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Mesophotic corals on the subtropical shelves of Lord Howe Island and Balls Pyramid, south-western Pacific Ocean

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Abstract

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Keywords

pacific, pyramid, balls, island, ocean, howe, mesophotic, lord, shelves, subtropical, corals, south-western

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Mesophotic corals on the subtropical shelves of Lord Howe Island and Balls Pyramid, southwest Pacific Ocean

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Abstract

Subtropical reefs are predicted to be dynamic areas of change under increased global sea-surface temperature warming. A critical knowledge gap exists for deeper, mesophotic corals in these higher latitude settings, where little is known about their spatial and depth distributions. At the latitudinal limits of coral reef growth in the Pacific Ocean, abundant mesophotic corals were revealed on the shelf surrounding the subtropical, mid-ocean island of Balls Pyramid. Our study extends these findings to the nearby Lord Howe Island shelf to assess mesophotic coral cover and explore spatial patterns in mesophotic benthic communities around these World Heritage, marine park protected islands. Underwater towed video data collected around Lord Howe Island (24 sites) were combined with existing benthic data from the Balls Pyramid shelf. Results showed that similar habitats occurred across both shelves, with communities varying between inner-, mid- and outer-shelf zones. Corals were most prevalent on the Balls Pyramid mid shelf, with selected locations around the Lord Howe Island mid shelf reporting similar cover (maximum site-average cover of 24%). The benthic

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Keywords: Reefs, Coral reefs, Seabed, Benthos, Biodiversity, Marine, Conservation

1. Introduction

Subtropical reefs have been identified as important systems to monitor and conserve under a changing climate (Beger *et al.* 2013; Makino *et al.* 2014). Intensifying and warming poleward-flowing ocean currents have resulted in the tropicalisation of subtropical and temperate waters, leading to substantial changes to the geographical distributions of some marine species (e.g. Cheung *et al.* 2012; Vergés *et al.* 2014). Many of these species have extended their latitudinal ranges through increased larval dispersal (e.g. corals in Yamano *et al.* 2011, fish in Vergés *et al.* 2014), with the magnitude and rate of species responses variable due to individual species traits (e.g. Byrne *et al.* 2011) and the complex interactions of biota to changing conditions at multiple spatial and temporal scales (Poloczanska *et al.* 2013). Large-scale shifts in the geographical distributions of coral reefs have occurred in response to past warming conditions (during the Last Interglacial and Holocene), where reefs expanded their ranges into higher latitudes and diminished in tropical regions (Kiessling *et al.* 2012). Understanding the occurrence and extent of past and present-day range shifts underscores the necessity to conserve and monitor areas at the latitudinal limits of species distributions as they are likely to be useful early indicators of ecosystem shifts and species range expansions.

Along the southeast Australian coast, the poleward flowing East Australian Current (EAC), which is the dominant regional oceanographic feature, is warming and strengthening, and is one of the global hotspots for increased sea-surface temperature (SST), (Hobday and Pecl 2014; Wernberg *et al.* 2011). The strengthening of the EAC results in warmer waters extending further south along the coastline and this has been associated with new records of *Acropora* species discovered on subtropical reefs along the mainland coast as far as 30°S (Baird *et al.* 2012). Offshore of the mainland coast, along the subtropical island and reef chain of the Lord Howe Rise, coral reef growth is more akin to tropical reefs due to the strong influence of eastward-flowing eddies of the warm EAC (Harriott and Banks 2002).

The two southern islands in the chain, Lord Howe Island (LHI, 31°33’ S, 159°5’ E, Figure 1) and Balls Pyramid (BP, 31°45’S, 159°15’E), encompass a unique mix of tropical and temperate marine life with some tropical corals surviving at their southernmost limits and some algae at their northernmost limits (Edgar *et al.* 2010; Keith *et al.* 2015; Veron and Done 1979). LHI supports the southernmost known extent of modern, Holocene and Last Interglacial coral reef growth in the South Pacific Ocean (Kennedy and Woodroffe 2000; Veron and Done 1979; Woodroffe *et al.* 2010). The submerged shelves surrounding LHI and BP also support extensive fossil coral reefs which form the southernmost range extent of Holocene coral reef growth (Linklater *et al.* 2015; Woodroffe *et al.* 2010).

Abundant mesophotic coral ecosystems (MCEs) were discovered on the submerged fossil reefs around BP (Linklater *et al.* 2016). MCEs are defined to typically occur in depths greater than 30–40 m depth and extend to the bottom of the photic zone (Kahng *et al.* 2014; Hinderstein *et al*. 2010). Scleractinian corals were recorded to extend to a maximum depth of 94 m depth, with average coral cover up to 19% for an individual transect (84% for an individual still image). The unanticipated abundance and wide depth range of coral populations was considered unique for this subtropical setting and raised the question of how coral distribution around BP compared to the adjacent shelf around LHI (24 km north) and whether this island platform also supported suitable habitat for modern coral communities.

The fossil reefs around both shelves occur at similar depths of 25–50 m, and cover approximately one third of the shelf area (Linklater *et al.* 2018). The extent of fossil reef growth was significantly larger (1.8 times larger in area) around LHI (155 km^2) compared to BP (87 km^2) and the LHI shelf possessed a greater proportion of shallower substrates, which relates to the larger size of the original volcano that formed LHI (Linklater *et al.* 2018). Due to the availability of substantial fossil reef substrate at similar depths to the BP shelf and the development of the modern coral reef in the shallow waters around LHI, it was considered likely that the LHI shelf also possesses mesophotic coral growth.

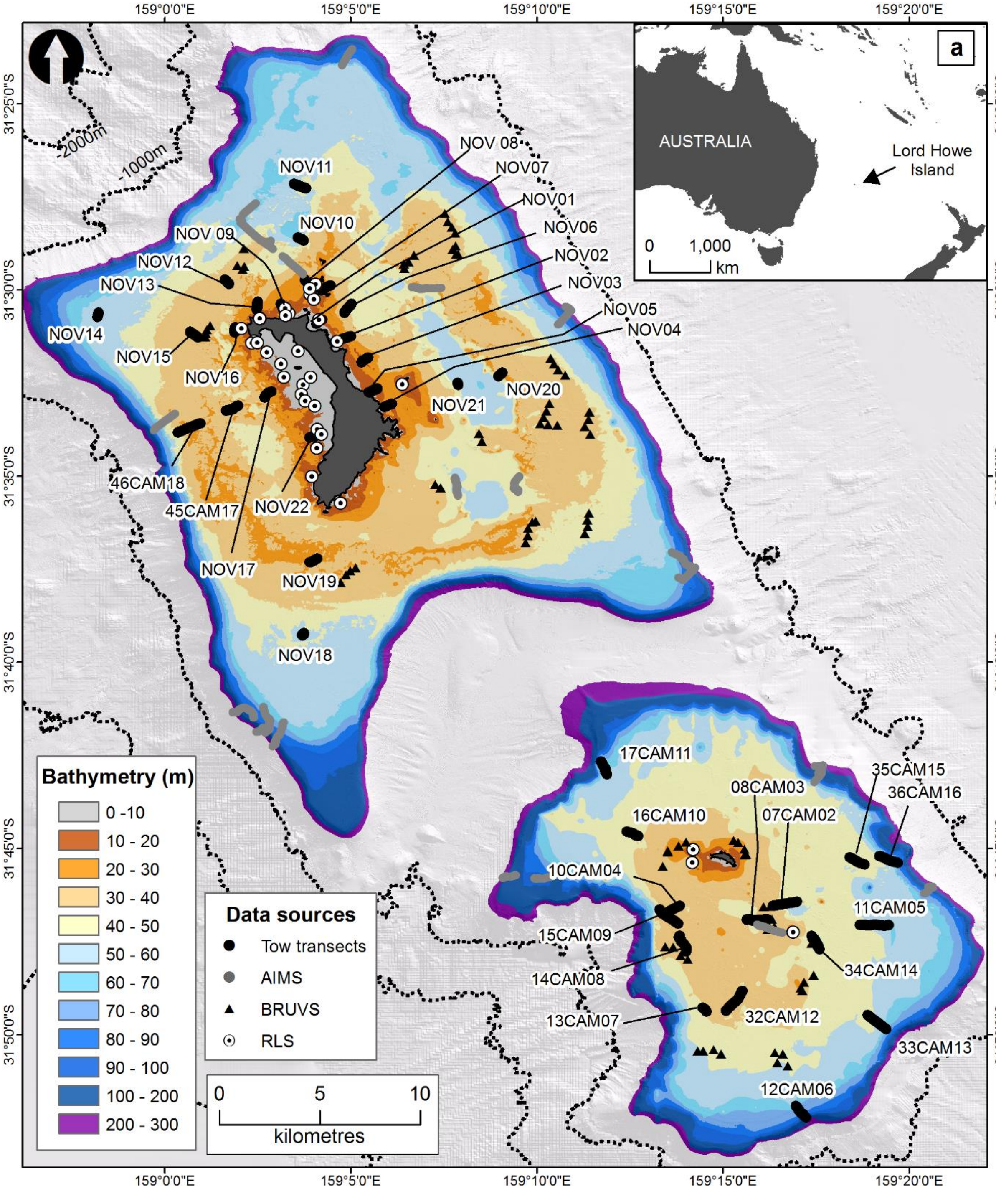

Figure 1 Location of tow transects collected around the Lord Howe Island shelf. Existing data shown for Reef Life Survey (RLS) sites (available online www.reeflifesurvey.com), Baited Underwater Video (BRUVS) sites (Rees 2017) and Australian Institute of Marine Science (AIMS) tow transects (Speare *et al.* 2004). Bathymetry colour scheme applied to shelf 0-300 m depth, with hillshade-only shown for depths >300 m. Isobaths displayed as dashed lines at 1000 m intervals; a) Inset map showing island location relative to the Australian mainland.

Coral refugia are areas where extant coral populations can survive while unfavourable environmental conditions persist. If coral populations can persist through adverse conditions in refuges, some corals may replenish degraded reef systems if conditions return to being favourable in the future (Bongaerts *et al.* 2010; Glynn 1996; Riegl and Piller 2003). MCEs, also termed ‘deep reefs’, have the potential to act as temporary climate refugia due to their depth range, which may minimise their exposure to increased sea-surface temperatures and intensified wave action (Bongaerts *et al.* 2010; Slattery *et al.* 2011). Higher latitude subtropical coral reefs and communities have also been hypothesised as suitable habitats for potential coral expansion and temporary refugia, in addition to isolated islands, areas of upwelling and seamounts (Couce *et al.* 2013; Glynn 1996; Riegl and Piller 2003; Tittensor *et al.* 2010). The LHI and BP shelves possess a number of the attributes of proposed refugia environments, including subtropical locality and mid-ocean isolation with availability of mesophotic reef substrates (Linklater *et al.* 2016; Linklater *et al.* 2018) and deep shelf flanks (Kennedy *et al.* 2011). Anthropogenic impacts are minimised through Commonwealth and state marine park protections (Department of Environment 2018; NSW Marine Parks Authority 2010), and the islands have been inscribed on the World Heritage List since 1982. The high conservation protections, together with the island’s isolation and restricted resident and tourist populations (Lord Howe Island Local Environmental Plan 2010), result in limited anthropogenic impacts.

Areas of suggested climate refugia are not necessarily immune to multiple stressors associated with climate change, such as bleaching (e.g. (Harrison *et al.* 2011; Smith *et al.* 2016) and acidification (Tittensor *et al.* 2010), and further studies are required to determine their potential vulnerabilities as well as benefits (Bongaerts *et al.* 2017; Smith *et al.* 2016). Refugia potential has been explored at Lord Howe Island’s shallow reefs by a number of studies investigating coral accretion rates, recruitment and competition (Anderson *et al.* 2015; Cameron and Harrison 2016; Dalton and Roff 2013; Harrison *et al.* 2011; Hoey *et al.* 2011; Keith *et al.* 2015). Analysis of decadal datasets suggest coral populations have remained stable, which indicates resilience to climate change to date (Dalton and Roff 2013), and the area is considered a stronghold for local, brooding species (Keith *et al.* 2015). The limitations of refugia have been identified as high algal abundance, low coral recruitment and slow growth rates (Anderson *et al.* 2015; Hoey *et al.* 2011), as well as low success of larval establishment for spawning coral species (Keith *et al.* 2015). The islands are also considered ‘marginal’ for corals in terms of low aragonite saturation, which may limit coral growth under increased warming (Hoegh-Guldberg *et al.* 2007; Kleypas *et al.* 1999b).

Assessing refugia potential requires complex analyses of species composition, thermal tolerances, reproductive processes, connectivity and larval supply (Cacciapaglia and van

Woesik 2015; Cameron and Harrison 2016; Davies *et al.* 2016; Davies *et al.* 2017), but the critical first step is to establish if corals are present and to what spatial extent they occur. The identification of abundant extant coral populations on the BP mesophotic shelf (Linklater *et al.* 2016) raised the question of whether similar habitats occur around nearby LHI and what role these shelves may have in supporting corals into the future. Higher-latitude mesophotic reefs are poorly understood and few studies have investigated the role of these environments in supporting scleractinian corals (e.g. Linklater *et al.* 2016; Rooney *et al.* 2010; Venn *et al.* 2009). An understanding of the structure and composition of reef communities in this setting is required to address the current knowledge gap of MCEs in higher latitude locations. In this global hotspot of oceanographic change, it is important to establish baseline knowledge of benthic community composition to enable monitoring of community shifts over time.

Our study aimed to: 1) characterise the benthic communities of the LHI mesophotic shelf; 2) explore spatial distributions of communities around the LHI shelf; 3) compare and contrast benthic composition on reef features of the LHI shelf to the already documented benthic communities of the BP shelf. We hypothesised that the LHI shelf possessed mesophotic corals colonising the extensive submerged fossil reefs, similar to those reported around BP. Understanding the relative capacity of the mesophotic shelves to support modern coral growth will help to assess their potential suitability for coral reef expansion in the future. This information will provide important baseline data for use in the management of this globally significant marine park and World Heritage area.

2. Methods

In our study, towed underwater images were collected from 24 sites around the LHI shelf on two voyages. The first voyage was undertaken on the Marine National Facility R.V. *Southern Surveyor* in February 2013 (SS2013_v02) with still images collected using the Shallow Underwater Camera Model 2 at 5 second intervals. During this survey 767 images were collected from two sites around the LHI shelf (45CAM17 and 46CAM18). The second voyage was undertaken on the NSW Department of Primary Industries vessel *Tursiops* in November–December 2013, with images collected using the NSW Office of Environment and Heritage towed camera. The November–December 2013 voyage collected a further 6,587 images (captured at 3 second intervals) from 22 sites around the LHI shelf (NOV01-22). This new dataset collected around the LHI shelf was combined with classified tow data for 1,381 stills (15 sites) presented for the BP shelf in Linklater *et al*. (2016).

This study focussed on broad patterns in shelf zones around LHI and between the two shelves to elucidate spatial variations in the distribution and abundance of benthos, with particular focus placed on scleractinian corals. Data were integrated with detailed benthic community data presented in Linklater *et al.* (2016). Benthic data for the two shelves were related to the high-resolution (5 m cell size) bathymetry model and geomorphic feature classification produced by Linklater *et al.* (2018).

The sampling design of this study considered existing data and long-term monitoring locations (Figure 1). Sampling was stratified by shelf-reef zones (inner, mid, outer) and attributed with the shelf region (e.g. north). Sites were selected to complement other long-term monitoring locations and capture the spatial variation with depth and around the shelf. Inclement weather conditions restricted the collection of imagery on the mid- and outer-shelf regions around LHI, especially on the more exposed eastern margin, which were the primary target. For this reason, a greater number of shallower tows were conducted and data were thus subsampled to explore trends and compare with existing data for BP.

2.1 Still image analysis

The towed camera systems deployed on both voyages were equipped with a downward facing high-definition stills camera and forward-facing video camera, fitted with dual lights and Ultra Short Baseline (USBL) positioning. Cameras were towed approximately 1 m above the seafloor, in water depths ranging from 3–115 m along transect lengths ranging from 115–1,417 m (totalling 14 km for BP and 13 km for LHI). Tow data (inclusive of shallower data) are first presented and described in terms of broad trends in benthic composition; and subsampled data is subsequently used for statistical analyses as it represents a more spatially balanced sample of shelf reefs.

A total of 1,287 stills around LHI were extracted from 24 sites and classified for benthic composition. Image classification adopted the methodology described for the BP tow data in Linklater *et al.* (2016), whereby images were extracted every 10 m along the tow transects and were classified for percent cover with a 25-point overlay in Transect Measure v2.31 software (totalling 32,175 points). Sessile benthic organisms and sea urchins were classified within each image, and where these were absent, benthic substrates were classified. Benthos were classified using the terminology of CATAMI (Althaus *et al.* 2015) and terms were aggregated into Level 1 organism/substrate ‘Type’ (e.g. scleractinian corals), Level 2 ‘Morphology’ (e.g. encrusting) and Level 3 ‘Genus/species’ (e.g. *Acropora*). Genus and species classifications were only performed for selected organisms which were confidently recognisable. The diversity of organisms observed and the difference in morphology that can occur when organisms are at environmental extremities meant that classifications used in this study were conservative.

Subsampling was performed on the classified tow data to standardise sampling for quantitative and statistical analyses. This standardised approach was needed as tow transects varied in length, crossed multiple geomorphic feature types and had disproportionate sampling in sheltered, shallow waters due to adverse weather (Figure 1). Equal segments of 20 images (approximately 200 m in length) were manually extracted from each tow over the centroid of the dominant feature type, and data were averaged for each site (Figure 2). Reef features were given preference over basins as they were the focus of this study, and the centroid of the reef polygons were targeted to collect a representative sample of mesophotic reef habitat within each tow. Tows that crossed non-target features, including the shallow tows (NOV01, NOV04-05, NOV22) and basin areas (NOV06, 08CAM03), were excluded from analyses. Shallow habitats have been well-described by other studies (Edgar *et al.* 2010; Harriott *et al.* 1995; Veron and Done 1979) and basin features for BP are described in Linklater *et al.* (2016). The subsampling undertaken for this study resulted in 19 sites for LHI and 14 sites for BP. Reefs deeper than 20 m were mostly targeted, with depths of subsampled site data ranging from 14–58 m (Figure 6). Sites were grouped into shelf-reef zones (inner, mid, outer shelves) and regions (north, south, etc.) for analyses. Sites were well separated spatially, typically more than 1 km apart (closest sites 500 m apart). Global Moran's I was calculated for the encrusting stony coral variable using GeoDa software (Center for Spatial Data Science, University of Chicago), with results indicating spatial autocorrelation was not apparent (Global Moran's I = 0.09, pseudo p-value = 0.065).

Previous analyses for the BP shelf undertaken by Linklater *et al.* (2016) explored the relationship between the benthic communities and underlying geomorphology, and therefore extracted multiple, smaller segments (10 stills) for each geomorphic feature the tow crossed using detailed sub-categories of geomorphic features (e.g. upper mid-shelf reef, mid-shelf intra-reef depressions). This study extracted one subsample per tow (20 stills) over the dominant geomorphic feature, with the objective of exploring patterns in benthic distribution between and within shelf zones for the two shelves.

2.2 Environmental data and geomorphic classification

The high-resolution bathymetry model, with a 5 m cell size, and geomorphic feature interpretation presented by Linklater *et al.* (2018) were used as inputs for the environmental data in this study. Selected terrain variables, including slope and ruggedness for the island shelves were also sourced from Linklater *et al.* (2018). Additional derivatives were calculated from the bathymetry model, with the list of variables outlined in Table 1. Slope, ruggedness, depth range and standard deviation, and curvature were included as measures of surface complexity. Curvature represents topographical peaks and troughs and was calculated with ArcGIS Spatial Analyst, which uses a fixed 3 x 3 rectangular window, and with the landform curvature tool in the Geomorphometric and Gradient Metrics Toolbox (GGMT), which allows for user-defined scales (Evans *et al.* 2014). The scalable landform curvature produces a similar surface to topographic position index (TPI, also termed bathymetric position index or slope position). TPI and landform curvature grids were calculated at a set scale and compared with correlation tool in GGMT which showed 0.99-1 correlation between the grids. Therefore, these two parameters were considered interchangeable for the purposes of this study. Aspect (eastness and northness) was included as a surrogate for currents (Wright *et al.* 2012). Euclidean distance from land and the shelf break were included as surrogates for the potential influence of large-scale oceanographic processes such as upwelling and wave action. Latitude and longitude were also included, resulting in a total number of 16 variables tested.

Table 1 Terrain variables utilised by this study

Terrain variables	Tools and Parameters	References
Depth	Interpolation from multiple inputs	(Linklater *et al.* 2018)
Range	Focal statistics: Rectangle 3x3	ESRI ArcGIS
Standard dev.	Focal statistics: Rectangle 3x3	ESRI ArcGIS
Slope	Spatial analyst	ESRI ArcGIS
Curvature	Spatial analyst: curvature, plan, profile	ESRI ArcGIS
Landform curvature	Geomorphometric and Gradient Metrics Toolbox; 30 and 100 cell radius (rectangle)	(Evans *et al.* 2014)
Aspect - Eastness	Benthic Terrain Modeler (Sine transform)	(Wright *et al.* 2012)
Aspect - Northness	Benthic Terrain Modeler (Cosine transform)	(Wright *et al.* 2012)
Distance to land	Euclidean distance (m)	ESRI ArcGIS
Distance to shelf break	Euclidean distance (m)	ESRI ArcGIS
Ruggedness	Benthic Terrain Modeler (BTM); 3 cell radius	(Wright *et al.* 2012)

In the previous study by Linklater *et al.* (2016), Acoustic Doppler Current Profiler (ADCP) and backscatter data (surface hardness) were utilised to explore trends in benthic distribution around the BP shelf. ADCP data were not available for the LHI sites visited in the November 2013 survey, and backscatter multibeam sonar data were not available for the inner shelf as it was outside the coverage of the multibeam survey. Therefore, these variables were excluded from this study.

Geomorphic features around the two shelves were defined by Linklater *et al.* (2018). Feature boundaries were manually digitised, informed by bathymetry data, backscatter data, sub-bottom profiles, sediment and rock cores and sediment grabs. The classification of geomorphic features was used to separate the shelf zones into the aggregated terms: inner-, mid- and outer-shelf reefs. Inner-shelf reefs comprise fossil reefs and bedrock outcrops. Mid-shelf reefs comprise the upper, lower and intra-reef depressions of the mid-shelf fossil reef and mid-shelf patch reefs, and; outer-shelf reefs comprise the outer-shelf pavement, patch reefs and ridges, and terrace features.

2.3 Statistical analyses

Statistical analyses focused on exploring variation in benthos around the different shelf-reef zones and regions of LHI, and comparing the distribution of benthos to the BP shelf. Biota and substrate data were compared to terrain variables to explore patterns in their distribution that are influenced by surface complexity. Statistical analyses were first performed on the new data for the LHI shelf. Data for BP, presented in Linklater *et al.* (2016), were subsampled in the manner described above for the LHI data to capture consistent samples of shelf reef features. Subsampled data for LHI and BP were then integrated, and statistical analyses were repeated for the collated data.

Statistical analyses were performed in PRIMER-E Primer v6.1.15 with PERMANOVA+ v1.0.5 (Anderson *et al.* 2008; Clarke 1993). Abundance data were input as counts (totalling 25 counts per still) and were analysed as site-averaged data. Data were square root transformed to enhance the contribution of low abundance benthos and Bray-Curtis similarity resemblance matrices were computed. Benthic data were analysed at three classified levels of organism/substrate 'Type' (Level 1), 'Morphology' (Level 2) and 'Genus/Species' (Level 3). Site-averaged data at Level 3 were clustered into reef types using the hierarchical CLUSTER tool with Simprof test applied at 9,999 permutations. SIMPER analyses were performed on clustered data to explore within-group similarity.

Principal coordinates analyses (PCO) were performed on site-averaged data. PCO uses the rank-order of similarities from the resemblance matrix to project the data onto two principal coordinate axes to reduce dimensionality and visualise patterns in the data.

Analyses were then repeated at Level 3 using only the biotic data to explore the trends in community composition without the influence of substrate. Results containing both substrate and biotic data are denoted with ‘a’ and biotic data is denoted with ‘b’. Data were labelled with ‘Shelf Zone’ and scleractinian coral composition (Level 1 abundance) and displayed as a bubble plot. Correlations with benthic composition data (Level 2a, Level 3a and 3b) and environmental data were displayed as vectors.

Permutational MANOVAs (PERMANOVAs) were performed to test whether benthic communities (Level 2a, Level 3a and 3b) varied significantly between shelf zones. The ‘Shelf’ factor (i.e. LHI or BP) was combined with the ‘Shelf zone’ factor to create a new factor representing ‘Shelf-Shelf zone’ (e.g. “LHI shelf - Outer-shelf reef”) which was treated as a fixed factor as it represents the hypothesis being tested. The new extracted subsampled ‘Site’ locations were nested within the ‘Shelf-Shelf zone’ factor and treated as a random factor due to the nested relationship. Pairwise PERMANOVAs were performed using an unrestricted permutation of raw data and 9,999 permutations (Anderson *et al.* 2008).

Environmental data were input into Primer and data were analysed as site-averaged data. A Draftsmans Plot was produced to identify collinearity and explore the need to transform variables. A natural log transformation was applied to selected variables (slope, range, standard deviation, ruggedness), and all variables were normalised. The BIOENV procedure within the BEST tool was first applied with all variables included to explore the strongest contributors to variation in benthos. Collinear variables were removed, retaining the higher ranked variables. The BIOENV procedure was then repeated with the reduced selection of variables, with 9,999 permutations. The reduced selection of variables for the BIOENV procedure was performed for Level 2a, Level 3a and 3b data.

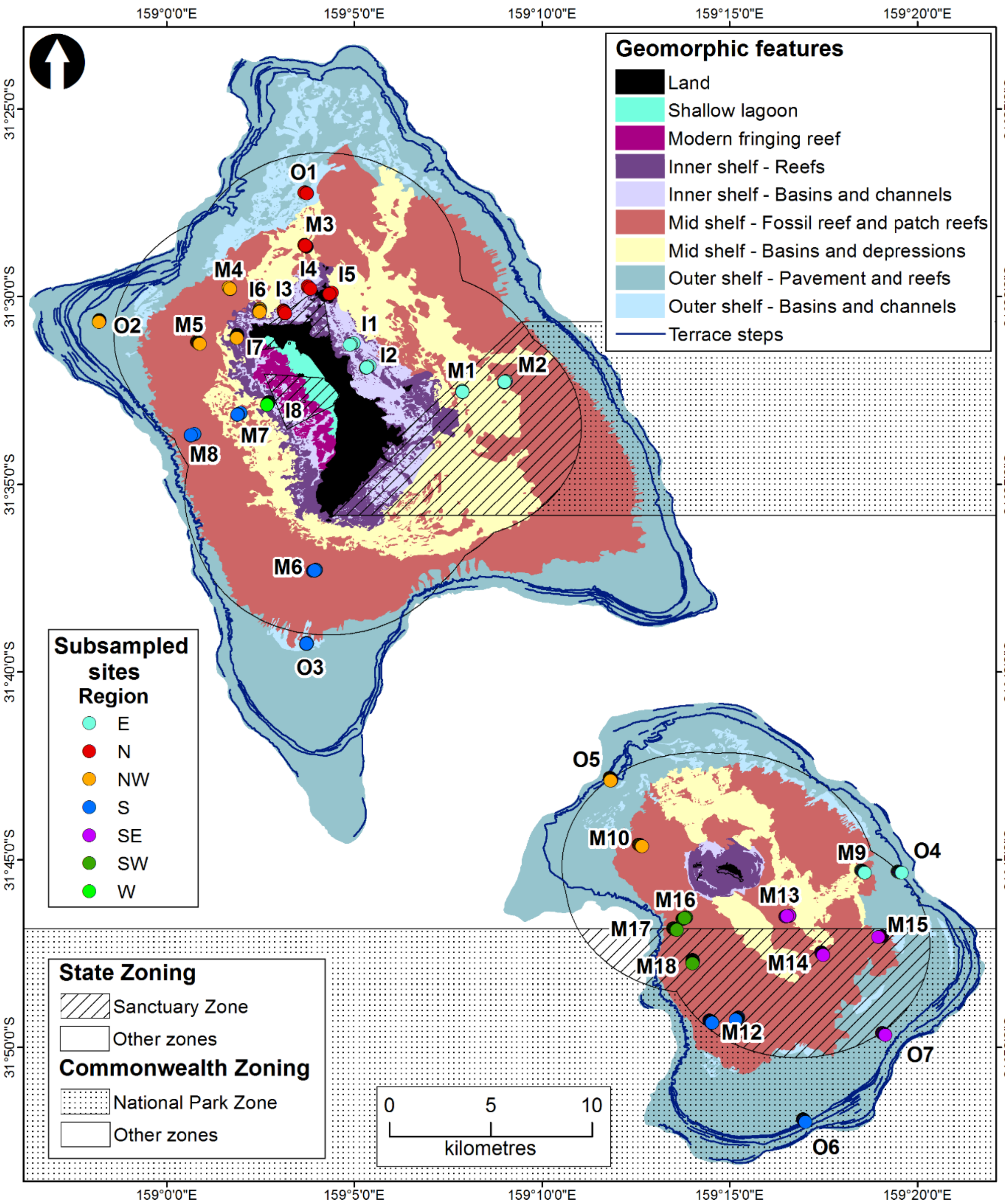

Figure 2 New sites subsampled over reef features for each shelf zone (inner, mid, outer). Sites contain 20 images each. "No take" protected areas shown for state ('Sanctuary Zones') and Commonwealth ('National Park Zones') marine park areas. Geomorphology classification sourced from Linklater *et al.* (2018).

3. Results

3.1 Lord Howe Island shelf

3.1.1 Benthic composition

Abundant algae, corals and sponges were evident colonising the shelf reefs around LHI, with summary tow statistics provided in Table 2. Classified benthic data are available at: doi:10.17632/x8v7yxzxj9.1. Across all classified tow transects, scleractinian corals were observed to occur from 6–60 m depth. Encrusting morphologies were the most dominant scleractinian coral morphology observed (57%), with sub-massive morphologies the second most common (19%). The highest average scleractinian coral cover (22%) was recorded on tow NOV20 (M2) on the eastern mid-shelf reef. The maximum scleractinian coral cover recorded around LHI was 64% cover on the southern fringing reef (NOV22), however this tow was excluded when subsampling data for subsequent statistical analysis (Section's 3.1.2 and 3.2) due to its shallow depth range (6–14 m).

Table 2 Summary statistics for tow data collected around the Lord Howe Island shelf. Abbreviations: Scleractinian coral cover (STC); average percent cover (Av), maximum percent cover (Max).

Tow	Sub. site	Start Coord (S, E)	End Coord (S, E)	No. stills	Depth range (m)	STC Av (%)	STC Max (%)
NOV01*	-	31.514928; 159.067896	31.513233; 159.070487	35	6 - 14	12	52
NOV02	I1	31.523379; 159.075980	31.520654; 159.083420	84	5 - 25	3	28
NOV03	I2	31.532393; 159.088100	31.530106; 159.091063	42	13 - 22	2	16
NOV04*	-	31.552273; 159.098383	31.550879; 159.101704	40	12 - 20	2	20
NOV05*	-	31.545660; 159.091281	31.544026; 159.095254	49	3 - 11	5	32
NOV06*	-	31.510041; 159.080519	31.506113; 159.083733	65	30 - 37	0	0
NOV07	I5	31.499353; 159.070661	31.497822; 159.074304	46	31 - 35	4	24
NOV08	I4	31.498510; 159.065231	31.495373; 159.062752	50	23 - 30	3	44
NOV09	I3	31.511804; 159.055022	31.506028; 159.051976	77	9 - 29	9	52
NOV10	M3	31.477785; 159.062203	31.476422; 159.059547	58	40 - 60	0	4
NOV11	O1	31.454347; 159.063196	31.452347; 159.057914	102	48 - 58	0	8
NOV12	M4	31.497294; 159.028787	31.495268; 159.026934	48	35 - 38	1	8
NOV13	I6	31.508638; 159.041164	31.505225; 159.041568	45	18 - 33	1	8
NOV14	O2	31.509952; 158.970373	31.511941; 158.969891	42	57 - 58	0	4
NOV15	M5	31.518686; 159.011473	31.521165; 159.014886	55	29 - 38	3	20
NOV16	I7	31.516604; 159.031556	31.518947; 159.031312	31	30 - 34	1	12
NOV17	I8	31.545371; 159.047868	31.548044; 159.044582	51	26 - 35	11	48
NOV18	O3	31.654553; 159.061629	31.653603; 159.062305	38	51 - 53	2	16
NOV19	M6	31.621746; 159.064916	31.620100; 159.068323	48	29 - 32	11	24
NOV20	M2	31.538523; 159.149481	31.536879; 159.151300	43	28 - 35	22	44
NOV21	M1	31.542411; 159.131439	31.541465; 159.131169	28	35 - 51	4	16
NOV22*	-	31.565531; 159.067106	31.565995; 159.064835	28	6 - 16	13	64
45CAM17	M7	31.553926; 159.027477	31.551671; 159.032968	67	26 - 38	4	28
46CAM18	M8	31.563718; 159.005892	31.559552; 159.016067	115	29 - 44	2	16

* Tows excluded from statistical analyses. Coordinates in WGS 1984 Zone 56S.

Depth zonation of benthic composition type (Level 1a) for the subsampled sites (14–58 m depth) around the LHI shelf is shown in Figure 3 and representative images of coral communities are shown in Figure 4. Overall, a shift in dominant benthos is apparent, where dominance in fleshy algae and sand in shallower waters shifts to a dominance of biogenic substrates and pebbles in deeper waters. Scleractinian coral composition was variable across all depths, with the highest abundance in 25–30 m depth. Black and octocorals also showed variable abundance across depths, with the highest average abundance in 35–40 m depth. Other colonisers, which predominantly comprised ascidians, urchins and bryozoans, were more abundant in depths less than 35 m. *Lissoclinum* sp. was the most common ascidian observed. In deeper waters (55–60 m), anemones and urchins were the primary component of other colonisers. *Prinocidaris* spp. was the most ubiquitous urchin species observed, with *Tripneustes* sp. observed to a lesser extent. Fleshy algae generally decreased with increasing depth, while crustose coralline algae increased in abundance from 25–55 m depth.

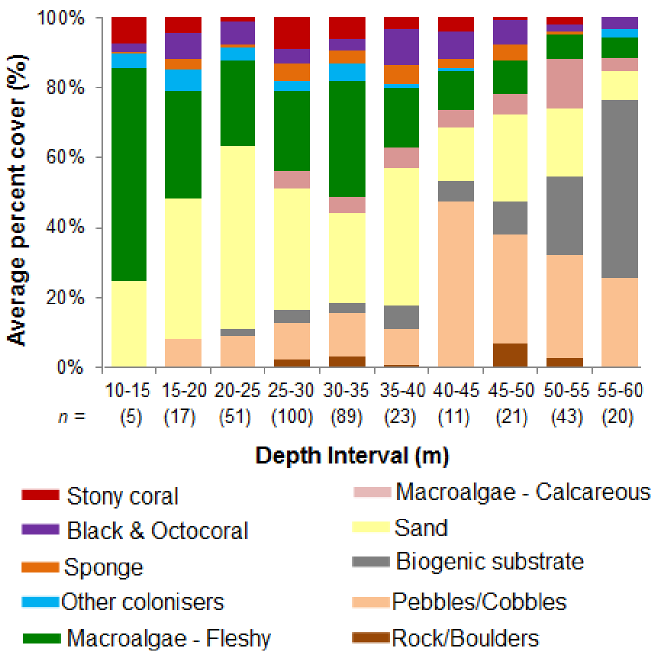

Figure 3 Depth zonation for subsampled sites around the LHI shelf, with number of stills (*n*) per depth interval indicated.

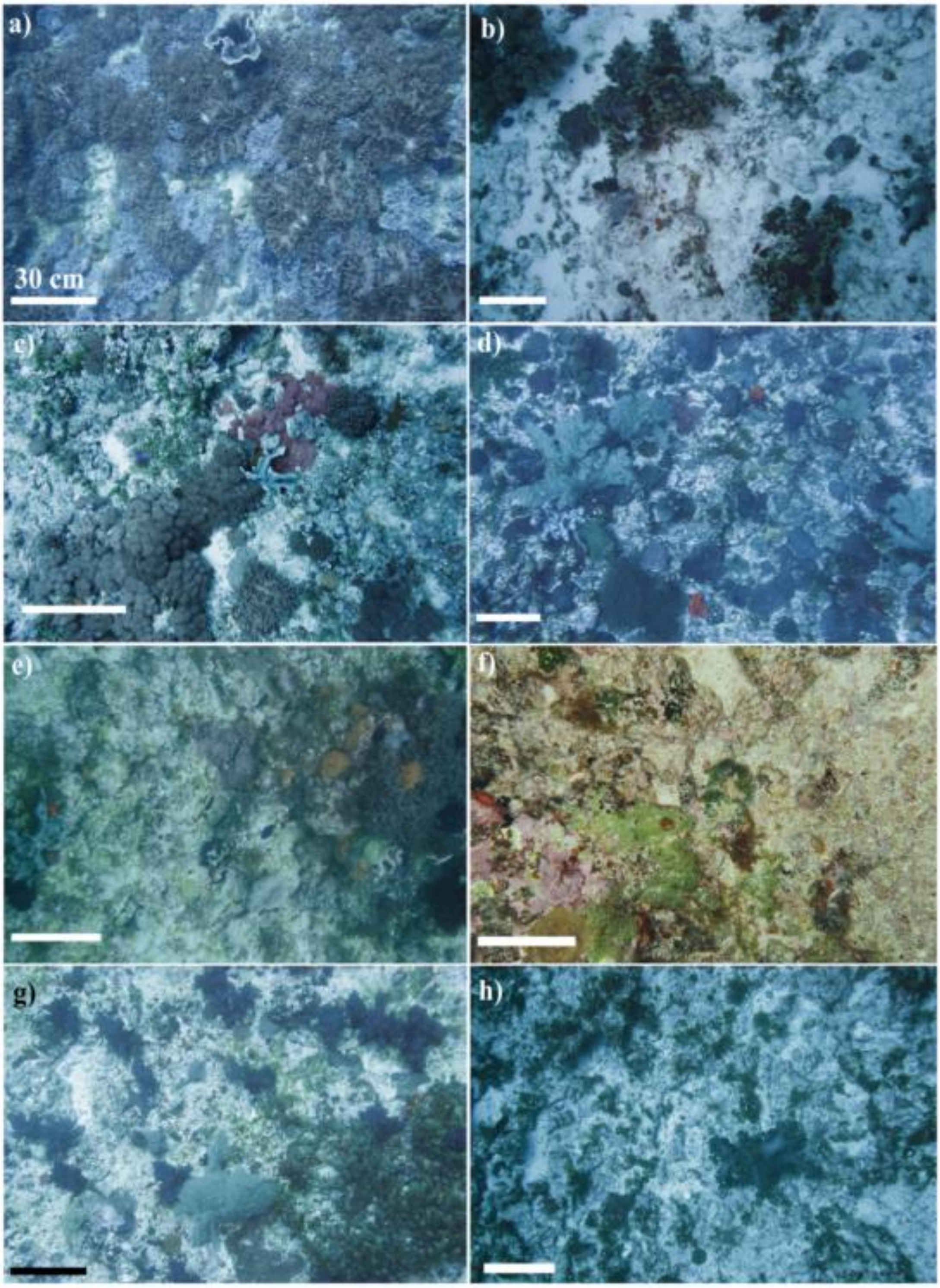

Figure 4 Benthos images for the LHI shelf: a) Northern inner-shelf reef (I4), massive digititate soft coral beds; b) Northwestern mid-shelf reef (M4), branching aborescent *Dendronepthya* sp. soft corals; c) Eastern inner-shelf reef (I2), *Xenia* sp. soft coral, encrusting scleractinian coral, erect sponge and *Caulerpa racemosa*; d) Eastern mid-shelf reef (M2), encrusting scleractinian corals and sea fans; e) Western inner-shelf reef (I8), mushroom leather and digitiate massive soft corals, encrusting scleractinian coral, erect sponge and bryzoans; f) Western mid-shelf reef (M7), encrusting scleractinian coral, crustose coralline algae, encrusting *Peysonnelia* sp. and *Caulerpa* sp., globose *Codium Spongisoum*; g) Southern mid-shelf reef (M6), branching soft coral

Dendronepthya sp., sea fans, encrusting scleractinian corals, sponge crusts and *Caulerpa racemosa*; h) Southern outer-shelf reef (O3), encrusting scleractinian corals, branching soft coral *Dendronepthya* sp., laminate *Padina* sp. and branching *Dictoyta* sp. algae. Scale bar in each image represents 30 cm.

The inner-shelf reefs around LHI were characterised by greater proportions of black and octocorals and other colonisers, occurring with sub-massive scleractinian corals, filamentous and branching algae which colonised structurally complex carbonate (calcarenite and reef limestone) and volcanic substrates. Fleshy algae and corals coexisted in close proximity, with *Asparagopsis* sp., *Chlorodesmis* sp., *Caulerpa racemosa* and *Codium spongiosum* common, and scleractinian coral *Isopora* sp. and soft coral *Xenia* spp. also common.

The inner- and mid-shelfs of LHI northern shelf comprised dense beds of massive soft corals, with high densities of digitate and ridge morphologies (including *Lobophytum* sp.) observed at sites I3, I4 and I6. Average black and octocoral abundance was greatest at northern site I4 (15%), where dense patches of massive soft corals were observed (Figure 4a).

The mid-shelf reefs around LHI, comprised reef limestone, were colonised by mixed encrusting benthos (algae, sponges, corals), with sand veneers across the reef surface. Similar to the northern inner shelf, high soft coral abundances (arborescent branching morphologies) were observed on the northern and northwestern mid-shelf reef tows of M3 and M4, where patches of *Dendronepthya* spp. were observed to be common. Substrate complexity was variable around the mid-shelf reefs. The mid-shelf reef surface was typically low-profile reef with cavities, with topographic complexity greatest on the upper mid-shelf reef features and around feature edges. The eastern LHI mid-shelf reef site M2 (28–29 m depth, Figure 4d) recorded the highest average scleractinian coral cover for the LHI shelf, 24%, which also had the equal highest maximum cover of 36% together with the inner western reef (I8). This site exhibited a steep elevation change rising from the mid-shelf basin to the top of the fossil reef rim.

The outer-shelf reefs comprised low profile carbonate pavements that transitioned to terraces with steep drop-offs and steps towards the shelf break. Rhodolith beds and bivalve beds, with sand veneers and encrusting and laminate algae, were characteristic of the pavement areas (Figure 4h). The highest average composition of biogenic material (including rhodoliths and bivalve beds) occurred on the outer shelf sites, comprising 51% of the northern LHI site O2 and 36% of the southern LHI site O3 (Figure 5). Fans and sea whips with sparse scleractinian corals colonised the carbonate surface, which typically exhibited low complexity over the pavement surface.

During image classification, other organisms of interest were noted that were not included as part of this study. These included fish, crustaceans, sea cucumbers, sea stars and a sea spider. Images of these organisms can be found in the online image library (doi: 10.17632/r49jptds7j.1). A sighting of the rare and protected Ballina Angelfish (*Chaetodontoplus ballinae*) was recorded at site 33CAM13 (O7) in approximately 50 m depth. Several endemic Doubleheader wrasses (*Coris bulbifrons*) were also sighted at 15CAM09 (M17), NOV02 (I1), NOV15 (M5) and NOV22. Notably, a dense colony of *Prinocidaris* urchins was observed on tow 46CAM18 (M8) which did not occur in such dense numbers elsewhere.

3.1.2 Benthic community analyses

PCO analysis of the LHI data showed the inner-, mid- and outer- shelf reefs form distinct groups separated from one another, with variation apparent within each zone (Figure 5a). The first two principal coordinates explained 30% and 18% of the total variation. Vector overlays of compositional data showed encrusting scleractinian corals and sponge crusts correlate to the mid- and inner-shelf reefs (Figure 5a). The mid-shelf reefs correlated to greater scleractinian coral abundance, with the eastern mid-shelf reef (M2) correlating to the highest recorded counts (Figure 5c). The northwest (M5) and southern (M6) mid-shelf reefs and western inner-shelf reef (I8) were also associated with greater scleractinian coral abundance.

The northern (O1) and northwestern (O2) outer-shelf reefs were associated with low scleractinian coral cover and greater abundances of rhodoliths and pebble substrates. Coralline algae and bivalve beds corresponded to the southern outer-shelf reef site (O3). Filamentous algae, sand waves, *Lobophytum* sp. Octocoral and *Lissoclinum* sp. ascidians corresponded to the north, eastern and northwestern inner-shelf reefs. Depth and distance from shelf were the environmental variables that showed the greatest correlation to inner-shelf reefs (Figure 5d). Latitude correlated to the northern and northwestern mid- and outer-shelf reefs at LHI, and distance from shelf correlated to the remaining mid- and outer- shelf reefs.

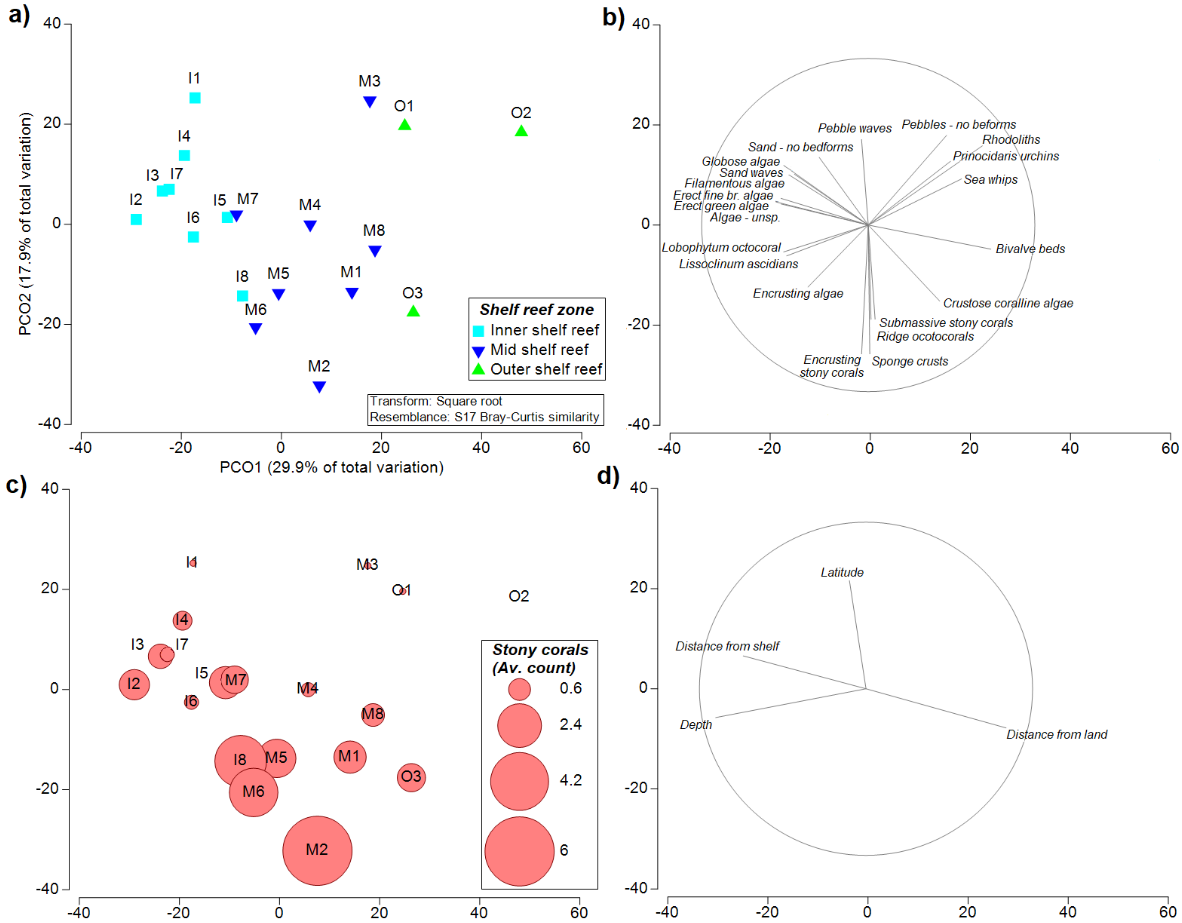

Figure 5 PCO results for the LHI shelf Level 3a data with substrate and biotc data: a) Shelf reef zone; b) Compositional vectors (Level 3a) overlain for vector correlations >0.5; c) Scleractinian (stony) coral abundance as average counts (Level 1) displayed as bubble plot; d) Environmental variables with vector correlations >0.5.

3.2 Comparison of Lord Howe Island and Balls Pyramid shelves

3.2.1 Benthic composition

The greatest proportion of biota relative to substrates occurred on the LHI eastern and southern mid-shelf reefs and around most of the BP mid-shelf reefs (with the exception of the northwest). Scleractinian coral cover was greater overall on the BP mid-shelf reef compared to the LHI inner- and mid-shelf reefs (Figure 6). Several of the subsampled sites around the BP shelf exceeded 50% maximum coral cover for an individual still, including the southeastern (76%), southwestern (72%), eastern (64%) and southern (56%) mid-shelf reefs and southern outer-shelf reef (52%). In comparison, the maximum coral cover around LHI was 36%. The highest average cover per site observed around BP, 25%, occurred on the southwest mid shelf (M17, 30–33 m depth), and was similar to the highest average coral cover per site of 25% on the eastern LHI mid shelf (M2). The outer-shelf reefs on both shelves exhibited the lowest coral cover, with the exception of the southern outer-shelf reef site on BP (O6, 59–69 m depth).

The inner- and mid-shelf reefs around LHI had greater proportions of black and octocorals. Black and octocorals were commonly observed around the BP shelf though they comprised a lower proportion (maximum per site average 5% at M13) relative to the LHI shelf (maximum per site average 15% at I4). The highest proportions of fleshy macroalgae across both shelves occurred on the inner-shelf reef sites around LHI, comprising 61% and 50% of the northwest (I7) and eastern (I2) sites, respectively.

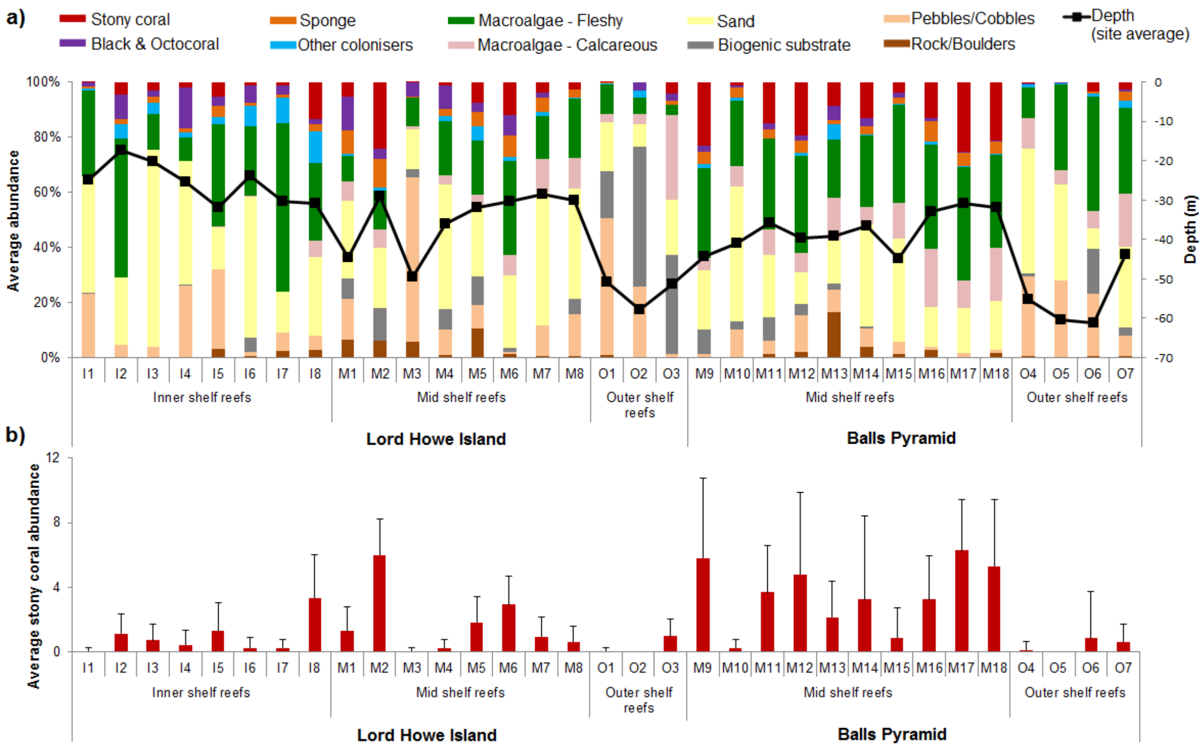

Figure 6 Adundance of benthos and substrates on the LHI and BP shelves: a) Benthic composition of subsampled sites for shelf zones, showing average abundance (counts) stacked for each site. Average depth is displayed as a secondary axis; b) Average scleractinian coral abundance (count) for each site, with standard deviation shown as positive error bar.

The outer-shelf reefs on both shelves exhibited greater proportions of pebbles, with these accounting for 50% of the site composition at the northern outer-shelf reef on LHI (O1). High abundances of biogenic substrates, including rhodoliths and bivalve beds (e.g. Figure 7), were also observed on the outer-shelf reefs around LHI. The northwest outer-shelf reef on LHI

(O2) contained 51% biogenic substrates and no scleractinian corals were recorded along this tow, which was similarly the case for the BP northwestern outer-shelf reef (O5).

Prolific carbonate production was demonstrated by the vast expanses of carbonate sand accumulations in basin areas and ubiquitous sand veneers on reef surfaces. Sandy seabed, especially sand veneers, form a high proportion of substrates across all sites, with a thin layer of sand common on the reef surfaces, indicating biogenic carbonate production across the shelf. Sandy substrates, with and without bedforms, occurred between reef outcrops. Volcanic material was occasionally observed close to the islands around LHI, but was only present in small quantities.

3.2.2 Benthic community analyses

Clustering of genus/species-level data at Level 3a (with both substrate and biotic data included) resulted in seven clusters of statistically different reef types (Table 3). Substrate data was included as it is considered an important component characterising reef habitats. PCO analysis for the two shelves combined showed that separation of the collective inner-, mid- and outer-shelf reefs are apparent. The first two principal components explained 20.2% and 19.8% of the total variation (Figure 7).

Most LHI inner-shelf reefs clustered together into Reef Type 2, which were characterised by octocorals and fleshy algae. PCO analyses show these sites were associated with massive ridge octocorals and filamentous fleshy algae, with moderate levels of scleractinian coral cover (Figure 9). The remaining inner-shelf reefs clustered with five mid-shelf reef sites around LHI into Reef Type 7, which exhibited similar community composition with greater cover of scleractinian corals and sponges. The majority of BP mid-shelf reef sites clustered into Reef Type 6, which also included the BP southeast outer-shelf reef and western mid-shelf reef at LHI. Reef Type 6 was associated with the highest levels of scleractinian coral cover, and correlated to increased cover of encrusting and sub-massive scleractinian corals, sponges and coralline algae. The southwestern mid-shelf reefs on BP and the eastern LHI mid-shelf reef M2 (which clustered into Reef Type 7) showed the highest association with scleractinian coral abundance. All of the BP mid-shelf reefs correlated to greater scleractinian coral abundance with the exception of the northwestern mid-shelf reef (M10).

The outer-shelf reefs on both shelves were associated with the occurrence of pebbles and rhodoliths. Reef Type 3 was characterised as sand inundated reefs encrusted with algae, and included a mix of mid- and outer-shelf reefs around LHI and BP. PCO analyses showed these reefs are correlated to sand and pebbles (with bedforms). Reef Type 4 is similar in composition to Reef Type 3, but with a greater composition of pebble and rhodolith beds. Reef Type 4 included the northern mid- and outer-shelf reefs at LHI (M3 and O1) and the southern BP outer-shelf reef (O6). Site O2 and O3 form their own distinct clusters as Reef Type 1 and 5, respectively. Reef Type 1 comprised biogenic and pebble beds with sea whips, and correlated to high cover of rhodoliths. Reef Type 5 was similar in composition to Reef Type 6, but with higher cover of *Dendronepthya* octocoral species.

SIMPER analyses indicated sand veneers were a top contributor to cluster separation across most groups, with macroalgae also commonly a top contributor. Within-group similarities were similar across all clustered reef types, with the highest within-group similarity for Reef Type 3 (61%) and the lowest for Reef Type 4 (53%).

Table 3: Clustered reef types for the LHI and BP shelves, with Level 3 input data. Av = average; Rugg = ruggedness.

Reef Type	Summary	Sites	Depth Range	Av Rugg	Av Slope	Description
1	Biogenic and pebble beds with branching octocorals and whips	O2	57–58 m	0.0005	1.8°	Branching octocorals, whips and urchins, with coralline and fleshy sheet-like algae. Substrate of pebbles, bivalve beds and rhodoliths.
2	Reef with octocorals and fleshy algae	I1, I2, I3, I4, I7	14–32 m	0.0006	4.2°	Massive digitate and ridge (incl. *Lobophytum sp.*) octocorals, encrusting scleractinian corals and ascidians (incl. *Lissoclinum sp.*). Algal communities of globose, encrusting and filamentous fleshy algae (incl. *Caulerpa peltata*, *Caulerpa racemosa*). Substrate of sand and pebble waves between reef outcrops.
3	Algal dominated reef	M7, M10, M15, O4, O5	25–64 m	0.0009	4.5°	Low profile, sand inundated reef with encrusting coralline and fleshy (incl. *Peysonnelia sp.*) algae. Sparse encrusting scleractinian corals and sponges.
4	Pebbles and biogenic beds with fleshy algae	M3, O1, O6	39–69 m	0.0013	4.9°	Pebbles and rhodolith beds with encrusting fleshy and coralline algae. Branching octocoral *Dendronepthya spp.* with sparse encrusting scleractinian corals.
5	Reef with branching soft corals and coralline algae	O3	51–52 m	0.0003	2.6°	Low profile reef with coralline algae and bivalve beds. *Dendronepthya spp.* common, with encrusting and foliose scleractinian corals.
6	Reef with scleractinian corals and fleshy algae	M8, M9, M11, M12, M13, M14, M16, M17, M18, O7	29–46 m	0.0004	2.0°	Encrusting scleractinian corals common, with sub-massive and foliose scleractinian corals and sponge crusts. Encrusting coralline and fleshy (incl. *Peysonnelia sp.*) and filamentous algae. Varying levels of cover of benthos.
7	Reef with scleractinian corals and	I5, I6, I8, M1, M2, M4, M5,	22–50 m	0.0010	4.8°	Encrusting scleractinian corals, sponge crusts, massive ridge (incl. *Lobophytum sp.*) and branching octocorals (incl.

octocorals	M6	*Dendronepthya spp.*), ascidians (incl. *Lissoclinum sp.*) and byrozoans. Reef outcrops with pebbles and bivalve beds.

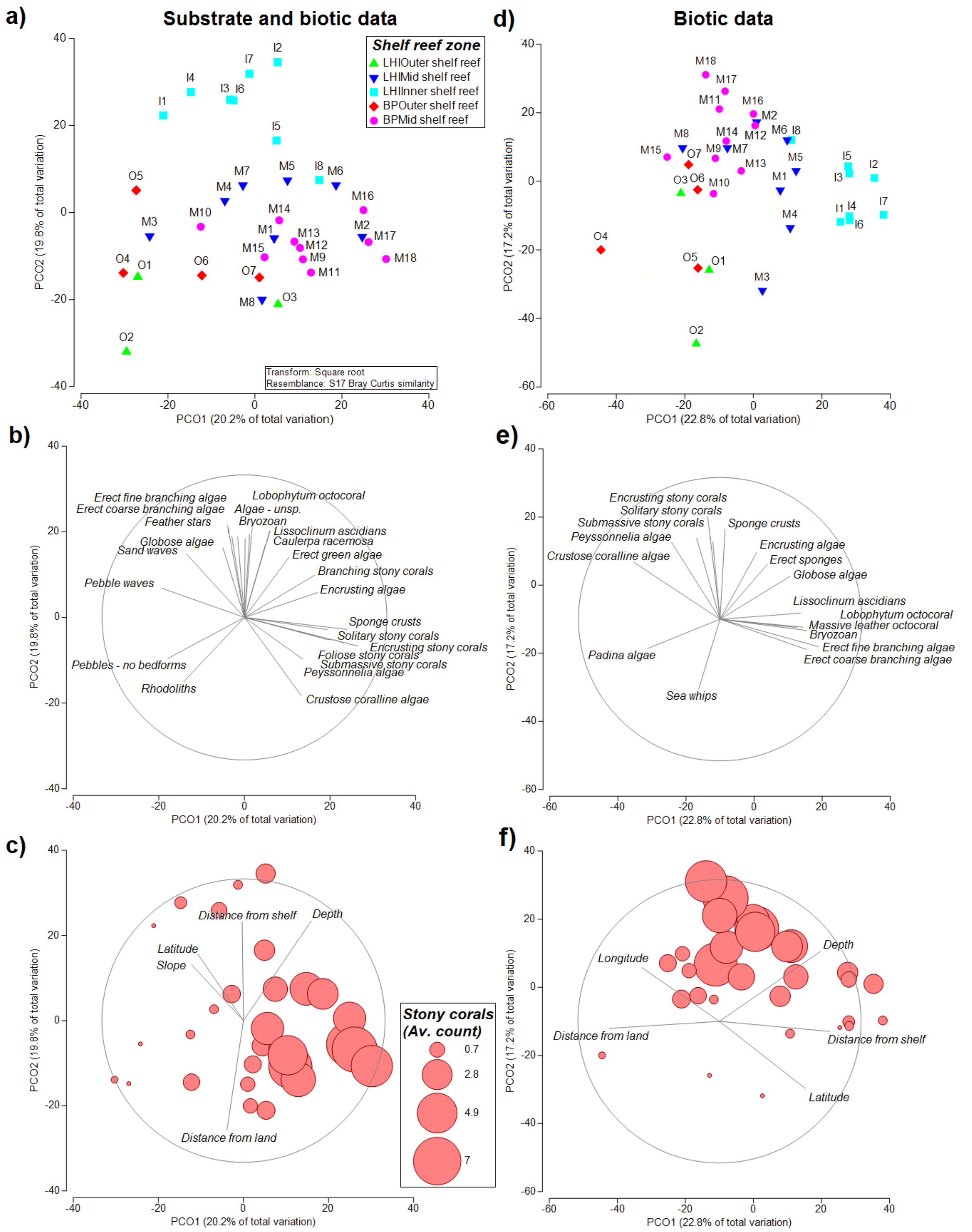

Figure 7 PCO results from LHI and BP shelf comparison with Level 3a (L3a) and Level 3b (L3b) data: a) Shelf reef Zone (L3a); b) Compositional vectors (L3a) overlain for vector correlations >0.5; c) Scleractinian (stony) coral abundance (Level 1) displayed as bubble plot with environmental vectors (L3a) overlain for vector

correlations >0.5; d) Shelf reef Zone (L3b); e) Compositional vectors (L3b) overlain for vector correlations >0.5; f) Scleractinian coral abundance (Level 1) displayed as bubble plot with environmental vectors (L3b) overlain for vector correlations >0.5.

PERMANOVA pairwise analyses at morphology (Level 2a) and genus/species levels with (Level 3a) and without (Level 3b) substrate data indicated significant differences between all shelf-reef zones, except for the LHI and BP outer-shelf reefs which were not significant (p(perm) = 0.0837) at Level 3b. The strongest difference in benthic composition was apparent for the BP mid-shelf reef and the LHI inner-shelf reef (p(perm)=0.0001 at Level 3b). The LHI inner- and mid-shelf reefs also showed strong differences, with the greatest difference also shown at Level 3b (p(perm)=0.0004). The weakest differences were apparent between the BP and LHI outer-shelf reefs at all levels. Generally, similar significance values were reported across all three levels analysed.

Table 4 PERMANOVA table Pairwise PERMANOVA results with 'Shelf-Shelf Zone' as a factor. Data shown for Level 2 (L2a, morphology) and Level 3 (L3a, genus/species) with substrate and biotic data, and L3 with biotic data only (L3b).

	LHI inner shelf (IS)			LHI mid shelf (MS)			LHI outer shelf (OS)			BP mid shelf (MS)		
	L2a	L3a	L3b	L2a	L3a	L3b	L2a	L3a	L3b	L2a	L3a	L3b
LHI IS		-			-			-			-	
LHI MS	**0.0008**	**0.0007**	**0.0004**		-			-			-	
LHI OS	0.0055	0.0059	0.0061	0.0115	0.0102	0.0123		-			-	
BP MS	**0.0002**	**0.0003**	**0.0001**	0.0123	0.0118	0.0115	0.0046	0.0039	0.0026		-	
BP OS	0.0020	0.0019	0.0023	0.0113	0.0081	0.0020	0.0296	0.0287	*0.0837*	0.0062	0.0051	0.0025

Bold text: p(perm)≤0.001; italicised text: p(perm) not significant.

3.2.3 Relationship to environmental data

Trends in PCO analyses indicated several environmental vectors correlated to the inner-shelf reefs at genus/species Level 3a (with and without substrate), including depth, distance from shelf and latitude, and the outer-shelf reefs correlated to distance from land. A weak association occurred between the distribution of mid-shelf reefs with longitude at Level 3b. Most other variables exhibited correlations less than 0.5 in PCO analyses. Insufficient replication existed to test the variation between shelf-reef zones and regions (e.g. north), although trends shown in the PCO indicated shelf-wide patterns in cover within reef features, with an apparent reduction in scleractinian coral cover on both shelves to the north.

BIOENV analyses of the relationship of genus/species-level (Level 3a) to environmental variables showed 0.589 correlation (significance level 0.01%) with depth, distance from land and latitude selected as the highest-ranking variables. With substrate data removed, the same variables were selected with a slight increase in correlation at 0.604 (significance level 0.01%). Similarly, at morphology-level (Level 2a), the same variables were selected with a 0.580 correlation (significance level 0.01%).

4. Discussion:

The data presented in this study is the first documentation of extensive mesophotic coral communities around the Lord Howe Island (LHI) shelf, and together with research completed around the Balls Pyramid (BP) shelf, fills a large knowledge gap in our global understanding of the distribution and composition of subtropical, mesophotic reefs. Collectively, these findings demonstrate the important role of subtropical island shelves in supporting mesophotic coral ecosystems.

4.1 Benthic community trends

Statistical comparisons of the reef features across the LHI and BP mesophotic shelves showed that the benthic communities differ between the inner-, mid- and outer-shelf reefs. The variation of benthic communities between shelf-reef zones supports the previous findings of Linklater *et al.* (2016) that the antecedent topography influences colonisation of modern benthos. Scleractinian corals were most prevalent on the southwestern and eastern mid-shelf reefs around BP, which has the greater extent and vertical relief of fossil reef growth and was inferred to be the windward setting that was more exposed to prevailing wind conditions during times of lower sea level (Linklater *et al.* 2015; Linklater *et al.* 2018). The elevated surface of the fossil reef structures likely provides enhanced exposure to light penetrating through the water column and cross-shelf currents which carry nutrients to support biota.

Shallow reefs in the northern region of the LHI shelf have been described as ‘rheophilic’, which refers to reefs characterised by strong currents (Environment Australia and NSW Marine Parks Authority 2001; Lindsay *et al.* 2008). The high abundance of soft corals on the mid-shelf reefs, including *Dendronepthya* spp., which are often associated with high flow areas (Poulos *et al.* 2013), suggests the northern mesophotic shelf experiences strong currents that enable rheophilic reef communities to extend to mesophotic depths. The northern region is characterised by channel networks infilled with sediment, inferred to be the leeward setting during times of lower sea level (Linklater *et al.* 2015; Linklater *et al.* 2018), which may provide less suitable substrate for hard coral growth.

Overall, the shelf reef zone appears to be a stronger indicator of benthic community assemblages than the environmental variables utilised in this study. Depth, distance from land/shelf and latitude were identified among the strongest variables relating to benthic composition in BIOENV and PCO analyses. The identification of depth as an explanatory variable is supported by the patterns in zonation documented across the two shelves in this study and in the preceding research by Linklater *et al.* (2016). Some communities, such as the sea whips on the outer-shelf reefs and terraces, appear to be structured by depth, whereas other communities, such as the massive soft coral beds on the northern LHI shelf, appear to be spatially clustered and are inferred to be structured by other variables such as current velocities. Distance from land/shelf break and latitude were included as surrogates for broadscale processes such as currents and exposure to wave action. The strong influence of these surrogate measures suggests complex dynamics, not well accounted for in this study, are important variables structuring communities around the shelf in addition to depth and geomorphology. Seafloor complexity measures, such as standard deviation, range and TPI, have been shown to be important variables explaining distribution of benthic and pelagic biota in other studies (e.g. Rees *et al*. 2018; case studies in Harris and Baker, 2012), and the contribution of these variables may be greater for individual species relationships.

Oceanographic data for mesophotic depths are difficult to collect at sufficiently high spatial resolution (to match terrain datasets) and are temporally variable, particularly for this exposed, mid-ocean setting. The apparent north-to-south variation in some communities, such as the massive soft corals and scleractinian corals, may be the result of oceanographic patterns or an artefact of sampling design and warrants further investigation. The inclusion of ocean temperature and current information is strongly recommended for future studies as it is likely that physical conditions play a vital role in structuring shelf communities. While variations in benthic communities occur within shelf features, the geomorphic features are considered to be a useful surrogate for benthos as similar habitats occur across the shelf reefs and basin areas, as shown by this study and prior research around the shelves (Brooke *et al.* 2012; Linklater *et al.* 2016).

A notable characteristic of the benthic communities observed on the shelves was the diversity of benthos. A diverse array of scleractinian corals, sponges, soft corals and algae proliferated, which is in contrast to trends in benthic communities observed at comparable depths around the southeast coast of mainland Australia where communities shift to sponge-dominated beyond 20–30 m depth (Jordan *et al.* 2010). The intermixing of algae and coral is a trait of LHI and BP recognised as globally uncommon as such communities typically exhibit greater patchiness in other tropical-temperate transition zones (Edgar *et al.* 2010). The inter-mixing of coral and algae was apparent across the all shelf zones on both shelves. In shallower waters these organisms were typically branching, filamentous (algae) or sub-massive (coral) morphologies, with the deeper shelf overwhelmingly dominated by encrusting morphologies.

4.1.1 Scleractinian coral cover

The key trend observed in relation to scleractinian coral distribution was the greater live coral cover associated with the southwest BP mid-shelf reef (30–33 m depth) and the LHI eastern mid-shelf reef (28–29 m depth). These features contained the highest average coral cover recorded for the subsampled dataset (24–25%), with comparably greater coral abundances than those observed around the deeper inner-shelf reef features at LHI. While the eastern mid-shelf reef at LHI featured similar coral cover, the LHI shelf was generally reduced in terms of coral cover compared to the BP shelf reefs. The outer-shelf reefs on both shelves had the lowest occurrence of corals, with the exception of the southern outer-shelf reef on BP.

The sampling design of this study focused on the mesophotic zone and did not examine the regions with the highest coral cover in the lagoon of the modern fringing reef, which have been reported at maximum values of 51% (Harriott *et al.* 1995) and 80% (Veron and Done 1979). These maximum percent cover values are comparable to those observed on the BP mid-shelf fossil reef (84% from an individual still, 19% maximum tow average in Linklater *et al.* 2016), highlighting the significance of these fossil reefs as coral habitat. The comparatively lower coral cover recorded around LHI may be due to sampling design as adverse weather prohibited more extensive sampling around the mid shelf.

Encrusting morphologies were the dominant scleractinian coral morphology observed, and these flatter morphologies have been attributed to high-energy currents, and lower temperature and light conditions (Hoogenboom *et al.* 2008). While the shelf experiences lower relative light compared to the shallows, light penetration at this location is recognised as exceptionally good and is reflected by the prevalence of zooxanthellate corals growing at depths greater than 90 m on the southern BP shelf (Linklater *et al.* 2016). High water clarity is supported by euphotic depth data extracted from MODIS satellite imagery by Huang (2013), which shows the euphotic zone typically extends 60–80 m around the LHI and BP shelves (based on zeu annual average for 2010).

Very few studies have focused on the combination of high latitude, mesophotic reef environments (e.g. Venn *et al.* 2009), and this study provides a case study of a higher latitude region with deep light penetration. The prevalence of scleractinian corals and diverse communities observed around the LHI and BP shelves support the emerging narrative of mesophotic coral ecosystems globally, which indicate coral communities extend far beyond the perceived optimal shallow depths (Kahng *et al.* 2014; Loya *et al.* 2016; Turner *et al.* 2017).

4.2 Implications for refugia

Due to the influence of the EAC in facilitating coral growth in this region, and given the strengthening predicted for the EAC (Suthers et al. 2011), these mesophotic shelves may provide a refuge environment for existing coral populations if conditions remain within their thermal tolerances. Considerable areas of reef habitat also occur across both shelves, which could support the establishment of new coral populations or other organisms arriving via long-term dispersal. The isolated geographic location and high protection status afforded to this marine park and heritage area maximises the chances of coral survival as direct anthropogenic stressors are relatively low.

Lord Howe Island was identified by Riegl *et al.* (2015) as an area of potential higher resilience to increased SST and nutrients based on an Indo-Pacific model exploring reef recovery. However, while the islands may benefit from an increased supply of warm water from the EAC, they are not immune to climate change impacts. The shallow lagoon reefs of LHI suffered a significant bleaching event in 2010 (Harrison *et al.* 2011), and is not known if prior bleaching events extended to the MCEs. The impacts of climate change on MCEs are not well understood as MCE research is an emerging field (Loya *et al.* 2016; Turner *et al.* 2017), but bleaching can occur on deep reefs when thermal tolerances are exceeded or from cold water intrusions (Menza *et al.* 2007; Smith *et al.* 2016). Higher latitude areas are also recognised as vulnerable to ocean warming due to lower aragonite saturations which may impede coral growth rates (Hooidonk *et al.* 2014; Kleypas *et al.* 1999a). Coral growth rates of some coral species at LHI appear to be reduced under warming conditions (Anderson *et al.* 2015), although growth rates in other high latitude locations have reported stable or increased growth for some species (Cooper *et al.* 2012; Ross *et al.* 2015).

To further address the potential of the LHI and BP shelves as refugia, further studies are required to determine species assemblages, genetic connectivity, reproduction modes and recruitment potential. Shallow coral species around LHI have been described as locally-sourced, brooding-dominated species which receive infrequent successful establishment of spawning coral species from tropical reefs to the north, including the Great Barrier Reef (Keith *et al.* 2015). Understanding the genetic connectivity of the MCEs around LHI and BP to the shallower reefs, and their connectivity to regional reef systems are critical areas for further investigation.

4.3 Implications for management

The sites with the greatest prevalence of corals on the southern BP shelf and eastern LHI shelf coincided with "no-take" fishing areas in the Lord Howe Island Marine Park. These "no take"zones in state waters connect to "no-take" zones in Commonwealth waters (Figure 2). Almost half (47%) of the BP shelf to the south is protected by "no-take" areas, and the southeast shelf around LHI is the only "no-take" mid-shelf area (16% of shelf area). While this study was not designed to test for marine park effects, the greater areas of coral cover appear to correspond to these protected zones. These communities are therefore well-protected by the existing marine park framework, together with its World Heritage listing, and benefit from the complementary management of the state and Commonwealth marine parks which offer contiguous "no-take" areas.

The characterisation of MCEs presented in this study contributes toward local knowledge of the diversity of habitats around the shelves, and fills the gap in coverage between shallow and deep coral habitats. Furthermore, these findings contribute toward global knowledge of the composition of MCEs at high latitudes, of which there have been few studies.

5. Conclusions

This study highlights the importance of mesophotic environments as coral habitat and the key role they can provide in discerning the impacts of a changing climate on patterns of benthic biodiversity. The key findings of this study are:

1. Mesophotic coral communities revealed to colonise the mid- and outer-shelf reefs around Lord Howe Island, with scleractinian corals occurring in greatest abundance on the eastern mid-shelf reef (maximum site average of 24% coral cover). The

occurrence of mesophotic corals on the Lord Howe Island shelf demonstrates the role of the submerged reefs as suitable coral habitat.

2. Greater overall abundance of scleractinian coral cover around the Balls Pyramid mesophotic shelf relative to the Lord Howe Island mesophotic shelf. While both shelves support live coral populations, the Balls Pyramid shelf appears to provide conditions more favourable for mesophotic coral growth.
3. Similar habitats documented across the mid- and outer-shelf reefs around Lord Howe Island and Balls Pyramid, with community composition differing between each shelf reef zone (inner, mid, outer reefs). The spatial variability of benthic communities suggests monitoring and management approaches should aim to capture representation of each shelf zone and region.
4. Prevalence of live coral populations which may persist as refugia under ongoing climate change, and extensive mesophotic reef substrate available for colonisation of new organisms.
5. Abundant corals in this mesophotic subtropical setting emphasises the need to survey mesophotic environments in subtropical and tropical locations to discern their biodiversity and potential importance for coral conservation.

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Conflicts of interest

The authors declare no conflicts of interest.

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