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

David A. Bowden*, Ashley A. Rowden, Daniel Leduc, Jennifer Beaumont, and Malcolm R. Clark.
*corresponding author

National Institute of Water and Atmospheric Research, Private Bag 14-901, Wellington, New Zealand.

e-mail: david.bowden@niwa.co.nz; ashley.rowden@niwa.co.nz; daniel.leduc@niwa.co.nz; jennifer.beaumont@niwa.co.nz; malcolm.clark@niwa.co.nz.

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 physico-chemical 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 ms^{-1} 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 chemoautotrophic (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-chemoautotrophic 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 seabed 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^2, 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 ($P \leq 0.04$) 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, $P \geq 0.05$), 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 (Antipatheria), 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 ≤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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References

Anderson, J.T., Van Holliday, D., Kloser, R., Reid, D.G., Simard, Y., 2008a. Acoustic seabed classification: current practice and future directions. Ices Journal of Marine Science 65 (6), 1004-1011.

Anderson, M.J., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9 (6), 683-693.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008b. PERMANOVA+ for PRIMER: a guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.

Barnes, R.S.K., Hughes, R.N., 1988. An introduction to marine ecology. Blackwell Science Ltd, Oxford.

Bax, N.J., Williams, A., 2001. Seabed habitat on the south-eastern Australian continental shelf: context, vulnerability and monitoring. Marine and Freshwater Research 52 (4), 491-512.

Benn, A.R., Weaver, P.P., Billet, D.S.M., van den Hove, S., Murdock, A.P., Doneghan, G.B., Le Bas, T., 2010. Human Activities on the Deep Seafloor in the North East Atlantic: An Assessment of Spatial Extent. PLoS ONE 5 (9).

Bolam, S.G., Coggan, R.C., Eggieton, J., Diesing, M., Stephens, D., 2014. Sensitivity of macrobenthic secondary production to trawling in the English sector of the Greater North Sea: A biological trait approach. Journal of Sea Research 85, 162-177.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the Spatial Component of Ecological Variation. Ecology 73 (3), 1045-1055

Boschen, R.E., Rowden, A.A., Clark, M.R., Barton, S.J., Pallentin, A., Gardner, J.P.A., 2015. Megabenthic assemblage structure on three New Zealand seamounts: implications for seafloor massive sulfide mining Marine Ecology Progess Series 523.

Boschen, R.E., Rowden, A.A., Clark, M.R., Gardner, J.P.A., 2013. Mining of deep-sea seafloor massive sulfides: A review of the deposits, their benthic communities, impacts from mining, regulatory frameworks and management strategies. Ocean & Coastal Management 84, 54-67.

Bowden, D.A., Rowden, A.A., Thurber, A.R., Baco, A.R., Levin, L.A., Smith, C.R., 2013. Cold Seep Epifaunal Communities on the Hikurangi Margin, New Zealand: Composition, Succession, and Vulnerability to Human Activities. PLoS ONE 8 (10), e76869.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Marine Ecology-Progress Series 254, 11-25.

Bremner, J., Rogers, S.I., Frid, C.L.J., 2006. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). Ecological Indicators 6 (3), 609-622.

Campbell, H., Malahoff, A., Browne, G., Graham, I., Sutherland, R., 2012. New Zealand Geology. Episodes 35 (1), 57-71.

CCAMLR, 2009. Report of the workshop on vulnerable marine ecosystems, La Jolla, CA, USA, 3-7 August 2009. Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR).

Clark, M., 2001. Are deepwater fisheries sustainable? - the example of orange roughy (Hoplostethus atlanticus) in New Zealand. Fisheries Research 51 (2-3), 123-135.

Clark, M.R., 2010. Effects of Trawling on Seamounts. Oceanography 23 (1), 132-133.

Clark, M.R., Althaus, F., Schlacher, T.A., Williams, A., Bowden, D.A., Rowden, A.A., 2015. The impacts of deep-sea fisheries on benthic communities: a review. Ices Journal of Marine Science.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User manual/tutorial. PRIMER-E Plymouth UK.

Collie, J.S., Hall, S.J., Kaiser, M.J., Poiner, I.R., 2000. A quantitative analysis of fishing impacts on shelf-sea benthos. Journal of Animal Ecology 69 (5), 785-798.

Cryer, M., Hartill, B., O'Shea, S., 2002. Modification of marine benthos by trawling: Toward a generalization for the deep ocean? Ecological Applications 12 (6), 1824-1839.

de Juan, S., Demestre, M., Thrush, S., 2009. Defining ecological indicators of trawling disturbance when everywhere that can be fished is fished: A Mediterranean case study. Marine Policy 33 (3), 472-478.

Diaz, R.J., Solan, M., Valente, R.M., 2004. A review of approaches for classifying benthic habitats and evaluating habitat quality. Journal of Environmental Management 73 (3), 165-181.

Dolan, M.F.J., Buhl-Mortensen, P., Thorsnes, T., Buhl-Mortensen, L., Bellec, V.K., Boe, R., 2009. Developing seabed nature-type maps offshore Norway: initial results from the MAREANO programme. Norwegian Journal of Geology 89 (1-2), 17-28.

FAO, 2009. International guidelines for the management of deep-sea fisheries in the high seas. Food and Agriculture Organization of the United Nations, Rome.

Gage, J.D., Roberts, J.M., Hartley, J.R., Humphery, J.D., 2005. Potential impacts of deep-sea trawling on the benthic ecosystem along the Northern European continental margin: A review. In: Barnes, B.W., Thomas, J.P. (Eds.), Benthic Habitats and the Effects of Fishing, pp. 503-517.

Genin, A., 2004. Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. Journal of Marine Systems 50 (1-2), 3-20.

Glasby, G.P., Wright, I.C., 1990. Marine mineral potential in New Zealand's Exclusive Economic Zone. Marine Mining 9 (3), 403-427.

Gordon, D.P., Beaumont, J., MacDiarmid, A., Robertson, D.A., Ahyong, S.T., 2010. Marine Biodiversity of <italic>Aotearoa</italic> New Zealand. PLoS ONE 5 (8), e10905.

Gray, J.S., Dayton, P., Thrush, S., Kaiser, M.J., 2006. On effects of trawling, benthos and sampling design. Marine Pollution Bulletin 52 (8), 840-843.

Greene, H.G., Yoklavich, M.M., Starr, R.M., O'Connell, V.M., Wakefield, W.W., Sullivan, D.E., McRea, J.E., Cailliet, G.M., 1999. A classification scheme for deep seafloor habitats. Oceanologica Acta 22 (6), 663-678.

Greinert, J., Lewis, K.B., Bialas, J., Pecher, I.A., Rowden, A., Bowden, D.A., De Batist, M., Linke, P., 2010. Methane seepage along the Hikurangi Margin, New Zealand: Overview of studies in 2006 and 2007 and new evidence from visual, bathymetric and hydroacoustic investigations. Marine Geology 272 (1-4), 6-25.

Hewitt, J., Julian, K., Bone, E.K., 2011. Chatham–Challenger Ocean Survey 20/20 Post-Voyage Analyses: Biotic habitats and their sensitivity to physical disturbance. New zealand Aquatic Environment and Biodiversity Report. Ministry of Fisheries, Wellington, New Zealand, p. 36.

Hiddink, J.G., Jennings, S., Kaiser, M.J., 2007. Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. Journal of Applied Ecology 44 (2), 405-413.

Hill, P., 2009. Designing a deep-towed camera vehicle using single conductor cable. Sea Technology 50 (12), 49-51.

Hinz, H., Prieto, V., Kaiser, M.J., 2009. Trawl disturbance on benthic communities: chronic effects and experimental predictions. Ecological Applications 19 (3), 761-773.

Hiscock, K., Tyler-Walters, H., 2006. Assessing the sensitivity of seabed species and biotopes - the Marine Life Information Network (MarLIN). Hydrobiologia 555, 309-320.

Howell, K.L., Mowles, S.L., Foggo, A., 2010. Mounting evidence: near-slope seamounts are faunally indistinct from an adjacent bank. Marine Ecology 31, 52-62.

ISA, 2007. Polymetallic sulphides and cobalt rich ferromanganese crust deposits: establishment of environmental baselines and an associated monitoring programme during exploration, Proceedings of the International Seabed Authority's workshop, Kingston, Jamaica, 6-10 September 2004. International Seabed Authority, p. 489.

Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. In: Blaxter, J.H.S., Southward, A.J., Tyler, P.A. (Eds.), Advances in Marine Biology, Vol 34. Academic Press Ltd-Elsevier Science Ltd, London, pp. 201-+.

Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., Somerfield, P.J., Karakassis, I., 2006. Global analysis of response and recovery of benthic biota to fishing. Marine Ecology-Progress Series 311, 1-14.

Lambert, G.I., Jennings, S., Kaiser, M.J., Davies, T.W., Hiddink, J.G., 2014. Quantifying recovery rates and resilience of seabed habitats impacted by bottom fishing. Journal of Applied Ecology 51 (5), 1326-1336.

Leduc, D., Rowden, A.A., Torres, L.G., Nodder, S.D., Pallentin, A., 2015. Distribution of macro-infaunal communities in phosphorite nodule deposits on Chatham Rise, Southwest Pacific: Implications for management of seabed mining. Deep-Sea Research Part I-Oceanographic Research Papers 99, 105-118.

Legendre, P., Borcard, D., Peres-Neto, P.R., 2005. Analyzing beta diversity: Partitioning the spatial variation of community composition data. Ecological Monographs 75 (4), 435-450.

Levin, L.A., Dayton, P.K., 2009. Ecological theory and continental margins: where shallow meets deep. Trends in Ecology & Evolution 24 (11), 606-617.

Levin, L.A., Sibuet, M., 2012. Understanding Continental Margin Biodiversity: A New Imperative. Annual Review of Marine Science 4 (1), 79-112.

Lundquist, C.J., Pritchard, M., Thrush, S.F., Hewitt, J.E., Greenfield, B.L., Halliday, J., Lohrer, A.M., 2013. Bottom disturbance and seafloor community dynamics: Development of a model of disturbance and recovery dynamics for marine benthic ecosystems. New zealand Aquatic Environment and Biodiversity Report. Ministry of Primary Industries, Wellington, New Zealand, p. 59.

Lundsten, L., Barry, J.P., Cailliet, G.M., Clague, D.A., DeVogelaere, A.P., Geller, J.B., 2009. Benthic invertebrate communities on three seamounts off southern and central California, USA. Marine Ecology-Progress Series 374, 23-32.

Murphy, R.J., Pinkerton, M.H., Richardson, K.M., Bradford-Grieve, J.M., Boyd, P.W., 2001. Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. New Zealand Journal of Marine and Freshwater Research 35 (2), 343-362.

O'Driscoll, R.L., 2004. Estimating uncertainty associated with acoustic surveys of spawning hoki (Macruronus novaezelandiae) in Cook Strait, New Zealand. Ices Journal of Marine Science 61 (1), 84-97.

O'Hara, T.D., 2007. Seamounts: centres of endemism or species richness for Ophiuroids? Global Ecology and Biogeography 16 (6), 720-732.

O'Hara, T.D., Rowden, A.A., Williams, A., 2008. Cold-water coral habitats on seamounts: do they have a specialist fauna? Diversity and Distributions 14 (6), 925-934.

Pitcher, T.J., Clark, M.R., Morato, T., Watson, R., 2010. Seamount Fisheries: Do They Have a Future? Oceanography 23 (1), 134-144.

Puig, P., Canals, M., Company, J.B., Martin, J., Amblas, D., Lastras, G., Palanques, A., Calafat, A.M., 2012. Ploughing the deep sea floor. Nature advance online publication.

Pusceddu, A., Bianchelli, S., Martin, J., Puig, P., Palanques, A., Masque, P., Danovaro, R., 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. Proceedings of the National Academy of Sciences of the United States of America 111 (24), 8861-8866.

Quinn, G.P., Keough, M.J., 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, p. 537.

Ramirez-Llodra, E., Company, J.B., Sarda, F., Rotllant, G., 2010. Megabenthic diversity patterns and community structure of the Blanes submarine canyon and adjacent slope in the Northwestern Mediterranean: a human overprint? Marine Ecology-an Evolutionary Perspective 31 (1), 167-182.

Ramirez-Llodra, E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., Van Dover, C.L., 2011. Man and the Last Great Wilderness: Human Impact on the Deep Sea. PLoS ONE 6 (8), e22588.

Rowden, A.A., Schlacher, T.A., Williams, A., Clark, M.R., Stewart, R., Althaus, F., Bowden, D.A., Consalvey, M., Robinson, W., Dowdney, J., 2010. A test of the seamount oasis hypothesis: seamounts support higher epibenthic megafaunal biomass than adjacent slopes. Marine Ecology 31, 95-106.

Thrush, S.F., Dayton, P.K., 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. Annual Review of Ecology and Systematics 33, 449-473.

Thrush, S.F., Dayton, P.K., 2010. What Can Ecology Contribute to Ecosystem-Based Management? Annual Review of Marine Science 2, 419-441.

Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. Marine Ecology Progress Series 318, 31-45.

Tyler-Walters, H., Rogers, S.I., Marshall, C.E., Hiscock, K., 2009. A method to assess the sensitivity of sedimentary communities to fishing activities. Aquatic Conservation: Marine and Freshwater Ecosystems 19 (3), 285-300.

Van Dover, C.L., 2014. Impacts of anthropogenic disturbances at deep-sea hydrothermal vent ecosystems: A review. Marine Environmental Research 102, 59-72.

Van Dover, C.L., Smith, C.R., Ardron, J., Dunn, D., Gjerde, K., Levin, L., Smith, S., Dinard Workshop, C., 2012. Designating networks of chemosynthetic ecosystem reserves in the deep sea. Marine Policy 36 (2), 378-381.

Vetter, E.W., Smith, C.R., De Leo, F.C., 2010. Hawaiian hotspots: enhanced megafaunal abundance and diversity in submarine canyons on the oceanic islands of Hawaii. Marine Ecology-an Evolutionary Perspective 31 (1), 183-199.

Williams, A., Bax, N.J., Kloser, R.J., Althaus, F., Barker, B., Keith, G., 2009. Australia's deep-water reserve network: implications of false homogeneity for classifying abiotic surrogates of biodiversity. Ices Journal of Marine Science 66 (1), 214-224.

Williams, A., Schlacher, T.A., Rowden, A.A., Althaus, F., Clark, M.R., Bowden, D.A., Stewart, R., Bax, N.J., Consalvey, M., Kloser, R.J., 2010. Seamount megabenthic assemblages fail to recover from trawling impacts. Marine Ecology 31, 183-199.

Wysoczanski, R., Clark, M.R., 2012. Southern Kermadec Arc – Havre Trough geohabitats. In: Harris, P.T., Baker, E.K. (Eds.), Seafloor geomorphology as benthic habitat: GeoHab Atlas of seafloor geomorphic features and benthic habitats. Elsevier, London, UK, pp. 853-867.

Zuur, A.F., Leno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1 (1), 3-14.

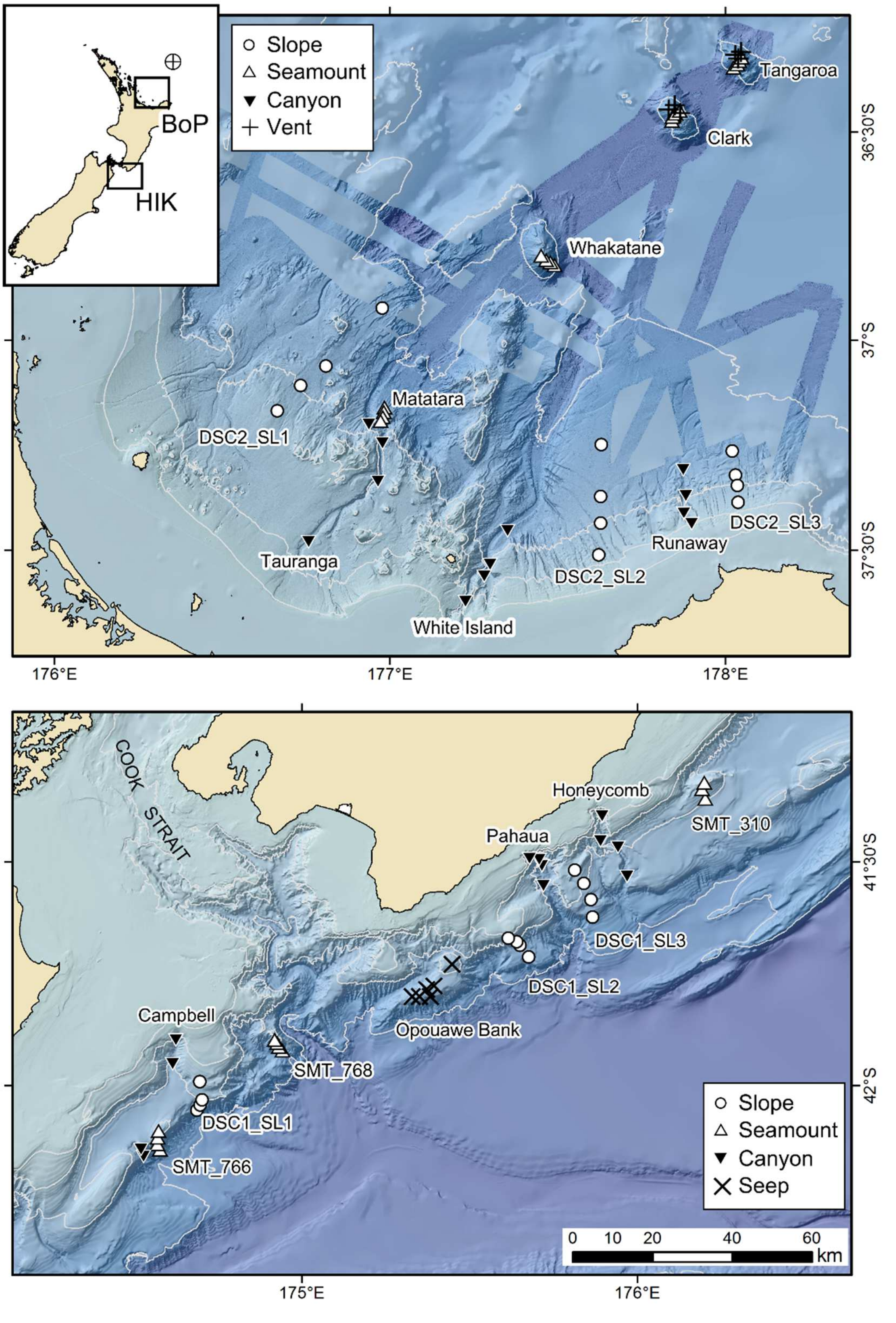

Figure 1. Sampling sites at features in the Bay of Plenty (BoP, top) and Hikurangi Margin (HIK, bottom) study regions, and their relative locations in New Zealand (inset – circled cross shows location of Brothers seamount on the Kermadec Ridge). Isobaths show 200, 500, 1000, and 2000 m depths. Scale bar applies to both regional maps.

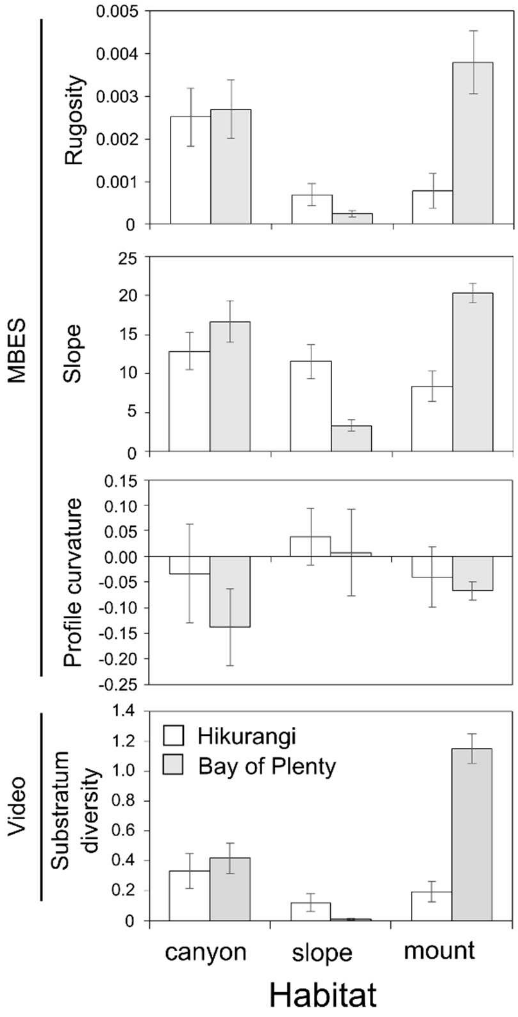

Figure 2. Physical seabed characteristics of canyon, slope, and seamount habitats on the Hikurangi Margin ('Hikurangi') and Bay of Plenty regions. The top three panels show representative metrics derived from multibeam echosounder data (MBES: rugosity, slope, and profile curvature as mean value per sample 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'(loge)).

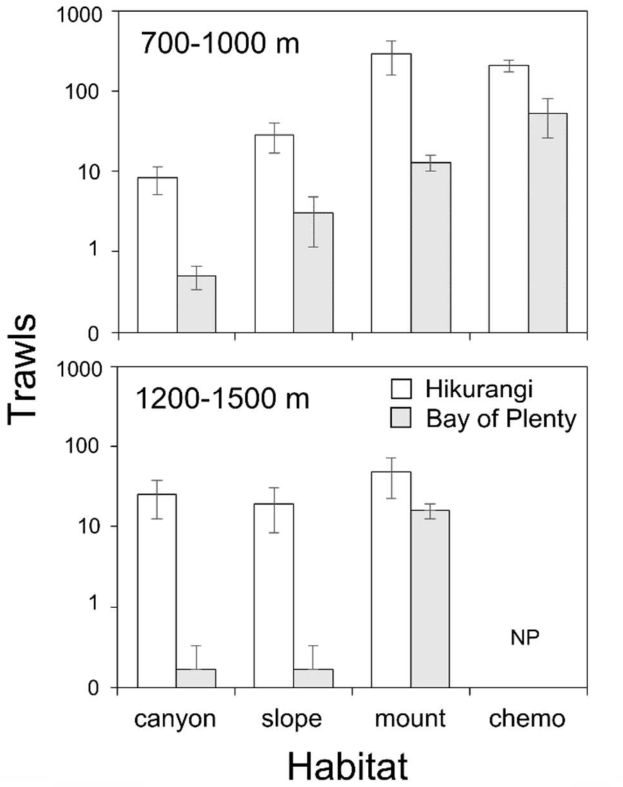

Figure 3. Cumulative trawl intensity in seabed habitats (canyon, continental slope, seamount, and chemosynthetic) of the Hikurangi Margin ('Hikurangi') and Bay of Plenty regions in two depth strata: 700-1000 m and 1200-1500 m. NP; no chemosynthetic habitats were present in the 1200-1500 m depth stratum 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.

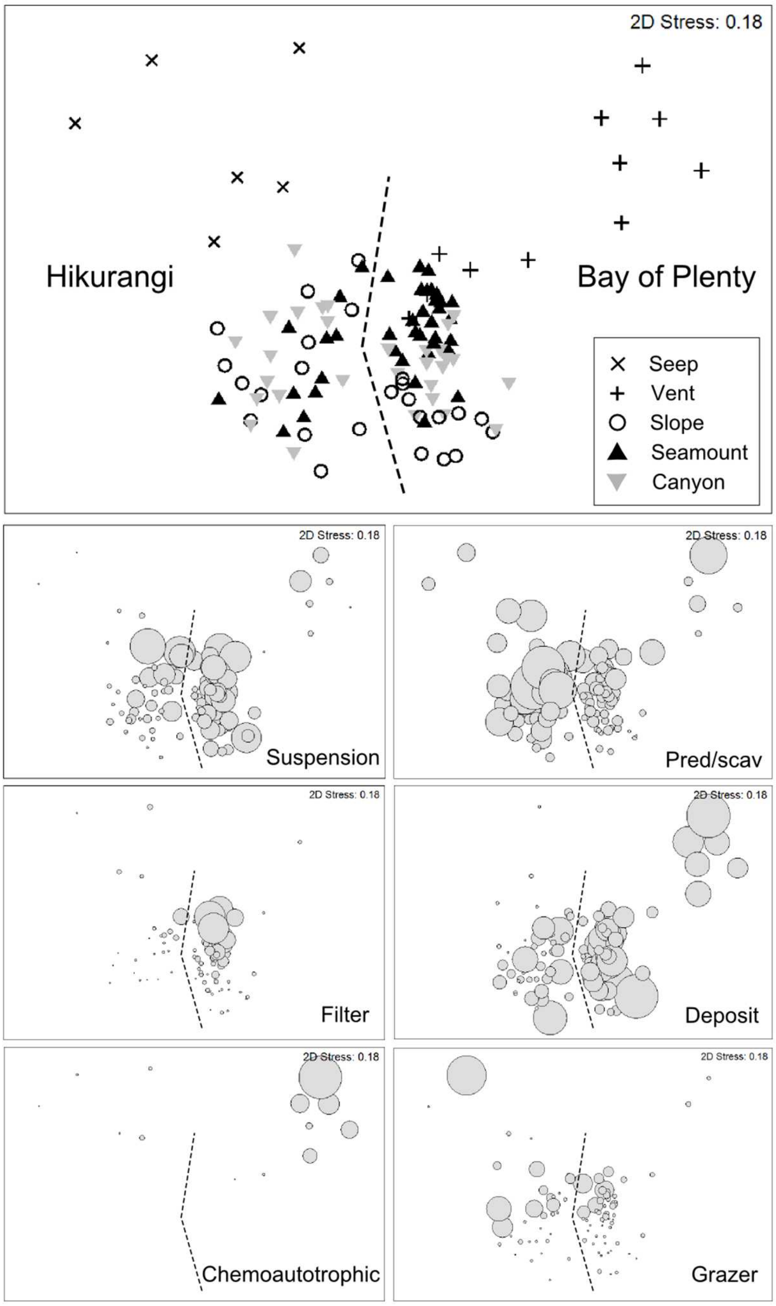

Figure 4. MDS ordination of Bray-Curtis similarities between mega-epifaunal benthic communities in five habitat types (cold seep, hydrothermal vent, continental slope, seamount, and canyon) sampled in two regions of the New Zealand EEZ: the Hikurangi Margin ('Hikurangi'), and the Bay of Plenty (left 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).

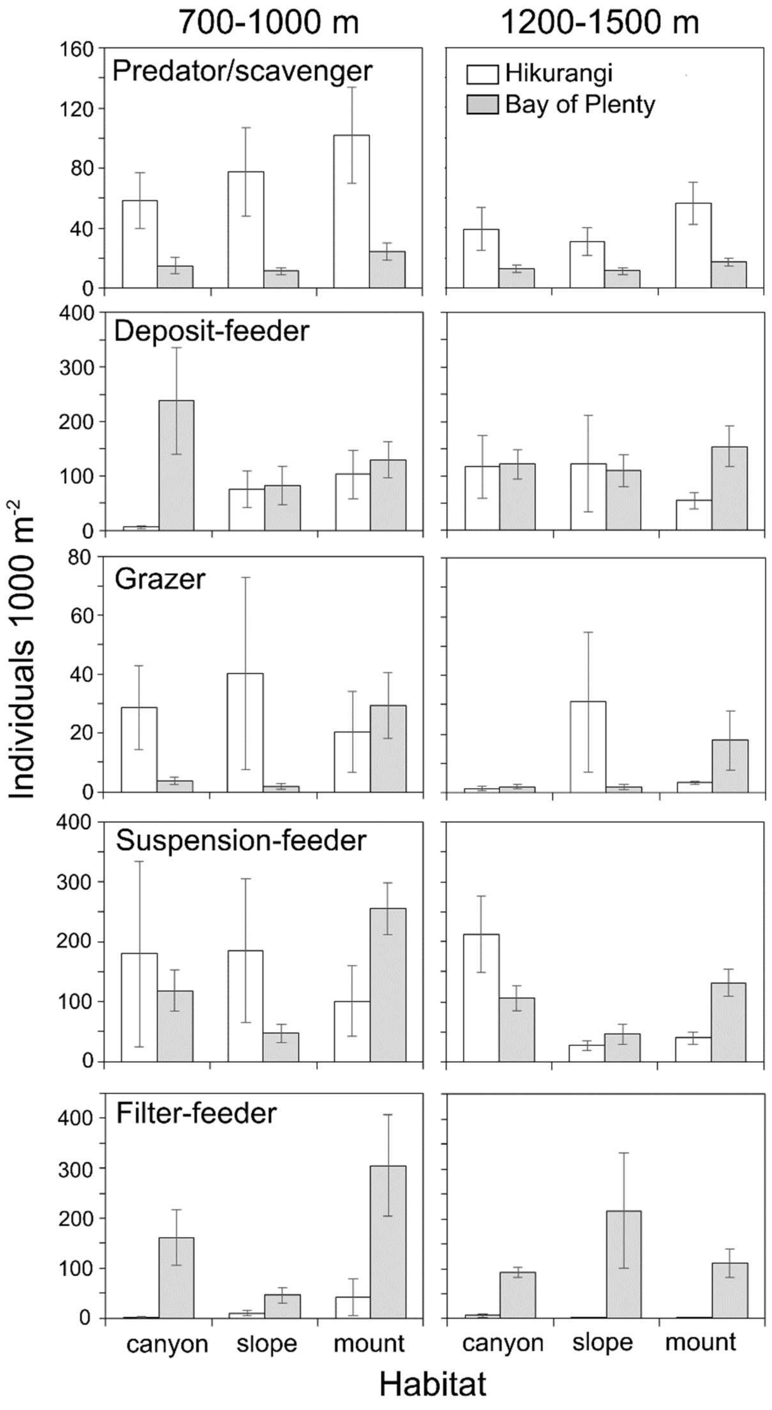

Figure 5. Densities of benthic taxa in five feeding groups (predator/scavenger, deposit-feeder, grazer, suspension-feeder, filter-feeder) in two depth ranges (700-1000 m and 1200-1500 m) in each of two regions of the New Zealand deep sea: Hikurangi Margin (‘Hikurangi’) and Bay of Plenty. Bars show means ± 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).

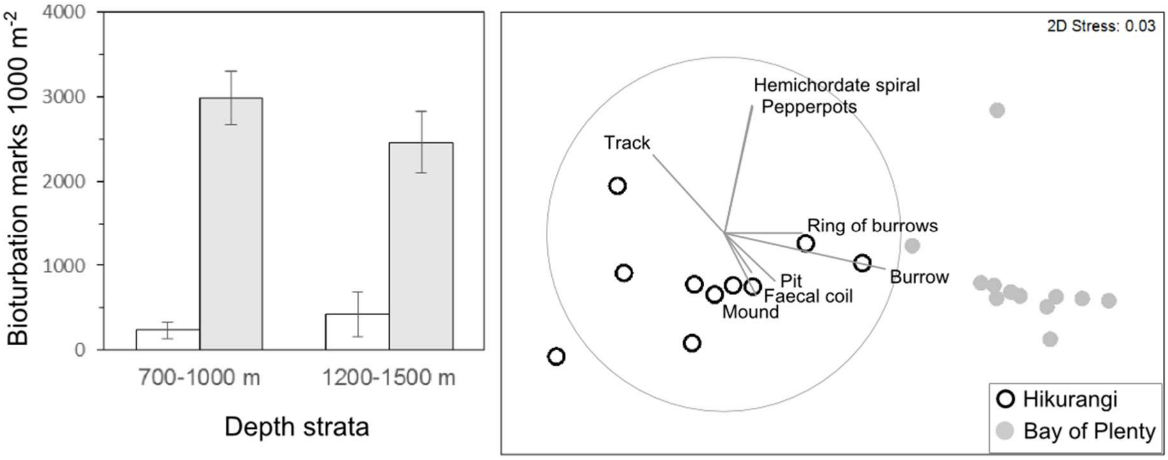

Figure 6. Bioturbation marks in muddy sediments. Left: density of all marks recorded in video transects from slope habitat with >97 % muddy sediments at two depth strata (700-1000 and 1200-1500 m) on the Hikurangi Margin (‘Hikurangi’, open bars) and Bay of Plenty (filled bars). Bars show means ± 1se 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.

Region	Habitat	Feature name	Depth stratum (m)	Station	Depth (mean, m)	Lat (mean)	Lon (mean)	Distance (km)
Bay of Plenty	canyon	Runaway	700	54	621	-37.4310	177.8940	0.96
			1000	59	867	-37.4027	177.8756	1.31
			1200	64	1228	-37.3648	177.8763	0.71
			1500	69	1421	-37.3034	177.8708	1.01
		Tauranga	700	126	650	-37.4744	176.7609	1.25
			1000	116	958	-37.3307	176.9598	1.27
				128	988	-37.3142	176.9801	0.82
				129	1064	-37.2253	176.9905	0.97
			1200	110	1165	-37.2514	176.9698	1.31
			1500	104	1435	-37.1932	176.9411	1.19
		White Island	700	157	674	-37.6142	177.2229	1.06
			1000	147	993	-37.5517	177.2828	0.92
				149	940	-37.5487	177.2707	1.13
			1200	141	1079	-37.5261	177.2995	0.97
			1500	134	1455	-37.4468	177.3519	0.74
	seamount	Clark	1000	93	1035	-36.4494	177.8433	0.82
				96	989	-36.4527	177.8385	0.65
			1200	35	1281	-36.4511	177.8518	1.20
				37	1190	-36.4576	177.8398	0.91
			1500	38	1461	-36.4662	177.8398	0.93
				94	1464	-36.4423	177.8561	0.95
		Matatara	700	132	830	-37.1971	176.9782	1.27
				159	790	-37.1957	176.9749	1.08
			1000	160	972	-37.1833	176.9785	1.04
				162	1039	-37.1802	176.9780	1.19
				167	1003	-37.1883	176.9793	1.36
			1200	163	1226	-37.1745	176.9726	0.95
				169	1208	-37.1819	176.9953	1.25
			1500	165	1483	-37.1578	176.9849	0.94
		Tangaroa	700	24	876	-36.3268	178.0360	0.75
			1000	26	1062	-36.3253	178.0402	0.85
			1200	20	1165	-36.3314	178.0219	0.50
				28	1204	-36.3218	178.0442	0.79
			1500	22	1543	-36.3379	178.0223	0.93
				30	1524	-36.3171	178.0527	1.21
		Whakatane	1000	75	955	-36.8180	177.4622	0.97
				76	924	-36.8065	177.4633	1.48

				79	1018	-36.8073	177.4677	0.96
				87	1039	-36.8006	177.4546	0.57
			1200	83	1203	-36.8058	177.4732	0.99
				89	1178	-36.7923	177.4531	0.97
			1500	85	1518	-36.8028	177.4816	1.01
				91	1492	-36.7788	177.4358	0.85
	slope	DSC2_SL1	700	1	728	-37.1652	176.6678	1.50
			1000	6	1028	-37.1053	176.7374	0.94
			1200	8	1203	-37.0577	176.8122	0.86
			1500	12	1491	-36.9209	176.9788	1.12
		DSC2_SL2	700	51	709	-37.5029	177.6175	0.85
			1000	47	994	-37.4312	177.6269	1.08
			1200	45	1198	-37.3683	177.6243	1.01
			1500	41	1495	-37.2426	177.6277	1.24
		DSC2_SL3	700	184	720	-37.3813	178.0319	1.18
			1000	180	1015	-37.3417	178.0298	1.26
			1200	177	1188	-37.3178	178.0237	1.22
			1500	174	1510	-37.2613	178.0137	0.97
	vent	Clark	700	98	888	-36.4488	177.8393	0.76
			1000	33	978	-36.4472	177.8385	0.91
				92	920	-36.4491	177.8399	0.72
		Tangaroa	1000	16	942	-36.3209	178.0293	1.02
				19	1066	-36.3311	178.0323	1.31
Hikurangi Margin	canyon	Campbell	700	123	613	-41.8943	174.6318	1.30
				90	646	-41.8923	174.6318	1.35
			1000	84	995	-41.9471	174.6182	1.52
			1200	102	1222	-42.1266	174.5393	1.48
			1500	99	1544	-42.1397	174.5474	1.51
		Honeycomb	700	56	604	-41.4102	175.8968	1.36
			1000	51	947	-41.4610	175.8966	1.19
			1200	48	1136	-41.4760	175.9466	1.04
			1500	45	1454	-41.5355	175.9707	1.17
				47	1388	-41.5390	175.9703	1.12
		Pahaua	700	29	620	-41.4910	175.6739	1.88
			1000	24	957	-41.4954	175.6959	1.95
			1200	20	1138	-41.5066	175.7133	1.08
			1500	11	1405	-41.5622	175.7298	1.90
	seamount	SMT_310	700	64	514	-41.3206	176.1944	1.53
				67	683	-41.3350	176.1893	1.31
			1000	70	989	-41.3659	176.1976	1.55
		SMT_766	1000	111	994	-42.1079	174.5757	1.25
				113	905	-42.1008	174.5746	1.06
			1200	109	1247	-42.1291	174.5733	1.43
			1500	82	1524	-42.1343	174.5851	0.54
		SMT_768	1000	133	951	-41.8926	174.9266	1.16
				135	1016	-41.9026	174.9359	1.47
				139	1074	-41.8951	174.9326	1.66
			1500	137	1424	-41.9140	174.9494	1.47
	slope	DSC1_SL1	700	119	710	-41.9863	174.7009	1.68
			1000	121	1054	-42.0327	174.7029	1.04
			1200	117	1298	-42.0413	174.6993	1.73
			1500	115	1435	-42.0476	174.6920	1.97
		DSC1_SL2	700	1	638	-41.6681	175.6351	1.77
				75	697	-41.6707	175.6283	1.77
			1000	3	1031	-41.6805	175.6369	1.13
			1200	5	1293	-41.6814	175.6535	1.36
			1500	8	1504	-41.7186	175.6715	1.68

DSC1_SL3	700	42	673	-41.5234	175.8085	1.68
	1000	39	940	-41.5496	175.8370	0.94
	1200	35	1126	-41.5937	175.8551	1.82
	1500	15	1527	-41.6318	175.8709	1.11

Table 2. Station data for chemosynthetic habitats used in these analyses.

Region	Habitat	Feature name	Depth stratum (m)	Voyage	Station	Depth (mean, m)	Lat (mean)	Lon (mean)
Hikurangi Margin	seep	North Tower	1000	SO191	106	1052	-41.7819	175.4014
				TAN0616	75	1052	-41.7819	175.4014
					76	1052	-41.7819	175.4014
					85	1052	-41.7819	175.4014
					114	1052	-41.7819	175.4014
					115	1052	-41.7819	175.4014
		Pukeko	1000	SO191	155	1060	-41.7859	175.3911
		South Tower	1000	TAN0616	117	1056	-41.7883	175.4087
					119	1056	-41.7883	175.4087
					120	1056	-41.7883	175.4087
					1075	1056	-41.7883	175.4087
		Tui	1000	SO191	108	815	-41.7215	175.4515
					129	815	-41.7215	175.4515
					154	815	-41.7215	175.4515
		Takahe	1000	SO214	64	1058	-41.7728	175.4275
					65	1058	-41.7728	175.4275
		Piwakawaka	1000	SO214	70	1095	-41.7944	175.3725
Bay of Plenty	vent	Brothers	1200	TAN1007	67	1248	-34.8818	179.0682
			1500		68	1432	-34.8828	179.0685
					70	1483	-34.8767	179.0706
					73	1552	-34.8759	179.0707
			1200		77	1284	-34.8824	179.0681
			1500		78	1836	-34.8610	179.0588

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.

Trophic group	Definition	Taxa	Rowden et al (2010)
suspension-feeder	passively trap water-borne food particles, including live prey, using external body structures	all corals, anemones, brisingid asteroids, Euryalida ophiuroids, *Dermechinus horridus*	Filter/Predator
filter feeder	actively pump water through body or shell to trap fine food particles	sponges, ascidians, brachiopods, bivalve molluscs	Filter-feeder
deposit-feeder	ingest sediments and food particles on or in the seabed	holothuroids, ophiuroids (except Order Euryalida), small natant decapods	Deposit-feeder
predator/scavenger	actively prey on live animals or consume dead animals	decapod crustaceans, galatheids, asteroids (except brinsingids), large natant decapods, errant polychaetes, opisthobranch molluscs, pycnogonids	Predator-Omnivore
grazer	remove attached organic particles from hard or soft substrata using abrasive mouthparts	echinoids (except *Dermechinus horridus*), non-predatory gastropod molluscs	Deposit-feeder
chemoautotrophic	Wholly or partly dependent on chemoautotrophic bacteria in reducing habitats	*Lamellibrachia* spp. worms, *Vulcanolepas* spp. barnacles, *Calyptogena* spp. clams, *Bathymodiolus* spp. mussels, *Alvinocaris* spp. natant decapods	NA

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.

Source of variation	df	SS	MS	Pseudo-F	P	permutations
Habitat	2	5258	2629	0.715	0.7008	720
Region	1	2064	2065	1.642	**0.0322**	9891
Stratum	3	17547	5849	1.155	0.3855	8779
Ha×Re	2	6639	3320	2.639	**0.0001**	9857
Ha×St	6	11831	1972	0.781	0.8047	9870
Re×St	3	11922	3974	3.159	**0.0001**	9837
Re× Ha×St	6	13107	2185	1.737	**0.0001**	9768
Residuals	62	77986	1258			
Total	93	225000				

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.

		Hikurangi Margin			Bay of Plenty		
Depth strata	Habitat comparison	t	P	perms	t	P	perms
All depths	slope *vs* chemo	2.1277	**0.0001**	9922	3.3013	**0.0001**	9946
	slope *vs* seamount	1.0019	0.4349	9927	3.1965	**0.0001**	9919
	slope *vs* canyon	1.0483	0.3400	9906	1.6389	**0.0051**	9922
	chemo *vs* seamount	3.1221	**0.0001**	9942	2.9792	**0.0001**	9922
	chemo *vs* canyon	2.4040	**0.0001**	9911	3.0378	**0.0001**	9926
	seamount *vs* canyon	1.3256	**0.0369**	9907	2.1988	**0.0001**	9921
700-1000 m	slope *vs* seamount	1.0085	0.399	5041	2.7622	**<0.001**	8252
	slope *vs* canyon	1.1028	0.237	1708	1.3212	0.052	5664
	seamount *vs* canyon	1.3125	0.051	5077	2.0936	**<0.001**	9870
1200-1500 m	slope *vs* seamount	0.8992	0.73	84	2.1333	**<0.001**	9072
	slope *vs* canyon	1.1488	0.175	1706	1.3689	**0.036**	462
	seamount *vs* canyon	1.4207	**0.04**	120	1.4219	**0.030**	9119

Table 6. Hikurangi Margin: SIMPER analysis for comparisons between benthic mega-epifaunal 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.

Taxon	Av.Abund Slope	Av.Abund Canyon	Av.Diss	Diss/SD	Contrib%	Cum.%
Ophiuroidea	7.59 (1.54)	49.66 (3.83)	3.79	0.87	5.55	5.55
Pennatulacea	14.14 (1.81)	77.15 (2.80)	3.77	0.52	5.51	11.07
Paguridae	21.84 (2.56)	17.26 (2.83)	3.47	0.98	5.09	16.15
Xenophyophoroidea	44.39 (2.42)	2.75 (0.62)	3.18	0.46	4.65	20.80
Actiniaria	10.91 (2.18)	18.65 (3.58)	2.94	1.30	4.31	25.11
Gorgonacea	9.62 (1.77)	24.9 (2.85)	2.93	0.94	4.30	29.41
Brisingida	0.55 (0.44)	33.09 (2.71)	2.55	0.56	3.74	33.15
Hydroids	4.74 (1.41)	19.92 (2.52)	2.53	0.85	3.71	36.86
Echinidae	18.76 (1.90)	3.4 (0.91)	2.53	0.55	3.70	40.56
Forcipulatida	14.4 (3.06)	7.35 (2.27)	2.52	1.15	3.68	44.24
Anthomastus spp.	6.0 (1.83)	10.19 (2.36)	2 .40	1.34	3.51	47.76
Ceriantharia	8.83 (2.54)	10.84 (2.40)	2.30	1.00	3.37	51.13
Cidaridae	15.18 (1.88)	2.47 (0.68)	2.23	0.57	3.26	54.39
Psychropotidae	7.84 (1.34)	4.07 (0.63)	2.00	0.61	2.93	57.32
Paxillosida	3.04 (1.23)	6.3 (1.58)	1.86	1.09	2.73	60.05
Quill worm	21.78 (1.77)	0.17 (0.19)	1.68	0.46	2.46	62.51
Demospongiae	5.35 (1.27)	3.48 (1.10)	1.62	0.99	2.37	64.87
Gastropoda	3.29 (1.45)	3.78 (1.52)	1.48	1.15	2.16	67.03
Laetmogonidae	7.09 (1.49)	0.25 (0.30)	1.46	0.84	2.14	69.17
Notomyotida	3.22 (0.91)	2.83 (0.80)	1.41	0.72	2.06	71.23
	Slope	Seamount				
Xenophyophoroidea	44.39 (2.42)	23.6 (3.16)	4.73	0.79	7.31	7.31
Paguridae	21.84 (2.56)	42.58 (4.92)	4.34	1.14	6.70	14.01
Quill worm	21.78 (1.77)	36.3 (2.15)	2.64	0.54	4.08	18.09

Echinidae	18.76 (1.9)	10.99 (1.62)	2.55	0.60	3.93	22.02
Ophiuroidea	7.59 (1.54)	10.07 (2.67)	2.32	1.15	3.58	25.60
Psychropotidae	7.84 (1.34)	9.42 (1.23)	2.27	0.68	3.50	29.10
Demospongiae	5.53 (1.27)	30.8 (2.69)	2.25	0.85	3.48	32.58
Forcipulatida	14.4 (3.06)	13.04 (3.23)	2.25	1.31	3.47	36.04
Actiniaria	10.91 (2.18)	13.21 (2.96)	2.16	1.38	3.34	39.38
Pennatulacea	14.14 (1.81)	6.09 (1.26)	2.08	0.74	3.21	42.59
Ceriantheria	8.83 (2.54)	15.09 (3.45)	1.99	1.05	3.08	45.67
Cidaridae	15.18 (1.88)	3.27 (0.69)	1.90	0.56	2.93	48.60
Gorgonacea	9.62 (1.77)	6.22 (1.56)	1.83	1.12	2.82	51.41
Scleractinia	18.07 (1.29)	25.4 (1.79)	1.67	0.51	2.58	53.99
Anthomastus spp.	6 (1.83)	2 (1.05)	1.60	1.23	2.47	56.47
Natantia	5.25 (1.96)	4.63 (1.65)	1.55	1.10	2.39	58.86
Paxillosida	3.04 (1.23)	4.45 (1.63)	1.54	1.14	2.38	61.23
Stylasteridae	30.15 (1.77)	3.53 (0.86)	1.48	0.50	2.28	63.52
Notomyotida	3.22 (0.91)	3.87 (0.95)	1.44	0.71	2.23	65.75
Laetmogonidae	7.09 (1.49)	2 (0.67)	1.38	0.85	2.13	67.88
Asteroidea	3.8 (1.77)	6.68 (2.24)	1.26	1.26	1.95	69.83
Gastropoda	3.29 (1.45)	3.92 (1.7)	1.25	1.22	1.93	71.75

	Canyon	Seamount				
Paguridae	17.26 (2.83)	42.58 (4.92)	4.18	1.14	6.35	6.35
Ophiuroidea	49.66 (3.83)	10.07 (2.67)	3.83	1.11	5.83	12.18
Xenophyophoroidea	2.75 (0.62)	23.6 (3.16)	3.70	0.79	5.62	17.80
Pennatulacea	77.15 (2.8)	6.09 (1.26)	2.96	0.45	4.49	22.29
Ceriantharia	10.84 (2.4)	15.09 (3.45)	2.76	1.03	4.20	26.49
Gorgonacea	24.9 (2.85)	6.22 (1.56)	2.52	0.89	3.83	30.32
Actiniaria	18.65 (3.58)	13.21 (2.96)	2.49	1.36	3.78	34.10
Brisingida	33.09 (2.71)	0.91 (0.68)	2.45	0.60	3.73	37.83
Hydroids	19.92 (2.52)	1.83 (0.84)	2.25	0.78	3.43	41.25
Demospongiae	3.48 (1.1)	30.8 (2.69)	2.22	0.84	3.37	44.62
Forcipulatida	7.35 (2.27)	13.04 (3.23)	1.99	1.30	3.02	47.64
Echinidae	3.4 (0.91)	10.99 (1.62)	1.93	0.68	2.93	50.57
Anthomastus spp.	10.19 (2.36)	2 (1.05)	1.92	1.18	2.91	53.48
Quill worm	0.17 (0.19)	36.3 (2.15)	1.73	0.41	2.63	56.12
Paxillosida	6.36 (1.58)	4.45 (1.63)	1.73	1.01	2.63	58.74

Psychropotidae	4.07 (0.63)	9.42 (1.23)	1.68	0.52	2.55	61.30
Asteroidea	2.84 (1.27)	6.68 (2.24)	1.60	1.21	2.44	63.73
Gastropoda	3.78 (1.52)	3.92 (1.7)	1.33	1.16	2.03	65.76
Notomyotida	2.83 (0.8)	3.87 (0.95)	1.32	0.70	2.01	67.77
Natantia	2.52 (1.54)	4.63 (1.65)	1.31	1.26	1.99	69.77
Buccinidae	1.96 (0.61)	3.03 (1.19)	1.29	1.00	1.95	71.72

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.

Taxon	Av.Abund Slope	Av.Abund Canyon	Av.Diss	Diss/SD	Contrib%	Cum.%
Phlebobranchia	123.68 (8.41)	59.05 (6.13)	5.53	1.01	9.34	9.34
Xenophyophoroidea	18.66 (2.12)	101.13 (6.04)	4.73	0.93	8.00	17.33
Holothuroid 4	27.68 (3.25)	30.1 (3.76)	3.56	1.15	6.01	23.35
Hexactinellida	5.21 (1.76)	45.06 (5.3)	2.97	1.14	5.02	28.37
Bryozoa	1.08 (0.6)	31.07 (4.13)	2.73	1.20	4.62	32.98
Ophiuroidea	19.45 (2.86)	9.7 (2.69)	2.34	0.92	3.95	36.93
Gorgonacea	11.36 (2.87)	25.66 (4.49)	2.31	1.38	3.90	40.83
Crinoidea	0.48 (0.38)	13.52 (2.6)	1.95	0.83	3.30	44.13
Natantia	23.39 (4.62)	41.31 (6.14)	1.92	1.48	3.25	47.38
Actiniaria	3.63 (1.25)	8.67 (2.25)	1.54	1.26	2.61	49.99
Caryophylliidae	9.15 (2.34)	6.18 (2.05)	1.54	1.16	2.60	52.59
Ceriantharia	6.7 (2)	3.91 (1.36)	1.47	1.24	2.49	55.08
Ascidiacea	0.08 (0.08)	23.72 (2.07)	1.40	0.54	2.36	57.44
Pennatulacea	3.95 (1.65)	6.08 (1.76)	1.30	1.08	2.19	59.63
Synallactidae	4.57 (1.58)	3.72 (1.47)	1.27	1.22	2.15	61.78
Antipatharia	0.21 (0.18)	5.05 (1.68)	1.21	1.24	2.04	63.82
Pelagothuriidae	2.82 (1.3)	4.27 (1.48)	1.11	1.05	1.87	65.70
Brachiopoda	0.18 (0.17)	4.9 (1.29)	1.05	0.76	1.78	67.47
Paguridae	1.81 (0.84)	3.36 (1.21)	1.04	1.12	1.76	69.23
Anthomastus spp.	3.33 (1.36)	1.83 (0.99)	1.03	1.18	1.75	70.98
	Slope	Seamount				
Phlebobranchia	123.68 (8.41)	33.43 (3.34)	5.42	1.14	8.13	8.13
Hexactinellida	5.21 (1.76)	104.74 (8)	4.33	1.19	6.50	14.63
Bryozoa	1.08 (0.6)	56.99 (6.39)	4.16	1.57	6.25	20.89
Demospongiae	0.63 (0.48)	48.53 (4.85)	3.03	1.03	4.55	25.43
Ophiuroidea	19.45 (2.86)	34.94 (5.05)	2.93	1.23	4.40	29.83
Gorgonacea	11.36 (2.87)	39.4 (5.3)	2.48	1.26	3.72	33.55
Natantia	23.39 (4.62)	62.78 (7.04)	2.37	1.08	3.55	37.10
Holothuroid 4	27.68 (3.25)	2.1 (0.52)	2.25	0.87	3.38	40.48

Xenophyophoroidea	18.66 (2.12)	8.45 (2.06)	2.17	1.07	3.25	43.74
Antipatharia	0.21 (0.18)	11.9 (3.07)	2.07	2.00	3.10	46.84
Caryophylliidae	9.15 (2.34)	13.11 (2.97)	1.70	1.35	2.55	49.39
Actiniaria	3.63 (1.25)	20.92 (3.05)	1.68	0.82	2.53	51.92
Elasipodida	0.89 (0.44)	24.47 (2.1)	1.65	0.56	2.48	54.40
Echinoidea	0.09 (0.09)	12.75 (2.14)	1.55	0.69	2.33	56.73
Crinoidea	0.48 (0.38)	10.91 (2.47)	1.51	1.09	2.27	59.00
Ceriantharia	6.7 (2)	4.02 (1.44)	1.24	1.19	1.87	60.87
Zoantharia	0.41 (0.37)	6.45 (1.41)	1.10	0.74	1.65	62.52
Scleractinia	0.07 (0.07)	8.59 (1.6)	1.08	0.66	1.63	64.15
Anthomastus spp.	3.33 (1.36)	5.34 (1.86)	1.08	1.24	1.62	65.77
Synallactidae	4.57 (1.58)	1.64 (0.87)	1.06	1.10	1.59	67.36
Pelagothuriidae	2.82 (1.3)	1.49 (0.44)	1.04	0.94	1.56	68.92
Pennatulacea	3.95 (1.65)	3.01 (1.17)	1.02	1.36	1.53	70.45
Brachiopoda	0.18 (0.17)	4.54 (1.07)	0.86	0.65	1.29	71.75
	Canyon	Seamount				
Phlebobranchia	59.05 (6.13)	33.43 (3.34)	3.44	1.34	5.96	5.96
Xenophyophoroidea	101.13 (6.04)	8.45 (2.06)	3.37	0.88	5.84	11.80
Hexactinellida	45.06 (5.3)	104.74 (8)	3.16	1.02	5.47	17.27
Bryozoa	31.07 (4.13)	56.99 (6.39)	3.04	1.35	5.26	22.53
Demospongiae	1.92 (1.13)	48.53 (4.85)	2.40	0.93	4.15	26.68
Holothuroid 4	30.1 (3.76)	2.1 (0.52)	2.33	0.95	4.04	30.72
Gorgonacea	25.66 (4.49)	39.4 (5.3)	2.06	1.24	3.57	34.29
Natantia	41.31 (6.14)	62.78 (7.04)	2.06	1.15	3.57	37.86
Ophiuroidea	9.7 (2.69)	34.94 (5.05)	1.93	1.04	3.34	41.20
Crinoidea	13.52 (2.6)	10.91 (2.47)	1.54	0.90	2.66	43.86
Ascidiacea	23.72 (2.07)	9.81 (1.11)	1.37	0.61	2.37	46.23
Elasipodida	0.16 (0.14)	24.47 (2.1)	1.35	0.50	2.35	48.58
Echinoidea	0.61 (0.27)	12.75 (2.14)	1.35	0.70	2.34	50.92
Antipatharia	5.05 (1.68)	11.9 (3.07)	1.35	1.39	2.33	53.25
Actiniaria	8.67 (2.25)	20.92 (3.05)	1.34	0.73	2.33	55.58
Caryophylliidae	6.18 (2.05)	13.11 (2.97)	1.33	1.26	2.31	57.89
Scleractinia	7.2 (1.29)	8.59 (1.6)	1.26	0.85	2.18	60.07
Brachiopoda	4.9 (1.29)	4.54 (1.07)	1.09	0.88	1.89	61.97
Ceriantharia	3.91 (1.36)	4.02 (1.44)	1.01	1.08	1.75	63.71

Pennatulacea	6.08 (1.76)	3.01 (1.17)	0.97	0.95	1.68	65.39
Zoantharia	0.25 (0.17)	6.45 (1.41)	0.96	0.69	1.66	67.05
Pelagothuriidae	4.27 (1.48)	1.49 (0.44)	0.94	0.90	1.62	68.67
Anthomastus spp.	1.83 (0.99)	5.34 (1.86)	0.92	1.15	1.60	70.27

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.

Region	Depth range	Variable	Cumulative Adj R^2	SS	Pseudo-F	P	R^2	res.df
Hikurangi Margin	700-1000	Lat^2 Lon Depth	0.23	28778			0.34	
		+ Substrate diversity	0.27	2953	1.9438	**0.0163**	0.07	17
		+ Trawl	0.30	2499	1.7144	**0.0481**	0.06	16
		+ mbes rugosity	0.32	1944	1.3634	0.1693	0.04	15
		+ mbes plan curvature	0.32	1599	1.1312	0.3367	0.04	14
		+ mbes STD	0.33	1558	1.1111	0.3522	0.04	13
	1200-1500	Lat^2 Lon Depth	0.13	20440			0.31	
		+ Substrate diversity	0.30	5261	3.8123	**0.0013**	0.18	11
		+ Trawl	0.32	1909	1.4385	0.1547	0.06	10
		+ mbes rugosity	0.33	1414	1.0735	0.3963	0.05	8
		+ mbes range	0.36	1724	1.3607	0.2170	0.06	9
		+ mbes STD	0.37	1412	1.1336	0.3468	0.05	7
Bay of Plenty	700-1000	Lat^2 Lon Depth	0.16	46821			0.24	
		+ Substrate diversity	0.27	7455	5.4922	**0.0001**	0.12	29
		+ Trawl	0.30	2577	1.9612	**0.0153**	0.04	28
		+ mbes rugosity	0.30	1628	1.2500	0.2146	0.03	27
		+ mbes range	0.31	1931	1.5109	0.0943	0.03	26
	1200-1500	Lat^2 Lon Depth	0.20	28692			0.29	
		+ mbes range	0.31	4899	4.5302	**0.0001**	0.12	22
		+ Trawl	0.33	1897	1.8197	**0.0256**	0.05	21
		+ Substrate diversity	0.34	1304	1.2667	0.2170	0.03	20
		+ mbes plan curvature	0.35	1388	1.3737	0.1543	0.03	19