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High coral cover on a mesophotic, subtropical island platform at the limits of coral reef growth

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ABSTRACT

Balls Pyramid is a volcanic monolith rising 552 m from the Tasman Sea, 24 km southeast of the Pacific Ocean's southernmost modern coral reef at Lord Howe Island. High resolution seabed mapping of the shelf surrounding Balls Pyramid has revealed an extensive submerged reef structure in 30–50 m water depth, covering an area of 87 km^2. Benthic community composition analysis of high-resolution still images revealed abundant scleractinian corals on the submerged reef, extending to a maximum depth of 94 m. Scleractinian coral occurred predominantly in 30–40 m depth where it comprised 13.3% of benthic cover within this depth range. Average scleractinian coral cover for all transects was 6.7 ± 12.2%, with the highest average transect cover of 19.4 ± 14.3% and up to 84% cover recorded for an individual still image. The remaining substrate comprised mixed benthos with veneers of carbonate sand. Benthic data were shown to significantly relate to the underlying geomorphology. BVSTEP analyses identified depth and backscatter as the strongest correlating explanatory variables driving benthic community structure. The prevalence of scleractinian corals on the submerged reef features at Balls Pyramid, and the mesophotic depths to which these corals extend, demonstrates the important role of this subtropical island shelf as habitat for modern coral communities in the southwest Pacific Ocean. As Balls Pyramid is located beyond the known latitudinal limit of coral reef formation, these findings have important implications for potential coral reef range expansion and deep reef refugia under a changing climate.

1. Introduction

It has been hypothesised that coral populations may be protected from climate-change impacts in 'refugia' (Glynn, 1996; Riegl and Piller, 2003) that occur in mesophotic depths (30–150 m depth) and at higher latitude locations, as they may be somewhat buffered from increased sea-surface temperatures (SSTs) and storm activity (Glynn, 1996; Riegl and Piller, 2003; Bongaerts et al., 2010; Slattery et al., 2011; Couce et al., 2013). Responses to changes will be spatially heterogeneous, and suitability to act as refuge environments will depend on regionally specific, ecosystem-scale responses to changes in climate condition (Pandolfi et al., 2011). In addition to acting as refugia, higher latitude regions may support increased coral populations as warmer ocean currents transport coral larvae poleward, leading to the latitudinal expansion of coral reef ranges. This can also be associated with tropical herbivores extending their ranges into temperate regions resulting in a community phase shift from macroalgal-dominated to coral-dominated when tropical fish herbivory increases (Vergés et al., 2014). Range expansions of modern corals have been documented in both the North and South Pacific Ocean (Yamano et al., 2011; Baird et al., 2012) and in the western Atlantic Ocean (Precht and Aronson, 2004). At the world's highest latitude reefs in Japan, the range extension of corals has been measured at rates up to 14 km/yr (Yamano et al., 2011). Predictive modelling of future climate scenarios suggests higher latitude regions may support coral reef range expansions where suitable substrate and light conditions are available (Couce et al., 2013; Freeman, 2015).

The discoveries of extensive coral populations at mesophotic depths and in higher latitude regions are challenging long-held perceptions of the 'known' geographical and depth distributions of corals (Celliers and Schleyer, 2008; Hinderstein et al., 2010; Thomson and Frisch, 2010; Bridge et al., 2012; Pyle et al., 2016). Coral communities in subtropical and mesophotic environments have been shown to exhibit high coral cover comparable cover to shallow, tropical systems (Thomson and Frisch, 2010), with up to 100% coral cover recorded along expansive

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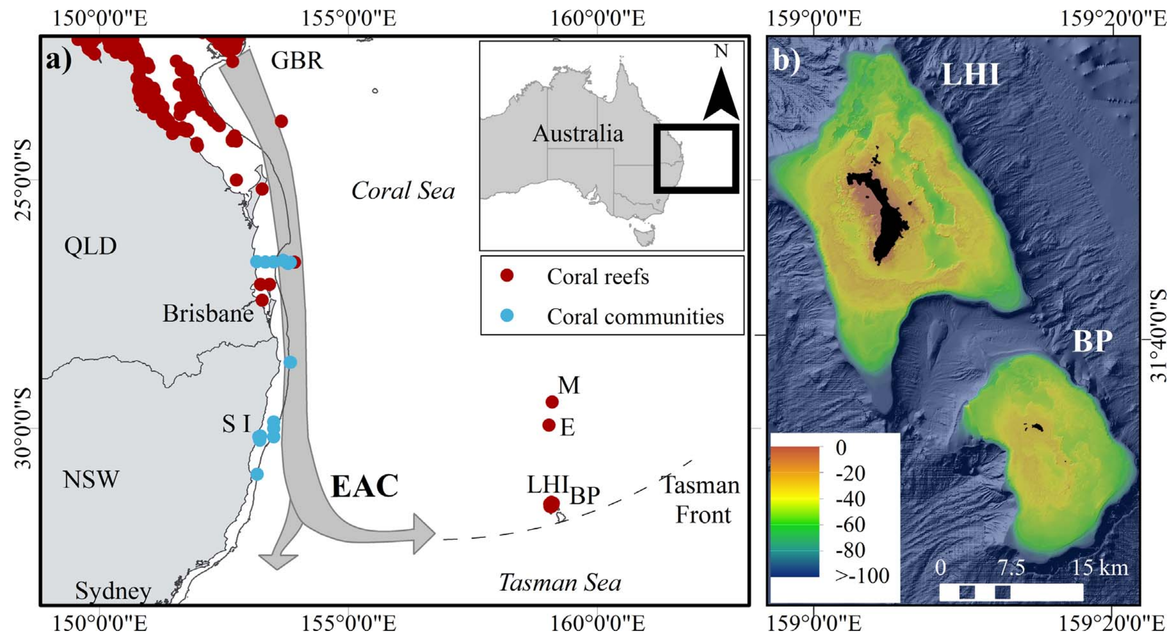

Fig. 1. a) The East Australian Current (EAC) flows south from the Great Barrier Reef (GBR), past the Solitary Islands (SI), with an east flow toward Balls Pyramid (BP), Lord Howe Island (LHI), Elizabeth Reef (E) and Middleton Reef (M); Coral reefs (dark red) and coral communities (light blue) dataset provided by UNEP-WCMC (ReefBase GIS); b) Hillshaded bathymetry sourced from Linklater et al. (2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

areas of the Hawaiian Archipelago in 50–90 m depth (Pyle et al., 2016). Species diversity can be lower in subtropical and mesophotic environments compared to tropical, shallow reefs (Sommer et al., 2013; Pyle et al., 2016), and reduced light availability can restrict the depth distribution of selected coral genera (e.g. *Acropora* and *Isopora*) and the potential for range expansion into higher latitudes (Muir et al., 2015a, 2015b). Coral reef research has historically focused on shallow, tropical reef ecology, and knowledge of subtropical and mesophotic reef environments is comparatively limited (Celliers and Schleyer, 2008; Menza et al., 2008), however studies into mesophotic ecyosystems are increasing exponentially as technology advances (Baker et al., 2016; Loya et al., 2016). Few studies have focused on the combination of mesophotic reefs in higher latitude environments (Venn et al., 2009; Rooney et al., 2010) and there is a clear need to investigate coral distributions in these regions and explore their potential role in providing substrates for future coral range expansion and refugia.

At the southern limits of reef formation in the Pacific Ocean, evidence of the poleward expansion of fossil reefs south of their modern distributions was recently discovered around the remote, mid-ocean island of Balls Pyramid (Linklater et al., 2015). Balls Pyramid is a volcanic pinnacle located 600 km off the mainland coast of southeast Australia and 24 km southeast of the Pacific's southernmost modern coral reef at Lord Howe Island. This new evidence of fossil reefs around the Balls Pyramid shelf highlighted the capacity of this subtropical platform to support substantial historical coral growth and suggested the mesophotic shelf may provide suitable substrate for modern mesophotic coral ecosystems.

Coral growth occurs in the Lord Howe region due to the warm-water currents delivered by the East Australian Current (EAC). The EAC consists of a dominant southerly flow primarily along the mainland shelf, but also generates eddies that travel eastward toward Balls Pyramid and Lord Howe Island. Modern-day southern range expansion of selected coral species has been documented along the southeast coast of Australia, attributed to a strengthening EAC (Baird et al., 2012). The shallow reefs around Lord Howe Island have been identified as potential coral refugia as the subtropical region may benefit from warmer waters delivered by an intensifying EAC (Hoey et al., 2011; Dalton and Roff, 2013; Keith et al., 2015). Decadal changes in community composition in relation to recent increases in sea-surface temperature suggest the shallow reefs around Lord Howe Island are relatively stable and may provide limited refuge potential for tropical coral populations (Dalton and Roff, 2013). However, for the Lord Howe region the benefits of an enhanced EAC may be confounded by vulnerabilities to coral bleaching (Harrison et al., 2011), reduced linear extension rates (Anderson et al., 2015), low recruitment success (Keith et al., 2015) and high macroalgal cover (Hoey et al., 2011). These factors have been shown to limit coral growth along the southwestern coast of Australia (Menza et al., 2007; Thomson et al., 2011; Abdo et al., 2012; Ross et al., 2015).

The role of high latitude, mesophotic coral ecosystems in supporting modern corals is little understood, as is their potential role as refugia under a changing climate. Due to its location at the critical threshold of coral reef formation in the Pacific, and the ongoing intensification of the EAC, the Balls Pyramid shelf is a key region to monitor species range extents and detect shifts in assemblages. In this paper we: 1) describe the distribution of modern coral populations on the fossil reefs; 2) quantify the composition of the mesophotic benthic communities; 3) examine the relationship between modern benthic communities and the underlying geomorphology; and 4) identify the environmental and oceanographic variables driving the spatial distribution of benthic communities, with a focus on scleractinian corals. This information provides a baseline understanding of benthic habitats and live coral cover for use in ongoing monitoring of the shelf and future assessments of refugia and expansion potential.

2. Methods

2.1. Study site

Balls Pyramid (31°45′S, 159°15′E) is a 552 m high volcanic pinnacle located within the Tasman Front at the boundary between the tropical Coral Sea and the temperate Tasman Sea (Fig. 1a). It is the southernmost island in a chain formed from hotspot volcanism that includes Lord Howe Island, and Elizabeth Reef and Middleton Reef approximately 200 km to the north. The pinnacle rises steeply from a shelf 22.8 km long and 16.2 km wide (260 km^2 area) and dominated by a submerged fossil reef in 30–50 m depth (Linklater et al., 2015). The shelf break occurs at 115–150 m depth, with a steep drop-off into