Outcropping reef ledges drive patterns of epibenthic assemblage diversity on cross-shelf habitats

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Abstract

Seafloor habitats on continental shelf margins are increasingly being the subject of worldwide conservation efforts to protect them from human activities due to their biological and economic value. Quantitative data on the epibenthic taxa which contributes to the biodiversity value of these continental shelf margins is vital for the effectiveness of these efforts, especially at the spatial resolution required to effectively manage these ecosystems. We quantified the diversity of morphotype classes on an outcropping reef system characteristic of the continental shelf margin in the Flinders Commonwealth Marine Reserve, southeastern Australia. The system is uniquely characterized by long linear outcropping ledge features in sedimentary bedrock that differ markedly from the surrounding low-profile, sand-inundated reefs. We characterize a reef system harboring rich morphotype classes, with a total of 55 morphotype classes identified from the still images captured by an autonomous underwater vehicle. The morphotype class Cnidaria/Bryzoa/Hydroid matrix dominated the assemblages recorded. Both α and β diversity declined sharply with distance from nearest outcropping reef ledge feature. Patterns of the morphotype classes were characterized by (1) morphotype turnover at scales of 5 to 10’s m from nearest outcropping reef ledge feature, (2) 30 % of morphotype classes were recorded only once (i.e. singletons), and (3) generally low levels of abundance (proportion cover) of the component morphotype class. This suggests that the assemblages in this region contain a considerable number of locally rare morphotype classes. This study highlights the particular importance of outcropping reef ledge features in this region, as they provide a refuge against sediment scouring and inundation common on the low profile reef that characterizes this region. As outcropping reef features, they represent a small fraction of overall reef habitat yet contain much of the epibenthic faunal diversity. This study has relevance to conservation planning for continental shelf habitats, as protecting a single, or few, areas of reef is unlikely to accurately represent the geomorphic diversity of cross-shelf habitats and the morphotype diversity that is associated with these features. Equally, when designing monitoring programs these spatially-discrete, but biologically rich outcropping reef ledge features should be considered as distinct components in stratified sampling designs.

Keywords: Bryozoa, Cnidaria, Continental shelf margin, Flinders Commonwealth Marine Reserve, Hydroid, Marine Protected Area, Porifera, Species diversity

Introduction

Shallow-water sessile invertebrate communities within diving depth (i.e. 0 - 30 m) have been widely studied with numerous papers examining their biology, ecology and distribution (e.g. Costa et al. 2009; Roberts et al. 2002; van Hooidonk et al. 2014). In addition, there has been a large research focus on cold-water corals in depth greater than 300 m (e.g. Althaus et al. 2009; Mohn et al. 2014; Tittensor et al. 2009; Waller et al. 2011).Recent video surveys reveal that epibenthic organisms found on the continental shelf beyond diving depth may be locally abundant and potentially represent a key ecological feature associated with rocky bottom structure along the mid-outer continental shelf margins (Bo et al. 2012; Cerrano et al. 2010). However, there is limited published data available, at sufficient spatial and biological resolution to describe the composition and distribution of these mid-outer shelf biological assemblages.

The role of epibenthic organisms, especially sessile invertebrate species, within the benthic ecosystem has been highlighted by previous studies. For example, cold-water corals promote habitat heterogeneity by increasing the physical complexity of the ecosystem at these greater depths (Baillon et al. 2012; Buhl-Mortensen et al. 2010). The prevalence of suspension feeders in these communities are important in the transfer of energy and biomass from the pelagic to the benthic by recycling particulate organic matter (POM) sinking from the upper photosynthetic regions (de Goeij et al. 2013; Gili and Coma 1998). More recently, de Goeij et al. 2013 suggest the role of sponges may be even more important than previously estimated, transferring both POM and dissolved organic matter (DOM) from pelagic to benthic systems where sponges form significant components of the faunal assemblage. Accordingly, epibenthic organisms such as porifera (sponges), antipatharians (black corals) and gorgonians (sea fans) are of crucial importance to the functioning of the sublittoral temperate assemblages occurring on hard, dimly-lit substrata (Gori et al. 2014; Ribes et al. 2003).

Despite the documented importance of shallow-water epibenthic communities, comparatively few studies in Australia have investigated the spatial variation in these potentially ecologically important assemblages along the outer continental shelf margins (but see McEnnulty et al. 2011; Williams et al. 2010). This trend is undoubtedly linked to the limitations associated with sampling in the outer continental shelf environments (Richardson and Poloczanska 2008), where accessibility and time constraints often impede rigorous fine-scale quantitative sampling (Poore et al. 2014). Previous studies focusing on shallow- (i.e. <30 m) and deep-water (i.e. >200 m) ecosystems provide important insights into spatial patterns of epibenthic assemblages in coastal and deep-water environments. For example, recent work has examined the effects of wave exposure and seafloor structure on the distribution of shallow-water invertebrates (Hill et al. 2014b). How these factors influence the spatial patterns of epibenthic organisms inhabiting outer continental shelf margins remains largely unknown.

The recent establishment of a network of Commonwealth Marine Reserves (CMRs) in shelf- to abyssal waters within Australia's EEZ (Department of Environment 2015) has driven increased studies of these outer continental self-margins and the habitats and assemblages they support, both for inventory of assets within CMRs and for establishing monitoring programs to track their effectiveness against management plans. On the shelf, such studies typically include using multibeam sonar mapping to define habitat characteristics prior to the biological survey phase (e.g. Lucieer 2013) as biological assemblages respond to physical characteristics of the benthic substrata in a predictable manner (Bax and Williams 2001; Hill et al. 2014b; Ierodiaconou et al. 2011; Post 2008; Williams et al. 2010; Williams and Bax

2001). As mapping programs have expanded, the results reveal regionally differing patterns in the geomorphology of rocky reef systems in shelf waters, that may, in turn, structure variation in the associated biota at multiple spatial scales (e.g. Monk et al. 2011; Williams et al. 2010; Zhi et al. 2014). It follows then, that biological inventory and monitoring programs would ideally be structured to account for such spatial variation, allowing for the importance of these structural controls to be properly defined.

In 2012, a shelf region of the shelf region of the Flinders Commonwealth Marine Reserve, off north-eastern Tasmania, Australia, was surveyed using multibeam sonar and an autonomous underwater vehicle (AUV), which collected precisely geo-located imagery of the seabed and associated biota, respectively. This survey revealed that the entire cross-shelf region was characterized by intermittent outcrops of slightly dipping sedimentary rock types that formed distinct outcropping reef features at eroded bedding planes. The outcropping reef features, up to 2 m in height, were often undercut forming small caves and ledges, and extended along the shelf for distances of 100s m to 1 km scales. Between successive step-features the reef was flat, smooth, usually sand-inundated and biologically depauperate, thus providing a distinct contrast with the outcropping reef features themselves, which were characterized by rich epibenthic assemblages. The objective of our study was to generate a detailed characterization of the biological variation associated with these outcropping reef features, a distinct geomorphic features in this region.

Methods

Study site

The study site was situated in the multiple use zone (IUCN VI) of the Flinders Commonwealth Marine Reserve (CMR; 40°37’S, 148°46’ E), which was established in 2007 and lies approximately 25 km offshore of the north-eastern coast of Tasmania, Australia (Figure 1). Within the multiple use zone of the CMR activities that impact on benthic habitats are prohibited (e.g., demersal trawling and scallop dredging). The study site covered ~ 26 km^2 of the CMR, and contained shelf, canyon head and slope features. This region was selected as it is considered a region of high biodiversity and productivity within the east Tasmania subtropical convergence zone (Schlacher et al. 2007).

The seafloor on the shelf was formed of soft sediment with isolated patches of low profile reef that are likely formed on sedimentary rock (likely sandstone) that preferentially erodes along bedding planes to form long, linear reef outcropping features of 1 - 2 m in height (Figure 2). The reef in this area was dominated by predominantly sessile invertebrates including hydrozoans, bryozoans, ascidians and sponges, which are thought to be typical of the broader region of eastern Tasmania (Andrew 1999; James 2014; Nichol et al. 2009).

Data acquisition

Multibeam sonar data

Bathymetry data were acquired using hull-mounted Kongsberg EM30[illegible] multibeam sonar (MBS) on the 22 m research vessel “Challenger”. The data were logged using Kongsberg acquisition software and post-processed using Caris HIPS and SIPS software to remove artefacts. The final bathymetric output was processed at 3 m horizontal resolution and subsequently used for AUV mission planning and delineating outcropping reef ledge features.

Autonomous underwater vehicle imagery

Seabed imagery was collected with a modified Seabed class AUV, the AUV *Sirius*. The AUV is described in Williams *et al.* (2012). Briefly, the AUV is equipped with stereo camera pair and strobes, and its' location calculated using a Doppler Velocity Log including a compass with integrated roll and pitch sensors, and Ultra Short Baseline Acoustic Positioning System (USBL) (for more details see Williams et al. 2012). Seabed images were collected with a synchronized pair of high-sensitivity 12 bit, 1.4 megapixel cameras (AVT Prosilica GC1380 and GC1380C; one monochrome and one color).

The start location of each of the 24 one km length AUV transects was determined using a probabilistic and spatially balanced survey design called Generalized Random Tessellation Stratified (GRTS). The GRTS sampling approach is a flexible strategy that can accommodate multiple survey objectives and provides unbiased estimates of habitats and taxa in the regions surveyed (Stevens and Olsen 2004). The intent of the GRTS approach was to provide quantitative estimates of the abundance (in our case proportion cover) of key biodiversity components of seabed fauna within a defined area, in this case an outer shelf reef system. As we were primarily interested in reef habitat within this region, the inclusion probability of transects was heavily biased towards transects that contained hard-substratum identified from the classification of MBS data collected in this region (Lawrence et al. 2015).

Each AUV transect was pre-programmed so that the AUV tracked the seabed at an altitude of 2 m at a cruising speed of 0.5 ms^{-1}, resulting in an approximate width of the field of view of 1.5 - 2.5 m per image. All surveys were conducted during daylight hours over three days in June 2013. AUV dives covered reef in depth ranges from *c* 60-90 m.

Data manipulation

To delineate the outcropping reef ledge features a bathymetric slope raster was calculated from the MBS data using Spatial Analyst in ArcMap 10. An arbitrary threshold of 1.5°, chosen visually based on a bathymetric hillshade of the area, was applied to the slope raster to define the extent and location of the outcropping reef ledge features (Online Resource 1). The Euclidean distance from these outcropping reef ledge features was calculated using Spatial Analyst in ArcMap 10. The Euclidean distance from nearest reef ledge feature was binned into the following classes: 0 m, 1 – 5 m, 5 – 10 m, 10 – 20 m, 20 – 40 m, 40 – 80 m, and > 80 m (Figure 2; Online Resource 1). Binning was done for ease of interpretation of biodiversity trends, and is hereafter referred to as "distance category".

One hundred and five images from the AUV transects were randomly selected for each distance category. Visual inspection of all selected AUV images was undertaken to ensure no overlap between subsequent images occurred. This was done to remove any possible double counting of organisms as consecutive AUV images can contain overlap resulting in the same organism occurring in consecutive images. Images assigned to the 0 m distance category were manually vetted to ensure they contained at least 90 % exposed reef.

The proportion cover of the taxon in the selected AUV images was obtained by scoring 25 random points superimposed on the image in TransectMeasure (SeaGIS). For each superimposed point the underlying taxon was identified to morphotype level using the Collaborative and Annotation Tools for Analysis of Marine Imagery (CATAMI) classification scheme (Althaus et al. 2015). CATAMI is a standardized national classification scheme that bridges the gap between habitat or biotope classifications and taxonomic classifications. It is a flexible, hierarchical classification that combines coarse-level taxonomy with morphology to allow for limitations in identifying biological taxa in marine imagery. It is important to note that by using CATAMI the classes identified in this study may reflect multiple morphometrically similar species or considerable morphological variation within a single species, and reflects an ongoing limitation in identifying taxa in marine imagery. Despite this inherent limitation, using broader morphological groups to calculate richness and other community metrics is known to correlate well with actual species richness and diversity in sessile invertebrates elsewhere (e.g., sponges Bell and Barnes 2001).

From the assemblage data, three measures of α diversity were calculated for each image, species richness (hereafter morphotype richness), Shannon diversity *H* index and Shannon's equitability (evenness). Morphotype richness and Shannon diversity *H* were calculated using the DIVERSE sub-routine in PRIMER v6 statistical software (Clarke and Gorley 2006). Shannon's equitability (evenness) was calculated manually in MS Excel. The different measures of α diversity were used as they provide complimentary metrics to capture biodiversity patterns. In addition, two measures of β diversity were also calculated using Jaccard and Sorensen indices. The latter was included as it places more emphasis on the shared species present rather than the unshared species that is captured by the former (Anderson et al. 2008).

Statistical analyses

Multivariate analyses were performed using the PRIMER v6 and PERMANOVA add-on package (Anderson et al. 2008; Clarke and Gorley 2006). A Bray–Curtis similarity matrix, based on proportion cover data, was used for multivariate analyses. A *dummy* variable of one was added to reduce the effect of sparse data (some images contained no biological morphotype classes) on the similarity measure (Clarke and Warwick 2001). No further data transformation was required after visual inspection of Shepard diagrams. Cluster analysis and non-metric multi-dimensional scaling (nMDS) were used to visualize the patterns in morphotype assemblages across distance categories. Distances among centroids were calculated for the assemblage nMDS to aid in interpretation of the graph.

The PERMANOVA routine, and associated pairwise comparisons, were used to compare the variation in morphotype proportion cover and composition across distance categories. The single-factor PERMANOVA with distance category as a fixed effect, and associated pairwise comparisons, were run with 9999 unrestricted permutations of the raw data. Using the Bray-Curtis similarity matrix, a distance-based test for homogeneity of multivariate dispersions (PERMDISP) routine was run to assess the dispersion assumption for PERMANOVA, with no strong dispersion differences between distance categories being detected.

The major morphotype classes responsible for within and between the distance categories similarity were determined using the similarity percentages routine (SIMPER; Clarke and Warwick 2001). This method examines the contribution of individual classes to Bray–Curtis similarity. Several key morphotype classes identified by SIMPER were superimposed on the nMDS ordination using the bubble plots to visually depict their proportion cover and distribution. Twenty percent similarity was overlaid on MDS plots.

Univariate analyses exploring the variation in α diversity (i.e. mean morphotype richness, Shannon's diversity *H* and evenness) between distance categories based on the Kruskal-Wallis non-parametric procedure, and pairwise comparisons using Nemenyi-test with Chi-squared approximation within PMCMR package in R version 3.0.3 (R Core Development Team 2014). Following Anderson et al. (2008), PERMDISP, based on Jaccard and Sorensen similarities, was used to assess differences in β diversity between distance categories.

Results

Fifty-five epibenthic morphotype classes (based on CATAMI classification) were recorded; they all had low proportion cover (Figure 3; Online Resource 2). The Bryozoan/Cnidaria/Hydroid matrix was the most dominant class across most distance categories (Figure 3; Online Resource 2). Encrusting sponges were the next most dominant class (Figure 3; Online Resource 2). Other morphotype classes recorded included representatives of sessile and mobile organisms from Ascidiacea, Bryozoa, Cnidaria, Echinodermata, Osteichthyes, Elasmobranchii, Mollusca, Phaeophyta, Polychaeta, Poriferia Rhodophyta, and Sipuncula worms (Online Resource 2).

The PERMANOVA revealed significant differences in morphotype assemblages between distance categories (pseudo-$F_{6,\ \text{72[illegible]}}$ = 31.26, $p < 0.001$; Figure 3). The nMDS ordination model (Figure 4a) confirmed that there was a gradient in morphotype assemblages as distance categories increased. The smallest Bray-Curtis similarity values were recorded at distance categories closer to the outcropping reef features indicating greater heterogeneity in morphotype classes on and around the outcropping reef ledges (Figure 4a; Figure 5). The 20 % similarity contour on the nMDS indicated that the morphotype assemblages were grouped in three distinct clusters: (1) assemblages on or near the outcropping reef ledge features (i.e. 0 m, 1 - 5 m), (2) assemblages affiliated with fringing low profile reef regions (5 - 10 m, 10 - 20 m), and (3) assemblages affiliated with sand inundated reef to full sand habitat that were greater than > 20 m from outcropping reef ledge features (i.e. distance categories 20 - 40 m, 40 - 80 m, > 80 m). This was supported by the pairwise analysis which revealed a significant difference ($p < 0.05$) between all non-adjacent distance categories.

The SIMPER analyses indicated that the difference in morphotype assemblage structure was influenced by proportion cover gradients in six morphotype classes (SIMPER, cut-off 70 %; Table 2). A strong proportion cover gradient in the morphotype class

Bryozoan/Cnidaria/Hydroid matrix was the primary driver in the dissimilarities in between all distance categories, with proportion cover steadily decreasing with distance from outcropping reef ledge features (Table 2; Figure 4b). Proportion cover gradients in the morphotype class “Erect branching sponges and encrusting sponges” also contributed to the dissimilarities between distance classes with exception to between 20 - 40 m and 40 - 80 m, 40 - 80 m and > 80 m, and 20 - 40 m and > 80 m (Table 2; Figure 4c, d). The presence of infaunal bioturbation (Figure 4e), morphotype classes “massive sponges” and “soft bryozoans” additionally contributed to the dissimilarity between some distance categories but to a lesser extent (Table 2).

The three α diversity metrics found similar trends. Morphotype richness varied between most distance categories and ranged from 0 to 11 organisms in the images (Figure 5a; Table 1a). Shannon-Wiener's *H’* varied between 0.13 and 1.98 (excluding 257 images with no biological morphotype classes recorded), while the evenness varied between 0.30 and 1.05. The Kruskal-Wallis procedure, and associated Nemenyi test pairwise comparison, indicated that morphospecies richness decreased significantly with increasing distance category (Figure 5a). Shannon-Wiener's *H’* and evenness both also decreased significantly over increasing distance category but plateaued from 20 - 40 m category (Figure 5a; Table 1b, c).

Beta diversity was relatively low and varied between 25 to 46 and 18 to 36 for the Jaccard and Sorensen measures, respectively (Figure 5b). These low measures of diversity, and the differences between them, are reflective of the fact that thirty percent of morphotype classes were observed only once (i.e. singletons). The PERMDISP routine found that β diversity varied significantly between most distance categories (Figure 5b). However, for the assessment of unshared classes, represented by Jaccard measure, non-significant differences were found between 0 m and 20 – 40 m, 1-5 m and 10 – 20 m, and 5 – 10 m and 10 – 20 m.

Similarly, for the assessment of shared classes, the Sorensen measure, non-significant differences were found between 0 m and 20 – 40 m, 1 – 5 m and 5 – 10 m, 1 – 5 m and 10 – 20 m, and 5 – 10 m and 10 – 20 m.

Discussion

Assemblage patterns and the importance of outcropping reef ledge features

The morphotype assemblages associated with the outcropping reef ledge features and adjacent sediment-inundated reefs in the Flinders CMR were characterized by six morphotype classes including; a Bryozoa/Cnidaria/Hydroid matrix, branching erect sponges, encrusting sponges, massive sponges, soft bryozoans and the presence of infaunal bioturbation. The dominance of the Bryozoa/Cnidaria/Hydroid matrix class is noteworthy in providing contrasts with previous published studies along Australia’s continental shelf margin which suggest that the epibenthic assemblages in similar depth ranges are often dominated by sponges (e.g. Fromont et al. 2012; Schlacher et al. 2007). This difference is potentially a result of the reduced wave energy along the Flinders CMR study area in comparison to the predominantly high-energy west-facing locations of previously highlighted studies. On such high-energy coasts depths well below 60 - 70 m (i.e. the depths sampled in this study) may be too disturbed by swell action, and associated sediment scouring, for delicate morphotype classes (such as Bryozoa/Cnidaria/Hydroid matrix class) to colonize successfully. However, along the more sheltered leeward side of eastern Tasmania, such as the Flinders CMR area, high-energy oceanic swells are much rarer, and seabed shear stress reduced relative to the high-energy west coast (Harris and Hughes 2012), possibly allowing these more fragile communities to thrive at depths up into the photic zone. This concept is supported by Bell and Barnes (2000) who suggest that fragile morphotype classes (such as Bryozoa/Cnidaria/Hydroid matrix and branching sponges) can only form in low swell energy environments. Although sediment scour and burial are recognized as important, little is known about the spatial extent and frequency on outer-shelf habitats (Harris and

Hughes 2012).Quantifying the natural spatial and temporal variability of these disturbances warrants further investigation (such as on-going monitoring at various temporal scales).

Our study also demonstrated that outcropping reef ledge features can strongly influence the patterns of proportion cover of epibenthic morphotype assemblages. The spatial pattern detected in the morphotype assemblage represents an assemblage ‘halo’ effect, or cline, around the outcropping reef ledge features and characterizes an ecologically important “high-point” (biologically and structurally) in the transition from outcropping to sediment-inundated reef habitats, as well as the importance of a spatially-controlled region of higher substrate complexity. The significant difference in the assemblage composition among distance categories (PERMANOVA pairwise comparisons) indicated that the turnover of morphotype classes occurs at relatively small spatial scales on these reef systems (i.e. 5 – 10 m’s). Similar assemblage halos around reef habitats have been noted in previous studies that examined the presence of reef on small-bodied epibenthic taxa (e.g. Langlois et al. 2006) and demersal fishes (e.g. Schultz et al. 2012) inhabiting the surrounding soft-sediments. While our study differs in the fact that we have recorded predominantly sessile morphotype taxa, which require hard substratum to attach themselves, the mobile nature of soft sediments inundating these reef systems allows physical characteristics of substrata to vary over small spatial scales (Paiva 2001) and time periods of days to weeks in relation to variations in wave and tide energy (Grant et al. 1997). It has been suggested that such factors lead to spatial variability at the scale of tens of meters (reviewed in Fraschetti et al. 2005), which is at the scale that we detected greatest changes in assemblage compositions (i.e. 5 - 10 m s). Sand inundation and sediment scour appear to be an important factor explaining spatial gradients and patchiness in epibenthic biota throughout the flat reef systems located on continental shelf throughout the Flinders CMR. However, the outcropping reef ledge features may provide a refuge against such disturbances, allowing the more fragile morphotype classes to colonize. It is the distance from these outcropping reef ledge features that provides the greatest spatial differentiation in our study.

There are some limitations to our study that should be noted. We have only investigated the influence of outcropping reef ledge features on the structuring of the observed morphotype assemblages at a single site, albeit over a large area. While it is clear that the presence of these hard outcropping reef features is a key driver in the structuring of these assemblages, previous research suggests that other environmental variables could be important. For example, Huang et al. (2011) found that mean bottom-water temperature, nitrate concentrations and depth were important variables in defining the distribution of sponge assemblages. Similarly, Bryan and Metaxas (2007) found that combinations of depth, temperature, slope, current, and chlorophyll a concentrations were important predictors in determining suitable habitat for deep-water gorgonian corals. Furthermore, factors such as recruitment and mortality (Keough and Downes 1982), larval distribution (Grantham et al. 2003), and currents (Cudaback et al. 2005) can influence the distribution of these assemblages, and could be considered, if data were available, for interpreting biodiversity trends observed in our study.

Conceptual diagram for outcropping reef ledge features

In light of our findings, we propose a conceptual diagram to describe the morphotype assemblages typical of the cross shelf reefs in this region (as indicated by more extensive unpublished surveying within the Flinders CMR). Shallow dipping rocks of sedimentary origin outcrop across the shelf and are preferentially eroded at bedding planes, producing an elongated sawtooth profile (Figure 6). The near vertical structures (*ca* 1 - 3 m in height) at the eroded bedding planes (outcropping reef features) can be linear and extend for many hundreds of meters where reef is exposed from the surrounding sediments (Figure 2). The steep surfaces and nearby boulders that are related to them are generally sediment free and covered with abundant, diverse and highly structured morphotype classes. At distances of as little as 5 m from this, on the low profile expanse of bedrock between consecutive steps, sediment inundation begins, restricting the ability of sessile morphotype classes to attach and be supported as they grow.

The importance of these outcropping reef features becomes apparent when compared to the continuous boulder fields commonly found further inshore on the continental shelf. These boulder field habitats are more homogenous at intermediate scales, with biota responding generally at fine-scale to local physical variables such as boulder aspect (Hill et al. 2014b).

Management implications

From a management perspective it is important to consider the difficulties of sampling such spatially-discrete, yet biological important outcropping reef ledge features. In many respects these outcropping reef ledge features are analogous to a river flowing through a desert, containing greater richness and diversity than the adjacent flat reef and sediment habitats. Sampling regimes and monitoring programs that do not account for such features through appropriately matched stratified sampling designs risk missing an understanding of the key structural controls on the distribution and abundance of many species that utilize this habitat preferentially.

Our data contained a relatively high prevalence of singletons (~ 30 %) and relatively low proportion cover. This is interesting because, despite scoring the imagery to the morphotype level, the percentage of singletons recorded is similar to but slightly less than that recorded in previous studies that have identified taxa to a lower taxonomic resolution (e.g., genus, species levels). For example, studies in north-eastern Australia and Western Australia have found that

48 – 60 % of Porifera species were restricted to samples from a single site within reef complexes (Fromont et al. 2006; Hooper and Kennedy 2002). Similar observations have been noted from survey regions in tropical north-western Australia (Przeslawski et al. 2014; Schönberg and Fromont 2012), where data from benthic surveys show that only a few epibenthic taxa (mostly Porifera) are ubiquitous (Heyward et al. 2010). Additionally, research in the shelf-break to continental slope canyon systems to the north and west of the Flinders CMR site have also noted similar patterns (albeit in deeper habitats > 120 m), with 76 % of Porifera species being restricted to a single site (Schlacher et al. 2007). This suggests that this low site-occupancy and potentially high levels of rarity (at scales of 10-100 s m) by epibenthic organisms may be a common feature of Australian continental shelf margins, and one that needs to be factored into biodiversity monitoring planning. Such species are unlikely to be suitable candidates for biodiversity monitoring and spatial planning. However, additional survey effort (using existing or newly collected datasets) is required to disentangle whether these rare species are in fact quite widely distributed but under sampled, or indeed, simply rare and patchy (Monk 2014). This is an important difference and determines the extent of conservation significance of the habitat features that support this diversity, and the scale at which such habitats need to be protected to capture and sustain this diversity. In the current study, for example, repeated replicate sampling along linear transects at increasing distances away from the outcropping reef features may be useful to help clarify the pattern of taxa turnover observed in the current study, determine the influence of disturbance on physical and biological regimes in epibenthic communities, and refine the spatial extent of reef influence on adjacent environments. Such information would complement spatially-balanced sampling approaches (Hill et al. 2014a), which could also be weighted to towards such spatial discrete features, and substantially improve our ability to plan future monitoring and biological inventory programs.

Conclusion

Our study demonstrated that reef features (such as outcrops and ledges) can strongly influence the patterns in proportion cover and composition of seafloor morphotype classes. The spatial pattern detected in the morphotype assemblage represented an assemblage halo effect around the outcropping reef ledge features. By creating ‘reef islands’ within reef patches, these features may represent an ecologically important high-point in the transition from exposed to sediment-inundated reef habitats. Even at our coarse morphotype taxonomic resolution, classes appear to be spatially-sparse with one third of morphotype classes being observed once. Monitoring of these spatially-discrete outcropping reef ledge features, that host the vast amount of emergent macro-faunal biodiversity in this region, will be important to evaluate the future success of this CMR. Additionally, if similar reef structures are found to be a common feature of cross-shelf habitats at national and global scales, future studies will need to account for these spatially-discrete, yet biologically rich, features in subsequent biodiversity inventory and monitoring.

Acknowledgments

This work has been funded through the National Environmental Research Program (NERP) funded by the Australian Government. The NERP Marine Biodiversity Hub is a collaborative partnership between the University of Tasmania, CSIRO Wealth from Oceans Flagship, Geoscience Australia, Australian Institute of Marine Science and Museum Victoria. Justin Hulls (UTas) provided significant technical support for field surveys and interrogation of AUV imagery. We would like to thank Oscar Pizarro, Ariell Friedman, Andrew Durrant and staff at the Australian Centre for Field Robotics (ACFR) University of Sydney for access to and running the AUV *Sirius.* AUV data was sourced from the Integrated Marine Observing System (IMOS) – IMOS is a national collaborative research infrastructure, supported by the

Australian Government. Ian Atkinson and Olivia Wilson (Geoscience Australia) are acknowledged for their assistance in the acquisition and processing of the multibeam sonar data. Emma Lawrence (CSIRO) is thanked for undertaking the AUV sampling design. Thanks also to Nic Bax, two anonymous reviewers and the Editor for their constructive comments on an early version of the paper. SN and JS publish with permission of the CEO, Geoscience Australia.

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Figure captions

Figure 1. Location of the outcropping reef features mapped by multibeam sonar and photographically sampled by autonomous underwater vehicle in the Flinders Commonwealth Marine Reserve. Black circles indicate locations of individuals images selected for interrogation. Zoom box (A) provides an example of the outcropping linear reef features.

Figure 2. Southwest-ward facing 3D representation of the reef features mapped by multibeam sonar and photographically sampled by autonomous underwater vehicle in the Flinders Commonwealth Marine Reserve. Color gradient indicates the distance categories used in assemblage analysis: 🟦 (0 m),🟩 (1 - 5 m),🟨 (5 - 10 m),🟫 (10 - 20 m),🟧 (20 - 40 m), 🟨 (40 – 80 m) and ⬜ (> 80 m).

Figure 3. Ranked mean proportion cover (dominance) per image (± S.E.) for morphotype classes contributing > 90% of the proportion cover within each distance category.

Figure 4. Non-metric multidimensional scaling ordinations for morphotype assemblages between distance categories. Hashed lines indicate 20 % similarity. A) Centroids of the total assemblage for each distance category: 1) 0 m (▲), 2) 1 - 5 m (▼), 3) 5 - 10 m (■), 4) 10 - 20 m (♦), 5) 20 - 40 m (○), 6) 40 - 80 m (×) and 7) > 80 m (+). B-E) Important morphotype classes identified in SIMPER analysis: bubble size indicates relative mean proportion cover (i.e. larger bubble = higher proportion cover). Example images of the morphotype classes are given in right column.

Figure 5. Mean variation (± S.E.) in α and β diversity measures across distance categories. a) α diversity. b) β diversity.

Figure 6. Conceptual diagram of the typical cross-shelf reef systems contained within the Flinders Commonwealth Marine Reserve. Outcropping reef features with complex and highly structured morphotype classes adjacent to, and on features, with sand inundation (grey shading) covering reef between ledge features, limiting growth of associated taxa.

Tables

Table 1. P-values from pairwise comparison of the morphotype assemblage relationship with distance categories using Nemenyi-test with Chi-squared approximation for (a) morphotype richness, (b) Shannon-Wiener's *H’*, and (c) evenness. Grey shaded cells indicate non-significant differences.

a)	**0 m**	**1 - 5 m**	**5 - 10 m**	**10 - 20 m**	**20 - 40 m**	**40 - 80 m**
1 - 5 m	0.91					
5 - 10 m	0.21	0.90				
10 - 20 m	0.00	0.10	0.79			
20 - 40 m	0.00	0.00	0.00	0.08		
40 - 80 m	< 0.001	< 0.001	< 0.001	< 0.001	0.91	
> 80 m	< 0.001	< 0.001	< 0.001	< 0.001	0.35	0.97
b)						
1 - 5 m	0.99					
5 - 10 m	1.00	0.99				
10 - 20 m	0.97	0.99	0.95			
20 - 40 m	< 0.001	0.001	< 0.001	0.02		
40 - 80 m	< 0.001	< 0.001	< 0.001	< 0.001	0.02	
> 80 m	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.20
c)						
1 - 5 m	0.99					
5 - 10 m	1.00	0.99				
10 - 20 m	0.97	0.99	0.95			
20 - 40 m	< 0.001	0.001	< 0.001	0.02		
40 - 80 m	< 0.001	< 0.001	< 0.001	< 0.001	0.02	
> 80 m	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.02

Table 2. Contribution, in percentage (%), of the groups obtained from the proportion cover data of the morphotype classes, which contribute to dissimilarities (cut-off 70 %) between distance categories. Percent contributions are presented in parentheses. Grey shading represents those pairs of distance categories that did not contain significantly different morphotype compositions.

	0 m	**1 - 5 m**	**5 - 10 m**	**10 - 20 m**	**20 - 40 m**	**40 - 80 m**	**> 80 m**
0 m	Bryozoa/Cnidaria /Hydroid matrix (57.08 %) Encrusting sponges (30.24 %)						
1 - 5 m	Bryozoa/Cnidaria /Hydroid matrix (37.11 %) Encrusting sponges (20.57 %) Branching erect sponges (12.49 %)	Bryozoa/Cnidaria /Hydroid matrix (64.64 %) Encrusting sponges (14.53 %)					
5 - 10 m	Bryozoa/Cnidaria /Hydroid matrix (38.07 %) Encrusting sponges (22.12 %) Branching erect sponges (10.12 %)	Bryozoa/Cnidaria /Hydroid matrix (37.40 %) Branching erect sponges (14.23 %) Encrusting sponges (13.00 %) Soft Bryozoa (5.66 %)	Bryozoa/Cnidaria /Hydroid matrix (70.92 %)				

10 - 20 m	Bryozoa/Cnidaria /Hydroid matrix (39.32 %) Encrusting sponges (23.03 %) Branching erect sponges (9.99 %)	Bryozoa/Cnidaria /Hydroid matrix (38.74 %) Branching erect sponges (14.50 %) Encrusting sponges (13.28 %) Soft Bryozoa (5.60 %)	▨	Bryozoa/Cnidaria /Hydroid matrix (76.62%)		
20 - 40 m	Bryozoa/Cnidaria /Hydroid matrix (41.27 %) Encrusting sponges (24.01 %) Branching erect sponges (9.43 %)	Bryozoa/Cnidaria /Hydroid matrix (40.97 %) Branching erect sponges (12.48 %) Encrusting sponges (12.88 %) Soft Bryozoa (4.97 %)	Bryozoa/Cnidaria /Hydroid matrix (41.33 %) Branching erect sponges (12.28 %) Encrusting sponges (8.24 %) Infaunal bioturbation (6.5 %) Massive sponges (3.79 %)	Bryozoa/Cnidaria /Hydroid matrix (43.21 %) Branching erect sponges (11.76 %) Infaunal bioturbation (9.[illegible]9 %) Encrusting sponges ([illegible].34 %)	Bryozoa/Cnidaria /Hydroid matrix (79.62 %)	
40 - 80 m	Bryozoa/Cnidaria /Hydroid matrix (42.45 %) Encrusting sponges (24.66 %) Branching erect sponges (9.37 %)	Bryozoa/Cnidaria /Hydroid matrix (42.59 %) Branching erect sponges (14.69 %) Encrusting sponges (13.06 %)	Bryozoa/Cnidaria /Hydroid matrix (43.44 %) Branching erect sponges (12.51 %) Encrusting sponges (7.72 %) Infaunal	Bryozoa/Cnidaria /Hydroid matrix (45.33 %) Branching erect sponges (12.08 %) Infaunal bioturbation (9.04 %)	▨	Bryozoa/Cnidaria /Hydroid matrix (82.30 %)

			bioturbation (5.28 %) Massive sponges (3.82 %)	Encrusting sponges (7.87 %)			
> 80 m	Bryozoa/Cnidaria /Hydroid matrix (43.35 %) Encrusting sponges (25.05 %) Branching erect sponges (8.76 %)	Bryozoa/Cnidaria /Hydroid matrix (43.23 %) Branching erect sponges (14.13 %) Encrusting sponges (13.25 %)	Bryozoa/Cnidaria /Hydroid matrix (43.92 %) Branching erect sponges (11.66 %) Encrusting sponges (7.59 %) Infaunal bioturbation (5.15 %) Massive sponges (4.00 %)	Bryozoa/Cnidaria /Hydroid matrix (45.39 %) Branching erect sponges (10.89 %) Infaunal bioturbation (9.31 %) Encrusting sponges (7.83 %)	Bryozoa/Cnidaria /Hydroid matrix (47.28 %) Infaunal bioturbation (16.83 %) Branching erect sponges (9.53 %)		Bryozoa/Cnidaria / Hydroid matrix (78.99 %)

Fig 1.

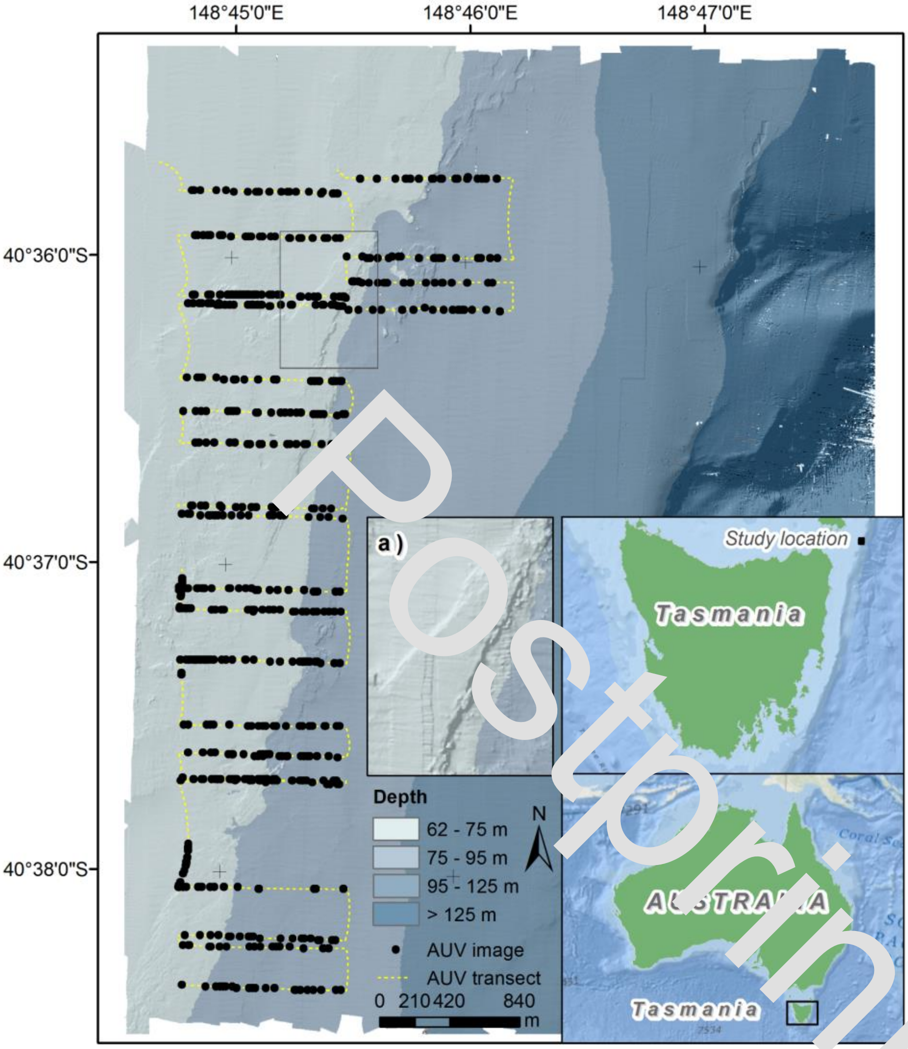

148°45'0"E
148°46'0"E
148°47'0"E
40°36'0"S
40°37'0"S
40°38'0"S
a)
Study location
Tasmania
AUSTRALIA
Tasmania
Depth
62 - 75 m
75 - 95 m
95 - 125 m
> 125 m
AUV image
AUV transect
0 210 420 840 m
N

Fig 2

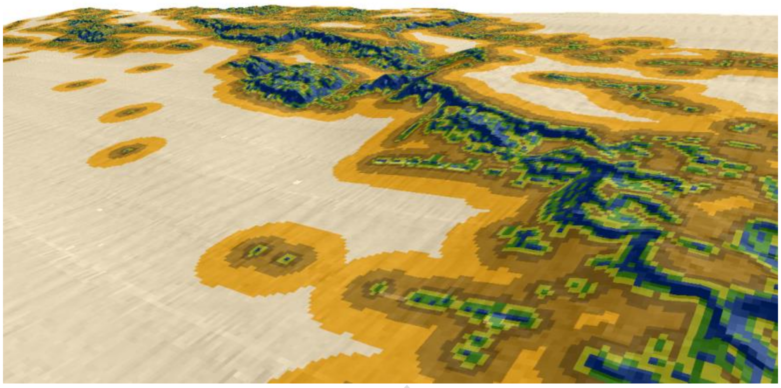
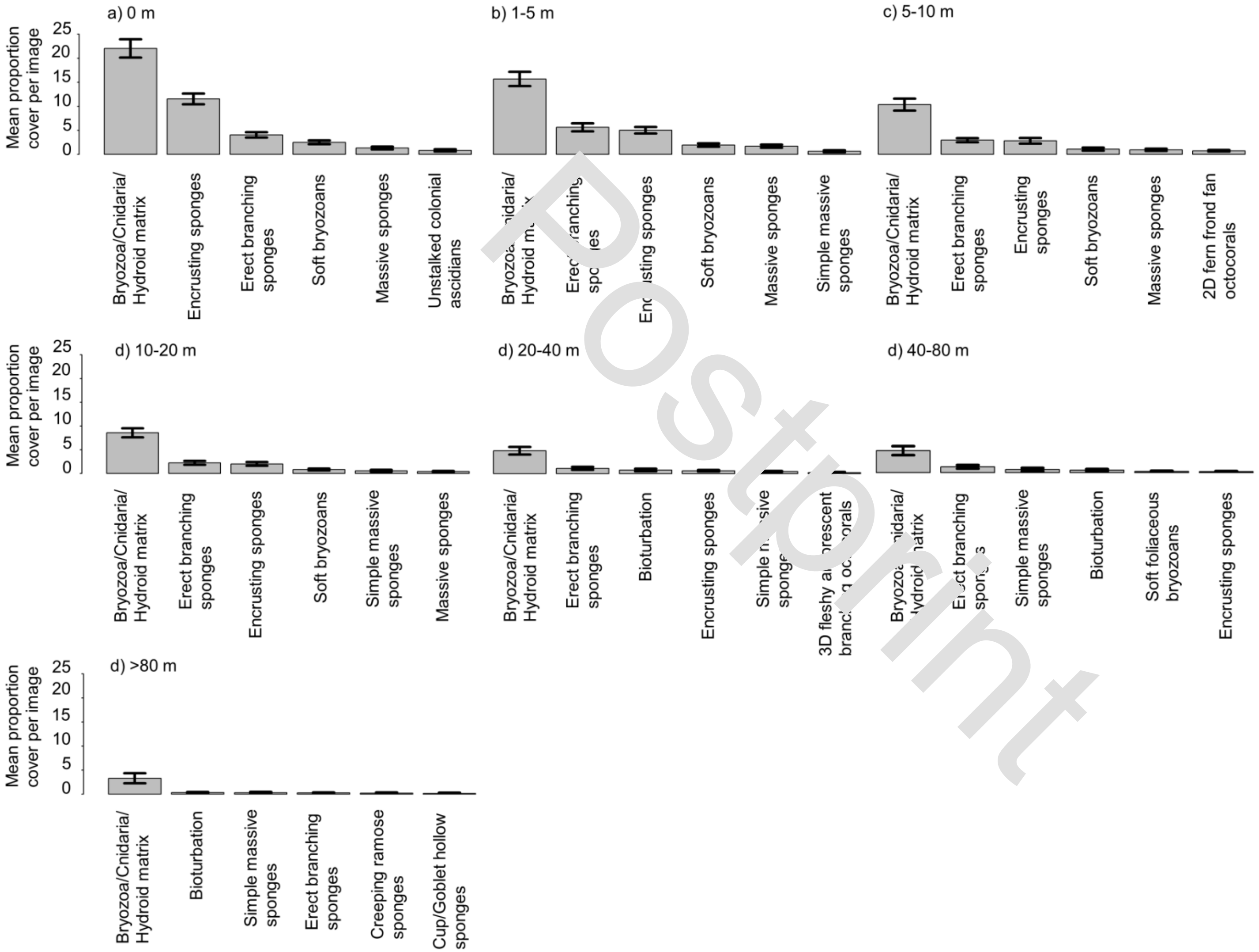


Fig 3



a) 0 m
Mean proportion cover per image
25
20
15
10
5
0
Bryozoa/Cnidaria/ Hydroid matrix
Encrusting sponges
Erect branching sponges
Soft bryozoans
Massive sponges
Unstalked colonial ascidians
b) 1-5 m
Bryozoa/Cnidaria/ Hydroid matrix
Erect branching sponges
Encrusting sponges
Soft bryozoans
Massive sponges
Simple massive sponges
c) 5-10 m
Bryozoa/Cnidaria/ Hydroid matrix
Erect branching sponges
Encrusting sponges
Soft bryozoans
Massive sponges
2D fern frond fan octocorals
d) 10-20 m
Mean proportion cover per image
25
20
15
10
5
0
Bryozoa/Cnidaria/ Hydroid matrix
Erect branching sponges
Encrusting sponges
Soft bryozoans
Simple massive sponges
Massive sponges
d) 20-40 m
Bryozoa/Cnidaria/ Hydroid matrix
Erect branching sponges
Bioturbation
Encrusting sponges
Simple massive sponges
3D fleshy arborescent branching octocorals
d) 40-80 m
Bryozoa/Cnidaria/ Hydroid matrix
Erect branching sponges
Simple massive sponges
Bioturbation
Soft foliaceous bryozoans
Encrusting sponges
d) >80 m
Mean proportion cover per image
25
20
15
10
5
0
Bryozoa/Cnidaria/ Hydroid matrix
Bioturbation
Simple massive sponges
Erect branching sponges
Creeping ramose sponges
Cup/Goblet hollow sponges

Fig 4

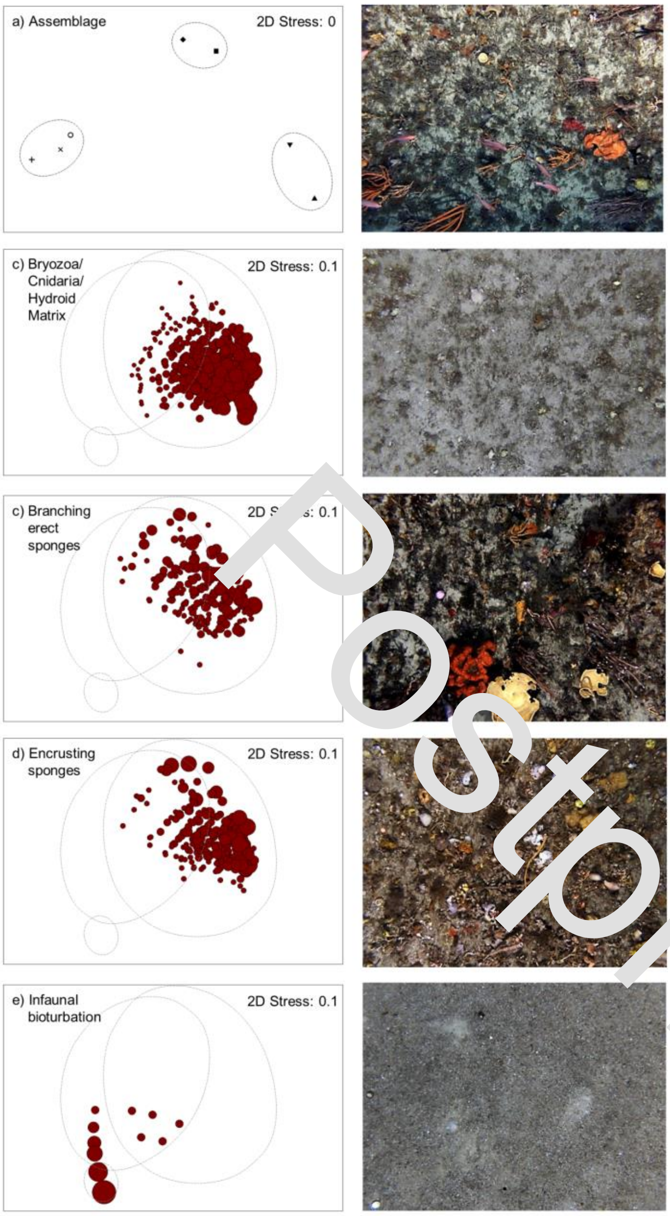

a) Assemblage
2D Stress: 0
c) Bryozoa/ Cnidaria/ Hydroid Matrix
2D Stress: 0.1
c) Branching erect sponges
2D Stress: 0.1
d) Encrusting sponges
2D Stress: 0.1
e) Infaunal bioturbation
2D Stress: 0.1

Fig 5

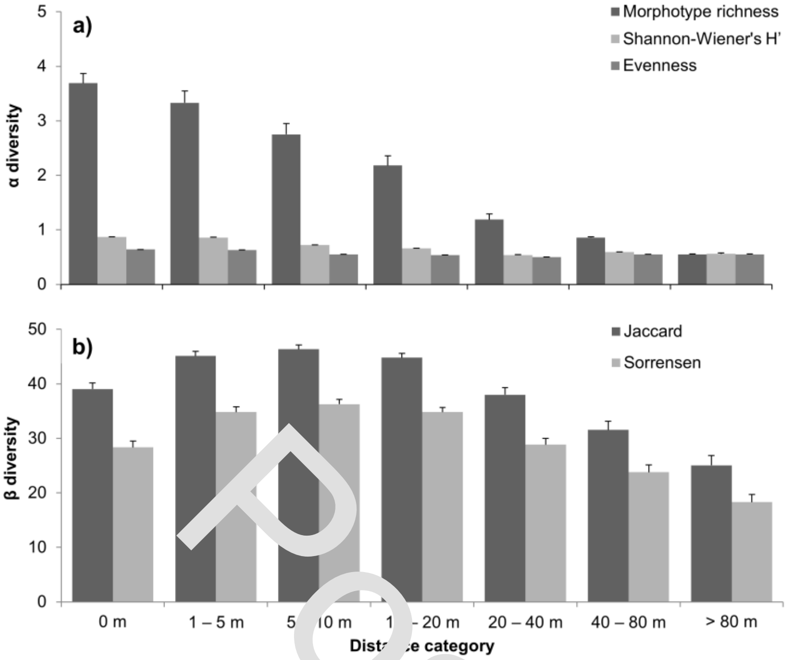
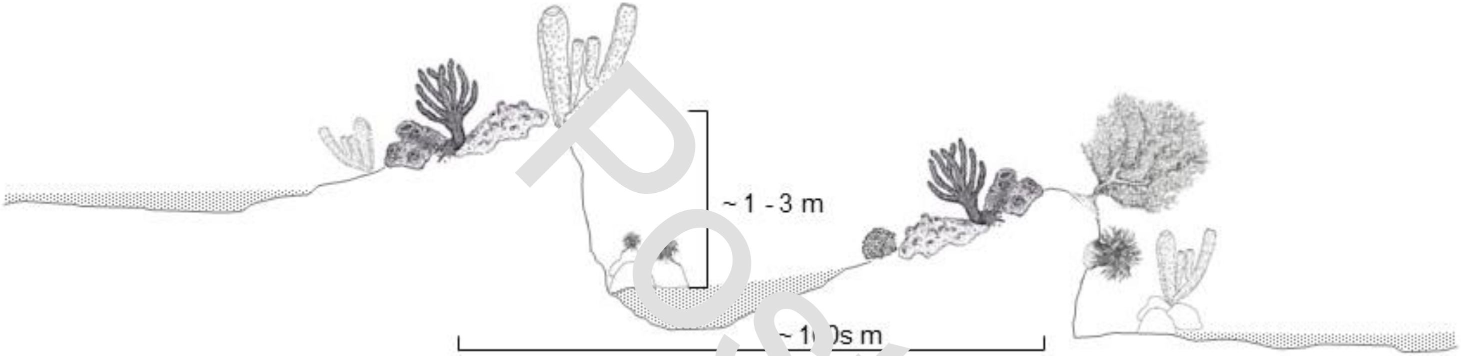

a)
Morphotype richness
Shannon-Wiener's H'
Evenness
α diversity
0
1
2
3
4
5
b)
Jaccard
Sorrensen
β diversity
0
10
20
30
40
50
0 m
1 – 5 m
5 – 10 m
10 – 20 m
20 – 40 m
40 – 80 m
> 80 m
Distance category

Fig 6



Online resource 1

Title: Outcropping reef ledges drive patterns of epibenthic assemblage diversity on cross-shelf habitats

Journal: Biodiversity and Conservation

Authors: Jacquomo Monk[1*], Neville Barrett[1], Nicole Hill[1], Vanessa Lucieer[1], Scott Nichol[2], Justy Siwabessy[2], Stefan Williams[3]

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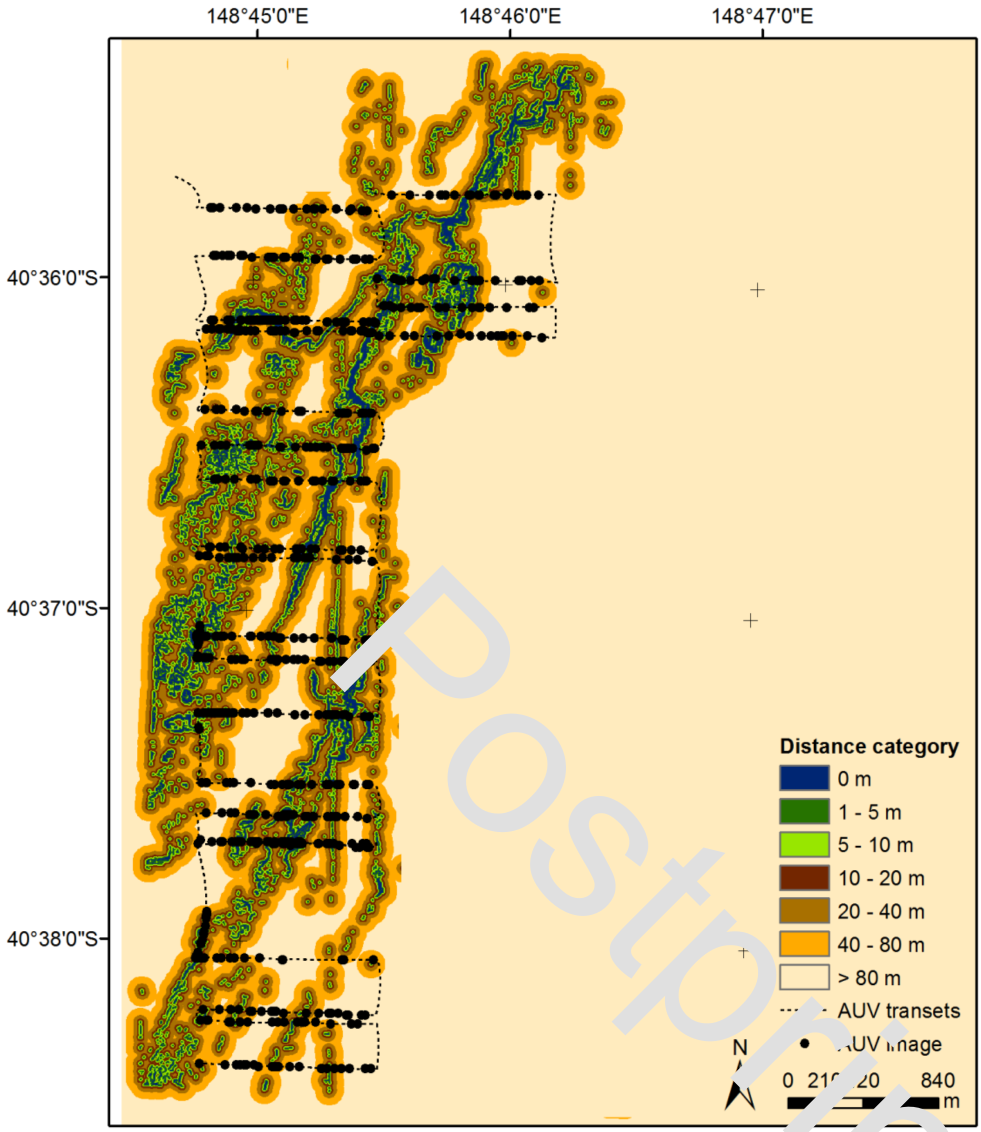

Figure 1. Distance categories from outcropping reef ledge features and position of the selected images from autonomous underwater vehicle used in the analysis of biodiversity trends in the Flinders Marine Reserve.

Online resource 2

Title: Outcropping reef ledges drive patterns of epibenthic assemblage diversity on cross-shelf habitats

Journal: Biodiversity and Conservation

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Table 1. Mean proportion cover for the morphotype and substrata classes observed in selected images from autonomous underwater vehicle surveys for each distance from nearest outcropping reef feature category.

Morphotype class	**Distance Category** **0 m**		**1-5 m**		**5-10 m**		**10-20 m**		**20-40 m**		**40-80 m**		**>80 m**	
	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error	Mean	Standard Error
Ascidians stalked (colonial)	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ascidians unstalked	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ascidians unstalked (colonial)	0.21	0.06	0.09	0.03	0.05	0.03	0.01	0.01	0.01	0.01	0.01	0.01	0.00	0.00
Ascidians unstalked (solitary)	0.19	0.05	0.05	0.02	0.11	0.04	0.04	0.02	0.00	0.00	0.00	0.00	0.01	0.01
Biota (unknown)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Bioturbation	0.00	0.00	0.09	0.09	0.04	0.02	0.06	0.02	0.19	0.07	0.11	0.05	0.09	0.03
Bryozoa/cnidarian/hydroid matrix	5.51	0.48	3.92	0.37	2.52	0.31	2.14	0.24	1.19	0.20	1.01	0.21	0.83	0.26
Bryozoa hard (branching)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.02	0.00	0.00
Bryozoa hard (fenestrate)	0.04	0.03	0.04	0.02	0.02	0.02	0.01	0.01	0.04	0.03	0.01	0.01	0.00	0.00
Bryozoa soft	0.63	0.10	0.49	0.09	0.28	0.08	0.11	0.05	0.03	0.02	0.01	0.01	0.03	0.02
Bryozoa soft (foliaceous)	0.01	0.01	0.09	0.04	0.02	0.02	0.08	0.03	0.03	0.02	0.06	0.03	0.03	0.02
Cnidaria colonial anemones zoanthids	0.03	0.02	0.01	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cnidaria corals black octocorals (2D fan)	0.00	0.00	0.04	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cnidaria corals black octocorals (2D fern frond)	0.06	0.03	0.10	0.04	0.19	0.04	0.07	0.03	0.01	0.01	0.01	0.01	0.00	0.00

Cnidaria corals black octocorals (massive soft corals)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Cnidaria corals black octocorals (whip)	0.01	0.01	0.06	0.02	0.15	0.04	0.03	0.02	0.01	0.01	0.00	0.00	0.02	0.01
Cnidaria corals black octocorals (3D fleshy arborescent)	0.17	0.05	0.13	0.04	0.14	0.05	0.10	0.03	0.06	0.04	0.02	0.02	0.00	0.00
Cnidaria corals black octocorals (3D non-fleshy arborescent)	0.00	0.00	0.04	0.02	0.01	0.01	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00
Cnidaria corals black octocorals (3D non-fleshy- bottle brush)	0.00	0.00	0.00	[illegible]	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cnidaria corals black octocorals (3D non-fleshy- bushy)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00
Cnidaria corals black octocorals (2D fern frond- complex)	0.00	0.00	0.00	0.00	0.00	[illegible]	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00
Cnidaria stony corals (solitary)	0.00	0.00	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cnidaria stony corals (solitary attached)	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.03	0.03	0.00	0.00
Cnidaria hydrocorals (branching)	0.00	0.00	0.01	0.01	0.00	0.00	0.00	[illegible]	0.00	0.00	0.00	0.00	0.00	0.00
Cnidaria true anemones (other anemones)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
Cnidaria tube anemones	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
Cnidaria hydroids	0.17	0.06	0.13	0.05	0.07	0.03	0.01	0.01	0.03	0.02	0.01	0.01	0.00	0.00
Cnidaria true anemones	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Echinoderms feather stars (unstalked crinoids)	0.00	0.00	0.00	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Echinoderms sea urchins (irregular urchins)	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Fishes bony fishes	0.01	0.01	0.03	0.02	0.01	0.01	0.02	0.01	0.01	0.01	0.00	0.00	0.01	0.01
Fishes elasmobranchs (rays/skates)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
Macroalgae encrusting (red)	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Macroalgae encrusting (red calcareous)	0.00	0.00	0.00	0.00	0.01	0.01	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00
Macroalgae erect coarse branching (brown-detached)	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Macroalgae erect fine branching (red)	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Molluscs (gastropods)	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Sponges crusts (creeping ramose)	0.11	0.04	0.02	0.01	0.07	0.03	0.04	0.03	0.00	0.00	0.04	0.02	0.06	0.04
Sponges crusts (encrusting)	2.89	0.28	1.26	0.17	0.70	0.15	0.50	0.10	0.15	0.04	0.05	0.02	0.01	0.01
Sponges erect forms (branching)	1.02	0.14	1.41	0.21	0.74	0.11	0.56	0.10	0.28	0.08	0.27	0.08	0.07	0.03
Sponges erect forms (laminar)	0.03	0.02	0.10	0.04	0.05	0.02	0.05	0.02	0.02	0.01	0.00	0.00	0.00	0.00
Sponges erect forms (palmate)	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sponges erect forms (simple)	0.03	0.03	0.01	0.01	0.02	0.01	0.05	0.02	0.02	0.01	0.00	0.00	0.00	0.00
Sponges erect forms (stalked)	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sponges hollow forms	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(barrels)													
Sponges hollow forms (cups and alikes)	0.01	0.01	0.05	0.03	0.01	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Sponges hollow forms (cup/goblet)	0.06	0.04	0.03	0.02	0.06	0.03	0.05	0.03	0.00	0.00	0.00	0.00	0.04	0.04
Sponges hollow forms (incomplete cup curled fan)	0.01	0.01	0.02	0.02	0.02	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.02	0.02
Sponges hollow forms (tabular)	0.02	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sponges hollow forms (tubes and chimneys)	0.04	0.02	0.11	0.05	0.09	0.03	0.03	0.02	0.04	0.02	0.01	0.01	0.00	0.00
Sponges massive forms	0.33	0.07	0.43	0.08	0.24	0.06	0.10	0.03	0.03	0.02	0.00	0.00	0.00	0.00
Sponges massive forms (balls)	0.04	0.02	0.03	0.02	0.03	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.01	0.01
Sponges massive forms (simple)	0.01	0.01	0.16	0.05	0.07	0.04	0.14	0.05	0.11	0.03	0.14	0.07	0.08	0.04
Worms (polychaetes tube worms)	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00
Substrata class														
Substrate unconsolidated soft (biogenic)	5.70	0.72	1.00	0.35	0.37	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Substrate unconsolidated soft (coquina shellhash)	0.00	0.00	0.02	0.01	0.12	0.10	0.05	0.04	0.09	0.03	0.05	0.02	0.04	0.02
Substrate unconsolidated soft (screwshells)	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Substrate unconsolidated soft (gravel 2-10mm)	0.00	0.00	0.00	0.00	0.08	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Substrate unconsolidated soft (pebble/gravel 10-	0.00	0.00	0.07	0.04	0.03	0.02	0.06	0.03	0.07	0.03	0.02	0.02	0.04	0.02

64mm)														
Substrate unconsolidated soft (coarse sand with shell fragments)	7.61	0.80	14.85	0.78	18.53	0.62	20.43	0.42	22.53	0.31	23.07	0.32	23.59	0.37
Substrate unconsolidated soft (sand/mud 2 mm no shell fragments)	0.00	0.00	0.07	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Substrate unconsolidated soft (mud/silt 64 um)	0.01	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Substrate consolidated hard (cobbles)	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.02	0.01	0.00	0.00	0.02	0.01
Substrate consolidated hard (rock)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00