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Deep-sea bio-physical variables as surrogates for biological assemblages, an example from the Lord Howe Rise

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ABSTRACT

Little is known about diversity patterns of biological assemblages in deep-sea environments, primarily because sampling deep-sea biota over vast areas is time consuming, difficult, and costly. In contrast, physical mapping capabilities are increasing rapidly, and are becoming more cost-effective. Consequently, the growing need to manage and conserve marine resources, particularly deep-sea areas that are sensitive to anthropogenic disturbance and change, is leading the promotion of physical data as surrogates to predict biological assemblages. However, few studies have directly examined the predictive ability of these surrogates. The physical environment and biological assemblages were surveyed for two adjacent areas – the western flank of Lord Howe Rise (LHR) and the Gifford Guyot - spanning combined water depths of 250-2200 m depth on the northern part of the LHR, in the Coral Sea. Multibeam acoustic surveys were used to generate large-scale geomorphic classification maps that were superimposed over the study area. Forty towed-video stations were deployed across the area capturing 32 h of seabed video, 6229 still photographs, that generated 3413 seabed characterisations of physical and biological variables. In addition, sediment and biological samples were collected from 36 stations across the area. The northern Lord Howe Rise was characterised by diverse but sparsely distributed faunas for both the vast soft-sediment environments as well as the discrete rock outcrops. Substratum type and depth were the main variables correlated with benthic assemblage composition. Soft-sediments were characterised by low to moderate levels of bioturbation, while rocky outcrops supported diverse but sparse assemblages of suspension feeding invertebrates, such as cold-water corals and sponges which in turn supported epifauna, dominated by ophiuroids and crinoids. While deep environments of the LHR flank and lower slopes of the Gifford Guyot were characterised by bioturbation with high occurrences of trails, burrows, and mounds, evidence for bioturbation was significantly less on the upper sections of Gifford Guyot, with mostly trails on the more sediment starved environments. The seamount summit also supported a variety of taxa, such as benthic ctenophores and rock-associated fishes that were not recorded in the deeper basin habitats. Physical characteristics of the seabed, particularly geomorphology, were good predictors of biological assemblage composition and percent cover of key taxa. Of the nine geomorphic classes assessed in this study, six predicted different physical habitats that supported distinct biological assemblages. However, other classes that were defined by spatial features (e.g., valleys, seamount dunes) where surficial physical variables were not unique, provided little predictive power of biological assemblages, but rather had characteristics that were shared with adjacent/surrounding geomorphic classes. Given the growing need to use surrogates in the management and conservation of marine environments, these results are promising. However, our findings suggest that there is a pressing need for careful testing and validation of surrogates, such as geomorphic classes, before classification schemes can be deemed effective and employed as a management tool to predict seabed habitats and their biological assemblages.

1. Introduction

The physical structure and composition of the seabed plays a critical role in the distribution and abundance of benthic assemblages. A wide range of physical variables are known to be important factors driving biological assemblage structure and species distributions (McArthur et al., 2010). For example, substrata type and complexity, topographic relief, sediment composition, and geomorphology of the seabed have all been identified as important descriptors of biological pattern (e.g., Jennings et al., 1996; Curley et al., 2002; Thrush et al., 2005; Anderson et al., 2009). Fine-scale bio-physical studies provide a critical understanding of these

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relationships, but the cost of biological sampling over large spatial extents is prohibitive, while direct extrapolation of fine-scale biological patterns over large management scales rarely captures the spatial complexity of these systems. Advances in acoustic technologies, such as multibeam and sidescan sonar, now mean that large areas of the deep seabed can be mapped quickly (on the order of $\sim$1000 km^2 per day at 1500 m depth) at high resolution ($\sim$30 m pixel) providing seabed maps that capture much of the physical complexity of the seabed (Gardner et al., 2003; Brown and Blondel, 2009). Where strong and predictable relationships exist between the physical structure of the seabed and the organisms that occur there, broad-scale ($\sim$100 km length scale) seabed maps or classifications may provide a valuable surrogacy tool for predicting large-scale occurrence, distribution, and abundance of marine organisms.

Classification of physical variables into seabed maps in the form of polygons, or surrogate classes (e.g., seascape, geomorphic, or habitat classes) is often used to infer biological patterns, and has been put forward as a potentially important management and conservation tool (e.g., Harris et al., 2005; Last et al., 2010; Anderson and Yoklavich, 2007). Given the increasing availability of habitat maps and the potential ability for habitat surrogates to be applied to management and conservation strategies, such as the designation of Marine Protected Areas (MPAs), it is necessary to examine and test the ability of surrogates to accurately predict biological pattern. An effective surrogate must be robust enough to take into account sources of mapping and biological uncertainty. For example, if a surrogate corresponds to the true habitat feature that the organism responds and orientates to (1:1 relationship), then it is likely to be a strong predictor in novel situations. Alternatively, a surrogate may implicitly, by virtue of its class definition, contain key finer scale habitat heterogeneity that, while unresolved at the map scale, still result in good predictive ability. Here, organisms may respond to finer-scale habitat heterogeneity and landscape features (e.g., edges), but these finer-scale habitat characteristics occur solely within a particular classification type. Regardless of the way in which a seabed class functions as a predictor, careful testing and validation are required before a classification scheme is deemed effective and employed as a management tool to predict seabed habitats and their biological assemblages.

Mapping the physical structure and composition of the seabed in shallow coastal environments has considerably advanced our understanding and management of these environments (e.g., Yoklavich et al., 2002; Rattray et al., 2009). Similar habitat mapping in deep-sea environments has received considerably less effort, largely due to the prohibitive costs associated with working in these remote environments. Consequently, mapping deep-sea environments and their biological assemblages and assessing the utility of physical surrogates has rarely been undertaken. Deep-sea benthic environments were once thought to be comparatively stable, comprising mostly homogeneous soft-sediments. But more recently the deep-sea benthos has been found to support high biodiversity (Dayton and Hessler 1972; Levin et al., 2001) and to be more dynamic and patchy than previously thought (Ruhl, 2008). Some have suggested that the biodiversity of some abyssal habitats may be comparable to tropical coral reefs (Grassle and Maciolek, 1992), although these patterns might be a function of low sampling effort over much vaster areas in the deep sea (Gray et al., 1997; Roberts et al., 2006). Geophysical studies of deep-sea environments have catalogued an assortment of geomorphic features including both physically complex raised features such as seamounts, banks, ridges and hydrothermal vents, as well as more expansive subdued features such as basins, valleys and abyssal plains (Heap and Harris, 2008). Biological studies have focused on features of particular interest such as seamounts and hydrothermal vents, reporting these features as biodiversity hotspots (Clark et al., 2006; Samadi et al., 2006; McClain, 2007). However, a lack of comparable studies on other deep-sea geomorphic features with similar/dissimilar substrata means there is inadequate information to provide a general view of the relationship between different geomorphic features and their biological assemblages (Przeslawski et al., 2011).

Cold water corals and sponges are important faunas of seamounts that are also found in other deep-sea systems, although information on the biology and distribution of deep-water sessile organisms is scarce (Stocks, 2004). Sessile suspension feeding faunas are often highly diverse in water depths of 200-1000 m, with some taxa occurring to depths of 4000 m (Freiwald et al., 2004). Many species of cold-water corals and sponges have emergent growth forms that provide food and shelter to other species (Beaulieu, 2001; Etnoyer and Morgan, 2005; Clark et al., 2006), and make them important habitat-formers that increase the habitat complexity of the benthos. Cold-water corals and sponges often have slow growth rates, fragile structures, and long lives compared to their shallow-water counterparts (e.g., bamboo coral in Andrews et al., 2009; Roark et al., 2009). As such, cold-water corals and sponges are particularly vulnerable to disturbance (Heifetz et al. 2009), with strong negative impacts of bottom trawling on cold-water-coral ecosystems found to last over a decade (Althaus et al., 2009). Changes in ocean circulation and acidification associated with climate change are also expected to affect growth and recruitment rates of cold-water-coral communities (Poloczanska et al., 2007). Consequently, there is strong management interest in the effects of human activities, such as coral harvesting, fishing and oil exploration, on these long-lived and fragile deep-sea organisms (e.g., Clark et al., 2006; Althaus et al., 2009).

Linking biological surveys with seabed maps provides a means to examine the feasibility of using physical habitat surrogates to predict biological assemblages. Video and camera surveys can traverse a broad range of deep topographic features over hard and soft substratum habitats to explicitly compare biological and physical patterns in the deep sea (Solan et al., 2003). Additionally, biological equipment, such as grabs, dredges and benthic trawls can also be deployed in a range of deep environments to provide fine-scale taxonomic resolution. Complementary video and camera surveys and *in situ* biological seabed sampling, when combined with physical data and maps, can provide comparative and detailed information on the distribution, abundance and spatial composition of benthic habitats and marine fauna and determine whether surrogates are effective predictors of biological pattern. In this study, we mapped the physical and biological environments of a 27,500 km^2 area in the northern section of the Lord Howe Rise (LHR) and examined the degree to which physical parameters of the seabed can be used to validate broad-scale geomorphic classifications and predict the composition of biological assemblages in these deep sea systems. Specifically, we measure the percent cover and presence of biological taxa from towed-video footage as a function of bathymetry, substratum hardness (backscatter), substrata type, habitat patchiness, and fine-scale geomorphology and relief. Biological epifauna and infauna were collected across the survey region to provide finer levels of taxonomic information and species-habitat associations. These data are then used to evaluate the viability of geomorphic surrogates in predicting biologically distinct assemblages in the deep sea.

2. Materials and methods

2.1. Study area

An area of $\sim$27,500 km^2 divided across two sections was surveyed on the northern part of the Lord Howe Rise plateau in

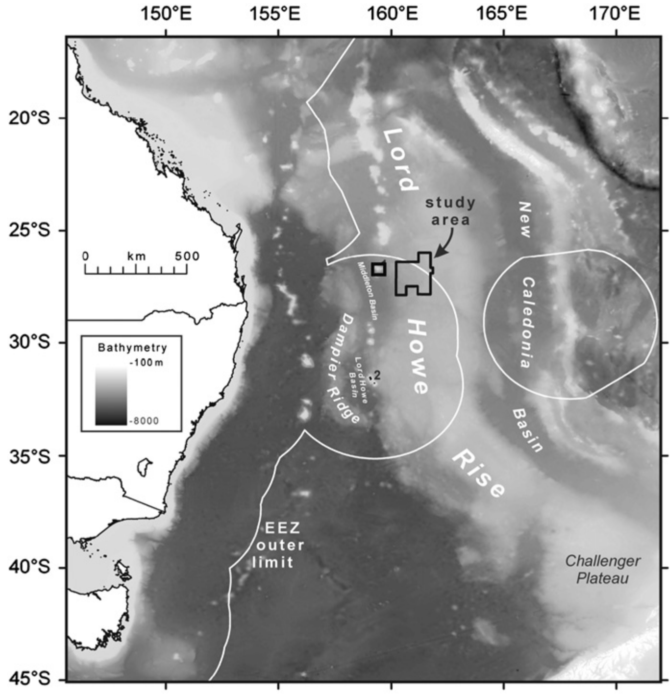

Fig. 1. Regional bathymetric map of the Lord Howe Rise (LHR) on the eastern margin of Australia. The two boxes show the location of the two study areas (Gifford Guyot, and the western flank of the LHR) on the northern Lord Howe Rise. LHI and arrow indicate the location of Lord Howe Island.

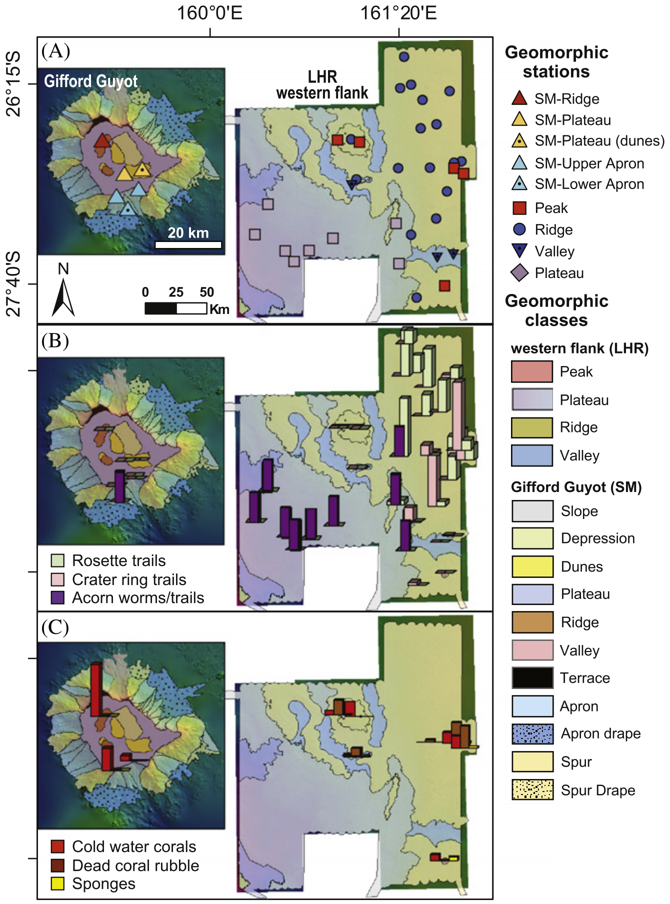

Fig. 2. Seabed bathymetric maps of the two study areas (Gifford Guyot, and the western flank of the LHR) on the northern Lord Howe Rise. (A) Station locations colour-coded by geomorphic classes, SM=Seamount; (B) Distribution and mean percent occurrence of three key soft-sediment fauna (rosette and crater ring trails and Acorn worms and trails (combined)), bar height range=1–34% occurrence; (C) Distribution and mean percent cover of three key rock outcrop fauna (cold-water corals, dead-coral rubble, and sponges), bar height range=1-18% cover.

the Coral Sea, between latitudes −26° to −28°S and longitudes 160° to 162° E on the outer reaches of Australia's Economic Exclusive Zone (Fig. 1). The LHR plateau is the largest bathymetric feature in the region extending 2800 km in length and covering an area of 1.95 million km^2 in water depths of 1300 m in the northeast (−26°18′S, 155°39′E) to 2600 m in the southwest (−27°50′S, 154°13′E). Previously, the geomorphology of LHR has been described only in general terms with the dominant features including an upper plateau, hills, valleys and terraces (Van der Linden, 1970), with greatest relief associated with the peaks of the Lord Howe seamount chain (Exon et al., 2004). The mapped area includes a ~25,500 km^2 area on the western flank of LHR, characterised by ridges, valleys, peaks and holes (Nichol et al., 2011), and a ~2,000 km^2 area that covers Gifford Guyot and surrounds. The guyot is a moderate-sized (>1600 km^2) flat-topped seamount that stands >2700 m high with a summit 260 m below sea-level (Heap et al., 2009), located approximately half way along the Lord Howe seamount chain (−26°45′S, 159°25′E) (Fig. 1).

2.2. Bio-physical data acquisition

The study area was acoustically surveyed in 2007 (7 October to 22 November) using a 30 kHz Simrad EM300 deep-water multibeam sonar system, mounted on the RV Tangaroa (Heap et al., 2009). The multibeam bathymetry was processed using Caris HIPS/SIPS v.5.4, and gridded to 50 m horizontal resolution, reflecting the beam footprint at nadir. Backscatter (or acoustic reflectance), which is a surrogate for substrate hardness, was processed using the methods described in Gavrilov et al. (2005) and gridded to 50 m horizontal resolution. The gridded bathymetry data were used to create a broad-scale geomorphic classification (>10 s km's) of the seabed (Nichol et al., 2011). Thus, geomorphic elements (e.g., peaks, holes, moats, scarps, polygonal furrows and aprons) were superimposed upon geomorphic units (e.g., ridges, valleys and plateaus), which were in turn superimposed over the Lord Howe Rise plateau.

To examine the fine-scale bio-physical composition and structure of the seabed within the mapped study area, 40 towed-video stations were sampled across the two survey areas (Fig. 2A) using the RV Tangaroa's towed video and still camera system DTIS (Deep Towed Imaging System): specific deployment details of the DTIS are provided in Heap et al. (2009). At each station an approximately 1 hr long video transect was surveyed (mean 52 min), with additional high-resolution (8-megapixel) still photographs captured every 15 s. Paired lasers, set 20 cm apart, projected onto the seabed within the field of view of the video and still camera provided a visual reference to help estimate the size of objects and organisms. In total, thirty two hours of seabed video footage, 6229 still photographs (i.e. those of sufficient quality) and 3413 seabed characterisations were acquired over ~64 linear km of seabed within the survey area. For each seabed characterisation, primary and secondary substratum type, geomorphology (bedform and relief), and presence of macro-biota (see Heap et al., 2009) were characterized using C-BED (Characterisation of the Benthos and Ecological Diversity) - the 3-tiered scheme of Anderson et al. (2008) and Nichol et al. (2009).

C-BED characterisations were scored for a 15-s section of video footage every 30 s along each video transect. Substratum composition (rock, boulders [>25 cm diameter], cobbles [6.5-25 cm diameter], sand and mud) was categorised into primary (>50% cover) and secondary (>20% cover) percent-cover using the protocol of

Stein et al. (1992), with substrata coded as 0, 20, 50, or 70% cover. Geomorphology was defined as a combination of 'bedform type' (e.g., sediment ripples, sediment waves, or hummocky) and 'vertical relief' (e.g., flat [0-0.3 m], low [0.3-1 m], moderate [1-3 m], high relief [>3 m], or rock wall [high relief and $>80^\circ$ incline]). Relief was an ordinal, semi-quantitative measure, with visual assessment of the seabed aided by the depth and altitude readings of the DTIS. Biotic composition was quantified by recording the presence of benthic macro-organisms identified to finest taxonomic category possible: groups (e.g., seastar and brittlestar), class (e.g., crinoids and anemones), broad ecological categories (e.g., fish, xenophyophores), or by the types of bioturbation (i.e. trails (evidence of epifauna), burrows and mounds (evidence of infauna), and distinct bioturbation marks (acorn worm trails, rosettes, and crater rings – Dundas and Przeslawski, 2009) (details in Heap et al., 2009). In addition, the percentage cover of key taxa (sponges, cold water corals, coral rubble, bioturbation) for each 15 sec period was post-processed to a precision of 5% intervals (0, 5, 10, - 100%). High-resolution still photographs and lasers were used to aid descriptions of the physical habitats and biota (e.g., xenophyophores and benthic ctenophores). Data were entered using a pre-programmed keypad (© 2008 Cherry) into 'GNav Real-time GIS Tracker' software (© Gerry Hatcher, 2002) following the protocol of Anderson et al., (2008) and Nichol et al. (2009).

Sediment and biological samples were also collected across the survey area using a range of sampling gear (Heap et al., 2009). Surface sediments were sampled at 35 stations using a benthic sled, grab, boxcore and piston core. Biological specimens were collected from 36 stations across the study area, with biota found on (*cf.* epifaunal) and in (*cf.* infaunal) sediments recorded from epifaunal (11 epibenthic sled and 13 dredges) and infaunal (15 boxcores) sampling gear (Heap et al., 2009). Specimens collected (e.g., molluscs, crustacea, ophiuroids, worms) are used to aid descriptions of the biological assemblages present within physical habitats of the northern LHR, but due to very low numbers are not included in analyses.

2.3. Analyses

Data were processed and analysed using SAS (Statistic Analysis System, SAS Institute Inc., 2001 v.9.1). Bathymetry and backscatter data, along with geomorphology categories, were acquired in ArcGIS (ESRI v.9.2). Area sampled per transect was calculated as the transect length (measured using the Hawth's Tools in ArcGIS) multiplied by transect width (estimated as 2 m field of view). Backscatter was treated in two ways: mean backscatter was calculated for each transect to represent the average substratum hardness, while the range of backscatter values represented the variability of hardness within the transect. Habitat relief was re-categorized as an ordinal variable with values of 1, 2, 3, 4 that corresponded with flat, low, moderate and high relief (incl. rock wall). Two forms of habitat patchiness were measured along each transect: the total number of substrata types (nhab) and the number of habitat transitions (patchiness) from one habitat type into another. Physical variables derived from multibeam variables (depth, mean and variability of substratum hardness) along with habitat variables such as substrata and relief were square root transformed to normalise data distributions and stabilise variance and mean relationships; 'patchiness', which was heavily right-skewed, was normalised by a $\log_{10}$ transformation; while 'nhab' was normally distributed and left untransformed. Means and standard errors were calculated for the percent cover estimates of key taxa (i.e. cold-water corals, sponges, coral rubble, and bioturbation) and are presented graphically. Percent occurrence estimates were calculated for substrata, geomorphology, and macro-organism categories as the number of 15-sec data points where the category type was recorded, as a function of the total number of points sampled within either a particular geomorphic class, or sub-class as defined.

The correlation structures of the physical and biological data were examined using Principal Components Analysis (PCA) using the SAS system PRINCOMP procedure on the correlation matrix of the transformed benthic habitat variables and the transformed biological variables. No excessive collinearity was observed and bivariate relationships between variables were generally linear or monotonic. To evaluate if geomorphic classifications, defined by the physical variables, were adequate predictors, and thus good surrogates of LHR biological assemblages at the scale of the survey area, we undertook a two-staged analytical approach. First, to examine the relationship between physical variables and geomorphic classes, we ran Canonical Discriminant Analyses (CDA) using the SAS system CANDISC procedure on the transformed physical variables. This method was then repeated on the transformed biological variables. Then, to evaluate how well geomorphic classes predicted the physical variables and the biological assemblages, Discriminant Function Analyses (DFA) were conducted on both the physical and biological data matrices using the SAS system DISCRIM procedure, with equal prior probabilities. DFA classification error rates (misclassification) were measured by cross-validation to determine if each individual sample was correctly classified into its defined geomorphic class. The null probability of random allocation to a category assuming equal priors was 0.167, with values higher than this in the DFA misclassification tables indicating better than random predictive ability. Classification Trees (CT) were also calculated using the rpart function (Therneau and Atkinson 2009) in the software package R for habitat and biota. CT were pruned to minimise re-substitution error, and cross validation rates were calculated, but are not presented as these provided no additional information.

3. Results

3.1. Geomorphology and sediments of the LHR and Gifford Guyot

The surveyed area of the western flank of northern LHR were characterised by a near continuous sediment cover across ridge, valley, plateau and basin features (25,500 km^2) (Nichol et al., 2011). The summit and upper slopes ($<\sim 1000$ m water depth) of the Gifford Guyot were draped in a thin layer of coarse sand, while the lower slopes of the seamount and LHR flank were draped in much finer-grained sandy-mud. Complex rocky features were also mapped on the Gifford Guyot and on the LHR flank but in total covered only 52 km^2 (2%) of the mapped area. On the LHR flank, rock outcrops were associated with 16 volcanic cones that ranged in height from 65-450 m (31 km^2, 0.11% of mapped area), four small ridges with heights up to 120 m (151 km^2, 0.6%), along with smaller outcrops identified from video that were too small to be resolved in the multibeam maps ($<$ 50 m in size, 1.1% of LHR video transects). On the Gifford Guyot, three isolated rocky ridges, 10-30 m high, were mapped on the summit (21 km^2, 1.3%), while the upper-slopes of the seamount had partially exposed rock ledges identified from video, but not resolved in the multibeam map (24.7% of upper-slope video transects). Complexity of the seabed was also scale dependent. While broad-scale features ($>$ 100's m) such as moats, polygonal cracks, and scarps were mapped (Nichol et al., 2011), video observations of these features identified mostly flat homogeneous soft-sediments (79% occurrence), with rare occurrences of sediment waves and ripples ($<$ 2%). Likewise, rock outcrops that were bathymetrically complex at broad-scales (10-450 m elevation) were at finer-scales of metres observed to be mostly low- or flat-relief surfaces with only rare occurrences of moderate to high relief outcrops (1.8 and 1.6%, respectively).

The volcanic peaks and small ridges of the LHR were mostly manganese-encrusted basalt with low-relief surfaces, making them relatively resistant to physical damage (e.g., anthropogenic impacts, such as trawling), with rare occurrences of higher relief structures. In contrast, the rocky ridges on the Gifford Guyot summit comprised more fragile limestone that is likely to be more vulnerable to physical disturbance.

3.2. *Geomorphic classes as surrogates for biological assemblages*

At broad spatial scales, physical variables distinguished six distinct geomorphic classes (peaks, seamount ridges, sediment-covered ridges, plateau, seamount plateau and seamount apron) out of the nine geomorphic classes sampled (Figs. 2, 3, Tables 1-3). Discrimination of the six classes was based on a combination of substrata type and/or sediment composition, depth, and the degree of habitat patchiness, while the remaining three classes displayed strong affinities with other classes (Figs. 2, 3, Tables 1-3). Assemblage composition also differed between the six geomorphic classes (Figs. 2B-C, 4, Table 3), indicating that these classes were valuable predictors of biological pattern. However, two additional geomorphic classes ('valleys' and 'seamount dunes') along with the lower section of the 'seamount apron' were the exceptions. The geomorphic class 'valley' was located at intermediate depths (1600–2200 m) between ridges and plateaus, but did not have distinct bio-physical characteristics; indeed, biological characteristics of valleys were indistinguishable from those of 'sediment-covered ridges' (Figs. 3, 4), and were subsequently pooled with sediment-covered ridges in further analyses. Similarly, 'seamount dunes' which were characterised by linear bedforms 2-6 m high with wavelengths of 150-250 m in the multibeam map, had bio-physical attributes that were indistinguishable from the adjacent and surrounding plateau (no dunes), and thus were pooled with seamount plateau (Figs. 3, 4). Although the upper-apron on the seamount was characterised by a distinct habitat and assemblage, the lower sections of this geomorphic class (seamount lower apron) had bio-physical characteristics that were more similar to the LHR plateaus, which occurred at the same depth (Figs. 2, 3). Given the lower number of stations (2 upper, and 1 lower) these geomorphic classes were analysed together, although misclassification rates were examined by sub-class (upper vs. lower) relative to other classes. The final six distinct geomorphic classes (incorporating the pooled sub-classes) predicted distinct habitat and assemblage types, although some similarities and overlaps, particularly between the sediment-covered ridge feature and the plateau, are described below and resulted in higher misclassification rates (Tables 1,2).

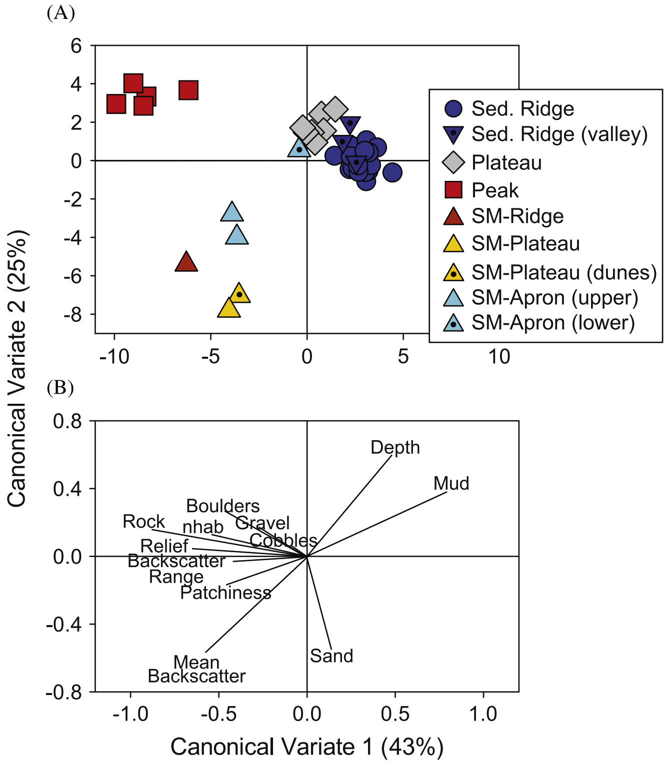

Fig. 3. . Ordination of the physical variables by Canonical Discriminant Analysis (CDA). (A) Reduced space plot colour coded by the nine geomorphic classes. (B) The structure coefficients of physical variables (labels are centred) associated with each axis. Vector lines describe the direction of change and correlation of physical variables with geomorphic classes. 'nhab' = number of habitats.

3.2.1. *Volcanic peaks (rocky outcrops)*

Sixteen volcanic peaks were mapped within the LHR flank survey area in depths of between 950-1700 m (Table 3; Nichol et al., 2011), with five peaks sampled across a similar depth range (1064-1628 m). The height of peaks ranges from 65-450 m with slopes of 10-30°. Volcanic peaks occurred in intermediate depths with high mean backscatter (broad-scale hardness) (Fig. 3), reflecting mostly homogeneous rocky substrata (71% of transects), with sandy-muds (15%) and mixed substrata (14%). Video characterisations identified that at fine-scales the sides of these peaks were of low (48%) or flat (44%) relief, with only rare occurrences of moderate relief (5%) or rippled sediments (3%). The rocky substrata of peaks had sparse coverage of sessile organisms, characterised by mixed cold-water corals (e.g., *Metallogorgia* sp., *Callogorgia* sp., black corals (Order: Antipatharia), sponges (Class: Demospongiae and Hexactinellida (glass sponges)), and dead coral rubble (Figs. 5, 6C,E,F,G,I, 7A,C), but supported no dense habitat-forming biota.

A diverse mixture of cold-water corals was present across much of

Table 1

Discriminant Function Analysis (DFA) cross-validation misclassification rates and sample effort for LHR Geomorphic classes determined from the physical data. Bold text and values depict the percentage of stations correctly classified for a given geomorphic class, while underlined values in other columns of a given row indicate the percentage of stations misclassified into other geomorphic classes. SM-Apron was analysed as a combined class, but misclassifications rates are separated here for interpretation. SM-Ridge had only one value, so the within-class covariance matrix could not be evaluated. Sed. Ridge = Sediment-covered Ridge.

Geomorphic Class (from)	**% classified (into)**						***No. of stations***
	SM-Ridge	SM-Plateau	SM-Apron	Peak	Sed. Ridge	Plateau	
SM-Ridge	**100**	0	0	0	0	0	*1**
SM-Plateau (+ SM-dunes)	0	**100**	0	0	0	0	*3*
SM-Apron (Upper)	0	0	**100**	0	0	0	*2*
SM-Apron (Lower)	0	0	**0**	0	0	100	*1*
Peak	0	0	0	**100**	0	0	*5*
Sed. Ridge (+ Valleys)	0	0	0	0	**83.33**	16.67	*24*
Plateau	0	0	0	0	44.44	**55.56**	*9*

Table 2
Discriminant Function Analysis (DFA) cross-validation misclassification rates and sample effort for LHR Geomorphic classes determined from the biological data. Descriptions and definitions are provided in Table 1.

Geomorphic Class (from)	% classified (into)						*No. of stations*
	SM-Ridge	SM-Plateau	SM-Apron	Peak	Sed. Ridge	Plateau	
SM-Ridge	**100**	0	0	0	0	0	*1**
SM-Plateau (+ SM-dunes)	0	**100**	0	0	0	0	*3*
SM-Apron (Upper)	0	0	**100**	0	0	0	*2*
SM-Apron (Lower)	0	0	**0**	0	0	100	*1*
Peak	0	0	0	**100**	0	0	*5*
Sed. Ridge (+ Valleys)	0	0	0	0	**79.17**	20.83	*24*
Plateau	0	0	0	0	11.11	**88.89**	*9*

Table 3
Biologically distinct geomorphic features: Geomorphic features were classified from seabed maps and physical data collected from the survey (TAN0713). Biological characterisations were determined from towed-video footage and still photographs of each geomorphic region. SM = seamount, H1 = habitat type 1, H2 = habitat type 2.

Geomorphic Feature	Area (km^2)	Depth range (m)	No. of video images	Dominant substrata	Characteristic biota	Vulnerability
Peak	30	1000-1650	916	Rock (Volcanic)	Sparse sessile invertebrates (e.g. octocorals, sponges)	High
SM-Ridge	21	260-300	77	Rock (Limestone)	Sparse sessile invertebrates (e.g. octocorals), SM fishes	Mod-high
Sediment-covered Ridge (+ Valley)	12,723	1300-1700	2,010	H1: Sandy-mud; H2: outcrops	H1: Bioturbation (e.g. crater ring trails); H2: sparse/dense sessile invertebrates	H1: Low; H2: High
Plateau (SM lower-apron)	12736	1700-2200	681	Sandy-mud	Bioturbation (e.g. acorn worms & trails)	Low Low
	208	2000-2200	25	Sandy-mud	Bioturbation (e.g. acorn worms & trails)	
SM-Plateau (+ SM-Dunes)	286	300-350	185	Sand & rubble (Limestone)	Low bioturbation, very sparse invertebrates, incl. benthic ctenophores.	Mod
SM-Apron (SM upper-apron only)	330	350-1500	188	Sand & rock (Volcanic & Limestone)	Low bioturbation, very sparse small invertebrates (< 3 cm height).	Mod

this habitat (55% total occurrence), but only in low percent cover (mean cover 4.5%, range 0-18%), while sponges (mostly glass sponges) were present in even lower percent cover (18% occurrence; mean cover 1%, range 0-20%; Fig. 5). Cold-water corals and glass sponges supported other species in their branches, such as brittlestars (e.g., *Ophiocreas oedipus*, *Ophiophycis johni*, *Asteroschema tubiferum*) and crinoids (Fig. 6B,E,G). Coral rubble (dead fragments of cold-water corals) was commonly recorded on the seafloor of all peaks (Figs. 2C, 5, 7C), with collections of sub-fossil corals (ages yet to be determined). The distribution of coral rubble was patchy with highest percentage cover recorded on the tops of peaks where in places it covered up to half of the seafloor (mean 5.3%, range 0-55%; Fig. 5). Importantly, live corals including the bamboo coral, *Keratoisis* sp., were only recorded in low numbers (0-4% mean cover). This low cover did not explain the amount of coral rubble present on volcanic peaks, indicating that coral rubble may have accumulated over long time periods, or possibly reflects some past die-off event. Motile species such as shrimp and prawns (10% occurrence), fishes (4%), and jellyfish (1%) were only sporadically recorded, while crinoids, including stalked forms (3%; e.g. Fig. 6A,D), brittlestars (1%) and seastars (1%) were rare.

3.2.2. Seamount ridges (rocky outcrops)

Three discrete seamount ridges were mapped on the Gifford Guyot summit in waters depths of 250-300 m (Heap et al., 2009). These seamount ridges varied in size (2-8 km long and 1-3 km wide) and height (10-30 m) and were characterised by high and variable backscatter hardness in shallow-water depths (Fig. 3). Only the largest ridge was sampled, which was characterised by rock substrata (94%) with some sandy sediments (6%) of mostly low relief (83%), with rare occurrences of either moderate or flat relief (7 and 6%, respectively). The seamount ridge also supported high occurrence (100%) but surprisingly low percent cover (13.1% +- 0.56% SE) of attached sessile invertebrates, characterised by a mixed cold-water coral (100% occurrence; mean cover 12.8%, range 2-22%) and sponge (10.4% occurrence; mean cover 0.2%, range 0-4%) assemblage (Figs. 2C, 4, 5, 7B). In contrast to the peaks on the LHR flank, cold-water corals on the Gifford Guyot were characterised by *Plexipomisis* sp., *Villogorgia* sp., *Muriceides* sp., *Psuedothesea* sp., *Narella* sp., *Keroeides* sp.. However, some cold-water coral genera (e.g. *Umbellulifera* sp., *Chrysogorgia* sp. D) were common to both peaks and seamount ridges. Seamount ridges also supported typical seamount fauna, including the seamount Xanthid crab, *Alainodaeus rimatara*, and high occurrences (34%) of seamount-associated fishes (e.g., *Parapercis binivirgata* (Fig. 7B), *Parapercis* sp. 2; *Hoplostethus intermedius*, rays, gurnard, small banded eel, *Neopriprion* sp., *Plectranthias* sp., *Eeyorius* sp., *Foetorepus* sp., Scorpaenidae, and the deep-water trumpetfish, *Fistularia commersoni*). In contrast, shrimp/prawns and jellyfish were absent from this geomorphic class.

3.2.3. Sediment-covered ridge (soft-sediment with isolated rocky outcrops)

The second most dominant geomorphic class was the 'sediment-covered ridge' that represented a large geomorphic ridge feature located along the eastern section of the LHR flank, in water depths of ~1300-1700 m (Table 3; Nichol et al., 2011). This ridge feature is draped in pelagic carbonate ooze up to ~500 m in thickness (Geoscience Australia, unpublished seismic data).

The surficial sediments covering the ridge and the valleys that bisect it, were both characterised from video as homogeneous flat bioturbated sandy-mud (92% occurrence), with occasional but discrete outcrops of hard substrata (7% occurrence), and rippled sands (1%; Fig. 3). The sediment-covered ridge (pooled with valleys) was characterised by high levels of bioturbation (81% occurrence, mean cover of 25%; Figs. 4, 5) that included a wide range of burrows (61% occurrence), trails (40%), and mounds (39%), as well as rosettes and crater rings (8.2% and 4.8% occurrence, respectively; Fig. 7G). Otherwise, few epifaunal organisms were recorded in these soft-sediments (Fig. 5). Finer-scale patterns were also present. Although rosettes and crater rings were often seen together, crater rings were more common in the sediment-covered ridge in northern regions, while rosettes were more common in mid-ridge regions (Fig. 2B), indicating that other factors varying over finer spatial scales were also important.

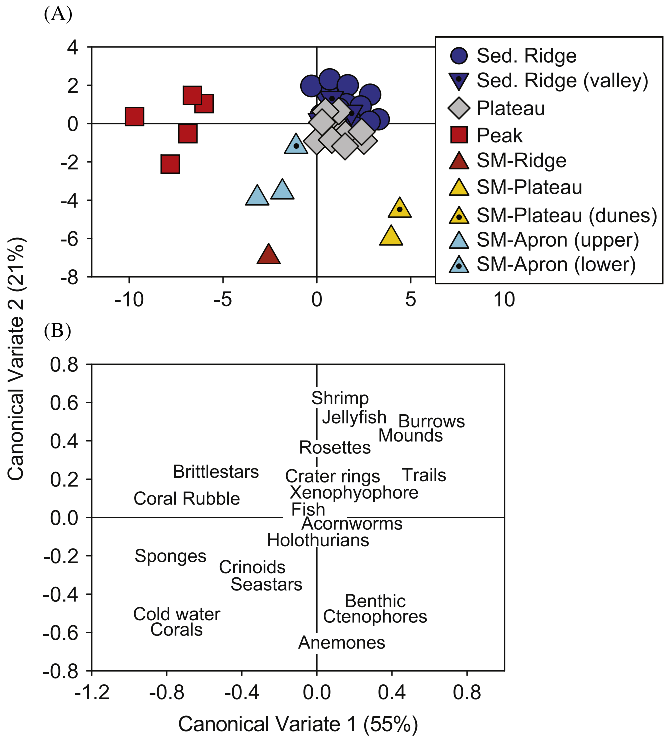

Fig. 4. Ordination of the biological variables by Canonical Discriminant Analysis (CDA). (A) Reduced space plot colour coded by the nine geomorphic classes. (B) The structure coefficients of the biological variables (labels are centred) associated with each axis.

Localised rock outcrops were also present within the sediment-covered ridge class, mostly along the flanks where slopes were greater than ~10°. These outcrops were observed in video, but only four were large enough to be resolved in the multibeam maps. Although rare in the sense of areal coverage, these rock outcrops supported some of the highest percent cover of sessile suspension feeders (up to 80%) (Fig. 7E). Within the sediment-covered ridge class, eight rock outcrops were sampled in depths ranging from 1350-1700 m. Ridge outcrops varied in size from ~3-70 m, and were mostly flat to low relief rock (36.5%, each), with rare occurrences of moderate (24.4%) or high (2.4%) relief features. Overall distribution of sessile invertebrates on these rock outcrops was highly patchy with an overall mean cover (7% ±2.1% SE, range 0-80%) dominated by diverse cold-water corals (5.8% ±1.9% SE, range 0-70%) and sponges (1.3% ±0.3% SE, range 0-10%) (e.g., Fig. 6B,H, 7E). Coral rubble (collections of sub-fossil corals) were also patchily recorded on these rock outcrops (mean cover 7% ± 1.1% SE, range 0-50%), with highest cover recorded on the largest (~22 km^2) rock outcrop (mean 18.6%, range 5-35%) (Fig. 2C). Golden corals (Family: Chrysogorgiidae) entwined with *Asteroschema tubiferum* brittlestars (Fig. 6B) were also characteristic of these ridges, along with bamboo corals, *Keratoisis* spp., which were more common in ridge-outcrops than all other geomorphic features. Motile species, such as shrimp/prawns (17%), fishes (10%), and jellyfish (7%) were ubiquitous (Fig. 4), with fish dominated by the family Macrouridae (grenadiers, rattails).

3.2.4. Plateau (soft-sediment)

The soft-sediment plateau was the most dominant geomorphic class of the LHR flank, and was also the deepest with water depths of ~1700-2200 m (Table 3; Nichol et al., 2011). This geomorphic class also supported the thickest deposit of pelagic carbonate ooze (~1-6 km in thickness: Geoscience Australia, unpublished seismic

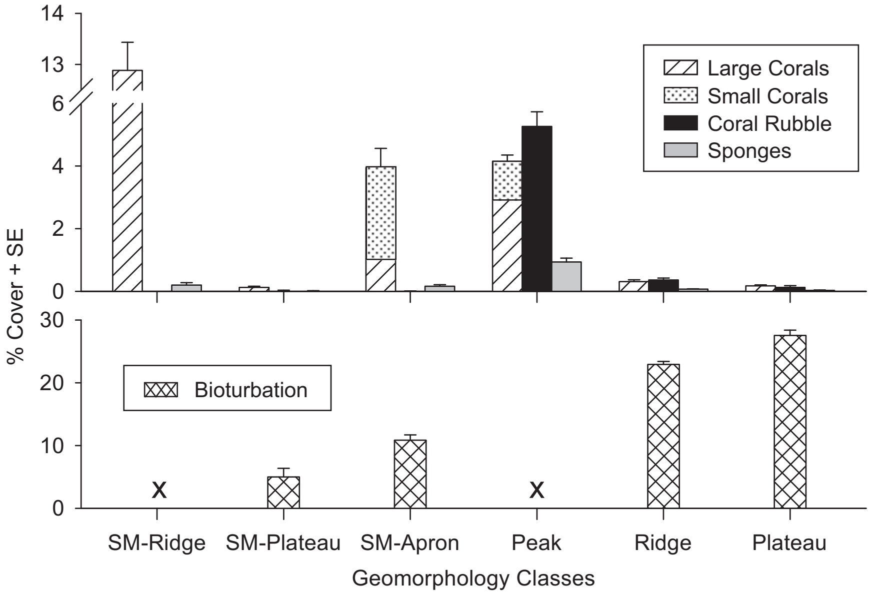

Fig. 5. Percent cover of key epibenthic taxa (cold water corals, sponges, and coral rubble) and bioturbation levels by geomorphic classes. SE = standard Error; x = no bioturbated sediments; small corals [< 3 cm height] large corals [≥ 3 cm height].

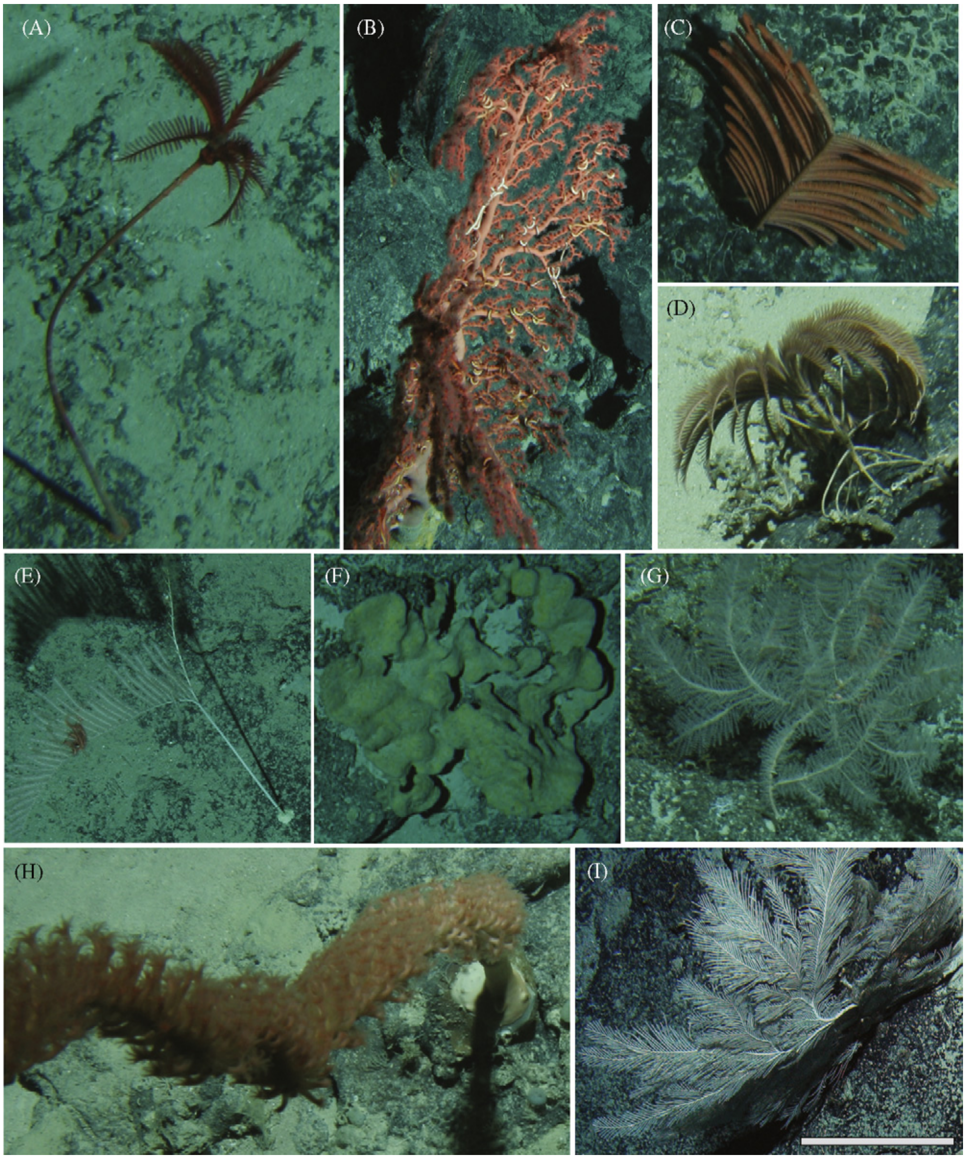

Fig. 6. Suspension feeding invertebrates of the northern Lord Howe Rise. (A) Volcanic Peak (1,580 m) with stalked crinoid attached to the seabed; (B) Sediment-covered Ridge with isolated rock outcrop (1386 m) supporting a gorgonian fan, *Paragorgia* sp. (Family: Paragorgiidae), with numerous brittlestars in its branches; (C) Volcanic Peak (1329 m) with attached black coral; (D) Volcanic Peak (1328 m) with stalked crinoid; (E) Volcanic Peak (1187 m) with large gorgonian fan, *Pleurogorgia plana* (Family: Chrysogorgiidae, golden corals); (F) Volcanic Peak with isolated rock outcrop (1015 m) with large yellow encrusting sponge; (G) Volcanic Peak (979 m) with branching gorgonian, *Thouarella* sp. (Family: Primnoidae, bottlebrush corals); (H) Sediment-covered Ridge (1526 m) with large unbranched whip-like gorgonian (Family: Primnoidae); (I) Volcanic Peak (975 m) with branching gorgonian (Family: Primnoidae).

data). The surficial sediments of the plateau were characterised by homogeneous flat bioturbated sandy mud sediments (100% occurrence) with no rock outcrops recorded. Based on surficial physical variables, plateaus were not uniquely different from other soft-sediment geomorphic classes (e.g., the sediment-covered ridge and valleys), except for their greater depth (Fig. 3). This deepest soft-sediment class did, however, support a different biological assemblage (Figs. 2B, 4, 5, Table 3). The plateau was characterised by the highest levels of bioturbation (99% total occurrence, including burrows [86%], trails [95%], and mounds [62%]; mean cover of 28%), the presence of acorn worms (Phylum Hemichordata, Class Enteropneusta) and their distinctive spiral or meandering trails (7% occurrence; 5.9 acorn worms and 56.1 acorn trails per km^2), and the absence of rosettes and crater rings (Figs. 2B, 5, 7H). Otherwise, like the sediment-covered ridge, the plateau supported very few epifauna, of which most were soft-sediment-associated invertebrates, such as gorgonian whips and sea-pens (6% total occurrence). On the flanks of Gifford Guyot, deeper parts of the seamount apron (lower apron >1500 m) supported habitats and assemblages indistinguishable from those of the plateau (Fig. 4, Tables 1, 2), suggesting that in terms of biological assemblages these features were not unique, but rather could be lumped into one geomorphic class. Motile species, such as shrimp/prawns (20%), fishes (5%), and jellyfish (1%) were again ubiquitous, with fish also dominated by the family Macrouridae (grenadiers, rattails).

Not all taxa were clearly separated between the sediment-covered ridge and the plateau. Instead, several taxa occurred across the boundaries of these two geomorphic classes, indicating that the depth distributions of taxa were not specifically correlated with geomorphic class boundaries. For example, acorn worms and their trails, which were recorded in depths of 1550-2200 m (Anderson et al., 2011), were one of the key taxa of the plateau. While 94% of all acorn worms and trails were recorded in the plateau, acorn worms and trails were also recorded in the deeper locations of ridges

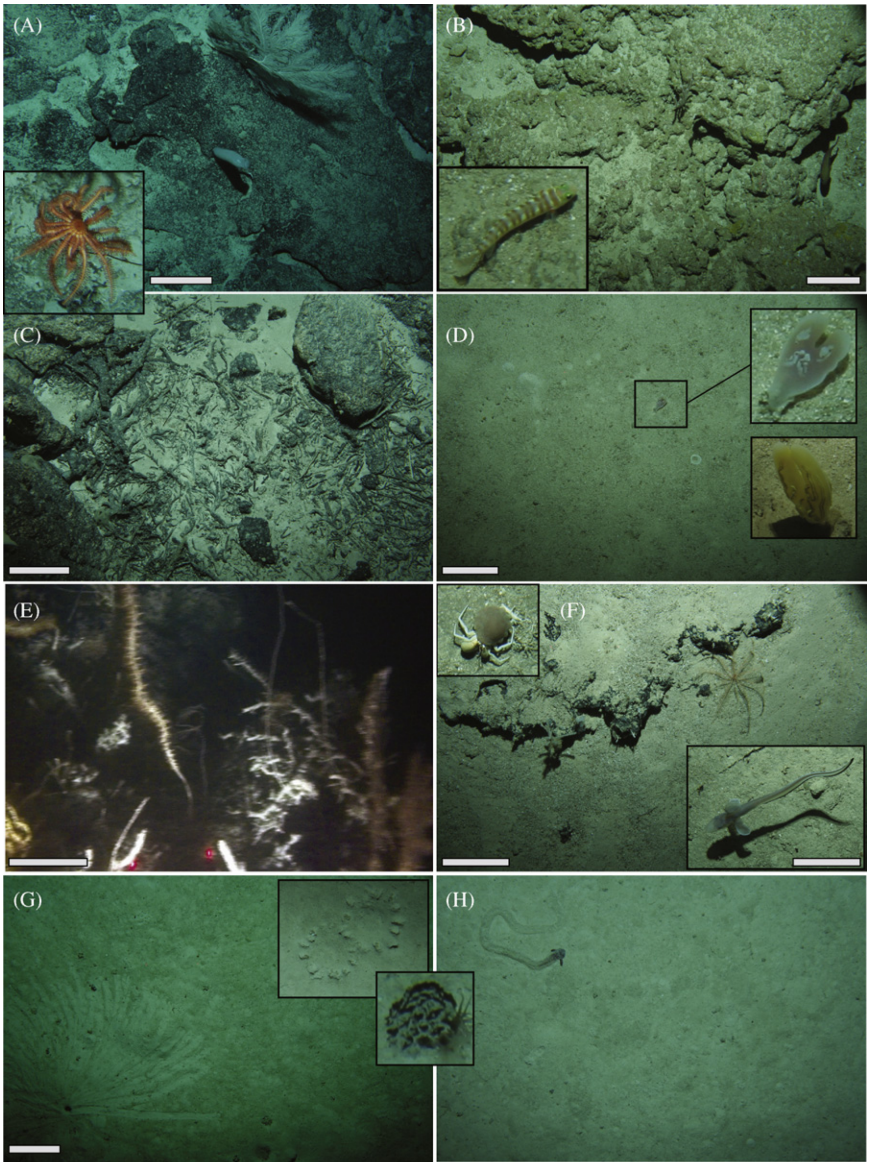

Fig. 7. Seabed habitat types and assemblages of the northern Lord Howe Rise. (A) Volcanic Peak (basalt) with tubular sponge and octocoral fan, [inset=orange crinoid – 115 mm diam.]. (B) Seamount Ridge (conglomerate limestone) with small octocoral and *Eeyorius* sp. [inset: *Parapercis binivirgata* - 110 mm TL]. (C) Volcanic Peak with dead Scleractinian rubble. (D) Seamount Plateau with benthic ctenophores (comb jelly) and sand dollars [top inset: benthic ctenophore - 120 × 70 mm], [bottom inset: benthic ctenophore - 56 × 29 mm]. (E) Sediment-covered Ridge with discrete rock outcrop and dense cover of octocorals. (F) Seamount upper-apron, with rock ledge draped in coarse sediment and shell debris with small octocorals and crinoid [top inset: hermit crab living under the zooanthid anemone, *Epizoanthus paguriphilus*, – 36 mm diam.], [bottom inset: Jellynose fish, *Ateleopus* sp., – 550 mm TL]. (G) Bioturbated sediment-covered ridge with rosette, [top inset=crater rings, ~235 mm diam.], [lower inset: Xenophyophore - ~35 mm diam.]. (H) Soft-sediment Plateau with acorn worm and its meandering trail. Scale bars=20 cm.

(> 1550 m: 6% of acorn worm and trail records) (Fig. 2B). Similarly, a commonly recorded reticulate xenophyophore - a large benthic deep sea foraminifera (Phylum Foraminifera, class Xenophyophorea) (Fig. 7G) - was often recorded in high numbers (up to 32 tests per still photograph) in depths from 1300-2200 m in both ridges (depths > 1300 m) and plateaus (all depths). This overlap in species distribution between ridges and plateaus may explain the higher misclassification rates between these two geomorphic classes (i.e. 20.83% of ridges misclassified as plateaus, and 11.11% of plateaus misclassified as ridges: Tables 1, 2).

3.2.5. Seamount plateau (soft-sediment and patchy rubble)

The summit of the Gifford Guyot incorporates a plateau in water depths of 260-350 m (Table 3; Heap et al., 2009), that is characterised by sand and muddy sand with high fine-scale patchiness (Fig. 3). Fields of sand dunes were distinguished on the plateau from multibeam imagery, but their physical and biological attributes were indistinguishable from the adjacent and surrounding plateau, suggesting that these geomorphic classes (i.e. seamount plateau and dunes) provide similar physical environments to biological assemblages, and therefore in terms of biological prediction should be combined. Seamount plateau, combined with seamount dunes, comprised homogeneous flat sands (79% occurrence) of variable thickness that were interspersed with patches of exposed low-lying limestone rubble (21% occurrence; Fig. 7D). The biological assemblage of the seamount plateau was also characterised by high occurrence of bioturbation (70% - burrows [48%] trails [34%], and mounds [30%]), but at significantly lower levels than other soft-sediment classes (mean cover of 5% ± 1.4%, range 0-15%; Fig. 5). Characteristic sessile invertebrates included benthic ctenophores ('comb jelly', order: Platyctenida; Fig. 7D), which were unique to this geomorphic class (47% occurrence), cold water corals (7.6% occurrence), soft-sediment anemones (2.4%) and sponges (1%), but overall their cover was negligible (mean cover 0.13 ± 0.037). The seamount plateau also supported a variety of seamount-associated epifauna dominated by the sand dollar, *Peronella hinemoae* (Echinoidea), but also included species unique to this geomorphic class (e.g., the brittlestars, *Dictenophiura platyacantha*; the cushion seastar, *Pteraster obesus*; and the predatory gastropods: *Phos alabastrum* and *Conus* sp. [possibly '*Conus luciae*']), along with more generic fauna (e.g., the brittlestar, *Ophiomusium scalare*). Motile species, however, such as shrimp/prawns (3%), fishes ($<2\%$, e.g. gurnard), and jellyfish ($<2\%$) were rarely seen in this habitat.

3.2.6. *Seamount Upper Apron (soft-sediment with rock outcrops)*

The sides (seamount apron) of the Gifford Guyot consist of debris slopes (angle of $\leq 19^\circ$) in water depths from 350 m at the edge of the summit down to 2300 m (Table 3; Heap et al., 2009). The upper-apron of the seamount (350-1500 m) was characterised by patchy rock and sand substrata in intermediate depths (Fig. 3) that represented low-lying rock ledges interspersed and partially draped by coarse sand and fine shell debris (Fig. 7F). In contrast to the lower apron, which was comprised of homogeneous bioturbated sandy-mud (see Section 3.2.4), the upper-apron was characterised by mixed rock and sand that comprised 49% of the seabed, interspersed with homogeneous sands (41%) or homogenous rock outcrops (10%). Upper-apron sediments were generally flat (91%) with some rippled sediments occurring near rock outcrops (9%), while rock ledges were mostly low-lying (50%) or flat (33%), with rarer occurrences of moderate (11%) and high (6%) relief. Sediments on the upper-apron also had the second lowest levels of bioturbation (36% occurrence, mean cover of 10.9% ± 0.83%, range 0-25%), second only to the seamount plateau (Fig. 5). Bioturbation was characterised mostly by trails (33%), while burrows were rare (10%) and mounds were absent, indicating that surface sediments of the upper-apron were stable enough to support epifaunal bioturbators, but were possibly too thin to support high levels of infaunal bioturbators. A key characteristic of the upper apron was the high occurrence (54%) and dominant cover (mean cover 4.2% ± 0.63%, range 0-45%) of very small (<3 cm in height) cold-water corals - possibly the lace coral, *Stylaster* spp. (Figs. 5, 7F). A range of fish species were unique to the upper apron. These included numerous big-spined boarfish *Pentaceros decanthus*, associated with the mixed rock and sand patches (8% occurrence); the thorny tinselfish, *Grammicolepis brachiusculus*; the Jellynose Fish, *Ateleopus* sp. (Fig. 7F); and the tripodfish, *Bathypterois longifilis*. Shrimp/prawns were common (11% occurrence) and included the armoured Goblin shrimp, *Glyphocrangon* sp., with gravid females. As with the summit, jellyfish were absent from the upper apron.

4. Discussion

4.1. *Spatial patterns of habitats and associated biota*

This study presents descriptive and quantitative information on deep-sea habitats of the northern LHR and provides the first comparative examination of the physical habitat and the biological assemblages across a range of deep-sea geomorphic features. Physical characteristics of the seabed, particularly geomorphology, were good predictors of biological assemblage composition and percent cover of key taxa. Of the nine geomorphic classes assessed in this study, six predicted different physical habitats that supported distinct biological assemblages. Two additional geomorphic classifications based on other criteria, such as shallow-gradients (e.g., valleys) or subsurface features (e.g., seamount dunes) where surficial physical variables were not unique, provided little discriminative power of biological assemblages, but rather had characteristics that were shared with adjacent/surrounding geomorphic classes. However, while different geomorphic classes in general had both distinctive habitat features and characteristic assemblages, substratum type (hard vs. soft substrata) and depth were the main variables driving these patterns.

The surveyed area of the northern LHR was characterised by overall low numbers and sparse cover of epifaunal organisms, both in the expansive soft-sediments and on the isolated rocky outcrops. Hard substrata supported diverse sessile and motile assemblages, but percent cover was extremely low compared to the availability of hard substratum. Studies in other deep-sea rocky environments have recorded dense assemblages of cold-water corals and sponges, particularly on the hard substrata of seamounts where matrix-forming corals can provide substantial refugia to a diverse epifauna (Koslow et al., 2001; Rogers et al., 2007; Pitcher et al., 2007). Depth-associated assemblage patterns have also been identified, with densities of sessile invertebrates decreasing with depth (Lampitt et al., 1986; Koslow et al., 2001; Rogers et al., 2007). Therefore, while the deeper rocky outcrops on the western flank of the LHR might be expected to support sparser assemblages, even the shallow rocky outcrops on the summit of the Gifford Guyot supported similarly low numbers and cover of epifauna.

Rocky habitats of the Gifford Guyot were rare (1.3% of mapped area), but supported a diverse albeit sparse epibenthic assemblage. The rocky outcrops of the seamount ridges were of sufficient size and height to support an extensive biological assemblage, yet bare rock was common. The seamount plateau and upper apron regions of the Gifford Guyot both had localised rocky outcrops thinly draped in coarse sands and shell debris. The likely instability and movement of coarse sediments over these low-lying rocky outcrops could severely impact the settlement, growth, and subsequent survival of sessile suspension-feeding invertebrates and may explain the low occurrence and density of suspension-feeding assemblages on this seamount. The presence of numerous but mostly small sessile invertebrates on the upper-apron, where large suspension feeding invertebrates were either rare or absent, also suggests that these areas may be regularly disturbed. It is unclear, however, whether the constant raining of sediments down these slopes inhibits the growth of species in this assemblage, or whether their small size reflects newly settled individuals re-colonising recently denuded surfaces following landslides or sediment burial. Therefore, while many seamounts may support dense coverage of cold water corals with high associated biodiversity (Koslow et al., 2001; Clark et al., 2006), others support much sparser assemblages (e.g., Sisters and Mongrel Seamounts, CSIRO unpublished data: Thresher *pers. comm.*; Gifford Guyot – *this study*). Consequently, it is clear that not all seamounts are equally capable of supporting high density assemblages even when rocky substrata are present. Variability in seamount species assortments and biodiversity are likely to reflect a breadth of environmental factors from broad-scale biogeographic, oceanographic, temperature and depth patterns, as well as finer-scale habitat structure and sediment dynamics, and anthropogenic impacts (Levin et al., 2001; Koslow et al., 2001; Stocks, 2004; Pitcher et al., 2007). If a representative portion of Australian seamounts were to be protected under a National Representative System of Marine Protected Areas then this variability must be taken into account.

In the deeper environments of the LHR flank, cold-water corals and sponges were recorded in all geomorphic classes. However, cold-water corals and sponges were only rarely recorded from the expansive sediment-covered ridge and the plateau on the LHR flank, where their occurrence and percent cover were negligible. Most cold-water corals and sponges from these deep-sea environments were associated with rocky outcrops of the volcanic peaks or the exposed rocky ridges. Although rocky outcrops were a limited habitat across the LHR flank (0.12% of the mapped area) the availability of rocky substrata was not limiting, as large areas of rock remained uncolonised. Most deep rock outcrops were characterised by sparse assemblages of cold-water corals and sponges. Only one small rock outcrop (3 × 5 m in size at 1630 m) supported a dense coral-dominated assemblage. While the movement of coarse sediments on the seamount may account for low densities of suspension feeders on the Gifford seamount, similar patterns are unlikely in these deeper basin environments. Soft-sediments were present in and around these deep rock outcrops, but the elevation of many of these features (e.g., volcanic peaks) makes disturbance from sediments unlikely. In addition, the one small outcrop supporting dense cold water corals was located in a silty low-relief environment, suggesting that the re-suspension of silt was not a deterrent to coral growth and cover.

Recent studies have identified that many deep-sea environments are often characterised by sparse cover of cold-water corals and sponges (Mortensen and Buhl- Mortensen, 2004; CSIRO unpublished data, Thresher *pers. comm.*). Several limiting factors have been suggested to account for fewer cold water corals in these environments, including temperature and salinity, limited food supply, and the depth of the aragonite-saturation horizon, (Gage and Tyler, 1991; Smith and Demopoulos, 2003; Roberts et al., 2006), although currently few data exist to investigate the relative importance of these factors. Measuring these factors is also problematic, especially where multiple factors are confounded (e.g., nutrients, and the water characteristics that supply them). Consequently, while substratum availability is a fundamental requirement, other resources are likely to be important in predicting the scarcity of deep-water sessile organisms.

While little is known about the distributions of cold-water corals and the processes that drive them, even less is known about the distributions of sub-fossil coral rubble, although a considerable number of studies have reported their occurrence. In this study, sub-fossil corals (coral rubble) were recorded and collected from the rock outcrops surveyed in both peak and ridge geomorphic classes. Percent cover of sub-fossil corals was highest on large outcrops and on the tops of volcanic peaks. Other studies have also recorded dead coral rubble, often in high densities and cover, particularly on seamounts and *Lophelia* banks (Clark et al., 2006; Roberts et al., 2006; CSIRO unpublished data, Thresher *pers. comm.*). Although cold-water corals are known to grow slowly and can live for extremely long time periods – up to 4000 years (Roark et al., 2009), it is currently unclear whether these long time periods explain the accumulation of coral rubble in these environments or whether some past die-off or disturbance event(s) may be responsible. Overlaying the distribution and abundance of live and dead coral structure on newly acquired seabed maps that resolve hard substratum features (e.g., peaks and large rocky ridges), combined with broader scale biogeographic knowledge, may provide the basis of a spatial and temporal framework to examine the processes affecting these deep-sea environments.

Although deep soft-sediment environments of the northern LHR supported high occurrences of low to moderate bioturbation, the epifauna responsible for this disturbance were only rarely seen. Infaunal assemblages ($>500\,\mu$m) were also sparse. Very few infaunal animals were collected from the sediments of the northern LHR, with no more than 8 species detected per 100 ml of 500 μm elutriated sediment (Heap et al., 2009). It is unknown if this reflects true low diversity and abundance of infauna or whether a prevalence of smaller-bodied ($<500\,\mu$m) or fragile fauna were simply not collected by the methods employed. More species were found in sediments from the deep flanks of the Gifford Guyot (2040-2423 m) than elsewhere in the survey area (Heap et al., 2009), but it is difficult to determine whether high species richness here is related to depth or other factors associated with seamounts. Previous studies in deep-sea soft-sediment plains have also recorded low numbers of animals, albeit with high species diversity (e.g., Gage, 1996; Levin et al., 2001). While differences in sampling methodologies used between studies may explain some observed differences, the fact that low occurrences of organisms were also recorded in the towed-video observations suggests some factors, such as nutrients, oxygen, or trace element levels, might be limiting infaunal numbers in this region. More extensive research is required on the infaunal assemblages of the LHR to examine how consistent these patterns of diversity and abundance are across the LHR and whether they vary with geomorphic class.

Faunal diversity and abundance can be strongly influenced by environmental factors, such as nutrients, oxygen, organic content, and trace element levels (Levin et al., 2001). Low nutrients, for example, can limit both the number and assortment of species in a region, while reductions in oxygen concentrations (oxygen-limited and energy-depleted) may lead to significant shifts in assemblage type and reduced biodiversity (Levin et al., 2001; Gooday et al., 2010). Sediment geochemistry of the northern LHR is characterised in detail in Radke et al. (2011) and is notable for low concentrations of most inorganic elements compared to global averages. In addition, moderate to high chlorin indices and low total organic carbon and nitrogen concentrations suggest low availability and freshness of organic matter, although still within normal values expected at these depths. While the geochemistry of these sediments identifies a sufficient food supply is present, it is unclear how these patterns vary by depth or geomorphic class. The relationship between infauna and geochemistry in the survey area also remains unknown but warrants further research particularly in relation to nutrient availability in the form of trace elements and organic matter.

4.2. *Geomorphic features as surrogates for biological assemblages and conservation tools*

How effective are geomorphic seabed classifications in predicting the physical setting of the seabed and their biological assemblages? Some classifications such as peaks and seamount ridges were very distinct from other classes on the basis of one or two obvious physical characteristics such as depth and seafloor hardness. Others were less distinct, but could be correctly classified on the basis of combinations of other more subtle physical variables, highlighting the multivariate nature of these seabed classes. Importantly, the distinction between seabed classes was, in most cases, reflected in the differences between the biological assemblages. Additionally, misclassification of seabed classes due to physical habitat differences was mirrored by a corresponding misclassification of the biological assemblage. This, in combination with what we know about habitat associations of deep-sea communities, indicates that the classification scheme reflects the importance of real habitat requirements for many organisms. However, as a caution we note that the numbers of stations in many of these geomorphic classes were very low due to the logistical constraints of deep-sea studies. There is a clear need to further assess the predictive effectiveness and assumptions of physical surrogates to avoid incorrect management decisions. In this study, six geomorphic classes provided clear discriminations of biological pattern, but this was mostly due to the fact the geomorphic classes reflected biologically important substrata and depth differences. Where depth differences were not incorporated into geomorphic classes (e.g., the lower vs. upper seamount apron), clear differences in assemblage types were observed, which resulted in high misclassification rates.

There is enormous potential for using physical variables as proxies or 'surrogates' to predict biological patterns, and as a consequence physical surrogates are often advocated as a tool for management and conservation. The inability to measure biodiversity and species and assemblage patterns over regional or national scales means that the use of physical surrogates is gaining momentum and will be more heavily relied on. However, clear evaluation of these tools has received less attention. Classification of large-scale geomorphology is now available for much of Australia's EEZ (Heap and Harris, 2008). At a regional-scale, geomorphic classes based on historical bathymetric and geological datasets have already been used as the foundation for the National Bioregionalisation of Australia (Department of Environment, 2004) and have subsequently been used to guide in the selection of representative habitats for inclusion in regional marine management and conservation plans around Australia (Harris et al., 2005, 2008). At broad spatial scales, or in cases where only sparse data sets exist, a number of workers advocate the use of abiotic (e.g., geologic and oceanographic) indicators of benthic habitats and ecosystems as proxies for biological communities and species diversity (Roff and Taylor, 2000; Roberts et al., 2003); it follows that applications of spatially more complete abiotic information should be employed to systematically map different habitats to support MPA design. Indeed, Greene et al. (1995, 1999) have devised a benthic marine habitat classification scheme that is strongly dependent upon seabed geology, whilst in Canada, Roff and Taylor (2000) and Zacharias and Roff (2000, 2001) use bottom physiography and oceanographic information in their hierarchical geophysical approach to classify and map marine environments.

This study identified that while surrogates (here geomorphic classes) may provide effective discrimination of habitats and biological assemblages across broad spatial scales (i.e. 10-100's of km's), it is critical that the correlation between physical variables and biological pattern be assessed. Where surrogates are distinguished by unique classes of physical variables, then biological discriminatory power is likely to be strong. In contrast, abiotic descriptors based solely on other factors such as subsurface features, while valuable are less likely to provide discriminatory power to detect different biological assemblages. To predict seabed habitats and biological assemblages across larger regional scales, such as the entire LHR, further testing would be required, but might be achieved using the NORFANZ benthic invertebrate data (Williams et al., 2011) and the National Institute of Water and Atmospheric Research (NIWA) 2007 benthic invertebrate data from the Challenger Plateau, south-eastern end of the LHR (NIWA, unpublished data).

5. Conclusions

The northern LHR was characterised by relatively sparse faunas for both the expansive soft-sediment environments and discrete rock outcrops. Geomorphic classes were good predictors, and therefore surrogates, of benthic habitats and biological patterns. Substratum type and depth were the main variables driving benthic assemblage composition, with soft-sediments characterised by low to moderate levels of bioturbation, while rocky outcrops supported sparse assemblages of suspension feeding invertebrates, such as cold-water corals and sponges that supported a diversity of associated fauna (e.g., brittlstars, crinoids, crustacea, seastars, and anemones). The occurrence and density of bioturbation increased with depth. The deep sediments of the western flank of the LHR supported high occurrences of bioturbation, characterised by a range of trails (evidence of epifauna) and burrows and mounds (evidence of infauna) as well as taxa specific trails, such as acorn worm trails, and trails in the form of rosettes and crater rings. In contrast to these deep environments, the sediment starved habitats of the Gifford Guyot supported significantly lower levels of bioturbation, characterised mostly by trails. Bioturbators require sediment to move through, and therefore this pattern of higher bioturbation with depth may simply reflect greater sediment deposition with depth. The summit of the seamount also supported a variety of taxa, such as benthic ctenophores and rock-associated fishes that were not recorded in the deeper basin habitats, but again were characterised by sparse assemblages. To manage and conserve these deep-sea environments, we need a better understanding of the ecology and distribution of deep-sea assemblages and the inter-relationships between habitat-forming species, such as cold water corals, and associated benthic communities. Similarly, if consistent national and international conservation strategies are to be applied to these environments, then a broader understanding of the distribution and ecology of deep-sea communities across a range of different habitats is needed to establish the generality of a surrogates approach in the deep sea.

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