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Abstract

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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 km². 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 $6.7 \pm 12.2\%$, with the highest average transect cover of $19.4 \pm 14.3\%$ 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.

Keywords: Coral reefs; mesophotic reefs; subtropical reefs; Balls Pyramid; coral expansion; refugia

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 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; Muir et al., 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 ecosystems are increasing exponentially as technology advances (Baker et al., 2016; Loya et al., 2016). Few studies have focussed 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 (Figure 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 km² 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 abyssal plains down to >3,000 m depth (Figure 1b).

The waters surrounding Lord Howe Island and Balls Pyramid contain a unique mix of tropical and temperate marine benthic and demersal species with high endemism and biodiversity (Veron and Done, 1979; de Forges et al., 2000; Edgar et al., 2010). These unique attributes are recognised through World Heritage (UNESCO, 2015) and Marine Protected Area status (NSW Marine Parks Authority, 2010; Department of Environment, 2016), with 47% of the shelf area surrounding Balls Pyramid incorporating no-take reserves. The Balls Pyramid shelf is an area of active carbonate production (Kennedy et al., 2002; Linklater et al., 2015), with stony corals observed at mesophotic depths (Speare et al., 2004). An extensive fossil reef also surrounds Lord Howe Island (Woodroffe et al., 2010) where modern coral reef structures have established and flourish despite conditions of low winter SST (minimum

weekly SST < 18°C) and low aragonite saturation (Ω arag=3.28-3.35, Kleypas et al., 1999). At comparable latitudes on the Australian mainland coast around the Solitary Islands (SI), corals occur in similar conditions, though do not form an accretionary coral reef structure and instead form coral communities which colonise bedrock outcrops (Figure 1a, Veron et al., 1974). High energy wind and waves are experienced along the Lord Howe coastlines, with prevailing southeast swell directions in the summer and southern swells in the winter.

Figure 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).

2.2 Still image analysis

Underwater images of the seabed were collected using the Geoscience Australia Shallow Underwater Camera Model 2 towed video system, deployed from the Marine National Facility *R.V. Southern Surveyor* during a voyage in February 2013 (SS2013_v02). The system was equipped with downward-facing high-resolution stills camera (Nikon D700 SLR; images captured at 5 second intervals), continuous forward-facing standard-definition video, dual lights and Ultra Short Baseline (USBL) positioning. Cameras were operator controlled and towed approximately 1 m from the seafloor at 1–1.5 knots in 30–115 m water depth. The camera system was deployed along 15 transects (269–1,417 m in length) and collected 4,638 still images.

Images were corrected with Adobe Photoshop CS6 to enhance brightness. Timestamped still images were georeferenced with USBL positional information in HoudahGeo v4.0.1 and the image coordinates were imported as point shapefiles into ESRI ArcGIS v10.1. To account for spatial autocorrelation, the georeferenced image points were sub-set at 10 m intervals which equates to approximately 15-20 seconds of footage. Point locations were converted to line shapefiles and ET Geowizards v11.1 'Station Points' tool was used to create 10 m-spaced points along the transect. These station points were spatially joined to the image locations to create a sub-set of 1,381 images at approximately 10 m intervals (Figure 2).

Images were scored for benthic organisms and substrates using a 25 point grid overlay (34,525 points) in SeaGIS Transect Measure v2.31. Sessile benthic organisms were documented in this study, with the addition of sea urchins due to their influence on habitat (Valentine and Edgar, 2010). Substrate was recorded where no biota were visible. The organism/substrate beneath each point was recorded, with percent cover for each still image calculated as the number of points for each category divided by 25. Organism data were imported into PRIMER v6.1.15 and PERMANOVA+ v1.0.5 for subsequent analyses (Clarke, 1993; Anderson et al., 2008). Data were imported as abundance counts, square root transformed and a Bray-Curtis Similarity Resemblance Matrix was produced. Data were binned into depth intervals for further analysis of benthic cover trends.

Terms for the classification benthic organisms and substrates conform to CATAMI, which is a hierarchical, morphology-based classification system developed to standardise nomenclature of underwater image analyses (Althaus et al., 2013). CATAMI classes were modified into two levels describing organism/substrate 'type' (e.g. stony corals) and 'morphology' (e.g. stony corals-encrusting). Genus- and species-level classifications were additionally attributed for selected conspicuous organisms (see Appendix 1), including the coral genus *Acropora* which was included due to its recognisable morphology and relevance to regional studies (e.g. Muir et al., 2015a). A comprehensive classification of scleractinian coral species is currently being undertaken as part of a separate study. In this study 'stony corals' and 'scleractinian' coral terms are used interchangeably and refer to 'true' hard corals from the Order Scleractinia (Class Anthozoa, Phylum Cnidaria). Under the CATAMI framework, 'black and octocorals' are a combined class described by morphology (e.g. fan). A small number of organisms remained unidentified due to difficulties with interpretations from still imagery, and on a few occasions stony corals may have been misclassified as

octocorals when they had extended polyps. Mesophotic coral ecosystems (MCEs) were described as Upper (30-60 m depth) and Lower (>60 m depth) mesophotic zones to align with global descriptions of MCEs (Slattery et al., 2011; Loya et al., 2016). Definitions of terms used in this study are shown in Table 1.

Figure 2 Flow chart indicating processing steps for still image analyses, habitat classification and exploratory testing of relationships with geomorphology and environmental variables. Data were classified into three community levels: organism type, organism morphology and habitat class.

Table 1 Definition of terms used in this study.

Feature	Definition	Reference
<i>Reef</i>	A mass (or group) of rock(s) or other indurated material lying at or near the sea surface that may constitute a hazard to surface navigation	(IHO, 2008)
<i>Coral reef</i>	A tract of corals growing on a massive, wave resistant structure and associated sediments, substantially built by skeletons of successive generations of corals and other calcareous biota	(Done, 2011)
<i>Coral community</i>	Any benthic community with a hard coral component, whether reef-forming or otherwise	(Harriott and Banks, 2002)
<i>Mesophotic coral ecosystem</i>	Characterised by the presence of light-dependent corals and associated communities that are typically found at depths ranging from 30 to 40 m and extending to over 150 m in tropical and subtropical regions	(Hinderstein et al., 2010)
<i>Basin</i>	A depression, in the seafloor, more or less equidimensional in plan and of variable extent	(IHO, 2008)
<i>Channels</i>	Relatively elongated, low lying areas that dissect shallower seafloor	(Abbey et al., 2011)
<i>Depressions</i>	Closed-contour, low-lying areas surrounded on all sides by shallower seafloor	(Abbey et al., 2011)
<i>Platform</i>	Low-gradient, low-relief surface of extensive horizontal dimensions	(Beaman et al., 2008)
<i>Terrace(s)</i>	An isolated (or group of) relatively flat horizontal or gently inclined surface(s), sometimes long and narrow, which is(are) bound by a steeper ascending slope on one side and by a steeper descending slope on the opposite side	(IHO, 2008)
<i>Shelf break</i>	The line along which there is a marked increase of slope at the seaward margin of a continental (or island) shelf	(IHO, 2008)
<i>Slope</i>	The deepening sea floor out from the shelf-break to the upper limit of the continental rise, or the point where there is a general decrease in steepness	(IHO, 2008)

2.3 *Habitat classification*

Classified image data were aggregated into habitat categories using the Cluster tool in PRIMER, with a Similarity Profile Analysis (SIMPROF) test applied to determine the significance of the cluster separation. At 65% resemblance, 13 statistically significant groups and 6 other groups were defined and these were manually refined to 10 distinct habitat categories upon visual inspection of the still images assigned to each cluster. A one-way Similarity Percentage (SIMPER) was subsequently performed on the habitat categories in order to determine within-group similarity and the benthic cover that contributes most to variation between groups.

2.4 *Relationship to geomorphology*

A Permutational ANOVA (PERMANOVA) was performed in PRIMER to test whether community composition is significantly different across geomorphic features (Clarke, 1993; Anderson et al., 2008). The null hypothesis (H_0) stated no difference in benthic composition for different features. Geomorphic features were defined and mapped in a previous study by Linklater et al. (2015), with feature definitions shown in Table 1. Because tow transects crossed multiple geomorphic features, equal segments of 10 images (approximately 100 m in length) were sub-sampled within each feature to create 57 sites (Figure 3). For three sites (OR1, OR4 and OT5), only 7–8 images were extracted due to the narrow feature geometry. Each geomorphic feature was replicated in at least one other video transect location, except for the outer-shelf basin category which is represented by only one transect and was therefore excluded from the analysis. To ensure the unbalanced nature of the design did not affect the PERMANOVA outcome; analyses were repeated with a balanced design which tested a random selection of 3 sites per geomorphic feature.

Figure 3 Sub-samples extracted from tow transects (bold text) as equal segments over consistent geomorphic features around Balls Pyramid. Geomorphic features: mid-shelf basin (MB), mid-shelf inter-reef depressions (MRD); mid-shelf upper reef (MRU); mid-shelf lower reef (MRL); outer-shelf basins (OB); outer-shelf platform (OP); outer-shelf reef (OR) and outer-shelf terrace (OT).

PERMANOVA analyses were performed at three community levels: 1) organism/substrate morphology; 2) organism/substrate type; and 3) habitat class. Habitat classes were imported as presence/absence data and a Bray-Curtis Similarity Resemblance Matrices produced. ‘Geomorphology’ remained a fixed factor, with ‘Sites’ nested within the geomorphic features treated as a random variable. PERMANOVA analyses were performed as a Main test Type III (partial) sum of squares with an unrestricted permutation of raw data method and 9,999 permutations. A pair-wise PERMANOVA was additionally undertaken to test the significance of differences between each geomorphic feature. Principal Coordinate analysis (PCO) was performed on site-averaged data to graphically represent variation within and between the geomorphic features.

2.5 Relationship to environmental variables

The relationships between benthic community data and environmental parameters were evaluated to determine the factors driving the spatial distribution of biota. Terrain variables were derived from a 5 m resolution bathymetry model produced by Linklater et al. (2015), sourced primarily from multibeam echosounder data acquired using a Kongsberg EM300 30kHz system during the *R.V. Southern Surveyor* voyage (Table 2). Slope, rugosity, range, standard deviation, curvature and Bathymetric Position Index (BPI) were included as measures of seabed complexity. Euclidean distance from land and the shelf break were used as surrogates to capture trends that may relate to nearshore processes around the island, such as wave action, and processes occurring around the shelf break, such as upwelling. Aspect was included as a surrogate for exposure to long-term currents (e.g. Ierodiaconou et al., 2011). Aspect was transformed to a linear measure and mean linear direction was calculated using the methodology of Jammalamadaka and SenGupta (2001).

Acoustic backscatter data and current velocity data were acquired onboard the *R.V. Southern Surveyor*. Backscatter represents a relative measure of surface hardness based on sonar reflection intensity, and was collected using a Kongsberg EM300 30kHz system and processed using CMST GA-MB Toolbox (Gavrilov et al., 2005). Acoustic Doppler Current Profiler (ADCP) data were collected from a RDI os75. Current flow velocities within the subsamples ranged 0-0.35 m/s, and flows around the shelf were observed to be highly spatially variable with strong cross-shelf currents exceeding 0.4 m/s. ADCP functionality was reduced as the system is designed for deeper water and was operated in externally triggered mode due

to the concurrent operation of a TOPAS sub-bottom profiler. Depth-binned eastward (u) and northward (v) values were attributed to the closest classified image, matching the appropriate depth interval where the data were available. Preliminary interpretations of the values in each depth bin suggest the water column is well mixed.

Table 2 Terrain and oceanographic variables.

Variables	Tools and parameters	Cell size	Reference
<i>Depth</i>	Interpolation from multiple inputs	5 m	Linklater et al. (2015)
<i>Range</i>	Focal statistics: Rectangle 3x3	5 m	ArcGIS
<i>Standard dev.</i>	Focal statistics: Rectangle 3x3	5 m	ArcGIS
<i>Slope</i>	Spatial analyst	5 m	ArcGIS
<i>Curvature</i>	Spatial analyst: curvature, plan, profile	5 m	ArcGIS
<i>Eastness</i>	Spatial analyst; Sine transform	5 m	ArcGIS
<i>Northness</i>	Spatial analyst; Cosine transform	5 m	ArcGIS
<i>Distance to land</i>	Euclidean distance	5 m	ArcGIS
<i>Distance to shelf break</i>	Euclidean distance	5 m	ArcGIS
<i>Rugosity</i>	Benthic Terrain Modeler (BTM)	5 m	Wright et al. (2012)
<i>Bathymetric Position Index (BPI)</i>	BTM; Standardised; Annulus window: 5 m inner radii; 15, 25, 50, 100 and 250 m outer radii	5 m	Wright et al. (2012)
<i>Backscatter</i>	Processed with CMST GA-MB Toolbox	5 m	Gavrilov et al. 2005)
<i>ADCP (u, v)</i>	Closest discrete value attributed to site	-	-

Terrain ($n=17$) and oceanographic variables ($n=2$) were combined with depth, latitude and longitude coordinates to create a suite of 22 environmental variables. A Draftsmans Plot was generated in PRIMER to identify the variables which required transformation and which showed co-linearity. Range, slope, rugosity and standard deviation variables were Log-transformed and all data were normalised. Finescale analyses were performed using benthic data for individual images (10 m spaced points) within each sub-sampled site, and broadscale analyses were performed using averaged benthic data for each sub-sampled site. Mean linear direction values were used to replace ‘eastness’ and ‘northness’ for site-averaged analyses.

BIOENV and BVSTEP procedures within the BEST tool in PRIMER were used to explore the correlations of environmental variables to the benthic community data (Anderson et al., 2008). BIOENV analyses were first performed with no permutations to explore all possible combinations of variables in order to identify the stronger-performing variables. Co-linear datasets were then removed and analyses were repeated with a reduced selection of variables using the BVSTEP procedure with 9,999 permutations.

3 Results

3.1 Benthic cover and depth zonation

Benthic cover on Balls Pyramid shelf comprises a high proportion of soft-substrate sands and gravels and mixed tropical and temperate carbonate-producing benthic organisms, including a prevalence of stony corals. Stony coral cover was shown to be greatest on the upper mid-shelf fossil reef surface (Figure 4), where species of reef corals of the genera *Porites*, *Montipora*, *Turbinaria*, *Dipsastraea*, *Paragoniastrea*, *Echinophyllia*, *Leptastrea*, *Homophyllia*, *Oulophyllia*, *Goniopora*, *Leptoseris*, *Acanthastrea* and *Coscinaraea* were common (Figure 5a, Figure 6). *Acropora*, *Pocillopora* and *Cycloseris* were also occasionally observed (e.g. Figure 5b). Average scleractinian coral cover across all transects was $6.7 \pm 12.2\%$, with cover ranging 0-19.4%. The highest recording of stony coral cover per individual still was 84% in 30 m depth on the southwest upper mid-shelf reef (15CAM09) on the transect which also had the highest average coral cover of $19.4 \pm 14.3\%$ (Table 3).

Ten distinct habitats were defined among the diverse mesophotic coral ecosystems observed (Figure 6). Sites with high stony coral cover separated into a distinct cluster representing stony coral-dominated reef habitat, which had a within-group similarity measure of 79.3% (Figure 6a, Appendix 2). The maximum water depth of stony corals recorded from point-count analysis was 86 m, at which they adopted the encrusting morphology most commonly observed for scleractinian corals in the region (39.5% of all corals recorded were encrusting, Figure 7). The deepest recording of *Acropora* sp. occurred at 48 m depth (Figure 5b). As the sub-sampling approach and point-count classification may not capture the deepest corals, the images excluded during sub-sampling were examined for scleractinian coral occurrences beyond 86 m depth, with the deepest record of 94 m observed on the southern outer-shelf terrace (12CAM06, Figure 4).

Figure 4 Hillshaded bathymetry of the Balls Pyramid shelf, showing percent cover of stony coral communities per still image along tow-video transects. Depth contours displayed at 200 m intervals beyond 100 m depth.

Table 3 Summary statistics for tow-video data collected on Balls Pyramid shelf.

Transect	No. stills	Depth range (m)	Avg. stony coral cover (%) $\pm$ std dev	Max. stony coral cover (%)
07CAM02	107	36 - 50	3.8 ± 7.6	36
08CAM03	98	37 - 43	0.2 ± 1.7	16
10CAM04	80	32 - 35	15.4 ± 14.2	48
11CAM05	138	43 - 53	2.1 ± 6.7	52
12CAM06	80	59 - 115	1.1 ± 6.0	52
13CAM07	27	38 - 40	14.4 ± 19.3	56
14CAM08	97	31 - 38	10.1 ± 13.0	72
15CAM09	110	30 - 41	19.4 ± 14.3	84
16CAM10	58	40 - 44	2.3 ± 6.7	40
17CAM11	77	53 - 72	0.0 ± 0.0	0
32CAM12	140	34 - 39	13.9 ± 14.2	60
33CAM13	118	42 - 68	2.8 ± 6.5	48
34CAM14	83	35 - 48	6.7 ± 12.4	76
35CAM15	78	43 - 49	9.9 ± 16.8	64
36CAM16	90	51 - 75	0.4 ± 1.7	12

Figure 5 a) Mesophotic coral assemblage at 39 m depth (13CAM07) with genera: 1-6 *Paragoniastrea* spp.; 7-8 *Turbinaria* sp.; 9-10 *Dipsastraea* sp.; 11 *Echinophyllia* sp.; 12 *Leptastrea* sp.; 13 *Goniopora* sp.; 14-15 *Homophyllia* sp.; and 16 *Oulophyllia* sp.; and b) Tabulate *Acropora* sp. at 48 m depth (35CAM15).

Figure 6 Representative images from habitat classification: a) Stony coral-dominated; encrusting and submassive scleractinian corals (e.g. *Dipsastraea* sp., *Oulophyllia* sp., *Turbinaria* sp., *Porites* sp.) with *Halimeda* sp. and filamentous red algae, mid-shelf lower reef, 37 m depth; b) Black coral and octocoral-dominated; fans with encrusting scleractinian corals, encrusting green and calcareous red algae, mid-shelf upper reef, 34 m depth; c) Mixed biota – Higher cover; encrusting and submassive scleractinian corals (e.g. *Montipora* sp., *Paragoniastrea* sp., *Echinophyllia* sp., *Coscinaraea* sp., *Acanthastrea* sp.), encrusting algae and branching octocorals (*Dendronephthya* sp.), mid-shelf upper reef, 39 m depth; d) Mixed biota – Lower cover; encrusting scleractinian corals (e.g. *Montipora* sp., *Leptoseris* sp., *Homophyllia* sp.) with urchins (*Prionocidaris* sp.), encrusting and filamentous algae and bivalve beds, mid-shelf lower reef, 42 m depth; e) Other coloniser-dominated; Sea anemones (*Entacmaea quadricolor* and *Heteractis crispa*) and urchins (*Prionocidaris* sp.) on encrusting coralline algae with a sea star, outer-shelf reef, 46 m depth; f) Algal-dominated; laminate brown algae, encrusting coralline algae and encrusting sponge, mid-shelf lower reef, 46 m depth; g) Sparse algae with sand/pebbles/reef; sand inundated reef and cobbles with sparse branching, laminate and filamentous algae, with bivalve beds, mid-shelf basins and channels, 47 m depth; h) Rhodolith beds; rhodolith beds and sands, sparse algae, outer-shelf terraces, 75 m depth; i) Pebble-dominated; pebble stones and gravels with shells, urchin spines, rhodoliths and sands, outer-shelf terraces, 64 m depth; j) Sand-dominated; sand waves, mid-shelf basins and channels, 43 m depth.

Diverse octocorals and black corals were observed across all depths, with whips occupying the deeper shelf >79 m (Figure 7). Several species of branching octocoral genus *Dendronephthya* were frequently observed, with massive soft corals also common, including the occasional genus *Lobophytum*. Black coral and octocoral-dominated habitats (Figure 6b), which encompassed a broad range of morphologies within the ‘black and octocoral’ organism class, exhibited the lowest within-group similarity (65.8%).

Habitats described as ‘mixed-biota’ were defined where no organism/substrate dominated composition but instead contained a diverse array of corals, sponges and algae. These mixed habitats were differentiated into classes which contained higher (Figure 6c) and lower (Figure 6d) relative cover of benthic organisms. Sea anemones and urchins were common in the habitats dominated by ‘other colonisers’ (Figure 6e) although their contributions to within-group similarity were only minor at 1.6% and 0.3%, respectively. Sea anemone species *Entacmaea quadricolor* and *Heteractis crispa* were observed, and *Prionocidaris* spp. were the most prevalent urchins, with *Diadema* spp. and *Tripneustes gratilla* occurring to a lesser extent.

Calcareous red algae were the most prevalent algal taxa (61% of all macroalgae recordings). Encrusting coralline algae were ubiquitous, as were non-calcareous encrusting red algae of the genus *Peyssonnelia*. Similarly, for green algal species, encrusting algae were the most common morphology observed, with *Caulerpa peltata* and other *Caulerpa* species prevalent, together with *Codium* spp. and calcareous genera *Halimeda*. Around the deeper shelf, branching brown algae, such as *Dictyota* spp., and laminate *Padina* sp. were more commonly observed, with sparse fleshy red algae which extended down to 69 m depth, with brown and green algae down to 81 m depth. Macroalgae were a high contributor (within 90% of cumulative total) to within-group similarity for most habitats and characterised the algal-dominated reef habitats (Figure 6f), as well as sand inundated reef and pebble substrates (Figure 6g).

Soft substrates were widespread and comprised entirely calcareous material with no volcanic sediment observed. Biogenic substrates formed a distinct habitat including rhodolith beds, with bivalve beds occasionally present (Figure 6h). Pebbles and carbonate sands were the highest contributors to within-group similarity for most of the defined habitats, and formed distinct habitats (Figure 6i and Figure 6j, respectively), with sand-dominated habitats exhibiting the highest within-group similarity (87.2%).

Figure 7 Box plots for stony corals, black corals and octocorals, soft substrates and macroalgae. Upper and lower box boundaries represent 25th and 75th percentile; horizontal line represents median; asterisk represents arithmetic mean; and bars represent minimum and maximum values. Stony coral morphologies with low abundance not shown, including: digitate ($n=5$), massive ($n=12$) and tabulate ($n=27$).

3.1.1 Upper mesophotic zone (30–60 m depth)

The upper mesophotic zone (30–60 m depth) contained 98.7% of all stony corals recorded, with the majority occurring in 30–40 m depth (76.2%). The 30–40 m depth interval contained the greatest proportion of visible benthic biota (63.0% of benthic cover), lowest soft sediment cover (34.0%) and highest proportion of stony corals (13.3%, Figure 8). Macroalgae cover remained high across all depths, with greatest occurrence at 30–40 m depth (42.4%). Sponges reached a maximum proportion of 4.5% of benthic cover at 30–40 m depth, and other colonisers (including sea anemones, bryozoans, ascidians and unidentifiable organisms) peaked at 1.3% of benthic cover at 50–60 m depth.

3.1.2 Lower mesophotic zone (60–115 m depth)

This zone was characterised by a greater proportion of soft substrates, black corals and octocorals, which occurred in greatest abundance at >80 m depth. Stony corals represented a smaller proportion of benthic cover in the lower mesophotic zone, comprising <3% of benthic cover in the 60-115 m depth range, with most still images exhibiting <10% stony coral cover. Exceptions to this occurred at 63 m depth on the southern outer-shelf where 52% stony coral cover was recorded (12CAM06). Additional exceptions of 20% and 12% cover were recorded at 63 m and 67 m depth, respectively (33CAM13). Biogenic substrates, which include rhodolith and bivalve beds, were more common at greater depths and reached a peak in composition at 70-80 m depth where they represented 18% of benthic cover.

Figure 8 Percentage composition of benthic cover by depth interval.

3.2 *Relationship to geomorphology*

Analyses of the tow-camera data sub-sampled by geomorphic feature provide a more detailed comparison of the benthic composition across shelf features (Figure 3, Appendix 3). Principal coordinates analysis showed the mid-shelf upper reef as the geomorphic feature most associated with higher stony coral cover and also highlights the role of the outer-shelf reefs in supporting comparable benthic cover to the upper mid-shelf reef at some sites (Figure 9). The mid-shelf basins showed the strongest association with sands and the outer-shelf terraces were most strongly associated with pebbles and biogenic substrates. Variability in benthic composition was most evident for basin and inter-reef depression features which ranged from soft sediment accumulations to low profile colonised reef.

PERMANOVA analyses showed that benthic composition varied significantly across geomorphic features at all community levels (Table 4). The PERMANOVA analyses performed with the random, equal sample showed that the unbalanced nature of the design did not affect the results, as significant relationships were achieved with both balanced and unbalanced designs. The ‘Geomorphology’ factor had larger Pseudo-F statistics than ‘Site’ factor in the unbalanced design, whereas the ‘Site’ factor had larger Pseudo-F statistics and higher significance-levels in the balanced design, which indicates more variation occurs between sites (from within geomorphic features) than between features. Pairwise PERMANOVA analysis comparing the benthic composition between features showed all features were statistically unique, with the exception of the outer-shelf reefs, mid-shelf lower reef and mid-shelf inter-reef depressions which were not significantly different from one another (Table 5).

Figure 9 Principal coordinates analyses (PCO): a) plotted by geomorphic feature; and b) plotted as a bubble plot of average stony coral count per site, overlain with vectors of benthic composition displayed with >0.6 correlation.

Table 4 PERMANOVA results for benthic community data at three levels: organism/substrate morphology; organism/substrate type; and habitat class.

Selection	Factor	Community level	Pseudo-F	p-value
<i>All sites</i>	<i>Geomorphology</i>	Morphology	10.98	0.0001
		Type	12.30	0.0001
		Habitat	6.73	0.0001
	<i>Site(Nested)</i>	Morphology	6.70	0.0001
		Type	6.59	0.0001
		Habitat	3.71	0.0001
<i>Random 3 sites</i>	<i>Geomorphology</i>	Morphology	6.18	0.0002
		Type	4.49	0.0001
		Habitat	1.75	0.0283
	<i>Site(Nested)</i>	Morphology	6.35	0.0001
		Type	7.98	0.0001
		Habitat	5.88	0.0001

Table 5 PERMANOVA pairwise analyses for organism/substrate type.

Geomorph Feature	MS-R-U	MS-R-L	MS-D	MS-BC	OS-R	OS-P	OS-T
MS-R-U	-						
MS-R-L	***	-					
MS-D	**	<i>ns</i>	-				
MS-BC	***	**	**	-			
OS-R	*	<i>ns</i>	<i>ns</i>	**	-		
OS-P	***	**	*	*	***	-	
OS-T	***	***	**	**	**	**	-

*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; *ns* = not significant

3.3 Relationship to environmental variables

Relationships to environmental variables were explored with BIOENV and BVSTEP analyses using finescale (individual classified points) and broadscale (site-averaged data) approaches (Table 6). Depth was identified as the strongest performing variable and was selected as the top variable for all community levels and scales. For broadscale data, backscatter was selected as the secondary explanatory variable for all community levels, with the highest correlation shown for organism/substrate type data ($Rho=4.87$, $p=0.0001$), followed by morphology-level data ($Rho=4.65$, $p=0.0001$). The weakest correlation occurred for habitats at the fine scale ($Rho=0.179$), although the relationship remained significant ($p=0.0001$), with depth and distance from land identified as the explanatory variables.

Table 6 BVSTEP results for finescale benthic data (individual image points) and broadscale data (site-averaged data).

Scale	Community level	Variables	Rho (correlation)	p-value
Finescale	Morphology	Depth	0.257	0.0001
	Type	Depth	0.299	0.0001
	Habitat	Depth, distance from land	0.179	0.0001
Broadscale	Morphology	Depth, backscatter	0.465	0.0001
	Type	Depth, backscatter	0.487	0.0001
	Habitat	Depth, backscatter	0.375	0.0001

4 Discussion

4.1 Benthic cover and depth zonation

The mesophotic shelf surrounding Balls Pyramid supports a complex mosaic of benthic habitats which demonstrates high habitat diversity. The scleractinian coral cover observed on the shelf is less than observed for the shallow reefs and lagoon around Lord Howe Island, although the maximum cover of 84% for an individual still, at 30 m depth, is high given its southerly location and mesophotic depths. The highest average cover of $19.4 \pm 14.3\%$ occurred on the southwestern mid shelf at $31^{\circ}46'S$ latitude, compared to the highest average coral cover around Lord Howe Island of 45.6% and 50.6% recorded at sites within the Lord Howe Island lagoon (Harriott et al., 1995), with Veron and Done (1979) estimating up to 80% cover. At comparable latitudes on the shallow high latitude reefs at $32^{\circ}S$ in Western Australia, Thomson and Frisch (2010) reported 72.5% maximum coral cover.

Scleractinian corals were found to extend to 94 m water depth, which is beyond the depths of 70 m recorded for high latitude reefs of Bermuda ($32^{\circ}N$, Venn et al., 2009) and 40-50 m for atolls in the northern Hawaiian Archipelago ($27^{\circ}50'N$), which extend deeper down to 153 m in the lower latitudes of the Archipelago (Kahng and Maragos, 2006; Rooney et al., 2010). On the shelf-edge reefs of the Great Barrier Reef (GBR) in tropical Australia, zooxanthellate corals have been observed at 75-100 m (Bridge et al., 2011; Bridge et al., 2012), with maximum depths of 125 m (Englebert et al., 2014). The deepest *Acropora* sp. recorded on the GBR was 73 m depth at a site ~2,000 km north of Balls Pyramid (Muir et al., 2015a). The maximum depth for *Acropora* sp. around Balls Pyramid occurred at 48 m, which is more akin to depth distributions observed in tropical settings than the neighbouring subtropical reefs along mainland Australia. In a global assessment of *Acropora* and *Isopora* depth distributions, Muir et al. (2015b) found trends of shallowing depth with increasing

latitude, and this deep occurrence of *Acropora* at Balls Pyramid forms an outlier to existing observations. These findings lend support to the emerging narrative that coral assemblages extend well beyond the perceived ‘optimal’ depths and geographical ranges, therefore emphasising the importance of exploring mesophotic communities in subtropical regions.

Cool-water influxes and reduced light penetration are key factors that restrict the maximum depth limits of MCEs (Bongaerts et al., 2010; Rooney et al., 2010; Bridge et al., 2011). Light availability is not considered to impede coral growth at Balls Pyramid as the deep recordings of scleractinian coral and green algae in >80 m depth provide evidence of photosynthetic processes, thus demonstrating high water clarity. As 91% of the shelf area occurs at depths of 30-90 m (Linklater et al., 2015), there is potentially sufficient light available for coral growth across the majority of the shelf. However, coral growth is likely limited by the cooler waters delivered to Balls Pyramid from the northwards movement of the Tasman Front. In particular, corals recorded on the shelf edge of Balls Pyramid would be exposed to episodic, cooler upwelling currents that rise from depths of >3,500 m (Middleton et al., 2006; Kennedy et al., 2011). The maximum depths of organisms reported in this study may be underestimated due to the image sub-sampling and point-count method of classification, and therefore organisms may occur deeper than reported.

4.2 Relationship to geomorphology and environmental variables

Despite the high proportion of scleractinian corals observed on the mid- and outer-shelf reefs, the coral communities observed in this study do not appear to be forming a complex, vertical reef framework and are therefore considered to be communities that form a veneer over fossilised reef rather than a true ‘coral reef’. However, given the abundance of scleractinian corals observed across the shelf, there may be locations where a modern coral reef structure is forming but was not observed during our sampling effort.

The occurrence of modern coral growth on fossil reef structures at Balls Pyramid highlights the role of antecedent topography in providing substrate for coral colonisation. Fossil reef features form an elevated topography in relation to the surrounding basin and platform features, which likely benefits corals by providing greater access to light and reduced sedimentation. The association of modern coral with the upper mid-shelf reef suggests these features hold the greatest potential as refugia or expansion substrate. The outer-shelf reefs also have the potential as suitable coral habitat as they exhibit comparable

composition to the mid-shelf reefs at selected sites. The important role of geomorphology in influencing benthic community distribution supports previous studies which have linked geomorphology to infaunal (Brooke et al., 2012; Anderson et al., 2013) and epifaunal (Przeslawski et al., 2011) assemblages on the Lord Howe Island shelf and Lord Howe Rise. The higher significance and Pseudo-F statistics for the 'Site' factor within the randomised sub-sample indicates there is inherent variation within the geomorphic features at different sites around the shelf. Therefore, geomorphology is considered to structure broad patterns in community distributions but does not account for the diversity within features.

Depth and acoustic backscatter showed the highest correlations with benthic data at the broadscale, site-averaged level, with weaker correlations demonstrated for the finescale imagery data. The selection of backscatter as a top explanatory variable likely relates to the proportion of soft-substrates within the samples, as sands and pebbles were identified in PCO analysis as the key components differentiating site composition. Due to its mid-ocean and tropical-temperate position, currents at this transition zone are highly complex and variable, both spatially and temporally. The ADCP data included in our analysis represents the best available data collected from the survey, however it only captures a limited snapshot of a complex hydrodynamic environment. Neither ADCP data nor aspect variables (surrogates for longer-term current patterns) were identified as explanatory variables in BVSTEP analyses, however hydrodynamic regime has been previously identified as a key driver structuring shallow coral communities around Lord Howe Island, where a fringing reef has formed around a sheltered lagoon that contains patch reefs (Veron and Done, 1979; Edgar et al., 2010). Unlike Lord Howe Island, sheltered environments do not occur in the shallows around the Balls Pyramid pinnacle and it instead remains highly exposed.

4.3 Implications and limitations for refuge capacity

The presence of abundant scleractinian corals on the Balls Pyramid shelf contributes evidence in support of the hypothesis that the region may act as a refuge habitat for extant coral communities and may support potentially larger coral populations. Should conditions remain favourable, the extant corals could persist in the climate refugia and maintain a genetic pool for future larval replenishment. The information presented in this study highlights the need for detailed investigations into the composition of mesophotic coral

species assemblages and their relationship to shallow-water assemblages in order to further assess refugia potential.

The potential benefits of warming sea-surface temperatures and high water clarity may, however, be countered by a number of factors which may limit refuge potential. Mesophotic and high latitude reefs remain vulnerable to bleaching from both sustained warm-water events and cold-water intrusions (Menza et al., 2007; Abdo et al., 2012). Shallow reefs around Lord Howe Island have suffered extensive bleaching when unseasonably high temperatures occurred in the lagoon (Harrison et al., 2011), and it is unknown whether deeper reefs were affected by this event. Increased acidification (Couce et al., 2013) and high macroalgal cover (Hoey et al., 2011) may also inhibit coral growth at this higher latitude location. Some coral species at Lord Howe Island have shown declines in accretion (Anderson et al., 2015), however contrasting trends have been observed for other high latitude areas (Cooper et al., 2012; Ross et al., 2015). High rates of *in-situ* sedimentation may impede coral development, particularly with prevalent flat morphologies of corals which are susceptible to smothering (Stoddart, 1969). Competition with macroalgae has also been identified as a potential limiter to refugia capacity in this region (Hoey et al., 2011). The co-occurrence of coral and algae is a unique trait of the region (Edgar et al., 2010) and the prevalence of algae is not believed to hinder coral growth. However, competition with macroalage may become of greater risk if conditions, such as sustained reccurent bleaching, compromise coral growth.

Refuge capacity may also be limited by low success rates of larval recruitment, which has been documented for the shallow corals around Lord Howe Island (Hoey et al., 2011). Warmer temperatures have been linked to a reduction in recruitment success along the southernmost reefs of the African coast (Schleyer et al., 2008). Genetic connectivity of shallow corals between Lord Howe Island and the GBR, which lies over 1,000 km to the northwest, has been shown to be limited given the region's isolation (Ayre and Hughes, 2004), though long-distance migration occurs to Lord Howe Island with enough frequency to maintain genetic diversity at evolutionary time scales (Noreen et al., 2009). It is critical to determine the pelagic larval duration and mortality rates for the species of corals which occur around the mesophotic shelf, and to understand how life history traits interact with ocean currents to limit or enhance dispersal. Understanding the success rates as well as the source, exchange and survival of coral larvae between the upper and lower MCEs and surrounding

reef systems is essential to further assess the role of deep reefs as refugia (Bongaerts et al., 2010; Holstein et al., 2016).

The assessment of refugia potential by this study is limited to evidence of the occurrence of modern corals which may remain as extant populations under future climate scenarios, and the availability of suitable substrates that may support new colonisation. Detailed assessments of the mesophotic coral assemblages are required to understand connectivity of corals in the region and better assess refugia potential. Information on larval life histories and dispersal could be coupled with oceanographic models and climate scenarios to predict potential shifts in species distributions and identify vulnerabilities of the shelf to likely impacts of future changes in climate.

4.4 Implications for management

Under rapidly shifting climatic conditions, an increased focus is needed on the conservation management of higher latitude and deeper reef systems (Hinderstein et al., 2010; Beger et al., 2013; Makino et al., 2014). Given their potential to act as refugia, there is a pressing need to better understand the characteristics and potential role of these systems under changing global environmental pressures and assess their resilience to these changes (Lesser et al., 2009; Slattery et al., 2011). Protecting potential refuges from anthropogenic impacts through the provision of no-take areas has been identified as an urgent priority in order to sustain reef ecosystems (Beger et al., 2013). Fortunately, the high level of conservation afforded to the Balls Pyramid region is ideal for long-term monitoring of the impact of environmental change on the composition of MCEs, latitudinally and with depth. Results from this study provide robust baseline data, and it is recommended that repeated surveys be undertaken to monitor any changes in community composition and scleractinian coral cover on the submerged features around Balls Pyramid.

5 Conclusions

The Balls Pyramid shelf is characterised by diverse reef and soft substrate habitats, colonised by mixed tropical- and temperate-associated organisms with extensive, healthy scleractinian coral communities. Areas of high scleractinian coral cover were recorded at several sites, with the highest average coral cover of $19.4 \pm 14.3\%$ recorded per transect

(average cover $6.7 \pm 12.2\%$ across all transects) and a maximum cover of 84% recorded per still. Corals were found to extend to depths to as great as 94 m, demonstrating high water clarity. Statistically significant correlations were found between benthic communities and geomorphology and environmental variables. Depth appeared as the strongest environmental driver explaining benthic community distributions, with the strongest correlation evident for 'broadscale' (site-averaged) data classified at the organism/substrate 'type' community level. Benthic data were shown to be highly statistically different across geomorphic features at all community levels. Our results point to the important role of mesophotic ecosystems on fossil reef structures for sustaining extant coral populations. Moreover, their provision of substrate that could potentially provide refugia for scleractinian coral communities into the future is highlighted and further research into refugia potential is strongly encouraged.

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Appendix 1: Benthic categories (modified CATAMI nomenclature)

Organism Type	Morphology	Genus/Species	Code
<i>Rock/Boulder</i>			HD_RB_1
<i>Cobbles</i>			HD_CB_1
<i>Biogenic substrate</i>	Bivalve beds		SO_B_TOT_1
	Rhodoliths		SO_B_B_2 SO_B_R_2
<i>Pebble/gravel</i>	No bedforms (waves/ripples)		SO_P_TOT_1
	Bedforms		SO_P_NW_2 SO_P_W_2
<i>Sand/mud</i>	Sand veneer		SO_S_TOT_1
	No bedforms (waves/ripples)		SO_S_V_2
	Bedforms		SO_S_NW_2 SO_S_W_2
<i>Macroalgae</i>	Calcareous - Branching		M_TOT_1
	Calcareous - Encrusting		M_B_C_2 M_E_C_2
	Fleshy – Branching	<i>Halimeda</i>	M_B_F_2
		<i>Dictyota</i>	
		<i>Codium</i>	
		<i>Codium spongiosum</i>	
	Fleshy – Encrusting		M_E_F_2
		<i>Caulerpa</i>	
		<i>Caulerpa peltata</i>	
		<i>Peyssonnelia</i>	
<i>Black & Octocorals</i>			M_Oth_F_2
		<i>Padina</i>	
	Branching - Fleshy		BO_TOT_1 BO_B_F_2
	Branching - Non-Fleshy	<i>Dendronephthya</i>	BO_B_NF
	Branching - Other		BO_Ot_2
	Encrusting		BO_E_2
	Fan		BO_F_2
	Massive		BO_M_2
	Organ pipe coral	<i>Lobophytum</i>	BO_Or_2
	Whip		BO_W_2
<i>Stony corals</i>	Branching		STC_TOT_1 STC_B_2
		<i>Acropora</i>	
	Digitate		STC_D_2
	Encrusting		STC_En_2
	Foliose		STC_F_2
	Massive		STC_M_2
	Solitary		STC_So_2
	Sub-massive		STC_SM_2
	Tabulate		STC_T_2
		<i>Acropora</i>	
<i>Sponges</i>			S_TOT_1
	Crust		S_C_2
	Erect forms		S_E_2
	Hollow forms		S_H_2
	Massive forms		S_M_2

Organism Type	Morphology	Genus/Species	Code
<i>Hydrocorals</i>			OC_Hyco_1
<i>Hydroids</i>			OC_Hydr_2
<i>True anemones</i>			OC_Anem_2
<i>Tube anemones</i>			OC_Tube_2
<i>Ascidians</i>			OC_Asc_2
		<i>Lissoclinum</i>	
<i>Bryozoans</i>			OC_Bry_2
<i>Feather stars</i>			OC_Fea_2
<i>Sea urchins</i>			OC_Urc_2
		<i>Diadema</i>	
		<i>Prionocidaris</i>	
		<i>Tripneustes gratilla</i>	
<i>Unknown</i>			OC_Unk_2

Appendix 2: SIMPER analyses results

Habitat classes with number of stills (*n*) per class, SIMPER results of average similarity (Sim%), top organism/substrate contributing to variation (up to $\geq 90\%$), cumulative contribution (Cumul %) for each habitat class.

<i>Habitat</i>	<i>n</i>	<i>Sim %</i>	<i>SIMPER</i>	
			<i>Contributor</i> ^a	<i>Cumul %</i>
<i>Stony coral dominated</i>	4	79.3	Stony corals	65.5
			Macroalgae	100
<i>Black and octocoral dominated</i>	18	65.8	Macroalgae	34.7
			Black & Octo	61.1
			Sand	76.3
			Stony corals	91.1
<i>Algal dominated</i>	117	72.9	Macroalgae	58.8
			Sand	92.8
<i>Mixed biota – Higher cover</i>	390	74.6	Macroalgae	42.9
			Sand	67.3
			Stony corals	90.3
<i>Mixed biota – Lower cover</i>	117	74.9	Macroalgae	39.2
			Sand	69.2
			Biogenic	89.5
			Stony corals	95.5
<i>Other coloniser-dominated</i>	71	71.9	Macroalgae	44.8
			Sand	70.6
			Pebbles	92.0
<i>Sparse algae with sand/pebbles/reef</i>	263	76.6	Sand	51.0
			Macroalgae	80.1
			Pebbles	98.6
<i>Rhodolith beds</i>	93	70.5	Pebbles	40.2
			Biogenic	68.9
			Macroalgae	93.8
<i>Pebble dominated</i>	219	72.4	Pebbles	63.5
			Sand	87.3
			Macroalgae	97.2
<i>Sand dominated</i>	89	87.2	Sand	86.3
			Pebbles	99.7

^a Included contributor's $\geq 90\%$ cumulative total

Appendix 3: Benthic composition of sub-sampled sites

Average abundance counts within sub-samples from each geomorphic feature around the Balls Pyramid shelf. Black and octocorals abbreviated to “Bl. & Octo” in table. Geomorphic features: mid-shelf basin (MB), mid-shelf inter-reef depressions (MRD); mid-shelf upper reef (MRU); mid-shelf lower reef (MRL); outer-shelf basins (OB); outer-shelf platform (OP); outer-shelf reef (OR) and outer-shelf terrace (OT).

Sites	Rock	Cobble	Pebble	Biogenic	Sand	Macro-algae	Stony coral	Bl. & Octo	Sponge	Other
MB-1	0.0	0.6	0.6	0.0	20.9	2.9	0.0	0.0	0.0	0.0
MB-2	0.0	0.1	1.3	0.0	23.6	0.0	0.0	0.0	0.0	0.0
MB-3	0.0	0.4	9.7	0.0	14.8	0.1	0.0	0.0	0.0	0.0
MB-4	0.0	0.1	4.1	0.0	20.4	0.4	0.0	0.0	0.0	0.0
MB-5	2.2	1.8	0.2	1.2	9.6	9.3	0.2	0.0	0.1	0.4
MB-6	0.1	1.2	2.6	1.5	11.2	8.3	0.1	0.0	0.0	0.0
MB-7	0.0	0.1	15.8	0.0	9.0	0.1	0.0	0.0	0.0	0.0
MRD-1	0.6	0.1	10.1	5.9	3.6	4.0	0.3	0.0	0.4	0.0
MRD-2	0.8	0.3	0.2	0.0	3.2	15.0	3.1	0.2	2.2	0.0
MRD-3	0.2	1.3	2.5	0.0	8.2	10.9	0.9	0.0	0.9	0.1
MRD-4	0.0	0.9	8.5	6.5	5.2	3.9	0.0	0.0	0.0	0.0
MRD-5	0.2	0.1	6.1	2.6	2.5	9.9	2.5	0.3	0.4	0.4
MRD-6	0.0	0.4	2.1	0.8	6.9	7.9	2.6	3.0	1.0	0.3
MRD-7	0.1	0.3	1.1	1.6	5.0	12.0	3.0	0.5	1.2	0.2
MRD-8	0.9	0.8	3.6	0.0	8.1	7.0	2.4	0.9	0.7	0.6
MRL-1	0.0	0.0	3.1	3.9	5.8	11.2	0.7	0.1	0.2	0.0
MRL-2	0.0	0.5	4.5	0.2	12.7	5.6	0.1	0.0	1.3	0.1
MRL-3	0.8	0.2	1.5	0.0	3.7	15.8	1.7	0.3	0.9	0.1
MRL-4	0.8	0.7	2.8	0.0	11.2	7.7	0.4	0.3	1.0	0.1
MRL-5	0.6	0.7	3.2	0.9	10.9	7.5	0.2	0.4	0.2	0.4
MRL-6	0.1	0.0	0.2	0.0	7.0	14.1	1.2	0.0	2.0	0.4
MRL-7	0.2	0.1	4.5	0.0	9.1	10.5	0.2	0.1	0.1	0.2
MRL-8	0.2	0.2	7.1	0.0	8.9	7.0	0.5	0.0	0.9	0.2
MRL-9	0.1	0.1	1.4	0.5	8.0	9.8	2.6	0.3	1.9	0.3
MRU-1	0.2	0.0	0.0	0.0	5.6	12.5	5.1	0.1	1.2	0.3
MRU-10	0.2	0.0	1.2	2.2	5.0	11.2	4.1	0.5	0.6	0.0
MRU-11	0.0	0.3	1.7	1.7	4.4	11.3	4.3	0.3	0.9	0.1
MRU-12	0.0	0.0	0.5	0.6	5.4	9.1	6.6	0.7	2.1	0.0
MRU-13	2.4	0.0	0.0	1.2	3.9	10.0	2.6	2.4	0.4	2.1
MRU-14	0.1	0.0	0.1	1.4	9.4	9.2	2.1	1.6	0.8	0.3
MRU-15	0.0	0.0	0.2	0.7	6.5	9.7	5.8	0.7	1.3	0.1
MRU-16	0.1	0.0	8.3	0.4	11.5	4.6	0.0	0.0	0.1	0.0
MRU-2	0.2	0.0	0.1	0.0	3.1	13.6	7.1	0.1	0.8	0.0
MRU-3	0.1	0.0	0.0	0.0	3.5	13.8	5.6	0.2	1.7	0.1
MRU-4	0.0	0.0	0.0	0.0	4.5	13.5	4.9	0.3	1.7	0.1
MRU-5	0.1	0.0	0.1	0.0	3.9	12.3	6.9	0.0	1.4	0.3
MRU-6	0.5	0.5	0.0	0.0	2.5	15.2	3.4	1.0	1.7	0.2
MRU-7	0.7	0.3	0.6	0.0	4.4	14.7	1.9	0.4	1.5	0.5
MRU-8	0.3	0.2	0.3	0.0	4.6	13.4	4.9	0.1	1.1	0.1
MRU-9	0.0	1.2	4.8	3.3	3.9	7.9	2.7	0.9	0.2	0.1
OB-1	0.6	0.0	13.0	0.0	8.4	2.5	0.0	0.0	0.1	0.4
OP-1	0.0	0.0	9.3	0.1	7.6	7.8	0.0	0.0	0.2	0.0
OP-2	0.0	0.0	6.3	0.0	6.7	10.7	0.0	0.0	0.0	1.3
OP-3	0.0	0.0	10.2	0.5	9.6	4.2	0.0	0.1	0.0	0.4
OP-4	0.0	0.0	4.4	0.1	12.6	7.3	0.1	0.1	0.2	0.2
OP-5	0.0	0.0	13.8	1.6	6.0	3.6	0.0	0.0	0.0	0.0

Sites (cont'd)	Rock	Cobble	Pebble	Biogenic	Sand	Macro- algae	Stony coral	Bl. & Octo	Sponge	Other
OP-6	0.2	0.0	6.5	0.2	8.5	7.9	0.5	0.0	0.2	1.0
OP-7	0.0	0.1	7.1	2.4	7.0	7.8	0.1	0.0	0.0	0.5
OR-1	0.0	0.0	5.9	0.0	7.6	11.0	0.0	0.4	0.0	0.1
OR-2	0.2	0.0	0.4	0.0	5.4	14.8	1.7	0.0	1.0	1.5
OR-3	0.0	0.1	0.7	1.6	5.8	11.5	3.0	0.4	1.5	0.4
OR-4	0.0	0.0	3.9	0.9	2.4	14.7	2.1	0.0	0.6	0.4
OT-1	0.0	0.0	17.4	2.1	3.0	2.3	0.0	0.0	0.0	0.2
OT-2	0.0	0.1	19.5	1.6	2.9	0.9	0.0	0.0	0.0	0.0
OT-3	0.0	0.0	7.8	10.2	0.8	6.0	0.1	0.0	0.0	0.1
OT-4	0.1	0.0	17.2	0.5	3.1	2.5	0.1	1.0	0.4	0.1
OT-5	0.0	0.1	18.7	2.6	1.4	2.1	0.0	0.0	0.0	0.0

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