Discussion

This study demonstrates that mesophotic reefs in the Great Barrier Reef region contain diverse benthic megafaunal communities, including several taxa previously not recorded from the region. The data also suggests 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 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 was collected by CTD casts IODP Expedition 325 (Webster et al. 2011), and indicate a strong thermocline occurring at depths >60 m at Hydrographers Passage (Figure 4). This data only represents 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).

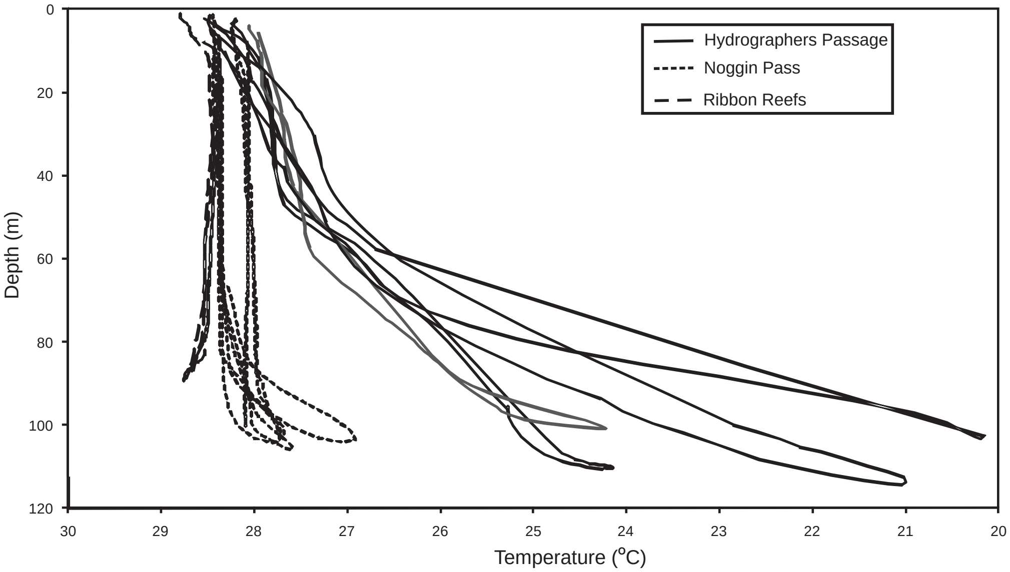

Figure 2.4: Temperature versus depth plots for three of the four sites sampled during the present study. Temperature data were collected on a separate expedition to the shelf-edge reefs in March 2010.

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 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 2.5 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.

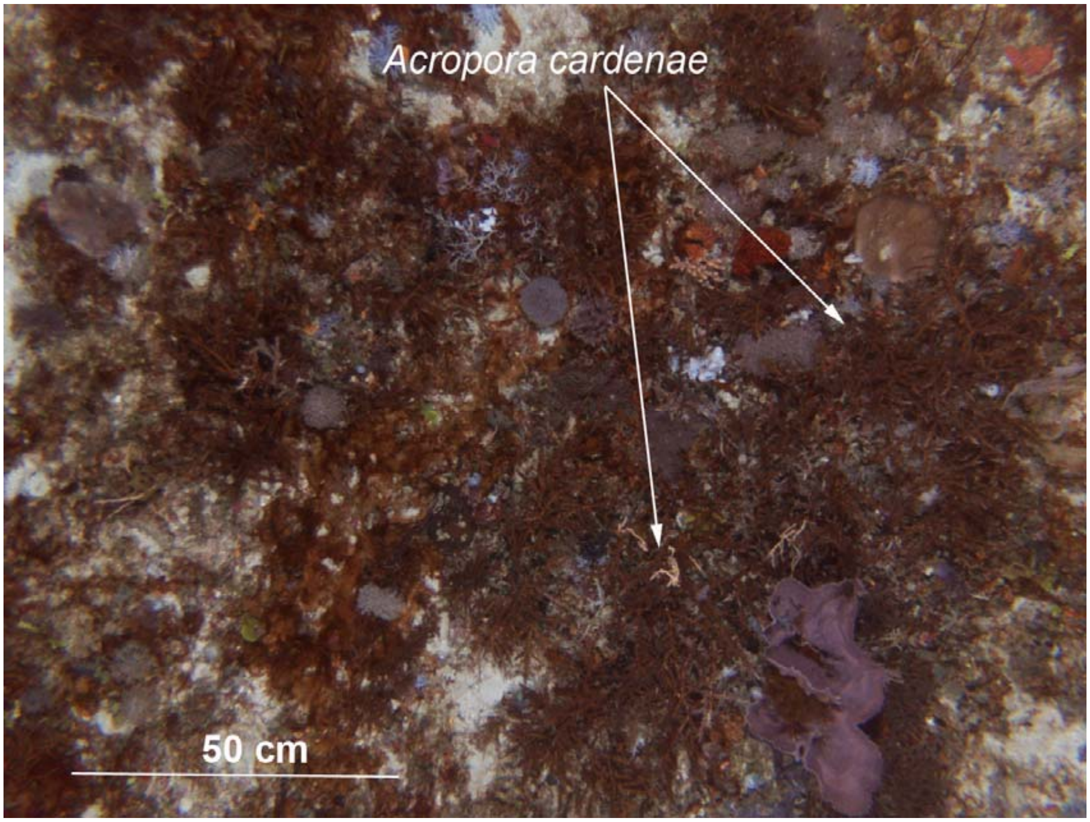

Figure 2.5: *In-situ* photograph of *Acropora cardenae* taken by autonomous underwater vehicle at a depth of ~50 m at Hydrographers Passage.

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; Rooney et al. 2010), 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 et al. 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 to 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 1257 shallow (≤18 m) transects, whereas it took only 23 dredges in this survey to yield 22 genera. Richness of heterotrophic octocorals on the shallow GBR is highly variable but generally low in most areas: only 11% of the 1257 shallow-water surveys recorded more than six genera of heterotrophic octocorals and 48% recorded none at all. In contrast, 26% of the deep dredges contained at least six heterotrophic octocoral genera, and only 22% 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 suggest 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., *Melithaeidae* and *Subergorgia*) were not recorded in this study. Seven genera (*Heliania*, *Keroeides*, *Muricella*, *Nicella*, *Paracis*, *Pteronisis* and *Callogorgia*) 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 1257 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 22 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 also found on shallow offshore reefs. These results suggest that the occurrence of heterotrophic octocorals in shallow waters 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 was not collected (Expedition 325 Scientists). Such strong currents promote suspension feeding and are associated with fast growth rates in heterotrophic octocorals (Fabricius et al. 1995a, 1995b), 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 which 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 provides a refuge for 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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Chapter 3

Changes in composition of sessile benthic megafaunal communities in response to variations in topography and substrata through the mesophotic zone

Images taken by AUV were used to characterise communities of sessile benthic megafauna along a depth gradient from 50-150 m at Hydrographers Passage. Sessile benthic megafauna identified communities were correlated to environmental variables depth, slope, aspect, rugosity and substrate type. The research presented in this chapter addresses research aims 1 and 2.

This chapter is presented in the form of a research paper and has been published in the international journal *Coral Reefs 30: 143- 153*. The paper has six co-authors and their contributions are as follows:

- Dr Terry Done provided editorial support and provided guidance on the interpretations and ideas discussed within the paper
- Dr Robin Beaman conducted the multibeam swath mapping on board the RV *Southern Surveyor*, and provided guidance on the processing of swath data and editorial support.
- Mr Ariel Friedman generated rugosity, slope and aspect grids on AUV stereo-images for the AUV transect and provided the explanation of the technique in the methods section.
- Dr Stefan Williams and Dr Oscar Pizarro collected the AUV data on board the RV *Southern Surveyor*.
- Dr Jody Webster provided funding for the RV *Southern Surveyor* expedition, and also provided editorial support.

Topography, substratum and sessile benthic megafaunal relationships on a tropical mesophotic shelf margin, central Great Barrier Reef, Australia

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Abstract

Habitats and ecological communities occurring in the mesophotic region of the central Great Barrier Reef (GBR), Australia, were investigated using Autonomous Underwater Vehicle (AUV) from 51 to 145 m depth. High-resolution multibeam bathymetry of the outer-shelf at Hydrographers Passage in the central GBR revealed drowned or submerged linear reefs with tops at 50, 55, 80, 90, 100 and 130 m separated by flat, sandy inter-reefal areas punctuated by limestone pinnacles. Cluster analysis of AUV images yielded five distinct image groups based on their sessile benthic megafauna, with rugosity and the presence of limestone reef identified as the most significant abiotic factors explaining the distribution of sessile benthic megafaunal communities. Reef-associated megafauna occurred in three distinct communities: (1) a shallow (<60 m) community dominated by photosynthetic taxa, notably scleractinian corals, zooxanthellate octocorals and photosynthetic sponges; (2) a transitional community (60 to 75 m) comprising both zooxanthellate taxa and azooxanthellate taxa (notably gorgonians and antipatharians); and (3) an entirely azooxanthellate community (>75 m). The effects of depth and microhabitat topography on irradiance most likely play a critical role in controlling vertical zonation on reef substrates. The lower depth limits of zooxanthellate corals are significantly shallower than that observed in many other mesophotic coral ecosystems. This may be a result of resuspension of sediments from the sand sheets by strong currents, and/or a consequence of cold water upwelling.

Keywords: mesophotic, community structure, vertical zonation, AUV, Great Barrier Reef.

Introduction

Mesophotic Coral Ecosystems (MCEs) are deep-fore-reef communities that generally occur from ~30 m to the bottom of the photic zone (Lesser et al. 2009; Kahng et al. 2010). They have been recorded in many locations throughout the tropics, including the Caribbean (e.g. Fricke and Meischner 1985), Enewetak (Colin 1986; Colin et al. 1986), Johnston Atoll (Maragos and Jokiel 1986), Hawaii (Grigg et al. 2002; Grigg 2006; Kahng and Kelley 2007), and the Red Sea (Fricke and Knauer 1986). Despite the low ambient light of the environment, MCEs generally contain zooxanthellate corals (e.g. Grigg 2006; Lesser et al. 2009; Kahng et al. 2010). Due to logistical and technological restrictions, information on both biotic and abiotic aspects of MCEs remains extremely scarce, particularly when compared with shallow-water coral reefs. Their nature is only beginning to be revealed through recent advances in SCUBA technology (closed-circuit rebreathers, mixed gases), robotics (Autonomous Underwater Vehicles and Remotely Operated Vehicles), and high-resolution multibeam bathymetric mapping. Recent studies of Indo-Pacific MCEs from Hawaii (Kahng and Kelley 2007; Rooney et al. 2010) and American Samoa (Bare et al. 2010) using remotely operated vehicles (ROVs) show that MCEs provide important habitat for a large variety of species. While MCEs host many shallow-water species, they also contain a high number of depth-endemic species of fishes and invertebrates (Thresher and Colin 1986; Macintyre et al. 1991; Pyle et al. 2008).

On the Great Barrier Reef (GBR), submerged shelf-edge reefs, first identified by Harris and Davies (1989), occur almost continuously for at least 900 km along the GBR margin (Hopley 2006). Studies have been conducted on the geomorphology of shelf-edge reefs of the GBR (Harris and Davies 1989; Hopley et al. 1997; Hopley 2006) and their potential significance as archives of sea level and climate fluctuation (Beaman et al. 2008); however, their ecology remains virtually unknown. Early observations of MCEs in the GBR were made in 1984 from a manned submersible to depths of >200 m on the front of Ribbon Reef No. 5 (described in Beaman et al. 2008) and Myrmidon Reef (Hopley et al. 2007). Living scleractinian corals were recorded as deep as 115 m at Myrmidon Reef, with 100% coral cover at ~90 m (Hopley et al. 2007). Scoffin and Tudhope (1985) noted that rock outcrops at 70 m in the central GBR were colonised by “conspicuous alcyonarians, sponges, soft and stony corals”. Given these previous observations, and the evidence for widespread occurrence of MCEs in the Indo-Pacific, it is likely that the submerged reefs of the GBR could also provide habitat for extensive and diverse mesophotic communities. The aims of this study were therefore: (1) to quantitatively describe the topography and substrates of a mesophotic reef habitat in the central GBR; (2) identify the sessile benthic megafauna utilising those substrates; and (3) investigate the effect of abiotic variables on the distribution of sessile benthic megafauna.

Materials and methods

Study area

This study was part of a research cruise on the RV *Southern Surveyor* undertaken in September-October 2007 to explore the outer-shelf of the GBR (Webster et al. 2008), and the study area is adjacent to Hydrographers Passage (19°40’ S, 150°14’ E; Figure 3.1a). The outer-shelf in this area is characterised by a gently north-easterly sloping shelf-edge margin which contains distinctive parallel reefs and terraces. The Hydrographers Passage region is subjected to particularly strong tidal currents. For example, the shallow-water reefs of the neighbouring Pompey Complex experience tidal currents in excess of 4 m s^{-1}, the strongest in the GBR (Hopley 2006). The major oceanographic feature on the outer-shelf seaward of the GBR is the southward-flowing East Australian Current (Church 1987).

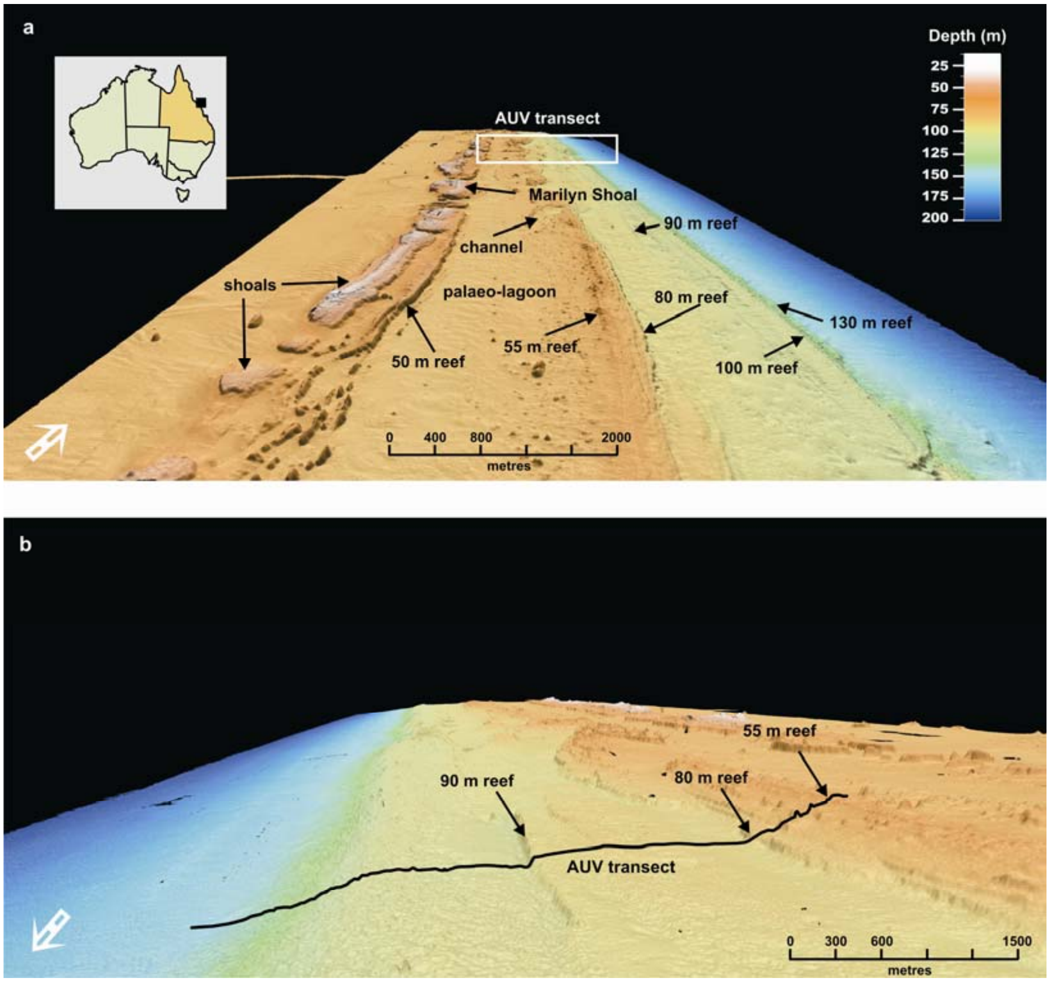

Figure 3.1: Study site at Hydrographers Passage: (a) looking north-west. Major reef features are the “shoals” and submerged reefs at 50, 55, 80, 90 100 and 130 m depth. Marilyn Shoal, which has previously been labelled in nautical charts, is shown for reference. Tidal channels bisect some reefs; (b) close up of the geomorphology along the AUV transect looking south-east.

Substrata, habitats and communities were examined using a combination of multibeam swath mapping and high-resolution AUV imagery (digital still photographs). Multibeam sonar was used to map and identify important geomorphic features (e.g. reefs) to a depth of 200 m. AUV imagery was used to define substrate composition and identify sessile benthic megafaunal communities from 51 to 145 m depth. A single Conductivity-Temperature-Depth (CTD) cast was also taken at 19˚ 38'S, 150˚ 17'E to a depth of 216 m (Webster et al. 2008; Table 2).

Bathymetry data

Multibeam bathymetry data were collected using a ship-mounted Kongsberg™ Simrad EM-300 multibeam swath mapping system, which operated at a frequency of 30 kHz and emitted a fanned arc of 135 beams per ping. Data were processed within Caris™ HIPS/SIPS software to remove erroneous values and to apply appropriate corrections (e.g. tides and sound velocity), then gridded into a BASE (Bathymetry Associated with Statistical Error) surface at 5 x 5 m resolution within HIPS/SIPS. The BASE surface pixel values were exported to ASCII XYZ (long/lat/depth) files, cropped to include ≤200 m depth (potential mesophotic habitat), and then imported into IVS3D Fledermaus™ for visualisation. ASCII files were also gridded within ArcGIS 9.3 to create XYZ-georeferenced raster layers for slope and depth. Depth values along the AUV transect were calculated from the multibeam data using the Spatial Analyst tool within ArcGIS 9.3. The total area mapped during the survey was 527 km^2.

AUV data

The University of Sydney's Australian Centre for Field Robotics provided the AUV *Sirius* for the study. *Sirius* collects a variety of physical and environmental data, including high-resolution stereo imagery, multibeam sonar, CTD, chlorophyll and turbidity (Williams et al. 2010). The AUV was programmed to travel at an altitude of 2 m above the seafloor at a speed of ~0.45 m s^{-1}. Pairs of stereo images were captured at 0.5 second intervals, which equates to a ~1.5 x 1.2 m image approximately every 22 cm. The AUV mission on 10 October 2007 lasted approximately four hours and contained a total of 7260 image pairs. The transect was conducted down slope from 51 to

145 m water depth. The total length of the transect was 3620 m. Georeferenced data collected by the AUV were converted into ArcGIS shapefiles and displayed in ArcMap 9.3.

To collect data on biota and substrate, every twentieth image pair was examined (n = 726), providing a quadrat at ~4.5 m intervals across the seafloor along the entire length of the transect (3620 m). Eight images were unusable because of poor image clarity, when the camera was either too close or too far from the seafloor to determine the composition of the image, resulting in a total of 718 images being used in statistical analysis. The relative abundances of sessile benthic megafauna in each image, as well as five different substrate types (sand, gravel, rubble, sediment-covered limestone and limestone; Table 3.1) were graded following the percent cover criteria of Done (1982) and collated into matrices.

Taxa were identified to lowest taxonomic unit (LTU) in the original data collection. Because rare taxa can create unpredictable relationships with environmental variables (Clarke and Warwick 2001), rare related taxa were merged prior to statistical analysis (e.g. the zooxanthellate octocoral genera *Sinularia*, *Sarcophyton* and *Lobotophytum* were merged into the family *Alcyoniidae*). In some cases, functional groups were used to more accurately differentiate between taxa when identification of species or genus was not possible from the AUV images (e.g. fan gorgonian). The combination of taxa produced 27 categories of sessile benthic megafauna for analysis.

Data analysis

Five image groups were identified using hierarchical cluster analysis based solely on their sessile benthic megafauna (Ward's sum of squares index; group-average linkage, after Done 1982). Data on sessile benthic megafauna were collected using ordered abundance categories, therefore no further transformations of data were performed. Broad taxon classes were also generated in order to clearly illustrate the dominant type of taxa contributing to each image group. LTU identifications (where possible) and taxa included in taxon categories and broad taxon classes are shown in the Appendix 1. Multidimensional scaling was performed on a Bray-Curtis similarity matrix based on the relative abundances of sessile benthic megafauna to explore relationships among image groups indicated by the cluster analysis.

The relationship between the relative abundance of sessile benthic megafauna and abiotic variables (depth, rugosity, slope, aspect and the relative abundance of the five substrate types) was investigated using the BIOENV function within the statistical program PRIMER (see Clarke and Warwick 2001; and Clarke and Gorley 2006 for detail on methodology and justification). The strength and significance of the relationship between the Bray-Curtis similarity matrix (megafauna), and a normalised Euclidean distance matrix based on the abiotic variables, was tested using Spearman rank correlation.

Depth values were derived from the multibeam bathymetry using ArcMap 9.3. *Rugosity*, *slope* and *aspect* were calculated using fine-scale triangular terrain reconstructions with centimetre resolution obtained from the AUV stereo images (Johnson-Roberson et al. 2010). *Rugosity* was calculated using a rugosity index by centring a window over each 1.5 x 1.2 m image pair and dividing the area of the contoured surface contained within the window by the area of its orthogonal projection onto the plane of best fit (Friedman et al. 2010). The contoured surface area was the sum of the areas of the triangles that make up the surface, and the plane of best fit was found using Principal Component Analysis. *Slope* for each image referred to the smallest angle between the plane of best fit and the horizontal plane. *Aspect* referred to the direction that the plane faced, which was measured as the angle between north and the horizontal projection of the vector normal to the best fitting plane.

Shannon's diversity index ($H' = -\sum P_i[\ln P_i]$ where P_i is the proportion taxon i contributes to the total score in any one image) was used as a measure of taxonomic diversity in each image. Continuous data (H', rugosity and limestone) were smoothed by calculating five-point running means (generated by averaging a band of five integer scores using a gliding window across the 718 images) to better reveal dominant trends along the transect. All statistical analyses were performed on raw data.

Results

Topography

The multibeam bathymetric mapping revealed a series of submerged reefs along the outer edge of the GBR shelf (Figure 3.1a). The submerged reefs closest to (~ 12 km from) emergent reefs (White Tip, Wyatt Earp and Rebe Reefs) form a semi-continuous line, rising from the seafloor at ~50 m depth to within 10 to 15 m of the surface. The submerged reefs were separated by deeply incised channels, up to 80 m deep and 200 to 1000 m wide. Seaward of these reefs (referred to in nautical charts of the region as “shoals”), a series of at least six submerged reefs, most of which rose a few metres above the surrounding seafloor, had their crests at depths of ~50, 55, 80, 90, 100 and 130 m (Figure 3.1a). Some of these features were continuous throughout most of the study site, whereas others only occurred intermittently. The 50 m reef (not included in the AUV transect) formed a semi-continuous feature throughout the study site, while the reefs at 55 m and 80 m (included in AUV transect) were relatively continuous in the southern section, but broken by several channels in the northern section (Figure 3.1a). The crests of both reefs were ~300 to 500 m apart, and the seafloor between them was stepped by numerous smaller terraces (Figure 3.1b). A 90 m reef occurred intermittently for about half the length of the study site including in the AUV transect (Figure 3.1b). A 100 m reef was present along almost the entire length of the study area, while a 130 m reef was well defined in the southern part of the study area, but more poorly defined in the AUV transect. The region between the 100 m and 140 m depth was composed of a relatively steep seafloor with a highly rugose topography (Figure 3.1b). The areas in between the reefs, identified as palaeo-lagoons by Webster et al. (2008), were flat and almost featureless. Above 100 m depth, they were punctuated by limestone pinnacles, interpreted as palaeo-patch reefs.

The substrate in the first 700 m of the AUV transect, which occurred on a topographic high at 50 to 75 m depth, was composed of a mixture of all five substrate types (Figure 3.2). Seaward of the 80 m reef was a rhodolith field with ~40% rubble (rhodoliths), 30% gravel and 30% sand. The rhodolith field gradually merged into a sand sheet at ~90 m depth which extended for over 1000 m. At its distal (seaward) edge it was punctuated by small limestone pinnacles, many of which were covered in sediment. At 90 m there was a reef composed predominantly of sediment-covered limestone, followed by another flat sandy expanse at ~100 m depth. Seaward of this sand flat, sand, gravel and rubble areas were interspersed with limestone blocks which rose up to five metres above the surrounding seafloor. Many of the limestone blocks were covered with sediment (visible in Figure 3.3b) with little or no bare limestone visible (Figure 3.3c). Although sediment-covered limestone occurred throughout the survey area, it was particularly abundant below 70 m depth. Beyond 140 m the substrate became flat and featureless, and was composed predominantly of sand and gravel.

Table 3.1: Definitions of substrate types.

Name	**Description**
Sand	Unable to distinguish individual grains in images; estimated grainsize < 2 mm.
Gravel	Larger than sand but smaller than rubble; estimated grainsize ~ 3-30 mm.
Rubble	Clasts > 30 mm grainsize but not firmly attached to the substrate.
Sediment-Covered Limestone (SCL)	Limestone which has been covered by sediment but appears hard underneath.
Limestone	Limestone protrudes above the surrounding seafloor; no soft sediment.

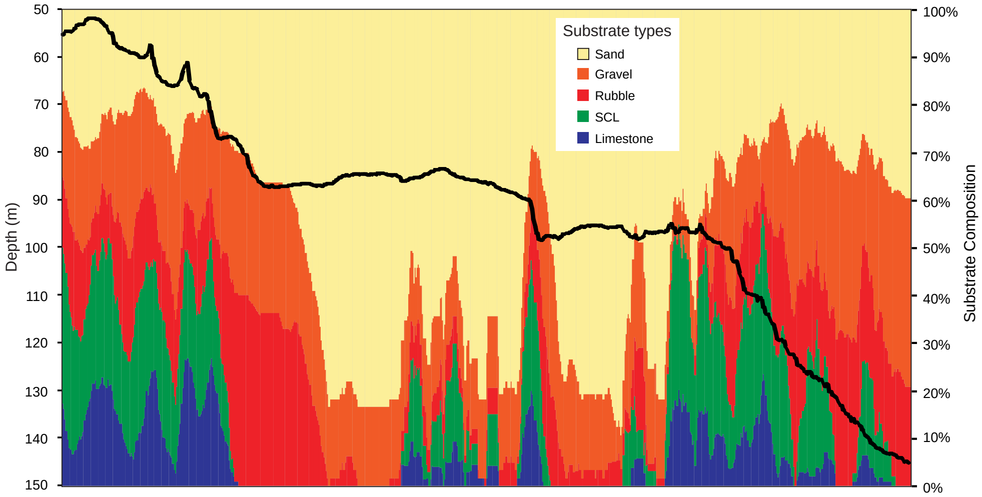

Figure 3.2: Substrate composition along the AUV transect. Ten-point running means of substrate types were used for clear visual interpretation. Depth profile (black line) is shown to indicate changes in substrate relative to depth and geomorphic features

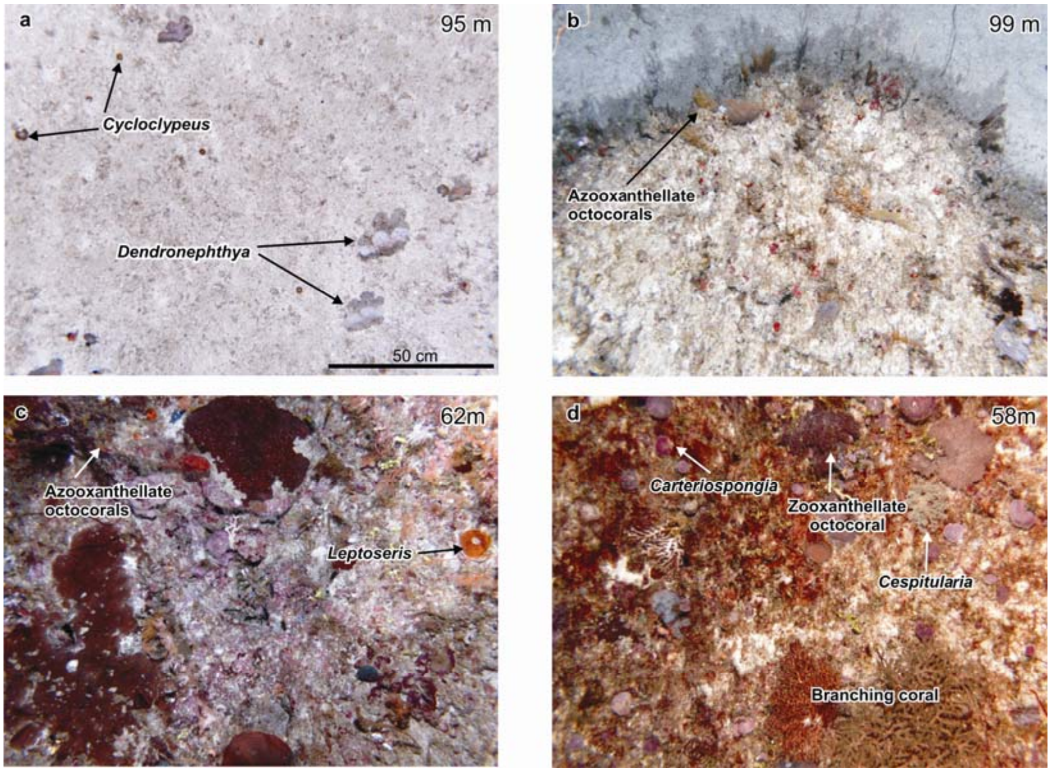

Figure 3.3: Examples of image groups, showing: (a) *Dendronephthya* colonies growing in soft substrate and the giant foraminifera *Cycloclypeus* on the sand sheet at 95 m depth; (b) diverse community of azooxanthellate filter-feeders (predominantly octocorals) growing on the crest of a sediment-covered limestone reef at 99 m; (c) transitional community composed of both zooxanthellate corals and filter-feeding octocorals growing on a limestone reef wall, 62 m; and (d) shallow-water community dominated by zooxanthellate octocorals, scleractinia and *Carteriospongia*, 58 m.

Sessile benthic megafaunal communities

Cluster analysis of the sessile benthic megafauna yielded five distinct image groups. A summary of the major contributors to each image group is shown in Figure 3.4, while the mean environmental properties, as well as diversity (H') are included in Table 3.2. Clusters 1 and 2 were found on soft, non-reef substrates (<5% mean limestone); clusters 3, 4 and 5 were reef-associated and contained significant amounts of limestone and sediment-covered limestone. Cluster 1 was the most common, occurring in 54% of images, and was defined by a paucity of sessile benthic megafauna. It occurred in low relief areas with a sandy substrate. Cluster 2 (28%) was also found on sandy substrates and exhibited low abundance of sessile benthic megafauna, apart

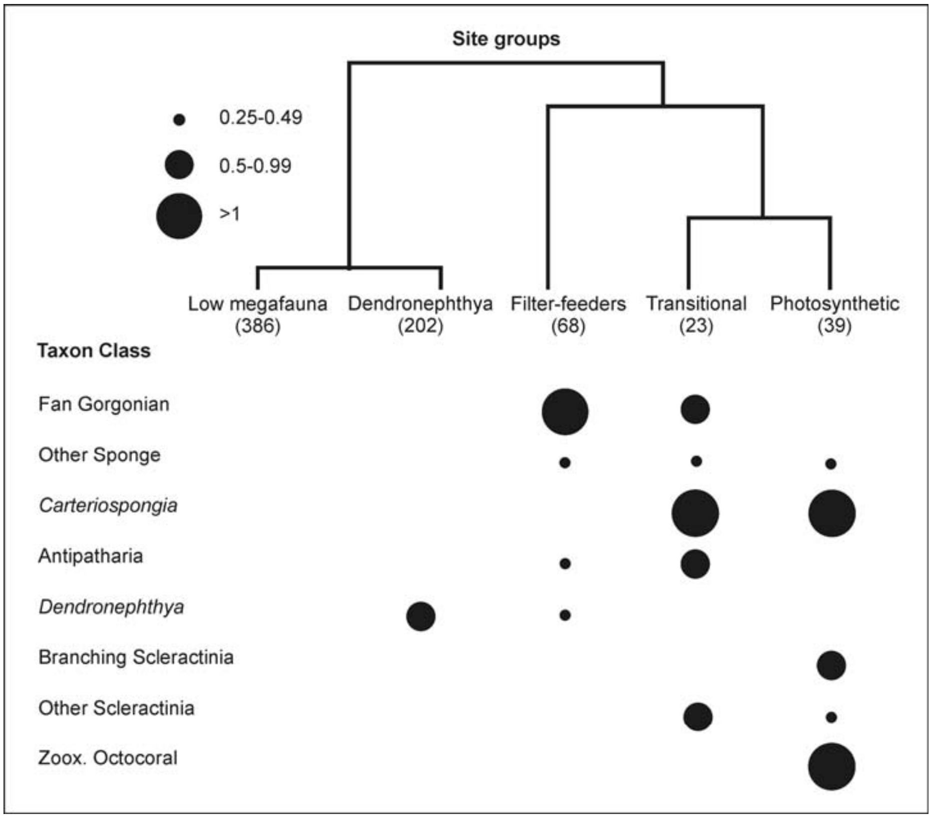

Figure 3.4: Contribution of eight most abundant taxon classes to the five image groups identified using cluster analysis. Membership of taxon classes is shown in Appendix 1. The number of images in each image group is shown in brackets. Circles represent the mean abundance per image of each taxon class to each image group.

Table 3.2: Mean values for abiotic variables and diversity for each image group. Standard deviation is also shown for rugosity index and slope. Values for the five substrate types were calculated using the 0-5 ordinal abundance categories.

Image group	**1**	**2**	**3**	**4**	**5**
Depth (m)	91	103	100	67	54
Rugosity Index	1.02 ± 0.04	1.07 ± 0.11	1.31 ± 0.23	1.24 ± 0.16	1.12 ± 0.07
Slope (˚)	5 ± 4	8 ± 9	22 ± 18	21 ± 13	6 ± 6
Sand	4.3	3.9	3.0	2.2	3.2
Gravel	2.1	2.3	1.7	1.7	2.4
Rubble	1.5	1.6	1.3	1.2	1.7
Sediment-Covered Limestone	0.6	1.4	3.4	3.2	3.4
Limestone	0.3	0.5	1.9	3.2	2.3
Diversity (H’)	0.1	0.6	1.2	1.4	1.3

from colonies of the azooxanthellate octocoral *Dendronephthya* growing in the soft substrate. Cluster 3 (9%) was dominated by azooxanthellate filter-feeders, particularly fan gorgonians. It was the dominant group on sediment-covered reefs below 75 m depth. Cluster 4 (3%) was a transitional community composed of a mixture of photosynthetic taxa and filter-feeders. It occurred in areas of high slope with a high proportion of limestone and generally in depths from 60 to 75 m. Cluster 5 (5%) occurred on limestone and sediment-covered limestone substrates in the shallowest parts of the transect (depths <60 m) and was dominated by photosynthetic taxa, particularly zooxanthellate octocorals and the phototrophic sponge *Carteriospongia*. Multidimensional scaling of sites based on their sessile benthic megafauna showed image group clusters to be well defined by a 2-dimensional ordination (Figure 3.5). The stress level of 0.12 indicated a good ordination, especially given the high number of samples (n=718).

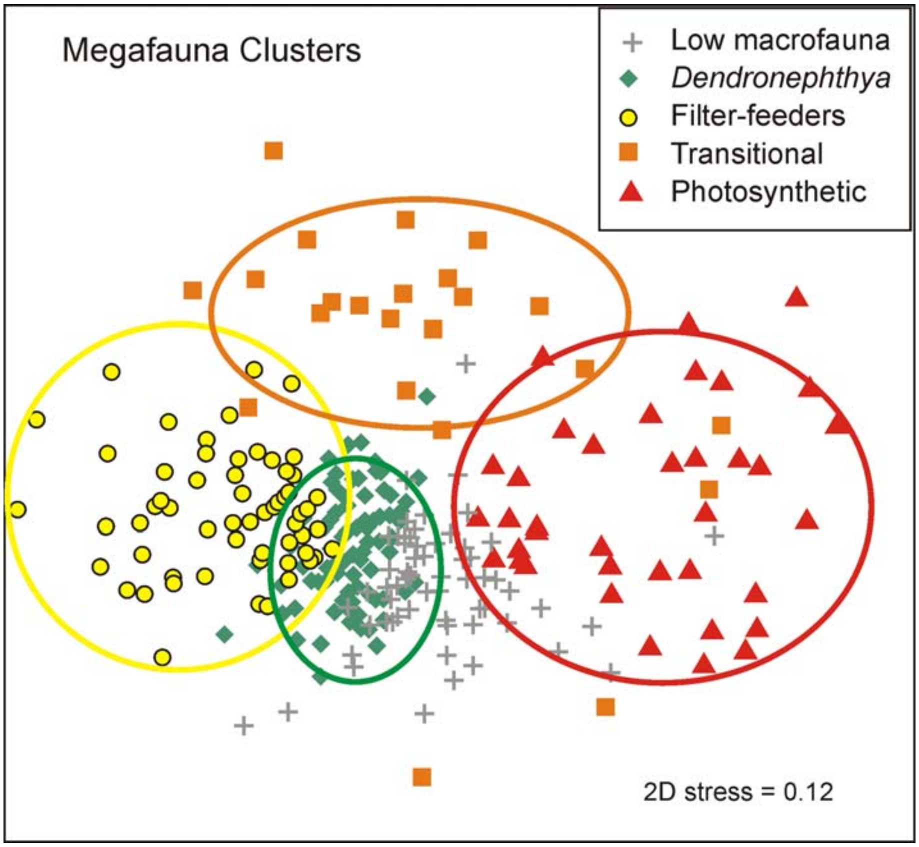

Figure 3.5: Multidimensional scaling plot of sites (AUV images) based on the relative abundance of sessile benthic megafauna. Colours correspond to image groups identified in cluster analysis ("Low sessile benthic megafauna" images not circled).

Vertical zonation of reef-associated sessile benthic megafaunal communities was clearly evident in the AUV transect and occurred in three distinct zones (Figure 3.6). Photosynthetic taxa were dominant on the reef top above 60 m depth (Figure 3.7a), with communities composed of zooxanthellate octocorals such as *Cespitularia* and Alcyoniids, a diverse assemblage of scleractinia including *Acropora*, *Montipora*, *Pocillopora* and *Seriatopora*, and *Carteriospongia*. From 60 to 75 m a transitional community occurred, comprising both photosynthetic and non-photosynthetic filter-feeding taxa. Fan gorgonians and antipatharians became more abundant (Figure 3.4), while the dominant zooxanthellate taxa were encrusting and platey scleractinia such as *Leptoseris* and *Echinophyllia*. Below 75 m, photosynthetic taxa became extremely rare, with reef communities dominated by a diverse suite of azooxanthellate octocorals, including *Annella*, *Chironepthya*, *Siphonogorgia*, *Echinogorgia*, *Zignisis* and Ellisellids, both branching (e.g. *Ellisella*) and non-branching (e.g. *Junceella*, *Viminella*).

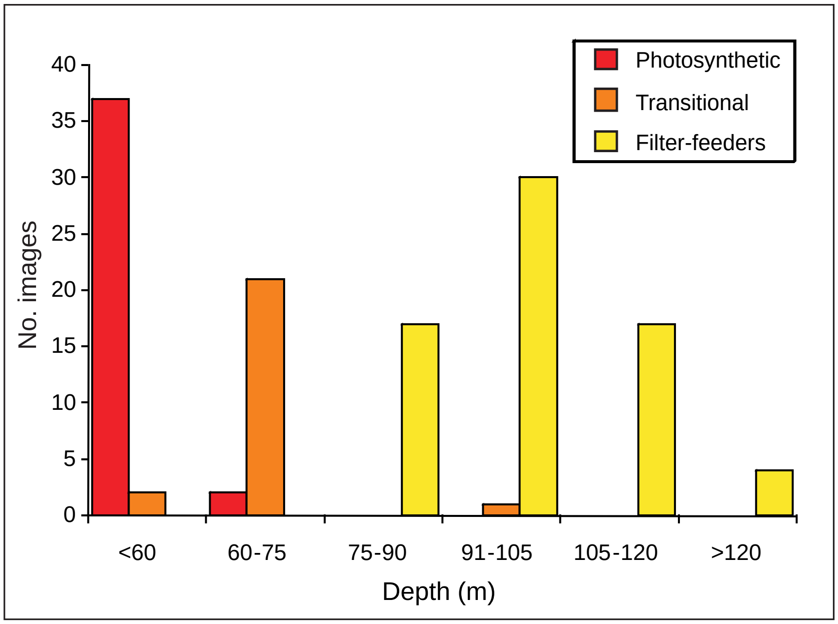

Figure 3.6: Depth zonation of three reef-associated image groups. The zooxanthellate group is dominant above 60 m, the transitional group from 60-75 m, and azooxanthellate filter-feeders are generally found in depths >75 m.

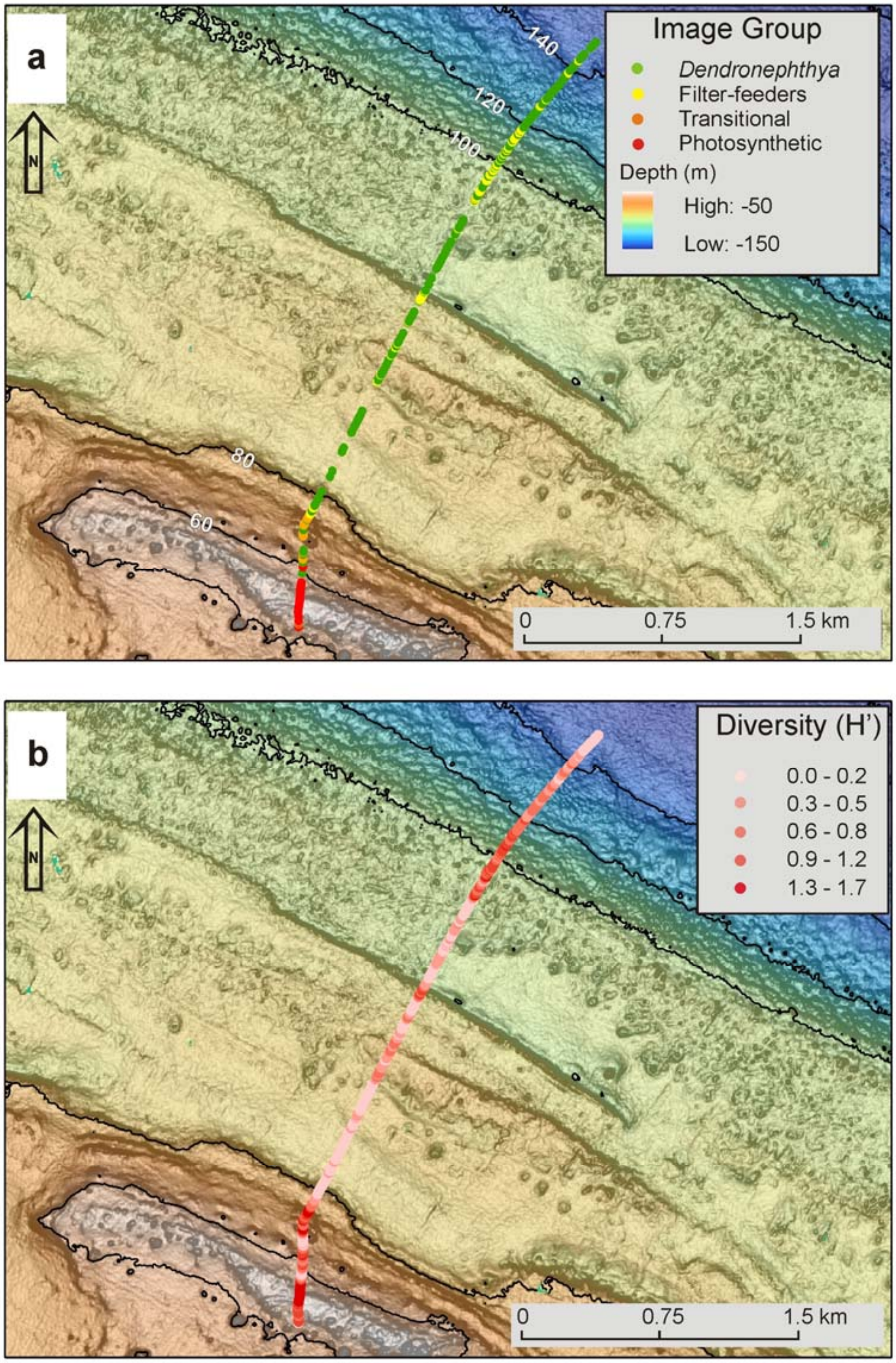

Figure 3.7: Maps of the AUV transect showing: (a) location of the image groups (“low megafauna” sites not shown); and (b) diversity (H’) calculated using five-point running means.

Diversity (H’) was highest on steep, rugose reef habitats <75 m depth (Figure 3.7b). Diversity on the rugose limestone substratum in 95 to 120 m was significantly higher than areas with soft substratum, but lower than on shallower limestone reefs <75 m. Non-reef substrates contained low diversity; however, the sand sheets did contain the giant (up to 10 cm diameter) benthic foraminifera *Cycloclypeus carpenteri*. Although it was not included as sessile benthic megafauna, it was relatively abundant (up to 10 m^{-2} in the AUV images) between 80 and 100 m depth. Significant spikes in diversity were observed in association with high limestone and rugosity values (Figure 3.8). The BIOENV analysis indicated that the abiotic variables *rugosity* and *limestone* best explained the variation observed in the relative abundance of sessile benthic megafauna among sites (Spearman rank correlation = 0.755). *Rugosity* had the strongest individual correlation (0.734).

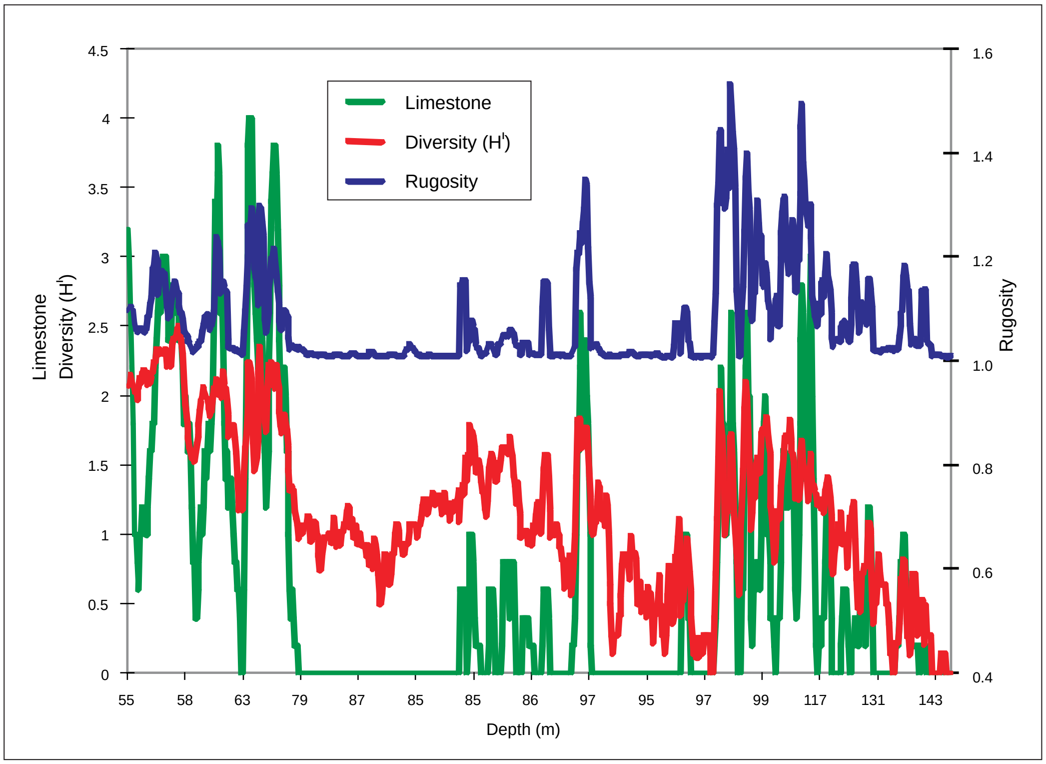

Figure 3.8: Diversity (H’) (red), limestone (score on 5 point scale) (green) and rugosity index (RI) (blue). All plotted values are five-point running means along the AUV transect.

Discussion

Topography and substrata

The submerged reefs at Hydrographers Passage appear to be part of an extensive and diverse but poorly characterised reef environment on the GBR outer-shelf. High-relief areas are built of reefal material and surrounded at their bases by rubble originating from the reefs. Large areas devoid of topographic highs allow the development of extensive sand sheets. Interestingly, a significant proportion of the reef limestone was covered in sediment, similar to that described from the deep reef slope at Enewetak by Colin et al. (1986). Strong currents in the region probably disturb the sand sheets, resuspending sediments and transporting them onto the reefs. The magnitude and periodicity of sediment transport onto the reefs may play an important role in determining community composition in several ways, discussed below, however it is difficult to speculate on the periodicity of these events and, consequently, how often limestone reefs may be free from sediment.

Controls on depth zonation and community composition

Substrate type clearly plays an important role in determining the distribution of sessile benthic megafauna at Hydrographers Passage. Diversity of both photosynthetic and filter-feeding sessile benthic megafauna at all depths was significantly higher on reef substrates than inter-reefal areas. However, other factors such as slope angle, habitat microtopography and oceanography also appear to play an important role in determining community composition.

Reduced irradiance with depth eventually limits the distribution of photosynthetic taxa (Kirk 1994), and consequently depth is an important determinant of community composition on MCEs (Kahng et al. 2010). Reef communities at Hydrographers Passage exhibited strong depth zonation (Figure 3.6), with the transition from communities dominated by photosynthetic taxa to filter-feeders; probably reflecting decreased irradiance with depth. Various studies (e.g. Brakel 1979; Ohlhorst and Liddell 1988; Liddell et al. 1997; Lesser et al. 2009) have shown that areas of high slope receive significantly lower levels of irradiance than horizontal surfaces. High slope may occur at different scales; large, steep walls obviously exhibit high slope, however microhabitat topography can also cause a significant reduction in irradiance (Ohlhorst and Liddell 1988). The method used to calculate rugosity and slope used in this study (see Friedman et al. 2010) ensured that rugosity and slope were independent. However, because both values were calculated over the same scale (1.5 x 1.2 m), an image may contain a topographically complex microhabitat (high rugosity), but low overall slope. Biologically, the effect is the same – high slope, regardless of scale, causes a reduction in irradiance which is probably the critical determinant in limiting the occurrence of photosynthetic taxa. On mesophotic reefs where irradiance is already significantly reduced by depth, relatively small increases in slope angle may be sufficient to affect community composition. Mean slope and rugosity values in sites dominated by photosynthetic taxa (6° ± 6 for slope and 1.12 ± 0.07 for rugosity) are substantially lower than in the transition zone (21° ± 13 and 1.24 ± 0.16) or on the deeper reefs (22° ± 18 and 1.31 ± 0.23) (Table 3.2). Although the exponential decrease in irradiance with depth is of obvious importance to photosynthetic taxa, slope angle also appears to play an important role in determining vertical zonation.

In some cases, rugosity values derived from AUV images may be amplified by living frame-building sessile benthic megafauna (such as branching Scleractinia or fan gorgonians) growing on the antecedent limestone framework. Nonetheless, it is clear that topographically complex reef habitats exhibit higher diversity than flatter areas. Moreover, the shallow, photosynthetic image group exhibits relatively low rugosity but high diversity of sessile benthic megafauna, including frame-building taxa such as Scleractinia. This indicates that despite the potential influence of living frame-builders on rugosity values, there is a clear correlation between overall rugosity of the substrate and high sessile benthic megafaunal diversity.

The influence of slope angle at Hydrographers Passage is well illustrated by examining the community composition of scleractinian corals. Although corals in intermediate depths (12-24 m) are often most abundant on steep slopes less prone to sediment accumulation, reduced irradiance on steep slopes can cause coral recruitment to shift to horizontal substrates in deeper water (Bak and Engel 1979; Birkeland et al. 1982). At Hydrographers Passage, the low-slope habitat on top of the 55 m reef contained the highest diversity of scleractinian corals, including branching species of *Acropora*, *Pocillopora*, and *Seriatopora*. Steeper areas in 60 to 75 m, contained much lower coral diversity, and were inhabited by flat, platey and encrusting forms such as *Echinophyllia* and *Leptoseris*. Colonies were typically dark in colour, suggestive of high zooxanthellae densities needed to meet energy requirements in low light (Fricke et al. 1987). Both genera are common inhabitants of MCEs in the Indo-Pacific (Kahng et al. 2010), indicating adaptation to light-limited environments, while their plating morphology and tendency to occur on vertical walls (Veron 2000) suggests they are susceptible to high sedimentation. The greater light availability on low slope reef tops therefore favours branching corals, which are better able to deal with sediments, while the steeper areas favour species adapted to utilise limited irradiance.

The AUV transect reveals scleractinia to be rare below 75 m at Hydrographers Passage, despite *Leptoseris* spp. being known to occur at depths well over 100 m elsewhere in the Indo-Pacific (e.g. Kahng and Kelley 2007; Maragos and Jokiel 1986; Fricke et al. 1987). Abundant *Leptoseris* (100% cover) was recorded at Myrmidon reef, only 340 km north-west of Hydrographers Passage, at 90 m depth (Hopley et al. 2007). Therefore, it is likely that local environmental and substratum conditions such as exposure to moving sediments are responsible for the shallow depth limit of *Leptoseris* at Hydrographers Passage, rather than insufficient surface irradiance. Although very high turbidity associated with the extreme tides and currents are known to affect coral communities on shallow-water reefs near Hydrographers Passage (Kleypas 1996; van Woesik and Done 1997), they are probably not important on MCEs that occur >15 km seaward of the emergent reefs. The dominant oceanographic feature in this area, the East Australian Current, brings clear, oceanic water to the mesophotic reefs, while data collected by the AUV during the transect indicated relatively low turbidity (~0.5 NTU). Therefore, sediments derived from the GBR lagoon would be unlikely to cause the shallow depth limit of scleractinian corals observed at Hydrographers Passage. However, the prevalence of sediment-covered limestone in the AUV transect indicates that localised currents may transport autochthonous sediments from the sand sheets to the reefs, particularly on the reefs seaward of the sand sheets (>75 m). Resuspension of sediments could affect the community composition in two ways: (1) by increasing turbidity near the seafloor, thereby reducing light penetration; and, (2) by smothering corals and inhibiting growth. Small amounts of sediment would probably be sufficient to exclude many of the flat, plating or encrusting corals which occur on MCEs.

Although azooxanthellate, filter-feeding octocorals were abundant on sediment-covered limestone reefs, they were generally concentrated along steep walls and the edges of reef crests - environments least likely to accumulate sediment. Liddell et al. (1997) showed sediment cover in low-slope habitats limited the diversity and abundance of benthic taxa on deep reefs (200 to 250 m depth) in the Bahamas, resulting in “small islands of suitable habitat surrounded by a desert of barren sand”. A similar pattern is seen in Figure 3.3b, which shows a diverse community of octocorals occurring on the steep crest of a reef, with low octocoral abundance away from the crest. Although reduced irradiance would not affect such taxa, they do appear to be negatively impacted by sediment accumulation, though not to the same extent as scleractinia.

Upwelling onto the GBR shelf at Hydrographers Passage, affecting both nutrient availability and temperature, may also play a role in determining the composition of sessile benthic megafaunal communities. Chlorophyll data collected by the AUV during the transect revealed chlorophyll levels up to 0.6 $\mu g\ l^{-1}$ at 100 m depth, significantly higher than the ~0.2 $\mu g\ l^{-1}$ at the sea surface. Octocorals are suspension feeders whose diet consists primarily of phytoplankton and other small (<20 µm) organic particles (Fabricius et al.

1995a, 1995b). Unlike Scleractinia, which possess highly developed stinging cells (nematocysts) ideal for zooplankton capture, octocorals contain few small nematocysts and rely on currents to provide nutrition. Current speed has been shown to affect food intake and growth rates in soft corals, with food intake highest at unidirectional, intermediate flow speeds (8-15 cm s^{-1}; Fabricius et al. 1995a, 1995b; Fabricius and Alderslade 2001). Increased levels of chlorophyll would represent a significant advantage for azooxanthellate octocorals, particularly phytoplankton-feeders such as *Dendronephthya* and may explain the abundance of azooxanthellate soft corals at Hydrographers Passage, particularly below 70 m. Data collected both by the AUV and the CTD cast suggest a thermocline may also exist at ~70 m, with temperature 25.5 ˚C at the surface, 24.5 ˚C at 70 m and falling to 18.5 ˚C at 140 m. Low temperature has been shown to limit coral growth on mesophotic reefs in Palau, where wide daily temperature fluctuations (commonly ~10 ˚C, up to 20 ˚C) resulting from large internal waves were implicated in the depauperate biological community on reef slopes from 60 to 120 m (Wolanski et al. 2004). These data only represent a “snapshot”, and unfortunately no long-term data exist for the region. However, the shift in community composition coinciding with observed thermocline depth suggests upwelling may also play a role in determining community composition.

In summary, the GBR at Hydrographers Passage contains an extensive mesophotic ecosystem composed of diverse reef and inter-reefal communities. The distribution of sessile benthic megafauna is closely correlated with rugose, limestone reef habitats, with different communities inhabiting reef and non-reef substrates. There is a distinct vertical zonation of sessile benthic megafaunal communities occurring on mesophotic reefs, with photosynthetic taxa dominating above 60 m depth, a transitional zone between 60 to 75 m, and a community dominated by azooxanthellate filter-feeders from 75 to 140 m depth. This study provides the first quantitative assessment of a mesophotic ecosystem within the GBRMP, and, with 900 km of shelf-edge reefs in the central GBR alone, the first insight into a potentially vast mesophotic ecosystem.

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Chapter 4

Composition of sessile benthic megafaunal communities along the Great Barrier Reef outer-shelf and their relationship to environmental variables

Images were selected at random from four AUV missions across three sites to identify changes in the composition of sessile benthic megafaunal communities along the GBR outer-shelf. There were significant differences in community composition between all three sites, and also between functional ecological groups inhabiting different finer-scale habitat types. Slope angle of the substrate, water clarity and water column productivity best explained the observed variation. The research presented in this chapter primarily addresses research aim 3, although it also informs the modelling study in aim 4.

This chapter is presented in the form of a research paper and has been published in the international journal Marine Ecology Progress Series 428: 63-75. The paper has six co-authors and their contributions are as follows:

- Dr Terry Done provided editorial support and provided guidance on the interpretations and ideas discussed within the paper
- Mr Ariel Friedman generated rugosity, slope and aspect grids on AUV stereo-images for the AUV transect and provided the explanation of the technique in the methods section.
- Dr Robin Beaman conducted the multibeam swath mapping on board the RV *Southern Surveyor*, and provided guidance on the processing of swath data and editorial support.
- Dr Stefan Williams and Dr Oscar Pizarro collected the AUV data on board the RV *Southern Surveyor*.

- Dr Jody Webster provided funding for the RV *Southern Surveyor* expedition, and also provided editorial support.

Variability in mesophotic coral reef communities along the Great Barrier Reef, Australia

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Abstract

The composition of sessile benthic megafaunal communities on mesophotic coral reefs (50 to 65 m depth) was investigated at three sites (Noggin Pass, Viper Reef and Hydrographers Passage) over 500 km of the Great Barrier Reef (GBR) shelf-edge, Australia. High-resolution stereo imagery was collected in four separate autonomous underwater vehicle (AUV) surveys and used to characterise the substratum and megafauna at each site (two surveys from Viper Reef, and one from each of Noggin Pass and Hydrographers Passage). Random sampling of 100 images from a 100 × 100 m area at each site indicated that non-reef habitats predominated and that megafauna were largely confined to reef habitats, while a more detailed investigation of these reef substrata revealed diverse benthic megafaunal communities that varied significantly both within and between study sites. There were consistent patterns in the functional ecological groups occupying particular finer-scale habitat types, with phototrophic taxa dominating the flatter tops of submerged reefs and heterotrophic suspension-feeders occupying steeper habitats. Slope angle, water clarity and productivity best explained the distribution of megafauna on reef habitats. Reduced photosynthetically active radiation (PAR) likely excludes most phototrophic taxa from steeper slopes. These results suggest that the extensive submerged reefs on the outer-shelf of the GBR harbour diverse mesophotic reef communities. Given these results, GBR mesophotic coral ecosystems deserve further study, not only of their benthic megafauna but also their fish and mobile invertebrate communities.

Keywords: mesophotic; coral; octocoral; community composition; autonomous underwater vehicle; AUV; Great Barrier Reef

Introduction

The Great Barrier Reef (GBR) extends ~2300 km along Australia's north-east coast (Hopley et al. 2007). Although the iconic emergent reefs are widely recognised, a vast submerged barrier reef system also occurs on the shoulder of the continental shelf and may be as long as the emergent GBR. A continuous line of submerged reefs has been documented occurring for over 800 km in the central GBR in 50 to 70 m water depth (Hopley et al. 1997; Hopley 2006). Submerged reefs have also been mapped on the steeper shelf margin of the northern GBR (Beaman et al. 2008) and also in the far north near Torres Strait (Harris et al. 2005). Studies on these reefs generally focused on their geomorphology (Harris and Davies 1989; Hopley 2006; Beaman et al. 2008); consequently, little is known about their ecology.

Mesophotic coral ecosystems (MCEs) are tropical coral reef communities that exist from ~30 m to the bottom of the photic zone, often exceeding 100 m in depth (Kahng et al. 2010). In recent years, they have been receiving increased attention from both scientists and managers due to an increasing awareness of both their intrinsic ecological character and biodiversity, and their potential to act as refugia for coral reef species as these areas become exposed to damaging environmental changes, such as rising sea surface temperatures and increasing incidence of severe cyclones (e.g. Bongaerts et al. 2010). Studies of MCEs have been conducted in the Caribbean and the Red Sea (Fricke et al. 1987) as well as several locations in the Indo-Pacific, including Johnston Atoll (Maragos and Jokiel 1986), Enewetak (Colin 1986; Colin et al. 1986), American Samoa (Bare et al. 2010) and Hawaii (Kahng and Kelley 2007; Rooney et al. 2010).

The vast majority of studies conducted on coral reefs worldwide have focused on shallow-water habitats <30 m deep, with the lower depth limit largely imposed by the use of SCUBA. Recent technological advances, such as multibeam sonar and autonomous underwater vehicles (AUVs) (e.g. Armstrong et al. 2006; Williams et al. 2010) have enabled the collection of remotely sensed data in deep water habitats and at multiple spatial scales. Moreover, use of such remotely sensed data to predict the distribution of benthic communities has greatly increased, particularly over large geographical areas (e.g. Kostylev et al. 2001; Mumby et al. 2004; Beaman and Harris 2007; Pitcher et al. 2007).

The distribution of MCEs across various spatial scales is determined by a combination of environmental factors including geomorphology, sedimentation, light availability and temperature gradients (Locker et al. 2010). However, the effect of these variables on MCE community structure remains poorly understood, particularly in the vastly understudied MCEs of the Indo-Pacific (Hinderstein et al. 2010, Kahng et al. 2010). Variations in physical water properties such as wave energy, water clarity, productivity and sedimentation both across and along the GBR shelf have been correlated with changes in community composition of shallow-water reef taxa including corals (Done 1982) and octocorals (Dinesen 1983, Fabricius and De’ath 2008). Coral species richness decreases with increasing latitude south along the length of the GBR (Veron 1995). However, changes in the composition of many communities are greater across-shelf, from turbid coastal habitats to the clear oceanic waters of the outer-shelf. Done (1982) showed coral community composition and richness varying across the central GBR both within and between reefs in response to predictable environmental parameters. On shallow-water reefs, overall diversity for both corals and octocorals peaks mid-shelf (Done 1982, Fabricius and De'ath 2008), although the distribution of octocorals varies substantially between phototrophic and heterotrophic taxa. Phototrophic octocorals in the GBR occur in a wide range of habitats, whereas heterotrophs exhibit limited ranges with highest richness occurring in regions of high productivity and water flow and low disturbance (Fabricius and De'ath 2008). An extensive study of continental shelf seabed habitats in the GBR suggests that local species composition and abundance in most biotas on the GBR are in large part driven by the local environment and not strongly correlated to cross-shelf position or latitude *per se* (Pitcher et al. 2007).

The GBR's submerged shelf-edge reefs are exposed to water that is generally clear and oligotrophic (Wolanski 1994), although modelling of long-term (30 year) water quality data by De'ath (2007) indicates pelagic productivity doubles from north to south along the length of the GBR outer-shelf. To date, no studies have attempted to examine how different environmental factors may affect community composition of the MCEs. Using the results of a semi-quantitative study at sites separated by up to ~500 km on the GBR outer-shelf (see Figure 4.1), this study provides the first investigation of possible environmental drivers of mesophotic reef community structure on the GBR. The study aims to: (1) determine the structure of sessile benthic megafaunal communities at three sites along the GBR shelf-edge; and (2) identify the physical/environmental factors that best explain the distribution patterns of sessile benthic megafauna.

Materials and methods

Study sites

Noggin Pass

The Noggin Pass site (10 km east of Noggin Reef at 17° 5’ 24” S, 146° 34’ 12” E; Figure 4.1) consists of a series of pinnacles, 20 to 50 m in diameter, which rise ~3 m above the surrounding seafloor (Figure 4.2a). These structures, occurring at a depth of 58 to 63 m, were interpreted by Webster et al. (2008) as palaeo-patch reefs. A channel occurs immediately to the south of the site, which is located ~700 m from the shelf break (120 m depth). The shelf itself at this latitude is generally steeper than at the other two study sites at Viper Reef and Hydrographers Passage.

Viper Reef

The Viper Reef site (18° 49’ 48” S, 148° 27’ 0” E; Figure 4.1) consists of two separate AUV surveyed areas located ~650 m apart: Viper North and Viper South (Figure 4.2b). The surveys were conducted ~1000 m from the shelf break (~130 m deep) seaward of a line of submerged shoals. These shoals are ~10 km seaward of the closest emergent outer-shelf reefs (Lion and Jaguar Reefs). The surveys covered two of a series of limestone pinnacles 20 to 80 m in diameter at a depth of ~56 m and rising 2 to 5 m above the surrounding seafloor.

Hydrographers Passage

The Hydrographers Passage study site (19° 24’ 0” S, 150° 15’ 0” E; Figure 4.1) is located 12 km north-east of the nearest emergent outer-shelf reef (Rebe Reef). The shelf break is located at ~130 m and lies nearly 3 km seaward of the site. The continental shelf in this area is wider and exhibits a shallower gradient than in the northern study areas (Hopley et al. 1997). The site is in a high-energy region exposed to strong tidal currents with small emergent reefs set back from the shelf-edge. A series of submerged coral shoals, located ~12 km seaward of emergent reefs, have been previously identified by the Great Barrier Reef Marine Park Authority and on nautical charts. The AUV survey (Figure 4.2c) was conducted on the seaward edge of a 500 × 200 m submerged reef that rises from

62 to 50 m depth, and included limestone pinnacles ~30 m in diameter that rise up to ~6 m above the surrounding seafloor.

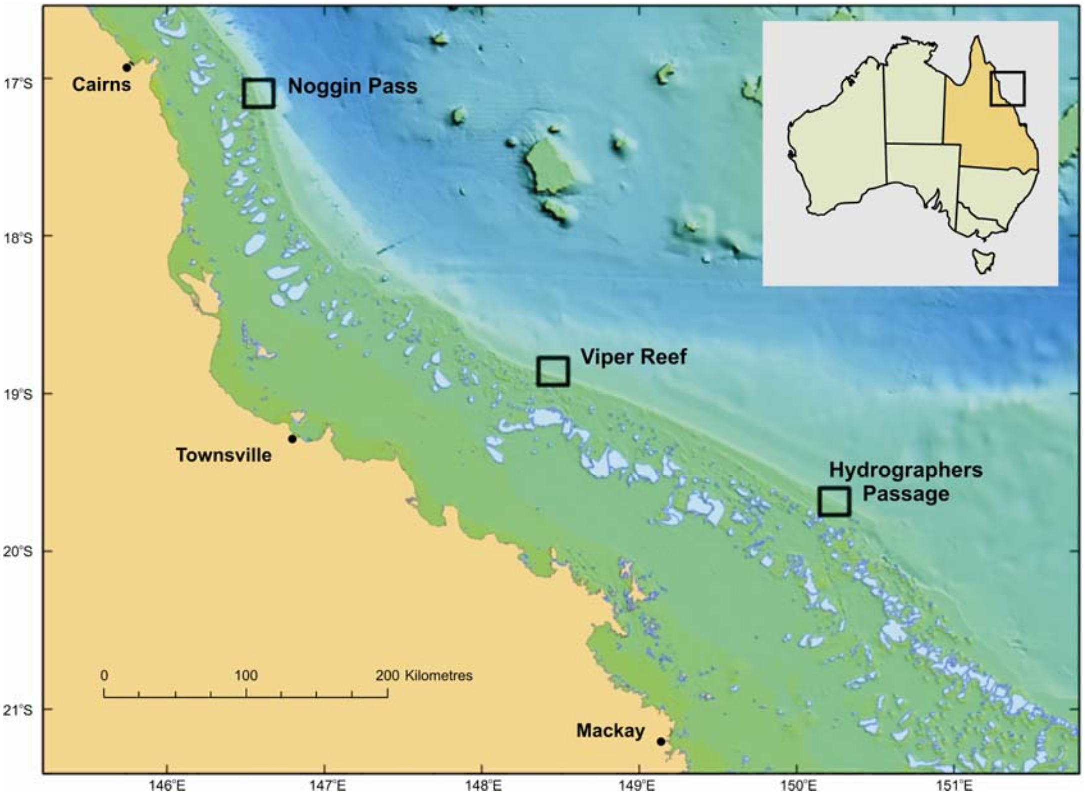


Figure 4.1: Study sites along the Great Barrier Reef shelf-edge. Surveys were conducted at Noggin Pass, Viper Reef and Hydrographers Passage from September to October 2007.

Topography

A topographic model of the seafloor at each site was created using multibeam bathymetry data collected using a ship-mounted Kongsberg™ Simrad EM-300 multibeam sonar system operated at a frequency of 30 kHz. Data were processed within Caris™ HIPS/SIPS software to remove erroneous values and to apply appropriate corrections (e.g. tides and sound velocity), then gridded into a BASE (Bathymetry Associated with Statistical Error) surface at 5 × 5 m grid resolution within HIPS/SIPS. The BASE surface pixel values were exported to ASCII XYZ (long/lat/depth) files, and gridded within ESRI™ ArcGIS 9.3 to create the topographic model in the form of xyz-georeferenced raster layers.

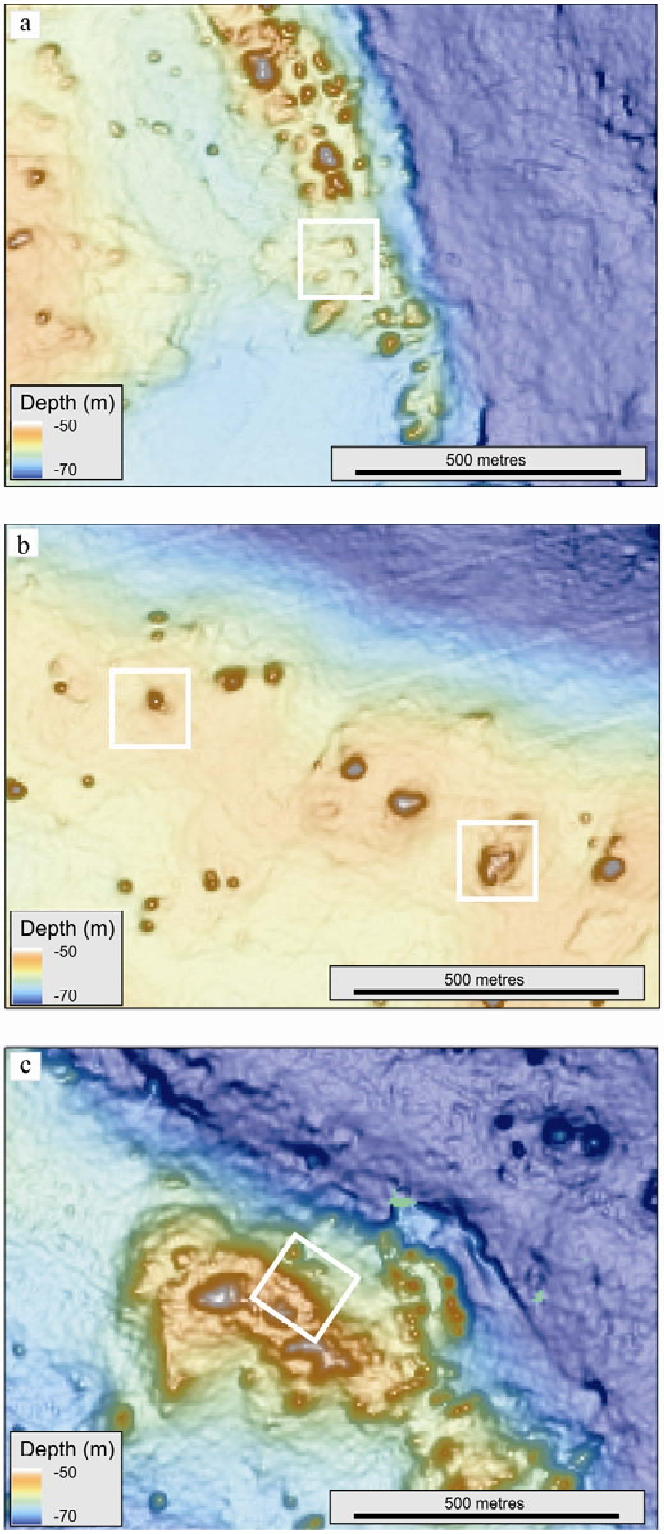


Figure 4.2: Multibeam bathymetric images of study sites. White squares indicate position of autonomous underwater vehicle surveys: (a) one at Noggin Pass, (b) two at Viper Reef, and (c) one at Hydrographers Passage.

AUV data

High-resolution, georeferenced stereoscopic images of the seafloor were collected at a rate of 2 Hz using the AUV *Sirius*, which was programmed to travel 2 m above the seafloor at a speed of 0.45 m s^{-1} (Williams et al. 2010). A total of four AUV surveys were conducted across three sites; two from Viper Reef (6 and 7 October 2007) and one from both Noggin Pass (3 October) and Hydrographers Passage (11 October). The primary aim of the research expedition was to investigate the nature of the submerged reefs from a geological standpoint, specifically to examine changes in reef growth and palaeo-environmental conditions since the last glacial maximum. The primary role of the AUV was therefore to provide high-resolution images of the reefs themselves (described in Williams et al. 2010) rather than to quantitatively assess the biota, which was a secondary goal of the expedition. Therefore, the analysis in this study required several different surveys conducted for geological purposes to be standardised for ecological analysis. Each survey was conducted using orthogonal line transects. The smallest total area covered by an AUV grid was 100 × 100 m (Noggin Pass); therefore, the other AUV surveys were clipped to this size.

Two surveys were conducted at Viper Reef to examine whether proximal sites contained similar benthos. Analysis was conducted at two spatial scales; initially, a site-scale analysis was conducted by randomly selecting 100 images from each survey (400 images in total) over each entire 100 × 100 m area. Analysis of these data revealed a high proportion of uninformative non-reef images (sand or gravel-dominated substrata) containing little or no sessile benthic megafauna; therefore, a more detailed examination of reef habitats was conducted by randomly selecting supplementary images from reef substrates (defined as >50% limestone or sediment-covered limestone). A total of 25 reef images were selected from each survey (100 images in total), which was found to be adequate to characterise the richer communities on reef substrata.

The characterisation of megafauna and substrata was made by detailed visual inspection of high-resolution images from the AUV. Data on substrata and biota were collected from each image using ordered abundance categories where 0 = no occurrence; 1 = present at <5% cover; 2 = 5–10%; 3 = 10–30%; 4 = 30–80%; and 5 = >80%. Sessile benthic megafauna (Porifera, Scleractinia, Antipatharia, Octocorallia, Actiniaria, Crinoidea and Ascidiacea) were identified to the lowest taxonomic unit reliably achievable from the images (primarily genera, but some species). In some cases (e.g. azooxanthellate octocorals), morphology was used for classification when identification of species or genus was not possible from the AUV images (e.g. fan gorgonian). Rare taxa (<2% occurrence), which can create unpredictable relationships with environmental variables (Clarke and Warwick 2001), were subsequently grouped together into "morphological units" before inclusion in analyses (see Appendix 2).

Abiotic data describing each image and to be used as potential explanatory variables were as follows: the relative abundances of five substratum types (*sand*, *gravel*, *rubble*, *sediment-covered limestone* [*SCL*] and *limestone*); *geomorphic zone* (classified as crest, depression, slope or flat calculated using the Benthic Terrain Modeller extension for ArcMap 9.3) (Wright et al. 2005); *rugosity*, *slope* and *aspect* (derived from stereo image reconstructions, described in the next paragraph); and *productivity* and *water clarity* (estimated for each site using long-term modelled data on chlorophyll and Secchi disk measurements).

Three-dimensional triangular mesh terrain reconstructions with ±10 mm resolution were created for each image using the stereo image pairs combined with information on vehicle position and orientation (Mahon et al. 2008, Johnson-Roberson et. al. 2010) and used to calculate rugosity, slope and aspect (see Friedman et al. 2010). *Rugosity* was expressed using a rugosity index (*RI)*, calculated by centring a window over each 1.5 × 1.2 m AUV stereo image pair and dividing the area of the contoured surface contained within the window by the area of its orthogonal projection onto the plane of best fit. The contoured surface area is the sum of the areas of the triangles that make up the surface, and the plane of best fit was found using principal component analysis. An *RI* value of 1 represents a completely flat surface, and this value increases with increasing fine-scale roughness. *Slope (S)* refers to the smallest angle between the plane of best fit and the horizontal plane. Fitting a plane to the data removes *S* from *RI* and ensures the two values are independent; although many rugose habitats also exhibit high slope, a steep flat plane (i.e. a reef wall) can be recognised as having high slope but low rugosity. *Aspect (A)* refers to the direction that the plane faces, which is measured as the angle between north and the horizontal projection of the vector normal onto the horizontal plane. Aspect values were transformed to harmonics (sin[a] and cos[a]) and treated as joint variables. Water column productivity and water clarity values were estimated from models of long-term GBR water quality at each site (see De'ath 2007) and accessed via the AIMS e-atlas (http://e-atlas.org.au/geoserver/wms). Where the model extends only to the edge of the emergent reefs (Viper Reef or Hydrographers Passage), estimates were obtained as close as possible to the study site (<10 km in both cases), which was deemed sufficiently accurate, particularly given the GBR-wide scale of the model. Being located on the outer-shelf, all sites were clear and oligotrophic compared to inshore regions. However there was variation between sites: water clarity was highest at Noggin Pass (Secchi depth = 20.1) and lowest at Viper Reef (17). Chlorophyll was twice as high at Hydrographers Passage (0.67 µg/l) than at the two more northerly sites (0.3 to 0.35 µg/l); however, all sites showed much lower chlorophyll levels than areas further inshore. All abiotic variables were normalised (mean = 0 and SD = 1) using PRIMER prior to statistical analysis.

Data analysis

Statistical analysis was performed using PRIMER v6 (Clarke and Gorley 2006). Statistical analysis used in PRIMER was performed on a Bray–Curtis similarity matrix (the complement of the dissimilarity matrix, B–C*100), the standard format for PRIMER. The ANOSIM (analysis of similarities) function was performed on a Bray–Curtis similarity matrix of the relative abundances of morphological units to determine the relationships and significance of variation observed in the four AUV surveys and across the three sites. ANOSIM is an approximate analogue for standard univariate one-way and two-way ANOVA tests. Similarity percentages (SIMPER) were used to examine the contribution of individual morphological units to variations indicated by ANOSIM. Hierarchical cluster analysis was performed to identify image groups based on their dominant sessile benthic megafauna (Ward’s sum of squares index; group-average linkage, after Done 1982). The influence of the abiotic variables on relative abundances of morphological units was also tested using the BIOENV function within PRIMER. Spearman rank correlation was used to determine the strength and significance of relationships between the Bray–Curtis similarity matrix (sessile benthic megafauna) and a normalised Euclidean distance matrix (based on the abiotic data). Multidimensional scaling (MDS) was used to illustrate the relative similarity among images and sites, as well as the relationship of images and image groups to the explanatory abiotic variables with a Spearman rank correlation >0.5. Shannon’s diversity index ($H' = 1 - \Sigma Pi[\ln Pi]$, where Pi is the proportion that MUi contributes to the total score in any one image) was calculated for each image as a measure of its taxonomic diversity.

Results

Site-scale community structure

Analysis at the scale of each 100 × 100 m site (400 images in total) showed that most of the seafloor was non-reef substratum containing very little sessile benthic megafauna. By comparison, separate analysis of ‘images from reef’ substrata revealed abundant and diverse sessile benthic megafaunal communities occurring in reef habitats. Cluster analysis of the site-scale data (not reproduced here) yielded five megafaunal image groups, of which one, based on shared absences, accounted for 316 (79%) of the images. This group included all the images of non-reef substrata (sand and gravel), of which most were without any sessile benthic megafauna at all (85, 96 and 91% at Noggin Pass, Viper North, and Viper South, respectively). Hydrographers Passage had fewer images with low cover of sessile benthic megafauna (44%). Although not quantitatively scored, algal colonisation of non-reef substrates was observed in the images and varied considerably between sites. The calcareous green alga *Halimeda* was ubiquitous in non-reef images at Viper Reef. Non-reef areas at Noggin Pass were generally completely bare; however, *Halimeda* growth was observed on lower reef slopes. *Halimeda* was scarce at Hydrographers Passage.

Communities on reef substrata

Communities of sessile benthic megafauna occurring on reef substrata showed considerable variation among all four surveys (Table 4.1). Dominant groups of sessile benthic megafauna identified were Porifera (sponges), Scleractinia (hard corals), Antipatharia (black corals) and Octocorallia (soft corals) (Figure 4.3, Table 4.2). Hard corals (particularly *Montipora)* occurred at all sites, although they were particularly dominant at Viper Reef (Figure 4.4a). Hydrographers Passage contained a high diversity of phototrophic octocorals (particularly *Cespitularia)* and the phototrophic sponge *Carteriospongia* in addition to corals (Figure 4.4b). By contrast, the large, distinctive heterotrophic octocoral *Annella* (Figure 4.4c) was particularly abundant at Noggin Pass, but rare elsewhere. Overall, both the richness of morphological units and diversity (*H*') was highest at Hydrographers Passage (32 morphological units, *H*' = 1.85), and only slightly lower at Noggin Pass (27 morphological units, *H*' = 1.81). Diversity was lower at both Viper Reef sites (24 morphological units, *H*' = 1.35 for Viper North; 26 morphological units, *H*' = 1.60 for Viper South).

ANOSIM indicated significant variation in abundance of sessile benthic megafauna between all three sites (Table 4.1). Noggin Pass and Hydrographers

Passage were more similar to each other than to Viper Reef. The two adjacent surveys at Viper Reef were more similar to each other than any other combination of sites, although the variation was still significant (Table 4.1). SIMPER indicated that the most important contributors to the observed variation were *Montipora*, *Annella* and *Carteriospongia*. Differences in the abundance of Montipora in combination with one other taxon explained 15 to 22% of the differences in all pairwise comparisons of sites: *Montipora* and *Annella* (Noggin vs. Viper), *Montipora* and *Carteriospongia* (Noggin vs. Hydrographers and Viper vs. Hydrographers). Variation in the relative abundance of *Montipora* explained 12.5% of the observed dissimilarity between the two Viper Reef surveys.

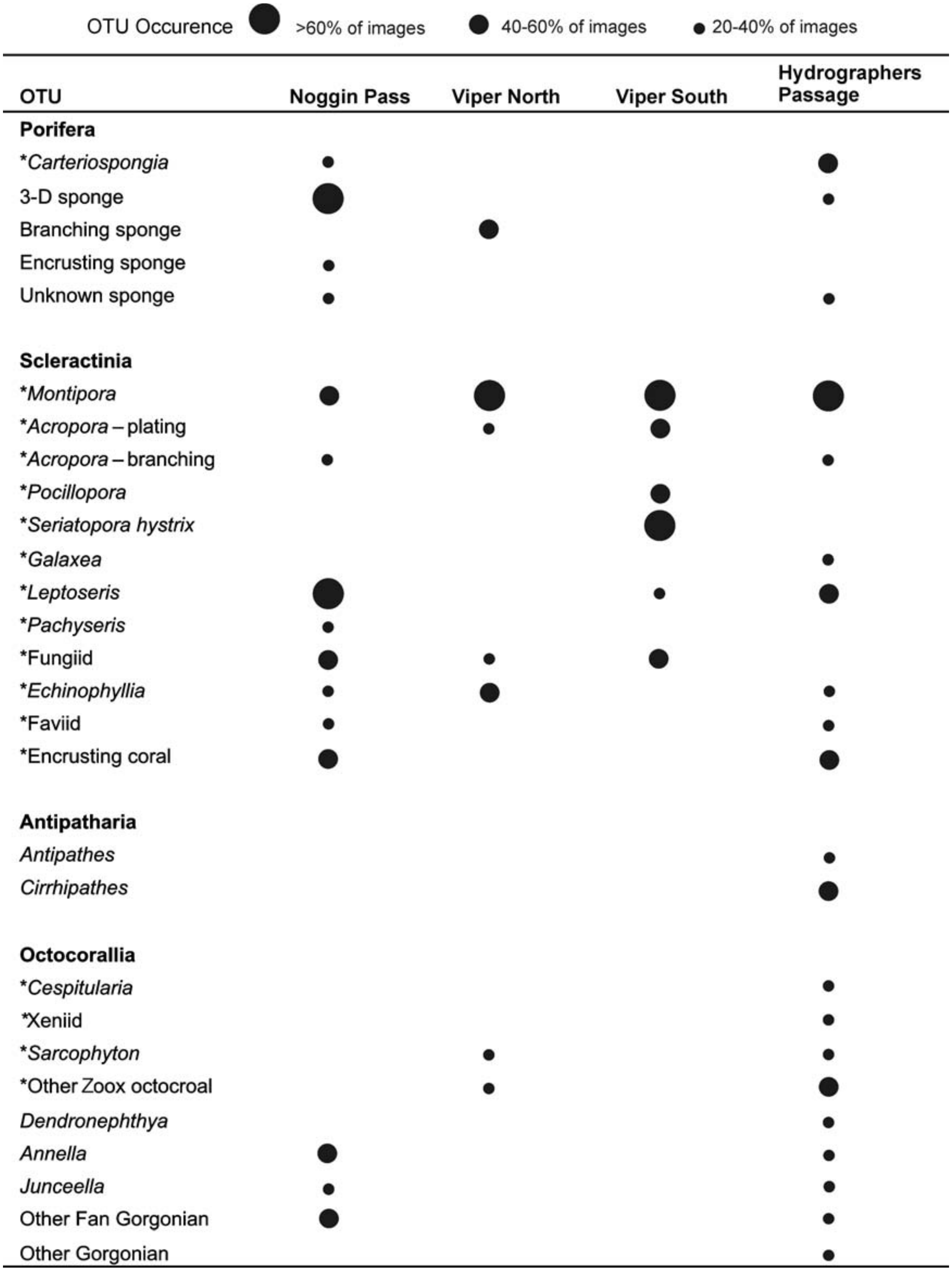
Table 4.1: Summary of ANOSIM results indicating variation in benthic composition between sites (latitudes) and AUV surveys on reef substrates. The lower the R-value, the more similar the sites. Latitude is recorded as 17˚S (Noggin Pass), 19˚S (Viper Reef), and 20˚S (Hydrographers Passage). AUV surveys are recorded as NP (Noggin Pass), VN (Viper North), VS (Viper South) and HP (Hydrographers Passage).

	Comparison	**R-value**	**Sig. level (p)**
(a) Sites (°S)	17˚ vs 19˚	0.541	0.001
	17˚ vs 20˚	0.289	0.001
	19˚ vs 20˚	0.548	0.001
(b) AUV Surveys	NP vs VN	0.475	0.001
	NP vs VS	0.488	0.001
	NP vs HP	0.289	0.001
	VN vs VS	0.175	0.002
	VN vs HP	0.373	0.001
	VS vs HP	0.484	0.001

Table 4.2: Summary of biotic and abiotic variables for the seven faunal dominance image groups identified using cluster analysis. Mean percent cover values are shown for benthic megafauna and substrata, calculated using the relative abundance scale described in the methods. Percent cover for any given score was considered as the mid-point for that category; a score of five in the data matrix was therefore estimated to represent 90% cover of that MU/substrate. Morphological units/substrata with % cover <2% are not shown, while abundances between 2-4% are indicated by a +. Standard deviations of percent cover for each MU are shown in brackets. * denotes phototrophic taxon. Diversity H' was calculated for all sites within the group combined.

Morphological Unit			**Fauna**	**Group**			
	1	**2**	**3**	**4**	**5**	**6**	**7**
No. Images	41	11	5	7	10	12	14
Porifera							
*_Carteriospongia_				23 (15)			6 (8)
Ianthella						+	
3-D sponge		+				4 (6)	+
Branching Sponge		+	+				
Unknown Sponge				+		+	
Scleractinia							
*_Montipora_	29 (19)	22 (18)	7 (7)	15 (6)	10 (18)	5 (6)	+
*_Acropora_ - plating	+			+			
*_Acropora_ - branching				4 (3)			
*_Pocillopora_	+						
*_Seriatopora hystrix_	+			+			
*_Galaxea_			48 (16)	5 (7)			
*_Leptoseris_		6 (5)		+	4 (6)	4 (5)	+
*_Pachyseris_		+				+	
*Fungiid	+				+	+	
*_Echinophyllia_		11 (16)					+
*Faviid		+					
*Encrusting coral		4 (4)		+	22 (12)	+	
Antipatharia							
Antipathes					13 (23)		
Cirrhipathes			+	+			
Octocorallia							
*_Cespitularia_			+	4 (4)			
*_Sarcophyton_				+			
*_Sinularia_				+			
*Xeniid				7 (9)			

*Other zoox. octocoral				5 (3)			
Annella						18 (14)	
Junceella				4 (3)		+	
Fan gorgonian				+	7 (8)	+	
Other gorgonian						+	+
Abiotic Variables (mean values)							
Rugosity Index (RI)	1.2	1.5	1.4	1.2	1.6	1.5	1.3
Slope (˚) (S)	20.3	37.7	17.8	15.4	49.5	43.0	30.4
Sand (%)	+	+	+	+	+	8	8
Gravel (%)					+	12	6
Rubble (%)						5	+
Sediment-Covered (%)	6	3	11	60	7	21	29
Limestone (%)	82	84	83	42	83	52	52
Diversity (H’)	1.5	1.8	1.3	2.4	1.6	1.9	1.6
MU Richness	32	23	9	26	20	21	32



OTU Occurence ⬤ >60% of images ● 40-60% of images • 20-40% of images

OTU	Noggin Pass	Viper North	Viper South	Hydrographers Passage
Porifera				
**Carteriospongia*	•			●
3-D sponge	⬤			•
Branching sponge		●		
Encrusting sponge	•			
Unknown sponge	•			•
Scleractinia				
**Montipora*	●	⬤	⬤	⬤
**Acropora* – plating		•	●	
**Acropora* – branching	•			•
**Pocillopora*			●	
**Seriatopora hystrix*			⬤	
**Galaxea*				•
**Leptoseris*	⬤		•	●
**Pachyseris*	•			
*Fungiid	●	•	●	
**Echinophyllia*	•	●		•
*Faviid	•			•
*Encrusting coral	●			●
Antipatharia				
Antipathes				•
Cirrhipathes				●
Octocorallia				
**Cespitularia*				•
*Xeniid				•
**Sarcophyton*		•		•
*Other Zoox octocroal		•		●
Dendronephthya				•
Annella	●			•
Junceella	•			•
Other Fan Gorgonian	●			•
Other Gorgonian				•

Figure 4.3: Abundance of morphological units in each autonomous underwater vehicle (AUV) survey. Circles: percentage of images in which each MU occurred, with larger circles representing higher percentage of images (morphological units occurring in <20% of images in all four AUV surveys not shown). Zoox.: zooxanthellate; *phototrophic taxon

Cluster analysis on the reef images (25 from each site) suggested seven image groups based on their sessile benthic megafauna (Table 4.2). Groups 1 (*Montipora* community) and 4 (*Carteriospongia*) were dominated by diverse phototrophic taxa, including various corals, zooxanthellate octocorals and phototrophic sponges. Group 2 (*Echinophyllia*) was characterised by corals from the family Agariciidae; although *Montipora* was commonly observed, it was not as dominant as in Group 1. Groups 5 (Azooxanthellate octocorals) and 6 (*Annella*) were dominated by heterotrophic suspension-feeding taxa in addition to *Montipora* and *Leptoseris*. Group 3 (*Galaxea*) was dominated by large colonies of the hard coral *Galaxea* but consisted of only five images, while Group 7 was a non-conformist group based on shared absences of most morphological units.

Most image groups were found predominantly at only one site (Figure 4.5a). The *Montipora* and *Galaxea* communities were common at both Viper Reef sites, while the *Annella* community was found exclusively at Noggin Pass. Hydrographers Passage was the most heterogeneous site, recording six of the seven groups, including all of the *Carteriospongia* group images and most of the Azooxanthellate octocorals group. BIOENV indicated the variables *slope*, *water clarity*, and *chlorophyll* best explained the observed variation in the relative abundances of megafauna across the four sites ($\rho = 0.458$). Interrelationships among the predictors and communities are indicated in Figure 4.5b. The influence of slope is revealed by the occurrence of heterotroph-dominated communities on the right of the figure (steep slopes), while autotroph-dominated communities (*Montipora* and *Galaxea*) occur to the left. The lower central position of the *Carteriospongia* community in Figure 4.5 possibly reflects its mixotrophic capacities in waters of higher productivity (see *Chlorophyll* vector in Figure 4.5b).

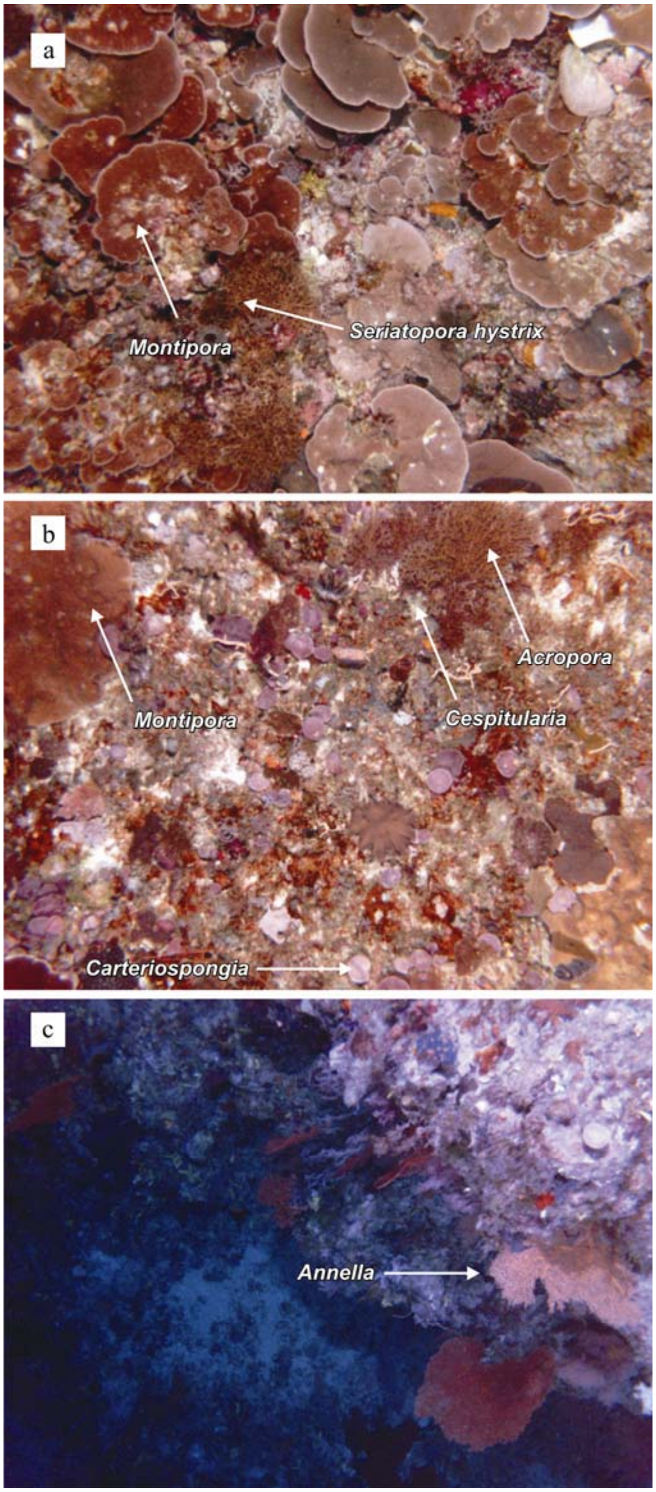


Figure 4.4: Representative autonomous underwater vehicle (AUV) images showing communities characteristic of each study area: (a) community heavily dominated by scleractinian corals at Viper Reef; (b) diverse phototrophic community occurring on a flat reef top at Hydrographers Passage; and (c) steep wall with abundant colonies of *Annella* at Noggin Pass.

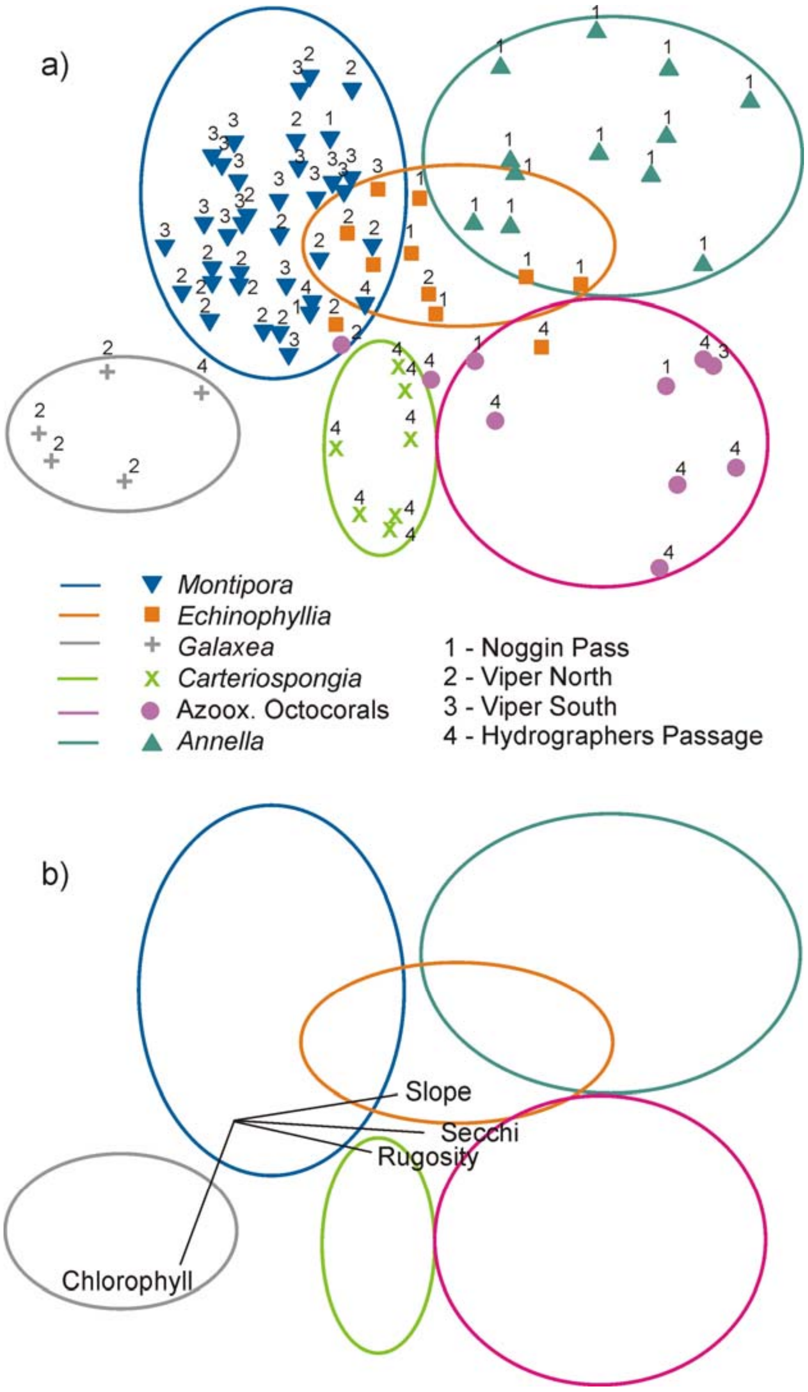


Figure 4.5: Multidimensional scaling diagram showing distribution of image groups based on relative abundance of sessile benthic megafauna relative to environmental variables. Colours represent image groups identified in cluster analysis; (a) Sites: 1 = Noggin Pass, 2 = Viper North, 3 = Viper South, 4 = Hydrographers Passage. Group 7 (non-conformist group) not shown. (b) Location of image groups relative to explanatory environmental variables (only vectors with Spearman rank correlation >0.5 are shown). Azoox. = azooxanthellate.

Discussion

Site-scale community composition

Not surprisingly, the best predictor of the presence of sessile benthic megafauna at the site scale was the presence of reef substrate, which clearly contained the highest abundance and diversity of sessile benthic megafauna. However, the overwhelming abundance of non-reef substrata in the random site-scale sampling was not suitable to identify explanatory variables other than substrate type. Nonetheless, these results show that submerged reefs of the GBR shelf-edge, formed by shallow-water coral communities during lower sea levels, now provide important habitat for MCE communities. The varying patterns of algal abundances on non-reef substrates between sites may reflect variations in localised upwelling and nutrient availability at different sites. The presence of *Halimeda* fields to 96 m depth in the central GBR (Drew and Abel 1988) was attributed to localised upwelling of nutrients onto the continental shelf, and Leichter et al. (2008) report similarly dense macroalgal communities at 50 to 60 m adjacent to the Florida Keys. Although the *Halimeda* fields observed at 55 to 60 m depth at Viper Reef did not correlate with higher surface chlorophyll, the reduced water clarity may indicate localised upwelling. In addition to encouraging algal growth, nutrient availability could be an important control on the composition of sessile benthic megafaunal communities on reef substrates. Species richness of heterotrophic octocorals on the shallow-water GBR is closely correlated with areas of high water-column productivity (Fabricius and De’ath 2008). Interestingly, very few heterotrophic suspension-feeders were observed at either Viper Reef site. There is also evidence that phototrophic corals may increase reliance on heterotrophy in nutrient-rich or light-limited environments (e.g. Anthony and Fabricius 2000, Leichter and Genovese 2006), although this is poorly quantified.

Community composition on reef substrata

This study revealed a consistent pattern of phototrophic taxa inhabiting the flatter tops of reefs and heterotrophic suspension-feeders occurring on steeper slopes. Light limitation is, by definition, an important factor driving MCE community structure (e.g. Kahng and Kelley 2007, Kahng et al. 2010), and the limiting effects of low ambient light levels at these depths may be exacerbated by relatively small increases in slope. The few obligate phototrophs that did occur on steeper slopes represent taxa commonly reported from MCEs elsewhere in the Indo-Pacific (Kahng et al. 2010), and probably have either a very broad ecological niche enabling them to survive in an extremely wide range of habitats (e.g. *Montipora*) or are “MCE specialists” (e.g. *Leptoseris*), which possess specific adaptations to low-light environments (Fricke et al. 1987).

Sedimentation has been shown to be an important control on growth of phototrophic taxa (e.g. Van Woesik and Done 1997, Fabricius 2005), particularly in inshore areas. Flat substrata in low flow areas are prone to sedimentation, limiting both the settlement of new recruits and the survival of established colonies (Fabricius 2005). Although MCEs generally occur in clear oceanic environments (Kahng et al. 2010), there is evidence that sediment downwelling may be an important factor in their community composition in some areas (Colin et al. 1986, Bridge et al. 2010). Many corals in mesophotic habitats adopt flattened morphologies to better intercept light (e.g. Jaubert 1977, Wallace 1978); however, this increases their vulnerability to sedimentation. Plating *Montipora*, which was abundant in this study, are particularly poor at removing sediment from their surface (Stafford-Smith and Ormond 1992). This may contribute to the occurrence of phototrophs on the tops of reef pinnacles, where they receive not only sufficient photosynthetically active radiation (PAR), but are also kept free of sediment. Heterotrophic, suspension-feeding taxa not dependent on light would be better able to utilise steep habitats less vulnerable to sedimentation.

Despite the consistent patterns in the distribution of functional groups, there were substantial variations in community composition between sites. These patterns may reflect variations in oceanographic conditions at each site, the ecology and life histories of different taxa, or spatial autocorrelation not detectable without replicates at each site. However, some insights may be obtained by comparing the patterns observed on MCEs to adjacent shallow-water reefs. Phototroph communities at Viper Reef and Noggin Pass were heavily dominated by hard corals (Figure 4.4a), while Hydrographers Passage exhibited a higher diversity of phototrophic taxa including zooxanthellate octocorals (particularly *Cespitularia*) as well as corals (Figure 4.4c). The emergent reefs near Hydrographers Passage (along with the southern Swain Reefs) contain the highest diversity of *Cespitularia* in the GBR (e-atlas, modelled using data from Fabricius and De'ath 2008), suggesting at least some observations in this study may reflect broad-scale distribution patterns rather than within-site differences.

Community composition for heterotrophs was similarly variable. Steep walls at Hydrographers Passage were colonised by a variety of heterotrophic octocoral taxa as well as *Antipathes*, whereas similar habitats at Noggin Pass were dominated by *Annella* (Fig .4c). Although heterotrophic octocoral taxa show relatively homogeneous habitat requirements (Fabricius and De'ath 2008), many exhibit limited ranges and/or patchy distributions within the GBR. This is probably caused by settlement of negatively buoyant brooded larvae only a few metres from the parent colony (Fabricius and Alderslade 2001). The ability of a wide range of taxa to utilise similar habitat combined with limited dispersal ability may cause significant heterogeneity in community composition on relatively small scales (metres to tens of metres) as well as between sites. Unfortunately, given the lack of replicates at each site, it is not possible to disentangle such small-scale, within-site variation from regional patterns.

Richness of heterotrophic octocoral taxa is strongly correlated with depth, current flow, slope and a lack of wave action, resulting in richness being highest in deep waters with high productivity where competition with phototrophs is less intense. In the GBR lagoon these conditions occur along inshore regions of the northern GBR (Fabricius and De'ath 2008). However, much more extensive areas with similar environmental conditions may also occur on many of the submerged reefs, particularly at Hydrographers Passage. At the depths examined in this study, the flat reef tops still receive enough light to allow competition from phototrophs. However steep walls and also deeper submerged reefs (described to 147 m depth in Bridge et al. 2010) may provide a habitat perfectly suited to heterotrophic octocorals.

Implications for GBR and Indo-Pacific MCEs

The development of tools to assess MCEs at large spatial scales using physical and environmental proxies is an important factor in overcoming current knowledge gaps regarding the nature and distribution of MCEs. The use of remotely sensed data is particularly important on the GBR, where MCEs occur far offshore, and restrictive diving legislation makes obtaining samples difficult. The vast majority of sessile benthic megafauna occur on reef substrates, and community structure is heavily influenced by fine-scale (decimetres to metres) topography. Predictive modelling of sessile benthic megafaunal communities on GBR MCEs would therefore require bathymetry and side-scan sonar data of sufficient resolution to detect topographic and substrate changes at these scales. This would be made possible by the collection of high- resolution (up to 5 × 5 m) multibeam and backscatter reflectivity data. However, the highest resolution digital depth models currently available for the GBR are 250 × 250 m (Lewis 2001). Large scale modelling of GBR MCEs in areas without high resolution AUV (or equivalent) data would require an understanding of mesoscale (10s to 100s km) variations in MCE biodiversity. For this purpose, representative replicated sampling is needed, and such sampling needs to be stratified to account for the local scale patterns, which were difficult to determine in the present study.

However, should such data be collected, it would no doubt be of significant interest to managers of the Great Barrier Reef World Heritage Area.

This study has demonstrated that diverse MCE communities occur for at least 500 km along the GBR shelf-edge. Given that submerged reefs have been documented occurring continuously from the Ribbon Reefs (15° S) to the southern edge of the Swain Reefs (23° S, ~350 km south-east of Hydrographers Passage) (Tilbrook and Matear 2008) as well as in the far northern GBR (10° S, and Gulf of Papua) (Harris et al. 2005), mesophotic reef communities probably exist for >1700 km along the GBR shelf-edge. The presence of diverse octocoral communities as well as large plating coral colonies supports the view that the submerged reefs are rarely subjected to disturbances such as storms and bleaching events. Although tropical cyclones are relatively common at all three sites (Massel and Done 1993), storms of sufficient magnitude to affect community structure at these depths are probably extremely rare. Massel and Done (1993) demonstrate that even as shallow as 12 m, waves and currents strong enough to dislodge massive corals are so rare that corals have a high probability of reaching 50 to 100 years old (unless they are killed by some other means). In addition, their location several kilometres offshore of emergent reefs means they would not be subjected to storm debris avalanches, such as those observed decimating mesophotic reef habitats in French Polynesia (Harmelin-Vivien and Laboute 1986). The presence of large colonies of both corals and heterotrophic octocorals at all sites suggests these reefs have not been affected by cyclone damage for many years, lending support to the hypothesis that MCEs may be important refugia for coral reef fauna. With shallow-water reefs under increasing pressure from both direct anthropogenic impacts and climate change, MCEs may become increasingly important to the health and resilience of coral reef ecosystems both in the GBR and elsewhere. Given these results, GBR MCEs deserve further study not only of their sessile benthic megafauna, but also of their fish and mobile invertebrate communities.

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Chapter 5

Habitat suitability modelling to predict the distribution of sessile benthic megafauna on mesophotic reefs and estimate the total amount of mesophotic reef habitat in the Great Barrier Reef World Heritage Area

Habitat suitability modelling was used to predict the occurrence and spatial extent of sessile benthic megafaunal taxa and communities at two spatial scales: a site-scale analysis from Hydrographers Passage and a regional-scale analysis for the entire Great Barrier Reef World Heritage Area. The results suggest that extensive mesophotic reef communities occur both on the deeper flanks of emergent reefs inside the GBR lagoon, and also on the submerged reefs of the outer-shelf. The research presented in this chapter primarily addresses research aim 4, but is informed by conclusions obtained from chapters 1, 2 and 3.

This chapter is presented in the form of a research paper and will shortly be submitted to the international journal Global Ecology and Biogeography. The paper has five co-authors:

- Dr Terry Done provided editorial support and provided guidance on the interpretations and ideas discussed within the paper
- Dr Robin Beaman conducted the multibeam swath mapping on board the RV *Southern Surveyor* and created the bathymetry layer used in the regional-scale analysis, provided guidance on the modelling techniques and provided editorial support.
- Dr Stefan Williams and Dr Oscar Pizarro collected the AUV data on board the RV *Southern Surveyor*.

- Dr Jody Webster provided funding for the RV *Southern Surveyor* expedition, and also provided editorial support.

Predicting the distribution and spatial extent of mesophotic coral reef habitat: A case study using the Great Barrier Reef, Australia

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Abstract

Predictive habitat models are an increasingly important tool for scientists and managers for identifying the distribution of species and/or communities which have not been extensively sampled, such as rare or cryptic species or communities in inaccessible habitats such as the deep sea. Mesophotic coral reef ecosystems (MCEs) are coral reef communities which occur in the lower photic zone. Because they occur below the depths accessible to traditional SCUBA surveys, the ecology of MCEs is poorly known. However, recent studies have indicated that MCEs contain unique ecological communities and may also provide vital refugia for corals and associated species from the effects of climate change. In this study, maximum entropy modelling techniques were used on data derived from high-resolution topographic mapping to identify potential mesophotic reef habitat for four genera (*Carteriospongia*, *Cespitularia*, *Annella* and *Dendronephthya*) and two community types (phototrophic and heterotrophic-dominated benthic communities) at two spatial scales in the Great Barrier Reef World Heritage Area (GBRWHA), Australia. Suitable habitat for phototrophs occurred on submerged reefs along the GBR outer-shelf and also on the deeper flanks of known reefs inside the GBR lagoon. In contrast, suitable habitat for heterotroph communities occurred primarily in deeper waters (90-120 m depth) along the GBR outer-shelf. The results indicate that almost 10 000 km^2 of MCE habitat occurs in the GBRWHA, of which only 763 km^2 is currently documented as reef habitat by GBRMP managers. This study also provides a framework for identifying MCE habitat in other parts of the world, including the poorly sampled Coral Triangle, the epicentre of coral reef biodiversity. Identifying potential MCE habitat which may provide refugia for coral reef species from environmental stress should be a priority for coral reef scientists and managers in coming decades to ensure their adequate protection.

Introduction

Species distribution models have been used in a variety of ecological applications, including predictive modelling of rare or endangered species (Raxworthy et al. 2003; Tinoco et al. 2009), conservation planning (Corsi et al. 1999; Ferrier 2002), invasive species management (Peterson 2003; Ward 2007), and predicting climate change impacts (Peterson et al. 2002; Guinotte et al. 2003). Unfortunately, in many cases biological survey data tend to be sparse and/or limited in coverage, making them unsuitable for many traditional modelling methods such as generalised linear models (GLMs) or classification and regression trees, which require accurate absence data (Elith et al. 2011). However in recent years, there has been significant improvement in the performance of models that require only georeferenced presence-only data (Raxworthy et al. 2003; Phillips et al. 2006; Phillips and Dudik 2008). The program MaxEnt uses maximum entropy techniques to create models of the relative probability of species distribution across a study area using presence-only data (Phillips et al. 2004; Phillips et al. 2006). MaxEnt has been used in both terrestrial and marine ecosystems and has been shown to perform favourably relative to other presence-only modelling techniques, particularly with small sample sizes (Phillips et al. 2006; Elith et al. 2006; Pearson et al. 2007; Elith et al. 2011).

The use of environmental surrogates to predict suitable habitat for species and/or communities over large spatial scales is of significant value to scientists and managers for identifying priority areas for conservation (Ward et al. 1999). In the marine environment, identification of hard-bottom habitat has been used as a proxy for biodiversity, particularly on coral reefs (e.g. Dunn and Halpin 2009). However, significantly more informative predictive models regarding the distribution of species or communities can be generated by using a greater variety of environmental data. Identifying the combination of environmental variables most predictive of a species or community enables predictions of suitable habitat in areas where biological survey data are unavailable. This is particularly useful for remote and/or inaccessible habitats such as in the deep-sea (e.g. Davies et al. 2008; Tittensor et al. 2009).

Mesophotic coral reef ecosystems, or MCEs, are coral reef communities which occur in the lower reaches of the photic zone (30-150 m depth) (Hinderstein et al. 2010). MCEs have received little research effort compared to their shallow-water counterparts due to their inaccessibility to traditional SCUBA surveys. However, recent technological developments such as autonomous underwater vehicles (AUVs) and remotely operated vehicles (ROVs) have led to a significant increase in MCE research in recent years (e.g Armstrong et al. 2006; Kahng and Kelley 2007; Bridge et al. 2011a, 2011b). This has been driven by recognition of both the unique biological character of MCEs, and also because they have the potential to act as refugia for corals and associated species from environmental stress such as warm-water bleaching and tropical storms (Riegl and Piller 2003; Hinderstein et al. 2010; Kahng et al. 2010; Bongaerts et al. 2010). There is also evidence spawning aggregations for a variety of fish species (including some of commercial importance) occur on mesophotic reefs (Nemeth 2005).

Given the well-documented degradation of shallow-water reefs from a variety of anthropogenic activities and the increasing threat of global climate change (e.g. Done 1999; Hoegh-Guldberg 1999; Hughes et al. 2003; Kleypas and Eakin 2007), MCEs may play a critical role in maintaining coral reef biodiversity in coming decades by providing both refugia for coral reef species and also a source of colonists to re-seed shallow-water habitats affected by an acute disturbance event. However, most studies of MCEs to date have been conducted in the western Atlantic (Armstrong et al. 2006) or Hawaii (Kahng and Kelley 2007; Rooney et al. 2010). Very little research has occurred in the Indo-west Pacific, despite this region containing substantially greater marine biodiversity.

Marine Protected Areas (MPAs) have become an important tool for conserving coral reefs from climate change and other human impacts (Salm et al. 2006; Almany et al. 2009). Ecological connectivity between reefs is a key consideration in the design of MPAs (McCook et al. 2009; Almany et al. 2009). However, the current knowledge gap with regard to MCEs generally results in their omission from coral reef connectivity models. Arguably, the contribution of MCEs to the overall function of coral reef ecosystems may be critical to assessing their resilience to the impacts of climate change. Given the logistical problems associated with direct observations of MCEs, predictive models of the potential location and extent of MCE habitat provide a critical first step for managers of coral reefs to gain maximum benefit from MPAs.

Coral reef habitat is currently regarded as occupying approximately 7% of the 348 000 km^2 Great Barrier Reef Marine Park World Heritage Area (GBRWHA). Although Pitcher et al. (2007) provide detailed models of the non-reef seabed communities on the continental shelf of the GBRMP, the study contained little data from the submerged reefs of the outer-shelf. Estimates of the total amount of reef habitat do take account of the extensive series of submerged reefs which occupy a significant area of the GBR outer-shelf (Hopley 2006; Hopley et al. 2007; Beaman et al. 2008), and have been shown to contain diverse mesophotic communities (Bridge et al. 2011a, b). Therefore, there may be a significant underestimation of the total area of coral reef habitat in the GBRWHA. Due to the potential importance of MCEs as refugia, accurate assessment of MCE habitats is an important component for understanding the ecological resilience of the GBR ecosystem. None of the myriad models of coral reef connectivity on the GBR (e.g. Wolanski et al. 1997; Ayre and Hughes 2000; Cappo and Kelley 2001; Bode et al. 2006) currently account for mesophotic reef habitat. If indeed MCEs are linked ecologically to shallow-water reefs, data deficiency regarding their location, extent and ecology represents a significant knowledge gap in understanding connectivity between reefs in the GBR ecosystem and, by extension, the effectiveness of management strategies to protect the GBR from both natural and anthropogenic threats.

In 2007, an expedition was conducted on board the RV *Southern Surveyor* to examine submerged reefs to depths of 150 m at four sites along the GBR shelf-edge (Webster et al. 2008). Data collected included high-resolution multibeam swath bathymetry, AUV imagery and specimens collected using a rock dredge, providing the first detailed assessment of MCE habitats on the GBR (Webster et al. 2008; Williams et al. 2010; Bridge et al. 2011a, 2011b, in review). In the present study, physical substrate properties derived from multibeam data are combined with occurrence records of sessile benthic megafauna from AUV images to generate habitat suitability models for MCE taxa and communities using maximum entropy modelling techniques at two spatial scales: (1) site-scale (~500 km^2 of MCE habitat at 5 x 5 m grid cell resolution), and (2) a regional (GBR-scale) with 100 x 100 m grid resolution. Although similar techniques have previously been applied to deep-sea coral communities (e.g. Davies et al. 2008; Tittensor et al. 2009), previous studies estimating the area of reef habitat in the United States for both shallow–water coral reefs (Rohmann et al. 2005) and

MCEs (Locker et al. 2010) have used only depth data as a predictor of potential coral reef habitat. Because reef distribution is generally patchy, this method causes substantial overestimation of the total area of reef habitat. This study uses high-resolution bathymetric data capable of resolving reef versus non-reef habitats, resulting in a significant increase in the accuracy and precision of habitat predictions and estimates. Therefore, this study provides a framework for future regional to global-scale modelling of coral reef habitats. Although this method may be utilised on a range of reef habitats it is particularly useful for predicting the occurrence of MCEs and, unlike previous studies, is conducted at a scale useful for marine managers. Given the potential importance of MCEs to coral reef resilience, this study will also provide scientists and managers with new information to better prepare coral reef ecosystems for the effects of global climate change.

Methods

Study Area

The GBR is composed of over 2900 individual reefs and stretches between approximately latitude 9˚S and 25˚S (Figure 5.1). The morphology of the GBR shelf-edge changes from north to south, being generally steeper in the north, and significantly affecting the morphology of the reefs which occur along it (Hopley 2006; Hopley et al. 2007). In the northern GBR, long, linear reefs located right on the shelf-edge form a true “barrier reef” system, with individual reefs up to 28 km long separated by narrow channels no more than one kilometre wide. A submerged reef has been observed at ~50 m depth to seaward of the Ribbon Reefs (Hopley et al. 2007; Beaman et al. 2008), however the shelf-edge is very steep and the 500 m isobath is reached only a few hundred metres from the emergent reefs. Below ~70 m the shelf becomes an almost vertical wall, leaving little space for the development of submerged reefs. South of about 16˚06'S, the shelf widens and most reefs are set back from the shelf-edge. This has allowed the development of an extensive series of submerged reefs, which run parallel to the

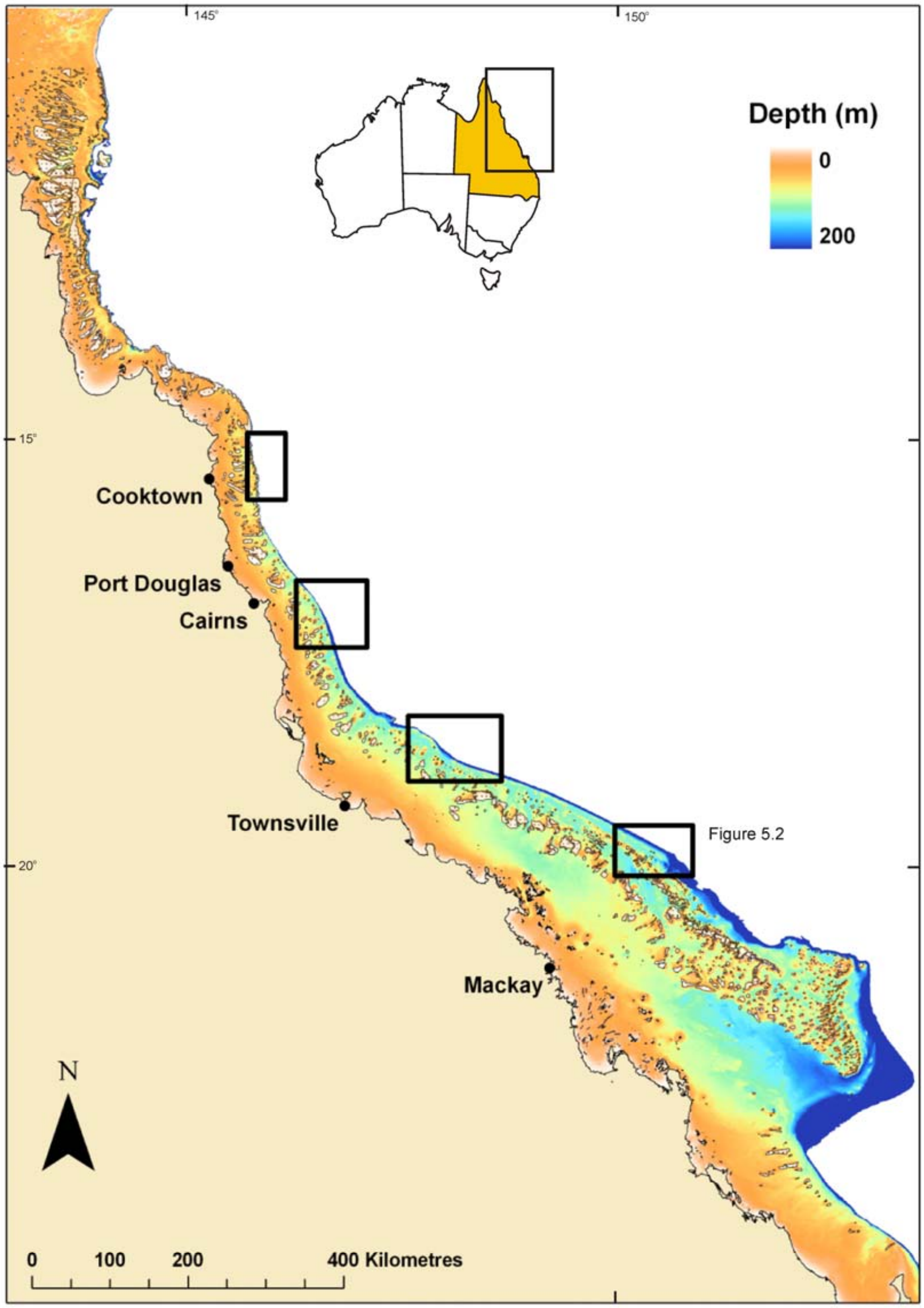


Figure 5.1: Digital Depth Model of the Great Barrier Reef World Heritage Area to the 200 m depth contour. Black outlines indicate locations of shelf-edge study sites examined in 2007

shelf-edge for over 800 km in the central GBR (Hopley 2006; Hopley et al. 2007). The low resolution model presented here covers the entire region from 10 to 25° S.

The high resolution model presented here covers the Hydrographers Passage region in the central GBR (19°40'S, 150°14'E; Figure 5.2). Here, the seafloor consists of a gently north-easterly sloping continental shelf margin, with lines of submerged reefs running parallel to the shelf break. The shallowest submerged reefs, located ~12 km seaward of the nearest emergent reefs, rise from ~50 m water depth to within 10-15 m of the surface. Beyond these shoals, the continental shelf slope is punctuated by at least six submerged reefs, with their tops at ~50, 55, 80, 90, 100 and 130 m (Bridge et al. 2011b).

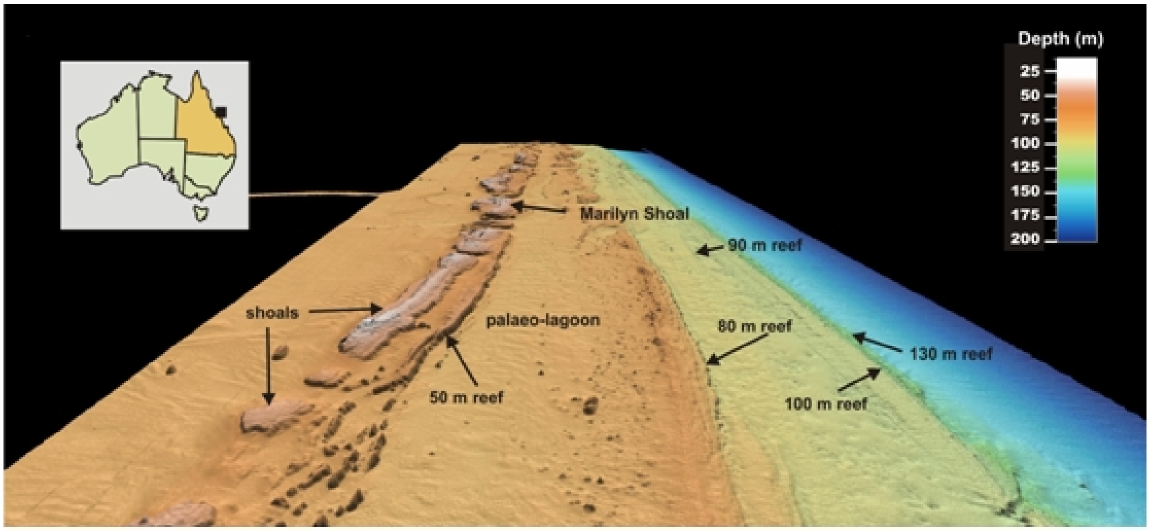


Figure 5.2: Bathymetry of Hydrographers Passage (5 x 5 m grid cells) showing the location of shoals and submerged reefs.

Species Records

High-resolution, site-scale models at Hydrographers Passage were developed for four genera commonly encountered during the RV *Southern Surveyor* expedition. MCEs are composed of a combination of phototrophic and heterotrophic taxa

(Bridge et al. 2011a), so therefore two genera of each trophic group were selected. The two phototrophic genera were the sponge *Carteriospongia* and the zooxanthellate octocoral *Cespitularia*. The two heterotrophs were both azooxanthellate octocorals, *Dendronephthya* and *Annella*. All four taxa appear to be relatively widespread on MCEs in the GBR. At the species and genus level, MCE community composition on the GBR varies considerably among sites, however there is much more uniformity among the trophic groups known to occupy certain habitats (Bridge et al. 2011a). Therefore, models investigating the extent of MCEs at a GBR-wide scale were conducted using trophic groups rather than specific genera. Models were generated for “phototrophic” and “heterotrophic” communities, based on their sessile benthic megafauna (Figure 5.3). Benthos and substratum occurrence records were taken from ten AUV surveys conducted between 28 September and 12 October 2007 (Webster et al. 2008). Phototroph communities consisted primarily of taxa which contain symbiotic dinoflagellates (*Symbiodinium* spp.), known as zooxanthellae. Taxa regularly observed in photosynthetic communities included zooxanthellate Scleractinia (e.g. *Acropora*, *Montipora*) and Octocorallia (e.g. *Cespitularia*), and phototrophic sponges (e.g. *Carteriospongia*). Heterotrophic communities consisted of zooxanthellae-free sessile benthic megafauna, which do not obtain any energy from by-products of photosynthesis, such as zooxanthellae-free Octocorallia (e.g. *Annella*, *Ellisella*), black corals (*Antipathes*) and wire corals (*Cirrhipathes* spp.). Occurrence records of species and communities were taken from ten AUV missions that covered all four sites examined during the RV *Southern Surveyor* expedition over 5° of latitude (Figure 5.1).

The variation in shelf morphology along the length of the GBR results in a substantially greater amount of space for the development of submerged reefs in the southern half compared to the steeply sloping north. This is particularly evident in the heterotrophic community which occurs in deeper waters 90-120 m deep; in much of the northern GBR these depths occur below the shelf break,

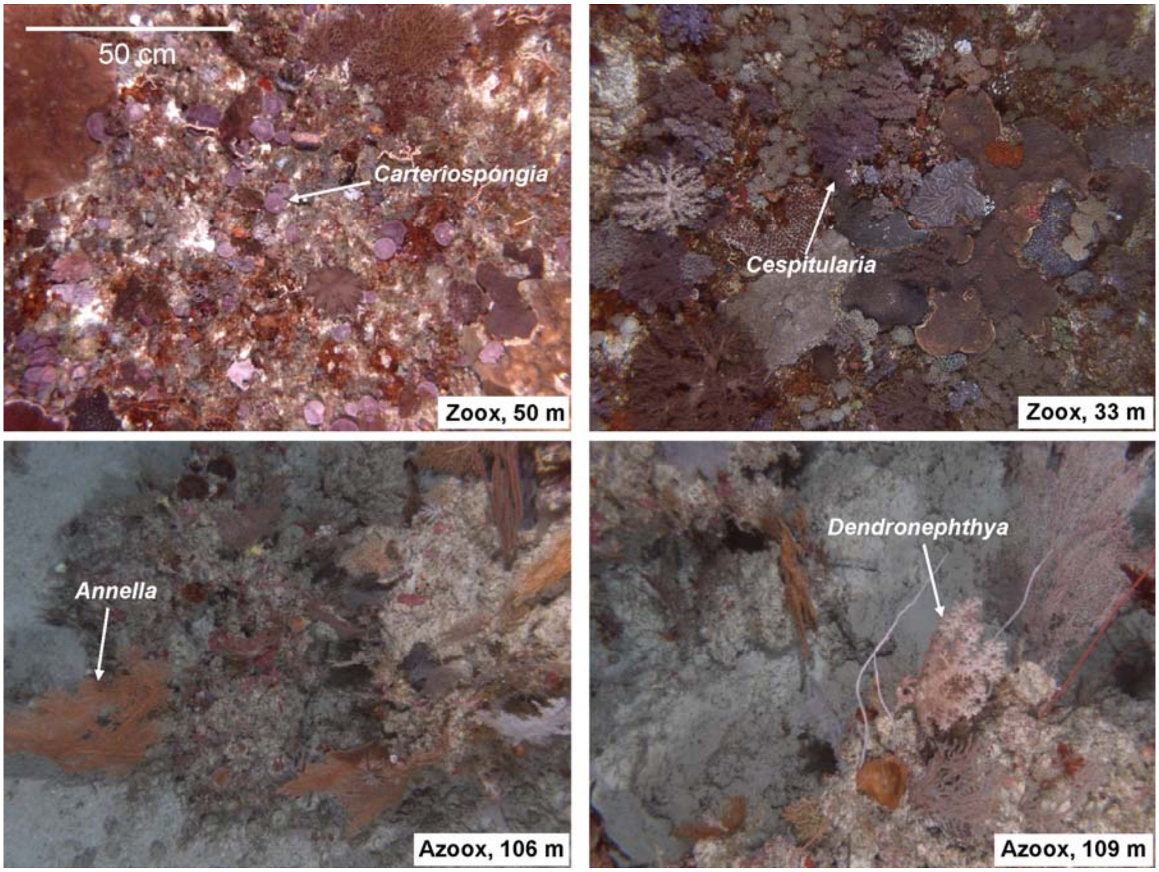


Figure 5.3: Examples of phototrophic (top) and heterotrophic (below) MCE communities, photographed using autonomous underwater vehicle (AUV). The four taxa used in site-scale models are indicated. Zoox. = Zooxanthellate (phototroph) community, Azoox. = Azooxanthellate (heterotroph) community

precluding the development of reefs during lower sea level stands. Therefore, a significantly higher number of occurrence records were found at the more southerly sites, particularly at Hydrographers Passage.

Environmental data

Environmental datasets for the high-resolution (5 x 5 m grid cell) models were derived from multibeam data collected on the RV *Southern Surveyor*. Data were collected using a ship-mounted Kongsberg™ Simrad EM-300 multibeam swath mapping system operating at a frequency of 30 kHz, with a swath width of 150° and 135 beams per ping. Multibeam bathymetric and acoustic backscatter data were processed within Caris™ HIPS/SIPS software to remove erroneous values and to apply appropriate corrections (e.g. tides and sound velocity), then gridded into a BASE (Bathymetry Associated with Statistical Error) surface at 5 x 5 m resolution. The BASE surface pixel values were exported to ASCII XYZ (long/lat/depth) files, cropped to include only <200 m depth values (potential mesophotic habitat), and then gridded within ArcGIS 9.3 to create georeferenced raster layers. Bathymetry data for the GBR-scale analysis were obtained from the “gbr100” grid, a new digital elevation model for the GBR with a resolution of 100 x 100 m (Beaman 2010).

Six environmental data layers were used in the high-resolution data study: *depth*, *slope*, *aspect*, *rugosity*, *geomorphic zones* and *substrate*. *Depth* values were derived from the multibeam bathymetry, and *slope*, *aspect*, *rugosity* and *geomorphic zones* were all derived from the digital elevation model and created in ArcGIS 9.3. *Aspect* and *slope* layers were both created using the relevant tools in the Spatial Analyst toolbox. *Rugosity* was generated using the Focal Statistics tool, which calculates a statistic (standard deviation) on a raster over a specified neighbourhood (in this case 3 x 3 cells). *Geomorphic zones* were generated using the Benthic Terrain Modeler (BTM) plug-in in ArcGIS to delineate the benthic zone boundaries of the physical landscape (Wright et al. 2005). BTM uses an input depth grid to generate Bathymetric Position Index (BPI) datasets through a neighbourhood analysis function. Positive cell values within a BPI dataset denote features that are higher than the surrounding area, such as ridges and pinnacles. Negative cell values within a BPI dataset denote zones that are lower than the surrounding area, such as canyons and gullies. BPI values near zero are either flat areas where the slope is near zero, or areas of constant slope where the slope is significantly greater than zero (Wright et al. 2005). For this study, grids were reclassified into four basic zones: crests, depressions, flats and slopes, using a 3° slope angle to differentiate between a flat and sloping seafloor.

Information on *substrate* was derived from sidescan data (available for Hydrographers Passage only). High backscatter values indicate the presence of harder (reef) substrate.

Modelling

Modelling was conducted using MaxEnt 3.2.19 (Phillips et al. 2004). MaxEnt uses environmental variable values at known species occurrence localities to impose constraints on the unknown distribution such that the mean and variance of the environmental variables in the model prediction are close to the empirical values of the occurrence data (Tinoco et al. 2009). The MaxEnt technique was used because: (1) it provides good estimates from a small number of occurrence records (Phillips et al. 2006; Hernandez et al. 2006); and (2) absence data is generally unreliable in poorly sampled regions, such as MCEs (Pearson et al. 2007).

Default model parameters used were a convergence threshold of 10^{-5} and a maximum iteration value of 500, which have been shown to achieve good performance on comparable datasets (Phillips and Dudik 2008). Model predictions are presented as cumulative probabilities, wherein the value of a given grid cell is the sum of that cell and all other cells with equal or lower probability (Phillips et al. 2006). Output cell values range from 0 to 1, indicating relative suitability (not probability) of occurrence. These values can be interpreted as an estimate of the probability of presence under a similar level of sampling effort as that used to obtain the known occurrence data (Phillips and Dudik 2008). Duplicate records (where multiple records were present within a single grid cell) were removed from the analysis, resulting in fewer occurrence records at the coarser grid resolution due to larger size of each grid cell. The relative importance of each environmental variable to the predictions of each model was identified using the jackknifing procedure within MaxEnt.

In each model, 70% of the occurrence localities were used as training data, with the remaining 30% used to test model results. The performance of both training and test datasets was evaluated using receiver operated characteristic (ROC) curves, with the area under the ROC curve (AUC) being a measure of model performance. In ROC analyses performed without true absence data, species able to exist in a wide variety of habitats have a smaller maximum achievable AUC than species with very specific habitat requirements (Phillips et al. 2006). Consequently, lower ROC values may be indicative of a broad ecological niche rather than poor model performance. In some cases low numbers of presence records may reduce the accuracy of AUC curves, therefore a separate “Leave one out” jackknifing procedure described by Pearson et al. (2007) was used to further test the strength of model predictions for the entire GBR. The procedure involves removing one occurrence locality from the dataset to test if the model can correctly predict that locality using the remaining occurrence records. The nature of the sampling effort (four sites along the GBR shelf) meant that many “samples” (AUV images) were in close proximity, leading to the potential for spatial autocorrelation. In order to minimise the effect of spatial autocorrelation on jackknife tests, all occurrence records from any one site were removed at the same time. The model was then run using all remaining sites to see if the model correctly predicted all the occurrence localities at the removed site.

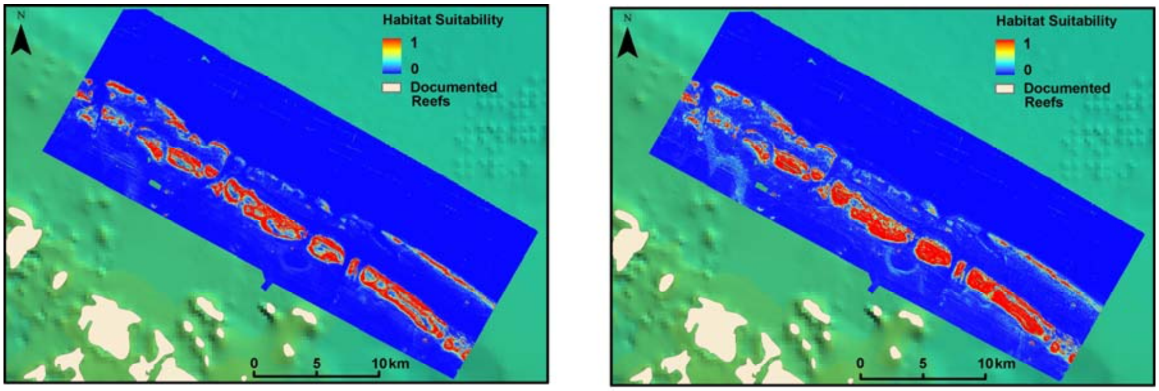
Modelling was conducted at two spatial scales, a high-resolution (5 x 5 m grid cells) site-scale and a lower-resolution (100 x 100 m) GBR-wide scale. One aim of the study was to examine the effectiveness of the lower-resolution bathymetry (available over far larger spatial scales) for predicting MCE habitat in areas where high-resolution bathymetry is currently unavailable. To investigate the effects of grid resolution on model predictions and the relative importance of environmental variables, identical occurrence data were used to model communities at Hydrographers Passage using both 5 x 5 m and 100 x 100 m grid cells.

The total area of MCE habitat in the GBRMP was estimated using cumulative probability model outputs that had been reclassified into Boolean maps using ArcGIS. The lowest presence threshold (Pearson et al. 2007) was used to determine areas of suitable habitat. This approach can be interpreted ecologically as identifying pixels predicted as being at least as suitable as those where a species' presence has been recorded. Consequently, it is a conservative estimate, identifying the minimum predicted area possible whilst maintaining zero omission error in the training dataset. Reef habitats are patchy in nature, and reef species on MCEs have been shown to be restricted to hard-bottom habitats (Bridge et al. 2011a; 2011b) which may not be easily distinguished at 100 x 100 m grid resolution. Therefore, conservative thresholds were likely to yield more accurate estimates of the true extent of MCE habitat.

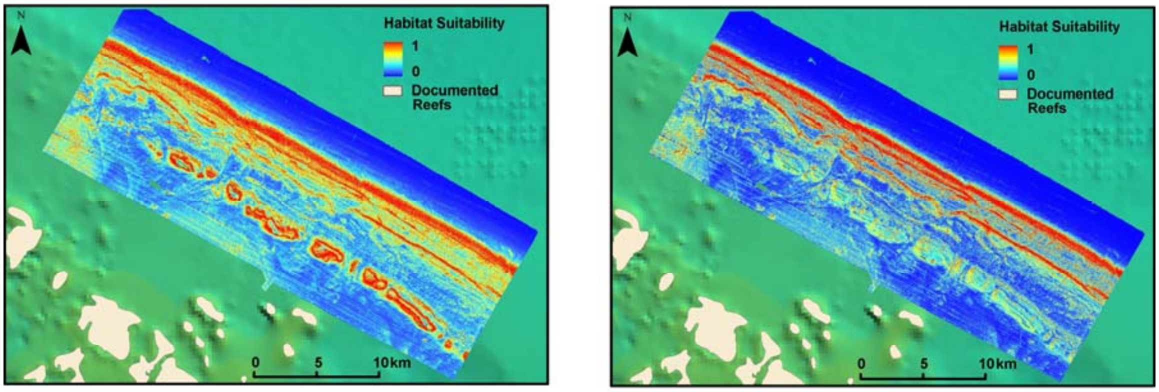
Results

High-resolution models (5 x 5 m grid)

The models indicated that the most suitable habitat for both phototrophic taxa, *Carteriospongia* and *Cespitularia*, occurs on the tops of submerged reefs above ~60 m depth (Figure 5.4 a, b) with habitat suitability low in other areas. The distributions for both taxa are similar, although *Carteriospongia* is absent from the very shallowest reef crests (~15-20 m depth). The most suitable habitat for the heterotrophic genera (Figure 5.4 c, d) occurred in deeper water (90-120 m), although suitable habitat was not as clearly associated with hard substrata. ROC curves (Figure 5.5) indicated that model results were accurate for all four genera; AUC values varied between 0.87 (*Dendronephthya*) and 0.99 (*Carteriospongia*) with AUC values higher for phototrophs than heterotrophs (Table 5.1). Both AUC values and mean habitat suitability for occurrence records were lower for heterotrophs, indicating habitat suitability was not as clearly defined as for phototrophs. Jackknifing indicated that *depth* was the most important environmental predictor of all four taxa (Figure 5.6). However, depth was less predictive of suitable habitat for heterotrophs than for phototrophs. The total amount of suitable habitat was also consistently higher for heterotrophic genera (Table 5.1).



a *Carteriospongia* b *Cespitularia*

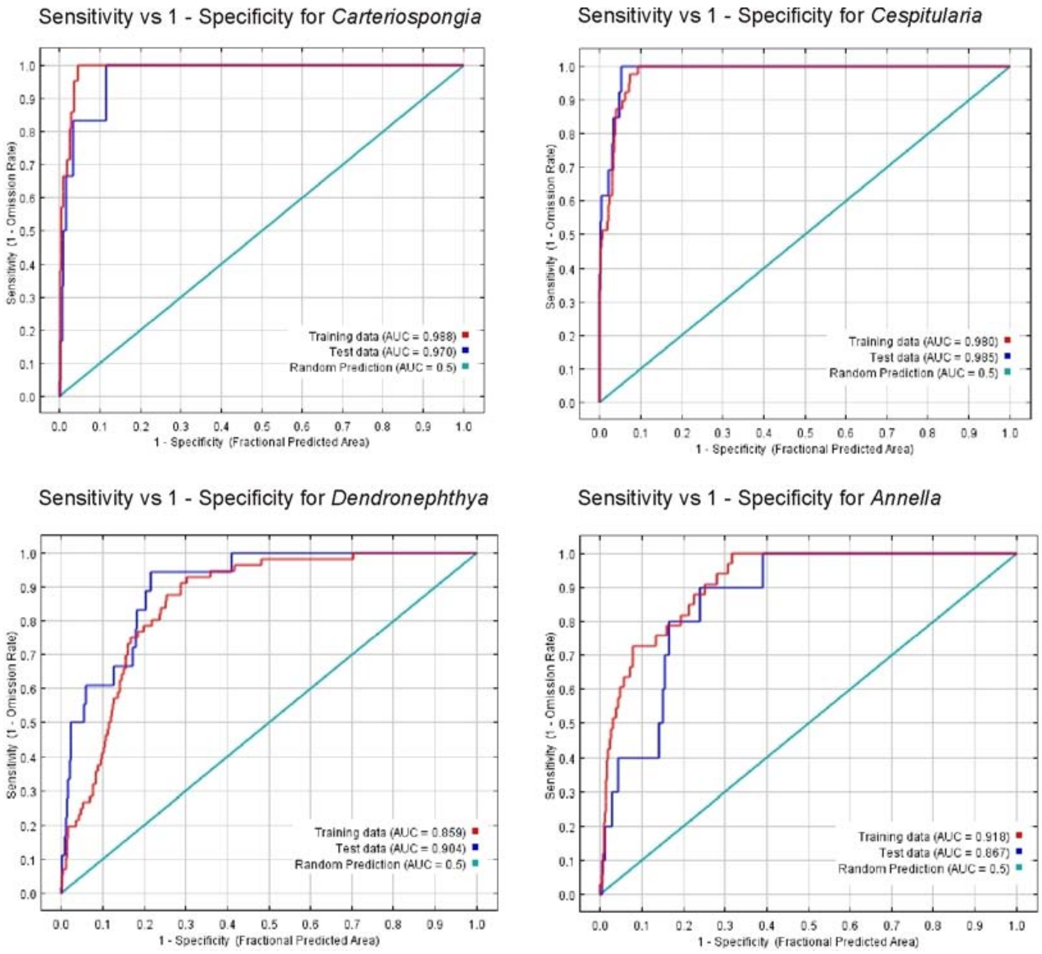


c *Dendronephthya* d *Annella*

Figure 5.4: Habitat suitability maps for *Carteriospongia*, *Cespitularia*, *Dendronephthya* and *Annella* from Hydrographers Passage created using 5 x 5 m bathymetry grids. The submerged reefs above 50 m depth showed high habitat suitability for phototrophic taxa (top); heterotrophic suspension-feeding taxa (below) had less defined habitat preferences, although the most habitat occurred on reef substrates between 90 and 120 m depth.

Table 5.1: Number of occurrences, Lowest Presence Threshold (LPT), Area Under the Curve (AUC) values, best predictor variables, and estimates of the total suitable habitat for each taxa and community in site-scale and regional-scale models

Region	**Resolution (m)**	**Species**	**No. Occurrences**	**LPT**	**Mean Suitability**	**Training AUC**	**Test AUC**	**Predictor Variables**	**Total Suita Habit (km^2)**
Hydrographers Passage	5 x 5	*Carteriospongia*	32	18	63	0.99	0.97	Depth	30
Hydrographers Passage	5 x 5	*Cespitularia*	64	10	64	0.98	0.99	Depth	47
Hydrographers Passage	5 x 5	*Dendronephthya*	79	13	62	0.86	0.9	Depth, substrate	333
Hydrographers Passage	5 x 5	*Annella*	46	12	59	0.92	0.87	Depth, substrate	65
Hydrographers Passage	5 x 5	Heterotroph	157	6	55	0.94	0.91	Depth, rugosity, slope, substrate	212
Hydrographers Passage	5 x 5	Phototroph	100	10	64	0.98	0.98	Depth, substrate	29
Hydrographers Passage	100 x 100	Heterotroph	26	12	52	0.94	0.8	Depth, slope	183
Hydrographers Passage	100 x 100	Phototroph	39	12	51	0.98	0.95	Depth, substrate	41
GBR	100 x 100	Heterotroph	26	32	56	0.99	0.99	Depth, rugosity, slope	2659
GBR	100 x 100	Phototroph	15	18	66	0.98	0.99	Zones (crest/slope), rugosity	6008



Sensitivity vs 1 - Specificity for *Carteriospongia*

Sensitivity vs 1 - Specificity for *Cespitularia*

Sensitivity vs 1 - Specificity for *Dendronephthya*

Sensitivity vs 1 - Specificity for *Annella*

Figure 5.5: Receiver Operating Characteristic (ROC) curves for the four taxa examined using 5 x 5 m bathymetry grids at Hydrographers Passage. The area under the curve (AUC) values indicate that all models perform well, although the broader niche of *Annella* and *Dendronepthya* is reflected in the lower ROC values.

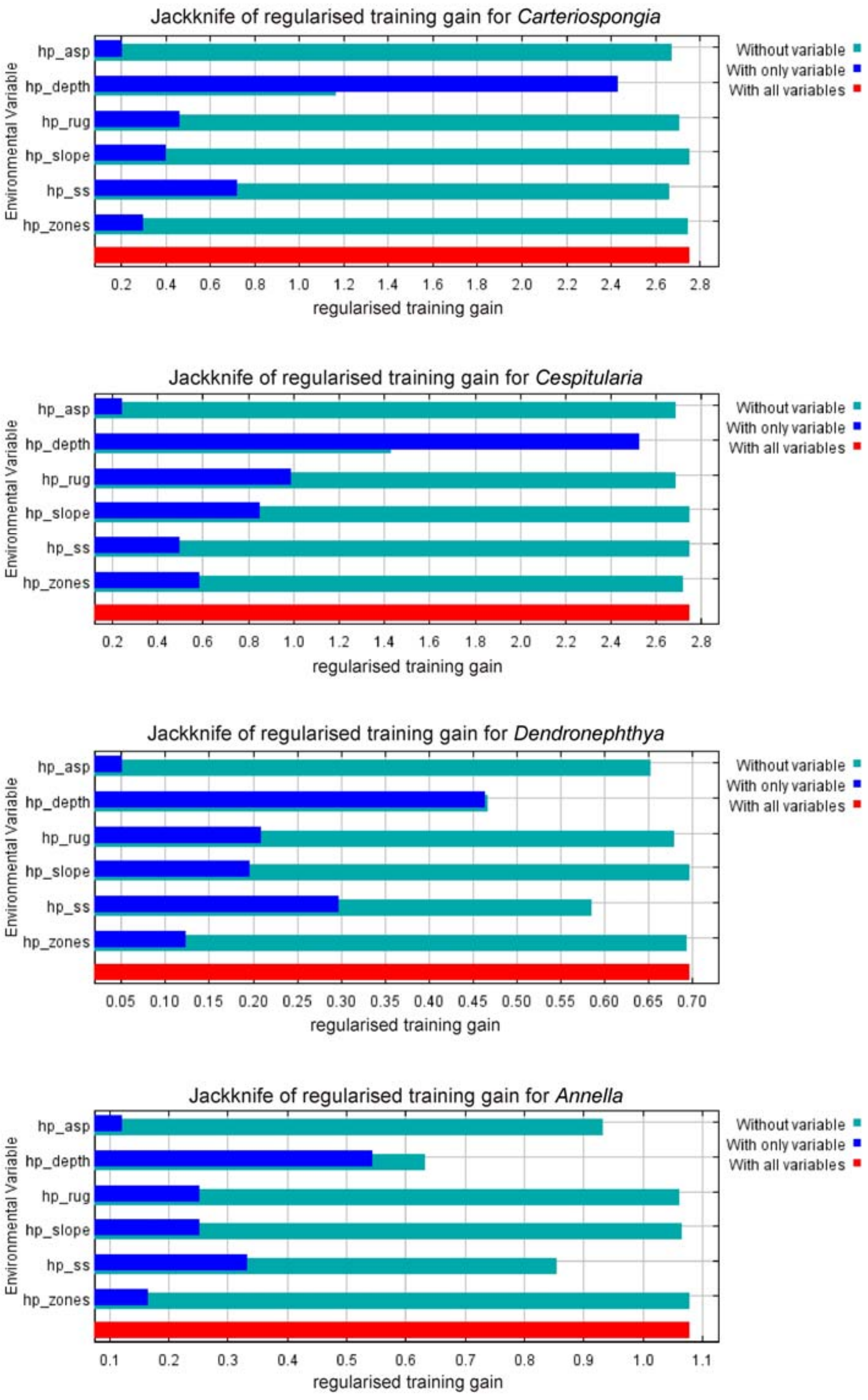


Figure 5.6: Relative importance of six environmental variables used for predicting suitable habitat for the four genera at Hydrographers Passage, measured using jackknifing. *Depth* was the most important variable for all four genera, although it was considerably more important for phototrophs.

Extrapolation to GBR-wide scale (100 x 100 m)

Predictive models of the Hydrographers Passage site using 100 x 100 m grid cells produced similar species distribution maps for both phototroph and heterotroph communities as the 5 x 5 m model. For phototrophs, both models clearly showed high habitat suitability on the tops of the shoals at depths <60 m (map not shown), while the most suitable habitat for heterotrophs occurred in the 90-120 m depth range (Figure 5.7). AUC values remained similarly high in both models (Table 5.1). The total area of suitable habitat predicted by the models at both scales was similar for both phototrophs and heterotrophs. *Depth* was the most important determinant of suitable habitat at both resolutions for both phototroph and heterotroph communities.

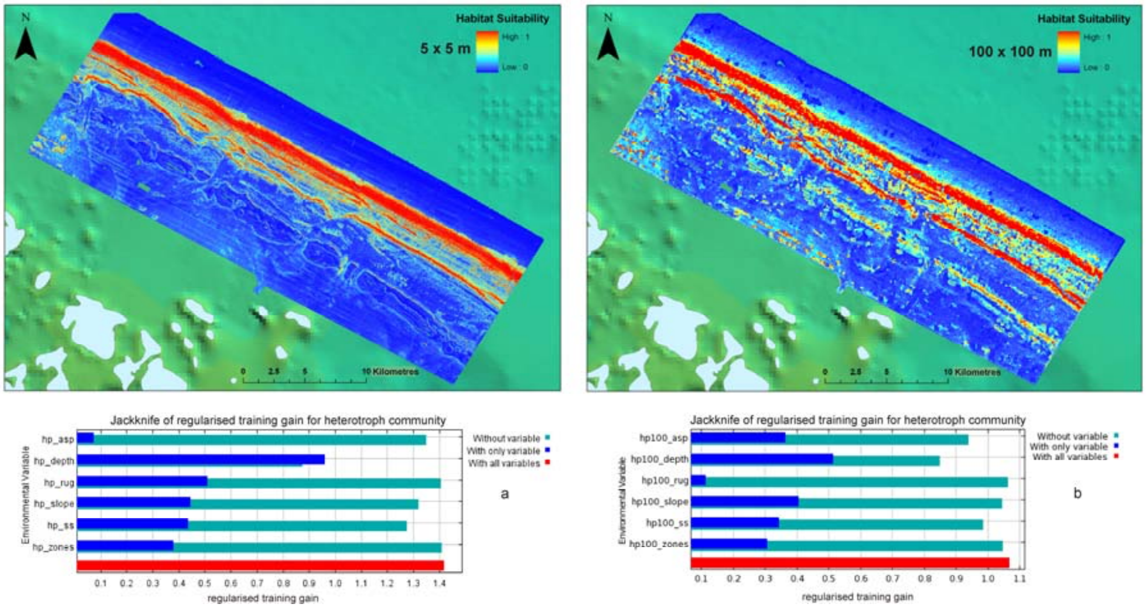


Figure 5.7: Comparison of species distribution maps and jackknife measure of environmental variable importance for heterotrophic MCE community between 5 x 5 m (a) and 100 x 100 m (b) grid cells. Both models clearly show highest habitat suitability occurring on submerged reefs between 90-120 m depth. *Depth* was the most important predictor variable in both cases, but was more predictive in the high-resolution model.

The GBR-scale model using 100 x 100 m bathymetry predicted the existence of suitable habitat for both phototrophic and heterotrophic MCE communities along the entire length of the GBR (Figure 5.8). For heterotrophs, suitable habitat was generally restricted to the outer-shelf region, with little suitable habitat occurring inside the GBR lagoon (Figure 5.8a). In contrast, phototroph communities occurred both on the submerged reefs along shelf-edge and also within the GBR lagoon (Figure 5.8b). On the steep, narrow shelf-edge in the northern GBR, phototroph communities were predicted only in the narrow strip immediately seaward of the emergent reefs, however in the southern GBR, suitable habitat was also predicted on the deeper flanks of emergent reefs. ROC curves (Figure 5.9a) show model accuracy remained consistently high for both phototroph and heterotroph communities (AUC 0.98 and 0.99 respectively; Table 5.1).

The “leave one out” jackknifing procedure indicated that model predictions were relatively accurate in most cases. For phototrophs, 13 of 15 known occurrence records were predicted correctly. All occurrences were predicted correctly when Ribbon Reefs, Noggin Pass, Viper Reef and North Hydrographers Passage sites were removed, with 4 of 6 occurrences correctly predicted when Southern Hydrographers Passage was removed. The two sites that were not predicted correctly had values only slightly lower than the lowest presence threshold (~0.10), illustrating the conservative nature of the estimates. For heterotrophs, 18 of 30 known occurrence records were correctly predicted. The lower accuracy was due to the large number of occurrence records at one site (southern Hydrographers Passage), which contained 25 of the 30 presence records. All incorrect predictions bar one occurred when this site was removed, leaving only five occurrence records. The total area of “reef” habitat predicted by the model represented ~2.4% of the total area covered by the environmental layers for phototrophs and 1% for heterotrophs; therefore, successful predictions of MCE habitat when occurrence records are removed are highly unlikely to be due to random chance.

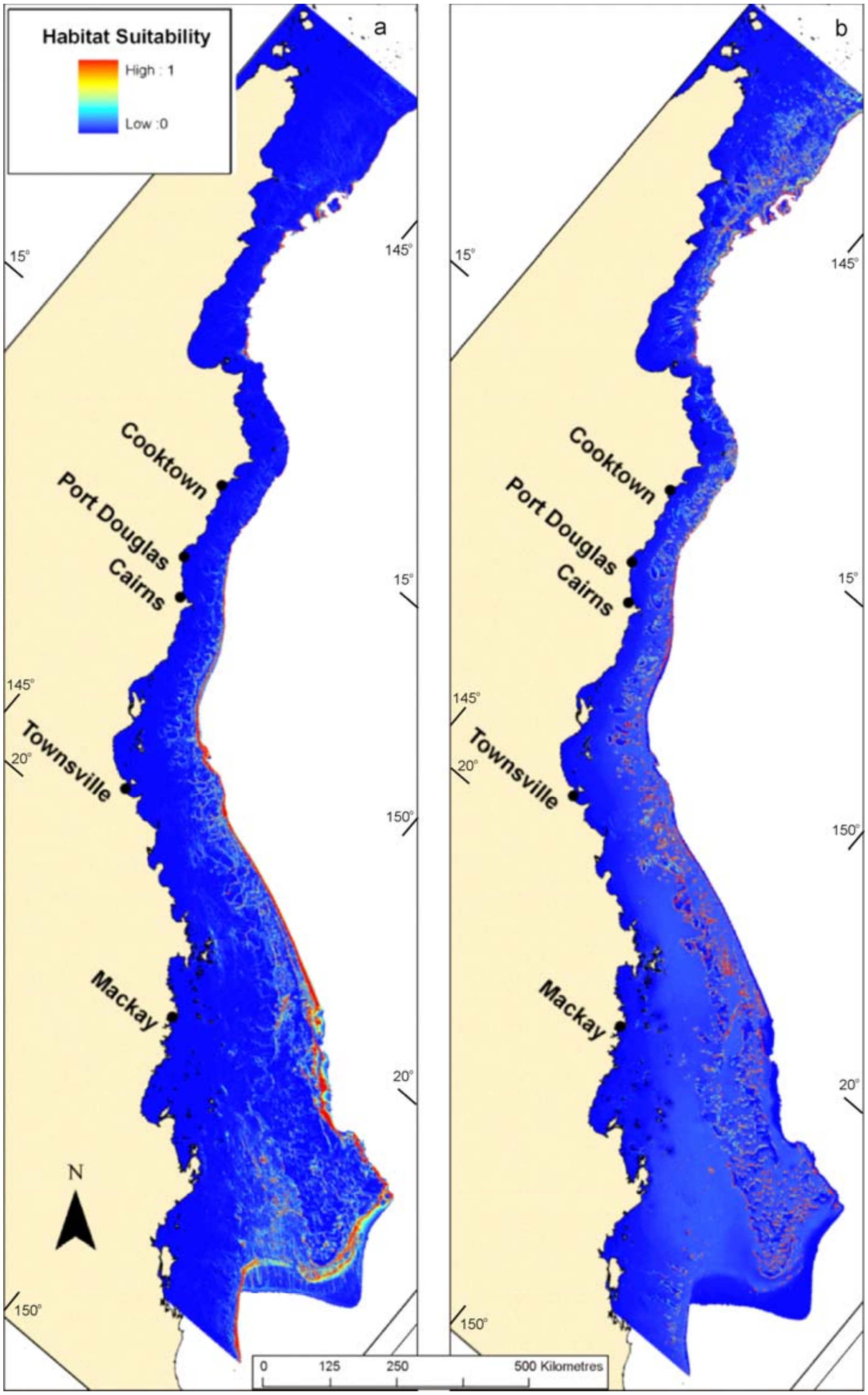


Figure 5.8: Species distribution maps for heterotrophic (a) and phototrophic (b) MCE communities in the GBRWHA. Areas with high habitat suitability occur on both submerged reefs along the shelf-edge and on the deeper flanks of documented reefs within the GBR lagoon, particularly in the central and southern GBR. Suitable habitat for heterotrophs is generally restricted to deeper waters along the shelf-edge of the GBR, with little suitable habitat occurring inside the GBR lagoon.

Geomorphic zone was the most important predictive variable for phototrophic MCE communities, with high habitat suitability occurring on slopes and crests and low suitability on flats and depressions. In contrast to most model predictions, *depth* contributed very little (Figure 5.9b). Heterotroph habitat suitability was best predicted by *depth*, followed by *rugosity* and *slope*. Variability in predicted habitat suitability between phototrophic and heterotrophic communities is illustrated in Figure 5.10, which shows a section of the central GBR east of Townsville (~19˚S). The white dotted areas represent regions of the GBRMP currently regarded as reef habitat. Suitable habitat for phototrophic MCE communities is clearly shown to occur along the shelf-break, corresponding to the submerged reefs of the central GBR shelf-edge identified by Hopley (2006). However, the model also suggests that the deeper flanks of reefs occurring inside the lagoon may also provide suitable habitat for these communities. In contrast, the GBR lagoon provides very little suitable habitat for heterotrophic MCE communities, however suitable habitat is not as clearly associated with submerged reef habitat.

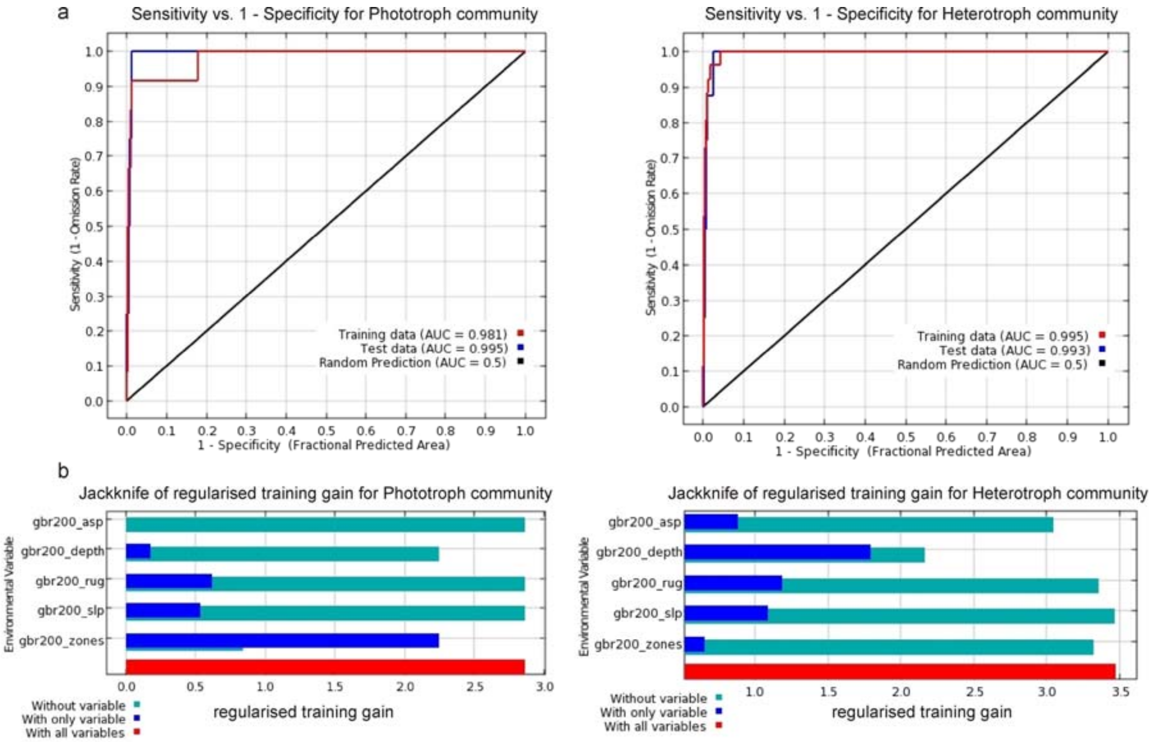


Figure 5.9: ROC curves (a) and jackknife measure of environmental variable importance (b) for phototrophic and heterotrophic MCE communities on the GBR. ROC curves indicate that the models provide good predictions relative to known occurrences. For phototrophs, *geomorphic zone* is clearly the best predictor variable at this scale; phototroph communities were closely correlated with ‘crest’ and ‘slope’ geomorphic zones, but rare on ‘flats’ and ‘depressions’. *Depth* is clearly the most important predictor variable for heterotrophs.

Using the lowest presence threshold of 0.32 for heterotrophs and 0.18 for phototrophs (Table 5.1), the total amount of MCE habitat in the GBR is estimated to be almost 9000 km^2. This is composed of ~6000 km^2 of habitat suitable for phototroph MCE communities, and ~2700 km^2 of heterotroph habitat. Only 763 km^2 of this potential MCE habitat occurs in areas currently recognised as reef habitat within the GBRMP. Figure 5.10a indicates that suitable habitat for phototroph communities along the shelf-edge is discontinuous. However, this observation is not consistent with the known distribution of submerged reefs, and is most likely due to low-resolution bathymetry data currently available in these areas being unable to resolve reef habitat.

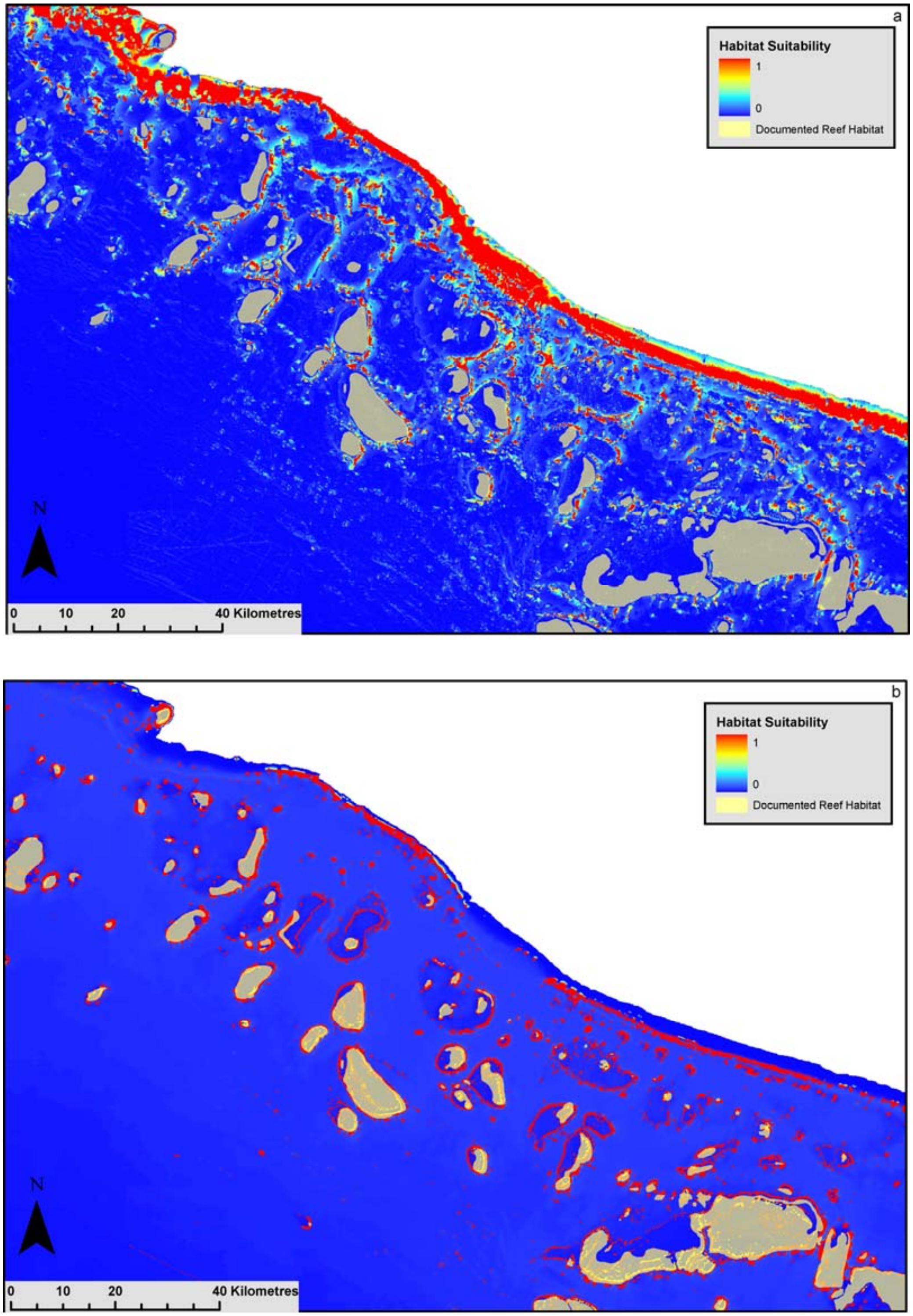


Figure 5.10: Close-up showing GBR-scale model predictions for a section of the central GBR; (a) phototroph communities can clearly be seen occurring both along the outer-shelf and along the deeper flanks of known reefs (indicated by black dots). The gaps in suitable habitat along the GBR shelf probably result from lack of data in these locations in the present gbr100 bathymetry; (b) highly suitable habitat for heterotrophs occurs primarily in deeper waters along the outer-shelf of the GBR.

Discussion

Identifying environmental variables responsible for the presence of mesophotic communities is difficult, and further research is required to better understand effects of both biological and environmental variables on the composition and structure of MCE communities with greater taxonomic resolution. Variables strongly correlated with high habitat suitability in this study are not necessarily important in themselves, but may instead be correlated with another important but unmeasured variable. For example, *depth* was shown to be an important predictor variable in most of the models in the present study, however this is likely to be related to other variables such as light irradiance or wave energy. This is further exacerbated by correlations between some environmental variables (e.g. slope and rugosity). Although MaxEnt is robust to this, it is nonetheless difficult to accurately identify individual environmental variables responsible for distribution patterns. Despite these difficulties, the results of the MaxEnt jackknifing procedure are useful in providing an estimation of relative importance of variables, and in the absence of more detailed environmental data represent an important first step in assessing the extent of MCE habitat in the GBRWHA.

Depth was the most predictive environmental variable for both phototrophic taxa at the 5 x 5 m grid resolution, which is hardly surprising given their need for sunlight to meet energy demands. However, *depth* had little influence on GBR-scale model predictions for phototrophs; instead, *geomorphic zone* (specifically slopes and crests) was the best predictor variable. This is likely due to the fact that the substantial area of non-reef seabed inside the GBR lagoon is not suitable habitat for these communities, despite occurring at suitable depth.

The models also indicate that similar communities occur both on lower reef slopes of shallow-water reefs inside the GBR lagoon as well as on the tops (crests) of submerged reefs on the outer-shelf. Although phototroph communities occur in both habitats, it is likely that these communities experience different oceanographic conditions and would also be expected to show variable response to environmental disturbances. For example, lower reef slope communities have been shown to suffer greater damage as a result of tropical storms than shallower areas (Harmelin-Vivien and Laboute 1986). However, many submerged reefs are not exposed to the debris avalanches which cause the majority of this damage, and therefore afford greater protection from tropical storms than lower reef slopes. Identifying differences in community composition and exposure to disturbances is an important consideration for assessing the refugia hypothesis, and should also be considered by managers when designing MPAs.

Less intuitively, *depth* was also the best predictor of suitable habitat for heterotrophs in both the site-scale and regional-scale models. Although heterotrophs do not rely on sunlight for energy, Fabricius and De'ath (2008) showed that taxonomic richness of heterotrophic octocorals on shallow reefs in the GBR increases with depth, and that heterotrophic octocorals generally have limited ranges and patchy distributions. Richness also increases with current strength, but is negatively correlated to wave energy. However, their study was conducted to a maximum depth of 18 m, with the authors noting that richness was still increasing at this depth. Although Bridge et al. (in review) show that there is considerable variation in the composition of heterotrophic octocoral communities between shallow and deep reef habitats, it appears that both generic diversity and habitat suitability for heterotrophic octocorals on the GBR is greatest (at least between 14 and 20˚S) at 90-120 m depth.

It is likely that the decreasing wave energy with depth corresponds to this increase in heterotrophic octocorals, and that the submerged reefs in this depth range therefore provide an ideal environment for these communities. Although there are undoubtedly other factors involved (e.g. less competition from phototrophs), it appears as though the deep submerged reefs of the GBR outer-shelf provide ideal habitat for a diverse range of heterotrophic octocorals. This influence of wave energy, particularly in the form of cyclones, is supported by the fact that shallow-water reefs in the far northern GBR, which experience fewer than five cyclones per century, contain high taxonomic richness of heterotrophic octocorals, even in shallow environments on offshore reefs (Fabricius and De’ath 2008). By contrast, the regions around Hydrographers Passage are exposed to more than 20 per century (Wolanski 1994). Cyclones appear to have a significant effect on the distribution of heterotrophic octocorals on most shallow-water reefs in the GBR, and result in their apparently patchy distribution. However, the deeper reefs of the GBR outer-shelf appear to provide a large, well-connected habitat for heterotrophic octocorals, and may therefore play an important role in the ecology of heterotrophic octocorals on the GBR.

Although these results indicate that the model presented here provides a valuable first insight into mesophotic reef habitat on the GBR, model results could be improved by the collection of additional data, such as a greater number and spatial extent of occurrence records. This model employs many techniques developed to survey rare species, largely because of the similarly low number of occurrence records. Unlike rare or cryptic species, increased sampling effort on the extensive MCE communities of the GBR would no doubt yield a corresponding increase in the volume of data. Such data would be most beneficial if it were collected over the entire length of the GBR. For heterotrophs in particular, occurrence records are heavily biased towards Hydrographers Passage, largely because the shelf morphology in that region leads to a large available habitat which is easily sampled by AUV.

Similarly, better information on other environmental data (e.g. chlorophyll and currents or benthic stress) would likely improve model predictions. Currently, these data are unavailable at the resolution required for predictive modelling of MCE communities in the GBR. Collection of such data would be highly beneficial, and combined with greater sampling effort would allow predictions of individual taxa, rather than the basic ecological communities presented here. Further, the results of the model presented here are significantly better in regions where high-resolution bathymetry data are currently available (e.g. Hydrographers Passage). Model predictions would be greatly improved by the collection of high-resolution multibeam data in regions which are currently not surveyed. Combined with a better understanding of the ecology and life history of MCE taxa, these data would enable more detailed and sophisticated modelling of MCEs in the GBR.

Significance of MCE models to management

The models of Hydrographers Passage suggest that the shallower submerged reefs (often referred to as “shoals”, Figure 5.2) likely support phototroph-dominated MCE communities. These shoals are common features along much of the shelf-edge in the central GBR, and generally rise to within 10-25 m of the surface. Very few shoals are classified as reef habitat within the GBRWHA, however preliminary data shows that they often contain high coral cover. Fig 5.11a shows high cover of both hard corals and octocorals on one such shoal at Hydrographers Passage. In addition to providing extensive reef habitat, there is also mounting evidence that these shoals provide refugia from disturbance events. The shoal in Figure 5.11b, located 12 km south of Noggin Reef at 17°S, was in the region affected by Severe Tropical Cyclone Larry in March 2006. The Australian Institute of Marine Science’s Long-Term Monitoring Program showed that live coral cover on Noggin Reef decreased significantly from 2003 to 2007 surveys, and was still only moderate (10-20%) when resurveyed in 2009 (http://data.aims.gov.au/reefpage2/rpdetail.jsp?fullReefID=17008S&sampleType=MANTA, accessed June 2011). By contrast, the shoal community shows high coral cover and little evidence of disturbance. Similarly, the coral community in Fig 5.11c (photographed in 2003) appeared unaffected by the mass bleaching event that affected proximal reefs (e.g. Myrmidon Reef) in 2002. None of the three shoals in Fig 5.11, which span over 500 km section of the central GBR, are currently classified as reef habitat by GBRMP management. The apparent resilience of these regions to environmental disturbance suggests these areas should be given significantly greater attention by both scientists and managers for their potential importance to the functioning of the GBR ecosystem as a whole.

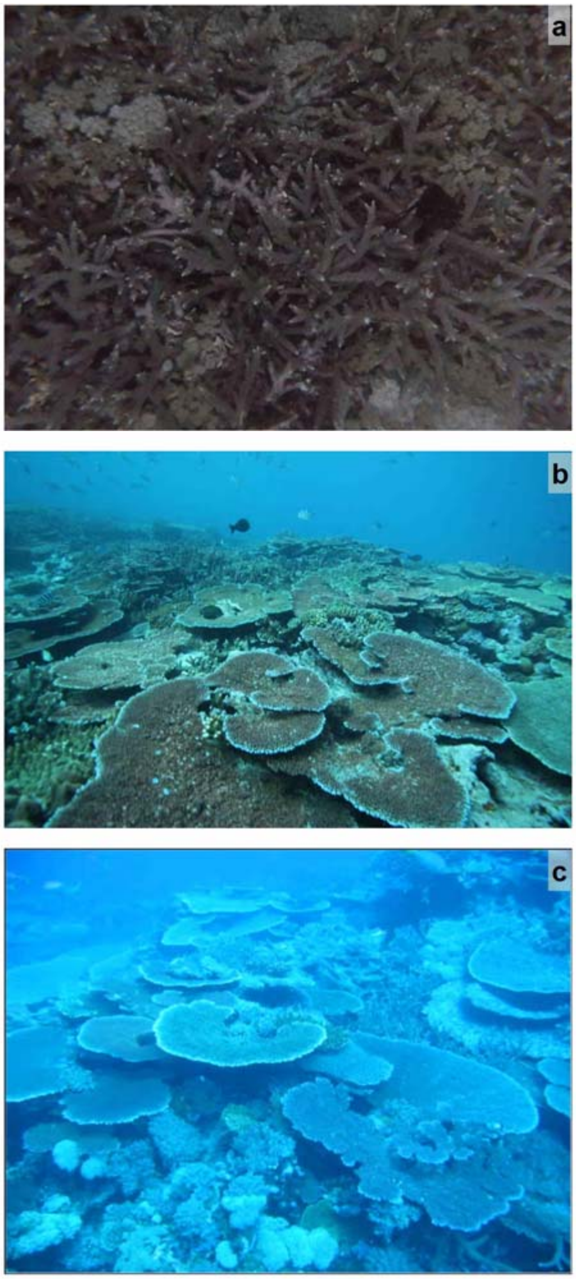


Figure 5.11: Examples of high coral cover on undocumented submerged reefs (known collectively as “shoals”) in 10-25 m depth on the GBR outer-shelf; a) ~15 m depth, Hydrographers Passage; b) offshore from Cairns (photo by D. Kline, University of Queensland); c) near Myrmidon Reef, Townsville (photo M. Wakeford, AIMS).

The models presented here provide a valuable first step in quantifying MCE habitat within the GBRWHA. The findings of this study will be valuable to marine managers because they illustrate the utility of available remotely sensed data for identifying coral reef habitats which cannot be detected using most commonly used methods. Data of this nature is constantly being updated, and new, higher-resolution datasets are regularly created. Datasets for a wide variety of environmental variables, including bathymetry, temperature, chlorophyll, aragonite saturation, are available at a global scale (albeit at lower resolutions than those presented here), and would be of significant value for creating predictive models of global mesophotic reef habitat. Such models would provide testable hypotheses about where MCEs may occur and would also be useful for scientists and managers for implementing networks of MPAs, particularly those aiming to incorporate susceptibility to climate change effects when prioritising MPA sites. Data of this nature would be particularly useful in areas such as the Coral Triangle. The coral reefs in this region are among the world's most diverse, but also the most vulnerable. As well as being buffered from environmental disturbance, the inaccessibility of MCEs makes them likely to be less exposed to other anthropogenic pressures, such as destructive fishing practices. Therefore, MCEs may be critically important to maintaining coral reef biodiversity in areas such as the Coral Triangle. Environmental data and models such as those presented here should be combined with greater sampling effort in order to better understand the role of MCEs and their relationship to the overall function of coral reef ecosystems.

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Chapter 6

Discussion and Conclusions

Thesis outcomes

The Great Barrier Reef World Heritage Area (GBRWHA) is one of the world's largest Marine Protected Areas (MPAs). However, a disproportionate amount of research on the GBR has focused on shallow-water coral reef habitats, which constitute only 7% of the 348 000 km^2 of the GBRWHA. The vast majority of research conducted on coral reefs to date has been conducted using SCUBA, and therefore mesophotic coral reef ecosystems (MCEs), which generally occur below the depths accessible to traditional SCUBA diving, have received limited research effort when compared to their shallow-water counterparts. Recent technological advances in both SCUBA technology (e.g. closed-circuit rebreathers) and robotics (autonomous underwater vehicles and remotely operated vehicles) have allowed scientists greater access to mesophotic coral reef ecosystems, and the last few years have seen increasing interest in MCEs from both scientists and marine managers. Although the GBR is among the most studied coral reef ecosystems in the Indo-Pacific, this thesis represents the first systematic and quantitative study of its deeper mesophotic coral reef communities.

The broad aim of this thesis was to examine the composition and extent of mesophotic coral reef communities in the GBRWHA and to identify environmental drivers of their distribution, and therefore represents an important step in understanding these ecosystems. It provides valuable baseline data for both scientists and managers about a poorly described habitat in the GBR, and can therefore be used to better understand patterns of biodiversity in the GBR ecosystem. More broadly, this study represents the first quantitative investigation of habitat-forming sessile benthic megafauna on mesophotic coral reefs in the Indo-west Pacific region. Based on analyses of the data collected on the 2007 RV *Southern Surveyor* expedition, this study draws the following conclusions about mesophotic coral reefs in the GBRWHA:

1. The submerged reefs occurring in the mesophotic zone of the GBRWHA contain diverse communities of sessile benthic megafauna. In general, the diversity of phototrophic taxa is highest in the shallower regions of the mesophotic zone <70 m deep, with deeper areas dominated by a diverse suite of heterotrophic suspension-feeding taxa. Relating this back to the research aim outlined in Chapter 1:

> *To identify sessile benthic megafauna occurring in the mesophotic zone of the GBRWHA and compare community composition on MCEs to adjacent shallow-water reef habitats*

This study identifies 29 hard coral species from 19 families and 24 genera of octocorals. Many of the hard corals represent species commonly encountered on shallow-water reefs; in contrast, many of the octocoral genera are absent or rare in shallow water. Twenty-two of the 24 genera of octocorals represented azooxanthellate genera, many of which appear to be widespread on mesophotic reefs. This is again inconsistent with observations in shallow waters, which indicate that many azooxanthellate octocorals have limited ranges.
Species-area modelling indicate that total diversity of hard corals in the region examined is ~84 species, suggesting that hard coral diversity on mesophotic reefs is considerably higher than previously thought.

2. Distinct communities of sessile benthic megafauna are observed both along a depth gradient from 50-150 m depth and in response to variations in substrate through the mesophotic zone. Analysis of AUV imagery identifies five

distinct groups of sessile benthic megafauna which all occur in clearly defined habitats. Relating this conclusion back to the research aim outlined in Chapter 1:

> *To identify how the composition of sessile benthic megafaunal communities change in response to variations in topography and substrata along a depth gradient through the mesophotic zone from 50-150 m water depth*

The first clear division occurs between reef and non-reef habitats. The majority of non-reef habitats contain no sessile benthic megafauna, although in some places they are inhabited by the heterotrophic octocoral *Dendronephthya*. Reef substrata exhibit greater topographic complexity than non-reef habitats, and contain diverse communities throughout the 50-150 m depth range. However, vertical zonation of sessile benthic megafaunal communities is apparent, with reef habitat above 60 m depth dominated by phototrophic taxa and below 75 m characterised by heterotrophic suspension-feeders. There is also a distinct transitional zone between 60 and 75 m which contains a combination of both of these groups. The effects of depth and microhabitat topography on light irradiance most likely play a critical role in controlling the composition of sessile benthic megafaunal communities on reef substrates.

3. Composition of sessile benthic megafaunal communities shows considerable variation both within and between sites along the GBR outer-shelf, although there were consistent patterns in the functional ecological groups occupying certain habitat types at all sites. Phototrophic taxa were observed on the flatter tops of submerged reefs, while steep walls were occupied by heterotrophic suspension-feeding taxa. Relating this back to the research aim outlined in Chapter 1:

> *To identify how the composition of sessile benthic megafaunal communities changes at a standardised depth (50-65 m) along the GBR margin and to identify geophysical variables responsible for those changes*

It is clear that the composition of sessile benthic megafaunal communities is controlled by a combination of physical, environmental and ecological interactions, and further sampling effort is required in order to predict the composition of sessile benthic megafaunal communities on MCEs in the GBR. However, it is clear that composition of MCE communities is spatially heterogeneous along the GBR. This finding is inconsistent with patterns reported from MCEs in other parts of the world (e.g. the Caribbean), where community composition appears to be homogeneous among geographically isolated sites. Slope angle, water clarity and productivity appear to be important environmental variables for explaining the variability observed among and between sites. Within a site, reduced light irradiance on steeper slopes likely limits the occurrence of phototrophic taxa in these habitats. Variability in water clarity and nutrient availability along the length of the GBR is likely to cause variation among sites. These results suggest that the MCE communities occurring on the GBR outer-shelf contain diverse communities that may exhibit considerable variation in composition.

4. Predictive habitat models were generated for four common mesophotic taxa at Hydrographers Passage using 5 x 5 m grid resolution bathymetry data. Data of this resolution is not available for a significant proportion of the GBR outer-shelf, therefore lower-resolution (100 x 100 m grid cell) data was used to estimate the extent of MCE habitat occurring in the GBRWHA. Relating this back to the research aim outlined in Chapter 1:

> *To examine whether predictive modelling techniques can be used to accurately predict the distribution of suitable habitat for sessile benthic megafauna and to estimate extent of mesophotic coral reef habitat in the GBRWHA.*

Predictive modelling is clearly a valuable tool which can be used to identify the potential distributions of MCEs in the GBRWHA, and can also be used for regional-scale analysis in other parts of the world. Site-scale modelling of two phototrophic (*Cespitularia* and *Carteriospongia*) and two heterotrophic (*Annella* and *Dendronephthya*) taxa at Hydrographers Passage using 5 x 5 m grid resolution provides accurate estimations of the occurrence of suitable habitat for these taxa. At a GBR-scale, occurrence records are currently too sparse to model the distributions of individual taxa. However, jackknife testing indicates that 100 x 100 m grid resolution data is capable of predicting the distribution of phototroph and heterotroph-dominated communities, even in a topographically complex and heterogeneous system such as the GBR. Using a conservative "lowest presence threshold" for defining suitable habitat, the model indicates that the total amount of potential mesophotic reef habitat is ~10 000 km^2, or approximately 50% of the area currently classified as reef habitat in the GBRWHA. This represents a significant proportion of total reef habitat within the GBRWHA, and combined with the diverse ecological communities described in chapters 2, 3 and 4, suggests that MCEs in the GBR warrant attention to ensure their adequate protection.

Geophysical variables as predictors of MCE communities

The results of this thesis conclusively show, for the first time, that the submerged reefs occurring in the mesophotic zone along GBR outer-shelf contain diverse ecological communities. The results of chapters 3 and 4 indicate that substratum, water depth and seafloor topography are all important geophysical variables which can be used to determine the composition of sessile benthic megafaunal communities on MCEs in the GBRWHA.

Substrate

Hard, reef substrata were shown to harbour a much greater abundance and diversity of sessile benthic megafauna than soft-bottom, non-reef habitats. All but a few taxa were found exclusively on reef substrata, and even those that did occur in non-reef habitats (e.g. *Dendronephthya*) were generally also found on reefs. Data collected by autonomous underwater vehicle (AUV) suggested that non-reef substrata at most sites were characterised by bare sand, although much of the non-reef area near the Viper Reef site was dominated by *Halimeda* meadows with sporadic aggregations of the Fungiid coral *Diaseris distorta*. Although depauperate in sessile benthic megafauna, sandy non-reef habitats in 60-90 m depth often contained a number of individuals of the giant benthic foraminiferan *Cycloclypeus carpenteri*. In addition, the crests of large sand dunes at ~60 m depth on the leeward side of the submerged shoals at Hydrographers Passage contained dense aggregations of the brittlestar *Ophiopsila pantherina* (Beaman et al. *in press*).

Depth

The cross-shelf profile in Hydrographers Passage (Chapter 3) revealed a distinct transition from a phototroph-dominated community (<60 m depth) to one dominated by heterotrophic suspension-feeders below a depth of 75 m, with a transitional community occurring in 60-75 m. Light irradiance is clearly an important determinant of community composition on MCEs (Lesser et al. 2009; Kahng et al. 2010), and decreasing light irradiance with depth eventually imposes a maximum depth limit on the distribution of phototrophic taxa. Shallower mesophotic communities (50-60 m depth) examined in this study contained diverse phototrophic communities, including a wide range of hard corals. In contrast, only a few deep specialist phototrophic taxa (e.g. *Leptoseris*) were found in deeper waters below 70 m.

Heterotrophic communities observed in this study were dominated by azooxanthellate octocorals. Although previous studies indicated that many heterotrophic octocoral taxa exhibited patchy distributions and limited ranges (Fabricius and De’ath 2008), these results indicate that many of these taxa are widespread on the deeper reefs of the GBR outer-shelf. One of the major reasons for this may be that unlike adjacent shallow reefs, deeper submerged reefs are not subjected to damage from tropical cyclones. This finding has important implications for understanding patterns of biodiversity and connectivity in the GBRWHA.

Topography

In addition to a general shift from phototroph-dominated to heterotroph-dominated communities with increasing depth, seafloor topography also appears to play an important role in determining the composition of sessile benthic megafaunal communities on MCEs. It has already been established that hard substrata contain greater diversity than soft-bottom habitats, however detailed examination of reef habitats (Chapter 4) revealed variation in community composition between the flatter tops of reefs and steeper reef walls. Although there was significant variation in the community composition between sites, there were consistent patterns in the functional ecological groups occupying particular fine-scale habitat types. In general, steep reef walls contain a higher abundance of heterotrophic taxa than flatter reef tops, and this is most likely due to decreased light irradiance on steeper slopes.

Other environmental drivers of community variability

The results in chapters 3, 4 and 5 identify depth and seafloor topography as the important environmental drivers of MCE communities, however there are likely to be other important environmental variables for which quantitative data was not available. Some variables may not even be particularly important in themselves, but are instead proxies for other important environmental drivers. For example, the reduction in light irradiance with increasing depth is probably a more important factor in MCE community composition than depth *per se*. In fact slope, optical water clarity and depth are all correlated to light irradiance, and it is in fact light irradiance, along with substratum, that is probably the most critical factor affecting the composition and distribution of MCE communities at low taxonomic resolutions and across large spatial scales. However, Chapter 4 showed that despite the consistent patterns in the functional ecological groups occupying particular habitat types, each of the sites examined here contained a different suite of taxa. This is contrary to the general pattern observed on shallow-water reefs, where similar reef environments right along the length of the GBR are dominated by similar suites of species (e.g. Done 1982). Therefore, there are likely to be factors which are also important in determining MCE community composition, particularly at higher taxonomic resolutions. Two possible reasons for the variations observed in community composition between different sites:

1. Variations in the physical environmental parameters (e.g. water column productivity);
2. Life history traits of the individual species (e.g. brooding versus broadcast spawning).

Nutrient availability

Various studies have shown that upwelling of cold, nutrient-rich waters occurs at a number of locations along the GBR shelf (Wolanski and Pickard 1983; Wolanski 1994; Brinkman et al. 2002). Such upwelling can cause significant variation in physical environmental parameters such as water temperature and nutrient availability. In an extreme example in Palau, daily temperature fluctuations of up to 20 ˚C were observed and cited as a possible reason for depauperate mesophotic communities (Wolanski et al. 2004). Although temperature fluctuations of this magnitude have not been observed on the GBR, the upwelling of nutrients has been shown to affect the composition of benthic communities in non-reef habitats such as *Halimeda* banks (e.g. Drew and Abel 1988), and could play an important role in determining the structure of MCE communities by favouring taxa better able to feed heterotrophically. Upwelling of nutrients would be of obvious benefit to azooxanthellate octocorals which feed on phytoplankton, however it may also help to determine the composition of hard coral communities.

Many of the hard corals observed on mesophotic reefs in this study also occur in shallow, inshore turbid reef environments (DeVantier et al. 2006). It has been suggested for some time that corals living in turbid, low-light conditions may have an enhanced ability to feed heterotrophically (Anthony and Fabricius 2000), and this ability would clearly be advantageous in deep, light-limited habitats. In a study of *Stylophora pistillata* across a depth range of 0-70 m, Mass et al. (2010) suggest that light irradiance at greater depth is insufficient to meet the corals metabolic demands, and therefore colonies existing in deep water must be supplementing their energy requirements by heterotrophic feeding. Increased knowledge of both upwelling along the edge of the GBR and the effects of nutrient enrichment on benthic MCE communities is likely to be an important development in understanding the community ecology of MCEs in the GBR and elsewhere.

Life history traits

Another factor to consider when attempting to predict MCE community composition is the life history traits of the individual MCE taxa, such as methods of reproduction (brooding versus broadcast spawning). The hard coral species observed in this study comprise both brooding and broadcast-spawning taxa, and further sampling could yield important information on the effect of different spawning methods. This question also has important ramifications for the refugia hypothesis; for example, the brooding coral *Seriatopora hystrix* shows evidence of genetic divergence across habitats which may affect the ability of deep populations to recolonise shallower habitats (Bongaerts et al. 2010; Van Oppen et al. 2011). The ecology of most azooxanthellate octocorals is poorly known, however at least some species appear to be brooders, with well-developed larvae often settling only a few metres from the parent colony. Combined with being restricted to specific fine-scale habitat conditions (low wave energy, high water flow), this has led to patchy distributions for many taxa on shallow-water reefs in the GBR. However, the results presented here indicate that many heterotrophic octocoral taxa are widespread at mesophotic depths. This suggests that the mesophotic reefs of the GBR provide an extensive, well-connected habitat for these taxa, and as such may play an important role in the connectivity of the GBR ecosystem.

Application to other parts of the world

This study provides the first quantitative assessment of MCEs in the GBRWHA, but also the first large-scale examination of MCE communities in the Indo-west Pacific, the epicentre of marine biodiversity. Currently, the best-known MCEs in the world are those in Hawaii and the Caribbean. However, the diversity of coral reef biota in these regions is an order of magnitude lower than in the Indo-west Pacific, therefore investigating MCEs in this region should be a priority for scientists attempting to understand the ecology of mesophotic coral reefs. Examining regions of high biodiversity is particularly critical for assessing the refugia hypothesis, since those areas of highest biodiversity are likely to be the highest priority for conservation. In places such as Indonesia, the relative inaccessibility of MCEs may afford them protection against direct human impacts which have severely affected so many shallower reef habitats in the region. Assessing biodiversity in these regions and implementing MCEs into management decisions should be a priority for managers aiming to minimise the loss of biodiversity in areas such as the Coral Triangle.

The technical and logistical difficulties involved with direct sampling and surveying of MCEs means that predictive modelling will be critically important to identifying and managing MCEs around the world. As such, it would be of great benefit to conduct a habitat assessment of MCEs at a global scale. The results of Chapter 5 suggest that if mesophotic coral reefs are included in estimates of reef habitat, the GBRWHA contains 10 000 km^2 of reefs that are currently classified as non-reef habitats. Modelling reef distribution in the GBR is challenging because it requires depth models of sufficient resolution to resolve the complex mass of reefs, however this is not the case in some other regions. Guinotte (2006) demonstrated the utility of environmental data at 1 x 1 km resolution for predicting mesophotic reef habitat on the North West Shelf of Australia, and concluded that there was approximately two times the amount of reef habitat occurring below 20 m depth than above. Environmental variables used in this study are now available globally at the 1 x 1 km scale, and could be used to develop models in areas of conservation priority, such as the Coral Triangle. Development of a global model of MCE habitat would be of particular value for managers in mitigating impacts such as overfishing and climate change.

Future Research

Although this thesis focused primarily on sessile benthic megafauna, there are several other key taxa occurring on MCEs which should be considered for future studies. The most obvious of these are reef-associated fish communities. Mesophotic reefs in other parts of the world have been shown to contain a variety of depth-endemic fish species (e.g. Pyle et al. 2008). In addition to these mesophotic curiosities, MCEs may also provide home to a wide variety of fish species common to shallow-water reef communities. Data from deeper habitats of Scott Reef, Western Australia, showed that there was significant overlap of many fish species between shallow and deep habitats (Andrew Heyward, pers. comm.), with the main difference in community structure being a lower abundance of grazers (e.g. Acanthurids) caused by the lower abundance of algae. This observation addresses another important component of the refugia hypothesis – while corals and other sessile benthic megafauna cannot move in response to a disturbance, motile fauna such as fish may seek refuge in deeper habitats following disturbance events such as cyclones or bleaching. Addressing these questions is an important step in understanding the response of the overall GBR ecosystem to the effects of climate change.

In addition, MCEs may harbour spawning aggregations for a variety of fish species, including some of commercial importance. For example, spawning aggregations of the red hind (*Epinephelus guttatus*) were shown to occur on MCEs in the United States Virgin Islands (Nemeth 2005). This led to the establishment of the Red Hind Bank Marine Conservation District and the total closure of the area to fishing in 1999 to protect brood stock. Fish communities occurring on MCEs in the GBRWHA remain virtually unstudied, however, there is anecdotal evidence that MCEs may contain high fish biomass. ROV observations of the MCEs at Hydrographers Passage taken during the 2010 IODP drilling expedition showed large numbers of fish schooling around the reefs (Figure 6.1). Further research should be dedicated to understanding the role of MCEs as fish habitat, particularly with regards to species of commercial importance.

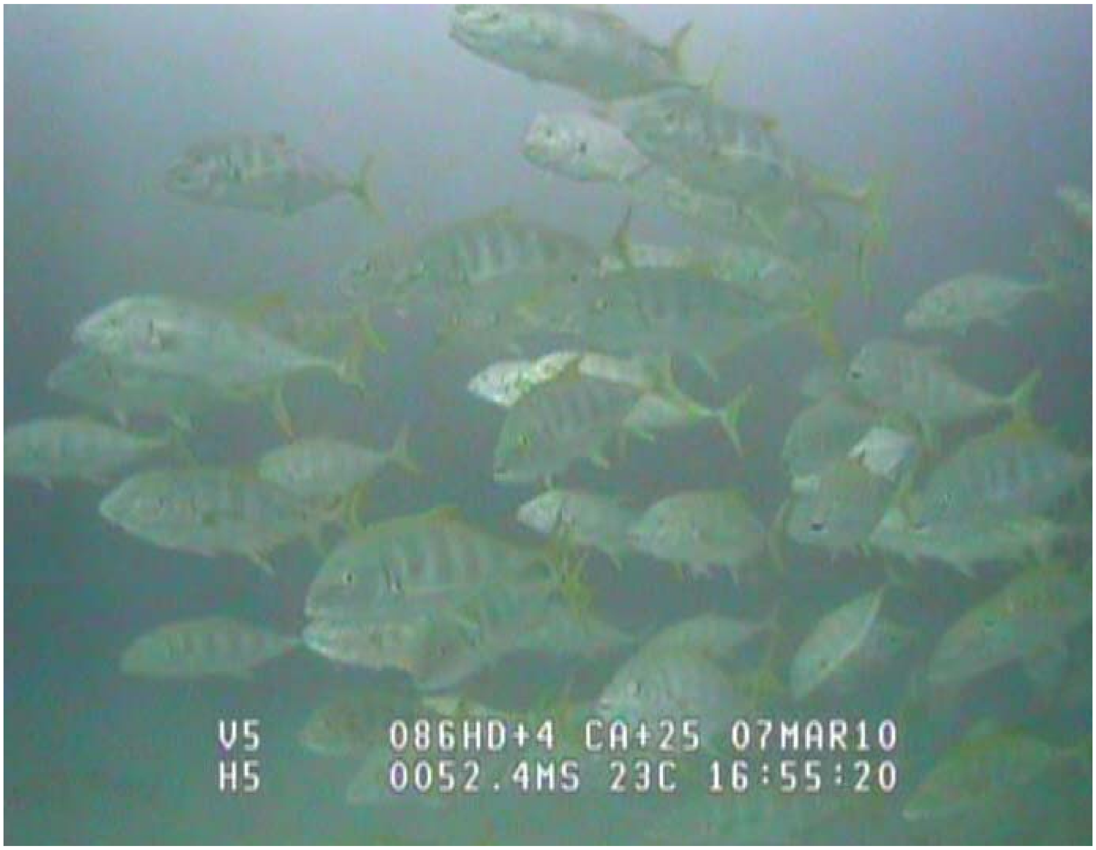

Figure 6.1: School of golden trevally (*Gnathanodon speciosus*) observed near a submerged reef at 52 m depth at Hydrographers Passage by ROV (photo courtesy of ECORD).

The vast majority of data collected during this study were collected in the “deeper” regions of the mesophotic zone, with limited examination of the upper mesophotic region (30-50 m). This region is likely to have more species in common with shallow-water habitats, however, it is still likely to be afforded some protection from disturbance. Therefore, investigations of these regions will be of critical importance to assessing the refugia hypothesis. The GBR outer-shelf contains a very large number of submerged reefs with tops in 10-40 m depth, some of which are marked on nautical charts. In some locations, these areas may even be examined using conventional SCUBA. Unfortunately, current regulations in Queensland governing scientific research diving are highly restrictive and contain no scope to utilise the new diving technologies regularly being employed to study MCEs in other parts of the world. Hopefully this will change in the future, because SCUBA studies of MCEs would be achievable at a fraction of the cost of the 2007 RV *Southern Surveyor* expedition. Preliminary observations of some of these habitats taken both by recreational divers and by AUV (Fig 5.11 in previous chapter) suggest that many of these areas contain high coral cover and are also buffered from some environmental disturbances. Therefore, these habitats warrant further study.

The modelling data presented in Chapter 5 clearly shows the benefits of collecting high-resolution bathymetric datasets. Unfortunately, many of the techniques used to obtain bathymetry data on the GBR (e.g. Laser Airborne Depth Sounder or LADS) do not penetrate into the mesophotic zone. While limited sections of the GBR shelf-edge are well mapped (e.g. Hydrographers Passage, Figure 3.1), there are still large “white areas” along the GBR shelf where no source bathymetric data are available. Obtaining multibeam bathymetry for the GBR outer-shelf sufficient to resolve submerged reef habitats would be of great benefit to studies of MCEs in the GBR. Similar problems occur in GBR-scale models of other environmental parameters such as optical water quality and bottom currents. Although these areas may be well offshore and consequently harder to survey than inshore regions, incorporation of physical, biological and environmental data from the outer-shelf would allow a greater level of understanding of the GBR ecosystem as a whole. This is an important consideration for both scientists and managers, particularly when trying to predict the effects of climate change on the GBR ecosystem over coming decades. Such modelling efforts would be greatly enhanced by the collection of long-term environmental data such as temperature, light and pH.

Concluding Remarks

Mesophotic coral reef ecosystems are among the least-studied coral reef habitats. This thesis provides the most comprehensive study of mesophotic coral reef ecosystems to date anywhere in the Indo-west Pacific region. It also represents the first quantitative assessment of habitat-forming sessile benthic megafauna occurring in the mesophotic zone of the GBRWHA. The results of this thesis provide valuable data for scientists aiming to understand the ecology of mesophotic coral reef ecosystems and their relationship to shallow-water reef habitats, and also for GBRWHA managers, who can now incorporate MCE habitats into management decisions. These results show that the submerged reefs of the GBRWHA outer-shelf contain diverse communities of sessile benthic megafauna. Further research should be directed towards better understanding spatial and temporal dynamics in the ecology sessile benthic megafauna, as well as fish and mobile invertebrate communities. In addition, greater attention should be given to connectivity between shallow and deep water reef habitats, particularly to investigate the potential for deep reef habitats to act as refugia and provide a source of colonists to re-seed shallow-water reefs affected by environmental disturbance.

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Appendices

Appendix 1: Taxa included in taxon matrix collected for Chapter 3. “Taxon Category” lists the 27 categories under which data were analysed for statistical analysis. To clearly display broad taxon classes and their relative importance to different site groups, these 27 categories were condensed into Taxon Classes, seen in column 2. “Taxa included” shows the taxa that were able to be identified, and which group they were included in. Many taxa were unable to be resolved to species level from the AUV images, particularly taxa such as octocorals, which require examination of sclerites for accurate identification, even to generic level.

Taxon Category	**Taxon Class (Fig.3)**	**Taxa Included**
Carteriospongia	Carteriospongia	*Carteriospongia foliascens*
Light brown thinly branching sponge	Other Sponge	ID unknown
Purple Vase Sponge	Other Sponge	ID unknown
Encrusting Sponge	Other Sponge	ID unknown
3D Sponge	Other Sponge	Diverse taxa, ID unknown
Montipora	Other Scleractinia	Several encrusting and plating species of *Montipora*
Leptoseris	Other Scleractinia	Multiple species, ID not possible from AUV images
Echinophyllia (Mycedium)	Other Scleractinia	Multiple species, ID not possible from AUV images
Fungiid	Other Scleractinia	*Fungia sp.* and *Diaseris distorta* identified in dredge samples
Branching Coral	Branching Scleractinia	Plating and branching *Acropora*, *Pocillopora*, and *Seriatopora hystrix* identified from dredge samples
Plating Coral	Other Scleractinia	ID unknown
Encrusting/Massive Coral	Other Scleractinia	ID unknown
Antipathes	Antipatharia	ID unknown
Cirrhipathes	Antipatharia	ID unknown
Stichopathes	Antipatharia	ID unknown
Other Antipatharian	Antipatharia	ID unknown
Cespitularia	Zoox Octocoral	ID unknown
Alcyoniid	Zoox Octocoral	*Sarcophyton*, *Lobophyton*, *Sinularia*
Other zooxanthellate octocoral	Zoox Octocoral	Xeniidae
Dendronephthya	Dendronephthya	Species ID unknown
Fan Gorgonian	Fan Gorgonian	*Annella* most abundant. *Siphonogorgia*, *Chironepthya*, *Echinogorgia*, *Zignisis* also identified from dredge samples
Branching Ellisellid	Ellisellid (not shown)	*Ellisella*
Non-branching Ellisellid	Ellisellid (not shown)	*Viminella, Junceella*
Other Gorgonian	Other Gorgonian (not shown)	ID unknown
Zoanthid	Zoanthid (not shown)	*Acrozoanthus*, other IDs unknown
Hydroid	Hydroid (not shown)	ID unknown
Crinoid	Crinoid (not shown)	Several taxa, IDs unknown

Appendix 2: Morphological Units used in site-scale habitat analysis, Chapter 4.

Morphological Unit
Porifera
Branching Sponge
Light brown thinly branching sponge
Carteriospongia
Other Sponge
Unknown Sponge
Scleractinia
Montipora
Seriatopora hystrix
Branching Coral
Fungiid
Diaseris
Faviid
Goniopora
Leptoseris
Encrusting Croral
Plating Coral
Other Coral
Antipatharia
Antipathes
Cirrhipathes
Octocorallia
Cespitularia
Xeniid
Zooxanthellate octocoral
Anella
Branching Ellisellid
Unidentified Gorgonian/Azoox Octo
Whip Gorgonian
Fan Gorgonian
Crinoidea
Crinoid
Ascideacea
Ascidian

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Appendix 3: Morphological units used in classification of reef substrata, Chapter 4.

Morphological Unit (MU)
Sponges
Carteriospongia
Ianthella
3-D sponge
Branching sponge
Encrusting sponge
Unknown sponge
Scleractinia
Montipora
Acropora - plating
Acropora - branching
Pocillopora
Seriatopora hystrix
Euphyllidae
Galaxea
Leptoseris
Pachyseris
Fungiid
Echinophyllia
Mycedium
Blastomussa
Scolymia
Faviid
Goniopora
Encrusting coral
Antipatharia
Antipathes
Cirrhipathes
Octocorallia
Cespitularia
Tubipora
Dendronephthya
Sarcophyton
Sinularia
Xeniid
Annella
Branching Ellisellid

Junceella
Other soft coral
Fan Gorgonian
Other Gorgonian
Actiniaria
Heteractis crispa
Crinoidea
Crinoid
Ascideacea
Ascidian