



Benthic megafaunal community structure of cobalt-rich manganese crusts on Necker Ridge



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ABSTRACT

In the North Pacific Ocean, the seamounts of the Hawaiian Archipelago and the Mid-Pacific Mountains are connected by Necker Ridge, a 600 km-long feature spanning a depth range of 1400–4000 m. The Necker Ridge is a part of a large area of the central and western Pacific under consideration for cobalt-rich manganese crust mining. We describe the fauna and community structure of the previously unsampled Necker Ridge based on explorations with the submersible *Pisces IV*. On five pinnacles and a portion of the Ridge ranging from 1400 to 2000 m deep, 27 transects were recorded using HD video, and voucher specimens were collected to aid in species identification. The video was analyzed to identify and count the megafauna found on each transect and to characterize the substrate. Diversity increased from south to north along the feature. There was a significant difference in community structure between southern and northern pinnacles, with southern pinnacles dominated by crinoids of the Family Charitometridae and northern pinnacles dominated by octocorals, especially the Families Isididae and Chrysogorgiidae. DistLM demonstrated a correlation between community structure on the pinnacles and at least six environmental variables, including latitude, sediment cover, and oxygen concentration, but not including depth. The discontinuous and patchy nature of these distinct megafaunal communities highlights growing evidence that cobalt-rich seamounts are highly heterogeneous habitats, and that managing seamounts may require more complex regulations than treating them as a single ecological unit. These results suggest that extensive community analysis should occur at a given site to determine management priority areas, prior to consideration of that site for exploitation of natural resources.

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1. Introduction

Seamount habitats can be found in every ocean (Wessel et al., 2010; Yesson et al., 2011) and provide hard substrate for sessile fauna in areas that are otherwise open ocean or sedimented abyssal plain. Seamounts and related features like banks and ridges often have steep relief, and these steep sides are thought to locally accelerate currents (Genin et al., 1986; White et al., 2005). Increased flow rates can prevent sedimentation (Hjulström, 1935), disperse propagules more effectively (Thistle, 2003), and possibly increase the availability of food particles for filter feeders (Rogers, 1994).

The impacts of fisheries trawling on the dominant sessile seamount megafauna, in particular deep-sea corals and sponges (e.g.

Wilson and Kaufmann, 1987; Hogg et al., 2010), have been relatively well-documented (Probert et al., 1997; Koslow et al., 2001; Clark and Rowden, 2009; Clark et al., 2010; Anderson and Clark, 2003; Niklitschek et al., 2010; Althaus et al., 2009; Williams et al., 2010). However, another major threat to seamount fauna that is less understood is the proposed mining of deep-sea substrates for minerals like cobalt from manganese crusts (Clark et al., 2009; Hein et al., 2009, 2010; Mengerink et al., 2014). Mining practices would remove all biogenic structures along with the crusts from a target area, and could cause large sediment plumes that could smother sessile fauna > 100 km outside of the mining location (Schlacher et al., 2014). Manganese crusts were previously expected to have overall lower abundances of deep-sea megafauna (Grigg et al., 1987), but Schlacher et al. (2014) reviewed data to demonstrate that seamounts with cobalt-rich manganese crusts in the Hawaiian Archipelago had abundant megafauna with different community structure than seamounts outside the cobalt-rich area.

Management of areas targeted for mining may be hindered by a

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lack of understanding of the communities present on targeted features as well as a lack of understanding of species distributions and spatial variability in community structure on seamounts in general. Although we now have more insights into the communities on cobalt-rich crusts in the Hawaiian Archipelago (Schlacher et al., 2014), the Archipelago is outside the targeted mining area. Within the area targeted in the central Pacific for cobalt-crust mining, few seamounts have been explored. Thus, the goal of our study was to explore a feature, Necker Ridge, within the targeted area and to characterize the deep-sea invertebrate megafauna on cobalt-rich manganese crusts of the Ridge in terms of abundance, diversity and community structure. Necker Ridge is a > 600-km-long razorback ridge feature, centered at approximately 22°N and 167°W, and trending north at about 32° (Hein et al., 1985). This unexplored feature is a prime first study target within this region because it lies just outside of the Papahānaumokuākea Marine National Monument of the Northwestern Hawaiian Islands (NWHI). Besides having cobalt-rich manganese crusts, Necker Ridge appears to be the only bathyal, hard-substrate feature properly situated to connect deep-sea fauna on the Mid-Pacific Mountains, which are also under consideration for cobalt-rich manganese crust mining, to the nearest protected areas in the NWHI.

We expect that there will be some variation in communities found along the Necker Ridge. Although globally only 200–300 seamounts have been biologically sampled (e.g. Rowden et al., 2010), patterns of community structure are beginning to emerge that indicate seamounts and similar features like ridges are not homogeneous habitats (e.g. Baco, 2007; Etnoyer et al., 2010; McClain et al., 2010; Rowden et al., 2010; Schlacher et al., 2014; Long and Baco, 2014). Seamounts typically have rough and heterogeneous topography, which can create irregular current patterns and uneven distributions of sediments, resulting in extensive areas of hard substrates as well as soft substrate habitats. The microhabitats that result from these changes in topography and substrate type (Auster et al., 2005) can result in patchy distribution of initial recruits that serve to enhance the heterogeneity. The types of organisms that recruit to each microhabitat then provide biological structures for epifauna (e.g. Buhl-Mortensen et al.,

2010), and further increase the biological patchiness found on seamounts (McClain et al., 2010).

Variation in other environmental parameters also contributes to observed heterogeneity on seamounts. Like other deep-sea ecosystems, seamount communities may be structured by depth (Baco, 2007; McClain et al., 2010; Schlacher et al., 2014; Long and Baco, 2014). In fact, species turnover of 93% can happen over depth ranges as small as 200 m (Long and Baco, 2014). Similarity between communities has also been shown to decrease with distance between communities, even on a single seamount (Halfar and Fujita, 2007; Schlacher et al., 2014). On some features other environmental variables, e.g. oxygen, salinity, substrate chemical composition, and substrate type, appear to structure community changeover rather than depth or distance (Levin et al., 1991; Wishner et al., 1990; McClain et al., 2010; Bo et al., 2011; Sautya et al., 2011). Thus, a second goal of this study was to examine the relationship of observed faunal patterns on Necker Ridge to environmental parameters such as depth, temperature and substrate type. In the process of addressing these goals we gain further insights into the fauna of cobalt-rich crusts within the targeted mining area, as well as into the relationship of observed community structure to environmental parameters on seamounts in general.

2. Materials and methods

2.1. Video surveys and analyses

To sample and explore each site at Necker Ridge we carried out video transects and specimen sampling in October 2011 using the submersible *Pisces IV*, operated by the Hawaii Undersea Research Laboratory. Necker Ridge is approximately 1400–4000 m below sea level. Pinnacles along the ridge were chosen as optimal sampling sites (Fig. 1) due to the depth limitations of the submersible (max 2000 m) and the likelihood of finding similar habitats to those studied on Hawaiian Archipelago seamounts. We define pinnacles as features conical in shape with steep sides, which do not have enough vertical relief to be classified as knolls. One dive

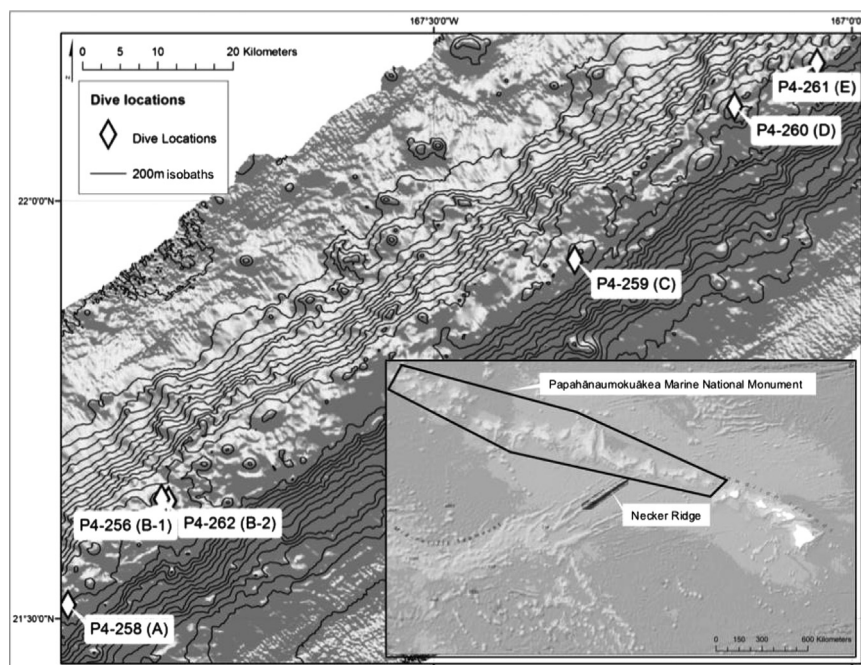


Fig. 1. Dive locations shown by diamonds and labeled by the *Pisces IV* dive number. Inset: Location of Necker Ridge relative to the Hawaiian Archipelago.

Table 1
Transect characteristics ordered from southernmost pinnacle to northernmost. Sampling began on pinnacle B though pinnacle A is the southernmost pinnacle, thus numbering is not sequential.

Transect	Latitude	Longitude	Max depth (m)	Length (m)	Time (min)	No. species	No. individuals	Fisher's (α)	Pielou's evenness (H')	Shannon's H' (\log_e)	ES ₁₀₀	ES ₅₀₀
A4S	21.517	-167.943	1745.10	718.28	15.83	21	63	3.8782	0.8440	2.5694	21.000	21.000
A5S	21.516	-167.937	1749.20	1061.30	17.00	17	94	3.3254	0.5951	1.6859	17.000	17.000
A6S	21.516	-167.937	1737.60	880.87	16.75	31	606	4.4971	0.3625	1.2446	12.482	28.959
B1S	21.634	-167.821	1748.10	1833.93	19.50	22	1124	11.0305	0.3591	1.1100	7.760	16.047
B2S	21.635	-167.818	1599.90	874.71	15.25	24	4528	6.0640	0.2860	0.9088	5.682	12.174
B3S	21.640	-167.817	1592.40	1568.43	15.55	32	5532	6.9120	0.1218	0.4220	5.748	14.386
B20S	21.655	-167.813	1922.70	574.48	15.33	42	486	8.6277	0.6538	2.4439	24.759	42.000
B21S	21.653	-167.815	1815.60	649.32	16.55	44	991	6.8892	0.4637	1.7547	19.350	36.518
B22S	21.650	-167.817	1700.20	645.95	15.17	22	2762	10.5838	0.1119	0.3459	5.157	12.205
B23S	21.649	-167.823	1701.10	775.25	15.00	25	1031	8.3683	0.2632	0.8471	10.073	19.726
B24S	21.646	-167.828	1603.10	626.04	14.50	39	6789	4.5443	0.1250	0.4579	6.335	15.523
B25S	21.646	-167.827	1603.00	857.40	15.00	29	4159	11.3199	0.1716	0.5778	7.042	14.111
B26S	21.645	-167.821	1501.30	653.54	15.00	42	2340	13.3169	0.5523	2.0642	18.045	31.501
B27S	21.643	-167.825	1500.90	604.69	15.42	42	2714	13.5043	0.4827	1.8042	16.230	29.798
C7N	21.936	-167.341	1894.70	782.26	12.33	20	79	9.3377	0.8525	2.5538	20.000	20.000
C8N	21.935	-167.339	1859.50	865.09	17.50	33	822	8.2265	0.4846	1.6944	16.767	28.969
C9N	21.930	-167.339	1852.90	840.92	15.33	36	307	11.1692	0.8014	2.8718	24.322	36.000
C10N	21.931	-167.335	1723.50	738.37	16.08	39	876	10.0380	0.6698	2.4538	18.505	33.543
C11N	21.929	-167.332	1706.10	743.46	15.92	24	889	10.7614	0.3466	1.1017	10.650	19.936
D12N	22.118	-167.133	1927.60	668.82	16.50	43	494	11.0291	0.7945	2.9884	27.696	43.000
D13N	22.121	-167.134	1936.00	792.65	15.00	37	201	9.4343	0.8239	2.9749	29.351	37.000
D14N	22.115	-167.137	1866.40	674.80	16.70	49	495	3.2630	0.7953	3.0951	28.897	49.000
D15N	22.113	-167.141	1748.30	560.68	12.50	47	1278	4.6188	0.7237	2.7706	24.096	40.848
E16N	22.172	-167.040	1840.40	562.65	16.50	46	2198	5.4747	0.5008	1.9172	17.987	32.733
E17N	22.168	-167.041	1830.20	563.10	16.00	51	1063	4.2041	0.7607	2.9909	26.374	44.633
E18N	22.166	-167.040	1813.30	601.74	16.33	53	1961	7.2699	0.6519	2.5882	23.595	40.338
E19N	22.164	-167.042	1729.90	608.41	17.00	49	1011	7.0524	0.7385	2.8743	25.454	41.654

was conducted on a portion of the ridge that was not a discrete pinnacle but was shallow enough to reach with the submersible. For simplicity of discussion, this site is also referred to as a “pinnacle” (pinnacle A). The greatest distance between the studied pinnacles is 117 km between pinnacles A and E.

To describe Necker Ridge and its fauna, HD video was recorded during quantitative submersible transects conducted at constant depth and speed. The transect locations are summarized in Table 1, and the full transect paths for each location are shown in Supplementary Fig. S1. During submersible dives it was observed that pinnacles on the northern half of the ridge appeared to have different communities compared to pinnacles on the southern half. A qualitative difference was also observed between transects on western slopes versus transects on eastern slopes. Based on these observations additional transects on both the east and west side of a single pinnacle (Pinnacle B) were incorporated to test these *a posteriori* hypotheses, but remaining time allowed for a second dive only on one pinnacle.

Before and after transects, individuals of the more abundant invertebrates were collected to serve as morphological voucher specimens. Total physical samples comprised 73 coral individuals across 33 species, 15 crinoid individuals across 5 species, and 20 sponge individuals across 9 species. Sponges and most octocoral families were identified by the authors and deposited in their respective museums. Additionally voucher specimens of crinoids were identified and archived by Dr. Charles Messing at Nova Southeastern University. After cataloging at the Smithsonian Natural History Museum, Chrysogorgiid octocorals in the genus *Iridogorgia* were sent to Dr. Les Watling at the University of Hawaii at Manoa and those in the genera *Chrysogorgia* and *Metallogorgia* were sent to Dr. Eric Pante at the University of La Rochelle for further identification.

Video transects were analyzed in 30-second intervals to fully capture the variability of the habitat. Organisms were identified to the lowest possible taxonomic unit and given unique identifiers if the species was unknown. Each video identification was also given

an identification confidence score on a scale of 1–4, with 4 being the least confidence. All confidence scores were kept in for descriptive statistics, but individuals with a confidence score of 4 were removed before multivariate analyses. Of the species observed, 58% were given binomial scientific names based on collected voucher specimens identified morphologically. For each visible individual that was counted, contact substrate type, relief (Wentworth, 1922; Parrish, 2007), rugosity, slope, and percent sediment cover were also measured (Supplementary Table S1). This video analysis method was used in Long and Baco (2014) and is similar to that described by Mortensen and Buhl-Mortensen (2004). For each transect, substrate categories were averaged over each 30-second interval, and then compiled to a percent occurrence for each transect (e.g. transect A1 had 57% boulder-type relief, 17% cobble-type relief, etc.). These measures were then further combined into “high” or “low” values so that analysis would cover categorized variables, and not a gradient of variables (Supplementary Table S1). Average salinity, dissolved oxygen, and temperature were gathered from submersible-mounted CTD data for each transect, but due to equipment malfunction, direct CTD measurements were missing for dive number P4-259 on pinnacle C. For this dive, CTD data from the NOAA World Ocean Database were used from within the same degree of latitude and longitude respectively (21°N and 167°W). Other transect scale variables include latitude, maximum depth, transect duration, transect length, mean direction, and the side of the pinnacle each transect was on (i.e. the small-scale topography can be sloping to the north (mean direction) but the whole transect was on the northwest side of the pinnacle). A combination of ultra-short baseline tracking of the submersible and Global Positioning System (GPS) tracking of the ship allows for each transect to be mapped in ArcGIS 10.0 using XY layers. The length of each transect was measured using the Geospatial Modeling Environmental package for R (Beyer, 2012). Mean direction was computed as in Long and Baco (2014) with the mean direction equations from Fisher (1995). Pinnacle side was assigned based on whether transects were on the northwest side

of a pinnacle or on the southeast side and coded as 0 or 1, respectively.

2.2. Statistical analyses

Statistical analyses were computed in either PRIMER v.6.1.15 (Clarke and Warwick, 2001) with the PERMANOVA add-on (Anderson et al., 2008) or R v.2.15.1 (R Core Team, 2012). Total species (S), number of individuals (N), Shannon's natural log base diversity index (H'), Pielou's evenness (J'), Fisher's alpha (α), and rarefaction curves to obtain ES_{100} and ES_{500} were calculated in PRIMER (Table 1). Shannon's H' is one of the most common diversity metrics reported, but this measurement is known to be difficult to relate across studies (Clarke and Warwick, 2001), thus we also report Fisher's α . Fisher's α is a diversity index that estimates the number of species in a sample expected to be represented by a single individual and is less sensitive to differences in sample size and differences in evenness than is H' (Hayek and Buzas, 1997). ES_{100} and ES_{500} are derived from Hurlbert rarefaction curves and represent the number of species expected in a given sample if the given number of individuals in the subscript were randomly taken from the sample (Hurlbert, 1971), and is an extrapolation from the total number of species and individuals collected. It also allows for more accurate comparison of samples of different sizes and takes into account both species evenness and richness. ES_{100} was chosen as a metric because the smallest samples had just under 100 individuals. ES_{500} was also chosen because most transects yielded a much larger number of individuals observed (Table 1).

Significant differences between diversity indices for north and south were calculated using t -tests with unequal variance in Microsoft Excel (2010). Although we attempted to make transects of equal length, there was some variation caused by currents affecting the submersible. In order to test for bias due to sample size, multiple regressions for each combination of transect duration and number of species, duration and number of individuals, transect length and number of species, and length and number of individuals were executed in R. Species count data for each transect were fourth-root transformed to reduce the influence of those few species that were ten-fold more abundant than others (Clarke and Warwick, 2001). For multivariate statistics, environmental variables were first normalized then assessed for independence in PRIMER using draftsman plots and pairwise correlations among variables. Normalized variables were then analyzed by Principle Components Analysis (PCA) to develop additional hypotheses. Community similarity was first analyzed with group average CLUSTER, then a Non-Metric Multidimensional Scaling (NMDS) plot was constructed to visualize the similarities between transects. One-way ANOSIM was analyzed between north and south pinnacle groups, with pairwise comparisons between all transects. A one-way SIMPER routine was analyzed using the pinnacles as units to find the organisms that best defined any pinnacle and best differentiated between pinnacles. Transect scale environmental parameters that defined the most variation in the abundance data were analyzed by DistLM using the AIC and Best criteria using the PERMANOVA add-on in PRIMER. Distance-based redundancy plots (dbRDA) and NMDS bubble plots were used to illustrate the relationship between the strongest variables as defined by DistLM and the similarities in community structure between transects.

3. Results

3.1. Pre-analysis data assessment

Transect lengths ranged from 561 to 1834 m (average 790 ± 293 m) and the duration ranged from 12.3 to 19.5 min

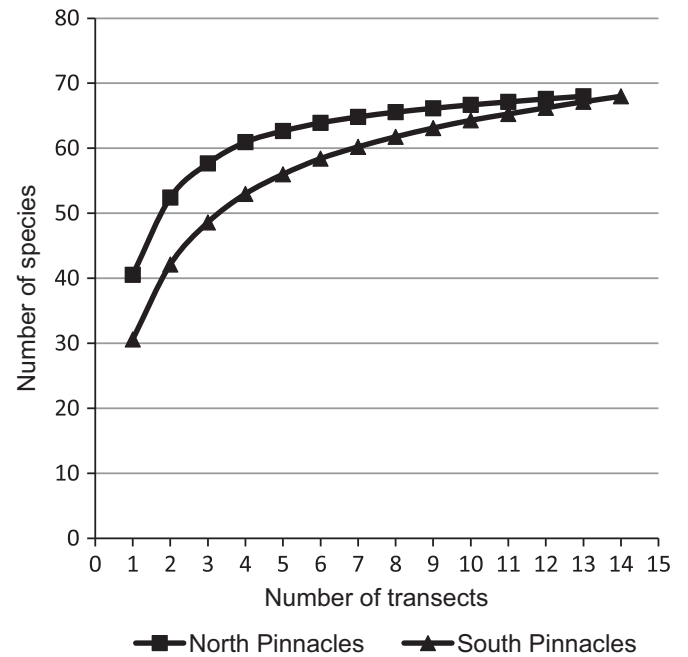


Fig. 2. Species accumulation curve for the north and south pinnacles.

(average 15.8 ± 1.4 min) (Table 1). Regressions (Supplementary Fig. S2) show no significant correlation ($p > 0.1$) for transect duration and number of species, duration and number of individuals, or transect length and number of individuals. Length and number of species did show a significant negative correlation ($p = 0.006$); however, because the relationship is opposite from what would be expected if there was bias due to sampling effort, this correlation was not considered a confounding factor. Draftsman plots demonstrated no correlation between the normalized variables at a limit of $r = \pm 0.90$, with the exception of a relationship between latitude and longitude. As a result, longitude was removed. The PCA of all environmental variables (not shown) did not provide information to build more *a posteriori* hypotheses. The species accumulation curves (Fig. 2) begin to reach an asymptote, suggesting the most common species present within our sampled depth zone on these features were sampled through video counts.

3.2. Descriptive and univariate statistics

Crinoids were the most abundant organisms overall (Fig. 3A) with 30,919 individuals counted over all transects (Fig. 3B). Members of the Family Charitometridae comprised 98% of the crinoid individuals. This family was represented by two species, *Glyptometra lateralis* and *Poecilometra acoela*. Five other species in three families represented the remaining 2% of crinoids. Anthozoans were the next most abundant class on Necker Ridge with 7955 individuals counted in all transects and 89% of these being representatives of the Octocorallia. The families Isididae and Chrysogorgiidae, (including the genera *Chrysogorgia*, *Rhodaniridogorgia*, *Metallogorgia*, and *Iridogorgia*), were the dominant families, comprising 41.8% and 38.2% respectively of the octocorals (Fig. 3B). These were also the most diverse octocoral families; 11 species belonged to the Isididae and 13 to the Chrysogorgiidae, with a further 3 assigned to another family, the Primnoidae. The remaining octocoral families were represented by only one or two species, giving a total of 42 octocoral species identified. Five sponge families on Necker Ridge were each also represented by only one or two species. Ascidians (2664 individuals) and ophiuroids (1085 individuals) were the next most abundant organisms; ophiuroids almost always occurred as epifauna on corals

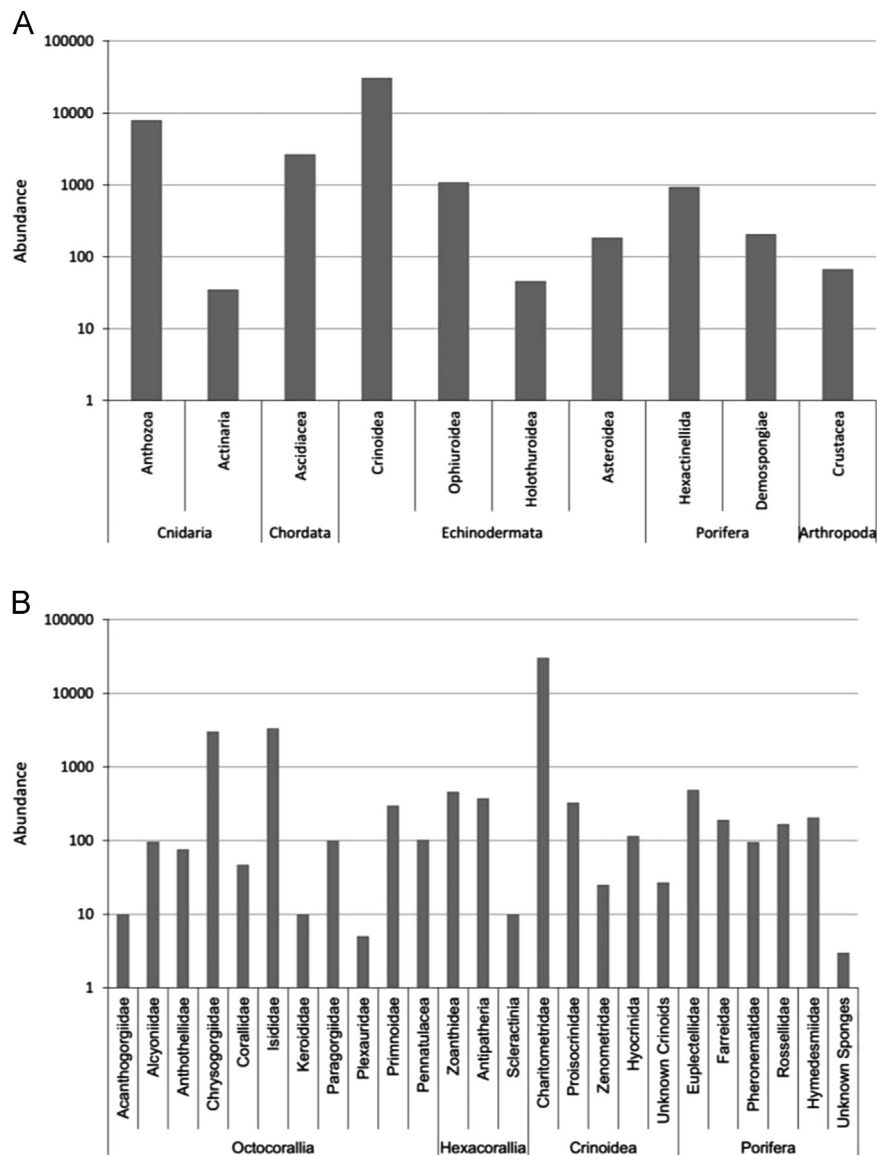


Fig. 3. (A) Abundance by class of all benthic organisms observed on Necker Ridge across transects. (B) Abundance of all organisms by family. Note the log scale on the y-axes in both panels.

and sponges while the brown potato-like ascidian *Styela* sp. was found in large groupings on hard bottom only on pinnacle E.

The five dominant animal taxa varied in abundance along the ridge; crinoids dominated on the southern pinnacles, A and B while corals dominated habitats on the more northerly pinnacles, D and E (Fig. 4). Pinnacle C shows a more even distribution of crinoids and corals with crinoids representing only slightly more than 50% of the individuals. In contrast, hexactinellid sponges were more evenly distributed across all of the peaks sampled rather than strongly dominating any one location. Pinnacle E had a very high mean abundance of ascidians compared to all other pinnacles on Necker Ridge.

Mean abundance of the coral and sponge families (Figs. 5 and 6) also show uneven distributions. Chrysogorgiidae and Isididae have a higher abundance on the northern pinnacles (C–E), while Antipatharians are the dominant corals on pinnacle A, and a more diverse mix of families occurs on B, including an abundance of Zoanthidea on one dive. Bamboo corals in the Family Isididae are widely distributed along Necker Ridge, but as we demonstrate in later analyses, different species are found between north and south pinnacles. Sponges were dominated by the Hexactinellida

with the Farreidae being most abundant on northern pinnacles and the Euplectellidae on southern pinnacles (Fig. 6). In contrast, the only family of demosponges, the Hymedesmiidae, was found throughout the Necker Ridge.

Diversity metrics (Table 1) also demonstrate the differences between pinnacles. In general many transects on the southern pinnacles have lower Shannon's diversity (H') compared to transects on northern pinnacles ($p < 0.001$). There is also a slight increase in the evenness (J) of the species distribution from south to north ($p < 0.001$), but there is not a trend with Fisher's α along the ridge ($p = 0.426$). The number of species (S) increases from south to north, and the expected number of species (ES_{100} and ES_{500}) also increases ($p < 0.001$ for both ES_{100} and ES_{500}). The number of individuals (N) shows a decrease from south to north ($p = 0.013$), but this trend is likely affected by the much higher numbers of individuals found on pinnacle B (range 486–6789 individuals per transect) compared to all other pinnacles (maximum 2198 individuals).

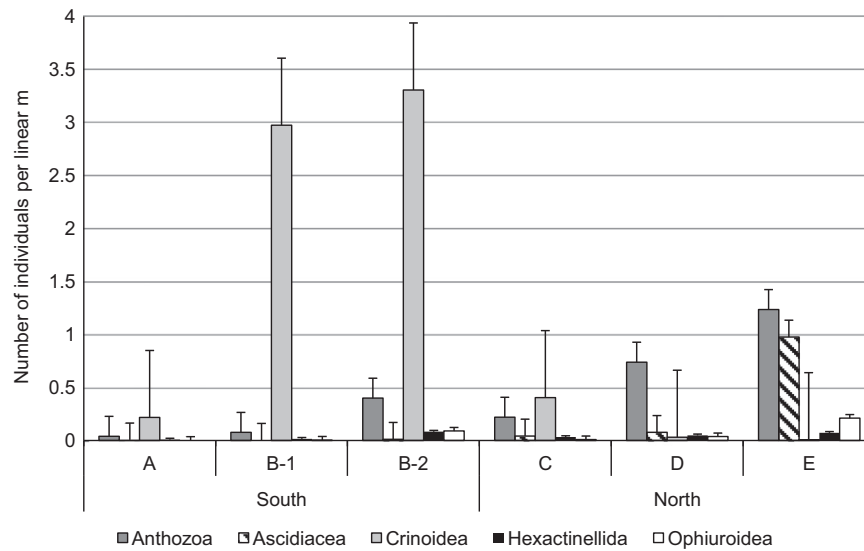


Fig. 4. Mean abundance of the five most common classes on Necker Ridge, calculated as number of individuals per transect divided by transect length. Error bars indicate one standard error.

3.3. Multivariate and environmental Analyses

Cluster analysis showed that at the 58% similarity level, transects split into 4 clusters, with similar groupings to the NMDS plot (Fig. 7A and B). Cluster I includes all transects from the northern pinnacles D and E (~70% similarity) with the exception of transect D13N. Cluster II includes most transects on pinnacle C along with transects that did not cluster within their respective pinnacles (A6S, B20S, B21S, and D13N). These transects form a large yet weakly structured cluster of samples that are more similar to northern sites than to southern sites. Communities found on all but two transects from pinnacle B form Cluster III and separate out from all other transects. The outlier dives on the southernmost pinnacle, A5S and A4S, cluster with one transect from pinnacle C (C7N) to form Cluster IV.

The NMDS (Fig. 7A) plot illustrates a similar pattern of community structure for transects within and among pinnacles. All but

two transects from both dives on the slopes of pinnacle B form a cluster to the upper left of the plot. The remaining two transects (B20S and B21S) were along a steep-sided edge on the northeast slope of the pinnacle. These transects group with pinnacle C, although B is closer to pinnacle A than to C. Transects A4S and A5S appear to be quite different from all other transects, including the third transect on the same pinnacle, A6S. Transects on the northern pinnacles D and E cluster separately from the other sites to the right of the plot, and transects from pinnacle C are spread out between pinnacle A and the outlier transects from pinnacle B. Pinnacle C is geographically closer to the northern sites (D and E) than the southern sites, but is more similar in assemblage composition to the southern pinnacles (A and B). One-way ANOSIM indicated significant differences in assemblage structure between northern (C–E) and southern pinnacles (A & B) ($p=0.001$). Pairwise tests in ANOSIM comparing the pinnacles (Table 2) showed that each north–south comparison was statistically significant

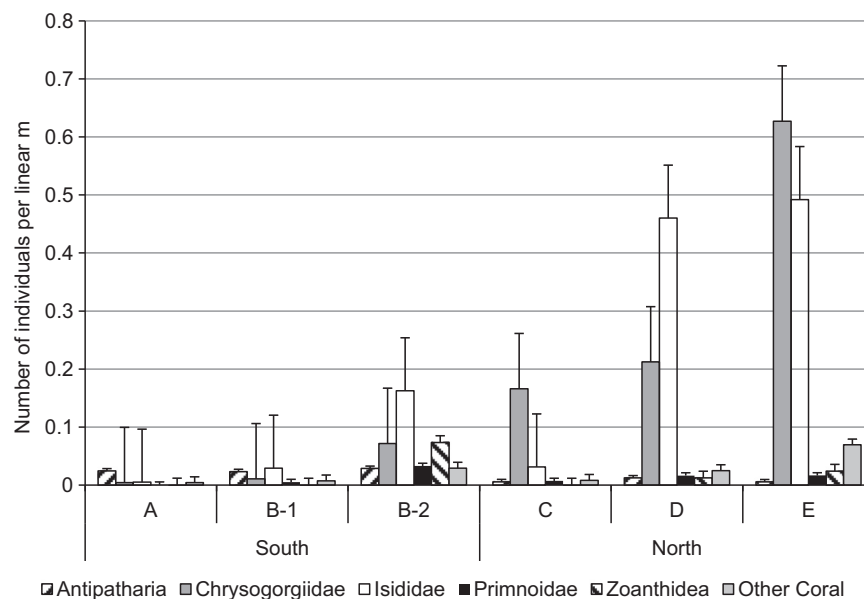


Fig. 5. Mean abundance of the most common coral taxa, calculated as number of individuals per transect divided by transect length. “Other corals” are those with fewer than 100 individuals on any site, which includes: Acanthogorgiidae, Anthothellidae, *Anthomastus*, Coralliidae, Keroididae, *Paragorgia*, Pennatulacea, Plexauridae, and Scleractinia. Error bars indicate one standard error.

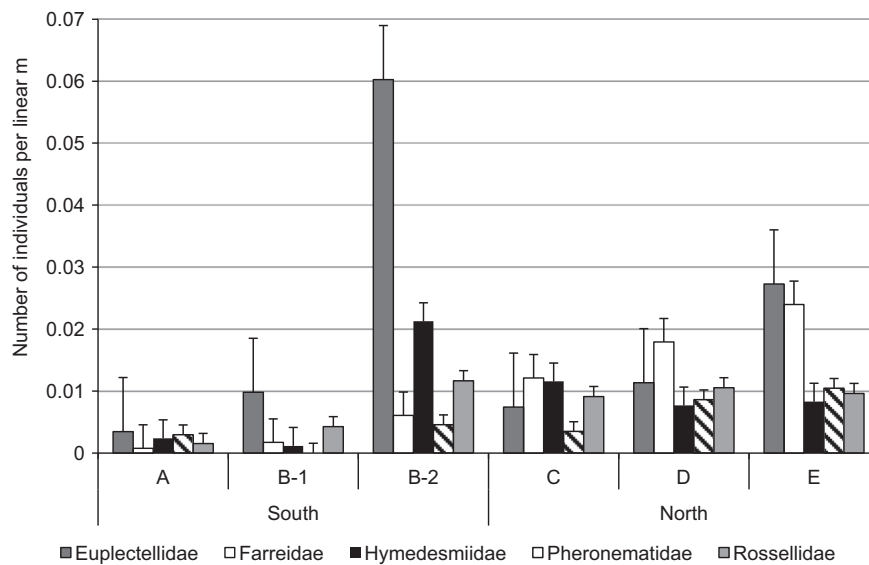


Fig. 6. Mean abundance of the sponge families found on Necker Ridge calculated as number of individuals per transect divided by transect length. One sponge species that could not be identified to family, identified as “unknown sponge” in this work, is omitted from the graph due to rarity. Error bars indicate one standard error.

($p < 0.05$) with the exceptions of the comparison of A–C. Within the northern group, the comparison of either pinnacles D or E to C was also significant, and within the southern group only the comparison of A to B-2 was significant.

SIMPER analysis identifies organisms that determine faunal similarities between assemblages from individual pinnacles. Fig. 8 shows the percent contribution at the genus or family level of all organisms. On the southern pinnacles A and B and the central pinnacle C, the highest percent contribution (between 10% and 17%) to community similarity within each pinnacle comes from the crinoid *Glyptometra lateralis*. For pinnacles B and C *Poecilometra acoela* is the second highest contributor to similarity within the pinnacle, while on pinnacle A the black coral *Bathypathes* sp.1 is the second highest contributor. The highest percent contributions on the northern pinnacles D and E are from the octocorals within the family Isididae and *Chrysogorgia* spp. (between 7% and 9%). *Chrysogorgia* spp. also makes a similar contribution to pinnacle C and on the northern pinnacles (7.5%). Sponges of the genus *Farrea* have a 6.9% and 6.5% percent contribution to the pinnacles C and D, although they represent less than 5% on all other pinnacles. The ascidian *Styela* sp. makes a similar contribution to the community on pinnacle E (7%) as Isididae sp. 1 (possibly *Acanella* sp.) and *Chrysogorgia* spp. The lower part of Fig. 8 has images of the species determined by SIMPER to have the highest contribution to similarity values within a given pinnacle. The gradual shift from crinoid dominated to coral dominated communities is apparent. The overlap of species on adjacent pinnacles suggests a more gradual shift in community structure rather than an abrupt community shift from northern to southern pinnacles.

Only a few species on Necker Ridge seem to be driving the differences between the pinnacles, mostly due to their extremely high abundances at one or two locations. SIMPER analysis shows that differences between northern (D and E) and southern (A and B) pinnacles are generally attributable to the much lower abundance of *Chrysogorgia* corals on the southern sites and the extreme abundance of the crinoid *Glyptometra lateralis* on the southern pinnacles (Supplementary Table S3). The abundance of the ascidian *Styela* sp. is also important to the differences between north and south locations. There is also a change in the coral community along the ridge; in pairwise comparisons between individual northern and southern pinnacles *Bathypathes* spp. and the sea pen *Distichoptilum* sp. are important for distinguishing the southern

pinnacles while *Chrysogorgia* spp., *Paramuricea* sp., and *Corallium* sp. are important in differentiating the northern pinnacles. The species that contribute to the difference of pinnacle E from all other pinnacles are the ascidian *Styela* sp., scleractinian hard corals, and the octocorals *Paragorgia* spp.

DistLM analysis reported nine environmental variables with a statistically significant correlation to the observed community structure (Table 3). The resulting model with the best AIC value included 6 of these, namely latitude, sediment cover, rugosity, oxygen, salinity, and temperature. The range of AIC values for the top 10 models from DistLM was from 176.29 to 176.89, which is a generally narrow range for AIC values. Typically a difference of at least 2 units demonstrates a real difference between models (Anderson et al., 2008; Burnham et al., 2011). However, models that have fewer variables are given more weight because each variable is providing more information, which is why the 6-variable model with the lowest AIC is determined as the most useful model by DistLM. The variables highlighted by the highest ranking model included latitude, percent sediment cover, percent high rugosity, oxygen, salinity, and temperature. Salinity and temperature are included in all top models, rugosity in nine, oxygen and sediment cover are included in six, and latitude is included in the top five models. Depth was only included in one of the top models. DistLM puts more weight on variables that describe new variation even if they are weakly correlated. As a result, percent high rugosity substrate was found to be important in the top models even though individually it explains a very small proportion of the variation (0.05) and is weakly correlated to the dataset on its own ($p=0.214$). Maximum depth was included in one model and percent high slope was chosen in two combinations. Pinnacle side was also chosen for one combination, even though it shows no correlation to the linear model ($p=0.774$). Though percent hard substrate is significantly correlated to community structure, it was not included in any combination, likely because another variable overlaps in the variation explained. The dbRDA plot (Fig. 9) from the top model of DistLM indicates that latitude shows the strongest relationship with the dbRDA1 axis (-0.735), suggesting it explains most of the variation in community structure, while the remaining variables have a stronger relationship with the dbRDA2 axis.

Bubble plots demonstrate the relationship between community structure and the 6 environmental parameters identified as

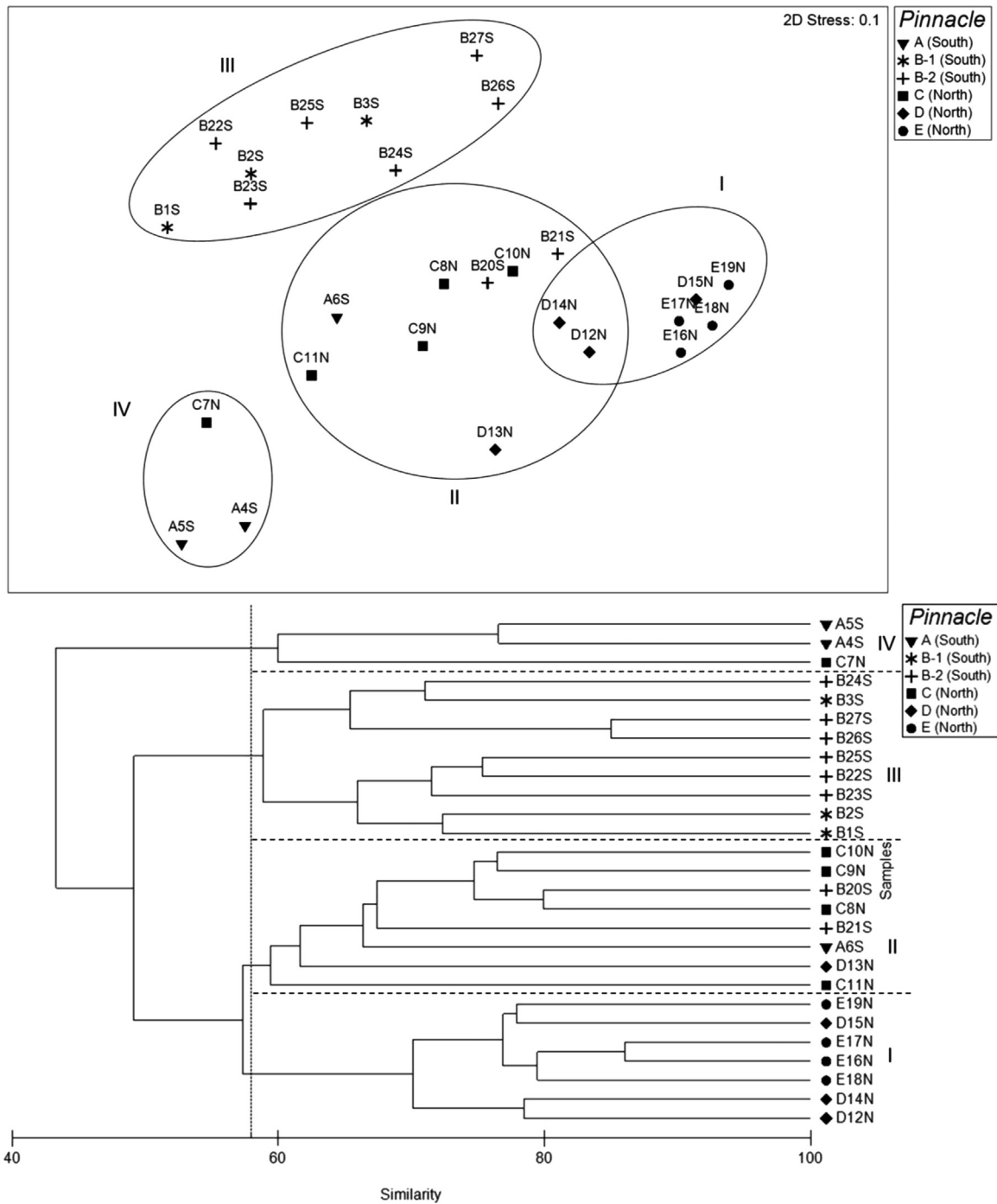


Fig. 7. (A) NMDS plot for transects on Necker Ridge. Symbols indicate which pinnacle transects sampled. Circles correspond to groups identified in cluster analyses in panel B. (B) Cluster diagram of transects using group average clustering method.

important by DistLM. Panel A suggests a strong pattern with latitude, confounded by the southernmost dive at site A (Fig. 10A). Fig. 10B indicates that the relationship between percent sediment cover and the community structure is not as clear, with transects to the left of the plot generally having higher sediment cover. The high sediment cover of A4S and A5S relative to all other transects could contribute to their distinctiveness. Although temperature was in all the top models, the bubble plot does not suggest a strong pattern with temperature, perhaps because the measured data only spans a range of 0.88 °C, with pinnacle A having the lowest temperatures of the sampled sites and many transects at pinnacle B having slightly warmer temperature than the other

sites (Fig. 10C). Oxygen also shows an interesting pattern in Fig. 10D, though less distinct than latitude; we see a slightly higher average oxygen on the southern pinnacles than on northern pinnacles, though there are exceptions. Bubble plots for percent high rugosity and salinity show no discernable trends (Fig. 10E and F).

4. Discussion

Consistent with the review of studies of cobalt-rich crust areas of the Hawaiian Archipelago (Schlacher et al., 2014), our observations show that seamounts within the targeted cobalt-rich

Table 2
Pairwise ANOSIM results for comparisons of pinnacle communities on Necker Ridge.

Pinnacles	R	P-value
B1 (South), A (South)	0.667	0.10
B1 (South), C (North)	0.559	0.036
B1 (South), D (North)	0.963	0.029
B1 (South), E (North)	1.0	0.029
B1 (South), B2 (South)	0.062	0.333
A (South), C (North)	0.415	0.054
A (South), D (North)	0.852	0.029
A (South), E (North)	1.0	0.029
A (South), B2 (South)	0.677	0.006
C (North), D (North)	0.5	0.008
C (North), 5 (North)	0.75	0.008
C (North), B2 (South)	0.287	0.035
D (North), E (North)	0.333	0.057
D (North), B2 (South)	0.504	0.006
E (North), B2 (South)	0.662	0.004

mining region do in fact host dense assemblages of structure-forming species, in contrast to early speculation that they might not (Grigg et al., 1987). The communities on Necker Ridge were dominated by crinoids, octocorals and sponges, with diversity increasing to the north along the Ridge. Community structure also varied significantly between pinnacles on the northern portion of the ridge compared to those on the southern end.

Histograms show a skewed distribution of sessile fauna on Necker Ridge, with two species of crinoids together being a full order of magnitude more abundant than all anthozoan species found, with most of these found on the southern portion of the feature. SIMPER analyses supports the abundance of crinoids on the southern pinnacles and corals on the northern pinnacles as some of the key contributors to dissimilarity of the north vs south pinnacles.

The highly uneven distribution of organisms along Necker Ridge calls into question why the southern sites support such large communities of crinoids, and why corals and ascidians are so much more abundant on the northern pinnacles? The distribution of organisms suggests that if primarily the environment determines the community structure, then there is likely a gradient of habitat change that has a strong impact on the types of organisms that occur along Necker Ridge. Alternative explanations for this variation in community structure across the Ridge may be related to larval supply or species interactions, such as competition.

4.1. Environmental variation as an explanation for north vs south patterns

One of the more intuitive environmental explanations for the higher abundance of crinoids on the southern portion of the ridge may be sediment cover. The southern sites tend to have higher percent sediment cover than the northern pinnacles, and sediment cover was highly correlated with community structure in the DistLM models (Table 3), supporting this hypothesis. In general filter feeders are thought to be highly sensitive to sedimentation (De Mol et al., 2005; Tompkins-MacDonald and Leys, 2008), but the high numbers of crinoids at locations with more sediment suggests a decreased sensitivity to sedimentation in the crinoids compared to the octocorals. Corals use mucus-covered polyps to filter-feed while crinoids use specially arrayed tube feet (Meyer, 1979). This may allow crinoids to be less sensitive to sediment loads, and previous studies have also found crinoids on substrates with relatively more sediment and with less abundant corals (Buhl-Mortensen et al., 2010; Bowden et al., 2011). However, if this were the single most important factor, we would expect sediment

levels to impact sponges, as they are also sensitive to sedimentation (Carballo, 2006; Tompkins-MacDonald and Leys, 2008), but sponges were common on some southern portions of the ridge, which supports the indication that sediment cover is not the only environmental element affecting community structure and species turnover.

Sedimentation can also be a proxy for current speed; sedimentation and current speed are inversely proportional so that hard substrate habitats with fast currents typically have low sediment cover. Necker Ridge seems to be characterized by fine sand grains, which Hjulström (1935) showed require an average velocity of 0.7 cm/s to maintain transportation of this size of sediments (*sensu* Press and Siever, 1986). A decrease in velocity by just 0.2 cm/s could cause the increased sediment cover seen at the southern sites. Depending on the geographic variation in current velocity across the ridge, there could be a lower velocity along the southern portion of Necker Ridge that promotes sedimentation at the southern pinnacles. Alternatively, the general morphology of the southern pinnacles could prevent the acceleration of the currents over the substrate as strongly as on the northern pinnacles. If the currents are weaker on the southern sites, there could also be a relationship between currents and the amount of food available to the filter-feeding organisms. Based on the trophic subsidy hypothesis (Genin et al., 1986; reviewed in Genin and Dower, 2007), without the accelerated currents, less food would be available on the southern pinnacles, which could prevent large coral forests from occurring. A larger food requirement by the corals compared to the crinoids would need to be determined experimentally, but this would also begin to explain how the sponge abundance is unaffected by location as they have the ability to actively pump water through their choanocytes.

Although percent sediment cover was an important variable, of all the environmental variables, latitude explained the most variation in community structure in the DistLM analyses. If latitude is excluded from DistLM analysis there is an 8.3% reduction in the variation of the community structure explained by other environmental variables. Latitude is likely a proxy for more complicated interactions between primary productivity, geomorphology, temperature, salinity, sedimentation, and/or oxygen, or other unmeasured parameters along the ridge. One possibility is that there may be a change in water mass across the feature. The strong correlations between temperature, salinity and oxygen with community structure could support such a change, but none of these water qualities show as clear of a pattern in the MDS bubble plots as latitude does and none of these were more than 48.4% correlated with latitude. There was only a 0.88 °C temperature range across all transects and any biological significance of this small difference is questionable. Changes in temperature values between pinnacles do not show the same gradient along the Ridge as community structure, but could potentially explain why the two southern pinnacles have different community structure.

Tidally rectified current patterns could be the source of temperature and oxygen differences (White et al., 2005), in which case the time samples were taken would affect the measured environmental conditions. Time series data is nearly nonexistent in this region, which limits the ability to consider the influence of tidally rectified current patterns. Though perhaps not due to water mass changes, oxygen concentrations could determine community structuring through the tidal movements; Vaquer-Sunyer and Duarte (2008) demonstrated that cnidarians had a sublethal oxygen concentration threshold approximately 1 mg/L less than the sublethal threshold for echinoderms. That difference is mirrored in the range of oxygen concentrations seen across Necker Ridge, but time series data would help determine the frequency and duration of any reduced oxygen level events. If the northern pinnacles are affected by lower oxygen concentrations for extended time

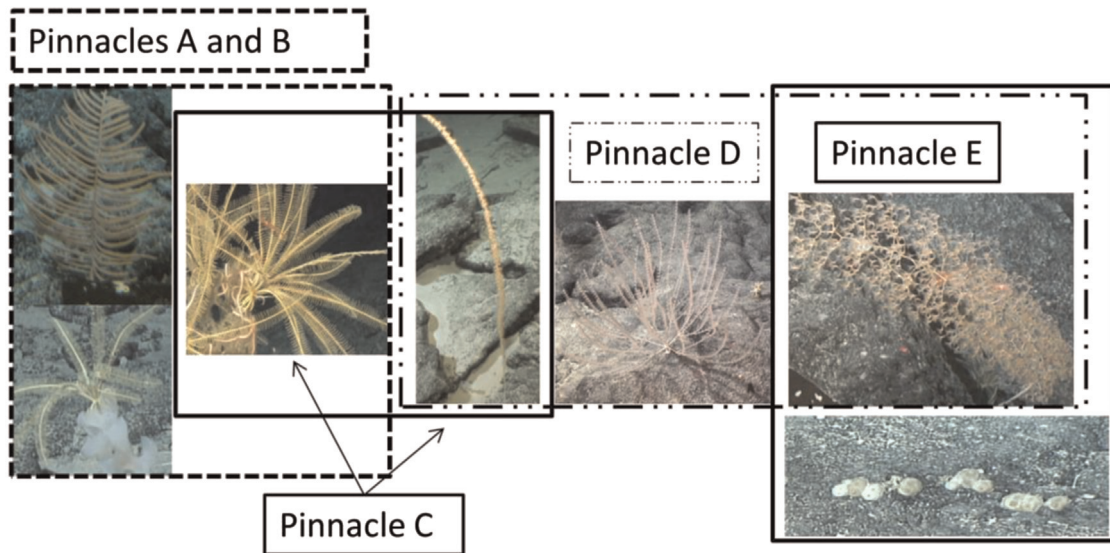
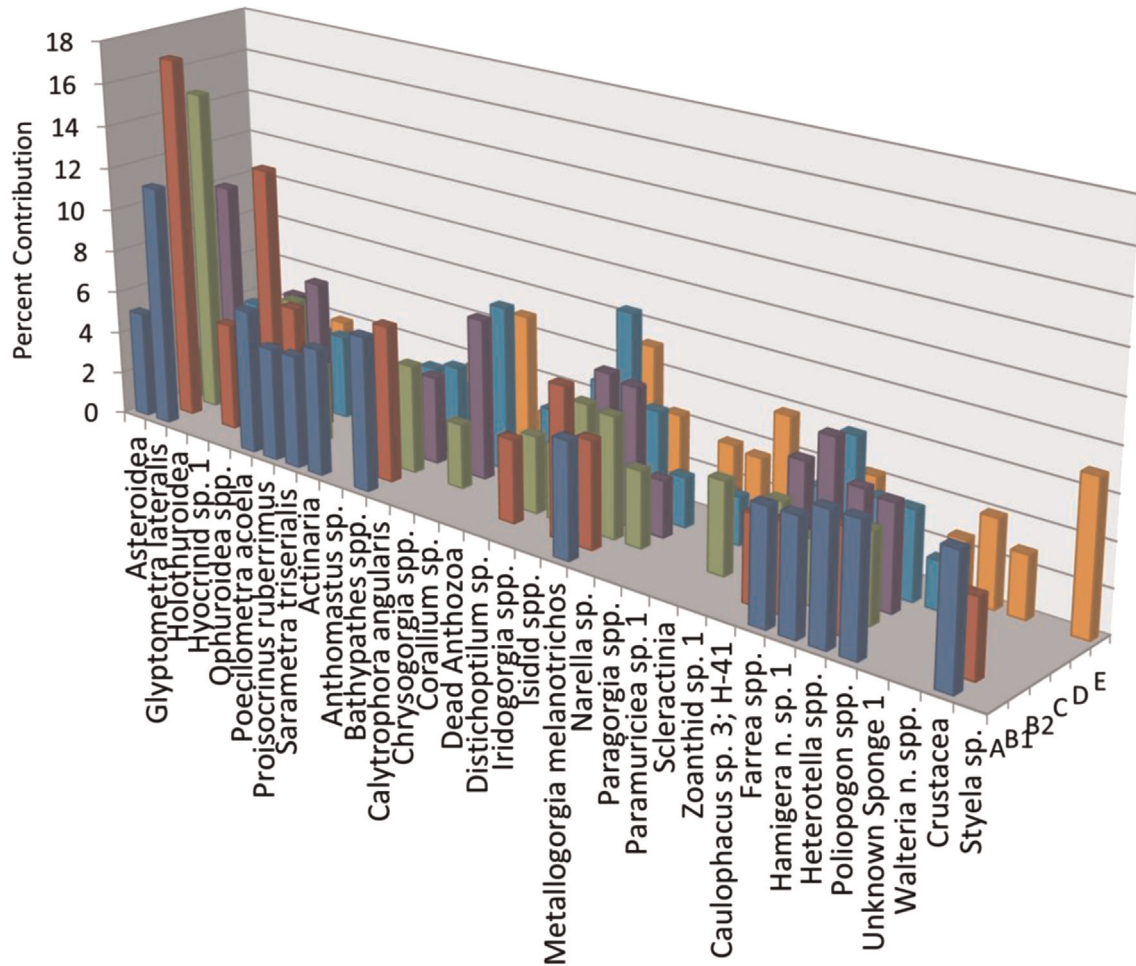


Fig. 8. SIMPER analysis of Necker Ridge fauna that define the community on a pinnacle. Organisms were grouped and analyzed by genus for easier display. Images show the community shift from south to north, starting from the top left to bottom right. Depicted species are: *Bathypathes sp. 1*, *Glyptometra lateralis*, *Poecilometra acoela*, *Isididae sp. 7*, *Isididae sp. 10*, *Chrysogorgia geniculata*, and *Styela sp.*

periods, echinoderms could be excluded from recruitment there. Besides crinoids, other echinoderms present included ophiuroids, asteroids, and brisingids. While the ophiuroids were relatively evenly distributed, the brisingids and other asteroids had higher abundance on the southern pinnacles. The environmental data from pinnacle C could also provide insight into the apparent community gradient. The central pinnacle has more similar oxygen

values to the southern sites, but temperature values similar to the northern sites, as well as a mix of high and low sedimented transects, which could explain the community on pinnacle C sharing traits with both northern and southern locations. Deep-sea organisms are typically sensitive to environmental changes (Dodds et al., 2007), thus these relatively small environmental differences could be influencing larval settlement or juvenile

Table 3
DistLM marginal tests and top 10 overall best model results. Significant *p*-values for individual variables are in bold.

No.	Variable	SS (trace)	Pseudo-F	<i>P</i> -value	Prop. of variation
Marginal tests					
1	Latitude	8593.7	10.032	0.001	0.28636
2	% Sediment cover	6512.8	6.9293	0.001	0.21702
3	% High rugosity	1569.0	1.3792	0.214	0.05228
4	Avg. oxygen (mg/L)	5238.7	5.287	0.001	0.17456
5	Avg. salinity (PSU)	2500.6	2.2725	0.045	0.08333
6	Avg. temp. (°C)	4409.0	4.3055	0.005	0.14692
7	Pinnacle side	618.14	0.52577	0.774	0.0206
8	% High relief	3774.1	3.5963	0.014	0.12576
9	Max depth	4630.1	4.5608	0.004	0.15429
10	Mean direction	442.94	0.37452	0.909	0.01476
11	% Hard substrate	4268.3	4.1453	0.002	0.14223
12	% High slope	3603.0	3.4111	0.014	0.12006
Overall best solutions					
AIC	<i>R</i> ²	RSS	Variables in best models		
176.29	0.63315	11,009	1–6		
176.62	0.65512	10,350	1–7		
176.68	0.59919	12,028	1, 3–6		
176.70	0.65404	10,382	1–6, 9		
176.80	0.65285	10,418	1–6, 12		
176.82	0.59712	12,090	3, 5, 6, 8, 10		
176.82	0.65258	10,426	2, 3, 5–8, 10		
176.86	0.67692	9695.7	3–8, 10, 12		
176.86	0.59652	12,108	5–8, 10		
176.89	0.67651	9707.9	2, 3, 5–10		

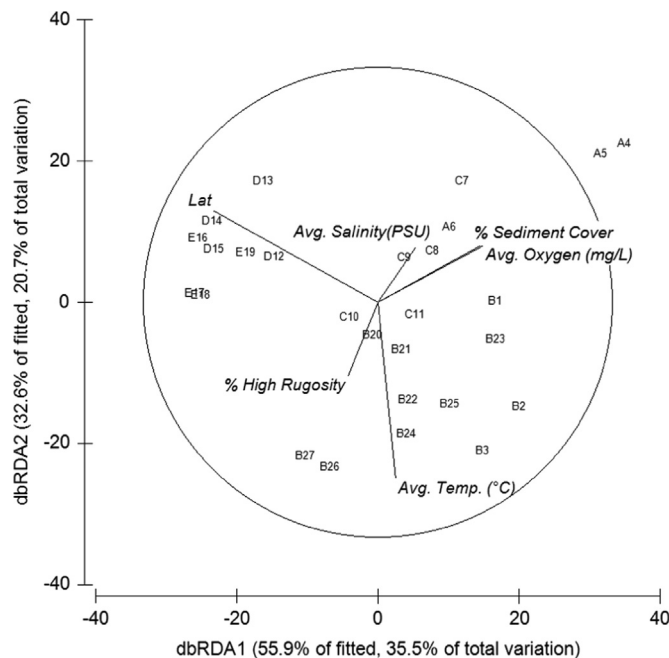


Fig. 9. dbRDA plot from environmental parameters chosen by the top DistLM model of community data compared to environmental factors. PC1 explains 36.6% of the total variation and PC2 describes 17.4% of the total variation. Six axes describe 63.3% of the overall variation. Point labels indicate the pinnacle and transect number.

growth of benthic organisms on Necker Ridge.

The distinct faunal changeover along a relatively small distance seen on Necker Ridge is surprising for a deep-sea habitat because many deep-sea species are thought to have wide dispersal capabilities and there does not appear to be any distinct barrier to dispersal for corals or crinoids along the ridge. However, as

discussed above, differences in environmental variables that describe habitats on seamounts can explain community structure variation at the scale observed in our study (20 km between pinnacles, across 117 km) Schlacher et al. (2014) demonstrated that taxa turnover increases on individual seamounts between sites with only a 1–2 km distance between them, even for deeper depth ranges (700–2000 m).

4.2. Biological and ecological explanations for north vs. south patterns

Deep-sea communities are not typically thought to be controlled by competition for space, but instead by recruitment limitation and the slow growth of most deep-sea megafauna (e.g. Rogers et al., 2007). However, on Necker Ridge there could be a competitive interaction between the crinoids and the corals and/or sponges. For example, there could be competition for space between crinoid and coral recruits, preventing coral–crinoid cross colonization. Both crinoid- and coral-dominated communities were often densely arranged and the high number of filter feeders per square meter could potentially prevent larval settlement (Dayton, 1971). An alternative is that with so many filter feeders present, there could be fairly high larval loss, with many larvae consumed before they can reach the substrate (Fabricius and Metzner, 2004). Another alternative is that there could simply be limited recruitment in general (e.g. Grigg, 1988), which in turn causes slow colonization along the ridge.

Another factor related to larval supply may be the composition of the source populations. We know there are rich and diverse coral and sponge communities to the north of Necker Ridge, on the Hawaiian Ridge, which could supply northern Necker Ridge communities with coral and sponge recruits, depending on current flow patterns. We do not know the community composition on the nearest seamounts to the south of Necker Ridge, the Mid-Pacific Mountains. If the Mid-Pacific Mountains are crinoid dominated, this could in part explain the dominance of crinoids on the southern portion of Necker.

Of these many possibilities, we speculate that there is a strong barrier to colonization for corals on the southern pinnacles in the form of higher sedimentation rates that prevent the larvae of many coral species from settling or surviving. If currents are slowed at the southern sites, then there could also be limited recruitment from outside the pinnacles that is reinforcing the differences between northern and southern sites. Empirical data on current velocities over time in this area would provide a clearer picture of how strongly the currents impact communities on Necker Ridge. Further studies on competitive interactions between corals and crinoids, as well as on tolerance of sedimentation by crinoids, would also help tease apart the potential reason for the variation in community structure seen at the shallowest portions of Necker Ridge.

4.3. Why not depth?

Typically in deep-sea habitats, including seamounts, there is a changeover in species composition with depth (e.g. Howell et al., 2002; Etter et al., 2005; McClain et al., 2010; Wei et al., 2010; Long and Baco, 2014). However, on Necker Ridge pinnacles the change in community structure is not as pronounced as the change along the latitudinal gradient. Maximum depth shows no trend on an NMDS bubble plot and was only included in one of the top ten models in the DistLM analysis. In the previously mentioned studies, where depth was found to be the major factor related to community structure, it is usually considered a proxy for other oceanographic variables that often change with depth. Where sampled on Necker Ridge, those same variables (temperature,

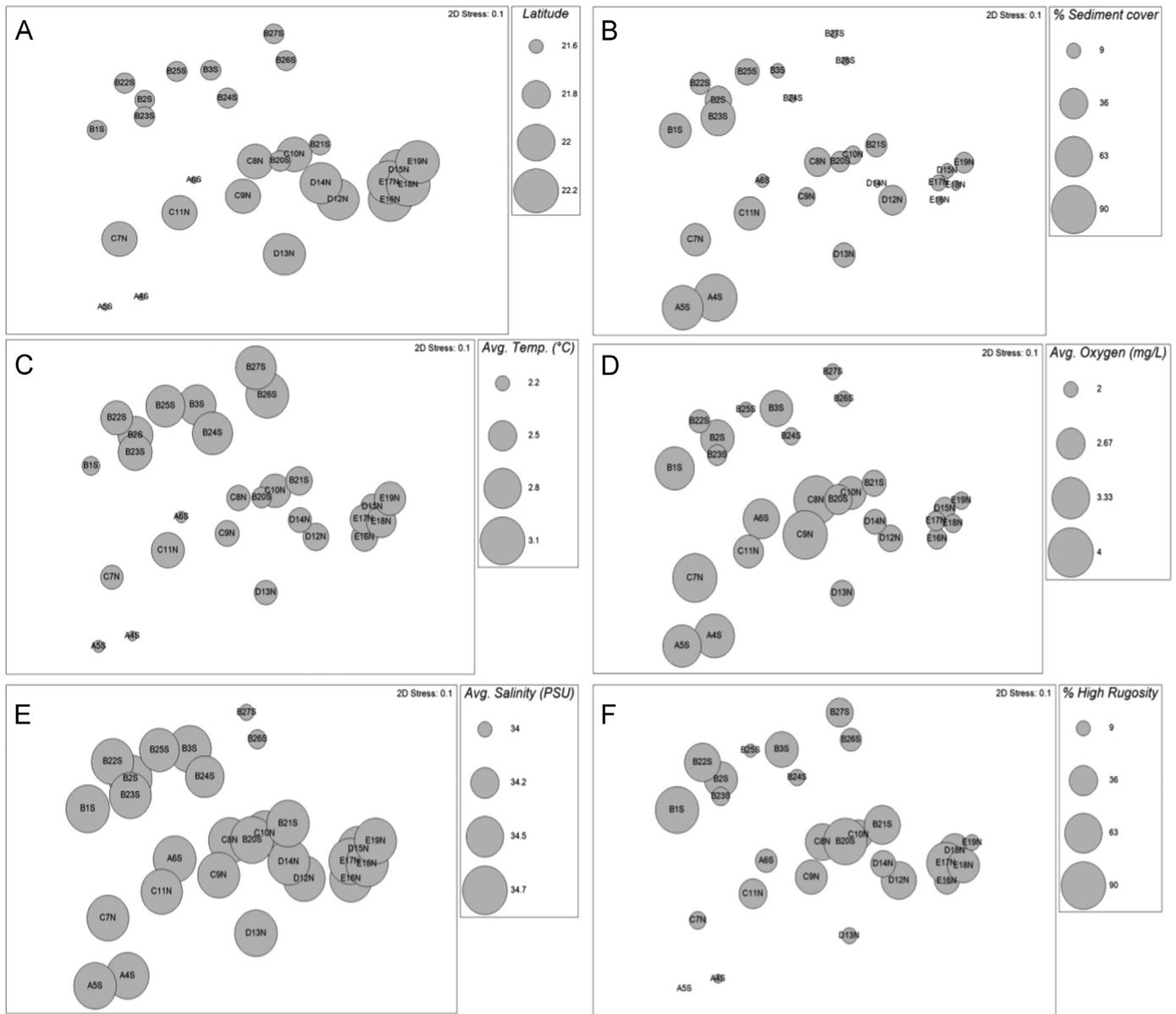


Fig. 10. MDS with bubble plot overlays for the six variables chosen as the top model in the DistLM analysis. Bubble size is related to the value of the environmental variable and each point is a transect. A – latitude, B – percent sediment cover, C – average temperature, D – average oxygen concentration, E – average salinity, and F – percent high rugosity.

salinity, oxygen, and sediment cover) seem to change more with location rather than depth. Another explanation for a lack of depth pattern is that sampling may not have covered a broad enough depth range for us to see a change in species composition with depth. [Howell et al. \(2002\)](#) found that the shallower depth zone in their study (150–700 m) had a much higher rate of faunal changeover than deeper bathymetric zones (nearly two-times greater than the 1500–2000 m zone). Consistent with this finding, the shallower Makapu'u deep-sea coral beds (320–530 m) in the Hawaiian Archipelago ([Long and Baco, 2014](#)) demonstrated a faster rate of faunal changeover than observed here on the deeper Necker Ridge. Thus we likely need to sample a larger depth gradient to fully resolve the species turnover on Necker Ridge.

5. Conservation implications

Cobalt-rich crust mining is quickly moving from theoretical mineral exploitation to active leasing ([Mengerink et al., 2014](#)), but

understanding of the distribution of fauna on these features as well as how human exploitation will affect these fauna is still minimal. The rich and diverse megafaunal community on Necker Ridge indicates that cobalt-rich crusts in the area of the central Pacific targeted for mining can support communities comparable in abundance and diversity levels to those that have been documented on other seamounts outside the cobalt-rich regions. These communities may not be uniform in composition across a given feature, as we find that there is a changeover in diversity and community structure moving from south to north across the pinnacles of Necker Ridge. We also see variation in community structure within a single pinnacle. These findings add to a growing body of evidence that deep-sea cobalt-rich seamounts are highly heterogeneous habitats and that extensive community analysis should occur prior to deep-sea areas being considered for exploitation of natural resources. The presence of multiple community types on seamounts and ridges indicates that managing seamounts may need to be more complex than treating them as a

single ecological unit.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2015.07.003>.

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