Deep-sea seabed habitats: do they support distinct mega-epifaunal communities that have
different vulnerabilities to anthropogenic disturbance?


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Abstract

Growing economic interest in seabed resources in the deep-sea highlights the need for
information about the spatial distribution and vulnerability to disturbance of benthic habitats
and fauna. Categorisation of seabed habitats for management is often based on topographic
features such as canyons and seamounts that can be distinguished using regional bathymetry
(‘mega-habitats’). This is practical but because such habitats are contiguous with others, there
is potential for overlap in the communities associated with them. Because concepts of habitat
and community vulnerability are based on the traits of individual taxa, the nature and extent
of differences between communities have implications for strategies to manage the
environmental effects of resource use. Using towed video camera transects, we surveyed
mega-epifaunal communities of three topographically-defined habitats (canyon, seamount or
knoll, and continental slope) and two physico-chemically defined meso-scale habitats (cold
seep and hydrothermal vent) in two regions off New Zealand to assess whether each supports
a distinct type of community. Cold seep and hydrothermal vent communities were strongly
distinct from those in other habitats. Across the other habitats, however, distinctions between
communities were often weak and were not consistent between regions. Dissimilarities
among communities across all habitats were stronger and the density of filter-feeding taxa
was higher in the Bay of Plenty than on the Hikurangi Margin, whereas densities of predatory
and scavenging taxa were higher on the Hikurangi Margin. Substratum diversity at small
spatial scales (<1 km) and trawl history were significantly correlated with community
composition in both regions. We conclude that, (1) a lack of consistent distinction between
communities raises questions about the general utility of topographically-defined mega-
habitats in environmental management, (2) fine-scale survey of individual features is necessary to identify the locations, characteristics, and extents of ecologically important or vulnerable seabed communities, and (3) evaluation of habitat vulnerability to future events should be in the context of previous and current disturbances.

Introduction

Increased economic interest in mineral and biological resources in the deep sea (deeper than ca. 200 m) raises concerns over potential effects of such exploitation on the sustainability of existing fisheries and wider ecosystem services. The United Nations General Assembly Convention on Biological Diversity (UNGA–CBD) has called for sustainable management of fish stocks through application of precautionary and ecosystem-based approaches to resource use, and international guidelines have been prepared to improve management of deep-sea fisheries and associated habitats in the High Seas (FAO, 2009). Similarly, the International Seabed Authority (ISA) has published guidelines for assessment of environmental impacts arising from exploration for seabed minerals, and promotes protection of the marine environment from such impacts (e.g. ISA, 2007). Implementation of such approaches, however, requires some understanding of the ecosystems in question, including their spatial distribution, constituent habitats, the fauna that characterise these habitats, and the relative sensitivities of these fauna to disturbance (Clark et al., 2015). As much of the deep seabed remains unexplored even in terms of basic topography, such understanding is lacking for most areas where resource use currently takes place or is likely to occur in future.

At present, most impacts from seabed resource use in the deep-sea occur on continental margins (Levin and Dayton, 2009; Levin and Sibuet, 2012; Ramirez-Llodra et al., 2011), the most pervasive of them being bottom-contact fishing (Benn et al., 2010; Cryer et al., 2002; Gage et al., 2005; Pusceddu et al., 2014; Thrush and Dayton, 2002). Continental margins are heterogeneous, consisting of a range of topographically-defined ‘mega-habitats’ (sensu Greene et al., 1999), including open slopes, canyons, banks, and knolls, and others, usually at smaller spatial scales (‘meso-habitats’, Greene et al. 1999), defined by their physicochemical properties, notably cold seeps. Impacts also occur in other habitats in the deep sea; particularly seamounts (Clark, 2010; Pitcher et al., 2010; Williams et al., 2010), and potentially at hydrothermal vents in future (Boschen et al., 2013; Van Dover, 2014). Ecological research in the deep sea to date has been concentrated largely on specific habitats in isolation, yet each habitat is embedded in a patchwork of others at landscape and regional
scales with few hard biological barriers between them (Levin and Sibuet, 2012). Thus, while individual habitats may be conveniently categorised on the basis of topography or chemistry alone, there is likely to be overlap in the faunal communities associated with them (Howell et al., 2010; Ramirez-Llodra et al., 2010; Rowden et al., 2010; Vetter et al., 2010). This overlap has implications for the way in which impacts of resource use on benthic habitats and communities are managed because concepts of sensitivity and recoverability (Bax and Williams, 2001; Clark et al., 2015; Hiddink et al., 2007; Tyler-Walters et al., 2009) used to gauge the likely ecological effects of disturbances are based on the specific sets of organisms that are associated with each habitat (e.g., CCAMLR, 2009; Williams et al., 2010).

Quantifying dissimilarity between faunal communities in different habitats has relevance for management because it indicates whether species or communities are restricted to a given habitat and thus provides some measure of the degree of connectivity between habitat types. This, in turn, has implications for the likelihood of recovery of populations or communities following disturbance because rates of recruitment are likely to be low if source populations are rare outside the disturbed area (Boschen et al., 2013). The effects of disturbances on benthic communities are determined by interactions between the physical, behavioural, and life-history traits of individual taxa (functional traits, sensu Bremner et al., 2003) and the characteristics of the disturbance itself (Gray et al., 2006; Hewitt et al., 2011; Thrush and Dayton, 2002). Some functional traits, such as suspension feeding and erect habit, are more sensitive to disturbance than others, particularly to disturbances associated with seabed trawling and mining that involve physical impact and resuspension of sediments (e.g. Bolam et al., 2014; Hiddink et al., 2007; Lambert et al., 2014; Tyler-Walters et al., 2009). Therefore, communities with low connectivity and high proportions of sensitive taxa are likely to be more vulnerable to disturbance than others. In deep-sea studies, however, information on the ecology of benthic fauna, particularly the reproductive and growth characteristics required for any assessment of recoverability, is often limited (Williams et al., 2010). This results in a restricted set of traits that can be assigned with confidence, with feeding mode (e.g. suspension-feeder versus deposit-feeder), mobility (e.g. mobile versus sessile), and body form (e.g. erect versus encrusting) perhaps the most reliable (Clark et al., 2015).

To make direct comparisons between the faunal communities in different habitats while minimising potentially confounding factors introduced by spatial separation (e.g. temperature and productivity gradients with latitude), comparative studies are best undertaken where habitats exist in close proximity to each other. New Zealand’s Exclusive Economic Zone
(EEZ) area is large, topographically diverse, and encompasses areas in which several seabed habitat types occur in close proximity to each other, thus affording opportunities to compare habitats while minimising spatial separation. The area is also rich in biological and mineral resources (Campbell et al., 2012; Glasby and Wright, 1990; Gordon et al., 2010), some of which are currently exploited. Since the 1970s much of the seabed has been subjected to varying intensities of bottom trawling by commercial fisheries for e.g., scampi (Metanephrops challengeri) (Cryer et al., 2002), hoki (Macruronus novaezelandiae) (O’Driscoll, 2004), and orange roughy (Hoplostethus atlanticus) (Clark, 2001), and there is increasing interest in the economic potential of seabed mineral resources (Boschen et al., 2013; Leduc et al., 2015).

Using towed camera systems, we surveyed benthic mega-epifaunal invertebrate communities in five contrasting seabed habitats in two regions of New Zealand’s EEZ to evaluate differences, if any, between habitats in terms of community structure, the trophic modes of the component taxa, and how these are related to differences in a range of physical environmental variables, including seabed topography and the intensity of bottom trawl fishing. As an indirect measure of community function, we also recorded the number and type of bioturbation marks, such as tracks and burrows, made in soft sediments by living organisms. The underlying hypotheses of the study are that (1) each of the habitats studied supports a distinct mega-epifaunal community type that can be consistently distinguished from others, and (2) because of this, the vulnerability to disturbance of these communities will vary predictably with habitat type.

**Methods**

**Study area and survey design**

Seabed invertebrate communities were sampled in two regions of New Zealand’s EEZ: the southern Hikurangi Margin off the south-east coast of the North Island, and the Bay of Plenty, off the central north-east coast of the North Island (Figure 1). These regions were selected because each encompasses a range of benthic habitats within a relatively restricted geographic area, thus facilitating formal comparisons between their associated faunas. In both regions, the continental slope is incised by canyons. On the Hikurangi Margin, canyons are interspersed with areas of open slope, elevated banks, knolls and seamount-like features and, on Opouawe Bank particularly, numerous active methane seeps (Greinert et al., 2010). In the Bay of Plenty region, canyons are interspersed with areas of open slope and knolls, while
more distinct seamount features associated with the southern end of the Kermadec Arc extend further offshore (Wysoczanski and Clark, 2012). Some of these seamounts are volcanically active and support communities of chemoautotrophic fauna associated with hydrothermal vents (Boschen et al., 2015).

Five habitat types were identified *a priori* for comparisons of benthic epifaunal community structure, three defined by their topography; open continental slope, canyon, and seamount, and two defined by their chemistry; cold seep, and hydrothermal vent. Dedicated sampling for this study was targeted primarily at the three topographically-defined habitat types, whereas data from the chemosynthetic habitats were sourced from other research programmes in the same survey regions. For this study, three or four features were selected in each region as representative replicates for each of the three topographic habitat types: slope, canyon, and seamount. Sampling of all topographically defined features was stratified into four target depths; 700, 1000, 1200, and 1500 m to enable evaluation of potential differences in community make-up with depth, although the summit depths of some seamounts were either shallower or deeper than 700 m. Cold seep and hydrothermal vent habitats were restricted in depth range and thus stratification was not relevant. At each depth stratum on each feature, benthic epifaunal and infaunal communities, as well as substratum properties, were sampled using towed cameras, corers, trawls, and epibenthic sleds, and prior to this all sites were mapped using multibeam echosounders (MBES). In this paper, we present data and analyses on benthic mega-epifauna (surface-dwelling invertebrate fauna larger than ca. 50 mm) recorded in towed camera transects.

**Video transects**

All towed camera transects from slope, canyon, seamount, and vent habitats were collected using NIWA’s Deep Towed Imaging System (DTIS, Hill, 2009) deployed from RV *Tangaroa*. In April 2010, voyage TAN1004 collected 38 camera transects from slope, canyon, and seamount habitats in the Hikurangi Margin region. In April 2012, voyage TAN1206 collected 60 transects from slope, canyon, seamount, and hydrothermal vent habitats in the Bay of Plenty region (Table 1). DTIS was configured with a high definition digital colour video camera (Sony, HD1080i format) angled forward at 45° from vertical, and a digital single lens reflex camera (Canon: TAN1004, EOS 350D, 8 megapixel; TAN1206, EOS 400D, 10 megapixel) angled vertically downwards. Full-resolution continuous video was recorded in-camera to miniDV tape and streamed in real time to the surface at lower resolution. Still images were taken automatically at 15 s intervals throughout all transects and
recorded in-camera. Transects were of 1 hour seabed duration at a target tow speed of 0.25 – 0.5 m$^2$ and height above seabed (altitude) of 1.5 – 3.0 m. The seabed position of DTIS was recorded via an ultra-short baseline (USBL) acoustic tracking system (Kongsberg HiPAP) and depth and altitude were recorded continuously via sensors mounted on the camera frame.

Data for seep habitats on Opouawe Bank on the Hikurangi Margin were taken from analyses by Bowden et al. (2013) based on voyages in 2006 (RV Tangaroa, TAN0616), 2007 (RV Sonne, SO191), and 2011 (RV Sonne, SO214). The towed camera system used on RV Sonne (Ocean Floor Observation System, OFOS, Bowden et al., 2013) was similar in specification to DTIS and operated by the same researcher (DAB) using the same protocols as for DTIS. Data from four transects using DTIS at hydrothermal vent communities on Brothers seamount in the Bay of Plenty region were added to the vent data from TAN1206: these were taken from analyses of transects from RV Tangaroa voyage TAN1007 (Boschen et al., 2015) (Table 2).

Environmental data

Seafloor morphology metrics to characterise habitats were derived from MBES data at each sampling site. All MBES data were gridded at 25 m resolution and metrics were calculated at 3 × 3, 7 × 7, and 15 × 15 focal mean scales (i.e. the extent of the surrounding grid over which mean values were calculated) for: average depth; depth range; slope; terrain rugosity; aspect; curvature; plan curvature, and profile curvature, plus the standard deviations of these measures at each focal mean. Because trawl fisheries have operated on the New Zealand continental shelf and margins over several decades and thus might be a confounding factor when evaluating differences in benthic community structure between regions and habitats, we included trawl intensity as an environmental variable in analyses. Data on bottom-contact trawl events were sourced for the period July 1980 to March 2011 from the trawl database of the New Zealand Ministry for Primary Industries. Trawling intensity for each benthic sampling site was calculated as the sum of all trawl lines intersecting a 2 km radius circle centred on the mid-point of the video transect (to match the precision of reported trawl trajectories and the length of video transects) during the 15 y period prior to sampling at that site (the maximum period for which records were available across all sites). For seep sites, the 2 km buffer was centred on site coordinates detailed in Greinert et al. (2010) and Bowden et al. (2013).
Video observations

The seabed distance of each transect was measured using the USBL position data in a geographic information system (GIS, ESRI ArcMap v.10.1) and mean transect width was calculated from a regression of measured video frame width against camera altitude (overall means for transect length and width were 1,350 m and 2.05 m, respectively). The full length of each transect was then reviewed using Ocean Floor Observation Protocol software (OFOP, www.ofop-by-sams.eu) to record three classes of data: substratum type, with continuous recording on an eight-category scale from ‘Bedrock’ to ‘Muddy sediment’; bioturbation marks, as counts of tracks, burrows, pits, faecal coils, mounds, and other traces of living organisms, and the identities and abundances of all benthic invertebrate fauna larger than ca. 50 mm. Substrate types were expressed as percentages of the full transect distance after correcting for any sections of the transect in which the seabed was not visible (e.g. because of excessive altitude, or contact with the seabed) and substratum diversity, as the Shannon-Weiner index ($H'$log$_e$), was calculated for each transect from these percentages. Fauna and bioturbation marks were recorded as counts per transect and then standardised to numbers per 1000 m$^{-2}$ of seabed, again allowing for obscured portions of transects.

In analyses of transects from the two principal voyages (TAN1004 and TAN1206), fauna were identified to the finest practicable taxonomic level, which ranged from species to phylum depending on taxon. Identifications for seep (TAN0616, SO191, and SO214) and vent (TAN1007) habitats were generally to coarser taxonomic resolution than for non-chemosynthetic taxa (e.g. all stony corals were recorded as ‘Scleractinia’) but at species or genus level for chemosynthetic taxa. To combine results from both regions and all voyages, all data were compiled into a single dataset and taxon labels were matched to a consistent taxonomic hierarchy by reference to the World Register of Marine Species (WoRMs, www.marinespecies.org). Three iterations of the final taxon list were then developed and evaluated in statistical analyses: (1) the full detail recorded from the video analyses; (2) a coarse level scheme in which all taxa were raised to the level of the most poorly-identified taxon (e.g. all sea-star species become ‘Asteroidea’, all snails become ‘Gastropoda’), and (3) a more refined scheme in which each taxon was assessed independently as to whether or not it represented a distinct identification that was recorded consistently throughout the dataset; if it was distinct (e.g. Brisingid asteroids) the original determination was retained but if not, it was aggregated to a coarser taxonomic level. These versions resulted in 295, 51, and 96 individual taxa in the detailed, coarse, and refined lists, respectively.
To characterise faunal communities by their ecological functions as well as by taxonomic composition, functional traits (Bremner et al., 2003) were assigned to each taxon in the data set. Because data from towed camera transects consist of only mega-epifaunal taxa and encompass a range of taxonomic levels, a simplified functional traits scheme was adopted consisting of six trophic modes: suspension feeder; filter feeder; deposit feeder; predator/scavenger; grazer, or chemosynthetic (see Table 3 for definitions). This scheme does not incorporate some traits that are fundamental in determining a taxon’s sensitivity to disturbance, particularly size and fragility, but other traits including mobility and body form, are, to an extent, implicit in the higher level trophic categories. Thus, suspension feeders have limited or no mobility and are erect, in the sense that they extend feeding organs into the water column, whereas predator-scavengers are mobile and not erect. Some of the trophic mode labels and the taxa assigned to them were revised from those previously used by Rowden et al. (2010) for slope and seamount benthos in the southwest Pacific. The principal changes were: distinction between suspension-feeders and filter-feeders; use of ‘predator/scavenger’ instead of ‘predator-omnivore’; the addition of ‘grazer’ to encompass taxa including echinoids and non-predatory gastropods that actively abrade particles from hard or soft substrata, and assigning non-chemosynthetic natant decapods as either ‘deposit-feeders’, for small and indeterminate taxa, or ‘predator/scavenger’ for large taxa including *Nematocarcinus* sp., and *Campylonotus* rathbunae. The latter change was made on the basis of assessments by Lundquist et al. (2013) and stable isotope analyses of species in the central New Zealand region (M. Pinkerton, NIWA, unpublished data).

**Statistical analyses**

Analyses of community structure, bioturbation marks, and environmental characteristics were run using multivariate statistical routines in PRIMER v.6 (Clarke and Gorley, 2006) with PERMANOVA+ (Anderson et al., 2008b). Analyses of fauna and bioturbation marks were conducted on separate matrices of Bray-Curtis similarities among transects, calculated from square root-transformed abundance data, to reduce the influence of highly-abundant taxa (Quinn and Keough, 2002). Bioturbation density comparisons were restricted to slope habitat transects in which seafloor substrata consisted of more than 97% muddy sediments, to ensure that similar soft-sediment habitats were being compared. General relationships among samples were visualised in non-metric multi-dimensional scaling (MDS) ordinations of the Bray-Curtis similarity matrices.
The relative influences of the *a priori* factors (habitat type, survey region, and depth stratum) on community structure were explored in 3-factor crossed PERMANOVA analyses, with habitat (slope, canyon, seamount, vent, seep) and depth stratum (700, 1000, 1200, 1500 m) as fixed factors, and survey region (Hikurangi Margin, Bay of Plenty) as a random factor. Because there were only three replicate measurements at each depth stratum within each habitat in each region, insufficient permutations were available to generate reliable significance tests for most pairwise comparisons of the interaction between habitat, depth stratum, and region. To overcome this, the PERMANOVA model was run using two coarser depth strata created by pooling the two shallower strata (700 and 1000 m) and the two deeper strata (1200 and 1500 m). These combined depth strata were then used in all subsequent faunal analyses. Three iterations of the analysis were run: the first including both regions but only the three topographically-defined habitats (because each of the chemosynthetically-defined habitats was represented in only one of the regions and we know, *a priori*, that the faunas of vents and seeps are largely distinct from each other), then for each region separately including all habitats. To determine whether any distinctions between habitats indicated by PERMANOVA were influenced by differences in multivariate dispersion, homogeneity of dispersions (as distances to centroids) among habitats within each region was tested using PERMDISP (Anderson *et al.*, 2006). Because effects attributed to one of the three main factors might also be influenced by other variables, including differences in the spatial proximity of sites and their trawling history, the PERMANOVA models were run using spatial metrics (latitude, longitude, and their quadratic and cubic components) and trawl intensity as covariates (Borcard *et al.*, 1992; Legendre *et al.*, 2005). Where factors were found to have a significant influence on benthic communities, pairwise tests were run to determine which comparisons were driving the higher level responses. SIMPER analyses (Clarke and Gorley, 2006) were run to identify the taxa contributing most to differences in community structure, first between regions for each habitat separately, then between habitats within each region. Probabilities here and in subsequent analyses were generated using 9,999 unique permutations of the data, where possible, otherwise with the maximum number available.

Relationships between benthic community structure and environmental predictor variables were explored using distance-based linear models (DISTLM, Anderson *et al.*, 2008b), initially for both regions combined, then for depth strata in each region separately. Environmental predictors included spatial, seafloor topography, substrate type, and fishing intensity variables. Selection of variables was based on pairwise correlations between
variables and the strength of their correlations with benthic community structure in the marginal tests of a trial DistLM analysis that included all variables: where two or more variables were strongly correlated with each other (r > 0.9) only the one ranked highest in marginal tests of the initial DistLM analysis was retained. This process yielded ten variables that were used in the final DistLM analyses: three spatial variables (latitude, longitude, and depth); five MBES seabed topography variables (seabed rugosity at 3×3 focal mean; the standard deviation of depth at 7×7 focal mean; the standard deviation of slope at 3×3 focal mean; plan curvature, and depth range at 7×7 focal mean); substratum diversity (H'(log_e), calculated from video observations of substratum type), and trawl intensity. To make some variables conform to approximate normality of distribution, log_{10}(x) or log_{10}(1+x) transformations were applied as appropriate (Zuur et al., 2010). The influence of each variable was tested first in isolation (marginal tests) and then in a combined model in which variables were added sequentially using a step-wise selection procedure based on the adjusted R^2 criterion.

Results

Topography and trawl intensity

Seamount habitats in the Bay of Plenty were steeper than those on the Hikurangi Margin (MBES slope measurements) and were more heterogeneous in terms of both rugosity at the scale of the MBES data and the diversity of substrate types at the scale of individual video transects (Figure 2). By contrast, continental slope habitats were steeper and more heterogeneous on the Hikurangi Margin than in the Bay of Plenty and, again, patterns were similar at both the MBES and video transect scales. Canyon habitats were broadly similar between the two regions in terms of all physical metrics. Cumulative trawl intensity over the 15 y period prior to sampling was higher on the Hikurangi Margin than in the Bay of Plenty in all habitats and both depths, with the highest intensities of trawling in both regions occurring on seamounts (Figure 3).

Community structure

The MDS ordination (Figure 4) indicated that: (1) mega-epifaunal communities in the two regions were distinct from each other; (2) both hydrothermal vent and cold seep communities were generally strongly distinct from those in all other habitats, although the hydrothermal vent communities from Brothers II seamount were more strongly distinct from other habitats in the Bay of Plenty region than were vent communities on Clark and Tangaroa seamounts,
and (3) while there was some differentiation between communities from slope, canyon, and seamount habitats in both regions, distinctions between habitats were stronger in the Bay of Plenty than on the Hikurangi Margin. These relationships were consistent regardless of which taxonomic aggregation level was used (‘full’, ‘coarse’, or ‘refined’), and unless specified otherwise, all subsequent results are based on the ‘refined’ taxon aggregation data.

These patterns were confirmed by the PERMANOVA analyses. Across all habitats and after accounting for spatial covariates, there was a significant overall difference between communities in the two regions of the study (Table 4, PERMANOVA, Region, P=0.0322). However, while neither Habitat nor Depth Stratum were significant in this analysis, all interactions with Region were (P=0.0001), indicating that any differences between communities in the four habitat types and across depth strata were not consistent between the two regions. Pairwise comparisons for the significant interaction between Habitat and Region showed that community distinctions between habitats (pooled across all depth strata) were less pronounced on the Hikurangi Margin than in the Bay of Plenty (Table 5). On the Hikurangi Margin, cold seep communities were significantly different from those in all other habitats (P=0.0001) and seamount and canyon communities at 1200-1500 m were marginally distinct (P=0.04). There was no clear differentiation between communities on the slope and those in seamount or canyon habitats at either depth. In the Bay of Plenty region, by contrast, all comparisons between communities in the different habitats were significant (P≤0.04) except for slope and canyon communities at 700-1000 m (P=0.052). There were no significant differences in multivariate dispersion between habitats within each region (PERMDISP, P≥0.05), with the exception of vent communities in the Bay of Plenty, which were more dispersed than those in other habitats (P=0.0001 for all comparisons).

Regional differences between communities were driven by a broad range of taxa, both through presence or absence in a given region and through differences in densities between regions (SIMPER by regions, detailed results not shown). In slope habitats, communities in the Bay of Plenty were characterised by the presence of solitary ascidians (Phlebobranchia) and a small holothuroid taxon (Holothuroid 4), and by higher densities of shrimps (Natantia), ophiuroids, gorgonian corals (Gorgonacea), and solitary corals (Caryophyllidae), while those on the Hikurangi Margin had higher abundances of asteroids (Forcipulatida), pagurid crabs (Paguridae), and echinoids (Echinidae and Cidaridae). In canyons, communities in the Bay of Plenty had higher densities of solitary ascidians, xenophyophores, sponges (Hexactinellida), shrimps, Holothuroid 4, bryozoans, and crinoids, whereas those on the
Hikurangi Margin had higher densities of ophiuroids, sea pens (Pennatulacea), anemones (Actiniaria), and pagurid crabs. On seamounts, communities in the Bay of Plenty had higher densities of sponges (Hexactinellida and Demospongiae), bryozoans, shrimps, gorgonian corals, solitary ascidians, ophiuroids, black corals (Antipatharia), solitary corals (Caryophyllidae), and crinoids, whereas those on the Hikurangi Margin had higher densities of pagurid crabs, xenophyophores, asteroids (Forcipulatida), and tube-dwelling anemones (Ceriantharia).

On the Hikurangi Margin, the marginally significant difference between seamount and canyon communities at 1200-1500 m depth was driven by higher densities of pagurid crabs, xenophyophores, tube-dwelling anemones, demosponges, asteroids (Forcipulatida, Asteroidea, Valvatida, Spinulosida), quill worms (*Hyalinoecia* sp.), and predatory gastropods (Buccinidae) on seamounts, and by higher densities of ophiuroids, pennatulaceans, gorgonean corals, anemones (Actiniaria), brisingid asteroids, hydroids, and *Anthomastus* spp. soft corals in canyons (SIMPER, Table 6).

In the Bay of Plenty region, significant differences between communities in all habitats resulted from differences in the densities of many taxa. For example, differences between slope and canyon communities across all depths were driven by higher densities of solitary ascidians, solitary corals, cerianthid anemones, and *Anthomastus* sp. soft corals in slope habitats, and by higher densities in canyon habitats of xenophyophores, holothuroids (Holothuroid 4, Synallactidae), hexactinellid sponges, bryozoans, gorgonian corals, crinoids, shrimps, anemones, ascidians, pennatulaceans, antipatharian corals, brachiopods, and other taxa (SIMPER, see Table 7 for details of all habitat comparisons).

Trophic structure

There were pronounced differences between regions and among habitats in the trophic structure of benthic communities (Figure 4, Figure 5). Across all habitats, pooling depth strata, predator/scavenger taxa were significantly more abundant on the Hikurangi Margin than the Bay of Plenty, whereas filter-feeder taxa were significantly more abundant in the Bay of Plenty (ANOVA, P<0.05 for both comparisons, Figure 5). Deposit-feeder densities were significantly higher in the Bay of Plenty than on the Hikurangi Margin in canyon habitats at 700-1000 m and seamount habitats at 1200-1500 m, but similar in all other comparisons. Suspension-feeder densities were significantly higher in seamount habitats in the Bay of Plenty than on the Hikurangi Margin. In canyon habitats at 1200-1500 m, however,
suspension-feeder densities were higher on the Hikurangi Margin, while at 700-1000 m in canyons, peak suspension-feeder densities were higher on the Hikurangi Margin but with high variance, driven largely by high densities of pennatulaceans at 700 m in Honeycomb Canyon. Grazers showed no overall trend but echinoids (primarily the regular urchin *Gracilechinus multidentatus*) occurred at high densities in localised patches in some canyon and slope habitats on the Hikurangi Margin.

**Bioturbation marks**

Total bioturbation densities in transects with substrata consisting of >97% muddy sediment were significantly higher at all depths in the Bay of Plenty than on the Hikurangi Margin (n=12 and n=10 transects, respectively, ANOVA P<0.001, Figure 6, left). Tracks (primarily those of predatory gastropods, pagurid crabs, and echinoids) were the only bioturbation mark type that occurred in comparable densities on the Hikurangi Margin; densities of all other types being higher in the Bay of Plenty (Figure 6, right).

**Relationship to environmental variables**

In the initial DISTLM model encompassing both study regions, the influences on community structure of each of the ten environmental variables in isolation were statistically significant (marginal tests, P<0.001). The spatial variables latitude$^2$ and longitude explained 19% and 16% of the total variance, respectively, followed by substrate diversity ($H'_{\log e}$, 12%), trawl intensity (6%), and the standard deviation of seabed slope (6%). The remaining variables, including depth, each explained ca. 5%. The full model (sequential tests) used nine of the ten environmental variables and explained 35% of the total variance in the community structure data (adjusted $R^2$). After allowing for the spatial variables (latitude$^2$, longitude, and depth), which explained 24% of variance, the most influential variable was substrate diversity ($H'_{\log e}$, 9%, P=0.0001), followed by trawl intensity (1%, P=0.0004). Each of the remaining variables explained $\leq$1% of the total variance and none were statistically significant in the model (P>0.05).

For the Hikurangi Margin at 700-1000 m, depth, substrate diversity, longitude, latitude$^2$, and trawl intensity, were significant in marginal tests (P<0.05), with depth (19%), substrate diversity (12%), and trawl intensity (8%) explaining the highest proportions of variance in community structure. The full model used eight of the ten environmental variables and explained 33% of the total variance in the data (Table 8). In sequential tests, the spatial variables explained 23% of variance and the most influential variables after allowing for
these were substrate diversity (7 %, P=0.0163) and trawl intensity (6 %, P=0.0481). The remaining variables used (rugosity, plan curvature, and standard deviation of depth) each explained ca. 4 % of the total variance and none were statistically significant in the model.

At 1200-1500 m, substrate diversity (18 %), depth (13 %), trawl intensity (11 %), and latitude$^2$ (11 %) were significant in marginal tests. The full model again used eight variables and explained 37 % of the total variance but the spatial variables accounted for only 13 % of the variance and substrate diversity was the only significant additional variable (18%, P=0.0013).

For the Bay of Plenty region at 700-1000 m, all environmental variables except for plan curvature were significant in marginal tests. Substrate diversity explained the greatest proportion of total variance in community structure (20 %) and depth range, rugosity, the standard deviation of depth, and trawl intensity each explained 13-14 %. The full model used seven variables and explained 31 % of variance in the data. The spatial variables explained 16 % and the most influential variables after these were substrate diversity (12 %, P<0.0001) and trawl intensity (4 %, P<0.0153). The standard deviation of slope and standard deviation of depth each explained ca. 3 % of variance but neither had a significant influence on the model. At 1200-1500 m, all variables except depth were significant in marginal tests, with substrate diversity (25 %), depth range (20 %), latitude$^2$ (19 %), the standard deviation of depth (18 %), and trawl intensity (17 %) explaining the highest proportions of variance. The full model again used seven variables and explained 35 % of variance. The spatial variables explained 20 % of variance and the most influential variables in sequential tests after these were depth range (12 %, P<0.001), and trawl intensity (6 %, P=0.0256), with substrate diversity and plan curvature each explaining ca. 3 %.

**Discussion**

The aim of this study was to ascertain whether there are general, and therefore predictable, distinctions between the mega-epifaunal benthic communities of a set of commonly encountered topographically-defined seabed mega-habitat types; canyons, seamounts, and open slope areas, as well as two chemosynthetic meso-scale habitats; cold seeps and hydrothermal vents. If they were distinct, such knowledge could help develop a framework on which to base environmental management decisions. Our results show that, while communities can sometimes be distinguished at the scales of these habitats, differences may not be consistent between regions (100s km scale), that there can be considerable overlap.
between the seabed habitats in terms of both physical characteristics and community composition, and that existing and historical anthropogenic disturbances, in this instance from trawling, may influence observed patterns.

Most taxa were not constrained to a single habitat type, and each habitat typically had mixed substrate and topographic characteristics. Importantly, neither the physical nor faunal distinctions between habitats were consistent between regions: the three topographically-defined habitats (canyon, slope, and seamount) and their epifaunal communities were more clearly differentiated from each other in the Bay of Plenty than they were on the Hikurangi Margin; the strongest correlations between community structure and environment were with substrate diversity at the scale of the video transects (<1 km) and trawl history, and the clearest distinction in the faunal data was that between the two regions of the study, rather than between habitat types. These results support conclusions of some existing studies (e.g. Howell et al., 2010; Lundsten et al., 2009; O'Hara, 2007) and suggest that simple categorisation of benthic communities on the basis of topographically defined habitat types is unlikely to be sufficient in itself for addressing the needs of management in the deep-sea. That is, spatial management measures based on the selection of topographically-defined habitats might suffice as a means to manage benthic community diversity in one region but fail in another.

That physical distinctions between habitats were more pronounced in the Bay of Plenty than on the Hikurangi Margin highlights one of the problems in any approach to classifying seabed habitats. In order to have general applicability, habitat definitions must be broad enough to encompass a wide range of variability in physical characteristics, yet the broader such definitions become the less likely they are to be useful for distinguishing between faunas. Characterisation of seabed habitats with remote acoustic sensing typically yields categories such as canyon, seamount, and slope, based on coarse-scale topography but may not discriminate ecologically important differences in factors such as substratum type. While hardness or softness of the seabed can be ascertained at local scales by interpretation of acoustic backscatter (Anderson et al., 2008a), more usually in deep-sea research, topographic measures such as angle of slope and terrain rugosity are used to infer the likelihood of hard or soft substrata being present (Diaz et al., 2004; Dolan et al., 2009; Greene et al., 1999). Our results indicate that substratum diversity at the scale of individual video transects (<1 km) has a strong influence on community structure and that key substratum types may not be confined to individual topographic habitats. For instance, while canyons in each region of
this study were generally comparable in their physical attributes, open slopes and seamounts were more variable; the Hikurangi Margin having areas of steeper, rougher, and more heterogeneous slope habitat than the Bay of Plenty, and seamounts that were consistently flatter, smoother, and more sedimentary. The overall predominance of soft sediment substrata on the Hikurangi Margin results in greater homogeneity of habitats than in the Bay of Plenty and, given the importance of transect-scale substrate diversity in the DistLM analyses, it is likely that the weaker habitat-based distinctions between faunal communities in the Hikurangi Margin is a reflection of this physical homogeneity.

Filter-feeding taxa were significantly more abundant in all habitats and depths in the Bay of Plenty than on the Hikurangi Margin, while the opposite was true for predatory and scavenging taxa. Trophic mode is constrained in part by characteristics of the physical environment that determine substratum type and the availability of food (Barnes and Hughes, 1988). The differences in feeding mode representation between regions in this study are, therefore, unlikely to be simple regional species pool effects. We expect sessile suspension- and filter-feeding taxa to predominate on undisturbed hard substrata in high-flow areas, and for such substrata to be more common on the steeper topographies of seamounts and canyons than on open slopes (Genin, 2004). In our data, this is supported for the Bay of Plenty region but not for the Hikurangi Margin, presumably because of the lack of distinction between physical habitats on the Hikurangi Margin noted above, where hard substrata are sparse on seamounts but present at some sites on the slope. Similarly, we would expect deposit feeders to be more common in habitats where there is accumulation of detrital material, such as canyon floors and, again, this is the pattern seen in the Bay of Plenty but not on the Hikurangi Margin.

If distributions of trophic functional types are influenced by substratum type, an obvious question here is why are physical seabed habitats less well-defined on the Hikurangi Margin? This is likely to be partly a consequence of regional differences in broad-scale topography and oceanography: the continental shelf and slope are narrower and steeper on the Hikurangi Margin than in the Bay of Plenty; the southern end of the Kermadec Ridge that terminates in the Bay of Plenty has no equivalent on the Hikurangi Margin, and proximity of the Hikurangi Margin study region to Cook Strait and the sub-tropical front creates a more dynamic and productive oceanographic regime than in the Bay of Plenty (Murphy et al., 2001). It is of interest, however, that the intensity of trawling and the density of bioturbation marks in sediments showed strong differences between regions: numbers of trawls per site were higher
in all habitats on the Hikurangi region than in the Bay of Plenty, whereas the density of
bioturbation marks was higher in the Bay of Plenty for all types except the tracks of mobile
organisms. Trawling is known to homogenise sediments at multiple spatial scales (Gray et
al., 2006; Puig et al., 2012; Pusceddu et al., 2014; Thrush and Dayton, 2002), and to cause
resuspension of sediments which may lead to down-slope sediment flows on the steep
gradients characteristic of canyon and seamount habitats (Puig et al., 2012). Trawling
disturbance can also modify the trophic structure of benthic communities by damaging
epifaunal suspension-, filter-, and deposit-feeders but favouring mobile scavenging and
predatory taxa (Collie et al., 2000; Hinz et al., 2009; Jennings and Kaiser, 1998; Kaiser et
al., 2006; Thrush and Dayton, 2010; Tillin et al., 2006).

In our data we see less physical distinction between habitats and higher densities of predator-
scavenger taxa and their tracks in all habitats on the more intensively trawled Hikurangi
Margin, and higher densities of filter-feeders and bioturbation in the Bay of Plenty. These
patterns are consistent with effects of seabed trawling reported elsewhere in the world (Puig
et al., 2012; Pusceddu et al., 2014; Tillin et al., 2006) but our data are insufficient alone to
conclude that this is a result of the difference in trawling intensity. For instance, regional
differences in sedimentation rates and the strength of near-seabed currents could potentially
generate similar patterns; bioturbation marks being erased more rapidly where these
processes are strongest. The predominance of mobile predator-scavenger tracks on the
Hikurangi Margin is perhaps the most compelling argument for a trawling-related effect
because, even if removal of marks through deposition and scouring were more rapid in this
region, we might still expect the two regions to be qualitatively similar in terms of the types
of bioturbation recorded.

These observations suggest a potential effect of trawling on the Hikurangi Margin that
warrants further dedicated study but it is of note here that we did not set out to evaluate the
effect of trawling, rather, it emerged as a significant variable that partially confounds our
original objective to compare communities between habitats. We think this is an important
point because the influence of trawl fisheries on observed benthic structure is likely to be a
pervasive, but not necessarily obvious, factor affecting continental shelf and margin habitats
world-wide. For management decision-making, the observed differences between regions
here highlight difficulties of interpretation associated with evaluating community structure
in areas that are already subject to differing levels of chronic anthropogenic disturbance (de
Juan et al., 2009). Thus, an initial inference from our results could be that benthic
communities in the Bay of Plenty are inherently more vulnerable to disturbance than those on the Hikurangi Margin because they have higher proportions of filter- and suspension-feeding taxa, which are known to be susceptible to damage from a range of disturbances (Bremner et al., 2006; Hiscock and Tyler-Walters, 2006). However, when the relative disturbance histories of the two regions are considered, it is also possible that the present composition of communities on the Hikurangi margin could be partly a consequence of modification of habitat and community structure by trawling. If this were the case, any environmental management process might also need to consider restoration of habitat and community structure (and thus of ecosystem function) in disturbed areas in addition to conservation of pristine or less-impacted areas that would currently rank highly for vulnerability.

In summary, our results show that there can be considerable overlap between deep-sea mega-habitats in terms of both their physical characteristics and their mega-epifaunal communities, and that any distinctions that exist between such habitats may not be consistent between regions. It is also relevant to environmental management considerations that seabed habitat heterogeneity at scales of <1 km (as recorded in camera transects) was correlated with faunal community structure and that the only habitats that were clearly distinct from surrounding habitats in their faunal characteristics were meso-habitats defined by chemistry rather than topography; cold seeps and hydrothermal vents. Given that these are at much smaller spatial scale than the topographically-defined habitats considered here, and are only defined by seabed sampling methods at 10m-100m scales (Bowden et al., 2013; Greinert et al., 2010), this distinction presents a challenge for developing general regional-scale management of deep-sea communities because it highlights that distinctive and potentially vulnerable communities exist within larger topographically-defined habitat categories (Van Dover et al., 2012).

While it may be possible in future to estimate with confidence the likelihood of occurrence of some small-scale habitats from topographic patterns at larger scales using predictive modelling, fine-scale seabed surveys are still required to confirm their presence and define their nature and extent. Because regional-scale information on seabed topography and habitats is constrained, at present, to relatively coarse scales (generally >250 m grid), the lack of consistent distinction between the communities of topographically-defined habitats in our results supports questions raised in previous studies about the general utility of such mega-habitat labels in environmental management decision-making (Howell et al., 2010; O'Hara...
et al., 2008; Williams et al., 2009). The obvious practical advantage of habitat classification based on such topographically-defined features, of course, is precisely that they are identifiable at coarse spatial scales and thus are valuable for initial delineation of areas where sensitive habitats are more likely to occur based on knowledge gained in other regions. Our results suggest that, while this level of habitat identification might be used as a pragmatic first stage in a management process, targeted fine-scale survey is required to assess the actual distribution of ecologically important seabed habitat patches, and thus to inform subsequent refinement of management strategies.

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Figure 1. Sampling sites at features in the Bay of Plenty (BoP, top) and Hikurangi Margin (HIK, bottom) study regions, and their relative locations in New Zealand (inset – circled cross shows location of Brothers seamount on the Kermadec Ridge). Isobaths show 200, 500, 1000, and 2000 m depths. Scale bar applies to both regional maps.
Figure 2. Physical seabed characteristics of canyon, slope, and seamount habitats on the Hikurangi Margin (‘Hikurangi’) and Bay of Plenty regions. The top three panels show representative metrics derived from multibeam echosounder data (MBES: rugosity, slope, and profile curvature as mean value per sample location ±1se). The lower panel shows substratum diversity from video transect observations of five substratum types (calculated from percent occurrence as Shannon-Weiner diversity $H'(\log e)$).
Figure 3. Cumulative trawl intensity in seabed habitats (canyon, continental slope, seamount, and chemosynthetic) of the Hikurangi Margin (‘Hikurangi’) and Bay of Plenty regions in two depth strata: 700-1000 m and 1200-1500 m. NP: no chemosynthetic habitats were present in the 1200-1500 m depth stratum in either region. Data are the number of individual trawl events intersecting a 2 km radius circle around each sampling site for the 15 y period prior to sampling and bars show means (±1se) of 3 to 6 sites per depth for each habitat type in each region. Trawl intensities are significantly higher (ANOVA, P<0.05) on the Hikurangi Margin in all habitats and both depth ranges. Note log scale on y axes.
Figure 4. MDS ordination of Bray-Curtis similarities between mega-epifaunal benthic communities in five habitat types (cold seep, hydrothermal vent, continental slope, seamount, and canyon) sampled in two regions of the New Zealand EEZ: the Hikurangi Margin (‘Hikurangi’), and the Bay of Plenty (left and right of the dashed line, respectively). The MDS is based on the square root transformed abundances of 96 taxa recorded in seabed video transects. Bubble plots show relative abundances of epifaunal taxa aggregated into six trophic modes (see Table 3 for definitions).
Figure 5. Densities of benthic taxa in five feeding groups (predator/scavenger, deposit-feeder, grazer, suspension-feeder, filter-feeder) in two depth ranges (700-1000 m and 1200-1500 m) in each of two regions of the New Zealand deep sea: Hikurangi Margin (‘Hikurangi’) and Bay of Plenty. Bars show means ± 1 se of counts from n≥5 video transects. Predator/scavenger densities are significantly higher in all habitats at both depths on Hikurangi Margin, and filter-feeder densities are significantly higher in all habitats at both depths in Bay of Plenty (ANOVA, P<0.01).
Figure 6. Bioturbation marks in muddy sediments. Left: density of all marks recorded in video transects from slope habitat with >97% muddy sediments at two depth strata (700-1000 and 1200-1500 m) on the Hikurangi Margin (‘Hikurangi’, open bars) and Bay of Plenty (filled bars). Bars show means ± 1se of n≥4 transects. Right: MDS ordination based on counts of the eight bioturbation types (burrow, pit, mound, track, ‘ring of burrows’, ‘pepperpots’, faecal coil, and hemichordate spiral) recorded. Vectors show relative contributions of each variable to the distribution of samples in the MDS and extend in the direction of increasing density.
Table 1. Details of camera transect stations sampled during voyages TAN1004 (DSC1) to the Hikurangi Margin and TAN1206 (DSC2) to the Bay of Plenty regions. Full names for named features are: Runaway Sea Valley; Tauranga Canyon; White Island Canyon; Clark, Whakatane, and Tangaroa Seamounts; Matatara Knoll; Campbell Canyon, Honeycomb Canyon; and Pahaua Canyon. Unnamed seamount features are labelled according to the New Zealand seamounts database (e.g. ‘SMT_310’), and slope areas are labelled with a voyage code and sequential identifier e.g. ‘DSC1_SL1’. Depth, latitude, and longitude are means of recorded start and end of video transects (note, where transects in canyons started on one wall and ended on the other, traversing the canyon floor in between, maximum depth is shown). Distance is the distance covered by the towed camera minus any sections where the seabed was not visible.

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<td></td>
<td>1200 77</td>
<td>1284</td>
<td></td>
<td>-34.8824</td>
<td>179.0681</td>
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</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>1500 78</td>
<td>1836</td>
<td></td>
<td>-34.8610</td>
<td>179.0588</td>
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</table>
Table 3. Trophic groups used in analyses of mega-epifaunal data from video transects. Equivalent categories used by Rowden et al. (2010) are shown for reference.

<table>
<thead>
<tr>
<th>Trophic group</th>
<th>Definition</th>
<th>Taxa</th>
<th>Rowden et al (2010)</th>
</tr>
</thead>
<tbody>
<tr>
<td>suspension-feeder</td>
<td>passively trap water-borne food particles, including live prey, using external body structures</td>
<td>all corals, anemones, brisingid asteroids, Euryalida ophiuroids, Dermechinus horridus</td>
<td>Filter/Predator</td>
</tr>
<tr>
<td>filter feeder</td>
<td>actively pump water through body or shell to trap fine food particles</td>
<td>sponges, ascidians, brachiopods, bivalve molluscs</td>
<td>Filter-feeder</td>
</tr>
<tr>
<td>deposit-feeder</td>
<td>ingest sediments and food particles on or in the seabed</td>
<td>holothuroids, ophiuroids (except Order Euryalida), small natant decapods</td>
<td>Deposit-feeder</td>
</tr>
<tr>
<td>predator/scavenger</td>
<td>actively prey on live animals or consume dead animals</td>
<td>decapod crustaceans, galatheids, asteroids (except brisingids), large natant decapods, errant polychaetes, opisthobranch molluscs, pycnogonids</td>
<td>Predator-Omnivore</td>
</tr>
<tr>
<td>grazer</td>
<td>remove attached organic particles from hard or soft substrata using abrasive mouthparts</td>
<td>echinoids (except Dermechinus horridus), non-predatory gastropod molluscs</td>
<td>Deposit-feeder</td>
</tr>
<tr>
<td>chemoautotrophic</td>
<td>Wholly or partly dependent on chemoautotrophic bacteria in reducing habitats</td>
<td>Lamellibrachia spp. worms, Vulcanolepas spp. barnacles, Calyptogena spp. clams, Bathymodiolus spp. mussels, Alvinocaris spp. natant decapods</td>
<td>NA</td>
</tr>
</tbody>
</table>
Table 4. PERMANOVA main effects results for 3-factor crossed analysis (habitat × region × stratum) after allowing for spatial covariates and trawl intensity. Significant results (P<0.05) are in bold. df, degrees of freedom; SS, sums of squares; MS, mean squares.

<table>
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<tr>
<th>Source of variation</th>
<th>df</th>
<th>SS</th>
<th>MS</th>
<th>Pseudo-F</th>
<th>P</th>
<th>permutations</th>
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<td>2629</td>
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<td>0.7008</td>
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<tr>
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<td>2064</td>
<td>2065</td>
<td>1.642</td>
<td>0.0322</td>
<td>9891</td>
</tr>
<tr>
<td>Stratum</td>
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<td>17547</td>
<td>5849</td>
<td>1.155</td>
<td>0.3855</td>
<td>8779</td>
</tr>
<tr>
<td>Ha×Re</td>
<td>2</td>
<td>6639</td>
<td>3320</td>
<td>2.639</td>
<td><strong>0.0001</strong></td>
<td>9857</td>
</tr>
<tr>
<td>Ha×St</td>
<td>6</td>
<td>11831</td>
<td>1972</td>
<td>0.781</td>
<td>0.8047</td>
<td>9870</td>
</tr>
<tr>
<td>Re×St</td>
<td>3</td>
<td>11922</td>
<td>3974</td>
<td>3.159</td>
<td><strong>0.0001</strong></td>
<td>9837</td>
</tr>
<tr>
<td>Re× Ha×St</td>
<td>6</td>
<td>13107</td>
<td>2185</td>
<td>1.737</td>
<td><strong>0.0001</strong></td>
<td>9768</td>
</tr>
<tr>
<td>Residuals</td>
<td>62</td>
<td>77986</td>
<td>1258</td>
<td></td>
<td></td>
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<tr>
<td>Total</td>
<td>93</td>
<td>225000</td>
<td></td>
<td></td>
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</table>
Table 5. PERMANOVA pairwise comparisons between benthic mega-epifaunal communities in slope, canyon, seamount, and chemosynthetic habitats in the Hikurangi Margin and Bay of Plenty study regions (pooled across all depth strata) and, for topographically-defined habitats, by depth strata (700-1000 m and 1200-1500 m) within habitats. Statistically significant differences (P<0.05) are shown in bold.

<table>
<thead>
<tr>
<th>Depth strata</th>
<th>Habitat comparison</th>
<th>Hikurangi Margin</th>
<th>Bay of Plenty</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>t    P    perms</td>
<td>t    P    perms</td>
</tr>
<tr>
<td>All depths</td>
<td>slope vs chemo</td>
<td>2.1277 0.0001 9922</td>
<td>3.3013 0.0001 9946</td>
</tr>
<tr>
<td></td>
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<td>1.0019 0.4349 9927</td>
<td>3.1965 0.0001 9919</td>
</tr>
<tr>
<td></td>
<td>slope vs canyon</td>
<td>1.0483 0.3400 9906</td>
<td>1.6389 0.0051 9922</td>
</tr>
<tr>
<td></td>
<td>chemo vs seamount</td>
<td>3.1221 0.0001 9942</td>
<td>2.9792 0.0001 9922</td>
</tr>
<tr>
<td></td>
<td>chemo vs canyon</td>
<td>2.4040 0.0001 9911</td>
<td>3.0378 0.0001 9926</td>
</tr>
<tr>
<td></td>
<td>seamount vs canyon</td>
<td>1.3256 0.0369 9907</td>
<td>2.1988 0.0001 9921</td>
</tr>
<tr>
<td>700-1000 m</td>
<td>slope vs seamount</td>
<td>1.0085 0.399 5041</td>
<td>2.7622 &lt;0.001 8252</td>
</tr>
<tr>
<td></td>
<td>slope vs canyon</td>
<td>1.1028 0.237 1708</td>
<td>1.3212 0.052 5664</td>
</tr>
<tr>
<td></td>
<td>seamount vs canyon</td>
<td>1.3125 0.051 5077</td>
<td>2.0936 &lt;0.001 9870</td>
</tr>
<tr>
<td>1200-1500 m</td>
<td>slope vs seamount</td>
<td>0.8992 0.73 84</td>
<td>2.1333 &lt;0.001 9072</td>
</tr>
<tr>
<td></td>
<td>slope vs canyon</td>
<td>1.1488 0.175 1706</td>
<td>1.3689 0.036 462</td>
</tr>
<tr>
<td></td>
<td>seamount vs canyon</td>
<td>1.4207 0.04 120</td>
<td>1.4219 0.030 9119</td>
</tr>
</tbody>
</table>
Table 6. Hikurangi Margin: SIMPER analysis for comparisons between benthic megaepifaunal communities across three habitat types (continental slope, canyon, and seamount). Based on Bray-Curtis similarities calculated from square-root transformed abundance data and the ‘refined’ taxon list with 70 % contribution cut-off. Av.abund, average abundance (untransformed individuals 1000 m-2, with average square root-transformed values in parentheses); Av.Diss, average Bray-Curtis dissimilarity between habitats; Diss/SD, average dissimilarity divided by its standard deviation; Contrib%, percentage contribution to average dissimilarity; Cum.%, cumulative percentage contribution to dissimilarity.

<table>
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<tr>
<th>Taxon</th>
<th>Av.Abund</th>
<th>Av.Abund</th>
<th>Av.Diss</th>
<th>Diss/SD</th>
<th>Contrib%</th>
<th>Cum.%</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>Canyon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ophiuroidea</td>
<td>7.59 (1.54)</td>
<td>49.66 (3.83)</td>
<td>3.79</td>
<td>0.87</td>
<td>5.55</td>
<td>5.55</td>
</tr>
<tr>
<td>Pennatulacea</td>
<td>14.14 (1.81)</td>
<td>77.15 (2.80)</td>
<td>3.77</td>
<td>0.52</td>
<td>5.51</td>
<td>11.07</td>
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<tr>
<td>Paguridae</td>
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<td>17.26 (2.83)</td>
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<td>0.98</td>
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<td>16.15</td>
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<td>2.75 (0.62)</td>
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<td>0.46</td>
<td>4.65</td>
<td>20.80</td>
</tr>
<tr>
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<td>18.65 (3.58)</td>
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<td>1.30</td>
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<td>0.94</td>
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</tr>
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<td>0.56</td>
<td>3.74</td>
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</tr>
<tr>
<td>Hydroids</td>
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<td>19.92 (2.52)</td>
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<td>0.85</td>
<td>3.71</td>
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</tr>
<tr>
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<td>0.55</td>
<td>3.70</td>
<td>40.56</td>
</tr>
<tr>
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<td>3.68</td>
<td>44.24</td>
</tr>
<tr>
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<td>Quill worm</td>
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<td>0.46</td>
<td>2.46</td>
<td>62.51</td>
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<tr>
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<tr>
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</table>

<table>
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<tr>
<th></th>
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<th>Seamount</th>
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<th></th>
<th></th>
<th></th>
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<tr>
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<td>3.47</td>
<td>36.04</td>
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<td>1.38</td>
<td>3.34</td>
<td>39.38</td>
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<tr>
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<td>0.60</td>
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<td>22.02</td>
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<td>Ophiuroidea</td>
<td>7.59 (1.54)</td>
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<td>2.32</td>
<td>1.15</td>
<td>3.58</td>
<td>25.60</td>
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<tr>
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<td>7.84 (1.34)</td>
<td>9.42 (1.23)</td>
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<td>0.68</td>
<td>3.50</td>
<td>29.10</td>
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<td>30.8 (2.69)</td>
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<td>3.48</td>
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<tr>
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Table 7. Bay of Plenty: SIMPER analysis for comparisons between benthic mega-epifaunal communities across three habitat types (continental slope, canyon, and seamount). Details as for Table 6.

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<th>Diss/SD</th>
<th>Contrib%</th>
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Table 8. Distance-based linear models (DISTLM) of benthic mega-epifaunal community variation in relation to environmental variables. Results are shown of sequential tests from separate models for 700-1000 m and 1200-1500 m depth ranges on the Hikurangi Margin and Bay of Plenty regions. Models used step-wise selection of variables based on the adjusted R² criterion. Three spatial variables were included as starting conditions for the model: latitude², longitude, and depth (sample depth in m). Explanatory variables: Trawl (log10(trawl intensity)); Substrate diversity (Shannon-Wiener diversity calculated from relative proportions of substratum types recorded in video transects), and MBES variables quantifying seabed depth range (range), standard deviation of depth (STD), rugosity, and plan curvature. Significant contributions to the models (P<0.05) are shown in bold.

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