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FEATURE ARTICLE

Megabenthic assemblage structure on three New Zealand seamounts: implications for seafloor massive sulfide mining

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ABSTRACT: Seamounts are recognized for their biological importance and, more recently, mineral wealth. However, in most cases the biological information required to assess the risk to seamount assemblages from mining is lacking. This study uses towed video footage and environmental data to investigate the patterns of megafaunal distribution, assemblage structure and association with environmental variables, both within and amongst 3 seamounts along the Kermadec volcanic arc in the New Zealand Exclusive Economic Zone. These seamounts represent different levels of hydrothermal activity, with an overlapping depth range: Rumble II East has no history of hydrothermal activity, Brothers is hydrothermally active and Rumble II West is predominantly inactive. All 3 seamounts fall within an area previously licenced for the prospecting phase of seafloor massive sulfide (SMS) mining. In total, 186 putative taxa were identified from video samples and assigned to 20 assemblages. Both seamount and *a priori* defined habitat (nested within seamount) contributed to explaining variation in assemblage structure, with a mixture of shared and unique assemblages found at each seamount. Magnetivity, as a proxy for hydrothermal activity, explained most of the variation in assemblage structure amongst seamounts, with depth, topography, substratum (and magnetivity for Brothers) explaining most within seamounts. Environmental management implications include the need to designate a network of 'set-aside' sites both within and amongst seamounts to adequately protect the range of faunal assemblages present. This study also suggests that inactive SMS areas may support faunal assemblages not found elsewhere within the region and would require suitable protection from mining activities.

An assemblage including corals, crinoids, ascidians and brittlestars on Rumble II West seamount, in the vicinity of SMS deposits.

Image: NIWA

KEY WORDS: SMS mining · Seamounts · Megabenthic · Distribution · Deep sea · Assemblages · Management

INTRODUCTION

Seamounts have considerable biological value, as potential stepping stones for dispersal (Hubbs 1959, Wilson & Kaufmann 1987), oases of high faunal abundance and biomass (Rowden et al. 2010b) and hotspots of species richness (Samadi et al. 2006,

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Morato et al. 2010), although not all seamounts have these characteristics (see review by Rowden et al. 2010a).

Seamount assemblages vary at multiple spatial scales, from habitat patches within a single seamount to variation amongst seamounts in the same or in different regions (Clark et al. 2010). For example, at Horizon Guyot, in the central North Pacific, aspects of the megafauna demonstrated random or patchy distribution at scales of 10 to 1000 m, with strong correlation to hard substratum distribution (Kaufmann et al. 1989). The degree of habitat diversity within a seamount can also influence faunal diversity, as found in the Gulf of Alaska, where the seamount with the greatest diversity in habitat (topography and relief) was characterized by the highest relative faunal diversity (Raymore 1982). Seamount habitats and faunal communities are shaped by a suite of environmental variables, including light levels, water column productivity and chemistry, hydrodynamic regime, seamount geomorphology, substratum type and hydrothermal activity (reviewed by Clark et al. 2010).

Seamounts are vulnerable to anthropogenic pressures such as fishing (Clark & Tittensor 2010) and, in the future, seabed mining (Halfar & Fujita 2007). Mineral resources at seamounts include cobalt-rich ferromanganese crust (also known as cobalt-rich crust or polymetallic crust) and seafloor massive sulfide (SMS) deposits. Of these 2 deposit types, SMS is expected to be mined at a commercial scale in the western Pacific in the near future (Nautilus Minerals Inc.: home page at www.nautilusminerals.com/s/Home.asp). SMS deposits form through hydrothermal circulation to create areas of hard substratum rich in sulfides and base metals. There are currently 165 deposits known globally (Hannington et al. 2011), which occur across a range of hydrothermal settings, as reviewed by Boschen et al. (2013).

Hydrothermal activity has considerable influence on benthic assemblages inhabiting seamounts that host SMS deposits. Hydrothermally active areas are colonised by a chemosynthetic assemblage of hydrothermal vent specialists (reviewed by Van Dover 2000, 2014). Hydrothermal vent fauna are typified by high biomass and low diversity (Grassle 1985) and rapid growth rates (Lutz et al. 1994). Hydrothermally inactive areas are colonised by 'background' fauna typical of hard substrata on seamounts, such as the sponges, hydroids, corals, anemones, squat lobsters, ophiuroids and holothurians inhabiting inactive areas of the Manus Basin (Galkin 1997). Over a scale of 10s to 100s of meters, chemosynthetic and background faunal assemblages exhibit zonation based on proximity to hydrothermal flow, with chemosynthetic assemblages existing in close proximity to hydrothermal flow and background assemblages existing at the vent periphery (Arquit 1990, Sudarikov & Galkin 1995). It has also been hypothesised that a third assemblage may exist at SMS deposit sites, one specific to the unique chemical environment of weathering inactive SMS deposits (Van Dover 2007, 2011).

In order to assess the vulnerability of seamount benthic fauna to mining activities, it is important to describe the structure and evaluate the variability of benthic assemblages, both amongst and within seamounts. There are very few studies that have investigated seamount faunas associated with mineral deposits. At Cross Seamount, in the Hawaiian Archipelago, cobalt-rich crust deposits were characterised by low diversity and low abundance of benthic megafauna (Grigg et al. 1987). A later study along the Hawaiian seamount chain found differences in benthic assemblage structure between seamounts located inside and outside the cobalt-rich crust region, driven by relative species composition and abundance, rather than species richness (Schlacher et al. 2014). The only study characterising benthic assemblages at SMS deposits was conducted at a proposed mine and reference site in the Manus Basin, off Papua New Guinea. Here, Collins et al. (2012) found 3 faunal assemblages in active areas, which were distinct from a 'peripheral assemblage' of *Abyssocladia* sponges, amphipods, stalked barnacles, squat lobsters, lepetodrilid limpets and thyasirid clams.

The main objective of the present study was to determine the broad-scale spatial variability in benthic megafaunal structure within and amongst seamounts of commercial interest for their SMS deposits along the Kermadec volcanic arc, within the New Zealand Exclusive Economic Zone (EEZ). This included the objective of investigating the hypothesised existence of an assemblage specific to inactive SMS deposits (Van Dover 2007, 2011). The study also aimed to identify the environmental variables associated with patterns in benthic assemblage structure. Assessing the variability in assemblage structure within and amongst seamounts, and in particular how SMS deposits contribute to assemblage structure in the region, will provide information essential to the environmental management of any future mining activities.

MATERIALS AND METHODS

Study area

Three seamounts were targeted for survey: Rumble II East, Brothers and Rumble II West (Fig. 1). These volcanoes were chosen to span a range of environments: Rumble II East is hydrothermally inactive with no SMS deposits, Brothers has large hydrothermally active areas where SMS deposits are forming and Rumble II West is predominantly hydrothermally inactive with inactive SMS deposits. These seamounts are ideal for a comparative study because they lie within 0.5° of latitude and have overlapping depth ranges (Rumble II East: 907 to 3017 m [Wright 1994]; Brothers: 1350 to 2250 m [Wright & Gamble 1999]; Rumble II West: 1194 to 2994 m [Wright 1994]). Both Brothers and Rumble II West have SMS deposits of potential interest to mining companies, with prospecting permits for both seamounts having been issued to Neptune Minerals in 2002 (Fig. 1; https://www.nzpam.govt.nz/cms/banner_template/CMINPSCURR).

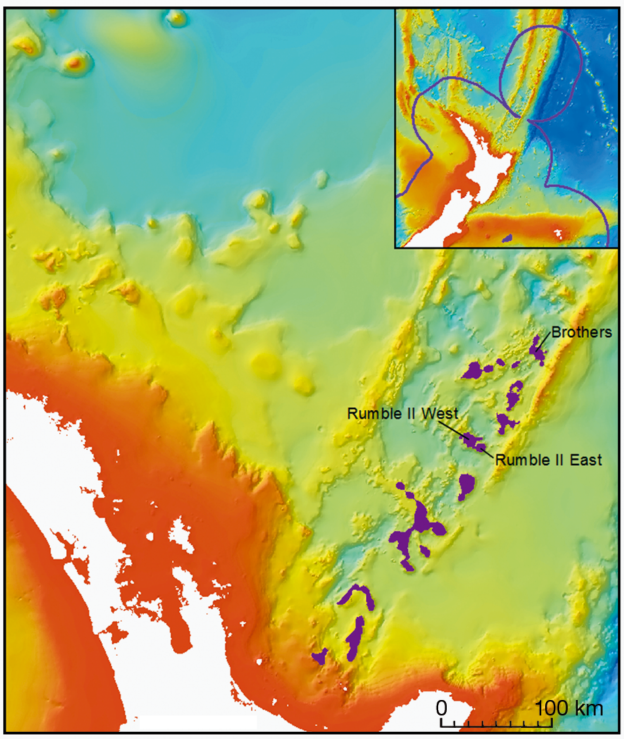


Fig. 1. Location of the seamounts Rumble II East, Rumble II West and Brothers in relation to areas licenced for seafloor massive sulfide (SMS) prospecting (purple shading). Inset: regional context of study area including northern New Zealand mainland and Exclusive Economic Zone (purple line)

Image data collection and analysis

Photographic transect data (video and still images) were collected during Leg 2 of the TAN1007 cruise on R.V. 'Tangaroa' between 29 May and 11 June 2010. Imagery was obtained using the NIWA deep-towed imaging system (DTIS) with a high definition digital video camera (Sony 1080i format) angled 45° forwards and a vertically orientated still image camera (Canon EOS 400D 10 mp). The ship travelled at 0.5 to 1 knots with the camera system being towed approximately 2 to 4 m above the seabed. A total of 51 transects over the 3 seamounts were of sufficient quality for analysis. Transects were distributed randomly amongst broad-scale habitat strata (caldera floor, caldera wall, seamount cone, seamount flank and chimney fields) defined *a priori* based on general topography from a multibeam survey undertaken during Leg 1 of the TAN1007 cruise on R.V. 'Tangaroa' between 12 and 29 May 2010 (Fig. 2). Transects were conducted to have as much overlap in depth range as possible between the same habitats on each seamount (Table 1). For analysis of the video (analysis of still images is not considered here), transects were divided into 200 m long contiguous samples (using GIS [geographical information system]) to enable greater spatial resolution of faunal distribution data. Two of the 200 m samples (each with only 1 faunal observation along their length) were excluded for statistical analysis purposes, leaving a total of 249 video samples (Table 1).

The video samples were analysed using Ocean Floor Observation Protocol (OFOP) software (Version 3.3.4a, Scientific Abyss Mapping Services, www.ofop-by-sams.eu/). Syncing video footage and navigation files through OFOP enables users to generate automatically geo-referenced faunal observation files during footage playback. All fauna were identified to the best taxonomic resolution possible. Some fauna could be confidently identified to species level, but the majority could only be identified to family level or higher. The faunal records obtained from video analysis were in the form of count data, which, due to changes in altitude along transects and the continuous nature of recording observations in OFOP, could not be translated to a true abundance. Instead, the frequency of observations was used to give an indication of relative abundance. The faunal observations from OFOP files were matched to their respective 200 m sample using a script written in R (http://www.r-project.org). Video samples where the camera altitude above the seabed was <1.0 m or >5.0 m were excluded to avoid bias in faunal obser-

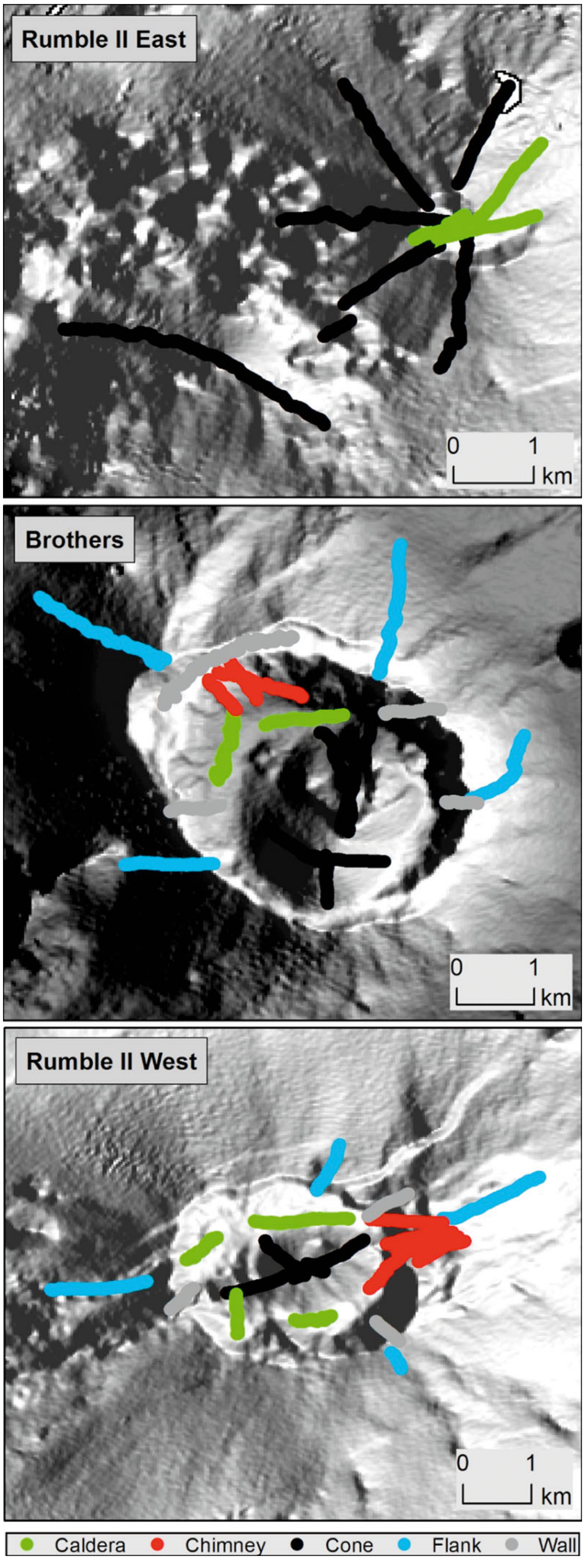


Fig. 2. Distribution of towed-camera transects across the 5 *a priori* defined habitat strata (caldera: caldera floor; chimney: chimney fields; cone: seamount cone; flank: seamount flank; wall: caldera wall) at the 3 study seamounts (Rumble II East, Brothers and Rumble II West)

vations resulting from camera altitude and consequent changes in image quality. The altimeter malfunctioned during 1 transect (Stn 33), so altimetry data were obtained by regression using the distance between the laser scaling dots on 101 still images from stations where altimetry was known. This regression was then applied to 128 images from Stn 33, to match the faunal observations in OFOP to their nearest altitude measurement as calculated from the images. Matched resemblance matrix tests (RELATE) in PRIMER 6 (Clarke & Gorley 2006) were used to assess whether the altitude within the range chosen for analysis and the percentage of excluded observations had an influence on the faunal distribution patterns observed. These pre-analysis tests revealed that neither altitude nor percentage of excluded observations had an influence that would likely confound the main analysis (i.e. the Rho values were very small; altitude = 0.087, number of excluded observations = 0.002).

Environmental data

Substratum type was described and identified from the video using OFOP. Substratum was described in a hierarchical fashion to include information on morphology/particle size class and potential chemical staining (Table 2). Substratum was quantified through semi-continuous recording, with observations being made every few seconds.

Position information was obtained from the DTIS navigation file. Additional environmental data—depth, backscatter (acoustic reflectivity), rugosity, aspect, slope and 3 measures of curvature (curvature, plan curvature, profile curvature: used to describe the relative position of terrain features)—were extracted from multibeam data, collected using an EM300 multibeam echo-sounder (IMHO) and processed using C&C Technologies HydroMap. Cleaned data were gridded to a resolution of 25 m cell size and exported to ESRI grid formats for use in ArcGIS. Backscatter data derived from multibeam were processed using SonarScope (Augustin & Lurton 2005). Processing consisted of statistical compensation of the signal as a function of its incidence angle on the seafloor, to attenuate the strong signal from specular reflection at the nadir and the rapid decrease of the signal strength with increasing incidence angle (Hughes Clarke et al. 1997, Le Chenadec et al. 2007, Fonseca et al. 2009). Magnetivity data were collected at 500 m resolution over all 3 seamounts during TAN1007 using a Sea Spy Magnetics overhauser

Table 1. Distribution of video transects and 200 m samples and their respective depth ranges, across the 3 seamounts and *a priori* defined habitat strata—caldera: caldera floor; wall: caldera wall; cone: seamount cone; flank: seamount flank; chimney: chimney fields

Seamount	Habitat substratum	Transects	No. of 200 m samples	Depth range (m)
Rumble II East	Cone	8	59	940–2110
	Caldera	4	17	1020–1400
Brothers	Cone	5	22	1200–1730
	Flank	5	30	1350–1960
	Caldera	2	11	960–1880
	Wall	4	22	1390–1700
	Chimney	3	11	1530–1910
Rumble II West	Cone	4	14	1160–1450
	Flank	4	16	1250–1710
	Caldera	4	18	1340–1450
	Wall	3	6	1190–1460
	Chimney	5	23	1180–1470
Total		51	249	940–2110

magnetometer, with data acquisition at 1 Hz using Marine Magnetics Sealink software. Magnetivity data were also obtained at 25 m resolution for Brothers Seamount (see Caratori Tontini et al. 2012a,b). The mean and standard deviation for each of the multibeam-derived variables and magnetivity at both spatial scales were calculated for each 200 m video sample. This was achieved by splitting the 200 m DTIS line segments into points with 1 m spacing along the track, and adding the grid cell value of all relevant layers as an attribute to the point layer. Mean and standard deviation for each relevant attribute value were then calculated for all points of 1 segment, generating a list of line segments and the mean and standard deviation for the underlying grid cell values. Means and standard deviations were calculated at different grid sizes (25 m and focal means of 3, 5, 7 and 15) to enable environmental influences on assemblage structure to be investigated at the most appropriate spatial scale. Focal means consisted of 3 × 3, 5 × 5, 7 × 7 and 15 × 15 grid cells of the original 25 m grids.

Table 2. Hierarchy used to describe substrata, including information on morphology/particle size class and chemical staining; '–' indicates no descriptor

Sediment type	Sediment descriptor	Final class
Lava	–	Lava
	Iron	Lava iron
	Sulfur	Lava sulfur
	Vent	Lava vent
Chimney	–	Chimney
	Sulfur	Chimney sulfur
	Vent	Chimney vent
Boulders	–	Boulders
	Sulfur	Boulders sulfur
	Vent	Boulders vent
Cobbles	–	Cobbles
	Sulfur	Cobbles sulfur
Pebbles	–	Pebbles
	Sulfur	Pebbles sulfur
	Vent	Pebbles vent
Gravel	–	Gravel
	Sulfur	Gravel sulfur
	Vent	Gravel vent
Sand	–	Sand
	Sulfur	Sand sulfur
Muddy sediment	–	Muddy sediment
Consolidated sediment	–	Consolidated sediment
Crust	–	Crust
	Iron	Crust iron
	Vent	Crust vent

Data analysis

The faunal distribution data from the video samples were analysed using multivariate routines in the statistical software package PRIMER 6 (Clarke & Gorley 2006) with PERMANOVA+ (Anderson et al. 2008). Prior to analysis, count data were transformed. After trialling a range of transforms, square root transformation was used, as it down-weighted the effect of abundant fauna sufficiently for the signal from rarer taxa to be observed, whilst still enabling the relative differences in abundance of taxa to influence the patterns in assemblage structure. A Bray-Curtis resemblance matrix was created from the transformed data. Hierarchical cluster analysis (CLUSTER) was performed on the resemblance matrix with a SIMPROF test (at $p = 0.05$) to determine sample group structure in the faunal data, i.e. identify 'assemblages'. Multidimensional scaling (MDS) plots were produced to visualise patterns in the grouping of samples associated with seamount, habitat and SIMPROF assemblage group. Similarity percentages—species contributions (SIMPER) was performed on the transformed data to identify the taxa characterising each SIMPROF assemblage group (with a 50% cumulative cut off).

The spatial variability in the assemblage structure, both amongst and within seamounts, was described using permutational multivariate analysis of variance

(PERMANOVA). Prior to PERMANOVA, the potential effect of multivariate dispersion was assessed using a distance-based test for homogeneity of multivariate dispersions (PERMDISP), with 999 permutations. Deviations from centroid was chosen as the method giving the best overall results in terms of Type I error and power (Anderson 2006). PERMDISP analyses suggested there was significant dispersion for both seamount (F = 6.9058, df1 = 2, df2 = 246, p[perm] = 0.001) and habitat (F = 6.9012, df1 = 4, df2 = 244, p[perm] = 0.001), but, as this dispersion occurred equally amongst different levels of the factors, it was not expected to affect the PERMANOVA results.

The effects of seamount and habitat nested within seamount were assessed using PERMANOVA, with Type III (partial) sums of squares, permutations of residuals under a mixed model and 999 permutations. Type III (partial) sums of squares was chosen as the most conservative model in which the order that terms are fitted is not important (Anderson et al. 2008). Permutation of residuals under a mixed model was selected as having the best power and being the most accurate regarding Type I error (Anderson & Legendre 1999, Anderson & ter Braak 2003).

The effect of environmental parameters on assemblage structure was assessed both amongst and within seamounts using distance-based linear models (DISTLM). Prior to DISTLM, draftsman plots and correlation matrices were produced to assess the distribution of each variable and to identify co-correlating variables. Where pairs of variables had a Pearson's correlation coefficient of 0.9 or larger, 1 of the co-correlating variables was excluded from the analysis. If variables demonstrated skew within the draftsman plots, they were square root transformed to normalise their distribution. Initially, DISTLM was run with topographic variables at different grid sizes (25 m and focal means of 3, 5, 7 and 15) to assess which spatial scale best explained the assemblage structuring observed. A focal mean of 15 (covering an area of 0.14 km^2) had the highest R^2 value for both the grouped variable and ungrouped variable models and was chosen for all further analysis.

For the amongst-seamount analysis, the environmental variables were grouped according to data type: depth, topography (rugosity, curvature, plan curvature, profile curvature, slope), magnetivity, substratum (backscatter and all substratum types without obvious hydrothermal signatures), substratum hydrothermal (substratum with observed venting, sulphur or iron staining), habitat heterogeneity (the standard deviation of environmental variables) and 2-dimensional space (latitude and longitude). Space was ultimately excluded from the analysis to avoid autocorrelation issues. DISTLM was performed by grouping variables by indicator as described above, with selection based on the Akaike information criterion (AIC), step-wise selection procedure and 999 permutations. AIC selection was chosen as the method to create the most parsimonious model, as it adds a 'penalty' for increases in the number of predictor variables (Anderson et al. 2008). Step-wise selection was chosen as it allows for both the addition and removal of a term to the model at each step (Anderson et al. 2008).

For the within-seamount analysis, DISTLM was first performed using the grouping of variables above, and then with the environmental variables ungrouped to investigate which individual variables were driving the observed patterns of environmental association with assemblage structure. For both of the above, DISTLM was performed using the same parameters as for the amongst-seamount analysis. Distance-based redundancy analysis (dbRDA) plots were used to provide the best possible 2-dimensional visualisation of DISTLM results for individual environmental variables at each of the 3 seamounts, with samples grouped by their SIMPROF assemblage and vectors proportional to their contribution to the total variation.

Assemblages identified by SIMPROF were mapped, using ArcMap 10, over digital terrain models generated from multibeam data.

RESULTS

Assemblage structure

In total, 186 putative taxa were identified from 249 video samples across the 3 seamounts. Cluster analysis indicated that the faunal records from the 200 m samples grouped both by seamount and by habitat within a seamount, which was visualised by MDS (Fig. 3A,B). PERMANOVA results indicated a significant influence of seamount (df = 2, SS = 1.30E5, MS = 65 055, Pseudo-F = 27.2, p[perm] = 0.001) and habitat nested within seamount (df = 9, SS = 1.08E5, MS = 12 036, Pseudo-F = 5.03, p[perm] = 0.001) on faunal distribution.

SIMPROF analysis identified 20 assemblages across the 3 seamounts, which were visualised by MDS (Fig. 3C). Six of these assemblages (d, f, j, l, q & t) were shared amongst seamounts, whilst 14 assemblages were unique to individual seamounts (Fig. 4). Of the shared assemblages, 4 were found at all seamounts

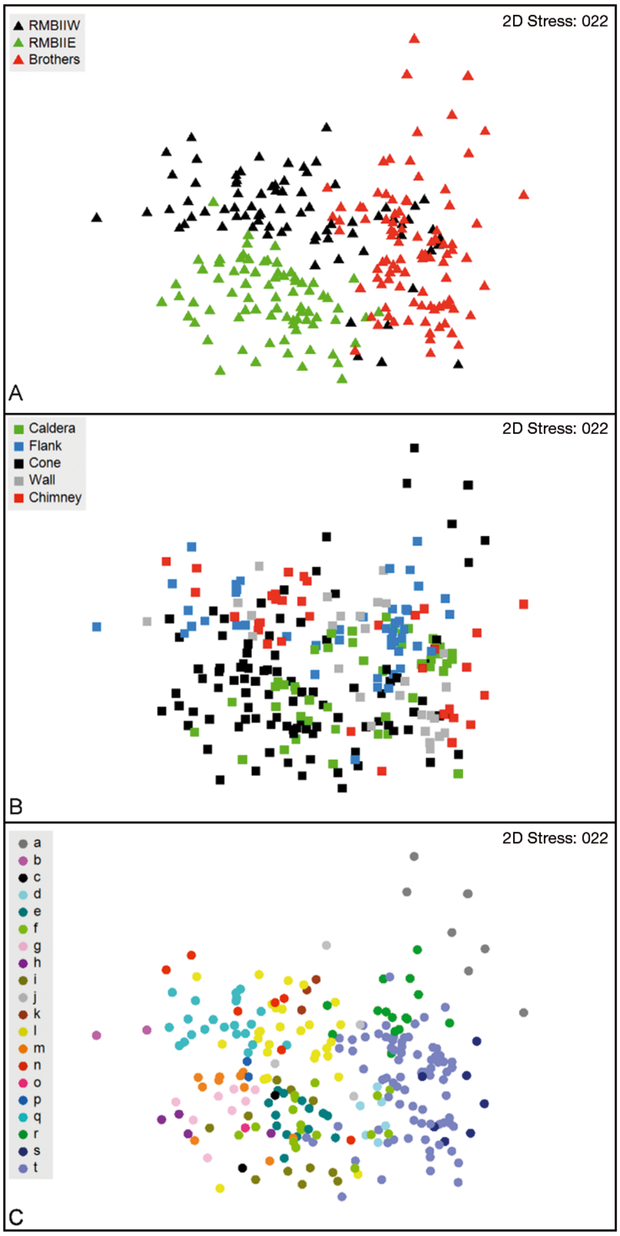


Fig. 3. Multi-dimensional scaling (MDS) plot of 200 m video samples labelled by (A) seamount (RMBIIW: Rumble II West; RMBIIE: Rumble II East; Brothers), (B) *a priori* defined habitat strata (caldera: caldera floor; flank: seamount flank; cone: seamount cone; wall: caldera wall; chimney: chimney fields) and (C) SIMPROF assemblages (a to t)

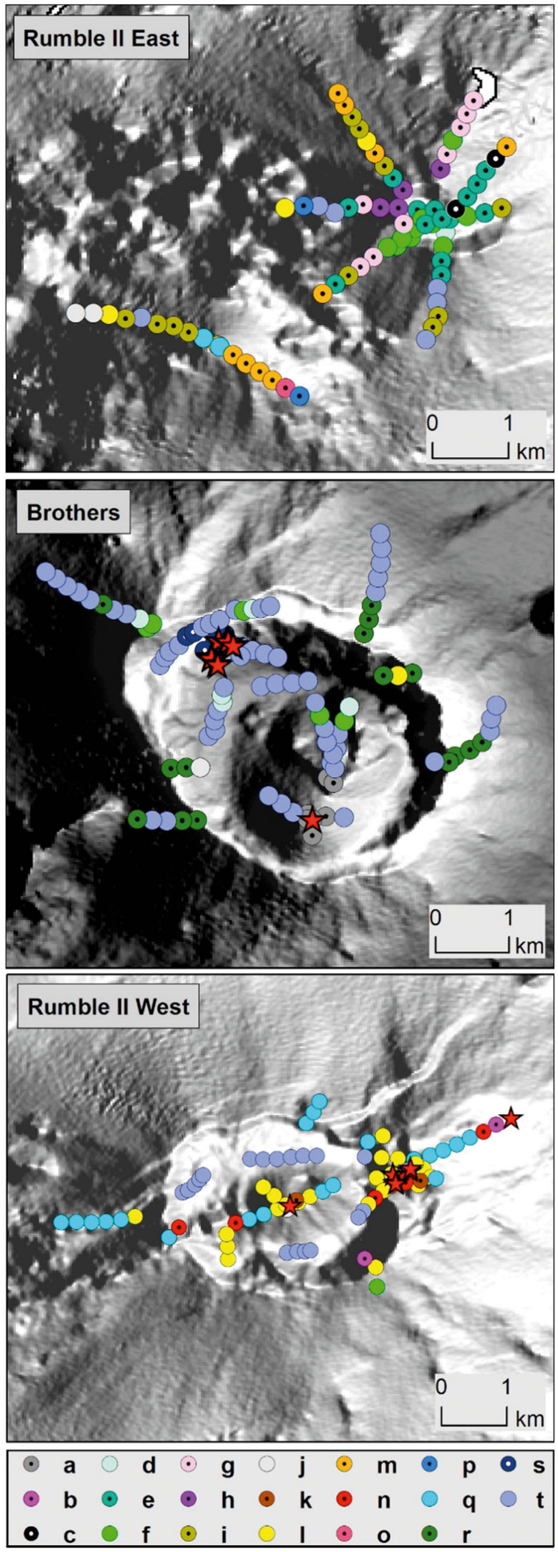


Fig. 4. Digital terrain model maps of SIMPROF assemblage (a to t) distribution over the 3 studied seamounts. Symbols with a black centre indicate assemblages unique to 1 seamount. Red stars indicate the locations of hydrothermal vent chimney structures from video observations

(f, j, l & t), 1 was shared between Rumble II East and Brothers (d) and 1 was shared between Rumble II East and Rumble II West (q). Rumble II East had a total of 14 assemblages, 8 of which were unique. Rumble II East assemblages required 3 to 5 taxa to make up 50% of the cumulative similarity between samples within an assemblage (Table 3). Brothers had 8 assemblages, 3 of which were unique, with only 1 taxon

Table 3. Taxon composition determined by SIMPER for the SIMPROF assemblages (a to t) unique to each of the 3 seamounts: Rumble II East (RMBIIE), Brothers and Rumble II West (RMBIIW), and shared between seamounts. Group similarity indicates the percentage similarity between 200 m samples within the assemblage group. The cut off for cumulative percentage to group similarity was 50%. Assemblage o was unique to Rumble II East, but only consisted of one 200 m sample and so could not be characterised by SIMPER analysis

Assemblage: group similarity (%)	Taxa (contributing %)	Cumulative (%)
RMBIIE		
c: 32.44	Actiniaria 2 (22.05), Ascidiacea 3 (15.59), Farreidae/Euretidae 2 (15.59)	53.23
e: 47.05	Xenophyophoroidea (27.68), Caridea (14.72), Hexactinellida 4 (11.49)	53.89
g: 43.61	Xenophyophoroidea (15.93), Hexactinellida 4 (13.98), Farreidae/Euretidae 2 (10.13), Stylasteridae (7.73), Comatulida (7.30)	55.12
h: 47.04	Primnoidae/Isididae 4 (16.99), *Rossella* sp. 1 (15.70), Hexactinellida 4 (11.95), Xenophyophoroidea (9.26)	53.89
i: 36.33	Zoantharia-colonised stalk (16.81), Hydrozoa 3 (16.25), Caridea (12.53), *Hyalonema* (*Oonema*) *bipinnulum* (10.26)	55.86
m: 45.40	Brachiopoda (41.98), Comatulida (7.75), Caridea (6.76)	56.48
p: 48.09	Farreidae/Euretidae 2 (21.60), Comatulida (19.32), Caridea (15.27)	56.19
Brothers		
a: 42.26	Alvinocarididae/Hippolytidae (58.38)	58.38
r: 58.40	Polychaeta (tubes) (66.56)	66.56
s: 59.96	Echiura 2 (66.16)	66.16
RMBIIW		
b: 33.90	Comatulida (58.58)	58.58
k: 42.90	Echiura (29.25)	61.45
n: 32.71	Scleractinia (branching) (37.85), Caridea (10.43), Schizopathidae (9.88)	58.16
Shared between seamounts		
d: 54.86[a]	Xenophyophoroidea (51.18)	51.18
f: 42.87[b]	Xenophyophoroidea (61.56)	61.56
j: 36.35[b]	Ophiurida (74.95)	74.95
l: 30.71[b]	Ophiurida (16.11), Caridea (14.91), Echiura 1 (8.62), Comatulida (7.81), Xenophyophoroidea (6.98)	54.42
q: 39.94[c]	Comatulida (20.35), Scleractinia (branching) (19.23), Schizopathidae (7.84), Primnoidae/Isididae 11 (6.47)	53.88
t: 34.37[b]	Caridea (56.65)	56.65

For assemblages found at multiple seamounts: [a]shared between Rumble II East and Brothers; [b]found at all 3 seamounts [c]shared between Rumble II East and West

required to make up 50% cumulative similarity within an assemblage (Table 3). Rumble II West had 8 assemblages, 3 of which were unique, with between 1 and 3 taxa required to make up 50% cumulative similarity within an assemblage (Table 3). The spatial location of unique assemblages on Brothers (a & s) and Rumble II West (b, k & n) coincided with records of hydrothermal vent chimney structures (Fig. 4); chimneys were generally hydrothermally active on Brothers and inactive on Rumble II West.

Environmental drivers of assemblage structure

The environmental drivers of differences in assemblage structure both amongst and within seamounts were identified using DISTLM. Amongst seamounts, the environmental variable groups included in the best model (R^2 = 0.32, RSS = 5.62) were (in order of decreasing importance) magnetivity, depth, substratum and topography (Table 4). Within seamounts, for Rumble II East the best model (R^2 = 0.38, RSS = 1.22E5) included depth, topography and substratum

Table 4. DISTLM Pseudo-*F*-values for the amongst-seamount (all) and within-seamount (RMBIIE, Brothers and RMBIIW) analyses. Displayed are the environmental variable groups selected by DISTLM as part of the best model; '–' indicates the group was available for the analysis, but not selected as part of the best model

Environmental variable group	Seamount Pseudo-*F*-values			
	All	RMBIIE	Brothers	RMBIIW
Topographic	4.039	2.484	5.029	1.949
Depth	6.882	6.935	3.745	2.231
Magnetivity	15.967	–	2.374	–
Substratum	5.421	1.859	2.542	3.508
Substratum hydrothermal	–	–	–	–
Habitat heterogeneity	–	–	–	–

Table 5. DISTLM Pseudo-*F*-values for the within-seamount (RMBIIE, Brothers and RMBIIW) analysis when variables were made available to the model individually. Displayed are the environmental variable groups selected by DISTLM as part of the best models; '–' indicates the variable was available for the analysis, but not selected as part of the best model. Co-correlates were variables that correlated with another variable at R = 0.9 or greater and were subsequently excluded from the analyses. SD: standard deviation

Environmental group	Environmental variable	Seamount Pseudo-*F*-values RMBIIE	Brothers	RMBIIW	Co-correlates
Topography	Plan curvature	3.444	–	2.189	Curvature[a,b]
	Profile curvature	1.929	–	3.158	Curvature[a,b]
	Curvature	–	7.114	–	–
	Aspect	–	4.816	1.972	–
	Slope	–	3.389	1.814	SD depth[b]
	Rugosity	–	–	1.905	–
Depth	Depth	6.935	8.317	7.061	–
Magnetivity	Magnetivity 500 m	–	3.889	1.830	–
Substratum	Lava	5.574	–	1.986	–
	Crust	–	4.323	1.680	–
	Boulders	–	–	11.317	–
	Cobbles	–	–	2.467	–
	Gravel	–	3.465	2.283	–
	Backscatter	2.351	6.138	–	–
Substratum hydrothermal	Chimney vent	–	4.008	1.831	–
	Chimney	–	–	1.851	–
	Crust iron staining	–	–	0.000	–
Habitat heterogeneity	SD slope	2.093	2.952	–	–
	SD magnetivity	–	–	2.448	–

[a]RMBIIE; [b]RMBIIW

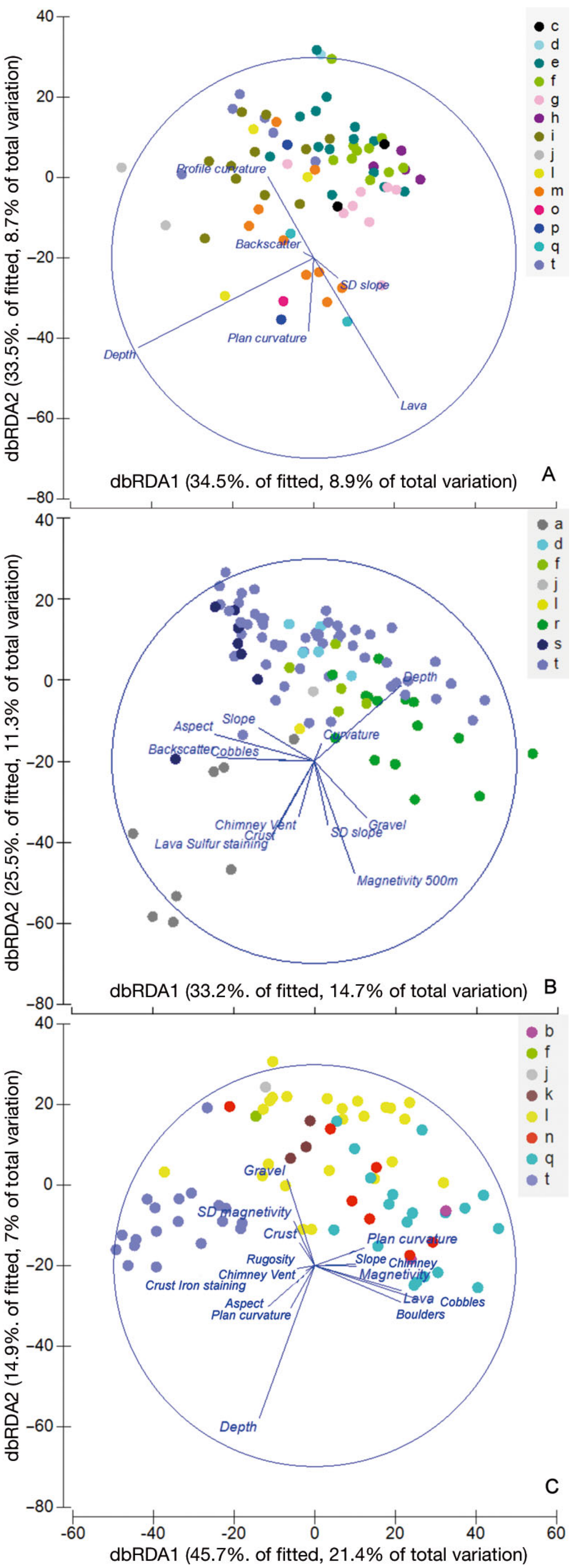
(Table 4). The best DISTLM model for Brothers (R^2 = 0.47, RSS = 1.33E5) included topography, depth, substratum and magnetivity (Table 4). At Rumble II West, the best model (R^2 = 0.43, RSS = 1.30E5) selected substratum, depth and topography (Table 4). Substratum hydrothermal and habitat heterogeneity were not included in the best model for any of the analyses.

The contribution of individual environmental variables to the models was assessed by running a DISTLM where the variables were ungrouped (Table 5). At Rumble II East, there were 24 variables available, of which 6 were included in the best model (R^2 = 0.26, RSS = 1.46E5). For Brothers, there were 41 environmental variables available, 12 of which were included in the best model (R^2 = 0.44, RSS = 1.39E5). Rumble II West had 31 environmental variables available, with 16 of these being included in the best model (R^2 = 0.47, RSS = 1.22E5). Depth was the only environmental variable to be included in the model for each of the 3 seamounts. The top 3 variables in terms of Pseudo-*F*-values were depth, lava and plan curvature at Rumble II East; depth, curvature and backscatter at Brothers; and boulders, depth and profile curvature at Rumble II West (Table 5). The importance of individual variable contribution to the models is visualised in the dbRDA plots (Fig. 5).

DISCUSSION

Assemblage structure and environmental drivers amongst seamounts

The seamounts selected for this study, Rumble II East, Brothers and Rumble II West, have different levels of hydrothermal activity and were expected to support different benthic assemblages. Analysis revealed that patterns in megabenthic assemblage structure differed both amongst seamounts and amongst habitats within seamounts. The patchwork of habitats observed at the studied seamounts also occurs elsewhere along the Kermadec volcanic arc at Rumble III and Rumble V Seamounts, with highly variable species diversity and density within and amongst seamounts (Clark & O'Shea 2001, Rowden et al. 2003). Patchy faunal distribution is common at seamounts generally, such as at Cross and Jasper Seamounts (Genin et al. 1986, Grigg et al. 1987) and Horizon Guyot (Kaufmann et al. 1989), where variability in the distribution of sessile filter feeders was associated with the occurrence of rocky prominences. These patterns reflect the variability of available habitats, where high between-habitat diversity supports high total seamount diversity (McClain et al. 2010).



The environmental drivers of assemblage structure amongst the 3 seamounts were magnetivity, depth, substratum and topography. Magnetivity can be a proxy for hydrothermal activity (Caratori Tontini et al. 2012a), with lower values occurring in regions of hydrothermal activity. The results of this study suggest that, at the seamount scale, hydrothermal activity (either current or past) is the main driver of differences amongst the 3 seamounts. Substratum and depth were also important influences on benthic assemblage composition on the Lord Howe Rise, Australia (Anderson et al. 2011), whilst substratum is an important structuring factor at seamounts generally, such as for coral communities associated with the stable rocky outcrops of Lo'ihi Seamount, Hawai'i (Grigg 1997). As well as being a key factor in the present study, topography also influenced community structure at Patton Seamount in the Gulf of Alaska, with the greatest diversity in topography and relief being associated with the highest faunal diversity (Raymore 1982).

There were 6 assemblages shared amongst the seamounts (d, f, j, l, q & t). The protozoan xenophyophores dominating assemblages d & f were also common in patches of soft sediment on the Lord Howe Rise (Anderson et al. 2011), the summit of Horizon Guyot and Magellan Rise in the North Pacific (Kaufmann et al. 1989) and seamounts in the eastern Pacific off Mexico (Levin et al. 1986). The ophiuroids dominating assemblages j & l are typically dominant components of the deep-sea benthic fauna on both hard and soft substrata (O'Hara 2007) and are abundant at other seamounts, such as Admiralty Seamount in the Antarctic (Bowden et al. 2011). Assemblage t was dominated by caridean shrimp and was especially prevalent at the seamounts with current (Brothers) and with relatively recent (Rumble II West) hydrothermal activity, which may suggest a vent association. A similar situation occurs at Kick'em Jenny Volcano in the Caribbean, where shrimp with no record of vent association exist in large numbers within the crater, potentially trapped during their downward diel vertical migration and subsequently becoming opportunistic vent residents (Wishner et al. 2005). Assemblage q was restricted to Rumble II East and West and was dominated by the long-lived and

Fig. 5. Distance-based redundancy analysis (dbRDA) plots to give the best possible visualisation of DISTLM results in 2-dimensional space for individual environmental variables at (A) Rumble II East, (B) Brothers and (C) Rumble II West. The coloured dots represent SIMPROF assemblages. Vectors are proportional to their contribution to the total variation (see Table 5)

slow-growing filter feeders typically associated with seamount hard substratum: comatulid crinoids, branching stony coral, schizopathid corals and primnoid/isidid corals. Assemblage q was not found on hydrothermally active Brothers, consistent with the findings of Clark & O'Shea (2001), who noted similar communities were almost entirely absent from the hydrothermally active Rumble III and Rumble V Seamounts. The absence of sessile, filter-feeding organisms was also noted at the volcanically and hydrothermally active peak of Northwest Rota-1 Volcano in the Mariana Arc (Limen et al. 2006) and has been attributed to environmental disturbance and the potentially 'hostile' geochemical conditions of hydrothermal activity (Grigg 1997).

Unique assemblage structure and the environment within seamounts

The unique assemblages at Rumble II East (c, e, g, h, i, m & p) were generally characterised by filter feeders, typical of communities associated with hard substratum on seamounts, such as ascideans, hexactinellid and stalked sponges, comatulid crinoids, brachiopods, stylasterids, primnoid/isidid corals and anemones. The occurrence of xenophyophores, with their preference for soft sediment, however, also suggests a degree of habitat patchiness within some of the samples. The abundance of sessile, filter-feeding organisms at Rumble II East can be partially explained by the distribution of lava and plan curvature, which were in the model and in combination define the occurrence of continuous hard substratum (lava) as well as ridges and valleys to funnel the currents (plan curvature: Wilson et al. 2007).

The unique assemblages at Brothers (a, r & s) had lower diversity, with each assemblage dominated by a single taxon: alvinocarid/hippolytid vent shrimp, tubed polychaete worms and echiuran worms, respectively. The vent shrimp and echiuran worm assemblages occur within areas of hydrothermal activity, with their low diversity being typical of hydrothermal vent communities (Grassle 1985). The alvinocarid/hippolytid shrimp at Brothers are presumed to be reliant on chemosyntheitc vent bacteria (Ahyong 2009), in a fashion similar to the closely related vent shrimp *Rimicaris exoculata* (Van Dover et al. 1988, Wirsen et al. 1993, Pond et al. 1997). Within the Southwest Pacific, alvinocarid shrimp also dominate hydrothermal communities on the active peak of Northwest Rota-1 Volcano (Limen et al. 2006), whilst *Lebbeus* hippolytid shrimp are exclusive to hydrothermally active sites, such as within the Manus and Lau Basins and the Okinawa Trough (Komai et al. 2012). The echiuran worms of assemblage s are not considered to be vent endemic. However, large populations may have established themselves in vent sediments in response to high levels of organic matter and hydrogen sulfide, as echiuran worms have been observed to dominate organically enriched intertidal areas (Stull et al. 1986). The dominance of polychaete and echiuran worms can be partially explained by curvature and backscatter in the model. Curvature is important for describing the relative position of terrain features and inferring current flow (Wilson et al. 2007), whilst backscatter is affected by the substratum characteristics of the seabed. In combination, curvature and backscatter represent the current flow and nature of the seabed and will influence the feeding ability of tube-dwelling polychaetes and echiurans (filter feeders and surface deposit feeders, respectively).

The unique assemblages at Rumble II West (b, k & n) exhibited relatively low diversity and high dominance, similar to the unique assemblages found at Brothers. Whilst assemblage n had higher diversity (branching stony corals, caridean shrimp and schizopathid corals), k and b were each dominated by 1 taxon: echiuran worms and comatulid crinoids, respectively. Although Rumble II West is generally considered hydrothermally inactive, previous hydrothermal activity may have enriched the sediments enabling large populations of echiuran worms to become established, as observed at Brothers. A high abundance of crinoids at Rumble II West has also been observed on the hard substrate of other seamounts, such as Davidson and Pioneer off California (Lundsten et al. 2009) and Admiralty Seamount (Bowden et al. 2011). The abundance of crinoids and corals in certain unique Rumble II West assemblages can be partially explained by the factors of boulders and profile curvature in the model. Taken in combination, boulders and profile curvature identify suitable elevated hard substratum, with higher current flow suitable for filter feeders. The occurrence of unique assemblages on Rumble II West coincided with video observations of hydrothermally inactive chimney structures, indicative of SMS areas. These chimneys provide elevated hard substratum and would be suitable habitat for filter feeders, as observed in the Manus Basin, where inactive chimneys are also colonised by sessile, filter-feeding organisms, such as sponges, hydroids, corals, anemones, squat lobsters, ophiuroids and holothurians (Galkin 1997, Collins et al. 2012).

Implications for the management of seafloor massive sulfide mining

The studied seamounts occur within areas originally licenced for SMS prospecting within the New Zealand EEZ. Prior to this study, little was reported on benthic assemblage structure at these seamounts, information essential for developing mitigation strategies for SMS mining.

The present study suggests considerable variability in habitat and biodiversity amongst seamounts. This is also the case when comparing seamounts of similar hydrothermal activity along the Kermadec volcanic arc: the alvinocarid/hippolytid shrimp observed on Brothers are absent from Rumble III, whilst the vent-endemic mussel *Gigantidas gladius* found at Rumble III and V is not present at Brothers (Clark & O'Shea 2001, Rowden et al. 2003). This has important implications for designing suitable strategies for mitigating the impact of mining activities on benthic fauna. One of these proposed strategies is the provision of 'set-aside' areas to preserve similar habitats and associated biodiversity within the region (International Seabed Authority 2010, Collins et al. 2013a,b). The high variability in seamount assemblages implies that protecting 1 seamount to enable mining at an adjacent seamount may not be a suitable strategy. Instead, to conserve the suite of assemblages present, it may be necessary to protect multiple seamounts or a network of sites. As impacts on SMS mining are expected to be localised (e.g. the majority of sedimentation impacts should occur within 1 km of the mining site; Coffey Natural Systems 2008), a network of smaller set-aside sites distributed within and amongst neighbouring seamounts may be a suitable strategy.

The unique assemblages at Rumble II West also suggest inactive SMS areas may support assemblages not found elsewhere in the region; individual taxa within these assemblages may be widely distributed, but the grouping of taxa to form these assemblages appears to be unique. This provides some support for the hypothesis that the unique environment of weathered inactive SMS deposits could host specific fauna (Van Dover 2007, 2011). The possibility of unique assemblages at inactive SMS deposits should be considered when designating set-aside sites, if they are to preserve local assemblage structure.

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