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RESEARCH PUBLICATION No. 109

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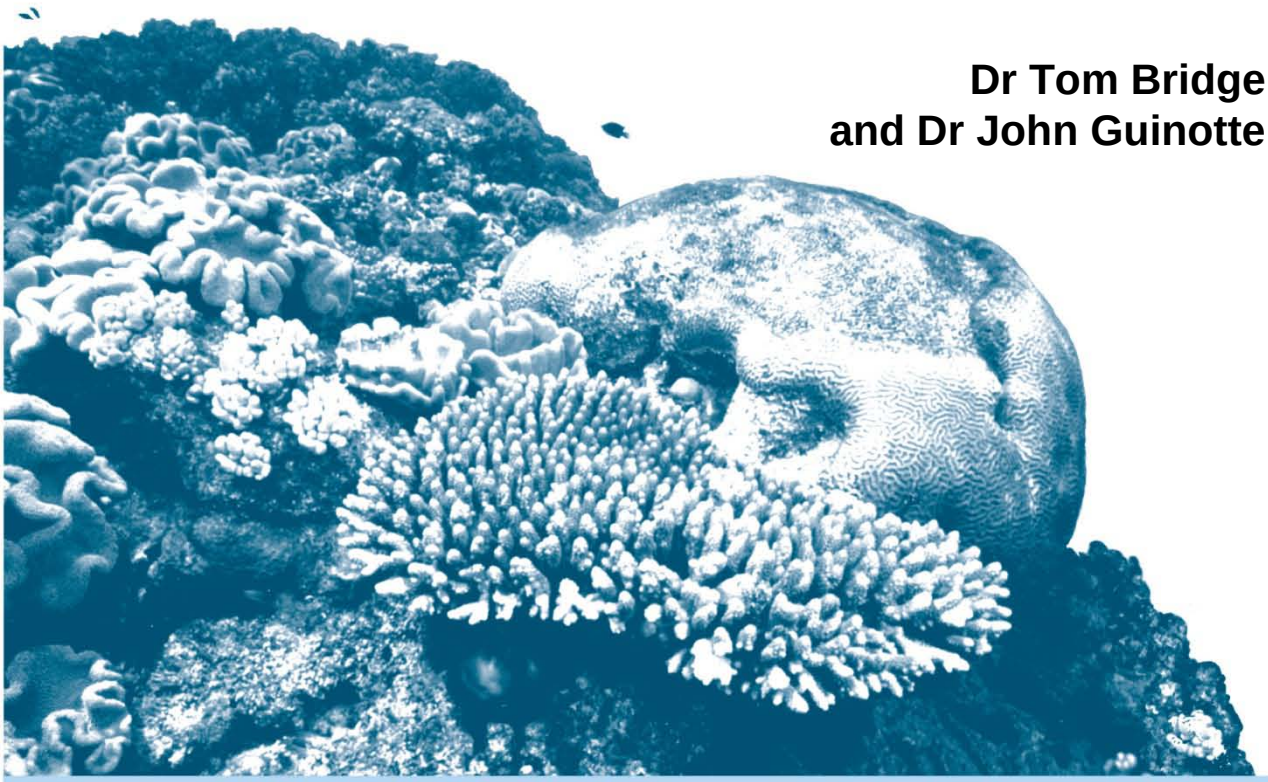
Their potential distribution and possible role as refugia from disturbance



Dr Tom Bridge
and Dr John Guinotte

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Their potential distribution and possible role as refugia from disturbance

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Australian Government
Great Barrier Reef Marine Park Authority

JAMES COOK UNIVERSITY AUSTRALIA

MARINE CONSERVATION INSTITUTE

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ACRONYMS USED IN THIS REPORT

MCEs.....Mesophotic coral ecosystems
LADS.....Laser Airborne Depth Sounder
CCR.....Closed-circuit Rebreather
ROV.....Remotely Operated Vehicle
AUV.....Autonomous Underwater Vehicle
NOAA.....National Oceanic and Atmospheric Administration
EAC.....East Australian Current
IMOS.....Integrated Marine Observing System
AIMS.....Australian Institute of Marine Science
LTMP.....Long Term Monitoring Program

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EXECUTIVE SUMMARY

This report reviews the most recent science regarding the potential distribution of mesophotic coral reef ecosystems (MCEs) throughout the Great Barrier Reef World Heritage Area, and discusses the potential importance of MCEs as refugia for corals and other sessile benthic megafauna from disturbance and as potential sources of coral larvae to disturbed shallow-water coral reefs. MCEs are zooxanthellate coral reef communities occurring in the intermediate depths of the photic zone (~30–150 metres) and have been documented in many regions of the world's oceans, including the tropical western Atlantic, Red Sea, and throughout the Indo-Pacific. MCEs are not as well studied as their shallow-water counterparts because they are found in waters that cannot be accessed safely with conventional SCUBA methods. However, recent advances in SCUBA technology (e.g. closed-circuit rebreathers and mixed gas diving) and robotics (autonomous underwater vehicles and remotely operated vehicles) provide a means to access MCEs, enabling scientists to document the unique mix of both shallow-water coral reef fauna and other species that are endemic to the mesophotic zone. The potential importance of MCEs as refugia areas from environmental disturbance and climate change makes them of great interest to managers of coral reef ecosystems, as illustrated by the United States' National Oceanic and Atmospheric Administration (NOAA) recently developing a Research Strategy for mesophotic coral ecosystems.

MCEs are found in deeper waters (~30–150 metres), which potentially provide an important refuge for corals and associated species from environmental disturbances. Recent observations have shown that MCEs are less likely to be affected by high sea surface temperature induced bleaching events that have caused substantial coral mortality on proximal shallow-water reefs. MCEs may also be important for recovery of disturbed coral reefs by providing sources of propagules to recolonise shallow-water reefs following disturbances, but this theory is largely untested. Preliminary studies indicate life history and ecological factors play important roles in the ability of corals to disperse from deep to shallow habitats. The environmental stability of many mesophotic habitats suggests MCEs could provide important refugia areas from climate change related impacts over the coming decades.

Predictive habitat modelling (Bridge 2012) indicates mesophotic coral ecosystems are widespread on the submerged reefs[1] along the Great Barrier Reef shelf-edge, and MCEs may constitute a significant proportion of total coral reef area in the Great Barrier Reef World Heritage Area. Autonomous underwater

[1] Submerged reefs are reefs which are not exposed at low tide

vehicles have documented diverse assemblages of sessile megabenthos in MCEs including a significant number of taxa not previously recorded in the Great Barrier Reef World Heritage Area. Studies of MCEs to date are not sufficient to determine spatial patterns and distributions of coral species and communities in the mesophotic zone in the entire Great Barrier Reef World Heritage Area. However, the observations do indicate the upper mesophotic zone (< 65 m depth) supports many common zooxanthellate corals found on shallow-water reefs, and deeper reef habitats (to a depth of 150 m) appear to be dominated by a diverse range of heterotrophic octocorals and other azooxanthellate benthos.

A pilot study was conducted near Myrmidon Reef to investigate the extent of damage to MCEs caused by Tropical Cyclone (TC) Yasi, a category 5 tropical cyclone that tracked through the Great Barrier Reef on 2–3 February 2011. Surveys of four sites (north-west Myrmidon, south-west Myrmidon, north-east Myrmidon and Thimble Shoal) revealed two distinct impact groups: (1) reefs with severe damage (NE Myrmidon and Thimble Shoal); and (2) reefs with minimal damage (NW Myrmidon and SW Myrmidon). The NW Myrmidon and SW Myrmidon sites were afforded some protection by the physical structure of the reef, but the NE Myrmidon site was exposed to full force cyclonic waves and experienced significant damage. The Thimble Shoal site experienced severe coral damage to a depth of approximately 40 m due to the absence of a reef flat. A comparison of coral damage observed on MCEs and shallow-water coral reefs indicated depth provided additional protection from cyclones in some cases, but factors including reef slope and wave exposure were important determinants of the degree of coral damage. Further, soft coral cover at mesophotic depths at undisturbed Myrmidon Reef sites was similar to soft coral cover values reported in shallower depths by the Australian Institute of Marine Science Long Term Monitoring Program prior to the 2002 bleaching event. Soft coral cover in shallower waters declined dramatically post-2002 and has not recovered. The results of this pilot study suggest soft corals may not have suffered significant bleaching mortality at mesophotic depths.

This report reviews the most recent science regarding MCEs in the Great Barrier Reef World Heritage Area and highlights their potential importance both as refugia and as potential sources of propagules to recolonise shallow-water habitats that have been subjected to environmental disturbance. The scientific literature is vast on the challenges coral reefs face: climate change (including increased frequency and severity of coral bleaching events and cyclones and ocean acidification), overfishing, and numerous terrestrial stressors. Many of these threats are predicted to amplify over the coming decades, putting increasing pressure on shallow-water reef systems. Predictive habitat models indicate extensive MCEs on the Great Barrier Reef are located along the outer-shelf and are therefore less likely to be impacted by terrestrial-based sources of disturbance (i.e. sedimentation, agricultural run-off, etc.). It is clear from the small amount of information available on MCEs that research effort, funding, and management policies directed towards MCEs have lagged behind their shallow-

water counterparts. In light of these facts it is critical reef scientists and managers gain a better understanding of MCE distribution, the functional roles MCEs perform, including their connectivity to shallower reef habitat and their significance as potential refugia areas throughout the Great Barrier Reef World Heritage Area. The aims of this report are therefore to: (1) provide an overview of the current state of knowledge of MCEs in the Great Barrier Reef World Heritage Area; (2) present the results of a pilot study from the Myrmidon Reef region to assess the damage sustained by mesophotic coral reefs from TC Yasi and compare the results to adjacent shallow reefs; (3) discuss the role of MCEs in ecosystem function, in particular the potential to act as refugia for corals and associated species from environmental disturbances and the effects of climate change; and (4) highlight areas for future research and suggest implications for management.

INTRODUCTION

Mesophotic coral reef ecosystems (MCEs) are tropical coral reef communities found at intermediate to lower depths of the photic zone. MCEs are characterised by the presence of light-dependent (zooxanthellate) corals and associated communities, and occur at depths from 30 to 150 m (Hinderstein et al. 2010; Kahng et al. 2010). MCEs are found in many regions of the world including the tropical western Atlantic (Armstrong et al. 2006; Smith et al. 2010) and the Indo-Pacific (Colin et al. 1986; Kahng and Kelley 2007; Bare et al. 2010; Bridge et al. 2011a; Bongaerts et al. 2011a). Darwin (1842) collected corals from mesophotic depths (128 m), but it was almost a century before the first *in situ* observations were conducted using SCUBA (Goreau and Wells 1967). In the 1980s, manned submersibles conducted detailed descriptions of the vertical zonation of coral reef communities in both the western Atlantic (Fricke and Meischner 1985; Reed 1985; Ohlhorst and Liddell 1988) and Indo-Pacific (Colin 1986; Colin et al. 1986; Thresher and Colin 1986). These studies reported diverse assemblages of benthic megafauna including scleractinian corals, octocorals, and sponges occurring to depths of 50 m or more. More recently, studies of MCEs using remotely sensed imaging techniques have been conducted in several locations in the Pacific Ocean including the Hawaiian Islands (Kahng and Kelley 2007; Rooney et al. 2010), American Samoa (Bare et al. 2010), the Great Barrier Reef (Bridge et al. 2011a, 2011b), and the western Coral Sea (Bongaerts et al. 2011a). These studies have increased scientific understanding of both the biodiversity of Indo-Pacific MCEs and the physical processes governing their community composition. Western Atlantic MCE coral assemblages appear to have high levels of regional similarity (Kahng et al. 2010), however no such patterns have emerged from studies of MCEs in the Indo-Pacific (Kahng et al. 2010).

Unlike shallower reefs, submerged reefs harbouring mesophotic coral communities are often too deep to be detected using remote sensing techniques such as Laser Airborne Depth Sounder (LADS) and space-based sensors. MCEs are also logistically difficult to study as they occur at or beyond the depths accessible to researchers using conventional SCUBA technology. Therefore, researchers have generally utilised either technical diving (closed- and open-circuit) or remote imaging systems such as remotely operated vehicles (ROVs) (Bongaerts et al. 2011a; Bo et al. 2011) or autonomous underwater vehicles (AUVs) (Armstrong et al. 2006; Williams et al. 2010) to explore MCEs. These tools are highly effective but very expensive due to the cost of the units and the ship time required to deploy them. For these reasons, MCEs have remained understudied and poorly understood, especially when compared to shallow-water coral reef habitats that can be surveyed easily and at lower costs using SCUBA. This is changing, however, as evidenced by a 2010 special issue focusing on MCEs in the journal *Coral Reefs*, and the development of a research strategy for MCEs by the United States' National Oceanic and Atmospheric Administration (NOAA; Puglise et al. 2009).

It has been suggested for some time that deep reef habitats may be less susceptible to some environmental disturbances, including warm-water induced coral bleaching, tropical cyclones and even crown-of-thorns starfish (Bak and Nieuwland 1995; Glynn 1996; Bongaerts et al. 2010a). Many disturbances currently impacting coral reefs are predicted to increase in frequency and severity due to climate change (Hughes 2003; Bellwood et al. 2004), and therefore MCEs may provide critical refugia for corals and associated species over coming decades. Unfortunately, long-term data on deep reef communities are scarce; however, one 20-year study of coral communities over a depth

range of 0–40 m in the Caribbean (Bak and Nieuwland 1995) does lend support to the refugia hypothesis. In that study, coral cover decreased significantly from 10–20 m but not at 30–40 m, while the number of colonies decreased from 10–30 m but not at 40 m. If these patterns are repeated in other locations around the world, MCEs may be able to maintain critical ecosystem functions and services even in areas where shallow reefs have become degraded. Furthermore, undisturbed deeper habitats may provide a source of propagules to repopulate shallow reefs which have suffered coral mortality. At present, evidence of this potential is conflicting. Populations of the coral *Seriatopora hystrix* from the northern Great Barrier Reef showed strong genetic partitioning of populations among habitat types, and experimental results indicated a decreased ability for transplanted corals to survive outside their native habitat (Bongaerts et al. 2010b). However, significantly less genetic partitioning was observed in the same species from Scott Reef, Western Australia (van Oppen et al. 2011). The ability of corals to disperse across habitats is likely to be influenced by a number of factors, including reproductive strategies (brooders/broadcasters), larval duration and local/regional oceanographic conditions, and further research is required to better address this question. Nonetheless, it is clear that mesophotic reefs are widespread throughout the Indo-Pacific and western Atlantic, and represent unique habitats worthy of further interest from both scientists and resource managers.

REPORT OBJECTIVES

The primary objective of this study is to provide an independent report summarising the current state of knowledge regarding the extent and ecology of MCEs in the Great Barrier Reef, and to discuss their potential importance as refugia for corals and associated species from environmental disturbances. The specific objectives are to:

- Provide an overview of the current state of knowledge of MCEs in the Great Barrier Reef World Heritage Area;
- Present the results of a pilot study from the Myrmidon Reef region to assess the damage sustained by mesophotic coral reefs from Tropical Cyclone Yasi and compare the results to adjacent shallow reefs;
- Discuss the role of MCEs in ecosystem function, in particular the potential to act as refugia for corals and associated species from environmental disturbances and the effects of climate change;
- Highlight areas for future research and suggest implications for management.

This information provides vital baseline data on an extensive but poorly characterised habitat within the Great Barrier Reef World Heritage Area, which can be used by management to improve the resilience of the Great Barrier Reef to current and future human and natural disturbances, including the effects of global climate change.

MESOPHOTIC CORAL REEF ECOSYSTEMS IN THE GREAT BARRIER REEF WORLD HERITAGE AREA

Physical oceanography of the Great Barrier Reef outer-shelf

The physical oceanography of the Great Barrier Reef system is complex and highly variable both latitudinally and across-shelf. Temperature, salinity, optical water quality, and water column productivity vary considerably in space and time and are strong drivers of coral distribution (Done 1982; Dinesen 1982). Although there are general latitudinal gradients (e.g. mean annual sea surface temperatures in the northern Great Barrier Reef average ~3 ˚C warmer than in the south), water column properties exhibit greater cross-shelf variability as coastal waters are influenced by terrigenous[2] sediments (Wolanski 1994). These variations are mirrored by changes in the ecology of shallow coral reefs, which show significant cross-shelf variation for a variety of taxa, including hard corals (Done 1982) and octocorals (Dinesen 1982; Fabricius and De'ath 2008). Variability in community composition is also influenced by physical variables such as wave energy and turbidity (hard corals and phototrophic octocorals) and water column productivity and current flow (heterotrophic octocorals). Submerged shelf-edge reefs occur largely outside the influence of many of these drivers of community structure because they are located far offshore (on the shoulder of the continental shelf) and are predominantly influenced by waters from the Coral Sea.

Surface waters (0–100 m) of the Coral Sea are relatively homogeneous with respect to salinity and temperature, but water column stratification leading to warming of surface waters may exist in summer during periods of low wind. The South Equatorial Current flows westward across the Coral Sea to the Great Barrier Reef shelf and bifurcates[3] upon reaching the eastern Australian margin between 14˚S and 18˚S (Figure 1). 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 Great Barrier Reef margin (Wolanski 1994; Brinkman et al. 2001). These internal waves result in episodic delivery of cold, nutrient-rich waters onto the continental shelf and potentially play an important role in the ecology of MCEs (Bongaerts et al. 2011b; Bridge et al. 2011a).

[2] Sediments derived from the erosion of rocks on land

[3] Splitting of the current into two branches

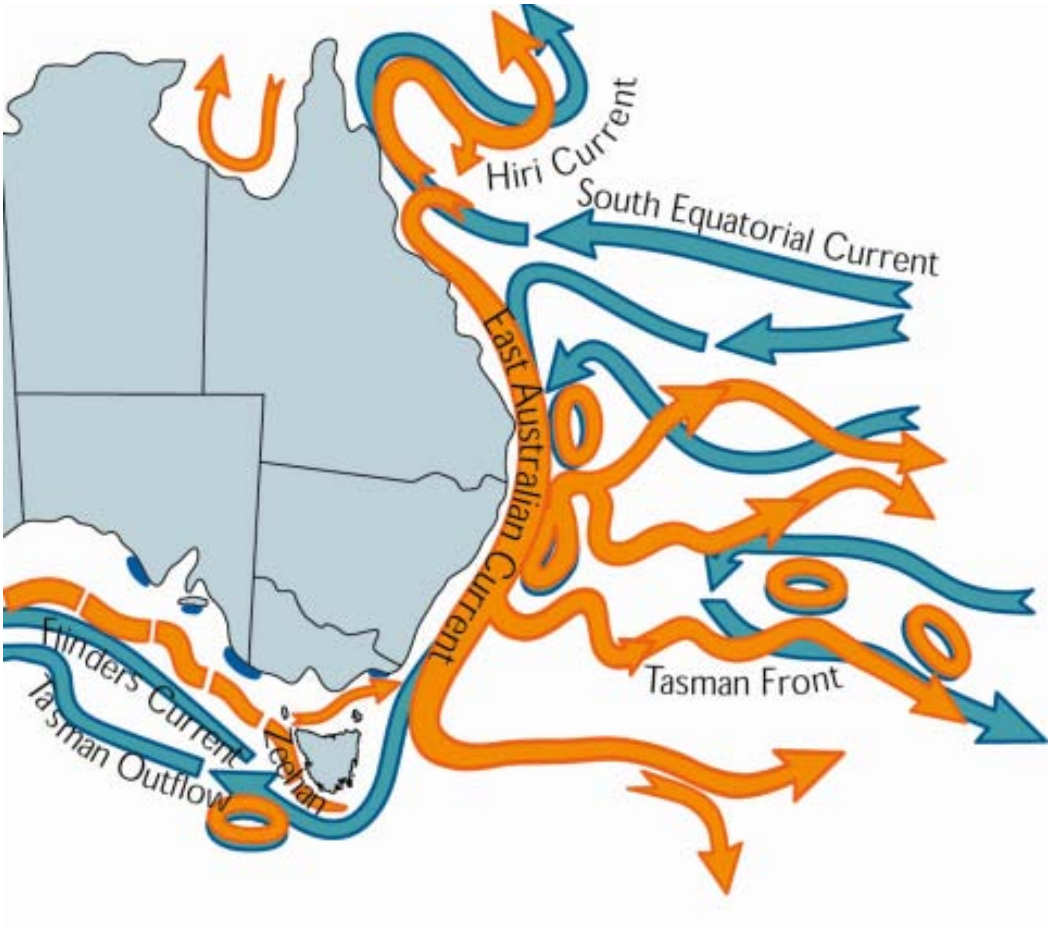

Figure 1: Oceanography of eastern Australia, showing bifurcation of the westward-flowing South Equatorial Current into the southward-flowing East Australian Current and the northward-flowing Hiri Current (from Ridgway and Hill 2009)

Variability in water column properties across and along the Great Barrier Reef results in highly variable light gradients throughout the water column, but zooxanthellate corals have been observed growing in mesophotic habitats with light levels as low as 0.07 per cent of surface irradiance (Kahng et al. 2010). Some deeper reef habitats of the Great Barrier Reef lagoon have been examined in detail (Pitcher et al. 2007), however, deeper communities in these areas contain very different assemblages to those occurring in the clear waters of the outer-shelf. In particular, inshore areas with higher turbidity are less likely to support zooxanthellate corals at mesophotic depths than outer-shelf reefs. SCUBA, ROV and AUV surveys of these outer-shelf shoals indicate that they support rich communities of zooxanthellate hard and soft corals to depths of over 40 m (Figure 4) (Beaman et al. 2011).

Submerged reefs on the shelf-edge of the Great Barrier Reef

The outer-shelf of the Great Barrier Reef World Heritage Area contains an extensive series of submerged shelf-edge reefs (Hopley et al. 2007) and is thought to support diverse mesophotic coral reef communities. Despite their apparent widespread

distribution in the World Heritage Area, these reef systems are poorly documented and are currently mostly unmapped. Some of the shallower outer-shelf reefs (often referred to as “shoals”) are marked on navigational charts and the *Great Barrier Reef Marine Park Zoning Plan* (2003), but the vast majority (particularly those occurring in waters > 30 m) remain uncharted. The descriptions of some non-reef bioregions of the Great Barrier Reef Marine Park, such as the Western Pelagic Platform, include references to “pelagic sediments punctuated by coral shoals”. However, many of these shoals are too deep (> ~25 m) to be identified by satellites or airborne imagery and are unlikely to be hazards for vessels. The areal extent of shoals that appear on navigational charts are often underestimated because only reef areas approaching the surface are mapped. These factors help to explain in part why the exact locations and spatial extent of MCEs are poorly documented on the Great Barrier Reef (Guinotte 2007).

In recent years, high-resolution multibeam bathymetric mapping has provided a detailed picture of submerged reef systems along some sections of the Great Barrier Reef outer-shelf (Beaman et al. 2008; Zieger et al. 2008; Bridge et al. 2011b; Abbey et al. 2011). The morphology of the Great Barrier Reef shelf changes significantly with latitude. The shelf is narrower and steeper in the north than in the south (Figure 2). 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). The northernmost 800 km of the Great Barrier Reef is occupied by deltaic reefs (at the northern extremity) and ribbon reefs. These reef types occur on the shelf-edge and exhibit a steeply sloping drop-off on their eastern side. This limits accommodation space for the development of submerged reefs to a narrow band immediately seaward of the emergent reefs, generally shallower than 70 m depth. Further to the south, reefs are set back from the shelf-edge and this has allowed the development of submerged reefs on the shoulder of continental shelf to depths of ~150 m.

The first quantitative study of submerged shelf-edge reefs of the central Great Barrier Reef was conducted by Harris and Davies (1989) using seismic profiling, side-scan sonar, and precision echo-sounding supplemented by submersible observations. They identified a series of submerged reefs between 15˚45’S and 21˚00’S off Cairns, Townsville and Hydrographers Passage. Hopley (2006) reported that these features occur almost continuously over 900 km along the central Great Barrier Reef margin and they have since been mapped as far south as the Swain Reefs (Tilbrook and Matear 2008). Research has focused primarily on reef geomorphology (Harris and Davies 1989; Hopley 2006; Beaman et al. 2008; Abbey et al. 2011) with little effort directed to the living mesophotic coral communities living on submerged reefs. Submersible observations conducted off Ribbon Reef No. 5, Myrmidon Reef, and Bowl Reef in 1984 indicated that submerged reefs were occupied by diverse mesophotic coral reef communities with living corals documented to depths exceeding 100 m (see Hopley et al. 2007; Beaman et al. 2008) (Figure 3).

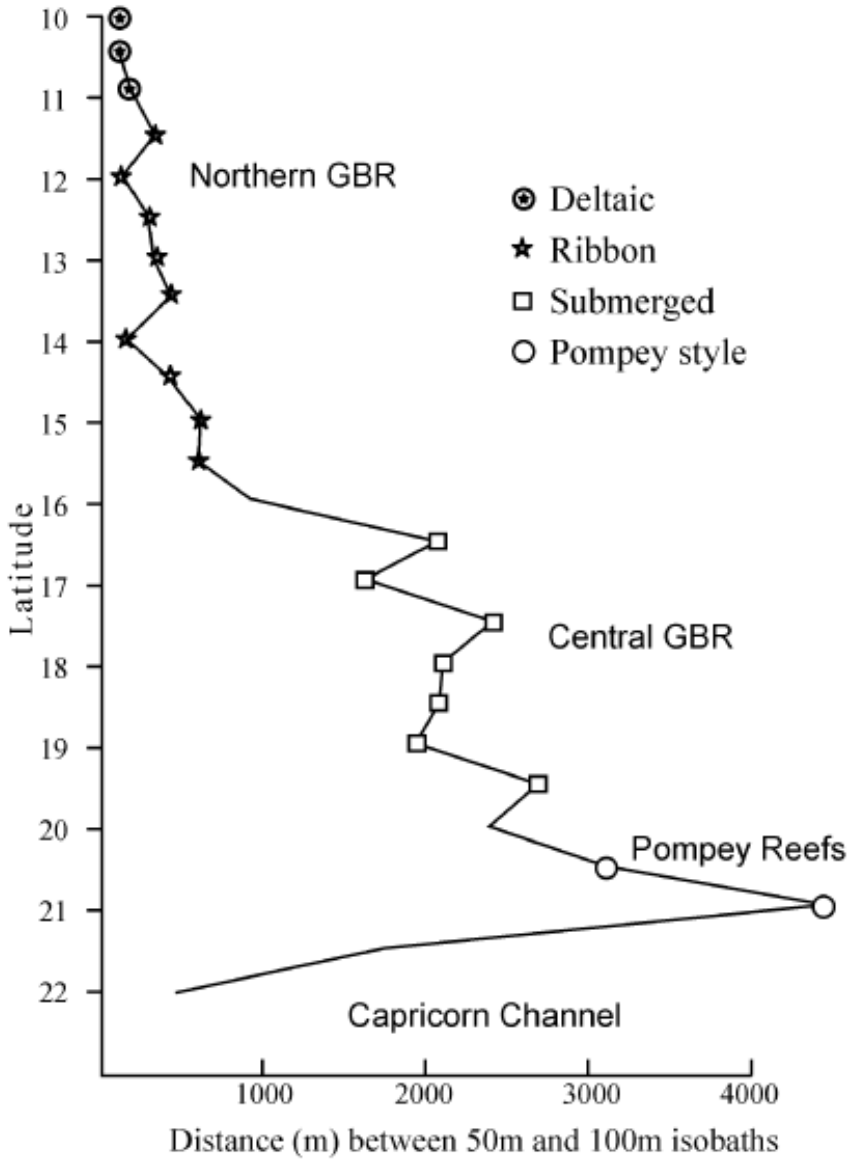

Figure 2: Variation in shelf morphology with latitude along the Great Barrier Reef margin (from Hopley 2006). Line indicates distance (in metres) between the 50 and 100 m isobaths for every 30' of latitude, as well as indicating the type of reefs occurring in each region. Shelf morphology exerts a strong influence on the occurrence and extent of submerged reefs along the Great Barrier Reef.

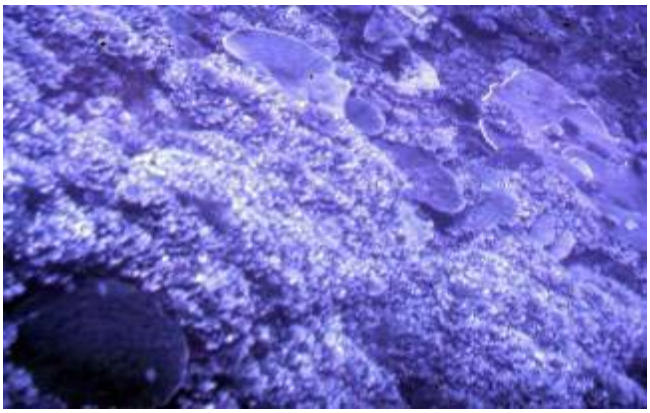

Figure 3: *Leptoseris*-dominated community at a depth of ~70 m at Myrmidon Reef in 1984. Photo: D. Hopley

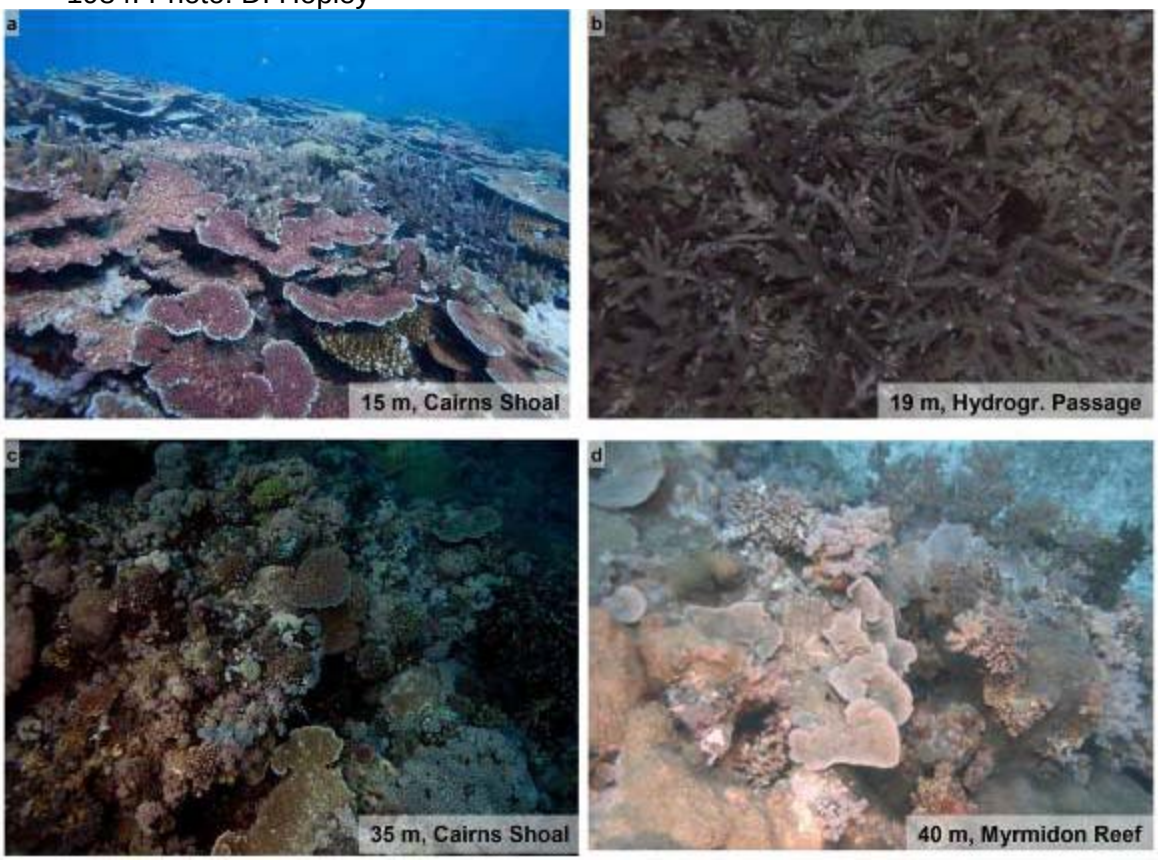

Figure 4: Examples of coral communities occurring on submerged reefs in the Great Barrier Reef World Heritage Area. The tops of some shoals occur above the mesophotic zone (a, b), while others are entirely mesophotic (c, d); (a) non-mesophotic coral area near Cairns (photo by Davey Kline); (b) non-mesophotic coral area near Hydrographers Passage (ACFR); (c) mesophotic coral area near Cairns (photo by Davey Kline); (d) mesophotic coral area near Myrmidon Reef (ACFR).

Mesophotic coral ecosystems on the Great Barrier Reef

The 2007 RV *Southern Surveyor* expedition was conducted by an international team of scientists (Webster et al. 2008) to investigate the submerged shelf-edge reefs first identified by Harris and Davies (1989) at four sites along 800 km of the Great Barrier Reef shelf-edge. The primary aims of the expedition were to: (1) examine the geomorphology of the Great Barrier Reef shelf-edge; (2) document the response of reefs to fluctuations in sea level; and (3) conduct biological surveys to document benthic biota. The expedition included high-resolution multibeam surveys at four sites along the Great Barrier Reef shelf-edge: (1) Ribbon Reefs; (2) Noggin Pass; (3) Viper Reef; and (4) Hydrographers Passage (Webster et al. 2008) (Figure 5). Bathymetry data were collected over an area ~4000 km^2 and confirmed prior observations indicating the outer-shelf of the Great Barrier Reef is occupied by a series of submerged reefs providing extensive potential coral habitat at mesophotic depths (Figure 6) (Webster et al. 2008). Optical imagery was collected using an AUV (Williams et al. 2010) and specimens were collected via benthic sled (Bridge et al. 2011c). This expedition was the most comprehensive study ever conducted on MCEs in the Great Barrier Reef World Heritage Area.

The gently sloping seafloor and series of parallel submerged reefs of Hydrographers Passage provided an ideal site to investigate depth zonation of mesophotic benthic communities during the expedition. AUV surveys conducted down-slope (50–150 m) revealed clear patterns in the zonation of sessile benthic megafauna along depth gradients (Bridge et al. 2011b). The upper mesophotic zone (> 60m depth) was dominated by a range of photosynthetic taxa, including hard corals, soft corals and phototrophic sponges, while deeper reef habitats (> 75 m) were colonised primarily by heterotrophic filter-feeders, including a diverse range of gorgonians, antipatharians, and some deep-water zooxanthellate corals (*Leptoseris* and *Echinophyllia* spp.).

Comparisons of the intermediate depths (50–65 m) where zooxanthellate corals are known to occur along the Great Barrier Reef outer-shelf revealed coral community composition was variable among sites, but also indicated there were consistent patterns in broad-scale habitat use by phototroph- and heterotroph-dominated communities (Bridge et al. 2011a). The tops of submerged reefs were flat or gently sloping and were dominated by phototrophic taxa, many of which also occur on shallow-water reefs. Steeper reef walls were dominated by heterotrophic octocorals and antipatharians; a likely function of decreased light irradiance on steeper slopes. Community composition between sites was not consistent; for example, phototrophic communities near Viper Reef were heavily dominated by hard corals (primarily *Montipora* sp.), whereas soft corals (primarily *Cespitularia* sp.) and phototrophic sponges (*Carteriospongia* sp.) occurred in high abundance at Hydrographers Passage (250 km to the south). The reasons for these patterns in community structure are currently unclear.

Specimens collected on the *Southern Surveyor* expedition indicated that mesophotic habitats support a combination of “depth-generalist” species that occur on shallow-water reefs but whose range extends into the mesophotic zone, and “depth-endemic” species that occur only in the mesophotic zone. Fabricius and De’ath (2008) collated SCUBA transects from over 1300 sites along the Great Barrier Reef and recorded 30 genera of heterotrophic octocorals. The 23 benthic samples collected on the 2007 RV *Southern Surveyor* expedition documented 25 genera, eight of which were not documented in the shallow-water surveys. Five were new records for the Great Barrier Reef World Heritage

Area. Scleractinian corals were also collected on the expedition and were identified to species where possible: three species of hard corals were new records for the Great Barrier Reef World Heritage Area (*Acropora elegans*, *Leptoseris striata* and *Pocillopora molokensis*). Several hard coral species (e.g. *A. elegans* and *A. cardenae*) that were previously considered extremely rare appeared to be abundant at mesophotic depths. Several other samples were unable to be identified to species level despite examination by expert taxonomists (Carden Wallace, Paul Muir, Michel Pichon). These may be new and undescribed species or known species whose morphology is substantially different at mesophotic depths. Estimates of hard coral diversity from the samples collected on board the 2007 RV *Southern Surveyor* expedition indicate species richness of coral communities at depths of 50–100 metres to be ~84 species (Bridge et al. 20112). Many of these represent taxa that are commonly found on shallow-water reef habitats and particularly on turbid inshore reefs (e.g. *Porites*, *Galaxea*, *Goniopora* and *Fungia*), indicative of their ability to acclimatise to the low-light conditions present in turbid and deeper areas. The upper mesophotic zone (30–50 m depth) is likely to support greater richness of corals due to higher light irradiance, but was not well sampled during the *Southern Surveyor* expedition. This is supported by preliminary results from a December 2011 expedition to the outer-shelf in the northern Great Barrier Reef (Mantis, Lagoon, Tydeman, Yonge and Number 5 Ribbon Reefs), which recorded ~150 species of corals in depths >30 m across the five sites (Bridge and Turak, unpublished data).

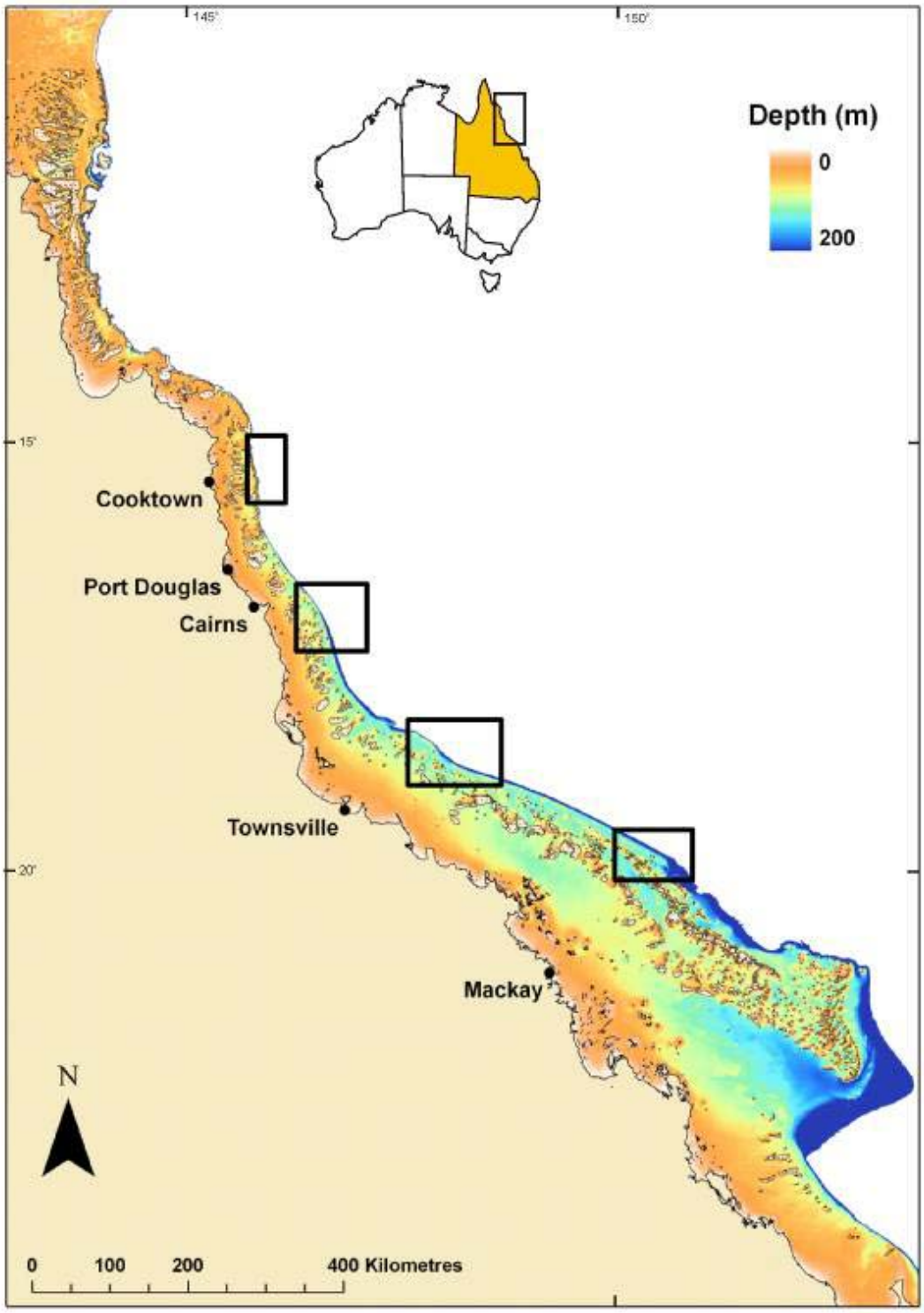

Figure 5: Location of four mesophotic study sites examined by the RV *Southern Surveyor* in September–October 2007 along the Great Barrier Reef outer-shelf. Bathymetry (0–150 m) from Beaman (2010).

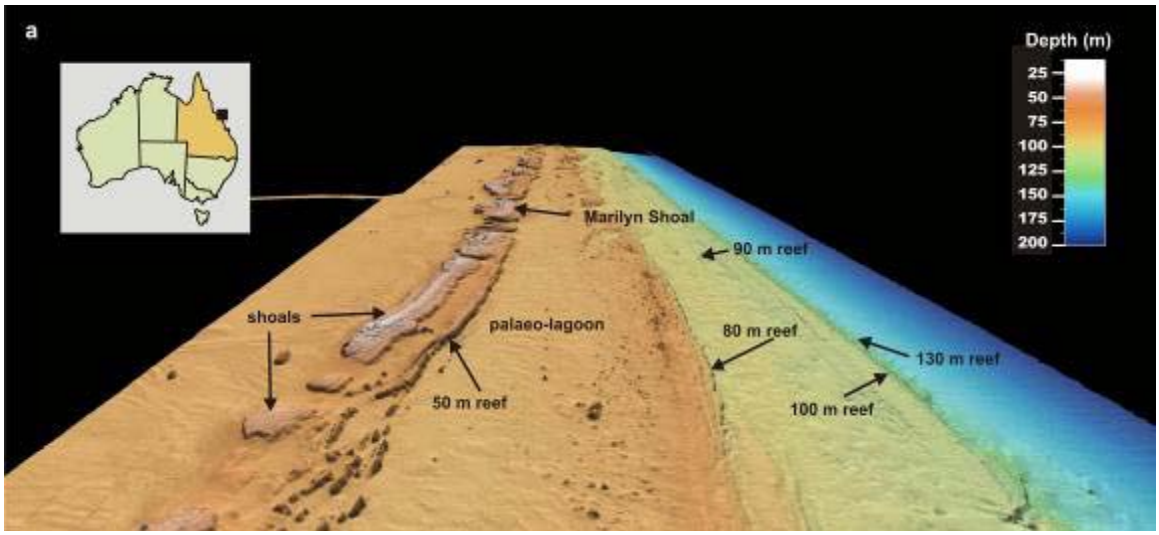

Figure 6: Multibeam bathymetric image of Great Barrier Reef outer-shelf at Hydrographers Passage, central Great Barrier Reef, showing location of submerged reefs (from Bridge et al. 2011b).

Predictive modelling of undocumented coral habitat

Physical and environmental drivers of species' distributions can be used as surrogates to predict the potential distribution of benthic marine ecosystems across large spatial scales and to identify priority sites for management (Ward et al. 1999; Davies and Guinotte 2011). Predictive habitat models use the location of species collected in the field to quantify the relative influence of environmental, physical and chemical drivers, and are particularly useful for predicting suitable habitats in areas where biological survey data are sparse (i.e. remote or inaccessible habitats such as the deep sea (Davies et al. 2008; Tittensor et al. 2009; Davies and Guinotte 2011). In 2001, Guinotte (2007) developed a predictive model of the distribution of coral reef habitat in the World Heritage Area using salinity, temperature, nutrients (nitrate and phosphate), bathymetry, light irradiance, and water clarity. The model used the highest-resolution bathymetric dataset available at the time (250 x 250 m) (Lewis 2001) and correctly predicted 90 per cent of documented reefs, and 93 per cent of reef absences within the Great Barrier Reef World Heritage Area. Model performance was highest in mid-shelf and outer-shelf regions and the model identified numerous "false positives" (modelled areas positive for reef habitat that were not documented in nautical charts) occurring in close proximity to the continental shelf (Figure 7). Guinotte (2007) suggested these false positives represented undocumented reef habitat because the depth range (25–40+ m) along the shelf was sufficient for coral growth. Subsequent field surveys conducted by the Australian Institute of Marine Science (AIMS) at two sites near Myrmidon Reef in 2003 confirmed model predictions and documented submerged reefs with high cover of both hard and soft corals (Figure 8). Interestingly, neither site showed any evidence of the bleaching event that severely affected Myrmidon Reef and other proximal reefs during the summer of 2002.

Guinotte's (2007) model was based on known thresholds for coral reef growth identified by Kleypas (1997) and probably underestimated the distribution of mesophotic coral communities. In a separate study, Bridge (2012) used Maxent (Maximum Entropy)

modelling to estimate MCE area for the Great Barrier Reef World Heritage Area using GBR100 (100 x 100 m bathymetric grid; Beaman 2010), geomorphic variables (slope, aspect, rugosity, geomorphic zone and seafloor reflectivity), and documented locations of mesophotic communities from a 2007 RV *Southern Surveyor* expedition (Webster et al. 2008). Maxent is a presence only modelling package that requires georeferenced occurrence data and is effective with small numbers of input sample locations (Phillips et al. 2004; Phillips et al. 2006). The model predicted the distribution of both phototroph- and heterotroph-dominated communities on submerged reefs (Bridge et al., in prep.), and indicated that mesophotic reefs occupy an area of > 7000 km^2 within the World Heritage Area. Phototroph-dominated communities occur primarily in two environments: (1) submerged reefs along the shelf-edge; and (2) deeper flanks of documented emergent reefs inside the Great Barrier Reef lagoon (generally around outer-shelf reefs). Bridge (2012) models predicted another 2000 km^2 of heterotroph-dominated reef habitat occurring along the deeper submerged reefs along the Great Barrier Reef shelf-edge. Model accuracy was evaluated using Receiver Operating Characteristic (ROC) curves, with the area under the ROC curve being a measure of model performance. In both cases, ROC values indicated high model accuracy (Bridge 2012, Figure 5.9).

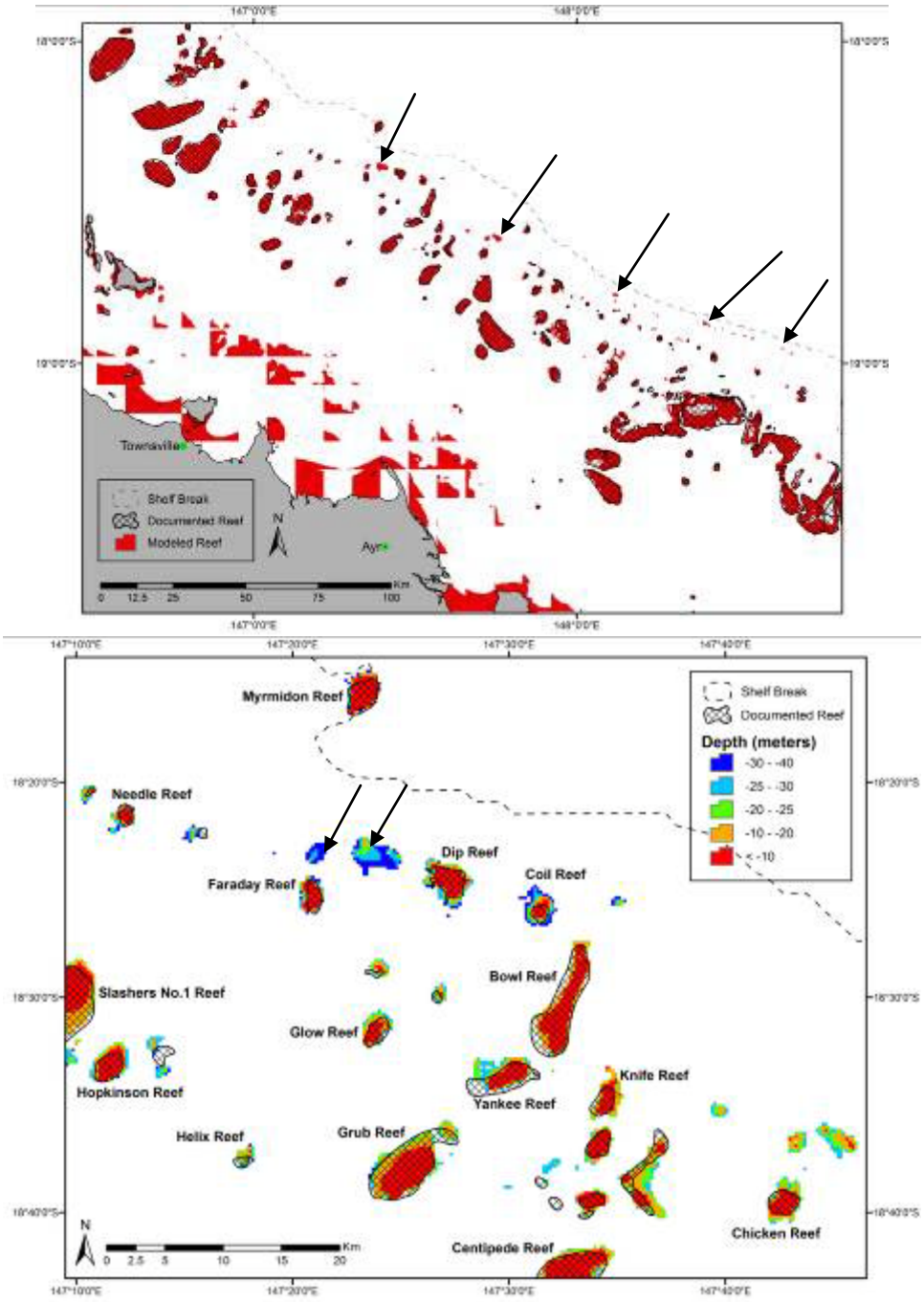

Figure 7: (top) Modelled reef habitat and documented reefs in central section of Great Barrier Reef Marine Park; spatial resolution 250 m x 250 m; black arrows highlight offshore areas where there is a high probability modelled reef habitat identifies undocumented reefs; (bottom) Location of modelled/undocumented reef habitat ground-truthed by AIMS divers, black arrows highlight two sites visited, legend shows depth ranges of modelled reef habitat (Guinotte 2007).

Figure 8: Undocumented submerged reef identified by predictive model near Myrmidon Reef (Guinotte 2007). Depth 25–40 m. Photo: Mary Wakeford, AIMS

PILOT STUDY OF MESOPHOTIC CORAL REEFS FOLLOWING CYCLONE YASI

Severe Tropical Cyclone Yasi was a category 5 storm that passed over the Great Barrier Reef on 2–3 February 2011. At its peak, it created wind gusts of 285 kilometres per hour and caused gale-force winds over 760 km of coastline from Cooktown to Mackay (Great Barrier Reef Marine Park Authority 2011). Reef Health and Impact surveys conducted along the length of cyclone-affected coast by the Great Barrier Reef Marine Park Authority (GBRMPA), AIMS and others immediately after the cyclone examined the severity and spatial extent of damage to reefs in the region. Surveys were conducted to a maximum depth of 15 m with the most severe damage (including removal of almost all sessile benthos and removal of the reef matrix) occurring on outer-shelf reefs within 100 km of the cyclone eye on the southern side of the cyclone track (Great Barrier Reef Marine Park Authority 2011). SCUBA restrictions limited surveys to shallow waters on emergent reefs and no data was collected from either submerged shoals or deep reef slopes adjacent to emergent reefs.

In July 2011, the Autonomous Underwater Vehicle (AUV) *Sirius* was deployed from the AIMS ship RV *Cape Ferguson* to examine the extent of cyclone damage along a depth gradient to depths of ~45 m. Surveys were conducted at three sites—Myrmidon Reef, Thimble Shoal and Helix Reef—to: (1) identify the extent of damage inflicted by TC Yasi on mesophotic coral communities; (2) examine variability in damage among different sites; (3) identify abiotic factors that may cause variation in cyclone damage; and (4) compare the results to those obtained from adjacent shallow-water surveys.

Methods

Surveys were conducted at sites in the central Great Barrier Reef: Myrmidon Reef (18.26˚S, 147.39˚E), Thimble Shoal (18.37˚S, 147.26˚E) and Helix Reef (18.63˚S, 147.29˚E) (Figure 9). These sites were selected to represent three different environments: lower reef slopes adjacent to emergent outer-shelf reefs (Myrmidon Reef), mid-shelf reefs (Helix Reef), and submerged shoals (Thimble Shoal). Surveys were conducted along a euphotic–mesophotic depth gradient from an upper depth of ~15–25 m depth (depending on reef morphology at each site) to a lower depth of ~45 m to determine whether or not deeper reef areas were less susceptible to cyclone damage than adjacent shallow reefs.

Three AUV missions were conducted at Myrmidon Reef (NW, SW, and NE corners of the reef) to examine the influence of reef aspect on coral damage (Figure 10a). The western side of Myrmidon Reef consists of a reef slope which plunges steeply from the surface to a depth of ~20 m. Below 20 m the substrate is predominantly sandy, but is punctuated by a series of patch reefs rising ~2–5 m above the surrounding sand. The eastern side of the reef has steep slopes with the SE side being too steep to conduct AUV or towed video transects (Hopley 1984). The Thimble Shoal survey was conducted as a transect across the top of the shoal (Figure 10b), which rises from ~50 m depth to within ~10 m of the surface at its shallowest point. The shallowest section surveyed by the AUV was ~15 m. The Helix Reef survey was conducted on the NW side of the reef (Figure 10c) so results could be compared to AIMS Long Term Monitoring Program (LTMP) observations.

Coral community data was collected by visual inspection of high-resolution georeferenced stereoscopic images of the seafloor collected by the AUV. A total of six AUV surveys (four from Myrmidon Reef, one from Thimble Shoal, and one from Helix Reef) were conducted from 23–25 July 2011. The relative abundance of nine biotic categories (branching coral, plating coral, massive coral, encrusting coral, other hard coral, zooxanthellate octocoral, azooxanthellate octocoral, sponge/other sessile benthic megafauna and macroalgae) was estimated for both the entire image and also for the proportion of the image containing hard substratum for 50 randomly selected images from each survey using a Rapid Ecological Assessment technique (DeVantier et al. 1998) (Table 1). Analysis of hard substratum provides better estimates of the comparative difference among sites, but comparisons of the entire image are more suitable for comparing mesophotic surveys to AIMS LTMP data.

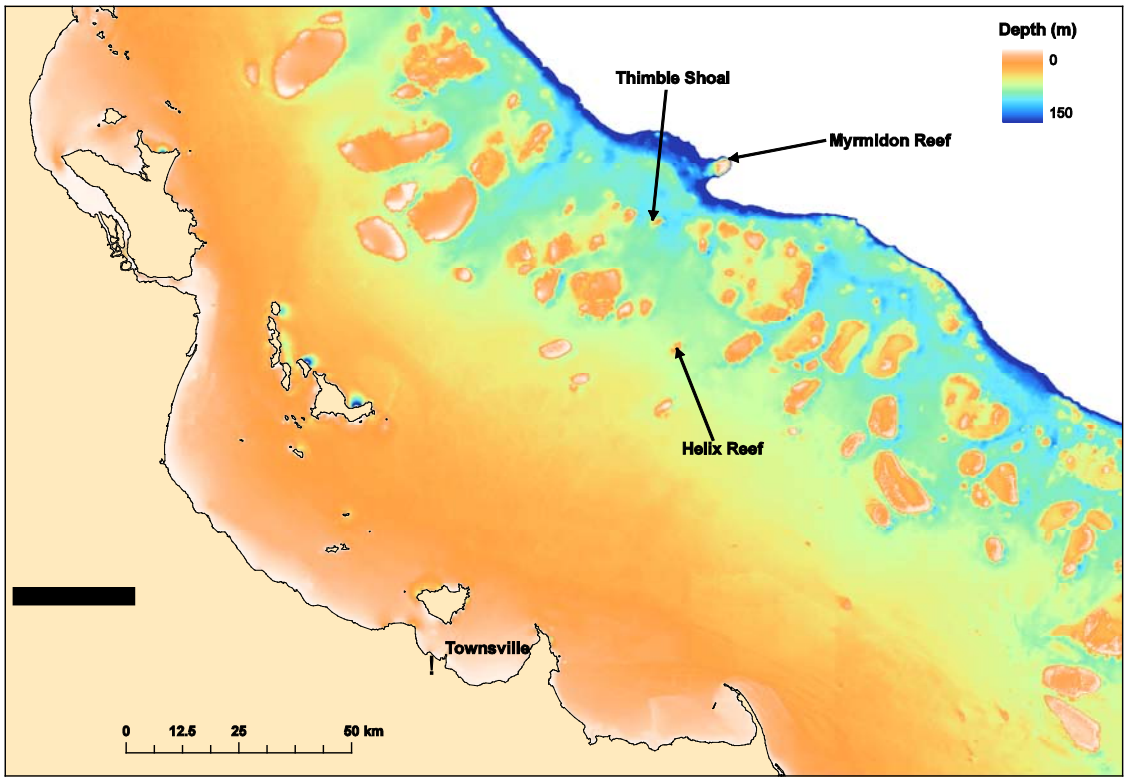

Figure 9: Bathymetry of the Great Barrier Reef to 150 m depth showing location of sites surveyed using AUV. Bathymetry data from Beaman (2010).

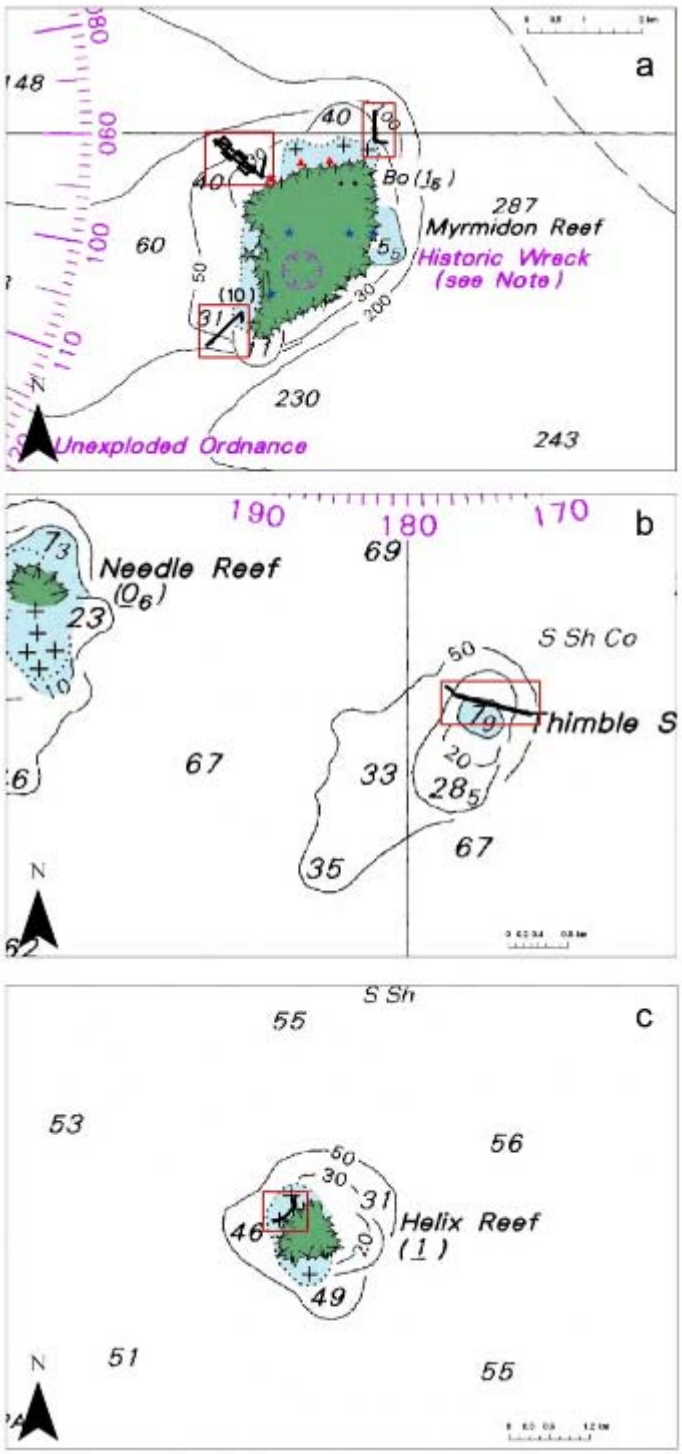

Figure 10: Location of AUV surveys at each site. Red boxes indicate the area that was surveyed, while black lines indicate the AUV track. Locations of shallow-water surveys at Myrmidon Reef are indicated by blue stars (GBRMPA) and red triangles (AIMS LTMP sites).

Table 1: Percentage cover categories used to analyse AUV images

Category	Percentage Cover
0	Not recorded
1	1–10
2	11–30
3	31–50
4	51–75
5	76–100

Abiotic data for substratum (sand, coral rubble, live coral rock) were collected using the same scale as the ecological data (Table 1). Additional abiotic data (various indices of rugosity, slope and aspect) were generated from three-dimensional reconstructions of AUV images (Friedman et al. 2010). Broader scale values were calculated by meshing together adjoining images over windows of five, 10 and 20 m centred on the randomly selected image. An estimate of cyclone exposure at the location of each image was also generated based on relative wave exposure and modelled using a fully automatic cartographic fetch model (Pepper and Puotinen 2009). Ten minute maximum wind speeds and directions at the surface were modelled based on the techniques described in Puotinen (2007) and Holland (2010). All analyses were conducted in the statistical program PRIMER v. 6 (Clarke and Gorley 2006).

A cluster analysis was performed on a Bray–Curtis similarity matrix of the relative abundance of each of the nine biotic categories. Analysis of Similarities (ANOSIM) was used to determine variability between sites. Similarity Percentages (SIMPER) were used to examine the key biotic components characteristic of each site, and BIOENV[4] used to identify abiotic variables which best explain the observed distribution of biota.

Myrmidon Reef is one of the best studied outer-shelf reefs in the Great Barrier Reef World Heritage Area and has a long history of ecological monitoring, including 21 AIMS LTMP surveys since 1988. The two most recent AIMS LTMP surveys were conducted in 2009 and 2011 and reported changes in shallow-water coral communities due to TC Yasi. AUV data collected for this pilot study was qualitatively compared to: (1) AIMS LTMP data from 2009 and 2011, and (2) data collected by the GBRMPA immediately following TC Yasi, to obtain insight into variability in spatial patterns of cyclone damage along depth gradients.

Results

Spatial patterns in communities and cyclone damage

Two sites (NW Myrmidon and SW Myrmidon) showed limited damage from TC Yasi, exhibiting high coral cover and few visible signs of damage to coral colonies. However, three sites (NE Myrmidon, Thimble Shoal and Helix Reef) appeared to have suffered extensive damage and had very low cover of sessile benthic megafauna. Interestingly, little coral rubble was observed in most locations; areas with low coral cover were generally completely devoid of three-dimensional structure. Examination of the biota at

[4] A tool within PRIMER for linking observed patterns in community structure to environmental variables

each site indicated Helix Reef (mid-shelf) contained different taxa to the four sites on the outer-shelf. Therefore, to maintain consistency in quantifying among-site variability, Helix Reef was excluded from further analysis.

The cluster analysis of hard substratum communities for the four outer-shelf sites confirmed visual observations and indicated two clusters: (1) images from NW and SW Myrmidon, and (2) images from NE Myrmidon and Thimble Shoal. The differentiation between the groups was clearly illustrated by ANOSIM (Global R = 0.648, ρ = 0.001). SIMPER analysis indicated over 60 per cent of the observed variation was due to zooxanthellate octocorals and macroalgae. Zooxanthellate octocorals were abundant at the undisturbed sites (NW and SW Myrmidon), but few in number at the disturbed sites (NE Myrmidon and Thimble Shoal). Macroalgae was observed on recently exposed hard substrata. Pairwise[5] ANOSIM tests of the four sites indicated there was no significant difference between NW and SW Myrmidon Reef sites, but there was a significant difference between the two disturbed sites (NE Myrmidon and Thimble Shoal). Disturbed sites were more similar to each other than to either of the non-disturbed sites. Two-way crossed ANOSIM (site and depth) indicated that depth was not significantly correlated to the observed distributions of biota.

Environmental variables explaining the observed variation

BIOENV analysis showed that the observed patterns in the distribution of sessile benthic megafauna could be explained by a range of environmental variables, although the relationship was not particularly strong (ρ = 0.208 for the best combination of variables). The most determinant combination of explanatory environmental variables were: rugosity, slope, mean depth and the number of nodes (another measure of rugosity). BIOENV did not identify wave exposure as a significant factor explaining community composition, but the sites with the highest (NE Myrmidon) and lowest (SW Myrmidon) exposure had the highest and lowest amounts of damage (Figure 11). All four sites were located in close proximity with maximum wind speeds of (30–35.7 m s^{-1}) and 17 hours of gales at all four sites. Thimble Shoal experienced low wave exposure in models, but experienced severe damage.

Comparison between deep and shallow communities

Comparison of post-TC Yasi coral communities at mesophotic depths with the GBRMPA shallow-water surveys conducted at Myrmidon Reef reveals interesting patterns. The GBRMPA surveys indicate damage was patchy across Myrmidon Reef, but the western side contained higher amounts of damaged coral, recently dead coral, and higher values for damage severity and extent. The western side also had higher overall coral cover (Table 2). The patterns for shallow-water reefs contradict patterns observed in AUV images, which indicated damage to mesophotic coral communities at both the NW and SW Myrmidon sites was low.

The location of AIMS LTMP sites 1 and 3 on the leeward side of Myrmidon Reef and the location of AUV surveys are shown in Figure 12. Site 1 is located adjacent to the NW Myrmidon AUV survey and Site 3 is located approximately halfway between the NW and NE Myrmidon surveys. LTMP surveys showed a decrease in cover of both hard and soft corals between 2009 and 2011 (Figure 13). Hard coral cover declined by 32 per cent at

[5] Test comparing two sites directly to each other, as opposed to all sites together

Site 1 and 25 per cent at Site 3 and was > 20 per cent at both sites post-Yasi. Soft coral cover also declined, although soft coral cover was low at both sites in 2009. Overall hard coral cover in the AUV surveys was similar to that observed for shallow-water habitats at NW and SW Myrmidon, but substantially lower for NE Myrmidon. However, soft coral cover was substantially higher at both NW and SW Myrmidon in the AUV surveys than in either of the 2009 or 2011 LTMP surveys.

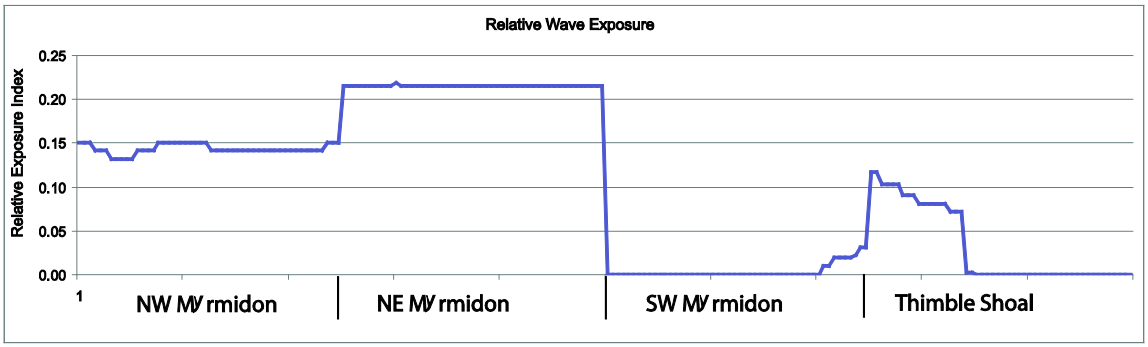

Figure 11: Model of cyclone exposure at the four outer-shelf reef sites

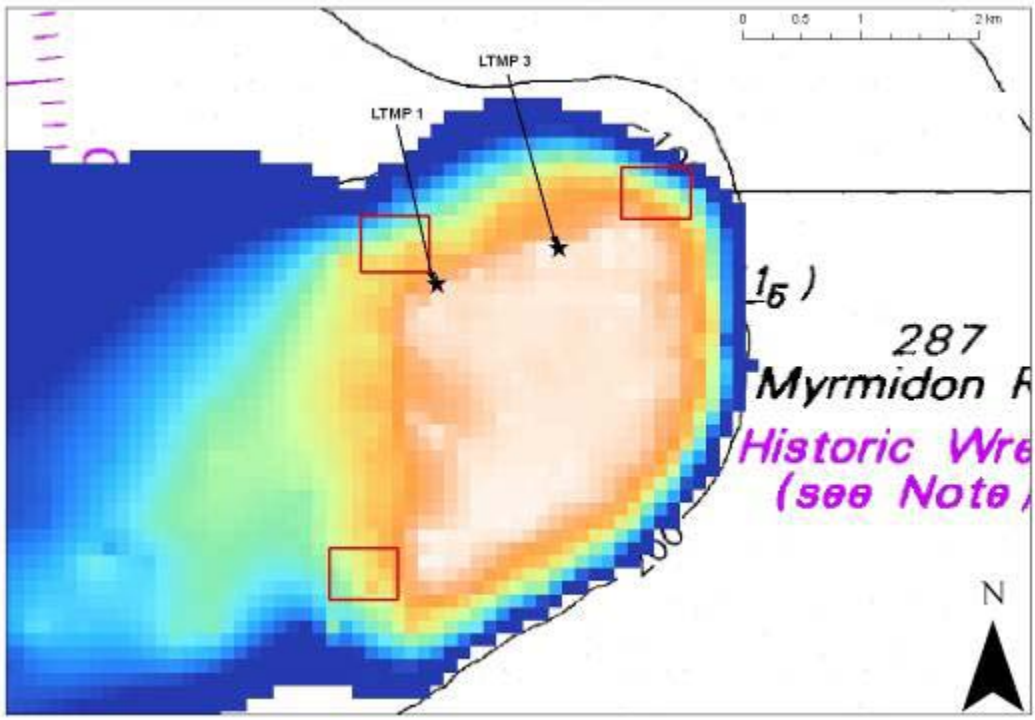

Figure 12: Location of AUV surveys (red boxes) and AIMS LTMP sites 1 and 3

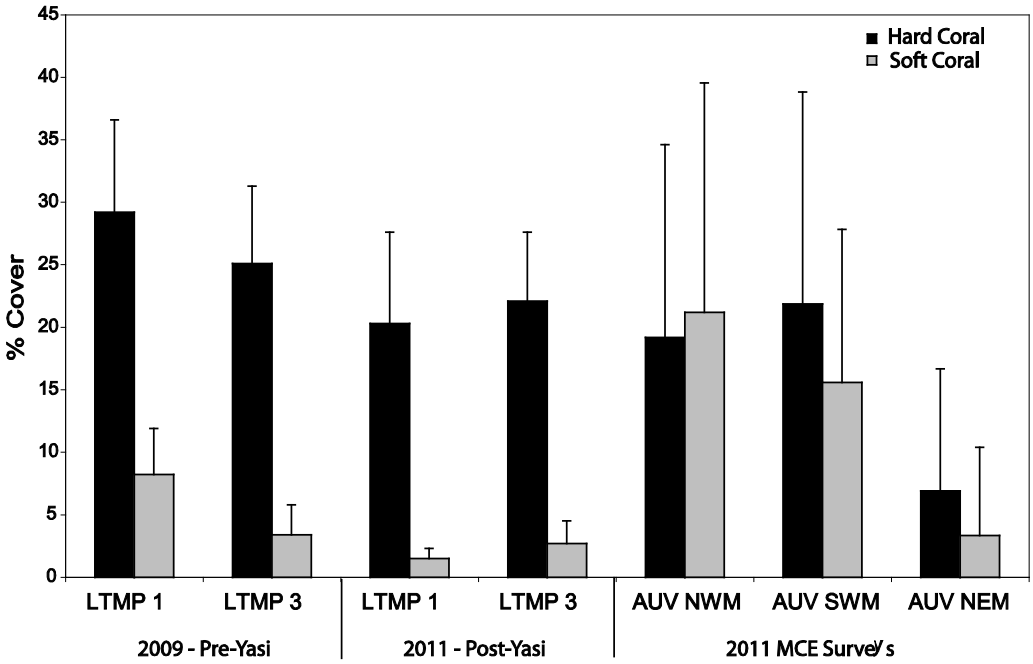

Figure 13: Comparison of coral cover at Myrmidon Reef in shallow (LTMP) and mesophotic (AUV) depths. NWM = NW Myrmidon, SWM = SW Myrmidon, and NEM = NE Myrmidon.

Table 2: Comparison of coral damage at east and west Myrmidon Reef reported by the Great Barrier Reef Marine Park Authority immediately following TC Yasi. Data presented are mean and standard deviation of the percentage cover of damaged coral, live coral, soft coral and recently dead coral and damage extent and severity indices developed by Great Barrier Reef Marine Park Authority. These indices are rated on a 0–5 scale, with 0 indicating no damage and 5 indicating extreme coral damage and high reef damage.

	Live Coral	Soft Coral	Damage Coral Cover	Recently Dead Coral	Damage Extent	Damage Severity
East	2.3 ± 2	0	26.5 ± 19	9.0 ± 14	0	0
West	12.4 ± 8	13.2 ± 21	37.6 ± 34	30.9 ± 36	9.1 ± 9	2.5 ± 2

Discussion

Spatial patterns in cyclone damage on submerged and mesophotic reefs

This pilot study provided an opportunity to study the effects of tropical storms on mesophotic communities under a "worst-case" scenario. TC Yasi was the largest and most intense cyclone to cross the Queensland coast in almost 100 years. Myrmidon Reef lies on the edge of the shelf and was subjected to TC Yasi's highly destructive winds (cyclone tracked 100 km north of Myrmidon). The geographic location of the reef was within the most heavily impacted region of the Great Barrier Reef World Heritage Area and the reef matrix received little protection (GBRMPA 2011).

This study confirmed the findings of earlier studies (Harmelin-Vivien and Laboute 1986) and reinforced that depth alone does not buffer mesophotic coral communities from reductions in coral cover when subjected to powerful category 5 cyclones. Cyclone damage varied considerably among mesophotic sites surveyed and between adjacent shallow and deep sites. The surveys conducted by the GBRMPA on Myrmidon Reef post-Yasi indicated the greatest coral damage occurred on the western side of the reef (although this was likely due in part to a higher pre-existing coral cover). However, deeper coral communities (NW and SW Myrmidon) suffered relatively minor and superficial damage despite wave exposure models indicating NW Myrmidon experienced high wave energy during the cyclone (Figure 11). The reef structure probably provided protection to MCEs on the western side of the reef, but the wave model indicates that the NE side of Myrmidon was exposed to the full force of the storm resulting in severe coral damage.

AUV images of Thimble Shoal showed very low coral cover in waters < 40 m depth despite the model indicating relatively low wave exposure. There are several possible reasons for this: (1) Thimble Shoal might have had low coral cover pre-Yasi (this is unlikely given reports of high coral cover from similar submerged shoals in the region); (2) Thimble Shoal's submerged coral communities were not protected from storm waves as were the MCEs on the western side of Myrmidon; or (3) errors in the wave exposure model. The wave exposure model indicated that half of Thimble Shoal experienced almost no wave exposure, but this probably accounts only for waves breaking on the shoal. Unlike the western side of Myrmidon, where the reef flat would have dissipated wave energy, cyclone waves probably broke directly on Thimble Shoal causing severe damage to coral communities and also to the reef matrix. The wave exposure model presented here only accounts for waves generated during the cyclone, not long-range swells. The size and intensity of TC Yasi probably generated significant long-range ground swells that would have impacted the reef prior to wind-driven waves from the cyclone. These swells were not included in the wave exposure model and probably impacted both NE Myrmidon and Thimble Shoal, while the western side of Myrmidon was protected by the reef flat.

The analysis indicated the distribution of benthic communities were positively correlated with rugosity and depth, and negatively correlated with slope. Small-scale rugosity values can be affected by the amount of living benthos because images with three-dimensional benthos (e.g. branching and plating corals) have higher rugosity than areas where corals have been removed. There was also evidence microtopography provided shelter for corals in some cases, particularly in disturbed sites. The few branching corals that survived the cyclone were located in crevices within the reef matrix. MCEs in high

slope areas are more susceptible to damage from debris avalanches, as reported by Harmelin-Vivien and Laboute (1986), and the high damage observed at the steeply sloping NE Myrmidon site may have been caused by debris avalanches rather than direct wave energy. In contrast, coral communities on the western side of Myrmidon reef are restricted to small patch reefs located in open, gently sloping, sandy areas away from the reef slope and were unaffected by debris originating from shallower depths. Depth appears to be another important factor in determining the susceptibility to damage at Thimble Shoal, where living corals were observed at 40 m depth with only macroalgae being present at shallower depths. This suggests that although depth alone is not able to completely buffer MCEs from severe cyclones, deeper coral communities are less likely to be as severely impacted as shallow communities.

Comparison of community composition on shallow versus mesophotic reefs

The results of this study indicate mesophotic hard coral cover at Myrmidon Reef is similar to adjacent shallow-water reefs, but soft coral cover is significantly greater at depth (Figure 13). Shallow-water soft coral cover at Myrmidon Reef declined substantially after the 2002 bleaching event and has shown minimal signs of recovery over the last 10 years (Sweatman et al. 2008). Upper mesophotic soft coral cover found in this study was similar to AIMS LTMP shallow-water values reported prior to 2002, and indicates that the 2002 bleaching may not have impacted soft corals at mesophotic depths. However, there is no evidence mesophotic soft corals have contributed to the recovery of shallow-water soft coral cover at Myrmidon Reef. The most abundant soft corals at Myrmidon Reef (*Efflatounaria* sp.) reproduce asexually via stolons (K. Fabricius, pers. comm.) and this characteristic would restrict the ability of *Efflatounaria* to disperse from the small patch-reef habitats of SW and NW Myrmidon to the main reef. Coral species with a higher capacity for larval dispersal over greater distances would probably recolonise disturbed shallow-water reefs more quickly.

Implications for the role of mesophotic coral reefs as refugia from environmental disturbance

A severe category 5 cyclone can cause significant reductions in MCE coral cover and this pilot study indicates mesophotic communities can be negatively impacted by cyclone waves to a depth of 45 m or more. However, this study found that deeper habitats afforded some protection by the reef itself were able to survive severe cyclones relatively intact while adjacent shallow-water coral communities experienced significant declines in coral cover. Deeper communities on the western side of Myrmidon Reef were relatively unaffected by TC Yasi and remain undisturbed. These undisturbed areas harbour several very large, fragile plating coral colonies that probably would not have survived the cyclone in shallower waters. Madin and Connolly (2006) reported large colonies of the plating coral *Acropora hyacinthus* were increasingly vulnerable to cyclone disturbance with increasing size. Given the importance of large colonies to broadcast-spawning species such as *A. hyancinthus*, the survival of large colonies at mesophotic depths may be a critical factor in the rate of recruitment and subsequent recovery of shallow-water reef habitats.

High soft coral cover at mesophotic depths lends support to the deep refugia hypothesis, indicating that deeper habitats at Myrmidon Reef may not have experienced significant mortality from the 2002 bleaching event. Coral recruitment from deep to shallow depths post-2002 appears minimal, but Myrmidon's MCEs may provide viable habitat for fish

and other mobile invertebrate communities that depend on soft corals for their survival. Undisturbed MCEs may play a critical role post-bleaching and reduce the probability of localised extinctions of dependent mobile organisms. MCEs may also play an important role in coral reef connectivity and population recovery for coral species capable of dispersing larvae over great distances.

MESOPHOTIC REEFS AS CORAL REFUGIA

Coral reefs are increasingly under threat from a variety of acute and chronic stressors acting at both global and local scales (Hughes and Connell 1999; Hoegh-Guldberg 1999; Hughes et al. 2003; Guinotte et al. 2003; Hughes et al. 2007; Wilkinson 2008). Approximately 15 per cent of coral reefs will be seriously threatened within the next 10–20 years and a further 20 per cent may be lost in the next 20–40 years (Wilkinson 2008). Consequently, identifying areas which may be naturally buffered from these stressors is a priority for coral reef managers (Riegl and Piller 2003). Deep reef habitats are generally regarded as being leading candidates for refugia (Bongaerts et al. 2010a), particularly from coral bleaching events caused by elevated sea surface temperature and light irradiance (Glynn 1996; Hughes and Tanner 2000; Riegl and Piller 2003). Similar theories have also been explored for other marine ecosystems (i.e. kelp communities) (Graham et al. 2007). There are currently two primary questions to answer when addressing the refugia hypothesis. Firstly, are deep reefs less susceptible to disturbance than shallow-water reefs? Although significant variability exists in susceptibility based on a range of factors including type of disturbance event (warm-water bleaching, tropical storm, etc.), the geographical location of the reef, reef geomorphology, and local oceanographic conditions, there is evidence indicating MCEs may be less susceptible to disturbance events. The second component of the refugia hypothesis involves investigating whether MCE areas that have escaped a disturbance event can provide a source of propagules to re-seed adjacent habitats which have suffered mortality (Hughes and Tanner 2000; Lesser et al. 2009; Slattery et al. 2011; Bongaerts 2011).

Bleaching

Mesophotic reef studies are few in number, but several observations across a wide geographic range indicate many MCEs have largely escaped the major bleaching events that have caused significant coral mortality on adjacent shallow reefs. Heyward et al. (2007) reported shallow-water corals (~10 m depth) on Scott Reef, Western Australia, suffered mortality of ~75 per cent from the global coral bleaching event of 1998, but no obvious mortality was observed in the mesophotic zone (25–75 m). Similar reports have emerged following other bleaching events, including the 2002 bleaching on the Great Barrier Reef (Guinotte 2007) (Figure 8) and also in Sumatra in 2010 (Bridge et al; in prep). However, most data assessing bleaching damage has been collected *post hoc* and long-term datasets are rare. Lack of long-term data and limited understanding of ecological processes on MCEs hampers the ability to conduct comparative studies, but evidence suggests that warm-water induced mass mortality of corals, which has plagued shallow-water reefs globally, is less common on MCEs even during severe bleaching events (Bongaerts et al. 2010b).

Cyclones

Coral bleaching is one of a myriad of threats facing coral reefs around the world; MCEs may also be buffered from other threats. Cyclones have been responsible for severe reductions in coral cover on the Great Barrier Reef (Done 1992; Gardner et al. 2005; Fabricius et al. 2008) with cyclone-affected reefs experiencing a mean decrease in coral cover of ~34 per cent per storm event (Osborne et al. 2011). The region has recently experienced three severe tropical cyclones in close succession: Larry (2006), Hamish (2009), and Yasi (2011), as well as a number of smaller cyclones. Storm-induced wave energy is negatively correlated with depth (Liddell and Ohlhorst 1988) and thus MCEs may be less susceptible to reductions in coral cover caused by tropical storms. Massel and Done (1993) reported massive scleractinian corals in shallow waters (12 m) were resistant to most storm waves, but Fabricius et al. (2008) reported significant coral damage (to at least 15 m depth) in offshore coral communities of the northern Great Barrier Reef following Cyclone Ingrid. MCEs may be less likely to experience direct damage from cyclones, but deep fore-reef communities remain at risk from debris avalanches resulting from shallow-water corals being dislodged and transported down-slope. In Tuamotu, French Polynesia, 100 per cent coral cover decline was observed at depths > 35 m following the cyclone season of 1982–83 (Harmelin-Vivien and Laboute 1986). The results presented in this study support the conclusion that depth alone is not a good determinant of cyclone vulnerability, with the steep outer-slope at NE Myrmidon Reef showing severe damage at all depths. However, deeper areas afforded some protection from the reef itself showed low damage at all depths.

Sedimentation

MCEs could be more susceptible to sedimentation than inshore reef habitats as they are not normally subjected to high sedimentation in outer-shelf areas and exist in light-limited environments. Colin et al. (1986) suggested downwelled sediments strongly influenced the abundance and lower depth distribution of corals on the deep fore-reef slope at Enewetak, a Pacific atoll surrounded by clear, oceanic water. Visibility in the deep lagoon was less than two metres and growth of phototrophic taxa was also restricted (Colin 1986). Strong bottom currents such as those at Hydrographers Passage may exert a similar influence on MCEs on the Great Barrier Reef outer-shelf by resuspending sediments from adjacent inter-reefal habitats (Bridge et al. 2011b), but MCEs on the outer-shelf are unlikely to experience high sediment run-off due to their geographic location.

Ocean acidification

Ocean acidification, arising largely from the human combustion of fossil fuels and resultant release of carbon dioxide to the atmosphere and uptake by the oceans, is cause for major concern among reef scientists (Kleypas et al. 1999; Hoegh-Guldberg et al. 2007; Anthony et al. 2007; Veron 2008). Decreasing aragonite saturation in the oceans is likely to lead to lower growth rates in scleractinian corals, and this may be detrimental to mesophotic corals which are likely to already exhibit slow growth rates. Ocean acidification is also expected to weaken reef structures, making them more susceptible to erosional forces and wave damage. MCEs are located at greater depths, experience less hydrodynamic stress than shallow-water reefs, and may be less susceptible to erosional forces.

Caribbean examples

Studies of the upper mesophotic zone adjacent to shallow-water reefs in Caribbean waters reported coral declines from disturbances in both shallow and deeper waters. A 30-year record presented in Bak et al. (2005) indicated no declines in coral cover or numbers of coral colonies on deep reefs, but did show a noticeable decline in coral diversity. Hughes and Tanner (2000) reported a long-term decline in coral cover and corresponding phase shift to an algal-dominated state at a depth of 35 m in Jamaica and Lesser and Slattery (2011) reported a similar phase shift on mesophotic reefs attributed to the introduction of the Indo-Pacific lionfish (*Pterois volitans*) to the Caribbean. Although declines in coral cover have also been observed on Indo-Pacific MCEs due to acute disturbance events such as tropical storms (Harmelin-Viviene and Laboute 1986), no studies have reported a resultant phase shift from coral-dominated to algal-dominated states.

Mesophotic coral ecosystems as sources of propagules

There is clear evidence that MCEs are less susceptible to some disturbances than their shallow-water counterparts, but the degree to which MCEs may be able to re-seed disturbed shallow-water habitats is less clear. The concept of connectivity between reefs has been studied for some time, particularly with reference to the design of marine protected areas (e.g. McCook et al. 2009; Almany et al. 2009), but only recently have studies been conducted examining vertical connectivity between deep and shallow reef habitats. Much of this connectivity work has been conducted on the Great Barrier Reef (Bongaerts et al. 2010b; van Oppen et al. 2011; Bongaerts et al. 2011b), but has been hampered by restrictive diving regulations limiting maximum depth limits to ~27 m. Nonetheless, the patterns observed in these studies provide a valuable insight into the potential value of MCEs as sources of propagules to re-seed shallow-water reef habitats.

The majority of work undertaken in this regard on the Great Barrier Reef has been conducted on the Pocilloporid coral *Seriatopora hystrix*. Bongaerts et al. (2010b) found populations of *S. hystrix* on the northern Great Barrier Reef showed strong genetic partitioning among habitats with populations in adjacent habitats ("Back Reef", "Upper Slope" and "Deep Slope") being genetically isolated from one another. High levels of genetic similarity were observed across similar habitat types at different locations. Transplant experiments, where corals were translocated from their native habitat to another environment, also showed that specific ecotypes were better suited to their native location. Survival of coral fragments transplanted outside their native habitat was low and no fragments from the "Deep Slope" habitat survived in either the "Upper Slope" or "Back Reef" habitats. This indicates that there appears to be little transportation of coral larvae among habitats, and therefore that deep to shallow recruitment of *S. hystrix* is unlikely. However, there are several important caveats that must be taken into account when considering these data: (1) stress of transplantation experiments on overall coral health, (2) variability in selective pressures between juvenile and adult corals, and (3) the effects of differing reproductive and life history strategies among species. Coral fragments in Bongaerts et al. (2011b) were transplanted as fragments from adult colonies and mortality of fragments transplanted from deep habitats may have partly resulted from instant light stress after transplantation. Secondly, selection pressures faced by juvenile corals at settlement may be very different from those faced by adults (Bak et al. 1979; Mundy and Babcock 2000). For example, many corals acquire symbionts horizontally (from the surrounding environment) as opposed to vertically (from

the maternal colony). *S. hystrix* acquires symbionts vertically from the maternal colony and also contain different symbiont types across their bathymetric range (Bongaerts et al. 2010b). Coral juveniles that acquire symbionts vertically will have the same clades of zooxanthellae as their parents (i.e. juvenile *S. hystrix* originating from a deep habitat will have characteristic deep symbionts). Bongaerts et al. (2011b) also reported host-symbiont assemblages for *S. hystrix* were stable associations (i.e. transplanted colonies did not shuffle their symbionts over time). *S. hystrix* also employs a brooding reproductive strategy (eggs develop within the parent colony and are released as larvae) and generally settles within 100 m of the parent colony (Underwood et al. 2007). These factors combined suggest *S. hystrix* is poorly suited to re-seed adjacent shallow-water reef habitats. Fortunately, the majority of Indo-Pacific coral species are broadcast spawners, acquire zooxanthellae horizontally (from the surrounding environment), and these species would be more likely to disperse and subsequently acclimatise to non-native habitats.

Van Oppen et al. (2011) reported data from Scott Reef, Western Australia, suggesting greater levels of population connectivity between deep and shallow *S. hystrix* populations. Genetic partitioning was observed on Scott Reef, but it was not as strong as the partitioning observed on the northern Great Barrier Reef. Coral specimens collected from Scott Reef were dominated by a single mtDNA lineage and showed no apparent host–symbiont specificity. Furthermore, assignment analyses of individual corals also provided evidence of gene flow between deep and shallow populations. One possible explanation for the variation in the level of genetic partitioning between the northern Great Barrier Reef and Scott Reef is the disturbance regime. The Ribbon Reefs on the northern Great Barrier Reef have seen relatively little disturbance in recent decades, but the shallow-water coral communities of Scott Reef were severely impacted by the 1998 bleaching event. The reduction in coral cover in shallow waters would have resulted in decreased competition for space and may have allowed deeper ecomorphs (colonies native and acclimatised to deep water) an opportunity to establish themselves in shallow-water areas (van Oppen et al. 2011).

The vast majority of Indo-Pacific coral species are broadcast spawners, acquire symbionts horizontally (Bongaerts et al. 2011b), and may be capable of substantially greater dispersal and more rapid acclimatisation to new environments. Many coral species occupying deep habitats (> 50 m) on the Great Barrier Reef occur over a wide depth range, and an even greater number of species common to shallow-water reefs are likely to be found in the upper mesophotic zone (30–50 m) (Bridge, unpublished data). In order to understand the ability of deep reefs to re-seed shallow environments there is an urgent need to identify patterns in genetic partitioning across a range of coral species that incorporate different life history traits and reproductive strategies. Identification of larval dispersal methods employed by mesophotic corals is also needed. Some coral larvae may settle preferentially at certain depths (Baird et al. 2003) and studies should be conducted on both pre- and post-settlement corals to identify selective pressures on larval and adult corals (Sammarco 1991; Connell et al. 1997; Mundy and Babcock 2000; Hughes and Tanner 2000).

IMPLICATIONS FOR MANAGEMENT

1. **Greater collaboration could occur between government agencies (e.g. AIMS, Geoscience Australia) to collect data from submerged reefs/MCEs.** In particular, collection of multibeam bathymetry would significantly improve identification of submerged reefs, and allow more accurate spatial modelling of mesophotic reef habitats.

2. **Estimates of the area of Marine Park habitats (including coral reefs and/or shoals) could be made on three dimensional as well as a two dimensional basis.** Currently, area is calculated as if looking at a flat surface from space. A substantial portion of the habitat area at depth is steeply sloping but reef area is classified as the horizontal reef outline as seen from above. More accurate and potentially more useful calculations will come from beginning to think three dimensionally.

3. **The future vulnerability of these reefs could be further investigated.** While deep reefs may not be as vulnerable to bleaching, cyclones and Crown-of-thorns starfish, they may be more at risk from ocean acidification and, perhaps most significantly, substantial sea level rises. While sea level rise has not been considered a major risk to individual reefs in the Great Barrier Reef, this may not be the case for deeper submerged reefs.

4. **MCE habitats could be given high priority status based on existing information regarding their potential role as refugia from disturbance,** MCE habitats that are not included in existing management plans are potentially threatened by current (i.e. commercial and recreational fishing) and future/unforeseen human activity (i.e. climate change pressures). MCE are potentially important refuges for fish during major disturbance events as well as possibly important refugia for coral recruitment following these events.

   The vast majority of coral species on the Great Barrier Reef are depth generalists aiding in the ability of MCE to act as critical refugia into the future. *Acropora* spp. appear to be more specialised but from an ecosystem goods and services perspective the large number of *Acropora* spp. may provide sufficient functional redundancy in the depth generalists to mean that while species richness may decline mesophotic refugia supports recruitment led recovery by generalist *Acropora* spp. The extent to which they act as sources of recruitment that speed the recovery of reef habitat in shallow water after a cyclone/ bleaching is currently unknown. A precautionary approach to management would suggest that emphasis be placed on protection of MCE habitats.

5. **Where deemed possible and appropriate, documented MCE habitats along the Great Barrier Reef could be added to existing long-term monitoring programs (e.g. AIMS LTMP).** The IMOS AUV facility utilised in the Myrmidon Reef pilot study (presented in this report) provides an ideal tool for monitoring the health and community composition of MCE communities in the Great Barrier Reef World Heritage Area. Tools such as AUV, ROV, towed video or drop cameras could be added to AIMS LTMP survey methods and utilised at new sites

identified by modelling and subsequent field surveys and incorporated into the LTMP over time.

6. **Representative MCE areas could be identified and included in future management plans.** Before inclusion in management plans, more precise definitions of submerged and mesophotic reefs will need to be developed (eg. minimum/maximum depths) and unmapped reefs identified. True mesophotic reefs that occur below 30 metres and are not currently mapped may represent a new bioregion/s classification in the Marine Park. Describing the typology of the deep water reefs (eg. hard coral dominated, octocoral dominated etc.) will be an important step in defining where submerged and mesophotic reefs are most important as potential refugia. Comparing this new reef definition and depth extent with existing definitions under the Great Barrier Reef Marine Park zoning plan 2003 will help identify which of the deep water communities of interest are already currently protected through zoning, and which are unprotected.

   Some mesophotic reefs may already be included within existing reef outlines. Present outlines are based upon available bathymetry which is of varied resolutions across the Marine Park. Improved bathymetry is crucial to building consideration of mesophotic reefs as specific habitats into spatial management arrangements in the future. Clearly defining these boundaries would enable a clear comparison of the amount of deep reef habitat inside the various Marine Park zones.

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