NIWA
Taihoro Nukurangi

Hikurangi Marine Reserve DTIS video analysis

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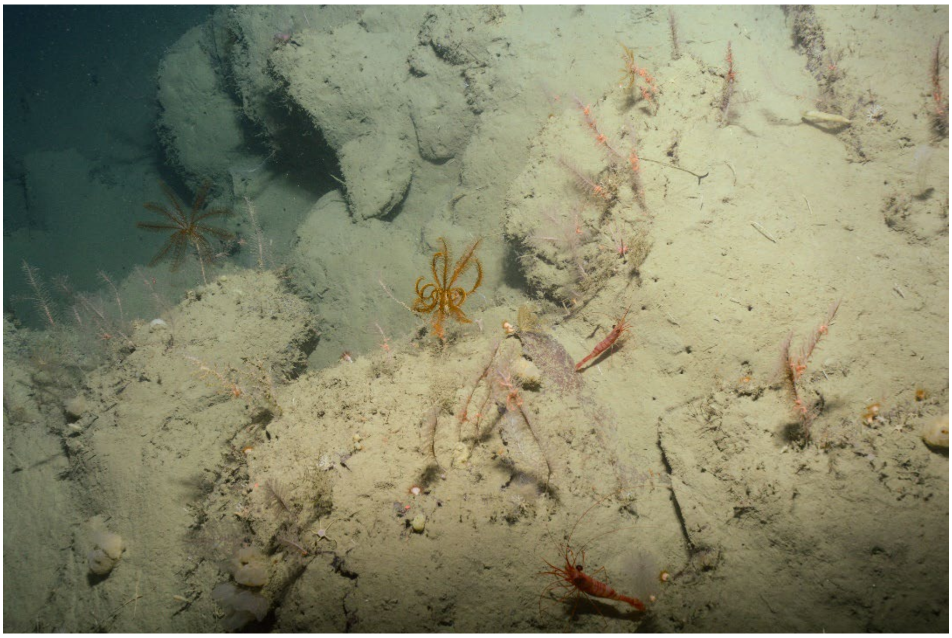

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Cover photo: seafloor photograph from the wall of Kaikoura Canyon (NIWA DTIS image TAN2203_011_085)

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Executive summary

This report presents analyses of high-resolution seafloor imagery from a recent survey of the Hikurangi Marine Reserve (HMR) and surrounding areas commissioned by the Department of Conservation, together with existing material from earlier surveys, to develop quantitative data about the distributions of seafloor habitats and invertebrate communities and fishes. The motivation for this research is to improve understanding of the highly productive marine ecosystem centred on Kaikoura canyon and address questions related to three key aspects of the HMR's design: 1) how well it represents habitats and faunal communities in the region, 2) whether its current boundaries are adequate to fulfil its intended role of conserving the ecosystem of the canyon, and 3) how it influences, or is influenced by, surrounding habitats outside its boundaries.

Thirty-one seafloor video transects, representing twenty-seven seafloor sites, were analysed for substrata, benthic invertebrates, and fishes. The total seafloor area analysed was approximately 102,000 m^2 (~1 km^2), from which 66,928 individual observations were recorded: 32,230 observations of invertebrate taxa, 18,093 observations of fish taxa, and 15,605 observations of substrate type. All individual observations were time-references and logged with spatial coordinates, enabling detailed analyses of the resulting data at both whole-transect and within-transect spatial scales. Higher-resolution still images were also analysed from two sites in Kaikoura Canyon to generate more detail in on-going analyses of the capacity of the seafloor community to recover from major disturbance events.

Multivariate analyses at the whole-transect scale indicated four broad invertebrate community types that were differentiated by the types of taxa present, their relative abundances, and by their measured diversity. Most of the sites within the current HMR boundaries represented a single community type (community I), with the other three community types occurring predominantly outside of the HMR on the walls of Kaikoura Canyon and Conway Trough (communities II and III) and on the shallow coastal shelf at the northern rim of Kaikoura Canyon (community IV). Community I was associated with fine soft sediments on the canyon floor and was characterised by high densities of the tube-forming foraminiferan *Bathysiphon filiformis*, with seastars and shrimps. Community IV at the two northern canyon rim sites was the most distinct from all others, with high abundance and diversity of sponges and associated fauna on mixed hard substrata.

These analyses show that while seafloor habitats and fauna on the floor of Kaikoura Canyon itself and on the northern floor of Conway Trough (Community I) are currently well-represented in the Hikurangi Marine Reserve, communities characteristic of neighbouring habitats on the canyon walls, around its rim, and on the coastal shelf adjacent to it, are not. Thus, the current boundary of the HMR is effective for conserving the high-density, soft sediment canyon floor community but modification to the boundary would provide more complete representation of the range of community and habitat types identified in the study area. We present five potential modifications to the HMR boundary, each of which would encompass one or more of the community types identified here. Because Conway Trough shares community types with Kaikoura Canyon but appears to be less susceptible to disturbance from major canyon flushing events, it might be of particular interest in relation to the functioning of the local ecosystem, serving as a refuge or reservoir for canyon floor populations that promote recolonisation of the main canyon system following flushing events.

1 Introduction

The Hikurangi Marine Reserve (HMR) was established in 2014, in response to the discovery of extraordinary, highly abundant, seafloor communities on the floor of Kaikoura canyon by De Leo et al. (2010) and the inferred role of the canyon in the wider ecosystem based on observations of elevated diversity and abundance of marine fauna (De Leo et al. 2010; Peters et al. 2022; Schiel et al. 2019). The HMR boundary encompasses the head of Kaikoura Canyon and part of Conway Trough, from the shoreline close to the head of the canyon south of Kaikoura peninsula, to a maximum depth of approximately 1500 m, most of the included seafloor area being the canyon floor (Figure 1).

The canyon is subject to natural disturbance in the form of turbidity flows or canyon flushing events triggered by slope instabilities and seismic activity (Mountjoy et al. 2018), which can have major impacts on the ecosystem of the canyon (Bigham et al. 2023; Mountjoy et al. 2018). In November 2016, the earthquake that struck the Kaikoura region of the South Island triggered a major canyon flushing event that transported an estimated 850 megatonnes of sediment from the canyon and into the deep ocean and had profound effects on the existing seafloor faunal communities (Mountjoy et al. 2018).

Prompted by the opportunity to study recolonisation and recovery processes following the 2016 canyon-flushing event, a series of surveys from 2017 to the present has substantially increased the volume of seafloor imagery available from within the HMR. While data from this image resource have been used in time-series studies of invertebrate community recovery in the canyon axis (Bigham et al. 2023), to date, they have not been applied to improving understanding of the ecological role of the HMR.

The Department of Conservation (DOC), through its National Marine Protection Programme, has a statutory requirement to review Marine Protected Areas (MPAs) and Section 8 of the Kaikōura (Te Tai o Marokura) Marine Management Act 2014 requires the Minister of Conservation to initiate a review of the operation and ecological effectiveness of HMR in 2024.

To help inform this review, DOC contracted NIWA in 2022 to conduct a survey of seafloor habitats and fauna within the HMR boundaries and in surrounding areas, with a focus on seafloor photographic transects to characterise invertebrate megafaunal distributions (organisms larger than approximately 5 cm). At the completion of the survey (Rowden et al. 2022) all material from the survey was archived until funding became available to process the imagery and feed the resulting data into evaluations of the ecological effectiveness of the HMR. In 2023, this funding became available and the present project (NOF-BIO-321) was instigated with the objective to analyse the archived imagery from voyage TAN2203 and thus generate data to inform assessment of the ecological effectiveness of the current HMR extent. This assessment centres on three sets of questions:

1. Does the reserve encompass a representative array of the marine habitats and faunal communities present in the vicinity of the Kaikoura Canyon? Which of these habitats or communities are protected in the marine reserve and which are not, and in what relative proportions? Which habitats/communities (if any) are overly represented in the reserve compared to others that are poorly represented or not at all?

2. Are the current boundaries of the marine reserve optimal? What boundary adjustments should be considered to improve the representativity of the marine

reserve and/or include any significant habitats/communities which are poorly or not protected within the reserve?

3. What are the edge effects of the reserve? How does the reserve influence adjacent seafloor habitats and fauna and vice versa? What effects are occurring around the boundaries of the reserve which might directly or indirectly influence habitats and communities within the reserve?

This report presents data from detailed post-voyage reviews of seafloor photographic transects from TAN2203 and earlier surveys, with analyses aimed at addressing the key questions around ecological effectiveness of the reserve, above, and thus informing the review of the HMR.

2 Methods

2.1 Study area and seafloor imagery

The study area centres on the Hikurangi Marine Reserve (HMR), encompassing areas surrounding it that were sampled during the DOC-funded survey, voyage TAN2203 (Figure 1). This survey was planned to include coverage of three primary seafloor habitat types that were defined *a priori*: canyon floor; canyon wall, and the coastal shelf at the rim of the canyon, spanning depths from approximately 50 to 1500 m and including sites inside and outside the HMR boundary. To aid evaluation of the representativeness of the HMR, emphasis was also given to areas either side of the arm of the HMR that extends into Conway Trough and to inclusion of sites thought to have been relatively unaffected by the 2016 flushing event, particularly in Conway Trough and the Kowhai Sea Valleys. Twenty sites were surveyed successfully during TAN2203, from a total of twenty-four in the initial plan (Rowden et al. 2022), and all of these were included in analyses for the present project.

Video transects from surveys prior to TAN2203 were also selected to augment those from TAN2203 and enable more extensive comparison of seafloor habitats and fauna within the HMR and those in areas surrounding it. The final selection consisted of thirty-one transects (Table 1): 20 transects from voyage TAN2203 (5 inside HMR, 15 outside); four transects from TAN2011 (3 inside, 1 outside); two transects from TAN1708 (both inside), and five transects from TAN0616 (all inside). This selection represents only 27 seafloor sites, however, because it includes two sets of three transects in which the same seafloor sites were sampled on successive surveys. These repeat sites were included in this analysis to contribute to an on-going initiative to study ecosystem recovery processes following the canyon flushing event triggered by the 2016 Kaikoura earthquake (Bigham et al. 2023; Mountjoy et al. 2018). Transects spanned a depth range from 33 to 1435 m, with an average seafloor distance of 1237 m (standard deviation 397 m). Because only one of the station numbers (the sequential number of events through an individual survey) was duplicated across surveys (station 095 occurring in both TAN0616 and TAN2011), transects are labelled in later analyses by station number alone rather than with the full survey prefix. To distinguish the two 095 stations, the 2020 transect was labelled 20_095. Because all transects at sites designated as ‘shelf’ in the original survey actually covered the transition from shelf to upper canyon wall, these transects are labelled here as ‘rim’.

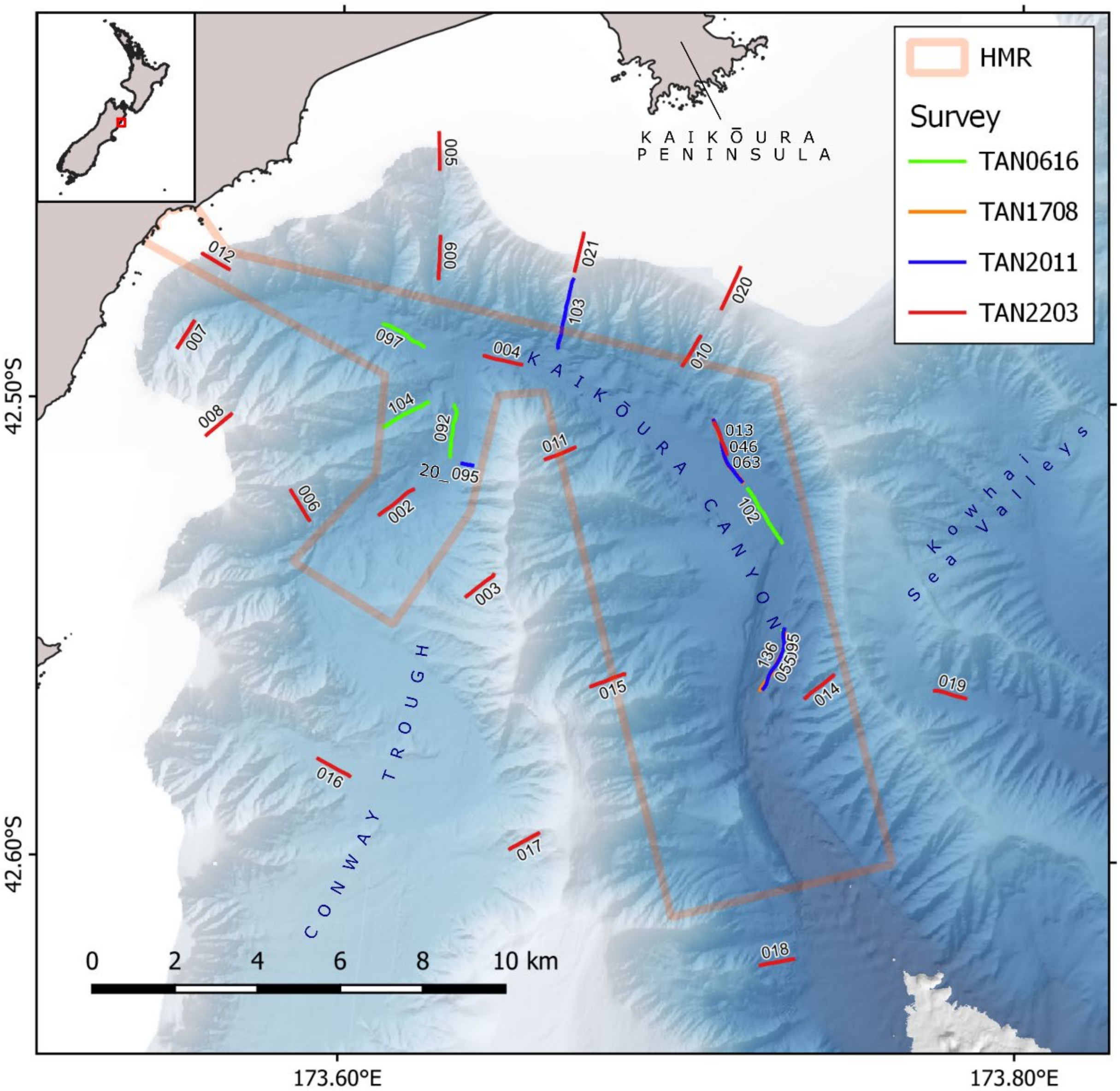


Figure 1: Kaikoura Canyon and the Hikurangi Marine Reserve, showing the locations of seafloor video transects analysed for the current project. Transects are colour-coded by voyage ('TAN' denotes RV Tangaroa, the first two numerals indicate year of survey and the last two numerals give the sequential number of the voyage in that year) and identified by station number within voyages. Inset map shows location within New Zealand and background multibeam echo-sounder bathymetry is from voyage TAN1707.

Table 1: Station data for video transects analysed in this project. Showing: year of survey; voyage code; station number; in or out of the Hikurangi Marine Reserve (HMR); morphological habitat class (Habitat); whether assumed to have been affected by the 2016 turbidity flow (TF); mid-point spatial coordinates; seafloor distance, and seafloor depths at start and end of transect.

Year	Voyage	Station	HMR	Habitat	TF	Lon. mean	Lat. mean	Distance (m)	Depth Start (m)	Depth End (m)
2016	TAN0616	092	in	floor	no	173.6328	-42.5067	1385	-1070	-1099
		095	in	floor	no	173.7307	-42.5531	856	-1376	-1402
		097	in	floor	no	173.6185	-42.4861	1679	-1085	-1028
		102	in	floor	no	173.7257	-42.5258	2109	-1351	-1305
		104	in	floor	no	173.6191	-42.5032	1597	-915	-1054
2017	TAN1708	063	in	floor	yes	173.7129	-42.5104	1886	-1213	-1304
		136	in	floor	yes	173.7282	-42.5573	1667	-1433	-1370
2020	TAN2011	046	in	floor	yes	173.7132	-42.5111	1813	-1212	-1303
		055	in	floor	yes	173.7289	-42.5562	1693	-1374	-1435
		095	in	floor	no	173.637	-42.5142	348	-909	-1088
		103	out	wall	no	173.6654	-42.4821	1761	-258	-1145
2022	TAN2203	002	in	floor	no	173.6164	-42.5224	1274	-1041	-1012
		003	out	wall	no	173.6414	-42.5405	1050	-588	-674
		004	in	floor	yes	173.6467	-42.4914	1243	-1159	-1192
		005	out	rim	no	173.6283	-42.4467	884	-33	-344
		006	out	wall	no	173.5883	-42.5239	949	-546	-845
		007	out	wall	no	173.554	-42.4861	1789	-431	-431
		008	out	rim	no	173.5651	-42.5051	957	-546	-226
		009	out	wall	no	173.6285	-42.4697	1018	-667	-830
		010	out	wall	no	173.7028	-42.4893	918	-695	-1053
		011	out	wall	no	173.6645	-42.5117	1010	-736	-970
		012	in	rim	no	173.5626	-42.4703	948	-50	-324
		013	in	floor	yes	173.7117	-42.5079	886	-1215	-1291
		014	in	wall	no	173.7416	-42.5621	1080	-1088	-1281
		015	out	wall	no	173.6791	-42.561	1142	-922	-716
		016	out	floor	no	173.5989	-42.5808	1125	-710	-698
		017	out	wall	no	173.655	-42.5962	1014	-371	-611
		018	out	wall	no	173.7301	-42.6223	1105	-1232	-1381
		019	out	floor	no	173.7801	-42.5636	1045	-1137	-1216
		020	out	rim	no	173.7144	-42.4754	1168	-105	-232
		021	out	rim	no	173.6694	-42.4684	955	-81	-155

All seafloor photographic transects were run using NIWA's Deep Towed Imaging System (DTIS, Bowden and Jones 2016; Hill 2009). DTIS records continuous colour video imagery and simultaneously takes high resolution downward-facing still images at 10-second intervals, with paired parallel lasers aligned with each camera to enable scaling of images. DTIS is towed at target speed of

0.25 ms^{-1} and target height above seafloor (altitude) of 2.5 m, usually along transects of 1 hour duration. Realised transect distance varies with current and sea-state but is generally in the range of 0.75 to 1.0 km.

The technical parameters of DTIS have been upgraded at times during its working life, with improvements to imaging systems and associated navigational systems. The main changes after 2006 (TAN0616) have been upgrades to the video and still image cameras and their housings, and improvements in the accuracy and consistency of vessel positioning and tracking systems. From 2006 to 2016, DTIS was configured with a video camera recording in HD1080i format and stills camera with 8-megapixel resolution, with both cameras in pressure housings with flat glass optical ports and oriented directly downwards towards the seafloor. In this configuration, the image frame width at target height above seafloor (altitude) was approximately 2 m for both cameras. In 2016, video format was upgraded to HD1080p (i.e., progressive scan rather than interlaced scan) and still image resolution was increased to 24-megapixels. The video camera orientation was also changed to approximately 45° forwards from vertical and housings for both cameras were changed to use dome ports, which increased the frame width to approximately 3 m at target altitude. RV *Tangaroa* was also upgraded with Dynamic Positioning and an upgraded ultra-short baseline (USBL) acoustic tracking system at this time, which enabled more accurate and consistent control of transect speed and direction, and improved the accuracy of recorded DTIS seafloor position data.

During DTIS deployments, a full record of navigational data is recorded, including the seafloor position and altitude of the DTIS vehicle throughout the transect and the ship's surface position, speed, and course. These data enable calculation of the seafloor distance covered during the video transect and the area of seafloor covered by the imagery, which in turn allows calculation of standardised population density estimates for benthic fauna.

2.2 Data extraction from video

Extraction of quantitative data from seafloor video transects for this project followed standard procedures developed by NIWA over more than 15 years of deep-water biodiversity surveys with the DTIS system. All data extraction was undertaken by two experienced NIWA analysts, working in close communication with each other and with taxonomists to ensure consistency of methods and identifications.

First, all of the high resolution still images from survey TAN2203 were reviewed to develop a reference set of taxon identification images – an image library – to be used as a reference when reviewing the video transects. Taxon names were assigned in consultation with relevant taxonomists and the NIWA Invertebrate Collection to confirm taxon identities. Because the taxonomic detail of individual organisms discernible in seafloor imagery varies depending on a range of factors, including orientation of the organism in relation to the camera, concealment behind substrata or other organisms, distance from the camera, and suspended sediments, the taxonomic assignments necessarily range from species-level, through coarser taxonomic levels (Family, Order, Class, Phylum), to operational descriptors (e.g., 'Worm (indeterminate)' or 'Bony fish') and thus include some overlap of labels. For instance, individual seastars within the same transect might be resolved to family or genus level where viewing conditions are favourable but as 'Asteroid' elsewhere. All levels are retained here, rather than aggregating to coarser taxonomic levels, to present the full depth of available information. In cases where additional taxa not in the initial image library compilation were encountered during review of the video imagery, frame-grabs were captured, shared with relevant taxonomists for determination, and the new taxon added to the library. All taxa recorded were placed in the context of standard taxonomic hierarchies by reference to the World Register of Marine Species (WoRMS 2019) .

The focus of the analyses was on benthic invertebrate fauna but all fish were also recorded, with identifications made by reference to an image identification library prepared at the same time as the one for invertebrates and using the same protocols. The data from observations of fishes are less detailed taxonomically than those for invertebrates because identifications are often compromised by angle of view (e.g., dorsal rather than lateral) and speed of movement, resulting in high proportions of coarse-level identifications (e.g., to the extreme level of 'bony fish'). Fish observations can also be less reliable for quantitative analyses because of the effects of potential avoidance or attraction behaviours that cannot be determined from the imagery alone. For these reasons, the fish observation data for the video analysis are presented here in only summary form as a table of taxon determinations, overall numbers, and number of sites at which present (Table A-1).

The full length of each transect was reviewed using Ocean Floor Observation Protocol software (OFOP, www.emma-technologies.com), in which observations of benthic fauna (invertebrates and fish) and substrate type are recorded by 'clicking' on labels in a set of lists compiled from the identification library. Each individual organism observed was recorded (although where faunal densities were higher than can be discriminated practically from video the recorded, numbers are indicative densities only) together with its spatial coordinates, depth, elapsed time along the transect, and UTC time of occurrence. Substrate type was recorded at frequent intervals and at each habitat transition throughout each transect, using categories based on the Wentworth scale (bedrock, boulders, pebbles, gravel, sand, and muddy sediment), along with *lebensspuren* (the visible life traces of fauna such as burrow holes, faecal trails, and feeding marks; here referred to collectively as 'bioturbation marks') and anthropogenic debris or disturbances, if encountered.

Output from each video review consisted of a data table in which all observations were logged in a single column, regardless of which category of observation they represent (i.e., invertebrate fauna, fish fauna, substrate type, bioturbation marks, and anthropogenic marks and debris). The observations were then separated out into fields for each category. Observations of fauna, bioturbation marks, and anthropogenic items were retained as discrete point records but substrate type is continuous throughout the transect (i.e., there is always a substrate in the image frame), so each observation was propagated forward in time at 1-second intervals until the next substrate type observation record occurred.

On completion of the stages above, audits of the observation data were run to check for and correct duplicated taxon names, mis-labelled taxa, non-benthic taxa, improbable taxa (this can occur when a neighbouring label in the OFOP lists is clicked rather than the intended one), and discrepancies in identifications among analysts. To enable standardisation of faunal counts per transect to unit area (individuals or colonies per 1,000 m^2 of imaged seafloor area) the total seafloor imaged area of each transect was calculated. Transect length was measured in a geographic information system (GIS, QGIS 3.16.11) by importing all USBL navigation points, converting these to line features for each transect, and calculating length using the *$length* command in QGIS. Video frame width values for each voyage were standard estimates used for previous video analysis projects (refs: DOC22306, ZBD2016-11). Widths were calculated as the average widths of 50 frames selected at random across transects (measured in ImageJ [imagej.nih.gov] using the DTIS laser points for scale), and total imaged area was calculated as the product of transect length and width.

2.3 Data extraction from still images

The primary focus of this project is the DTIS video imagery, because of the greater seafloor area that can be characterised using continuous imagery. However, there was also an opportunity to use analyses of still images from two transects from voyage TAN2203 (TAN2203_002 and TAN2203_004) to improve understanding of the timescales over which benthic communities in the canyon floor recover from canyon flushing events, building on the work of Bigham et al. (2023) and using the same methods. For this work, images were selected from portions of the two transects that overlapped with DTIS transects from four earlier surveys and had imaged seafloor areas in the range 0.5 and 2.5 m^2. The online image analysis tool BIIGLE 2.0 (Langenkämper et al. 2017) was then used to annotate all visible megafauna (invertebrates and fish > 2 cm; 41 labels), and all bioturbation marks ('lebensspuren') made by both epi- and infauna (18 labels). To estimate population densities of the benthic foraminiferan *Bathysiphon filiformis*, which occurs in high abundance in the canyon floor, numbers were estimated by counting individuals in randomly selected sub-areas within every fourth image along the transect (see Bigham et al. 2023 for details).

2.4 Data analysis

2.4.1 Video

The video observation data were summarised in two ways; at the level of the entire transect (*transect-level*) and at the level of 10 m along-transect segments within transects (*segment-level*). For transect-level data, counts were first summed then standardised to numbers per 1000 m^2 of seafloor imaged area. Transect-level data were used in community-level comparisons among transects. For segment-level data, each transect line feature was subdivided in GIS into 10 m segments (algorithm *grass7:v.split* in QGIS) and segment identities were then appended to each video observation using a spatial join (algorithm *native:joinattributesbylocation*), allowing observations to be summed by segment. Segment-level data were used for mapping distributions of fauna at finer (within-transect) spatial scales.

A suite of univariate metrics of community composition was generated from the invertebrate fauna density data at transect level (using PRIMER v7, www.primer-e.com, refs), of which four were chosen as summary metrics: the total number of individuals per transect (N); the total number of taxa per transect (S); Pielou's evenness (J'); and Simpson's diversity (1-Lambda'). These metrics were used to provide ecological context for patterns of similarity derived in subsequent multivariate analyses.

Multivariate analyses of community composition (also in PRIMER-E) were based on square-root transformed standardised abundance data (i.e., the transect-level data set as individuals 1000 m^{-2}) and the Bray-Curtis similarity metric, with each transect coded by three factors: *survey* (TAN0616, TAN1708, TAN2011, TAN2203); *HMR status* (in, out); *seafloor morphological habitat* (floor, wall, or rim). Four transects that intersected the HMR boundary at their deepest points were coded for *HMR status* as 'out'. For the two sites that were each sampled at three times, analyses were run initially with all transects included, to assess community change with time since the 2016 earthquake, and then with immediate post-earthquake transects removed to better represent current and pre-disturbance community structure. The relatively mild square-root data transformation was selected to reduce the influence of highly abundant taxa without masking abundance-related patterns. The analysis sequence then consisted of: 1) generation of a non-metric multidimensional scaling (MDS) ordination to visualise relative similarity of community composition among transects; 2) Cluster analysis with similarity profile test (SIMPROF, P at 0.05 significance) to identify statistically supported groups of transects, referred to as communities, and 3) the similarity percentages routine (SIMPER) to identify taxa contributing most to differences among these communities.

Segment-level data were used in GIS to explore the spatial distributions of individual taxa and higher taxonomic or informal groupings (e.g., Class, Sub-Class, 'Corals'). For each taxon or higher grouping, abundances (as counts per segment) were plotted as expanding symbols centred on the mid-point of each transect segment. Expanding symbols were constrained to five classes (using the Jenks Natural Breaks algorithm in QGIS), with symbol radius proportional to data values and maximum radius the same for all taxa regardless of absolute abundance values.

2.4.2 Still images

Faunal (invertebrates and fish) counts from still images were standardised to numbers per 1 m^2 of seafloor. These data were then added to the existing time-series dataset (10 years before the earthquake, TAN0616; 10 weeks after, TAN1701; 10 months after TAN1708; and 4 years after, TAN2011), generating a new time-step at 5.25 years after the canyon-flushing event triggered by the 2016 Kaikoura Earthquake. Here, we show summary results for subsequent analyses of these data, selected to demonstrate the extent to which benthic communities of the canyon floor within the HMR had recovered 5.25 y after the earthquake. The results centre on an updated version of the nMDS ordination adapted from Figure 2 in Bigham et al. (2023) with supporting statistical tests: PERMANOVA for significance of differences among communities at each time-step, and RELATE test of cyclicity (hypothesised return to pre-disturbance state) for the whole community response since the disturbance.

3 Results

Thirty-one seafloor video transects were analysed for substrata, benthic invertebrates, and fishes. The total seafloor area analysed was approximately 102,000 m^2 (~1 km^2), from which 66,928 individual observations were recorded: 32,230 observations of invertebrate taxa, 18,093 observations of fish taxa, and 15,605 observations of substrate type. Image quality was good throughout most transects but transect TAN2203_008, which crossed the canyon rim, had poor image quality through its first half, resulting in very few observations from the portion of the transect on the coastal rim before entering the canyon.

3.1 Seafloor substrata

Substrata within the HMR (Figure 2) were predominantly fine muddy sediments, with mixed hard substrata present only at the very head of the canyon (station 012) and deeper canyon floor transects (stations 055, 095, and 136). Canyon walls, including the ridge between Kaikoura Canyon and Conway Trough, were more heterogeneous, with areas of bedrock, boulders, and coarse aggregates as well as areas of muddy sediments. Transects 020 and 021, which traversed the northern rim of Kaikoura Canyon, encompassed extensive areas of mixed compacted gravels and sands on the shallow coastal shelf seafloor extending north from the canyon rim.

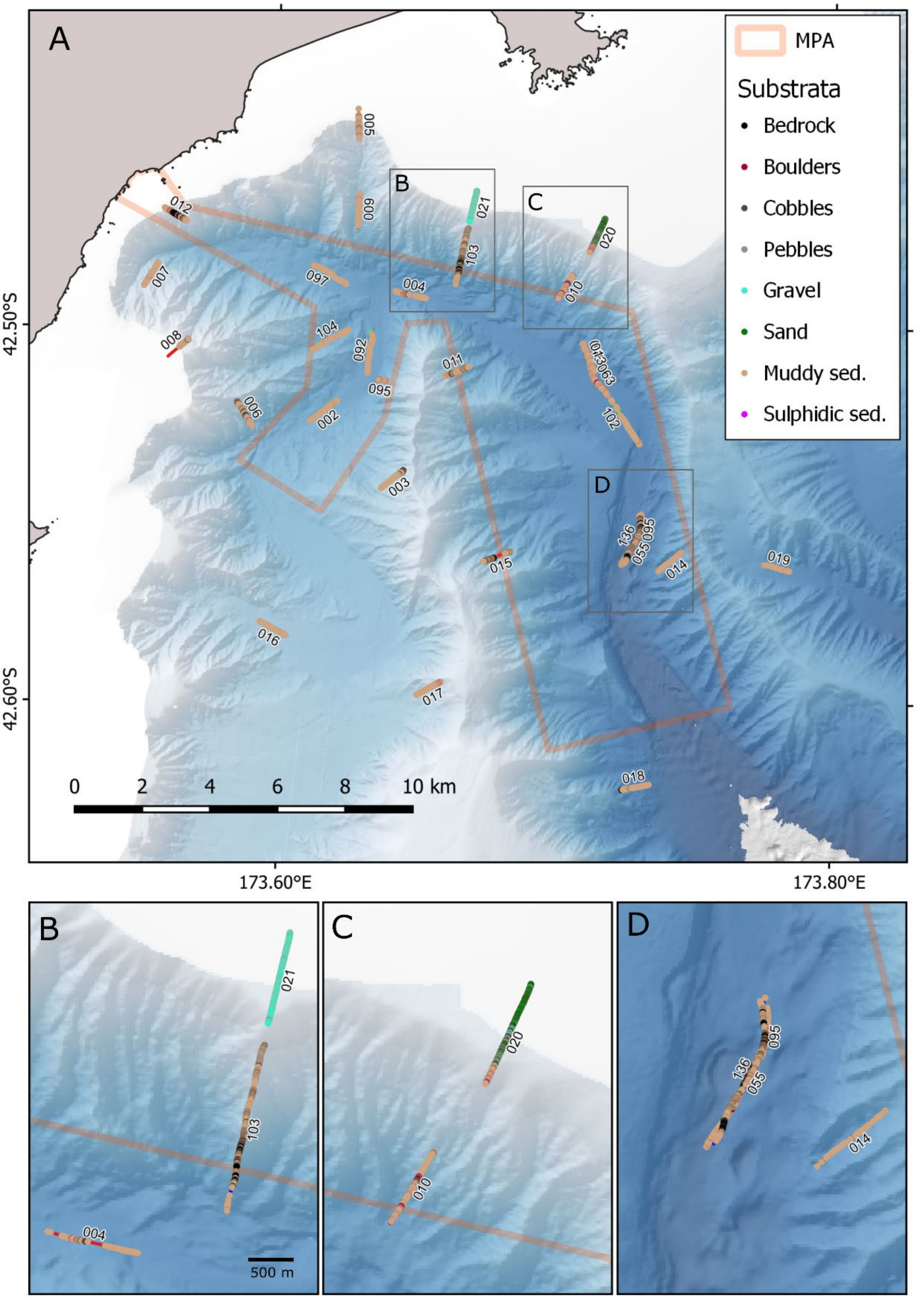


Figure 2: Seafloor substrata from video transect observations. Showing all transects analysed in this project (A), with detail of transects with heterogeneous hard substrata on the northern wall of Kaikoura Canyon (B, C) and on the deep canyon floor within the HMR (D).

3.2 Invertebrate fauna

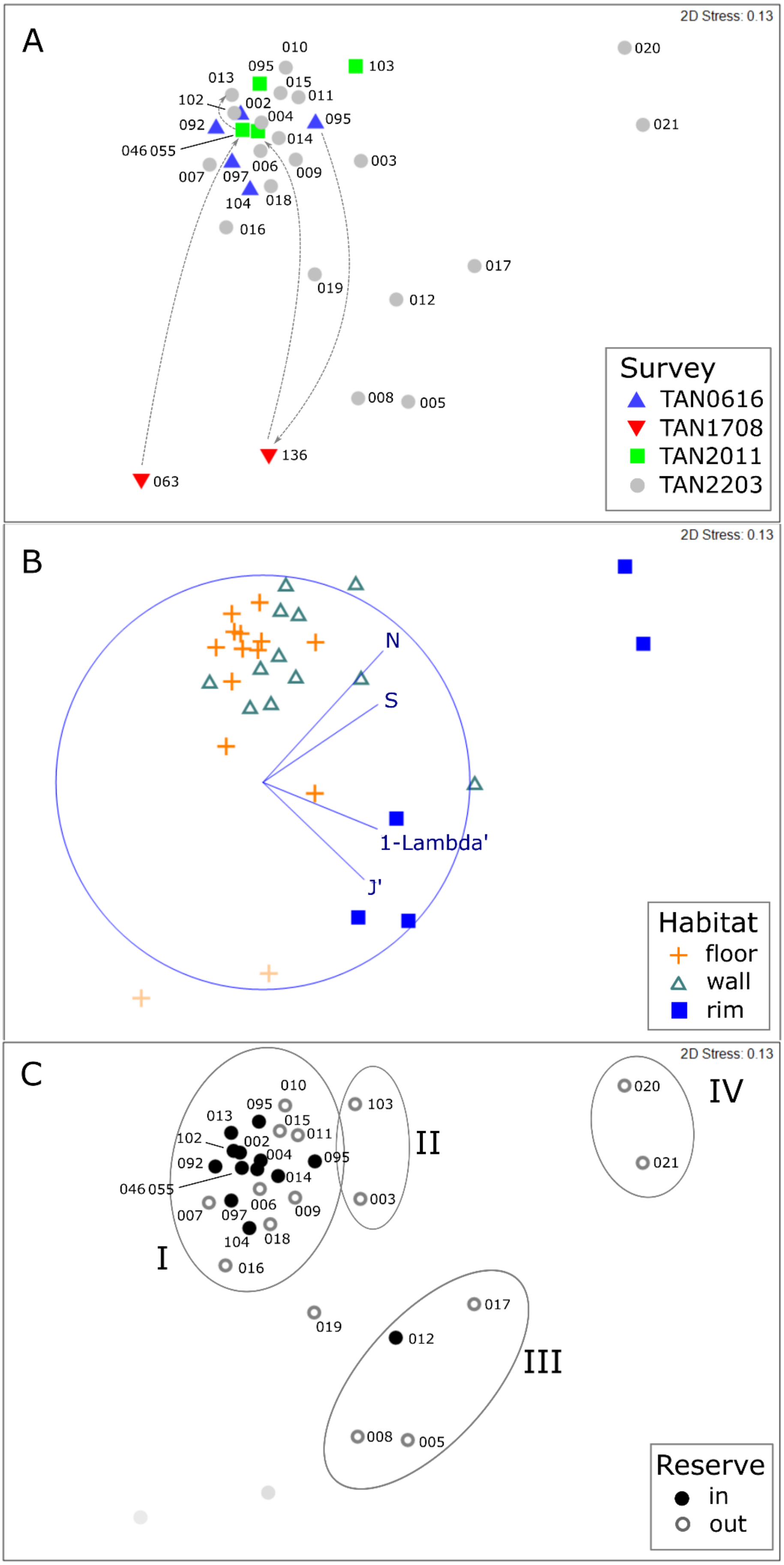
3.2.1 Community analyses

Because analysis of seafloor imagery inevitably yields observations at multiple overlapping levels of taxonomic detail (see Methods) and emphasises larger, more conspicuous taxa, values for taxon richness and abundance, along with metrics derived from them, are not definitive and cannot be compared with other studies or regions but provide an objective and internally consistent picture of distributions across the present study area.

In total, 102 invertebrate taxa were recorded, representing eleven phyla (Table A-1) and with highest numbers of taxa in Echinodermata (28 taxa), Cnidaria (22), Porifera (16), and Arthropoda (16). Most transects clustered strongly together in the nMDS ordination (Figure 3 A), indicating similar community structure. These transects were all from sites in the canyon floor and lower walls and were associated with lower diversity and evenness than transects from sites on the canyon rim (Figure 3 B). All rim sites were associated with higher diversity and evenness than canyon floor or wall sites; two of the rim sites (020 and 021), in particular, having the highest values of faunal abundance and taxon richness and being strongly distinct from all other sites.

The two floor sites that were surveyed at three times (one in 2017, 2020, and 2022, the other in 2006, 2017, and 2020) showed strong dissimilarity from the main cluster of transects immediately after the disturbance (TAN1708) but were strongly similar to it 5 years later (TAN2203). Because communities at these sites had returned to a state similar to their pre-disturbance state at the time of the last survey, the TAN1708 data were not included in subsequent analyses of community similarity.

SIMPROF grouping indicated four statistically supported clusters of transects, representing broad invertebrate community types (Figure 3 C,): Community I - the main group of 20 transects representing 18 canyon floor and wall sites and including all but one of the transects from inside the HMR; Community II - two transects from wall sites outside the HMR - one on the northern wall of Kaikoura Canyon that just intersects the HMR boundary at its deepest part, and one on the west side of the ridge separating Conway Trough from Kaikoura Canyon; Community III - a group of four transects; three from the rim-rim sites at the head of Kaikoura Canyon, one of which is inside the HMR, and one wall site from the west side of the ridge between Conway Trough and Kaikoura Canyon; Community IV - two transects from sites on the northern rim of Kaikoura Canyon. One transect in the Kowhai Sea Valley area (019) and thus the only site outside of both Kaikoura Canyon and Conway Trough, was not grouped but was intermediate between communities I and III.


A
2D Stress: 0.13
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136
063
Survey
TAN0616
TAN1708
TAN2011
TAN2203
B
2D Stress: 0.13
N
S
1-Lambda'
J'
Habitat
floor
wall
rim
C
2D Stress: 0.13
I
II
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IV
Reserve
in
out

Figure 3 (previous page): Megafaunal community similarity among sites: multi-dimensional scaling (MDS) ordination based on square-root transformed abundance data. Each point represents the community at a single site (transect; labelled by station number) and distance between points represents relative Bray-Curtis similarity; increasing distance representing decreasing similarity in community structure. All three panels show the same ordination, highlighting different aspects of the analysis. A: surveys on which the data were collected, with sites identified by station numbers. Two sites were sampled in three surveys and for these sites directional dotted lines indicate community change from before the 2016 Kaikoura earthquake (TAN0616) to approximately 1 year (TAN1708) and 5 years (TAN2203) years after it; the TAN1708 data points were omitted from subsequent analyses because the community at these sites had recovered to be strongly similar to their pre-earthquake state by 2022. B: similarity in relation to seafloor habitat type (canyon floor, wall, or rim), with vectors indicating correlation with univariate metrics of community composition (number of individuals (N), number of taxa (S), Simpson's diversity (1-Lambda'), and Pielou's evenness (J'). C: similarity in relation to the boundaries of the Hikurangi Marine Reserve (in or out), showing groups of sites identified as being statistically similar in faunal composition, i.e., communities (roman numerals, SIMPROF at p=0.05 significance level).

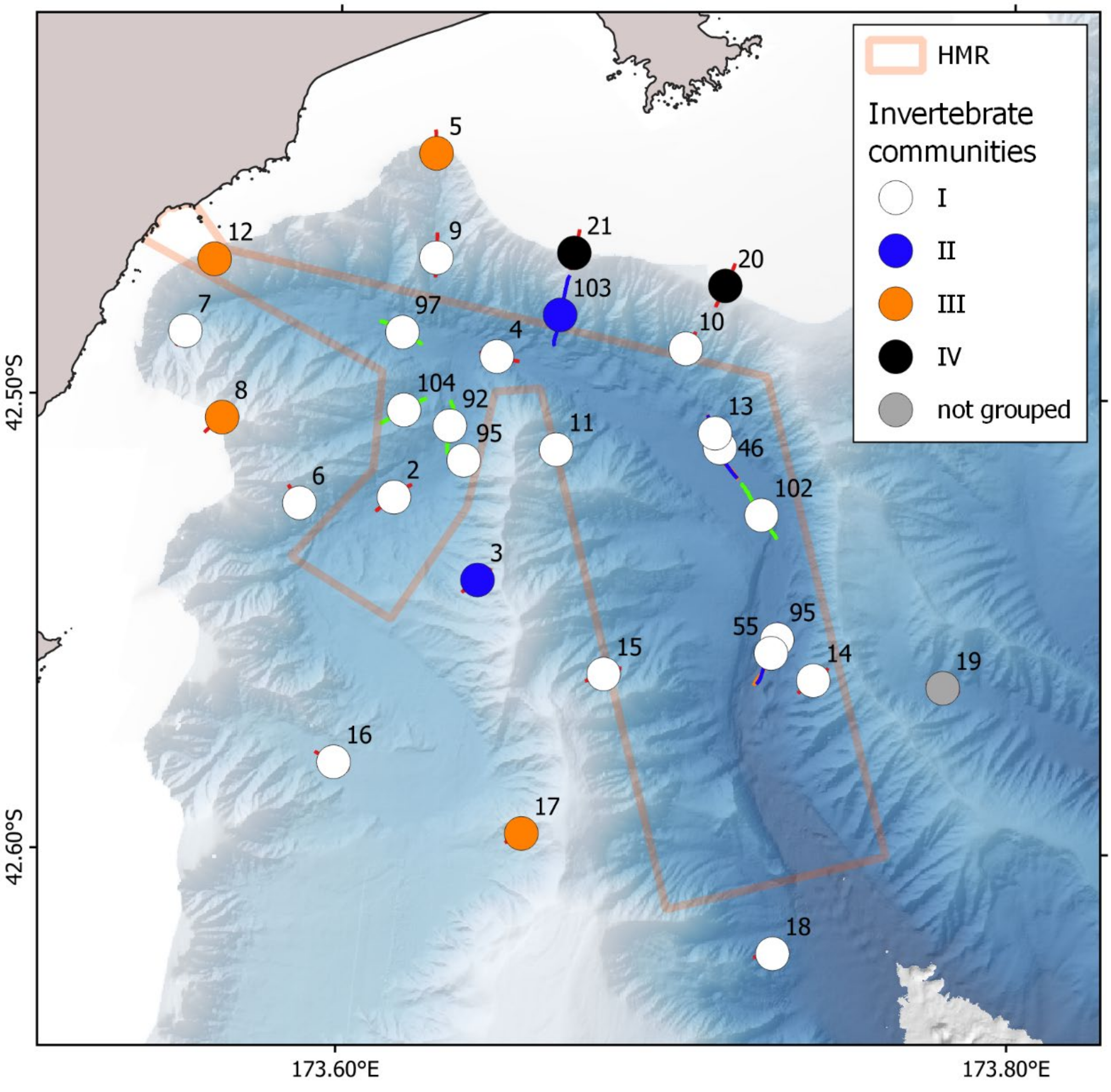

Figure 4: Distribution of seafloor megafaunal communities. Sites are grouped by the relative similarity of their community composition (taxa present and relative abundances) using a multivariate clustering algorithm with SIMPROF (at p=0.05) to determine the number of communities and group membership. One site (019) did not group with any others. For taxon composition of groups, see Table 2.

Table 2: Dissimilarity among communities identified by SIMPROF analysis. See nMDS Figure 2 for transect group memberships.

	Communities (ave. dissimilarity)		
	I	II	III
II	63.96		
III	81.97	76.12	
IV	95.72	85.54	93.10

Table 3: Invertebrate taxa characterising communities identified by SIMPROF analysis of among-transect similarities. SIMPROF groups were calculated using square root transformed abundance data and Bray-Curtis similarity. Characterising taxa were identified using Similarity Percentages Routine analysis (SIMPER). Table shows: number of transects per group (n); average within-group similarity (Group sim.); number of these transects within the Hikurangi Marine Reserve (HMR); taxon names; average within-group abundances (individuals 1000 m2 back-transformed from square-root values used in analyses); average similarity among transects within groups for each taxon; average similarity divided by the standard deviation of similarity for each taxon (a measure of consistency of contribution), and the proportion of total within-group similarity contributed by each taxon. Asterisks indicate taxa in groups protected under the Wildlife Act 1953.

Community	n	Group sim.	HMR	Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%
I	20	50.99	12	*Bathysiphon filiformis*	214.33	35.85	3.87	70.32
				Astropectinidae	41.47	7.46	0.92	14.63
				Crustacean (shrimp)	1.56	1.74	0.96	3.41
				Asteroid	0.69	1.22	0.92	2.40
				Anemones	1.04	1.17	0.80	2.29
				Primnoidae*	1.93	0.46	0.22	0.90
				Gracilechinus multidentatus	0.30	0.30	0.40	0.58
				Mollusc (gastropod)	0.12	0.28	0.38	0.55
II	2	40.91	0	*Bathysiphon filiformis*	135.96	14.99	NA	36.65
				Anemones	13.25	4.03	NA	9.86
				Sponge (Demospongiae)	5.71	2.57	NA	6.29
				Crustacean (pagurid)	7.29	2.19	NA	5.37
				Paramaretia peloria	3.35	2.08	NA	5.07
				Hydroids	2.72	1.59	NA	3.88
				Plexauridae*	1.74	1.47	NA	3.59
				Asteroid	1.39	1.34	NA	3.29
				cup corals (cup)*	3.03	1.34	NA	3.29
				Euryalida	1.06	1.20	NA	2.93
				Gorgonacea*	0.74	1.10	NA	2.68
				Crinoidea (motile)	1.25	1.10	NA	2.68
				Lipkius holthuisi	0.94	1.04	NA	2.54
				Mollusc (gastropod)	1.06	0.85	NA	2.07
				Molluscs (bivalves)	0.53	0.85	NA	2.07

Community	n	Group sim.	HMR	Taxon	Av.Abund	Av.Sim	Sim/SD	Contrib%
				Tube worms	3.20	0.78	NA	1.90
				Echinoid	0.27	0.60	NA	1.46
III	4	38.78	1	Crustacean (shrimp)	22.28	14.58	2.82	37.61
				Anemones	6.81	7.59	2.25	19.57
				Crustacean (Galatheidae/Chirostylidae)	5.71	5.78	3.28	14.90
				Bathysiphon	4.58	4.31	3.10	11.11
				Crustacean (crab)	1.66	2.98	3.20	7.68
				Pasiphaea	2.66	1.96	0.58	5.07
IV	2	35.84	0	*Australostichopus mollis*	57.00	7.58	NA	21.16
				Chalinidae	115.56	6.36	NA	17.73
				Sponge (Demospongiae)	36.84	4.30	NA	12.01
				Ascidians (clonal)	61.62	3.96	NA	11.05
				Tube worms	38.44	3.90	NA	10.88
				Poecilosclerid	42.38	2.41	NA	6.74
				Astrostole	2.37	1.65	NA	4.60
				Mollusc (gastropod)	4.58	1.25	NA	3.48
				Axinellidae	60.22	1.25	NA	3.48
				Myxillidae	1.19	0.69	NA	1.92
				Crustacean (pagurid)	1.19	0.62	NA	1.74
				Phorbas	0.66	0.62	NA	1.74

Community I was distinct from the other groups at dissimilarity levels ranging from 64 % (Community II) to 95.7 % (Community IV) (Table 2). It was the most uniform in composition (within-group similarity 50.99%) and was characterised by high densities of the tube-forming foraminiferan *Bathysiphon filiformis* (contributing 70.32 % of within-group similarity) and common occurrence of asteroids (primarily in the family Astropectinidae) and shrimps, these three taxa contributing more than 90 % of within-group similarity (Table 3). Other taxa associated with this group of transects occurred infrequently and at low densities (anemones, primnoid corals, and the regular urchin *Gracilechinus multidentatus*). Substrata associated with this community were predominantly fine muddy sediments (Figure 5) with infrequent areas of hard substrata draped with sediment.

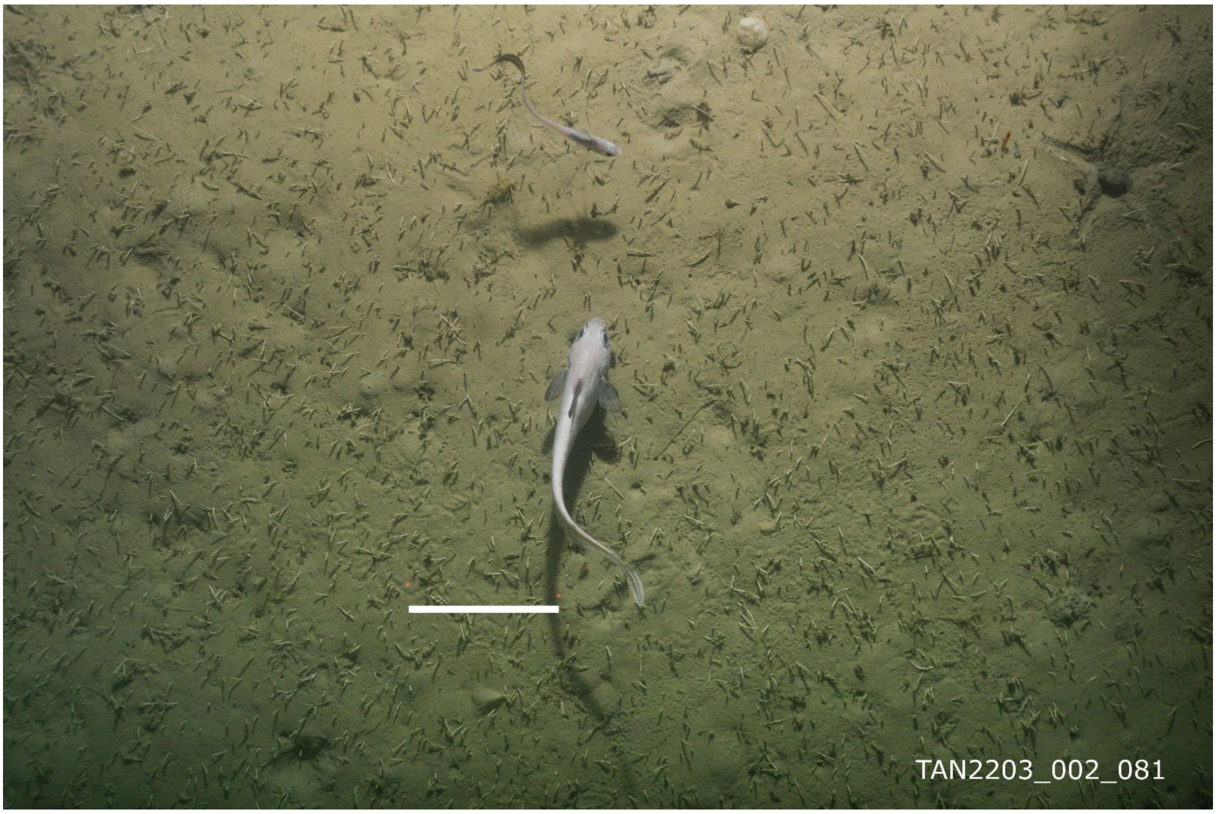

Figure 5: Community I: example image from the floor of Conway Trough within the HMR. Showing substrata of fine muddy sediments with high densities of the foraminiferan *Bathysiphon filiformis* (small tubes throughout image), impressions (lebensspuren) made by seastars (Class Asteroidea, top right), and rattail fishes. White scale bar shows 20 cm. Image from transect TAN2203_002.

Community II was distinct from other groups at dissimilarity levels ranging from 63.96 % (Community I) to 85.54 % (Community IV). This community was also characterised by *B. filiformis* but with a more diverse range of other taxa contributing to its within-group similarity, including anemones (9.89 %), sponges (6.29 %), pagurid crabs (5.37 %), and burrowing urchins (*Paramaretia peloria*, 5.07%). Other sessile and mobile taxa occurring at low densities, primarily in areas where hard substrata were exposed on canyon walls (Figure 6).

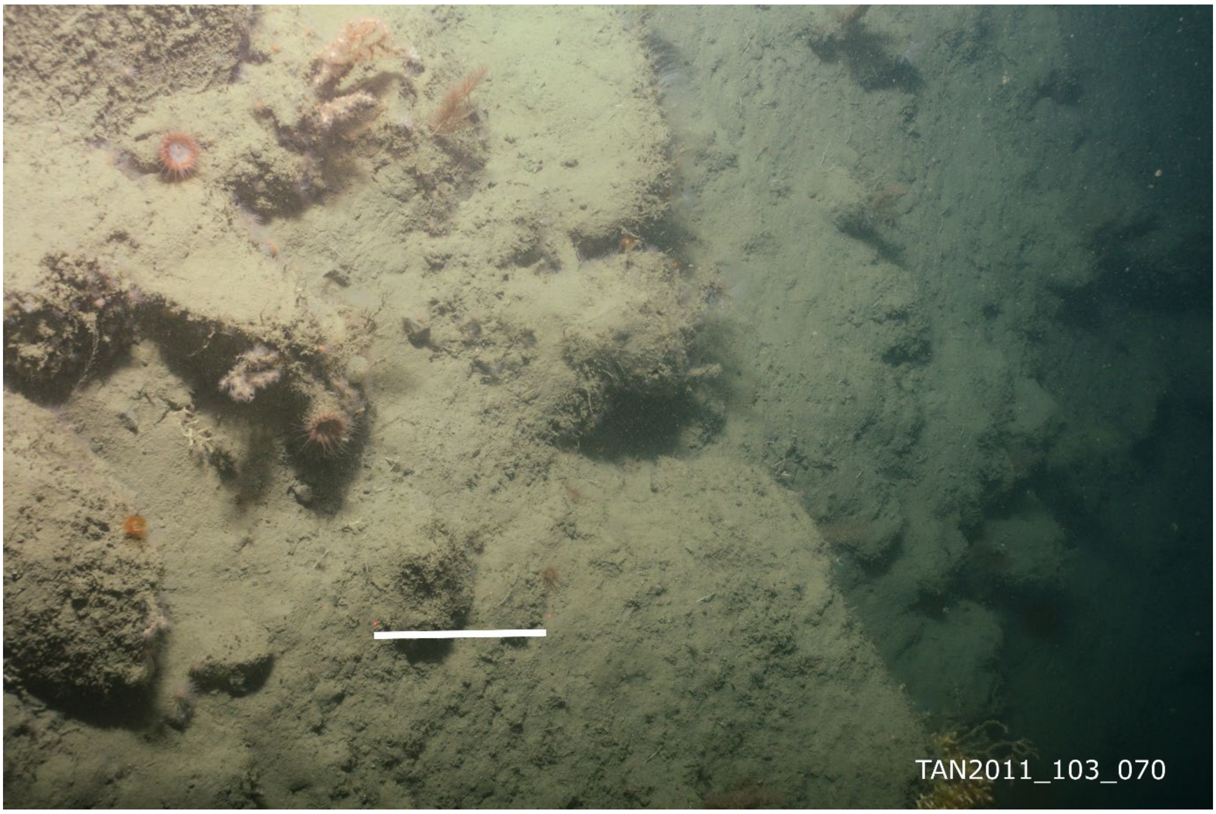

Figure 6: Community II: example image from the northern wall of Kaikoura Canyon, outside the HMR . Showing hard substrata draped with fine sediments and sessile invertebrate fauna including anemones and solitary and colonial corals. White scale bar shows 20 cm. Image from transect TAN2011_103.

Community III was distinct from other groups at dissimilarity levels ranging from 81.97 % (Community I) to 93.10% (Community IV). This community was characterised by sparse occurrence of few taxa but with densities more evenly distributed among them; shrimps, anemones, galatheid crustaceans, *B. filiformis*, and brachyuran crabs together contributing more than 95% to within-group similarity. Of the four sites at which this community type was observed, three were on the transition from shallow coastal rim to canyon wall at the head of Kaikoura Canyon, while the fourth was at the southernmost survey site on the eastern wall of Conway Trough. Substrata were primarily fine soft sediments but with areas of exposed hard substrata on the upper canyon walls. Suspended sediments caused poor visibility at all three of the rim sites (Figure 7).

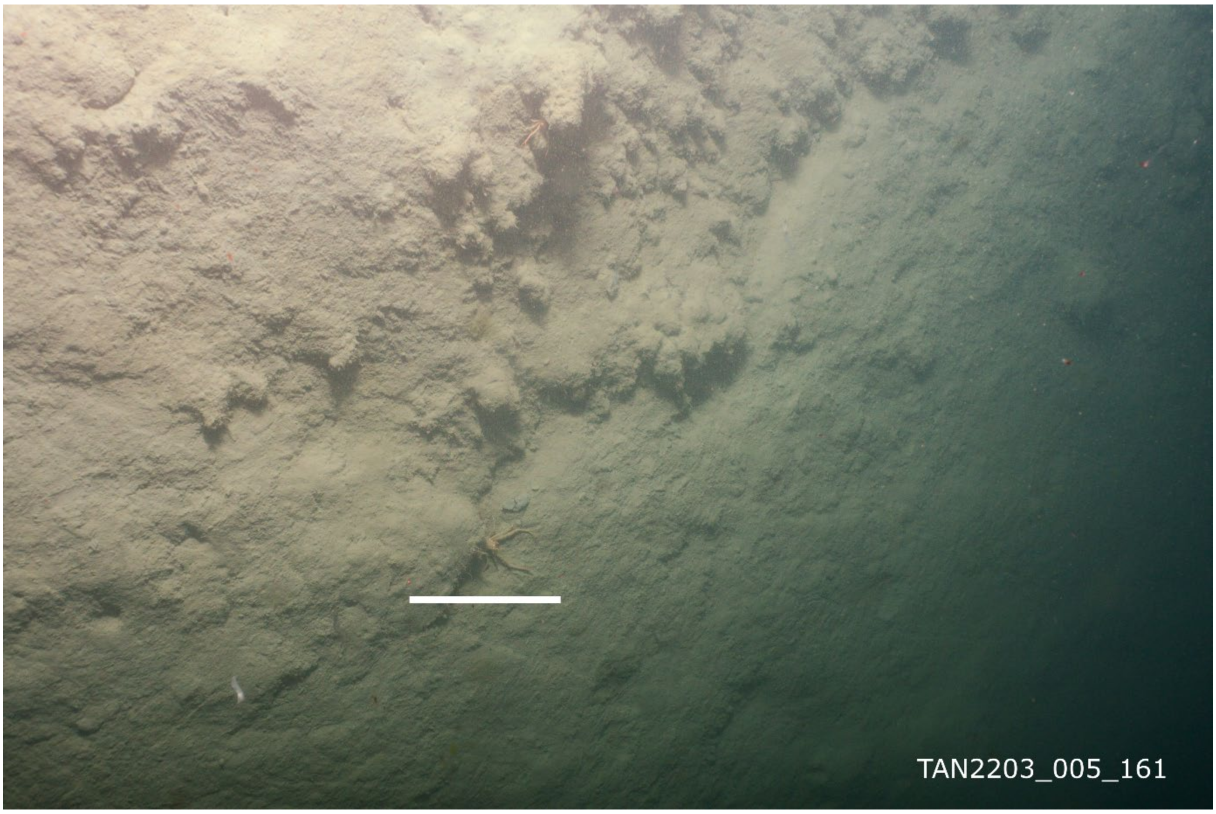

Figure 7: Community III: example image from the head of Kaikoura Canyon on the northern wall, outside the HMR. Showing fine sediments and sparse sessile invertebrate fauna including anemones and squat lobsters. White scale bar shows 20 cm. Image from transect TAN2203_005.

Community IV was strongly distinct from all other groups, at dissimilarity levels ranging from 85.54 % (Community II) to 95.72 % (Community I). This community was the most species-rich and was characterised by sponges (Class Demospongiae, including the taxon labels Chalinidae, Poecilosclerida, Axinellidae, Myxillidae, and *Phorbas* sp., and contributing more than 43 % to within-group similarity), the holothuroid *Autralostichopus mollis* (21.16 %), colonial ascidians (11.05 %), tube worms (10.88 %) and low recorded densities of other taxa including gastropod molluscs and pagurid crabs. Substrata were of compacted sand, gravel, and cobbles with thin overlay of fine sediments (Figure 8).

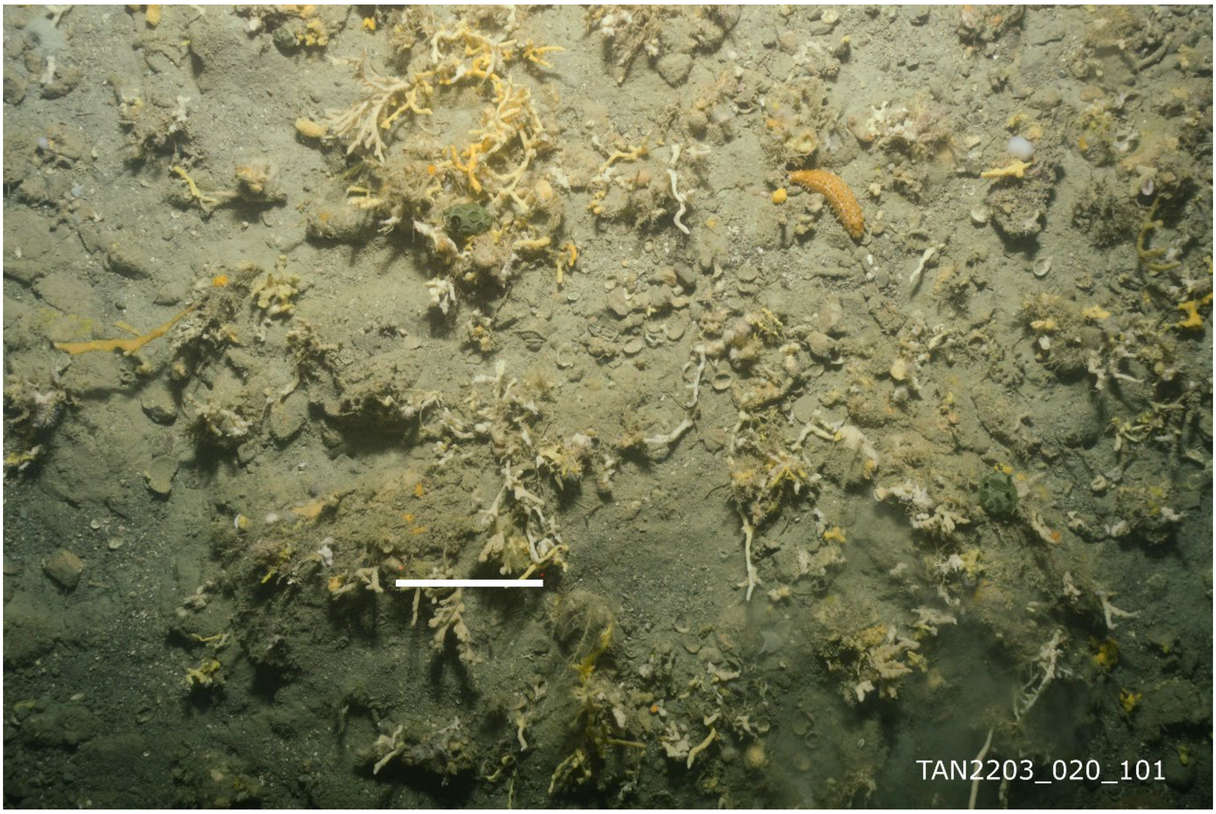

Figure 8: Community IV: example image of sponge-dominated seafloor invertebrate community on the coastal rim at the northern rim of Kaikoura Canyon. Showing substrata of compacted mixed aggregates and fine sediment overlay, sponges (Class Demospongiae), the holothuroid *Australostichopus mollis* (top right sector), colonial ascidians (pale diffuse forms), and other taxa. White scale bar shows 20 cm. Image from transect TAN2203_020.

The one ungrouped transect (TAN2203_019), from the floor of the westernmost of the Kowhai Sea Valleys, east of Kaikoura Canyon and outside the HMR, was intermediate in similarity between communities I and III (Percent similarity statistics cannot be calculated for single samples). The most obvious difference between this transect and those from the floors of Kaikoura Canyon and Conway Trough was the high density of burrows in the soft sediment substrata (Figure 9).

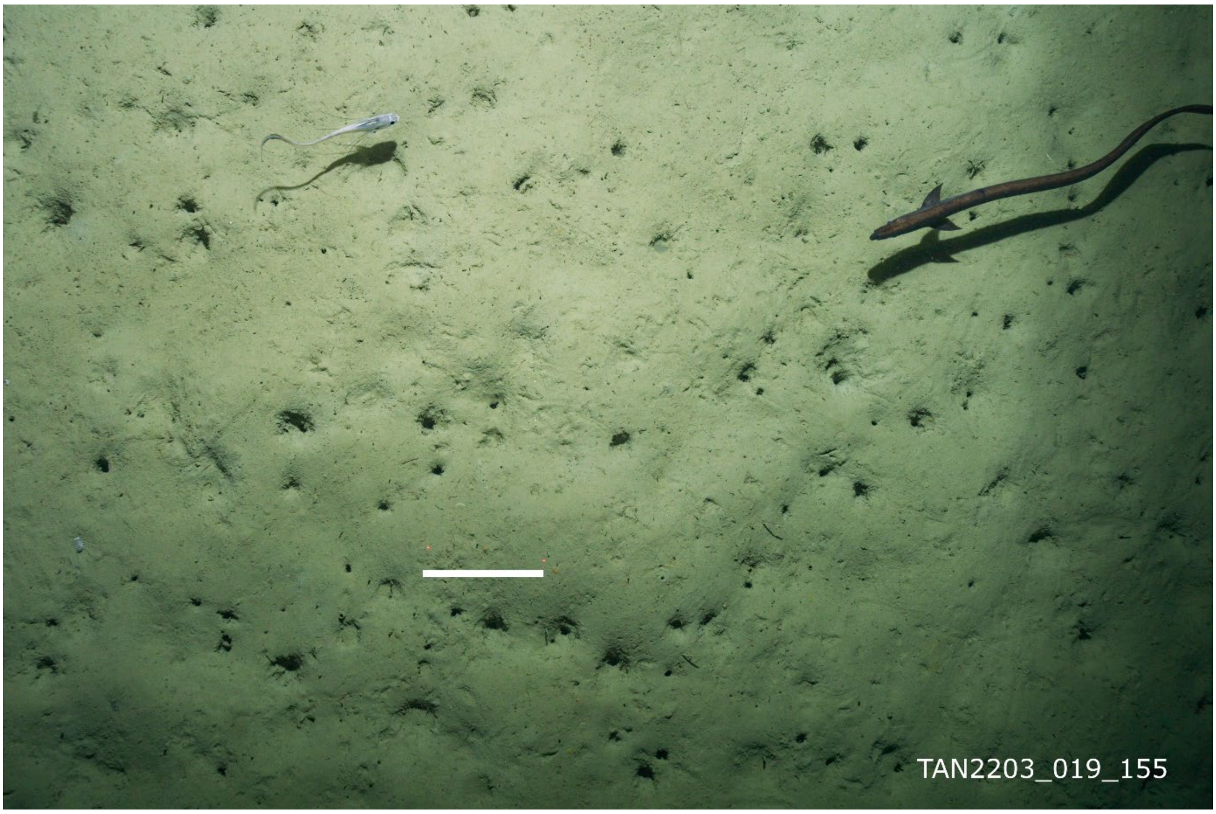

Figure 9: Example image from Kowhai Sea Valley floor, east of Kaikoura Canyon and outside the HMR. Showing substrata of fine muddy sediments with high densities of burrows. Note low density of *B. filiformis* by comparison with Kaikoura Canyon floor (Fig. 3-2). White scale bar shows 20 cm. Image from transect TAN2203_019.

3.2.2 Taxon distributions

Maps showing the relative abundances of selected invertebrate taxa and taxonomic groupings illustrate their distributions in relation to the boundaries of the HMR (Figure 10 to Figure 19). To show general patterns, taxa have been aggregated to higher groupings, primarily Class and Order levels but also the broader grouping of 'Corals', which encompasses all taxa recorded in the sub-classes Hexacorallia and Octocorallia. The distributions in these maps are summarised below:

The small, tube-forming foraminiferan *B. filiformis* was prevalent on soft sediments in all transects except for those at the transition between coastal rim and canyon wall (rim-rim sites), the southernmost Conway Trough wall site, and the one site in the Kowhai Sea Valleys (Figure 10).

Corals (hard and soft corals in the sub-Classes Hexacorallia and Octocorallia) were predominantly Primnoidae (1338 from a total of 1879 coral observations) and occurred on hard substrata at three wall sites in Kaikoura Canyon and one floor site in Conway Trough, with occurrences both inside and outside the HMR (Figure 11).

Sponges, predominantly taxa in the class Demospongiae, occurred at high densities in two transects on the northern rim of Kaikoura Canyon (020 and 021), both outside of the HMR, with only a few occurrences recorded on hard substrata elsewhere (Figure 12).

Holothuroid echinoderms (sea cucumbers, Class Holothuroidea) were associated with the high-density sponge habitats at the two easternmost sites on the northern rim-rim of Kaikoura Canyon, occurring throughout each of the transects at these sites (020 and 021) (Figure 13).

Asteroid echinoderms (sea stars, Class Asteroidea) occurred predominantly at floor and lower wall sites, with highest densities observed at deeper sites in Kaikoura Canyon, within the HMR (Figure 14).

Echinoid echinoderms (sea urchins, Class Echinoidea) occurred in locally high densities at wall sites, particularly along the northern wall of Kaikoura Canyon and at the most southerly site in Conway Trough. These were all soft sediment sites and occurrences were all of the burrowing urchin *Paramaretia peloria* (Figure 15).

Ophiuroid echinoderms (brittle stars, Class Ophiuroidea) were observed in low numbers and at only seven sites, with highest densities at sites on the northern wall of Kaikoura Canyon and on the ridge separating it from Conway Trough (Figure 16). Their distribution was similar to that of Decapod crustaceans.

Crinoid echinoderms (Feather stars, Class Crinoidea) occurred at low densities in only six transects, with highest numbers recorded at two wall sites and the deepest floor site in Kaikoura Canyon (Figure 17).

Decapod crustaceans, including all shrimps, crabs, lobsters, and squat lobsters, occurred at relatively low densities, with most records at sites on the ridge separating Conway Trough from Kaikoura Canyon and one site on the northern wall of Kaikoura Canyon (Figure 18).

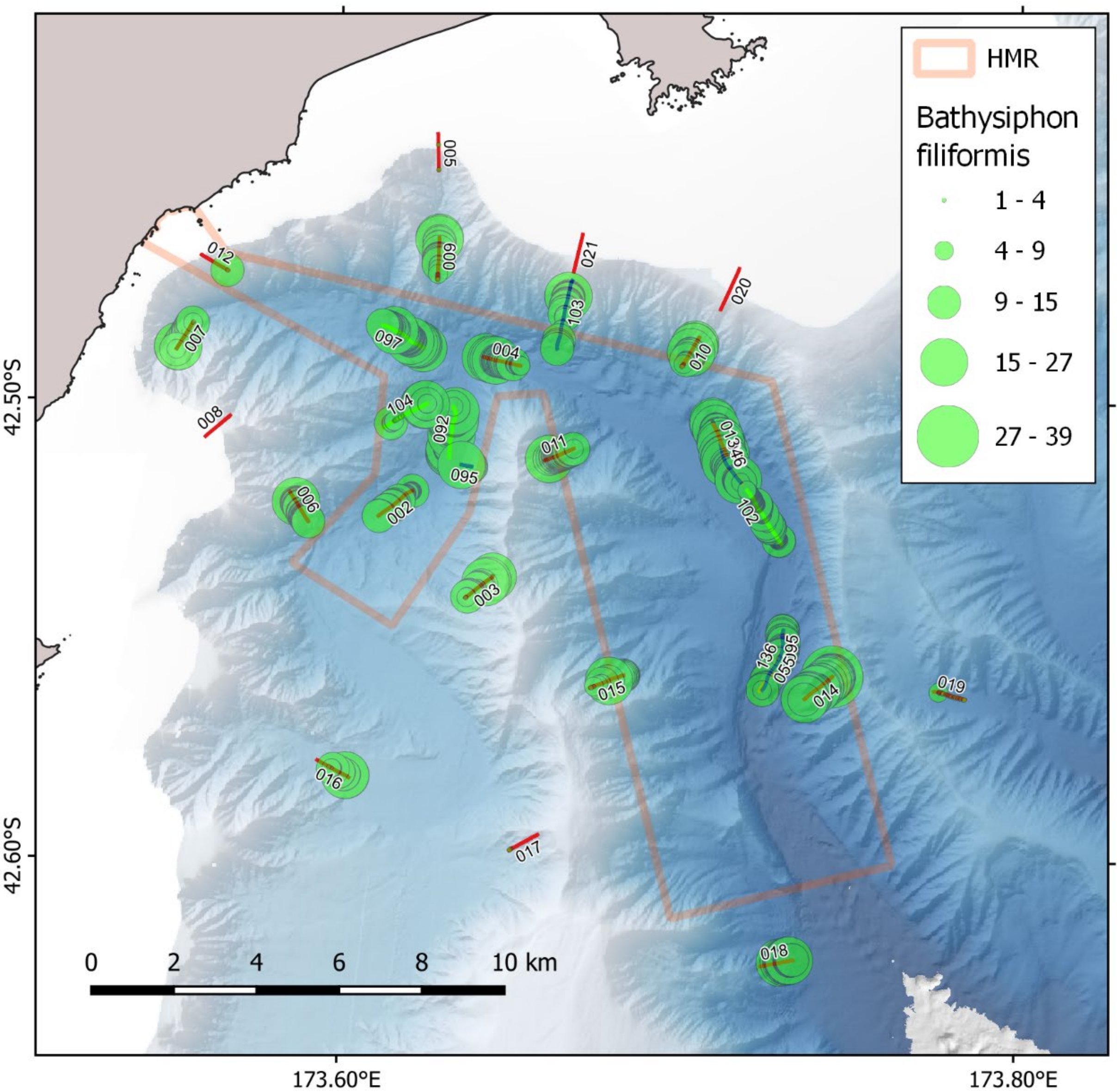

Figure 10: Distribution of the benthic foraminiferan *Bathysiphon filiformis* (Class Monothalamea) in relation to the Hikurangi Marine Reserve boundary. Green expanding symbols represent taxon occurrence and density (as individuals per 10 m segment of seafloor video transects). Symbol radius is proportional to taxon density in five bands, with band ranges determined using Jenks Natural Breaks and maximum radius constrained to 5 mm at full image resolution. Video transects (coloured lines as per Figure 1) are labelled with station number and the Hikurangi Marine Reserve boundary is indicated (HMR).

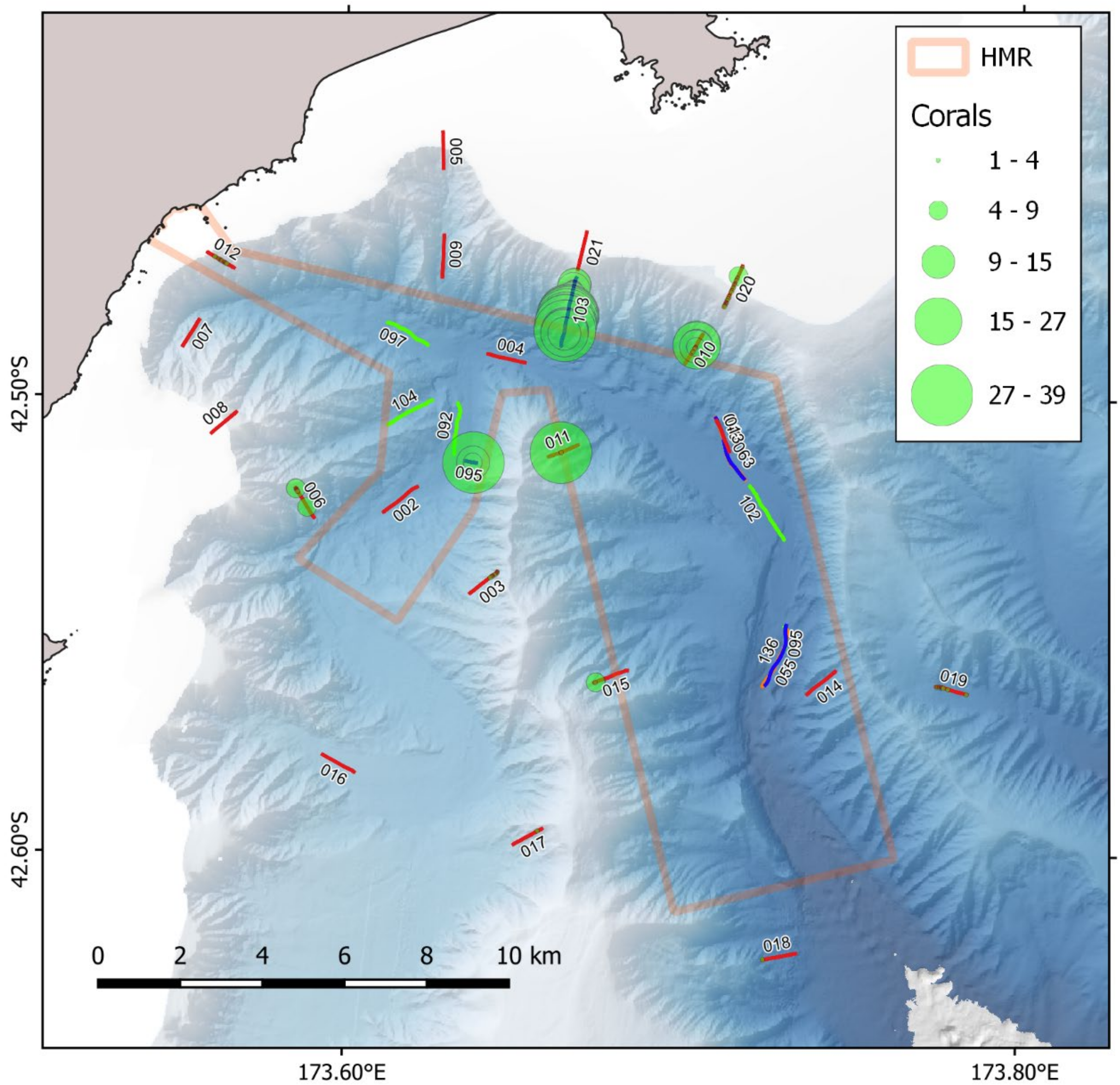

Figure 11: Distribution of hard and soft colonial corals (Class Anthozoa, Orders Scleractinia, Zoantharia, Scleralcyonacea, and Malacalcyonacea, and the superfamily Pennatuloidea) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Scleractinia; Alcyonacea; Gorgonacea; Primnoidae; Plexauridae; *Anthomastus* sp.; Isididae; *Solenosmilia variabilis*; and cup corals. Details as for preceding figure.

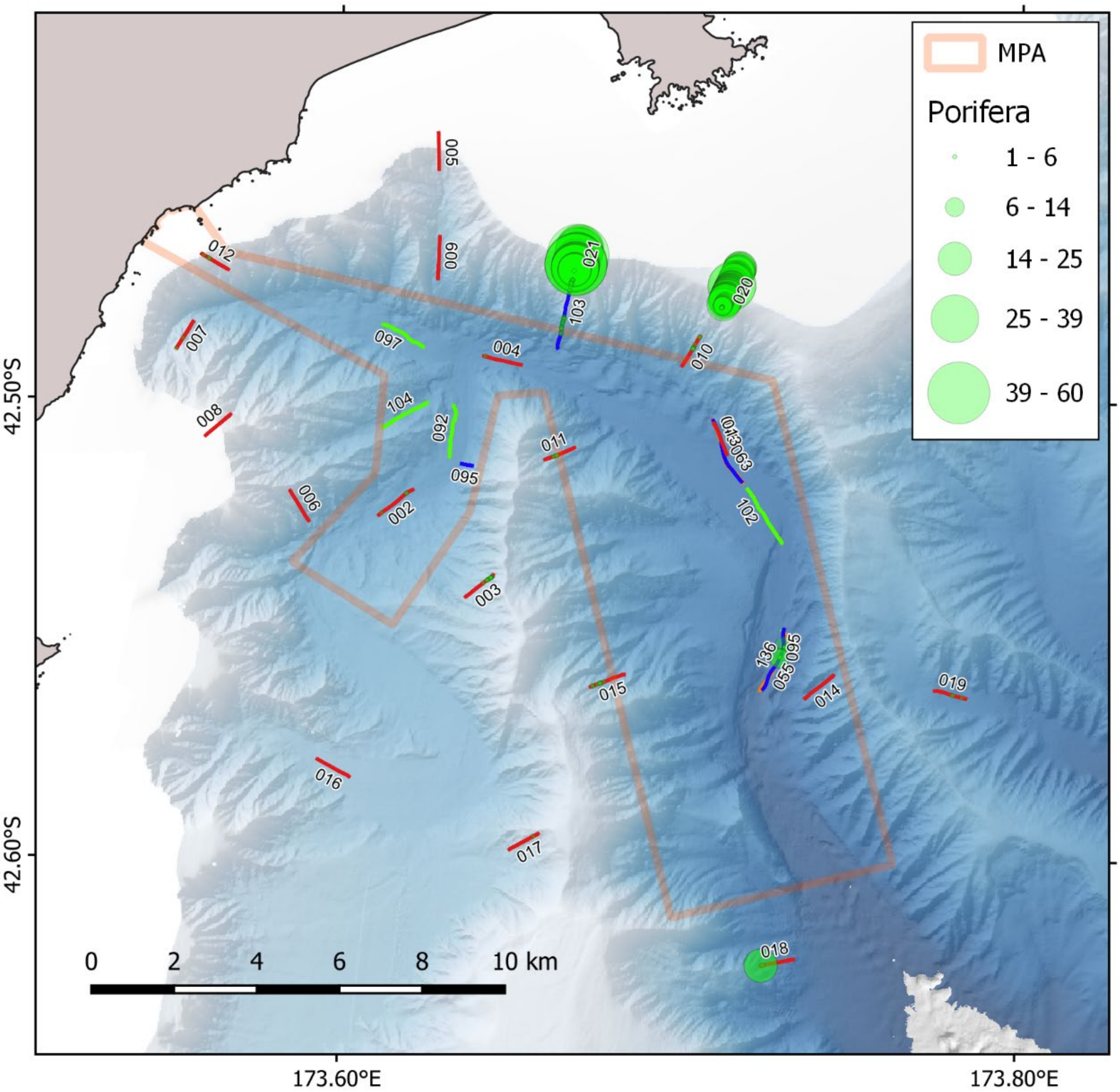

Figure 12: Distribution of Porifera (sponges; Classes Demospongiae and Hexactinellida) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Demospongiae; Hexactinellida; Axinellidae; *Axinella* sp.; *Darwiniella axeata*; Chalinidae; *Haliclona* sp.; *Phorbas* sp.; *Latruculia* sp.; Mycalidae; Myxillidae; Poecilosclerida; *Homaxinella* sp.; *Antarctotetilla leptoderma*; *Thenia novaezealandiae*; and *Poecillastra laminaris*. Details as for preceding figures.

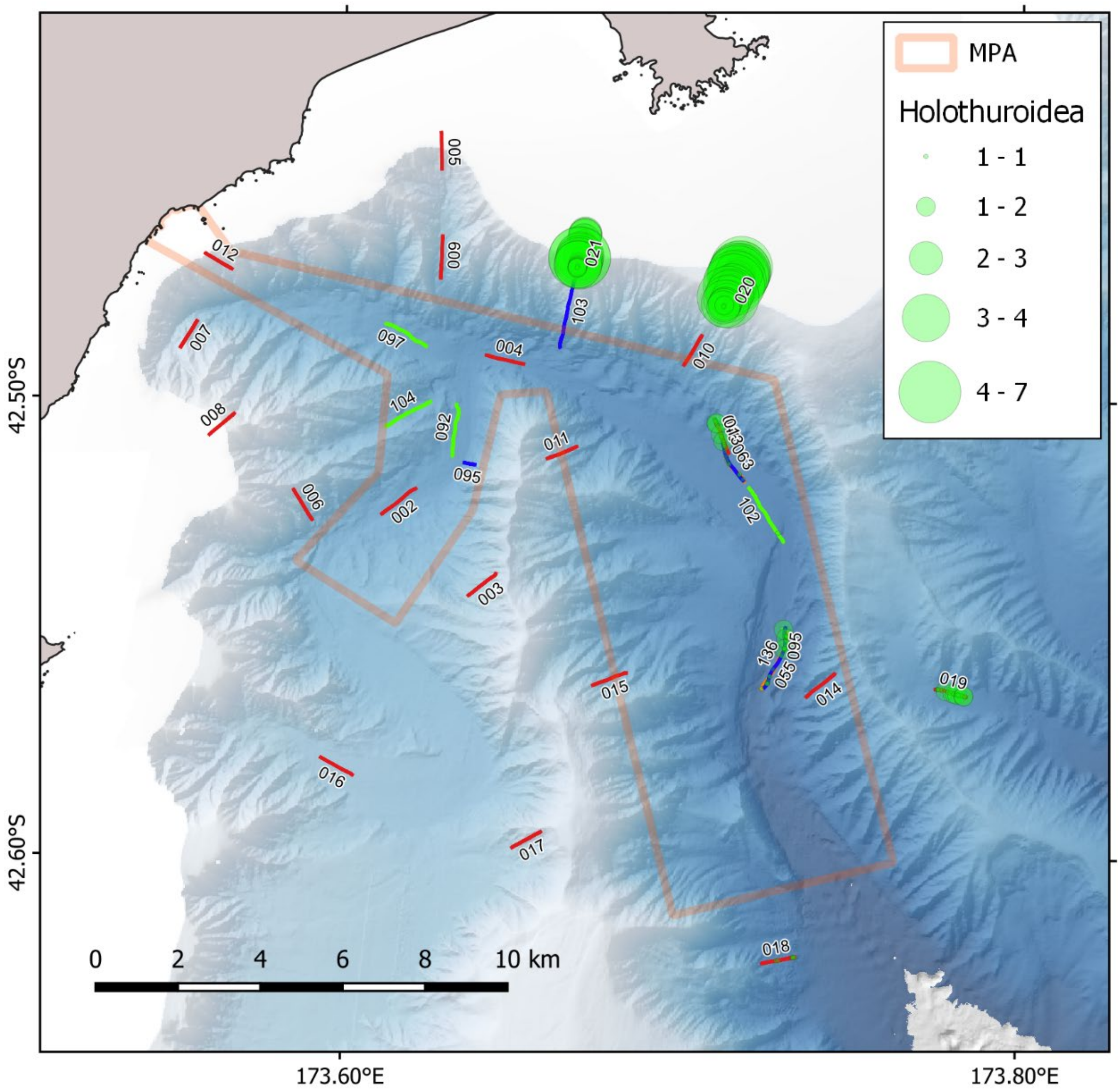

Figure 13: Distribution of holothuroid echinoderms (sea cucumbers; Class Holothuroidea) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Holothuroidea; Elasipodida; *Enypniastes eximia*; Synallactidae; *Australostichopus mollis*, and *Bathyplotes* sp. Details as for preceding figure.

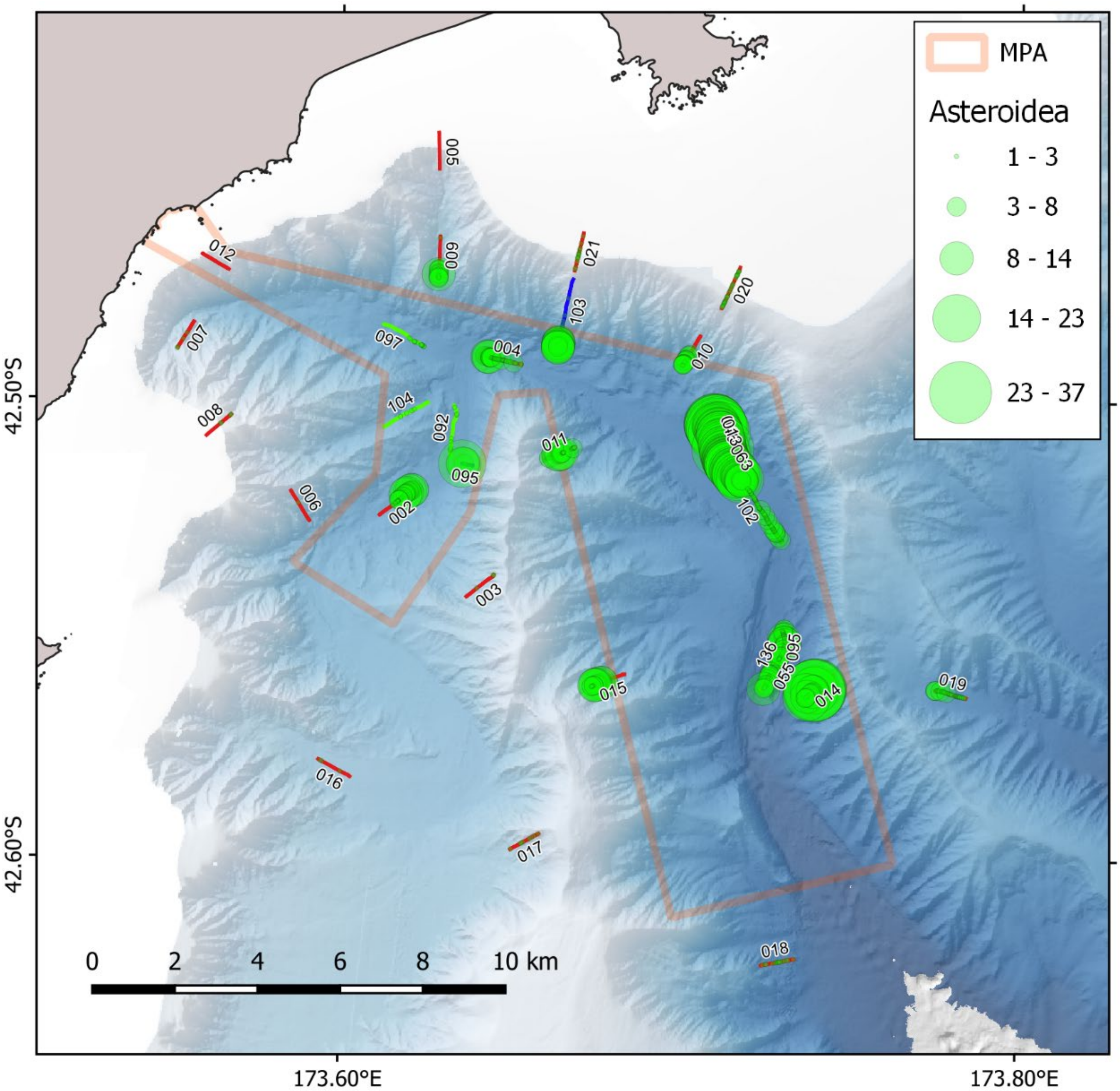

Figure 14: Distribution of asteroid echinoderms (seastars; Class Asteroidea) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Asteroidea; Brisingidae; Forcipulatida; *Astrostole* sp.; Asteriidae; Zoroasteridae; Astropectinidae; Goniasteridae; *Diplodontias* sp., and Odontasteridae. Details as for preceding images.

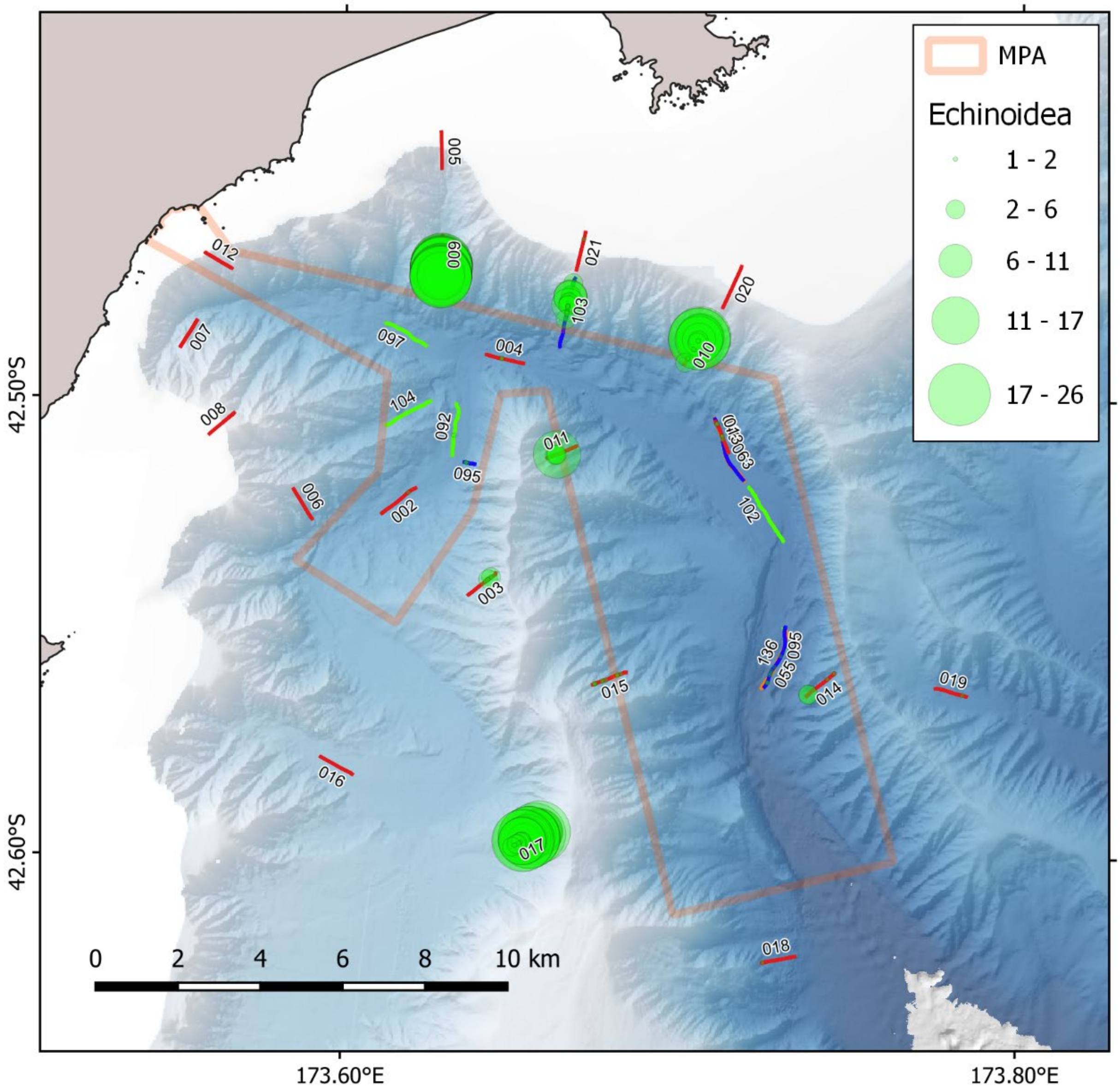

Figure 15: Distribution of echinoid echinoderms (urchins; Class Echinoidea) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Echinoidea; *Gracilechinus multidentatus*; *Pseudechinus flemingi*; *Paramaretia peloria*; Spatangidae; Cidaroida, and *Goniocidaris parasol*. Details as for preceding figure.

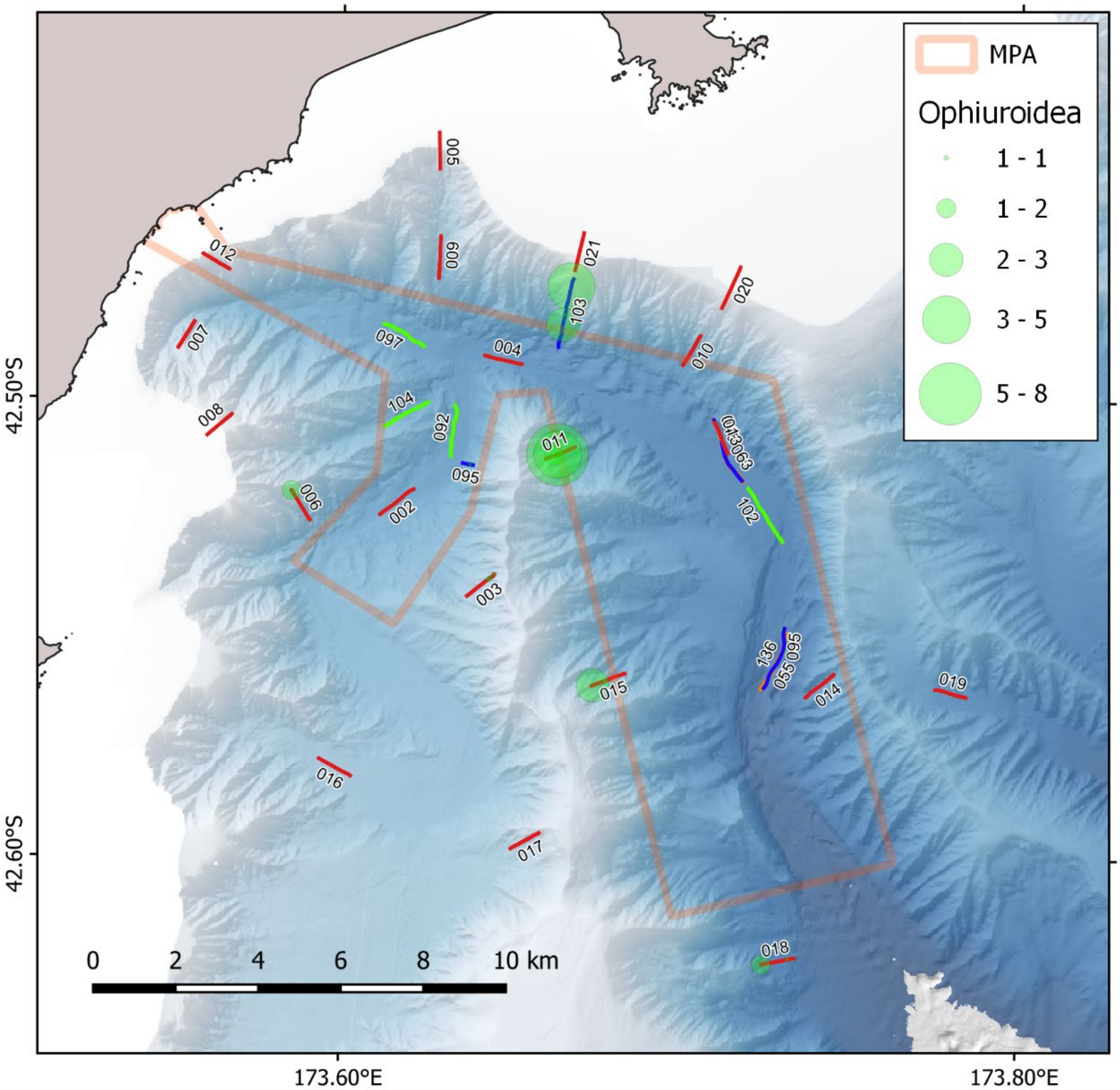

Figure 16: Distribution of ophiuroid echinoderms (brittle stars; Class Ophiuroidea) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Ophiuroidea; Euryalida, and Ophiurida. Details as for preceding figures.

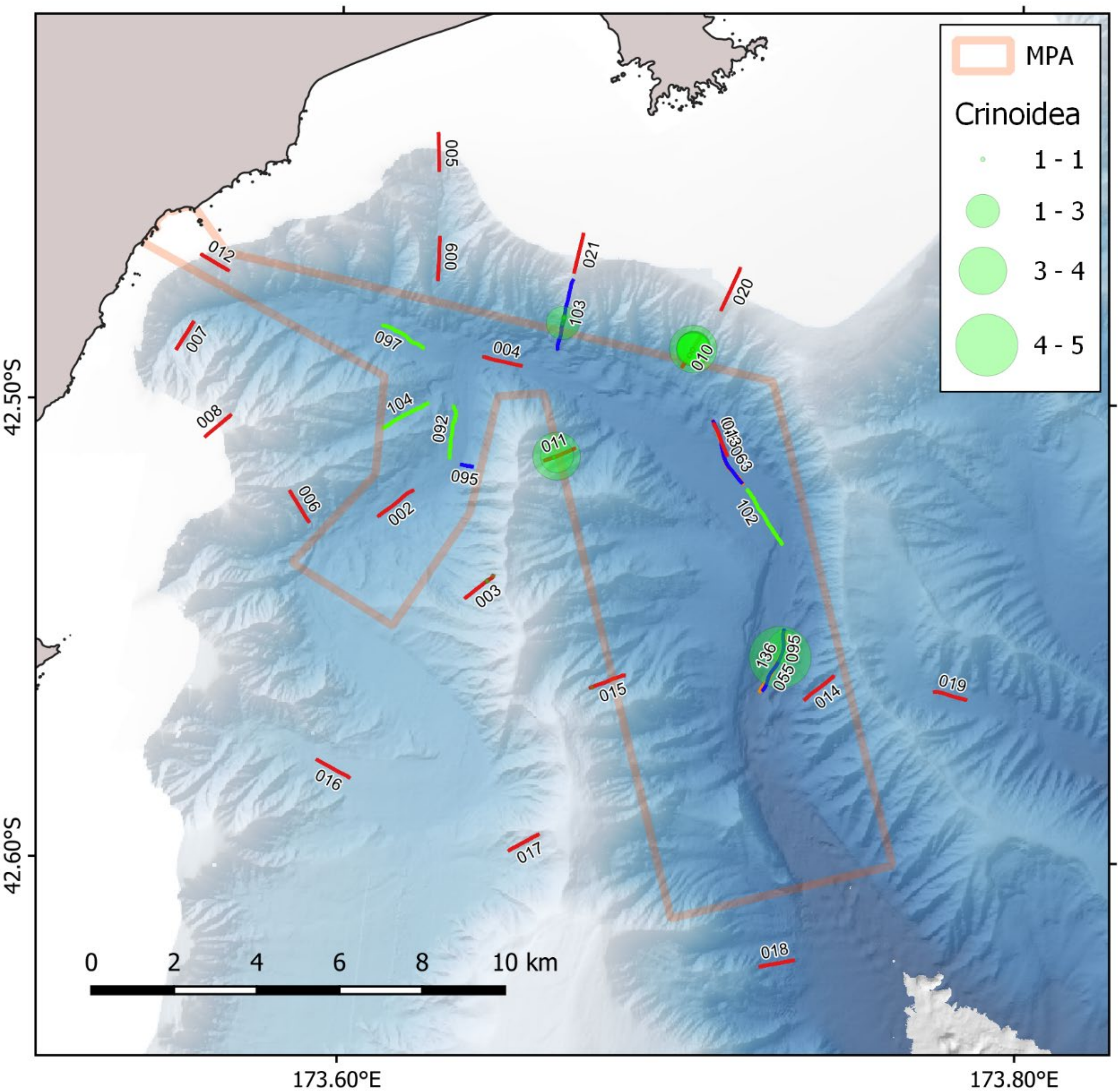

Figure 17: Distribution of crinoid echinoderms (sea lilies and featherstars: Class Crindoidea) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Crindoidea and Comatulida. Details as for preceding images.

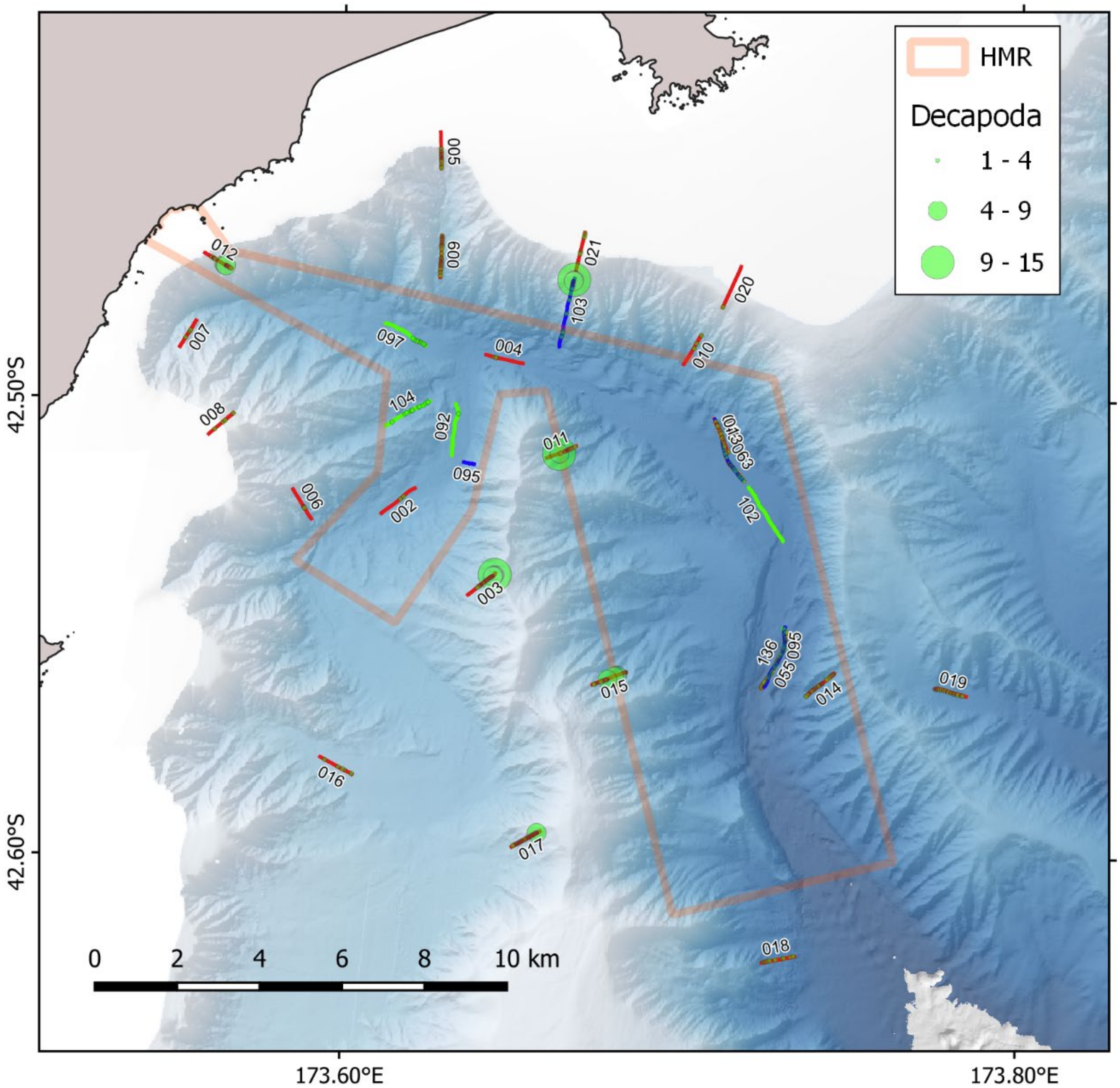

Figure 18: Distribution of decapod crustaceans (Order Decapoda) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Lobster; Brachyura; pagurid crab; Caridea; Galatheoidea; *Munida* sp.; *Metanephrops challengeri*; *Jasus edwardsii*; *Pasiphaea* sp.; Lithodidae; *Lipkius holthuisi*, and *Aristeaomorpha foliacea*. Details as for preceding figure.

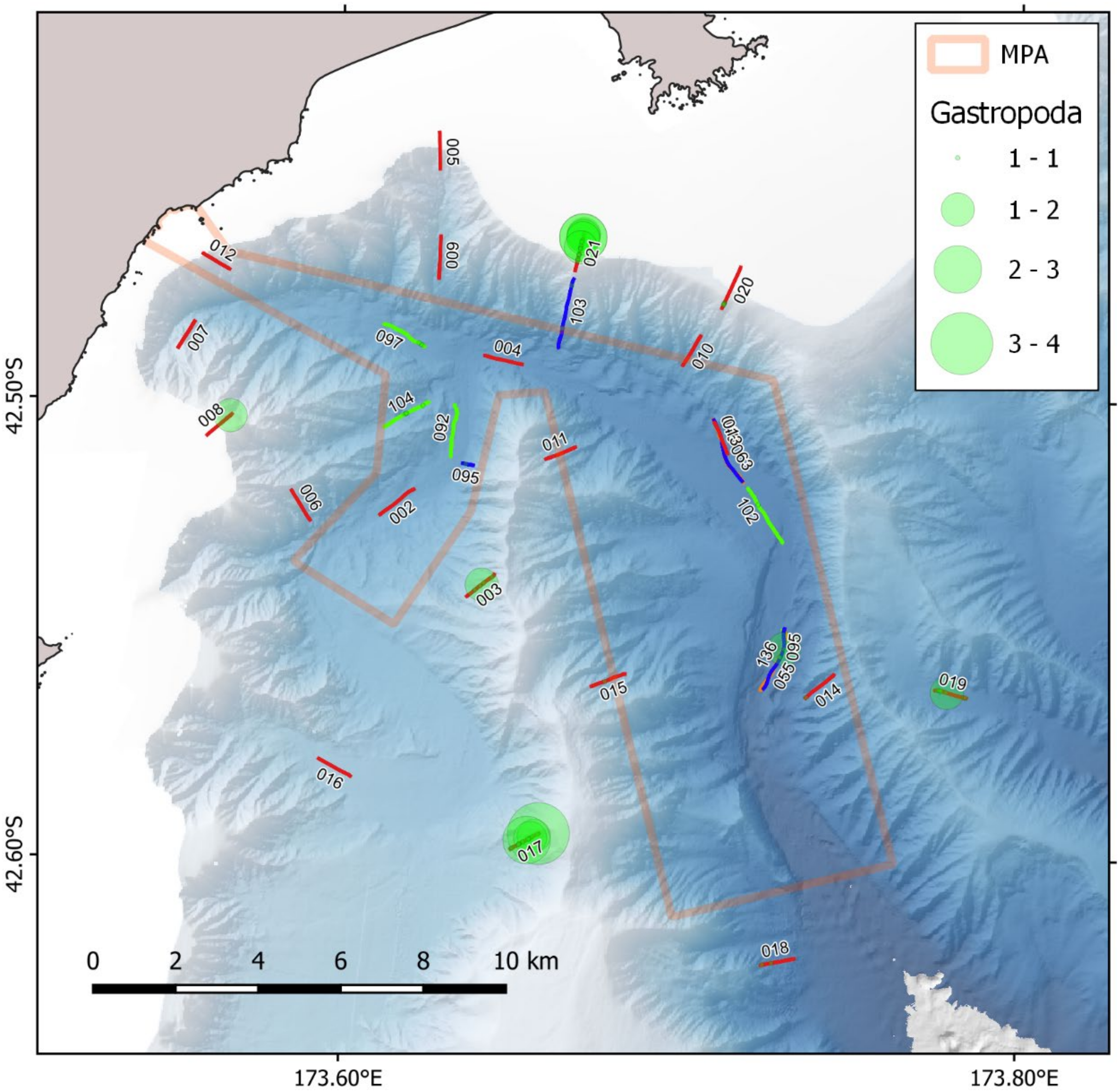

Figure 19: Distribution of gastropod molluscs (sea snails: Order Gastropoda) in relation to the Hikurangi Marine Reserve boundary. Taxon labels included are: Gastropoda; Volutidae, and *Pleurobranchaea maculata*. Details as for preceding figure.

3.2.3 Recovery of benthic megafaunal communities

Incorporating data developed here from analysis of still images from the 2022 survey into the existing time-series analysis of Bigham et al (2023) indicated that communities on the floor of both Kaikoura Canyon and Conway Trough had continued to recover towards their pre-disturbance states (Figure 20), with lebensspuren (as a proxy for infaunal megafauna) being closer to their pre-disturbance states than epifaunal megafauna. Although these data represent only two seafloor sites at the latest survey-point (TAN2203, 5.25 y after disturbance), the trajectories of communities at both of these sites through the time series show a movement in multivariate space towards convergence with their pre-disturbance states (Figure 20 B); the Kaikoura Canyon site (represented by transect TAN2203_004) showing more complete recovery than the Conway Trough site (TAN2203_002). PERMANOVA results showed that 5.25 y after disturbance the megafaunal communities (infauna and epifauna) at these sites still differed significantly from their pre-disturbance states ($p = 0.0001$). However, the indication in the MDS that communities at these sites were continuing a trajectory of recovery to their pre-disturbance states was supported by the RELATE test for cyclicity, which showed a marginal increase in strength (rho = 0.596, $p < 0.01$) from the value calculated without the data from TAN2203.

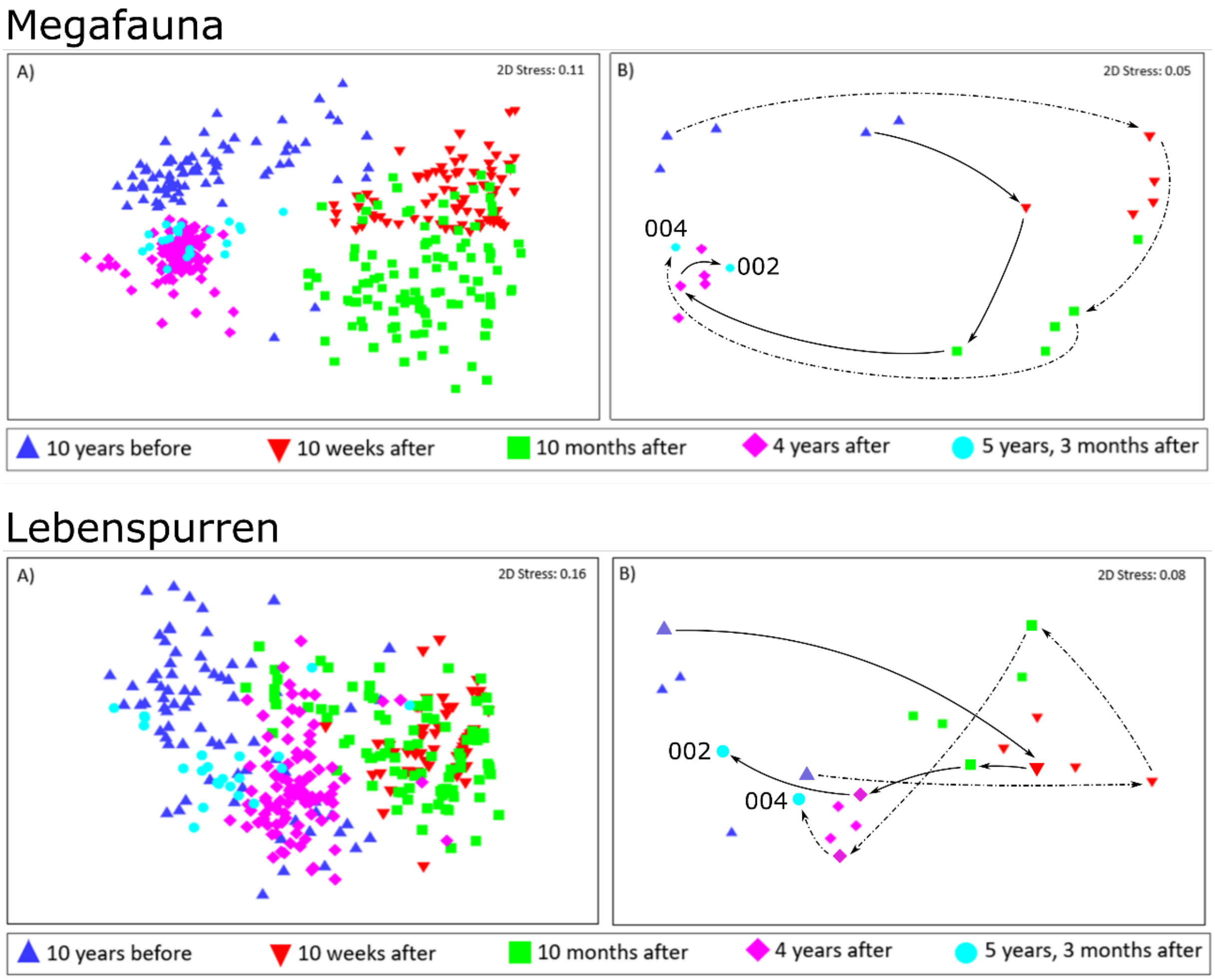

Figure 20: nMDS ordinations adapted from Bigham et al (2023) to incorporate additional data from analysis of bioturbation marks (lebensspuren) in still imagery from two transects from TAN2203. A) ordination using centroids from clusters of analysed still images ('sample groups' sensu Bigham et al 2023) from five surveys: TAN0616 (10 y before the Kaikoura earthquake); TAN1701 (10 weeks after); TAN1708 (10 months after); TAN2011 (4 y after), and TAN2203 (5.25 y after). B) ordination using whole-transect centroids with trajectories indicated for the two sites analysed under this project for the 5.25 y time point; transects TAN2203_004 on the floor of Kaikoura Canyon, and TAN2203_002 on the floor of Conway Trough. In both cases, the plots indicate that invertebrate communities have continued to recover, becoming more similar to their pre-disturbance states.

3.3 Fishes

The total of 18 093 fish recorded included 46 taxon labels, although this included the coarse-level labels 'rattails' and 'Macrouridae' (7 049 occurrences combined), 'bony fish (485 occurrences), and 'eels' (181 occurrences), each of which spanned multiple taxa at finer taxonomic resolution (Table A-2). Rattails, including hoki, were by far the most numerous fish taxon, with 15 882 occurrences recorded (87 % of all fish observations) and being present in all transect segments within Kaikoura Canyon, Conway Trough, and the Kowhai Sea Valleys and absent only from segments on the coastal shelf. Juvenile hoki (*Macrouronus novaezealdiae*) were present at high densities in two rim transects near the head of Kaikoura Canyon (995 records in TAN2203_008 and 530 in TAN2203_012).

4 Discussion

This study has analysed existing seafloor imagery from a recent DOC-commissioned survey of the Hikurangi Marine Reserve and surrounding areas, together with material from earlier surveys, to develop quantitative data about the distributions of seafloor invertebrates and fishes. The motivation for this research is to improve understanding of the highly productive marine ecosystem centred on Kaikoura canyon and address questions related to three key aspects of the reserve's design: how well it represents habitats and faunal communities in the region; whether its current boundaries are adequate to fulfil its intended role of conserving the ecosystem of the canyon, and how it influences, or is influenced by, surrounding habitats outside its boundaries.

4.1 Representation of habitats and fauna

These results show that while seafloor habitats and fauna on the floor of Kaikoura Canyon itself and on the northern floor of Conway Trough (Community I) are currently well-represented in the Hikurangi Marine reserve, communities characteristic of neighbouring habitats on the walls, around the rim of the canyon, and on the coastal rim adjacent to it, are not (Communities II, III and IV). Community II was most similar to Community I and was identified at only two sites, neither of which was inside the HMR and both of which were on wall habitats: one on the ridge between Conway Trough and Kaikoura Canyon, the other on the northern wall of Kaikoura Canyon. The main factor distinguishing these sites from those in Community I was a slightly higher incidence of hard substrata and sessile invertebrate taxa associated with it, including sponges, anemones, and corals (prediminantly primoidae). Community III was associated primarily with the shallow rim of Kaikoura Canyon at its head but also included one site from the eastern wall of Conway Trough. One of the four Community III sites (012 at the head of Kaikoura Canyon) was inside the HMR but this community was strongly distinct from most sites currently within the HMR and because it was characterised by low faunal abundances and relatively high evenness and diversity despite often poor near-seafloor visibility, it is likely that these canyon rim habitats harbour more diversity than is captured in the present analyses. Community IV, on the northern rim-rim of Kaikoura Canyon, is not represented in the HMR but was strongly distinct from all other communities in the study in terms of the taxa present and their overall diversity and abundance. These sponge-dominated communities have been surveyed previously by Page et al. (1993), who estimated that the community extended over approximately 4.5 km^2 on the rim edge of Kaikoura Canyon in depths of 80 to 105 m, in a survey area extending northwards from transect TAN2203_021. The one un-grouped site in the present study is in the Kowhai Sea Valleys, outside of the HMR, and is of interest here because it represents a valley floor habitat comparable to that of Kaikoura Canyon but which was not affected by the canyon flushing event that followed the 2016 earthquake. Although the present data include only this one example, the site is distinct in being the only one in which burrows are ubiquitous in the soft sediments of the valley floor.

4.2 Adequacy of reserve boundaries

The current boundary of the HMR is effective for protecting the high-density, soft sediment canyon floor community first identified by De Leo et al. (2010) (i.e., Community I). This assessment holds despite the exposure of the current reserve area to periodic catastrophic canyon-flushing events because evidence from Bigham et al. (2023) and the present study shows that this community has the capacity to recover to be near its pre-disturbance state within a decade. However, the current HMR extent has poor representation of the other community types identified here (Communities II, III, and IV, and the Kowhai Sea Valleys). Based on the data presented here, there are several potential boundary modifications that would improve substantially the representation of these benthic communities. Below, we describe five examples of such modifications that might be considered. The boundary modifications outlined here (Figure 21, A to E) have been drawn to ensure adequate representation of habitats and communities, encompassing examples of all seafloor communities identified in our analyses and representing the full heterogeneity of the seafloor environment in the study area. They are not definitive, however, their role being to inform the HMR review process by providing a range of potential extensions to the HMR that are supported by empirical data. Thus, the scope of any future boundary modifications, including the areas included and the precise position and alignment of their boundaries, would be decided by the review and consultation among relevant parties.

A. Community II is currently not represented in the reserve but a modification of the current HMR boundary joining the current southern extremities of the Conway Trough and the main Kaikoura Canyon arms of the reserve would encompass the ridge that separates these two features and the Community II transect 003 site. A slight deviation in this new line (Figure 21, line A) would also encompass the site of transect 017, yielding additional representation of Community III (currently represented only by transect 012 at the head of Kaikoura Canyon) in the reserve.

B. The diverse sponge-dominated communities on the northern rim-rim of Kaikoura Canyon (Community IV) are currently not represented in the HMR. Modifying the northern boundary from its current position at the base of the canyon wall to encompass the full height of the wall and extending approximately I km on to the coastal rim (Figure 21, line B) would protect Community IV sites 021 and 020. This extension would also improve representation of Community II by inclusion of site 103 on the lower part of the northern canyon wall.

C. Community III is currently represented by a single site at the head of Kaikoura Canyon. While modification A, above, would bring one more Community II site (017) into the reserve, this is perhaps not representative of the shallow canyon rim sites closer to the coast. If line B, above, were to be extended eastwards to the head of the canyon (Figure 21, line C), it would serve to include much of this habitat and the communities associated with it and would also encompass much of the known distribution of community IV (i.e., that which extends westwards beyond Line B).

D. An alternative or addition to C, above, would be to extend the HMR boundary from the south-western corner of the current Conway Trough arm of the reserve, around the canyon rim to encompass sites 006, 007, and 008 (Figure 21, line D). This would increase representation of Community III, as with option C, but not of the sponge Community (IV).

E. There is currently no representation of sea valley habitats adjacent to Kaikoura Canyon to the east, but the one transect analysed from this area (019) shows evidence of a benthic infaunal community that is materially different from any of those within the HMR, potentially because they are not subject to periodic disturbance from canyon flushing events. Extending the HMR boundary to the east, perhaps from the north-eastern corner of line B and the south-eastern corner of the current boundary (Figure 21, line E), would encompass valley floor and wall habitats in this area.

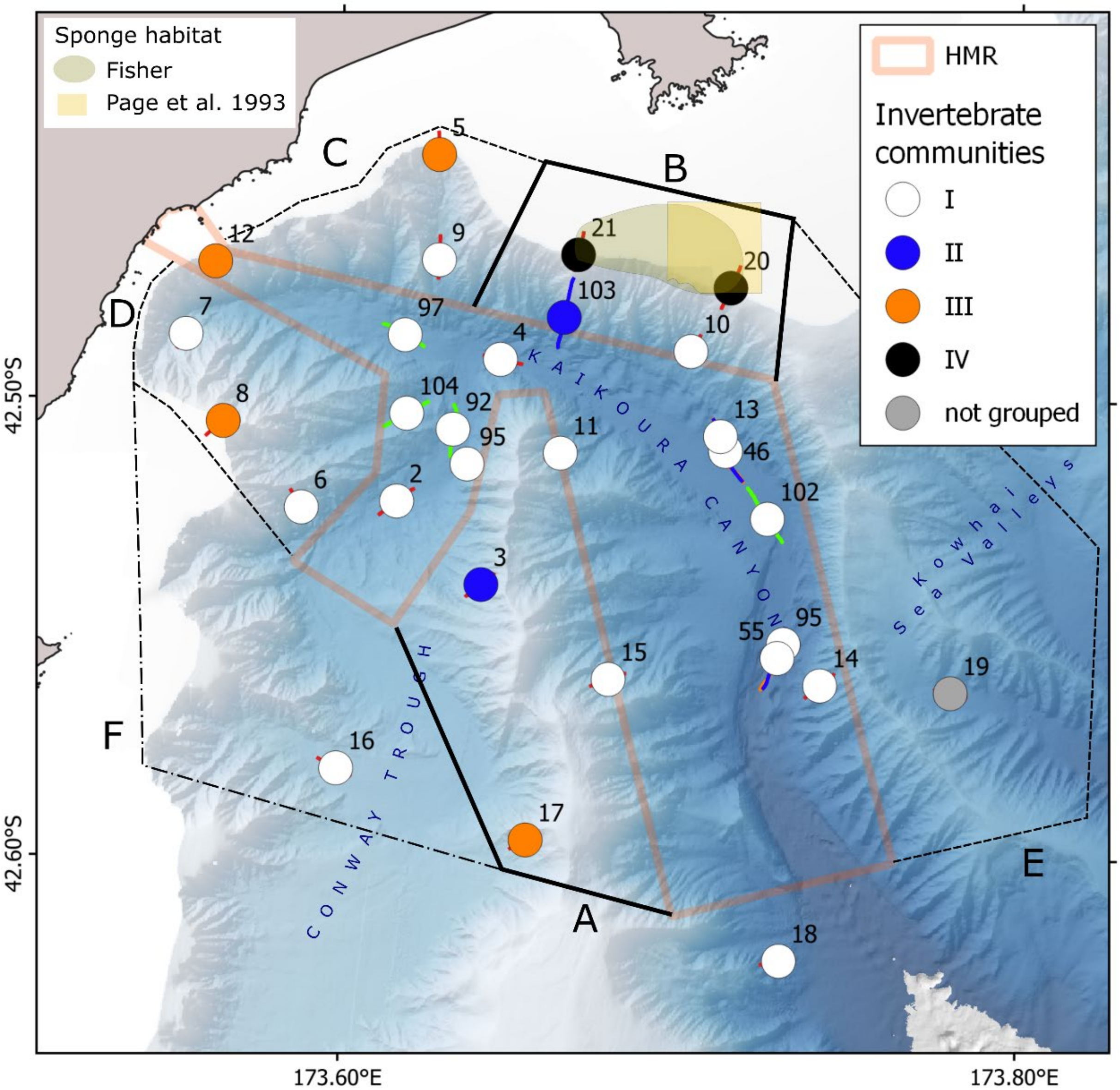

Figure 21: Hikurangi Marine Reserve: potential boundary modifications to improve representation of benthic habitats and invertebrate communities. Lines A to F (black solid and dashed) indicate possible boundary modifications to encompass community types and habitats that are currently either poorly represented or unrepresented in the HMR; see text for rationale. Polygons within line B indicate approximate extents of sponge-dominated rim community as identified by local fishers and Page et al. (1993). Coloured lines extending beyond symbols show video transect tracks, colour coded as per Figure 1.

4.3 Ecological effects of the reserve

From the present data, it is not possible to make definitive inferences about the influence the reserve has on surrounding areas. However, we know that the canyon system does have a significant influence on overall productivity in the area and transport of organic material to depth (De Leo et al. 2010; Mountjoy et al. 2018). In the present data, the abundance of rattail fishes within the canyon system suggests that the reserve protects a central part of the ecosystem that supports this productivity. However, if the heightened production is primarily a consequence of oceanographic focusing of organic material in the canyon axis and the canyon is also subject to periodic full flushing events, the more important ecological questions in relation to the reserve are likely to be; 1) where are the source populations of organisms that recolonise the canyon and thus regenerate production? and 2) are these populations currently protected by the HMR?

Few taxa appear to be shared between sites inside and outside the reserve other than in Conway Trough, which hosts the same communities found in the main arm of Kaikoura Canyon (Communities I and III, here). Because Conway Trough shares many characteristics with Kaikoura Canyon (community composition and habitat types) but appears to be less susceptible to disturbance from flushing events (Mountjoy et al. 2018), a plausible hypothesis is that this is a key area of source populations that seed the recovery of communities in Kaikoura Canyon after major disturbances such as the full canyon flushing event of 2016. If this hypothesis is correct, Conway Trough should be seen as a key component of the regional ecosystem and central to its extraordinary productivity. The lower (northern) part of Conway Trough is already included in the HMR but If the source population reservoir hypothesis is correct, it would argue for a further extension of the HMR boundary to include more of Conway Trough (e.g., Figure 21, line F). Of less direct relevance to the dynamics of the characteristic, high-productivity, floor communities in Kaikoura Canyon, the high-diversity communities on the northern rim of Kaikoura Canyon and adjoining rim also have potential to function as source population reservoirs for sponges and other sessile fauna to colonise exposed hard substrata within the HMR.

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Appendix A Taxon tables

Table A-1: Benthic invertebrate taxa recorded in seafloor video. Showing taxonomic groupings, total numbers of occurrences (count), and number of sites at which each taxon occurred (prevalence). The taxonomic resolution at which organisms can be identified from video is affected by variations in image quality between and within transects. 'Taxon observed' shows the labels applied during video analysis, whereas 'taxon aggregated' indicates where labels have been combined at coarser level to avoid potential duplication of taxa in the data.

phylum	class	order	family	taxon observed	taxon aggregated	count	prevalence
Annelida				Worm (indeterminate)	Worm (indeterminate)	3	1
	Polychaeta			Polychaete (errant)	Polychaete (errant)	16	3
				Tube worms	Tube worms	351	7
		Sabellida	Sabellidae	Sabellidae	Sabellidae (fan worm)	68	4
	Echiura (sub)			Echiura	Echiura	23	4
Arthropoda	Malacostraca	Decapoda		Crustacean (lobster)	Crustacean (lobster)	2	2
				Brachyura (crabs)	Brachyura (true crabs)	18	5
				Caridea (shrimps)	Caridea (shrimps)	525	25
				Crustacean (galatheid/Chirostylidae)	Galatheoidea	114	5
			Aristeidae	*Aristaeomorpha foliacea*	*Aristaeomorpha foliacea*	12	3
			Lipkiidae	*Lipkius holthuisi*	*Lipkius holthuisi*	224	12
			Lithodidae	Lithodidae	Lithodidae	6	4
			Munididae	*Munida* sp.	*Munida* spp.	8	1
			Nephropidae	*Metanephrops challengeri*	*Metanephrops challengeri*	1	1
			Paguridae	Paguridae	Paguridae	103	15
			Palinuridae	*Jasus edwardsii*	Crustacean (lobster)	1	1
			Pasiphaeidae	Pasiphaea	*Pasiphaea* sp.	77	7
		Isopoda		Isopoda	Isopoda	2	2
			Serolidae	Serolidae	Isopoda	4	3

phylum	class	order	family	taxon observed	taxon aggregated	count	prevalence
		Mysida		Mysida	Mysidacea	245	9
	Thecostraca			Cirripedia	Cirripedia	4	1
Brachiopoda				Brachiopoda	Brachiopoda	1	1
Bryozoa				Bryozoa – bushy	Bryozoa	34	4
				Bryozoa – filamentous	Bryozoa	3	2
Chordata	Ascidiacea			Ascidians (clonal)	Ascidians (clonal)	534	5
				Ascidians (solitary)	Ascidians (solitary)	31	6
Cnidaria	Anthozoa						
	Hexacorallia (sub)	Actiniaria		Actiniaria	Anemones	313	22
			Hormathiidae	Hormathiidae	Anemones	8	4
		Scleractinia			Scleractinia	9	2
			Caryophylliidae	*Solenosmilia variabilis*	Scleractinia	15	1
				Cup corals	cup corals	126	8
			Flabellidae	Flabellum	*Flabellum* sp.	3	3
		Zoantharia		Zoantharia	Zoantharia	13	5
			Epizoanthidae	Epizoanthus	Epizoanthus sp.	2	2
	Octocorallia (sub)			Octocorallia	Alcyonacea	9	2
				Gorgonacea	Gorgonacea	20	6
		Scleralcyonacea	Primnoidae	Primnoidae	Primnoidae	1338	6
			Coralliidae	Anthomastus sp.	Anthomastus sp.	277	1
				Heteropolypus sp.	Heteropolypus sp.	1	1

phylum	class	order	family	taxon observed	taxon aggregated	count	prevalence
		Pennatuloidea (super family)		Pennatuloidea	Pennatuloidea	4	3
			Kophobelemnidae	Kophobelemnon	Pennatulacea	1	1
		Malacalcyonacea	Alcyoniidae	*Anthothela* sp.	*Anthothela* sp.	1	1
			Isididae	Isididae	Isididae	10	2
			Plexauridae	Plexauridae	Plexauridae	50	5
	Ceriantharia (sub)			Ceriantharia	Ceriantharia	95	7
	Hydrozoa			Hydrozoa	Hydrozoa	68	5
		Anthoathecata	Stylasteridae	Stylasteridae	Stylasteridae	3	1
		Siphonophorae		Siphonophorae	Siphonophorae	47	10
Ctenophora				Ctenophora	Ctenophora	1	1
Echinodermata	Asteroidea			Asteroidea	Asteroidea	108	20
		Brisingida	Brisingidae	Brisingidae	Brisingidae	30	6
		Forcipulatida		Forcipulatida	Zoroasteridae/Asteriidae	3	2
			Asteriidae	Astrostole	*Astrostole* sp.	15	3
				Asteriidae	Zoroasteridae/Asteriidae	20	5
			Zoroasteridae	Zoroasteridae	Zoroasteridae/Asteriidae	160	8
		Paxillosida	Astropectinidae	Astropectinidae	Astropectinidae	5592	20
		Valvatida	Goniasteridae	Goniasteridae	Goniasteridae	13	1
			Odontasteridae	Diplodontias	Diplodontias	8	2
				Odontasteridae	Odontasteridae	1	1
	Crinoidea	Comatulida		Comatulida	Comatulida	1	1
				Crinoidea	Comatulida	45	6
	Echinoidea			Echinoidea	Echinoid	12	7

phylum	class	order	family	taxon observed	taxon aggregated	count	prevalence
		Camarodonta	Echinidae	*Gracilechinus multidentatus*	*Gracilechinus multidentatus*	56	9
			Temnopleuridae	*Pseudechinus flemingi*	*Pseudechinus flemingi*	11	3
		Spatangoida	Eurypatagidae	*Paramaretia peloria*	*Paramaretia peloria*	1198	10
			Spatangidae	Spatangidae	Spatangidae	92	2
		Cidaroida		Cidaroida	Cidaroida	204	5
			Cidaridae	*Goniocidaris parasol*	*Goniocidaris parasol*	2	1
	Holothuroidea			Holothuroidea	Holothurian	26	3
		Elasipodida		Elasipodida	Elasipoda	1	1
			Pelagothuriidae	*Enypniastes eximia*	*Enypniastes eximia*	43	7
		Synallactida		Synallactidae	Synallactidae	31	2
			Stichopodidae	*Australostichopus mollis*	*Australostichopus mollis*	350	2
			Synallactidae	Bathyplotes	*Bathyplotes* sp.	1	1
	Ophiuroidea			Ophiuroidea	Ophiuroidea	7	4
		Euryalida		Euryalida	Euryalida	31	7
		Ophiurida		Ophiurida	Ophiurida	1	1
Foraminifera	Monothalamea	Astrorhizida	Rhabdamminidae	*Bathysiphon* sp.	*Bathysiphon* sp.	15794	26
Mollusca	Bivalvia			Bivalvia	Bivalvia	17	5
		Ostreida	Pinnidae	*Atrina zelandica*	Bivalvia	1	1
	Cephalopoda	Octopoda		Octopoda	Octopoda	2	2
		Teuthida		Teuthida	Teuthidae	6	4
	Gastropoda			Gastropoda	Gastropoda	73	16
		Neogastropoda	Volutidae	Volutidae	Volutidae	5	1
		Pleurobranchida	Pleurobranchaeidae	*Pleurobranchaea maculata*	*Pleurobranchaea maculata*	12	1

phylum	class	order	family	taxon observed	taxon aggregated	count	prevalence
	Scaphopoda			Scaphopoda	Scaphopoda	2	1
Porifera	Demospongiae			Demospongiae	Sponge (demospongiae)	351	12
		Axinellida	Axinellidae	Axinellidae	Axinellidae	577	6
				Axinella sp.	*Axinella* sp.	1175	1
		Dendroceratida	Darwinellidae	*Darwinella oxeata*	*Darwinella oxeata*	2	1
		Haplosclerida	Chalinidae	Chalinidae	Chalinidae	779	3
				Haliclona sp.	*Haliclona* sp.	1	1
		Poecilosclerida	Hymedesmiidae	*Phorbas* sp.	*Phorbas* sp.	4	2
			Latrunculiidae	*Latrunculia* sp.	*Latrunculia* sp.	56	1
			Mycalidae	Mycalidae	Mycalidae	4	1
			Myxillidae	Myxillidae	Myxillidae	29	3
				Poecilosclerida	Poecilosclerida	346	3
		Suberitida	Suberitidae	Homaxinella	Homaxinella	17	3
		Tetractinellida	Tetillidae	*Antarctotetilla leptoderma*	*Antarctotetilla leptoderma*	4	3
			Theneidae	*Thenea novaezealandiae*	*Thenea novaezealandiae*	53	3
			Vulcanellidae	*Poecillastra laminaris*	*Poecillastra laminaris*	13	2
	Hexactinellida			Hexactinellida	Hexactinellida	21	6

Table A-2: Fish taxa recorded in seafloor video transects. Showing taxonomic groupings, total numbers of occurences (count), and number of sites at which each taxon occurred (prevalence). 'Taxon observed' shows the labels applied during video analysis, with accepted taxonomic names. Taxonomuc resolution varies depending on the quality of imaging and orientation of the fish in relation to the camera at the time of observation.

phylum	class	order	family	taxon_label	name	count	prevalence
Chordata	Elasmobranchii			Cartilagenous fish	Chondrichthyes	1	1
		Myliobatiformes		Rays	Myliobatiformes	2	2
		Rajiformes	Rajidae	Rough skate	*Dipturus nasutus*	2	2
				Skates	Rajiformes	13	5
		Squaliformes	Etmopteridae	shark (*Etmopterus* sp.)	*Etmopterus* sp.	78	16
			Centrophoridae	Shovelnose dogfish	*Deania calceus*	5	4
		Torpediniformes	Narkidae	Numbfish	Narkidae	9	1
		Selachii (infraclass)		Selachii	Selachii	10	9
	Holocephali	Chimaeriformes		Ghost shark	Chimaeriformes	24	12
	Myxini	Myxiniformes	Myxinidae	Hagfish	Myxinidae	17	2
	Teleostei			Bony fish	Osteichthyes	485	29
		Acropomatiformes	Epigonidae	Cardinalfish	Epigonidae	1	1
		Anguilliformes	Congridae	Conger eel	Congridae	98	11
			Syphobranchidae	Basketwork eel	*Diastobranchus capensis*	133	19
			Nettastomatidae	Duckbill eel	Nettastomatidae	20	7
			Syphobranchidae	Snubnose eel	*Simenchelys parasitica*	12	6
				Eels	Anguilliformes	181	26
		Centrarchiformes	Cheilodactylidae	Tarakihi	*Nemadactylus macropterus*	1	1
		Eupercaria incertae sedis	Labridae	Labridae (wrasses)	Labridae	5	1
		Gadiformes	Macrouridae	Rattails	Macrouridae	6868	28
				MACROURIDAE	Macrouridae	134	11
				Bollons rattail	*Coelorinchus bollonsi*	182	13

phylum	class	order	family	taxon_label	name	count	prevalence
				Carinate rattail	*Macrourus carinatus*	112	12
				Notable rattail	*Coelorinchus innotabilis*	37	6
				Serrulate rattail	*Coryphaenoides serrulatus*	3	1
				White rattail	*Trachyrincus aphyodes*	11	6
				Trachyrincus longirostris	*Trachyrincus longirostris*	496	18
				Four-Rayed Rattail	*Coryphaenoides serrulatus*	6504	25
			Merlucciidae	Hoki	*Macruronus novaezelandiae*	1535	7
			Moridae	Dwarf cod (*Notophycis marginata*)	*Notophycis marginata*	10	2
				Moridae (cods)	Moridae	32	10
		Notacanthiformes	Notacanthidae	Spineback eel	*Notacanthus* sp.	75	14
		Ophidiiformes	Ophidiidae	Ling	*Genypterus blacodes*	4	3
			Bythitidae	White brotula	*Cataetyx chthamalorhynchus*	3	2
		Perciformes	Percophidae	Opalfish	*Hemerocoetes* sp.	6	3
			Congiopodidae	Pigfish	Congiopodidae	3	1
			Pinguipedidae	Blue cod	*Parapercis colias*	6	1
			Hoplichthyidae	Deepsea flathead	*Hoplichthys haswelli*	16	3
			Sebastidae	Bigeye seaperch	*Helicolenus barathri*	7	3
			Sebastidae	Jock Stewart	*Helicolenus percoides*	840	7
			Pinguipedidae	Yellow cod	*Parapercis gilliesii*	10	1
			Zoarcidae	ZOARCIDAE	Zoarcidae	22	10
		Pleuronectiformes		Flatfish	Pleuronectiformes	3	2
		Syngthiformes	Centriscidae	Bellowsfish	Centriscidae	24	6
		Trachichthyiformes	Trachichthyidae	Orange Roughy	*Hoplostethus atlanticus*	48	14
		Zeiformes	Oreosomatidae	Oreos	Oreosomatidae	5	3