



Ocean Survey 20/20, Chatham Rise Benthos: effects of seabed trawling on benthic communities

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EXECUTIVE SUMMARY

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Trawl fisheries have direct impacts on seabed habitats and fauna that are likely to alter ecosystem function over time. In deep-sea soft sediments, such effects may be longer lasting than in shallower environments but few data are available from existing deep-sea fisheries. We used towed cameras and corers to survey benthic mega-epifaunal and macro-infaunal communities, together with bioturbation marks made by epifauna, burrowing infauna, and rat-tail fishes across gradients of cumulative trawl intensity on Chatham Rise, New Zealand. All survey sites were on uniform muddy sediment substrata, at depths from 458–614 m on the south and south-eastern flanks of the Rise, and selected to be within the hoki trawl fishery footprint. Sites were nominally grouped into two regions: south of Mernoo Bank (MERNOO), and along the south flank of the Rise east of Vryan Bank (SOUTH) but only in the SOUTH region were sufficient survey sites sampled to generate clear analyses. Relationships between benthic community structure and a range of environmental variables, including cumulative trawled seabed area summarised over the last 1, 5, and 20 years of available records, were explored using ordinations and distance-based linear models. Where relationships were detected, community effects were investigated in terms of univariate indices of community structure and variations in the abundances of individual taxa and functional traits.

Mega-epifaunal community structure and bioturbation marks were significantly correlated with trawling in the SOUTH region, where cumulative trawled area in the most recent year of fishing explained 10 to 17 % of total variance in community structure after allowing for spatial and depth effects. No correlations between macro-infaunal community and trawl intensity were detected, and in the MERNOO region, correlations with trawl intensity were weak for all data sets and varied depending on the trawl summary period used. The evenness and diversity of mega-epifaunal communities were highest in the least-trawled areas and lowest in the most-trawled areas, a pattern that was driven mainly by high abundances of small sessile suspension-feeders, small mobile deposit-feeders, and small predator/scavengers at the most intensively trawled sites in the SOUTH region. Taxa deemed most sensitive to trawl disturbance in *a priori* assessments were at lowest abundance at highest trawl intensities, whereas the most abundant individual taxa were all in the least sensitive and intermediate sensitivity groups, notably the solitary octocoral *Taiaroa tauhou*, the sea-pen *Kophobelemnon* sp., pagurid crabs, and the deposit-feeding quill worm *Hyalinoecia longibranchiata*. Across the entire study area, however, most taxa and most individuals were in the groups least sensitive to disturbance, with no taxa that would qualify as being highly sensitive to disturbance, such as larger corals, sponges, or bryozoans.

This is one of very few studies to assess the effects of trawling at sites entirely within the existing trawl footprint; all sites having been trawled to some extent, and with no un-impacted control sites or protected areas in which trawling had ceased. Thus, it represents a chronically disturbed system for which no pre-disturbance reference data are available. Our results indicate that high intensity trawling modifies the structure and functional composition of epifaunal communities in deep-sea soft sediment environments in ways comparable to those previously determined from studies in coastal and shelf depth fisheries, with reduction in the density of sensitive taxa and overall evenness and diversity. Such reductions in epifaunal diversity and the loss of functional types may have wider effects on the Chatham Rise ecosystem, including reduction in the availability of prey items for benthic-feeding demersal fishes. Failure to detect any effect of trawl history on macro-infaunal community structure in this study may be partly a consequence of inherently lower sensitivity to trawl disturbance of such fauna, but is also likely to be related to the coarse scale at which trawl data are available. This lack of spatial resolution in the trawl data will influence all such analyses but will be most pronounced for infauna because they are sampled at smaller spatial scales.

1. INTRODUCTION

1.1 Background

In May 2013, the Ministry of Primary Industries (MPI) submitted a successful proposal for use of Ocean Survey 20/20 (OS 20/20) ship time to study seabed habitats and fauna of Chatham Rise. In the subsequent contract between MPI and NIWA (Project ZBD201203 – Chatham Rise Benthos), two specific research objectives were agreed upon:

1. Determine whether there are quantifiable effects of variations in seabed trawling intensity on benthic communities,
2. Conduct seabed mapping and photographic surveys in previously un-sampled areas on the central crest of the rise.

The first objective was to focus on an investigation of fishing intensity effects on benthic habitats and fauna in hoki fishing depths (about 400–700 m) and, as far as possible, within a single class of the Benthic Optimised Marine Environment Classification (BOMECE, Leathwick et al. 2012). The second was to collect data from previously unsampled areas within the Central Chatham Rise Benthic Protection Area (BPA). Because the crest of Chatham Rise was of immediate topical interest to MPI, in relation to both the status of Benthic Protection Areas (BPAs) and an application by Chatham Rock Phosphate Ltd to mine in this area, Specific Objective 2 was undertaken first and results have been reported in two Progress Reports to MPI (Bowden & Leduc 2013, Bowden 2014), and a NIWA Client Report to CRP Ltd and MPI (Rowden et al. 2014). The present report covers the rationale, methods, results, and conclusions of Specific Objective 1: the study of the effects of gradients of bottom trawl disturbance on benthic communities.

1.2 Fishing effects

Trawling has impacts on seabed habitats and fauna that are likely to change ecosystem functioning (Jennings & Kaiser 1998, Thrush et al. 1998, Thrush & Dayton 2002, Kaiser et al. 2006, Puig et al. 2012, Pusceddu et al. 2014). Such modification of ecosystem functioning is of particular concern because of the potential for effects to propagate through to affect the fishery itself through ecosystem degradation (Kaiser et al. 2005). Short-term experimental studies have shown immediate changes in benthic habitats caused by trawling, ranging from conspicuous degradation of habitat structure, particularly for sponges and cold-water corals on hard substrata (Clark & Rowden 2009, Clark 2010, Williams et al. 2010), to shifts in the types of organisms present in soft muddy sediment substrata, with reduction or removal of larger, sedentary and erect sessile taxa, and increases in smaller mobile predatory or scavenging taxa (Thrush et al. 1998, Collie et al. 2000, Lambert et al. 2011). Estimates of relative sensitivities and recovery times of communities have been made based on such studies (Lambert et al. 2014) and studies of gradients of trawling intensity in areas subjected to chronic trawl disturbance have shown pervasive effects on community structure, which suggest that ecosystem processes have been degraded (Hinz et al. 2008, Hinz et al. 2009).

As traditional nearshore fishing grounds have become fully or over-exploited and demand for fish continues to increase, fisheries have expanded beyond continental shelves into the deep-sea (more than about 200 m). Soft sediment environments predominate in the deep-sea, constituting the largest biome on the planet, with high biological diversity and important roles in carbon sequestration and remineralisation of nutrients (Sanders & Hessler 1969, Rex 1997, Snelgrove 1999, Rex et al. 2006). Commercially important fisheries for deep-sea species have been developed in national and international waters since the 1970s and, while conspicuous effects on seamount habitats have been documented, there are concerns that effects on soft-sediment habitats may be pervasive (Thrush & Dayton 2002, Clark et al. 2016). Most studies of the effects of chronic trawl disturbance on soft sediments to date have been in shallow coastal or continental shelf environments (less than 200 m depth), and all but one in the northern hemisphere. Relatively little is known about the deep-sea in general, and understanding of the structure and functioning of deep-sea ecosystems

is arguably less well-developed than for any other major biome on Earth. If deep-sea fisheries are to be managed sustainably, it is important that their effects on the ecosystems in which they take place should be better understood.

Major commercial bottom trawl fisheries for benthic and demersal species in continental shelf and deep-sea depths have been in progress in the New Zealand region (exclusive economic zone and adjacent international waters) since the early 1970s. The main trawl fisheries are for scampi (*Metanephrops challengeri*) on continental shelves and slopes, orange roughy (*Hoplostethus atlanticus*) initially on continental slopes but now largely restricted to seamounts, and hoki (*Macruronus novaezelandiae*) on continental slopes in depths from 400 to 600 m. These are managed fisheries but the potential for ecosystem effects beyond the population dynamics of the target stocks is becoming an area of increasing concern (Clark 2001, Cryer et al. 2002, Clark et al. 2016) and MPI is currently funding research into such effects through projects including the present study and BEN2007-01; *Assessing the effects of fishing on soft sediment habitat, fauna, and process*.

The first published evidence anywhere in the world of the effects of trawling on benthic soft sediment community structure in the deep-sea, was from the New Zealand continental slope (Cryer et al. 2002). In a region subjected to a mixed trawl fishery in depths from 200–600 m, higher cumulative intensity of trawling, primarily for scampi, was associated with declines in the population densities of several benthic invertebrate taxa, and the species richness and diversity of the benthic invertebrate community overall. This study remains the only examination to date of the effects of chronic trawling on benthos in soft sediment habitats beyond continental shelf depths (deeper than about 200 m) and at spatial scales (tens of kilometres) appropriate to trawl fisheries. Although the findings of Cryer et al. (2002) are clear, the data used in their analyses were bycatch from research trawl surveys for scampi, and thus are likely to present a picture of community composition biased by the relative catchabilities of benthic taxa by trawls. Potential biases associated with use of scampi trawls to study benthic invertebrate communities include under-representation of infauna and smaller epifaunal taxa, and inaccurate estimates of population densities.

In this study, we build on the work of Cryer et al. (2002) by using dedicated benthic sampling methods to test the applicability of published results from fishing disturbance studies in coastal and continental shelf depths to a major off-shore deep-sea trawl fishery in New Zealand waters. Predicted changes in benthic communities with increasing disturbance from trawling include reduction in species richness and diversity, declines in the densities of emergent sessile taxa and large-bodied mobile taxa, and increases in the densities of small, mobile taxa, particularly scavengers and infaunal taxa (Jennings & Kaiser 1998, Thrush & Dayton 2002, Tillin et al. 2006, Hinz et al. 2009). In June 2013, during RV *Tangaroa* voyage TAN1306, we used a towed camera system and a multicorer to sample epifaunal and infaunal benthic invertebrate communities, respectively, across spatial scales from centimetres to kilometres that spanned gradients of cumulative bottom trawl intensity over a 20 year period on Chatham Rise, to the east of New Zealand's South Island.

2. METHODS

2.1 Study area

Chatham Rise is a continental rise extending eastwards from the South Island of New Zealand across approximately 10 degrees of longitude, with Mernoo Bank at its western end and the Chatham Islands at the eastern end. Because the Sub-Tropical Front coincides with, and is partially constrained by the rise, it is the most biologically productive fisheries region in New Zealand's exclusive economic zone (EEZ), with intense phytoplankton blooms propagating from west to east along its length (Chiswell 2001, Nodder et al. 2007, Nodder et al. 2012). Commercially important bottom trawl fisheries exploit populations of scampi (*Metanephrops challengeri*), hoki (*Macruronus novaezelandiae*), orange roughy (*Hoplostethus atlanticus*), and oreos (*Pseudocyttus maculatus*, *Neocyttus rhomboidalis* and others). Recent summaries of bottom-contact trawl history across Chatham Rise (Baird et al. 2011, Black et al. 2013, Black & Tilney 2015) show

highest trawling intensity, primarily from the hoki fishery, at 450–700 m depth west of Mernoo Bank and on the southern and northern central flanks of Chatham Rise (Figure 1).

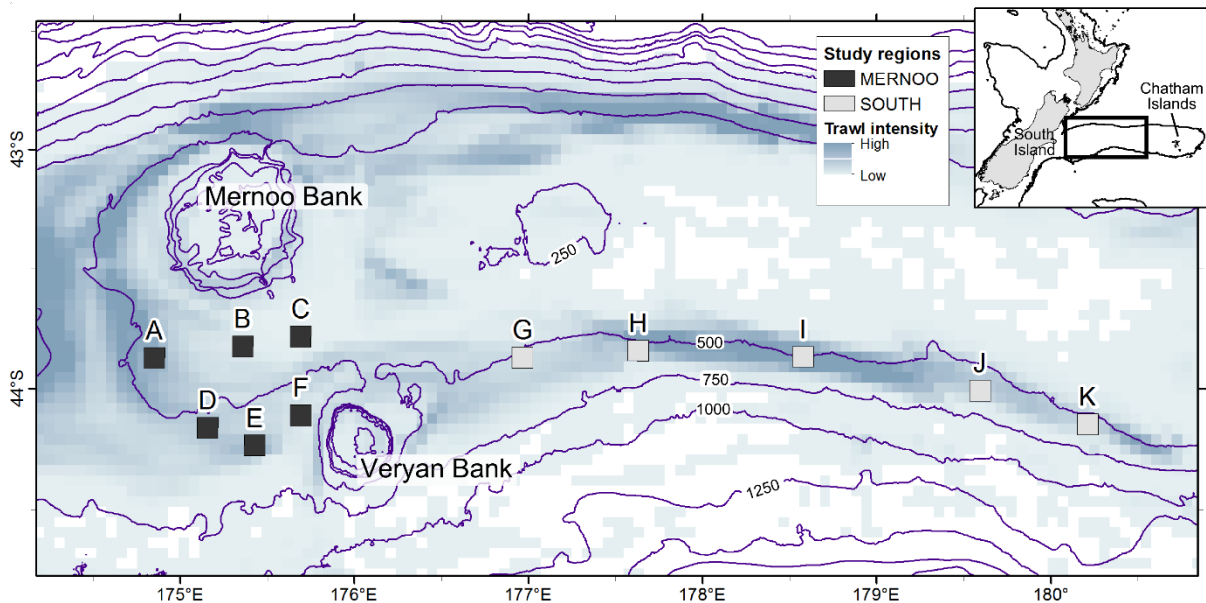


Figure 1: Chatham Rise, showing fishing intensity study survey boxes in the MERNOO (A to F) and SOUTH (G to K) study regions, with relative cumulative trawling intensity for the period 1989–2010 (blue shading; white cells have no recorded trawling). Isobath depths are in metres. Inset shows location of the study area in relation to New Zealand and the 1000 m isobath.

2.2 Survey design

Gradients of trawl intensity in the survey area co-vary with other major gradients, particularly depth and surface primary production at larger spatial scales, and seabed topography at smaller scales. To minimise the influence of these covariates, we constrained sites to be within the depth range of the trawl footprint (about 400–600 m) and allocated sampling into two spatial “regions”: one south of Mernoo Bank (MERNOO), the other on the central-southern flank of the rise (SOUTH). Within each region, we defined four (MERNOO) and five (SOUTH) alphabetically labelled 10 × 10 km survey “boxes” along gradients of cumulative trawl intensity (see Section 2.5 below). In the MERNOO region, two additional boxes (B and C) were defined to represent a largely unfished area, at shallower depth (about 400 m), reported by fishers to have high incidence of juvenile hoki. Boxes were defined at this scale to ensure that sampling spanned spatial scales appropriate for comparison with the summarised trawl intensity data. Seabed topography of each survey box was mapped using a multibeam echosounder (MBES, Kongsberg EM302) and gridded at 25 × 25 m resolution. Within each box, three randomly-selected “sites” were defined for sampling of benthic epifaunal and infaunal communities. Box selection was made, *a priori*, on the basis of available trawl history and regional bathymetry data but their fine-scale topography became apparent only when MBES surveys were completed at sea. In cases where MBES revealed more heterogeneous substrata, sampling was targeted at areas within the box where level muddy sediments were expected to occur (i.e. those that had low relief and uniform acoustic backscatter in MBES data). In boxes B, C, and F, however, video transects showed that all sites sampled were of heterogeneous substrata, to some extent (APPENDIX 1 – Maps), so sites from these boxes were excluded from analyses of trawling intensity effects. Because this resulted in data from only three survey boxes in the MERNOO region being available, the power of analyses to detect correlations with gradients of trawl intensity was reduced in this region. The final set of survey sites (Table A 1) spanned a depth range of 458–614 m (mean±sd, 533±40 m) and spanned latitudinal and longitudinal ranges of about 30 km and 450 km, respectively.

2.3 Epifauna sampling

Three video transects were run within each box, one at each sampling site (e.g., Figure 2), to record epifaunal invertebrates larger than about 5 cm ('mega-epifauna'), bioturbation marks, and substratum type. In boxes A, and J, transects were repeated because of initial failure of the still camera strobe; video was analysed from all transects, however, resulting in four analysed transects for each of these boxes. Transects were run using NIWA's Deep Towed Imaging System (DTIS, Hill 2009) configured with a high definition digital video camera (Sony, HD1080i format) angled forward at 45° from vertical, and a digital single lens reflex camera (Canon EOS 400D, 10 megapixel) angled vertically downwards. Pairs of parallel red lasers at 0.2 m spacing projected into the field of each camera enabled accurate scaling. 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) providing accuracy to about ±7 m at 500 m depth, and its depth and altitude were recorded continuously via sensors mounted on the camera frame.

2.4 Infauna sampling

Three multicorer samples were collected within each box, one at each sampling site (Figure 2, and Appendix 1), to sample macro-infaunal invertebrates (retained on a 300 µm mesh) and sediment characteristics. An Ocean Instruments MC-800A multicorer was deployed with four or eight tubes (9.52 cm internal diameter), depending on conditions, until a minimum of four satisfactory cores (with undisturbed sediment surface and at least 10 cm sediment depth) had been collected at each site. From these, two cores were processed for macro-infauna, one for sediment physical and chemical properties, and one for meio-infauna. Macrofauna cores were sectioned at sediment depths of 0–5 cm, 5–10 cm, and from 10 cm to the full depth of the core. Each section of the core was sieved separately on 300 µm mesh and preserved in 4 % borax-buffered formalin in filtered seawater. The core for sediment analysis was sectioned at 1 cm intervals from 0–10 cm sediment depth, then at 5 cm intervals to the bottom of the core, each section being sealed in a separate labelled plastic bag and stored frozen. Meiofauna were not analysed in this project but during sampling two sub-cores of 29 mm internal diameter × 50 mm sediment depth were collected from each sampling site, sectioned at 0–1 cm, 1–3 cm, and 3–5 cm sediment depths, and preserved in buffered 4% formalin with Rose Bengal dye.

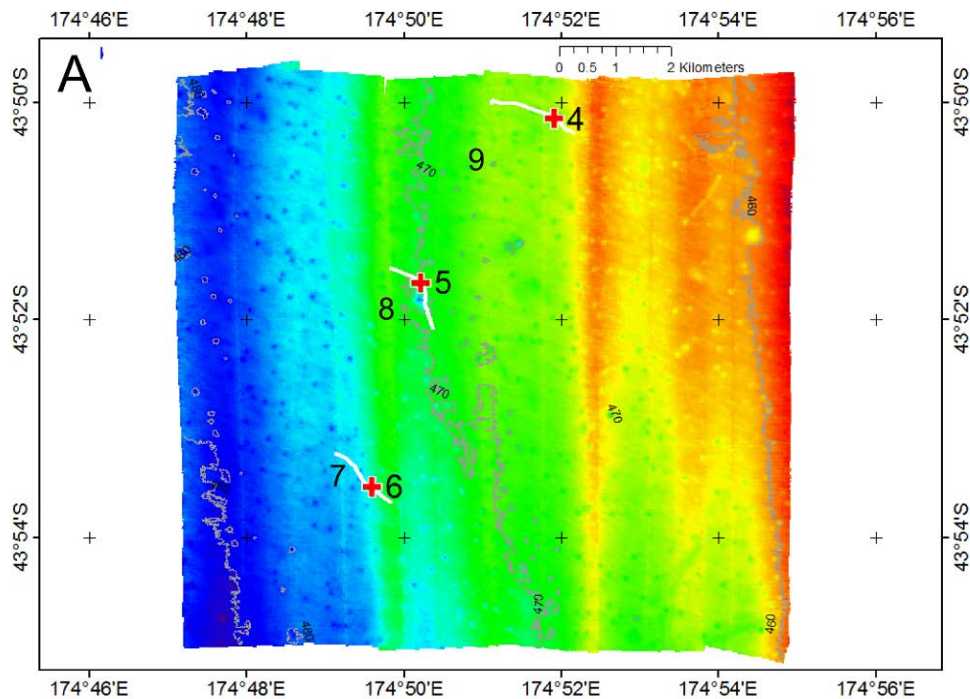


Figure 2: Example survey box (box A) in the MERNOO region, showing the MBES survey map (colour depth gradient fill) and the locations of the three DTIS camera transects (white lines) and three multicorer sites (red crosses), with associated station numbers, within it. Isobath depths in metres.

2.5 Trawl intensity data

Summary data on bottom contact trawl events in the New Zealand EEZ from 1989–90 to 2009–10 were sourced from MPI. Start and end point coordinates for each tow are reported routinely by vessels and these records have been compiled, audited, and summarised in MPI reports since 2011 (Baird et al. 2011, Black et al. 2013, Black & Tilney 2015). Annual summary data are provided at 5×5 km grid resolution as both the cumulative number of trawl events and the cumulative seabed swept area (km^2) occurring in each grid cell in each reporting year since 1989–90. For survey planning in this study, the most recent summary available was up to the 2004–05 fishery reporting year (Baird et al. 2011) but for subsequent analysis, revised analyses up to the 2009–10 year were available (Black & Tilney 2015). Initially, we evaluated both the number of trawl events and total swept area values in analyses but as results were very similar, we report only results using swept area. To compare the influence of long-term versus more recent disturbances, we generated cumulative totals of swept area covering three periods of the trawl record: the last 20 years (1989–90 to 2009–10, ‘20 y trawl’); the last 5 years (2004–05 to 2009–10, ‘5 y trawl’), and the last year (2009–10, ‘1 y trawl’) (Figure 3). As the 5 y summary was strongly correlated ($r \geq 0.9$) with both the 1 y and 20 y summaries, however, it was used only for initial explorations of the data and was excluded from formal analyses.

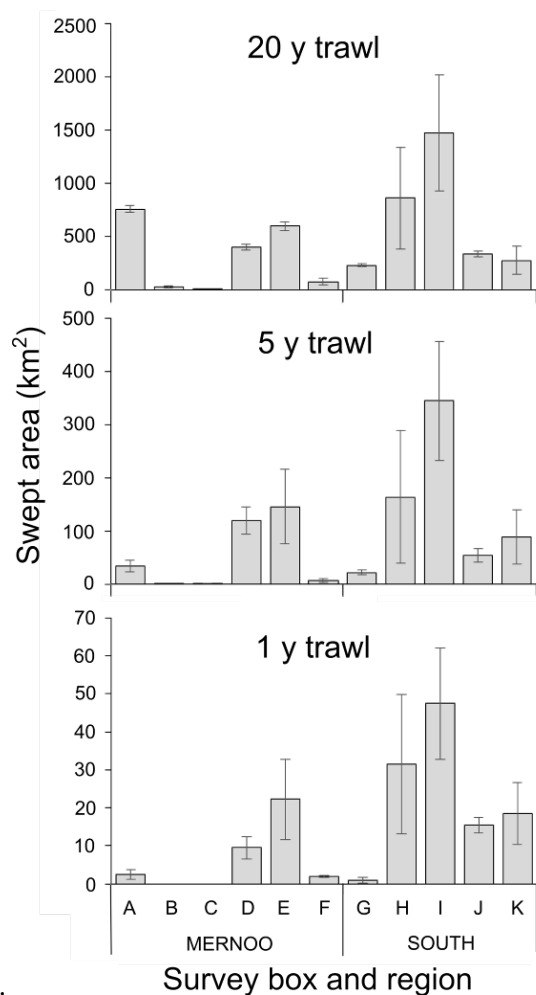


Figure 3: Trawl effort as the cumulative swept area in each of the 5×5 km grid cells occupied by sampling sites. Bars show means ± 1 standard deviation of $n=3$ sites in each of eleven survey boxes (A to K) in the two survey regions (MERNOO and SOUTH). Graphs show the cumulative swept area of trawls for the periods 1989–90 to 2009–10 (20 y trawl), 2004–05 to 2009–10 (5 y trawl), and 2009–10 (1 y trawl).

2.6 Primary production data

We used ocean colour estimates of surface chlorophyll *a* concentrations (chl_a_surf) from the NASA Ocean Data web site (<http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/8Day/9km/chlor/>) as a proxy for long-term primary production above each sampling site. The 1997–2010 mean was computed for the coordinates of each site, with the 9 km grid source data further composited to yield means across a 90×90 km area centred on each sampling site (S. Chiswell, NIWA, personal communication).

2.7 Sample Data

Seabed terrain metrics

Seafloor topography metrics were derived from MBES data in a geographic information system (GIS, ESRI ArcMap v.10.1). Metric calculation was based on the mid-point of each video transect and the recorded seabed position of each multicorer deployment. MBES data were gridded at 25 m resolution and values were calculated at 3×3 , 7×7 , and 15×15 grid cell focal mean scales for eight metrics: average depth; depth range; slope; terrain rugosity; aspect; curvature; plan curvature, and profile curvature, plus the standard deviation of each of these measures at each focal mean. This yielded a total of 48 metrics describing seabed topography at each sampling site. Obviously, many of these were strongly correlated with each other, so through an iterative process of examining correlation strengths and the effects of using different spatial

(focal mean) scales in trial faunal analyses (see Results, below), a subset of five variables, all at single grid cell or 3×3 focal mean scale, was arrived at for use in analyses: depth; aspect; profile curvature; rugosity, and depth range (Table 2).

Epifauna and bioturbation data from camera transects

All video transects were analysed but to avoid potential bias associated with differences in substratum type in the analyses of fishing intensity effects, transects were selected for quantitative analyses only if their substrata, as recorded in video observation logs, consisted of at least 97% muddy sediment. The only transects that did not meet this criterion were those in boxes B, C, and F. Two separate data sets were developed: one from analysis of the continuous video imagery, the other from the still images. The principal differences between these data sets are (1) the seabed area examined is much greater in the video than the still image data, (2) more smaller organisms are detected from the still images, and (3) the overall level of taxonomic resolution is finer from the still images.

For video data, the seabed distance of each transect was measured using the USBL position data in GIS (mean \pm sd; 1.42 \pm 0.35 km). Mean transect image width was 1.5 m, yielding imaged seabed areas per transect of about 2000 m². The full seabed duration of each video transect was reviewed by a single analyst using Ocean Floor Observation Protocol software (OFOP, www.ofop-by-sams.eu). All mega-epifauna (organisms larger than about 5 cm and visible at the sediment surface) and bioturbation marks (burrows, mounds, tracks, etc.) were recorded as counts and then standardised to numbers per linear kilometre of transect. Bioturbation marks provide some measure of the occurrence of infaunal taxa that are not captured in video imagery, as well as indicating relative levels of sediment re-working, which influences nutrient cycling at the seabed (Snelgrove 1999, Jennings et al. 2001, Thrush & Dayton 2002, Lohrer et al. 2004). Densities of thirteen types of bioturbation mark in soft sediments were recorded from the video transects (large burrows, small burrows, scampi burrows, paired burrows, rayed burrows, rings-of-burrows, tracks, mounds, pits, faecal coils, asteroid impressions, Flathead impressions, and rat-tail bite marks).

Taxonomists in New Zealand and abroad were consulted for identification of all invertebrate taxa and the higher resolution DTIS still images were referred to for confirmation of identities in the video. The full video fauna dataset consisted of 110 benthic invertebrate taxa at taxonomic levels from species to phylum. Although the taxon list was reviewed for accuracy and consistency of identification by both the analyst and the principal investigator, for some taxa, coarse-level labels, such as 'Asteroid', which were assigned where identification from video was uncertain, had potential overlaps with finer-level taxon labels. To determine what effect such overlaps might have on analysis results, a 'conservative' dataset was also generated in which all finer-level taxa associated with those for which appreciable numbers of such coarse-level observations had been made were aggregated to the coarser level. The principal groups to which this applied were Annelid worms, Anemones, Ascidians, Asteroids, Holothuroids, Pennatulaceans, regular echinoids, and sponges. Community resemblance matrices generated from these two versions of the faunal data (full and conservative) were compared using the RELATE routine in PRIMER (Clarke & Gorley 2006).

Because of the finer detail recorded from still images, their analysis was more time-consuming than for video transects, resulting in much smaller total sampled seabed area for comparable analysis effort. Images were selected to have framed seabed areas in the range 0.7 to 2 m² and, as far as possible, to be at even spacing along each transect. In each transect, 31 still images were analysed, resulting in analysed seabed area per transect of approximately 41 m². Using ImageJ software ([//rsbweb.nih.gov/ij/](http://rsbweb.nih.gov/ij/)), counts and identities of benthic invertebrate fauna and bioturbation marks were recorded, with substrate type recorded as percent area of the full image frame. Framed seabed area was calculated by scaling the images from the two laser points, and counts of fauna and bioturbation marks were standardised to numbers per square metre.

Infauna data from multicorer samples

Macro-infauna were sorted from sediment samples, assigned to coarse taxonomic groupings (Polychaeta, Amphipoda, Mollusca, etc.), and then identified and counted by specialist taxonomists for each group. The

resulting determinations and counts were compiled into a single dataset and audited for consistency prior to use in analyses. The final dataset of 257 taxa included some taxa conventionally assigned to the meiofauna, primarily nematodes, foraminiferans, harpacticoid copepods, and ostracods. Trial analyses were run including and excluding these taxa, and because results were very similar, the full, inclusive dataset was used in the final analyses. Because the full-detail data set spanned a wide range of taxonomic resolutions (species to phylum), which were not consistent between higher groups (phyla, classes), a conservative version of the data was developed in which taxa were aggregated to more consistent taxonomic levels; family-level for most taxa, including Annelida and Mollusca, but order-level for crustaceans and class-level for echinoderms. The aggregated data set consisted of 109 taxa and was compared against the full-detail data set in subsequent analyses.

Sediment data

From the multicorer deployments, the upper five centimetres of each sediment core was analysed for grain size composition (using a Beckman Coulter LS13320 laser diffraction particle size analyser), chlorophyll *a* (chl_a, µg g⁻¹), phaeopigment (phaeo, µg g⁻¹), particulate nitrogen (PN, %), and particulate organic carbon (POC, %) content. Pigments were measured spectrophotometrically following extraction in 95% ethanol, and PN and POC were measured using an Elementar C/N analyser following catalytic combustion at 900°C.

Functional traits and sensitivity to disturbance

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 epifauna and infauna datasets, separately (Table 1). For epifauna, four high-level trait categories were defined: position on or in the sediment; mobility; feeding mode, and body size. For each of these categories, a given taxon was scored against four (three for size) traits using the ‘fuzzy coding’ approach (Chevenet et al. 1994) in which the taxon can be represented in more than one trait. For instance, a taxon that can be both a deposit feeder and a scavenger would score 0.5 in each of these traits under the category ‘feeding mode’.

Following de Juan et al. (2009) and de Juan & Demestre (2012), each trait in each category was then ranked on a sensitivity scale from 0 (not sensitive) to 3 (highly sensitive) in terms of its expected sensitivity to bottom trawling. The trait attributions of each taxon were then multiplied by these rank weightings and summed to arrive at a sensitivity value for each trait for that taxon. Taxa were then assigned to sensitivity classes following Hewitt et al. (2011): first, all sensitivity values were summed across all traits for each taxon, yielding a single sensitivity value per taxon (ranging from 0 to 12 here), then the taxon list was divided into five sensitivity classes (G1, least sensitive, to G5, most sensitive) by splitting the sensitivity score range into approximately equal ranges.

Because the process of assigning traits and taxa to sensitivity ranks has the potential to introduce unintentional biases, particularly for little-studied deep-sea taxa, we also classified taxa into a set of trait-based classes by using k-means clustering (cascadeKM in R) on the matrix of trait scores without applying sensitivity weightings. This process defined six biological trait classes, the number of classes being determined by the Calinski-Harabasz criterion (Calinski & Harabasz 1974). The characteristic taxon traits represented by each class were identified using the similarities percentage (SIMPER) approach (Clarke & Gorley, 2015), and the relative abundance of each group was plotted in GIS to visualise distributions across the study regions.

For infauna, functional traits were initially assigned to all macrofaunal taxa but the confidence with which traits could be assigned varied and, for most taxa, was lower than for epifauna. Polychaete worms are among the most common and abundant macrofaunal taxa in deep-sea sediments, their taxonomy and ecology are well-defined, and a leading expert (Dr G. Read, NIWA) was available to the project, enabling functional traits to be assigned with greater confidence than for other groups. Therefore, traits analyses for infauna were restricted to annelid taxa.

Table 1: Functional traits assigned to epifaunal and infaunal annelid taxa (recorded in camera transects and multicore samples, respectively). Traits are in four functional categories and each trait is associated with an expected response to disturbance. Based on this expected response, traits are assigned a score ranking their likely relative sensitivity to bottom-contact trawling (0 least sensitive, 3 most sensitive).

Category	Traits		Response to disturbance	Sensitivity
Feeding	Epifauna	Infaunal annelids		
	Predator/scavenger	Predator/scavenger	Positive	0
	Deposit	Deposit/suspension	Neutral/negative	1
	Filter		Negative	2
Position	Suspension		Negative	3
	Deep burrowing	Subsurface (>2 cm)	Neutral	0
	Shallow burrowing	Surface (0–2 cm)	Neutral/negative	1
	Surface dwelling			2
Mobility	Erect			3
	Swimming	Mobile	Positive/neutral	0
	Crawling		Negative	1
	Sedentary	Sedentary	Negative	2
Body size	Sessile		Negative	3
	Small (<ca.5 cm)	Small-medium (0–5 cm)	Neutral	0
	Medium (ca.5–10 cm)			2
	Large (>ca.10 cm)	Large (> 5 cm)	Neutral/negative	3

2.8 Analyses

Analyses were divided into three stages: 1) description of patterns of variability in community structure and bioturbation among sites and in relation to trawling history, using unconstrained ordinations (non-metric multi-dimensional scaling, nMDS) of multivariate data, with the similarity percentages routine (SIMPER, Clarke & Gorley 2015) to identify characteristic taxa; 2) exploration of statistical correlations between community structure and environmental variables, including trawling, using distance based linear models (DistLM, Anderson et al. 2008), and 3) exploration of the influence of trawl disturbance on observed patterns in terms of univariate community indices, taxonomic composition of communities, types of bioturbation, and the functional traits of taxa and their sensitivities to trawling.

Description of pattern

Because different resemblance measures emphasise different aspects of community structure (Legendre & Legendre 1998), in initial analyses we explored the data using four measures: Bray-Curtis similarity; Hellinger distance; Chi-squared distance, and the modified Gower coefficient. Bray-Curtis is the most widely used of these measures in ecological research, and when used on untransformed abundance data, reflects both compositional differences and changing total abundance among sites. Chi-squared distance gives higher weight to rare than to common taxa and thus may be appropriate in cases where rare taxa are good indicators of special environmental conditions. Both Hellinger distance and the Modified Gower coefficient incorporate down-weighting of taxon abundances in their formulation. Hellinger transformation involves square-root transformation, while the modified Gower coefficient uses logarithmic transformation and allows the relative influence of species abundances versus species composition to be adjusted by choice of logarithm base (Anderson et al. 2006). Because of this capacity explicitly to adjust the relative influence of changes in taxon abundance, the Modified Gower coefficient is potentially the best candidate for use in the present study, in which changes in both taxonomic composition and abundance are expected. However, Clarke & Gorley (2015) caution that this resemblance measure is appropriate only for data that consist of true counts, in which abundances of observed taxa are integers, and not for densities of taxon counts standardised to unit sample size as used here.

To determine the extent to which variations in community (or bioturbation) structure were the result of differences in the taxa present or variations in their relative abundances, community resemblance among sites was compared using four treatments of the input data: untransformed; square root, $\log_{10}(x+1)$, and presence-absence. Untransformed data emphasise the influence of changes in abundances, square root and logarithmic transformations decrease the influence of highly abundant taxa, affording more influence to less abundant taxa, while presence-absence transformation attributes the same importance to all taxa, regardless of abundance.

To compare amongst these resemblance measures and transformations, a second-stage nMDS ordination (Clarke & Gorley 2015) was generated, providing a graphical representation of how similar each resemblance matrix is to the others. Ordinations were constructed initially with individual sites as the unit of comparison, then with box centroids (i.e., the mean similarity between boxes). As an initial visualisation of how similarities between survey boxes were related to gradients in cumulative trawl effort, trajectories from least- to most-trawled boxes in each region were overlaid on the box centroids ordinations.

Correlations with environmental variables

DistLM is a routine for modelling linear relationships between multivariate data and one or more predictor variables, using permutation methods to test the significance of relationships (Anderson et al. 2008). Outputs are in two stages: ‘marginal tests’ quantify the amount of variance explained by each predictor variable fitted individually, without the effect of other variables, while in ‘sequential tests’ variables that explain the greatest proportion of variance are selected first and others are added in order of the proportion of variance each one explains in addition to what is accounted for by the variables already fitted.

Initial selection of variables for use in DistLM models here was based on pairwise correlations between variables and the strength of their correlations with benthic community structure in the marginal tests of initial DistLM analyses that included all variables: where two or more variables were strongly correlated with each other ($r \geq 0.9$) only the one ranked highest in the marginal tests of the initial DistLM was retained. This process yielded 16 variables across five broad types (spatial, topographic, productivity, trawl history, and sediment properties) that were available for the final DistLM analyses (Table 2). As a consequence of this process, the 5y trawl summary was excluded from analyses of the MERNOO region, and both the 5 y and 20 y trawl summaries were excluded from analyses of the SOUTH region. The sediment variables were used in macro-infauna but not mega-epifauna analyses because as point-sampled metrics they were unlikely to be representative at the scale of the video transects. Because there is evidence that chronic disturbance from trawling can modify both physical and chemical sediment properties (e.g. Palanques et al. 2014, Pusceddu et al. 2014), additional macro-infauna analyses were also run excluding sediment variables for comparison.

All DistLM models were run using stepwise selection, the Adjusted R^2 criterion, and 9999 random permutations of the data. Initially, models were run without starting terms, allowing the selection procedure to add variables purely on the basis of their contribution to total explained variance, but because benthic communities are known to vary along spatial and physical gradients, they were also run with latitude, longitude, and depth (‘spatial’ variables) included as starting terms so that the influence of the remaining variables could be assessed after allowing for the influence of spatial separation between sites (Borcard et al. 1992, Meot et al. 1998). The latter was considered to be a more conservative approach to estimating the influence of trawling.

Table 2: Environmental variables used in analyses of benthic community data.

Type	Variable	Units	Abbreviation
Spatial	MBES depth	m	grid_25m
	Longitude	°	Lon_mean
	Latitude	°	Lat_mean
Topography	Aspect	°	aspect
	Profile curvature		curvature
	Depth range	m	range
	Rugosity		vrn
Productivity	Surface chlorophyll concentration	$\mu\text{g m}^{-3}$	chla_surf
Trawling	Cumulative swept area per 5×5 km grid cell 2009–2010	km^2	1y_trawl
	Cumulative swept area per 5×5 km grid cell 2004–2010	km^2	5y_trawl
	Cumulative swept area per 5×5 km grid cell 1989–2010	km^2	20y_trawl
Sediment	Mean grain size	mm	MEAN_grain
	Sorting		SORTING
	Phaeo pigments	$\mu\text{g g}^{-1}$	Phaeo
	Particulate nitrogen	%	PN
	Particulate organic carbon	%	POC

Influence of trawling

Four univariate indices of community structure were calculated: the total number of individuals (N); the total number of taxa (S); Pielou's evenness (J'), and Simpson's diversity ($1-\lambda'$). Values were calculated both for each sample (video transect or multicorer station) separately and summarised as means with standard errors for each survey box, and plotted against trawl history summaries.

To represent community sensitivity at each sampling site in terms of the sensitivity classes, we used two approaches proposed by Hewitt et al. (2011); one based on taxon abundances, the other on numbers of taxa (Hewitt et al. 2011's 'Method 2' and 'Method 3', respectively). For the abundance method, sensitivity scores were aggregated from taxon to site level by multiplying the sensitivity value of each taxon in a sensitivity class by its abundance at a given site, then summing the resulting values over all taxa in that class at the site. Weighted averages for each site were then calculated by dividing that sum by the total number of taxa found at the site. For the number of taxa method, the number of taxa in each sensitivity class was calculated and examined both as the proportion of the total number of taxa present at a site, and with no standardisation applied. Abundance-based and taxon-based values for the sensitivity classes were then plotted against trawl intensity at each sampling site and compared with hypothesised responses to disturbance. For sensitive taxa, the predicted response is a 'factor ceiling response', in which increasing fishing intensity exerts a control on how many such taxa occur at a site (Figure 4). For all univariate comparisons with trawl gradients, scatterplots and linear regression (using both ordinary least squares [OLS] and DistLM) were used to visualise and quantify the strength of relationships.

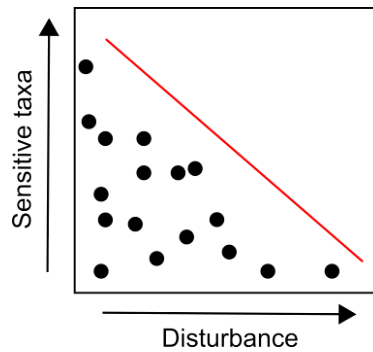


Figure 4: Conceptual plot of hypothesised response of taxa sensitive to disturbance, in which the number or abundance of such taxa is constrained beneath a ceiling that declines with increasing disturbance.

3. RESULTS

3.1 Description of pattern

Mega-epifauna

The final video fauna data set consisted of 41 915 counts of individual organisms representing 110 taxa across 10 phyla (Table A 2), with most taxa in the phyla Echinodermata (33), Cnidaria (25), Mollusca (14), and Arthropoda (12). Similarity matrices calculated from the full detail and conservative video fauna data sets were near-identical (RELATE, $Rho=0.98$, $P=0.01$), so the full detail set was used in all subsequent analyses. The still image fauna data set consisted of 6585 counts of 105 taxa, with a similar representation across phyla. Both data sets were analysed but results presented below are from the video data set only, with reference made to results from still images only where these add to or contrast with the video data.

On the basis of the second-stage ordination (Figure 5), we selected three resemblance matrices: Bray-Curtis similarity on both untransformed and $\log(x+1)$ transformed data to explore the influences of abundances and taxonomic composition, and Hellinger distance on untransformed data for comparison with Bray-Curtis resemblance. Chi-squared distance produced highly clumped arrangements of sites, with wide outliers, so was not pursued further. Comparison of ordinations based on untransformed, square root-transformed, and presence-absence data (Figure 6) showed that much of the variation among sites in the SOUTH region was driven by changes in taxon abundances rather than taxonomic composition; dispersion among sites in this region being greatest for ordinations of untransformed data. In the MERNOO region, dispersion among sites did not change appreciably with data transformation, suggesting influence of differences in both taxonomic composition and abundance.

Ordinations of box centroids, when overlain with trajectories of increasing cumulative trawled area over the 1 y and 20 y summary periods (Figure 7), showed that, whereas spatial patterns of trawling activity were largely consistent between the two trawl periods for the SOUTH region, they changed markedly in MERNOO. Thus, in the SOUTH region, box G was the least trawled and box I the most trawled in both summary periods, whereas in the MERNOO region box A was the most trawled over the 20 y summary but the least trawled in the 1 y summary. Communities in the least-trawled boxes (over 20 y) in each region, D in MERNOO and G in SOUTH, were more similar to each other than those in any other pairing, and were most dissimilar to those in the most trawled boxes in their respective regions (A and I in MERNOO and SOUTH, respectively).

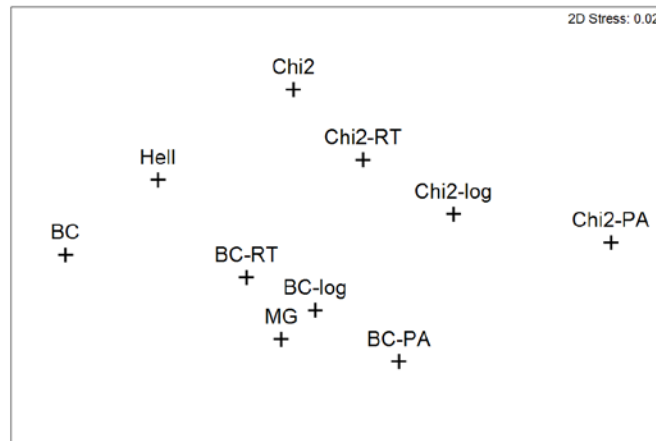


Figure 5: Mega-epifauna community data. 2Stage nMDS illustrating relationships between four resemblance measures (Bray-Curtis similarity [BC]; Hellinger distance [Hell]; modified Gower coefficient [MG], and Chi-squared distance [Chi2]) and for Bray-Curtis and Chi-squared distance, three data transformations (square-root, RT; $\log_{10}(x+1)$, log; and presence-absence, PA).

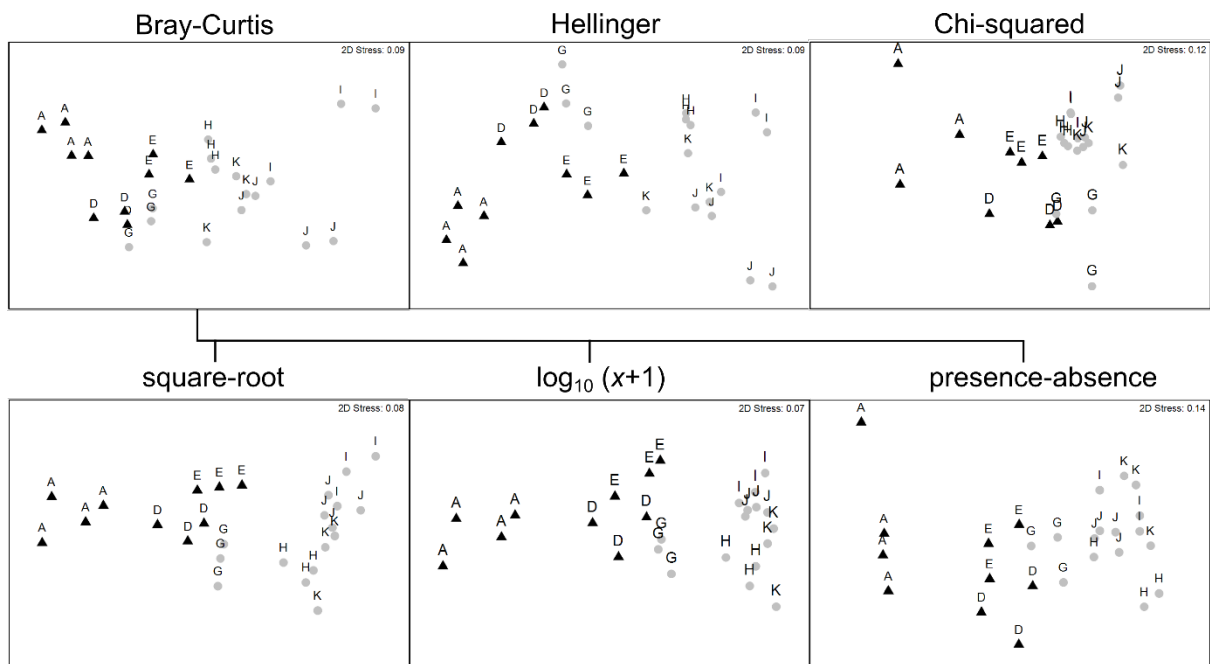


Figure 6: Mega-epifauna: nMDS ordinations of similarities between sites at all soft-sediment sites (>97% muddy sediments). Each plotted point represents mega-epifaunal community observed in a single video transect, differentiated by region (MERNOO, black triangles; SOUTH, grey circles) and labelled by survey box (A to K). Underlying data are taxon densities (individuals km^{-1}) from the full-detail taxon matrix, with separate ordinations shown for three resemblance metrics; Bray-Curtis similarity, Hellinger distance, and the Chi-squared distance, using untransformed abundance data, and for Bray-Curtis only, using square-root, $\log_{10}(x+1)$, and presence-absence transformations of the taxon density data. Note, station 3, box A was omitted from the ordination of Chi-squared distances because it was an extreme outlier (see top left site in the Bray-Curtis presence-absence ordination).

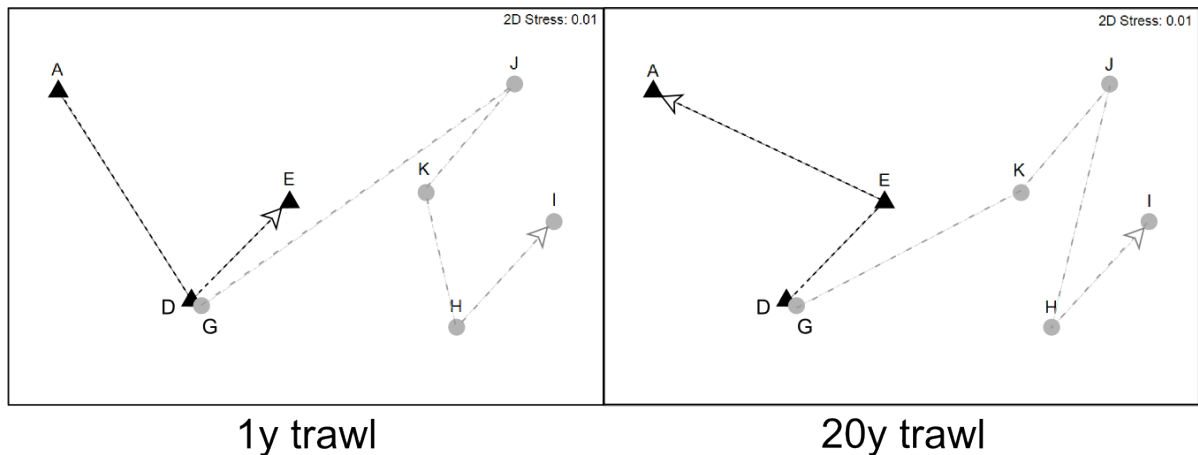


Figure 7: Mega-epifauna community change in relation to cumulative trawl disturbance; nMDS ordination of Hellinger distances among box centroids for survey boxes in the MERNOO (A-E, black triangles) and SOUTH (G-K, grey circles) regions, using untransformed abundance data. Superimposed lines with directional arrows show the gradients of increasing average cumulative trawled area over the full 20 years of records (1989 to 2010, '20 y trawl') and the latest year of records (2009–2010, '1 y trawl') per site in each survey box. Ordinations in the left and right panels are identical, with only the trawl gradient trajectories changing.

Mega-epifaunal communities in the lowest trawl intensity boxes D and G were distinguished from those in other boxes primarily by higher abundances of the soft corals *Anthomastus* sp., and *Telesto* sp., solitary scleractinian corals (*Flabellum* spp.), and the quill worm *Hyalinoecia longibranchiata* (Table A 4, Table A 5, and Figure 8). Sites in boxes I and J that were outliers in the untransformed data ordinations were distinct from others in the SOUTH region because of very high densities of the solitary octocoral *Taiaroa tauhou* (box I) and the sea-pen *Kophobelemnon* sp. (box J), high densities of pagurid crabs (I and J), and low densities or absence of most other taxa. Communities in Box H, which had the second-highest trawl intensity in the SOUTH region after box I, were characterised by *T. tauhou*, pagurids, and quill worms. Communities in the most-trawled box in the MERNOO region, box A were distinguished from those in the other two boxes in the MERNOO region primarily by the absence of *Anthomastus* sp., the presence of the urchin *Phormosoma bursarium*, higher densities of a type of small, erect, sessile polychaete worm (identified as “Onuphidae”) and *Brucerolis* sp. isopods, and lower densities of *Flabellum* sp., *T. tauhou*, quill worms, *Telesto* sp., and several other taxa. Within-box community similarities were in the range 64–68 % in the MERNOO region and 49–75 % in the SOUTH region (SIMPER, Table A 4), and dissimilarity between boxes was about 63 % in MERNOO but ranged from 59 to 83 % in SOUTH region, the strongest contrast being between the least- and most-trawled boxes in the region (G and I, respectively, SIMPER, Table A 5). Representative seabed photographs from the most- and least-trawled survey boxes in each region (A and D, respectively in MERNOO, and I and G, respectively in SOUTH) are shown in Figures 9 to 12.

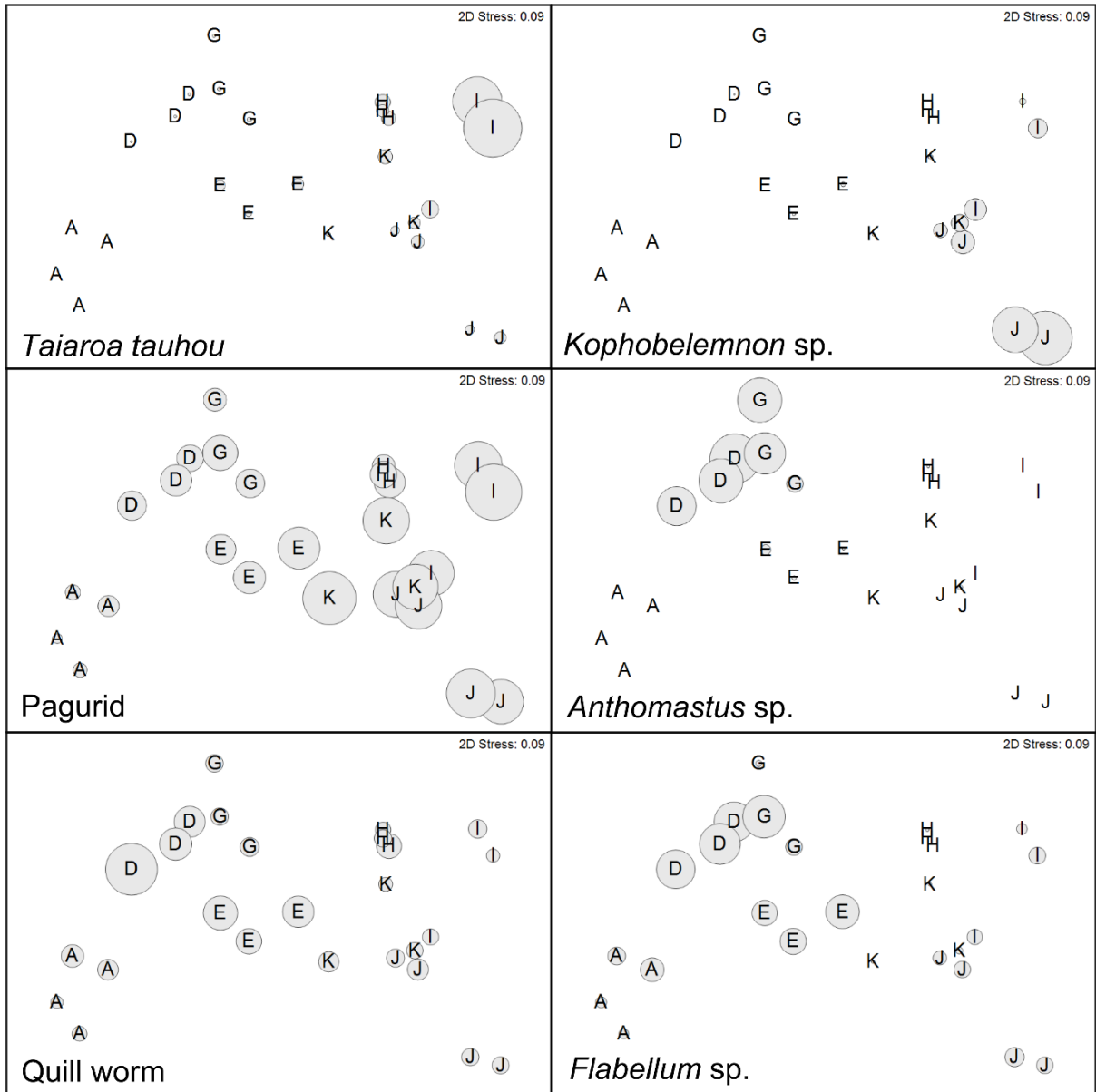


Figure 8. Mega-epifauna nMDS ordination (Hellinger distances) with superimposed bubble plots showing relative abundances of taxa identified by SIMPER as contributing to community dissimilarities between the least-trawled (D and G) and most-trawled (A and I) boxes across both regions, based on 20 y trawl summary. Bubble diameters are scaled to a standard maximum size for each taxon and thus show relative densities within, but not between, panels.

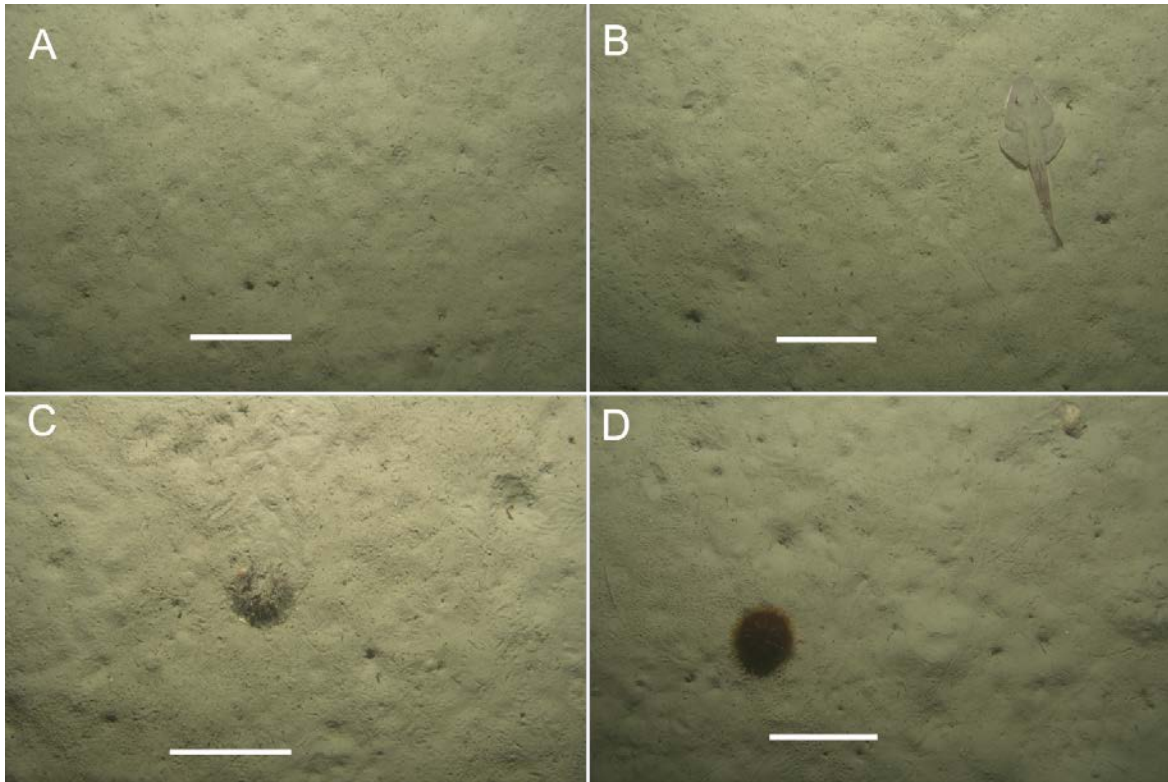


Figure 9: Box A (MERNOO region, highest trawl intensity), seabed photographs showing (A) muddy sediments, and (B) flathead fish, (C) burrowing urchin, and (D) the urchin *Phormosoma bursarium*. Scale bars show 20 cm.

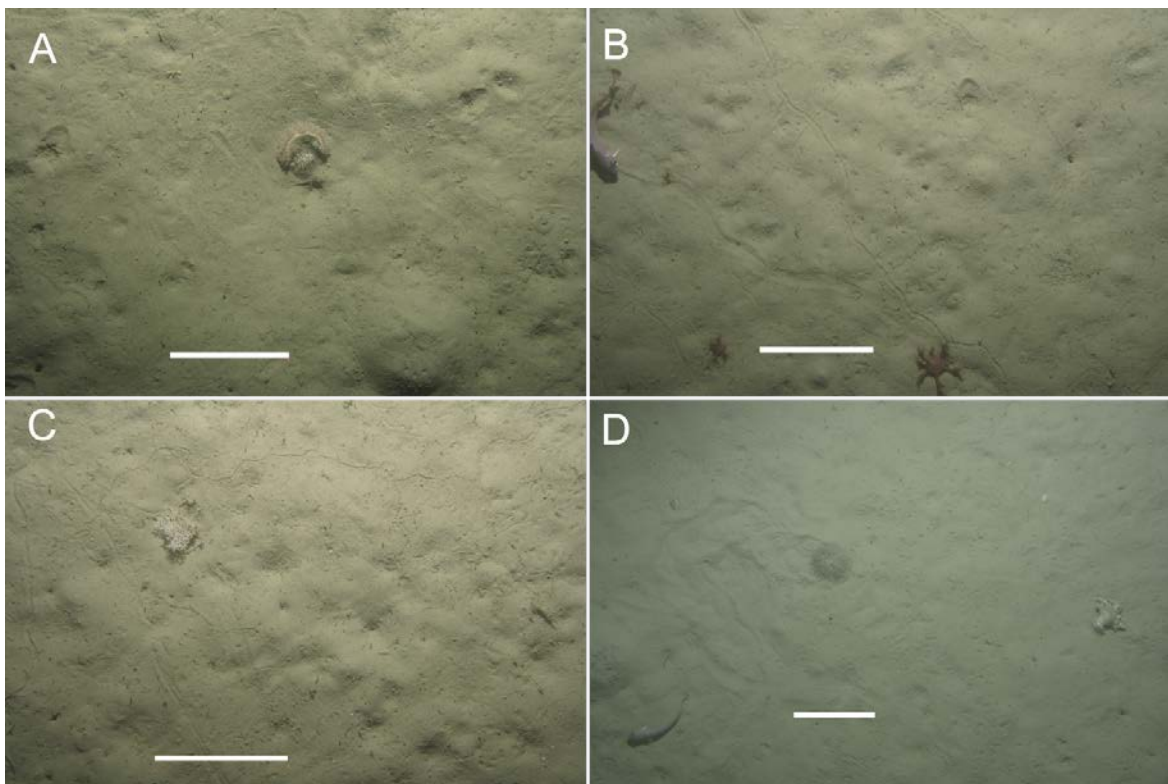


Figure 10: Box D (MERNOO region, lowest trawl intensity), seabed photographs showing muddy sediments with (A) *Flabellum* sp. scleractinian coral, (B) *Anthomastus* sp. soft coral, (C) bryozoan, and (D) burrowing urchin.

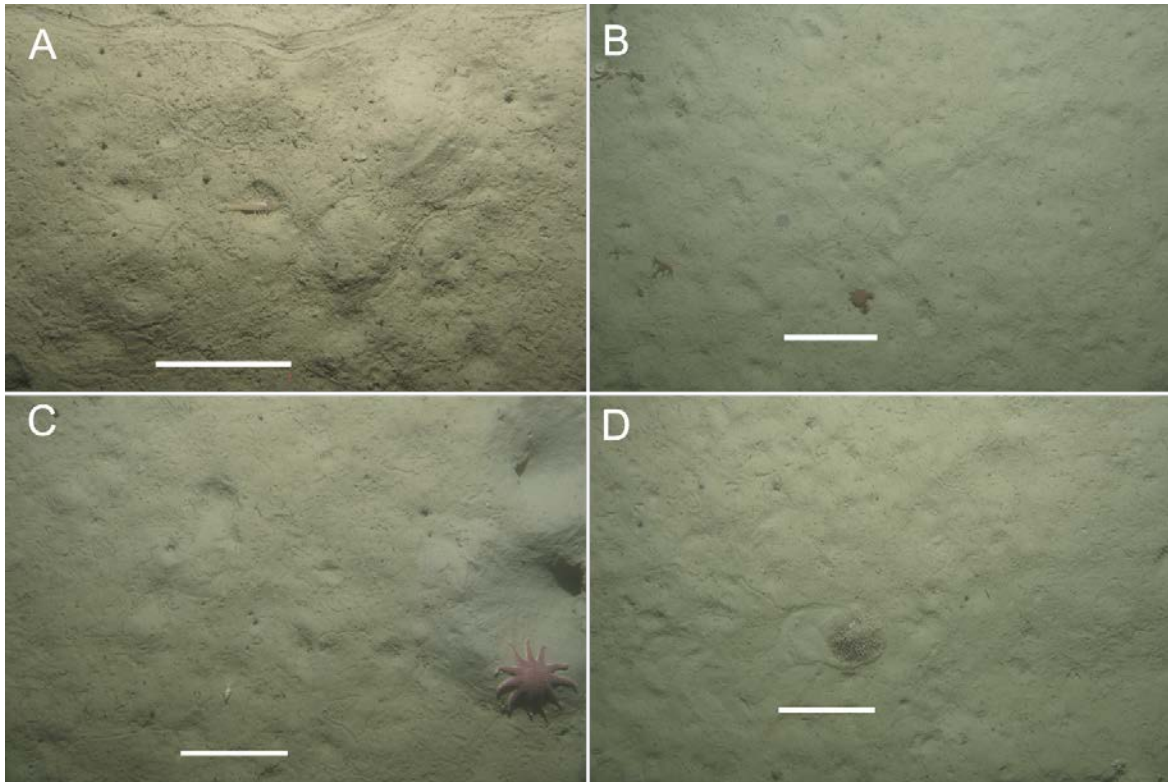


Figure 11: Box G (SOUTH region, lowest trawl intensity), seabed photographs showing muddy sediments with fine-scale texturing from biological activity (tracks, mounds, etc.) and (A) shrimp, (B) *Anthomastus* sp. soft coral, (C) *Solasteridae* asteroid, and (D) burrowing urchin. Scale bars show 20 cm.

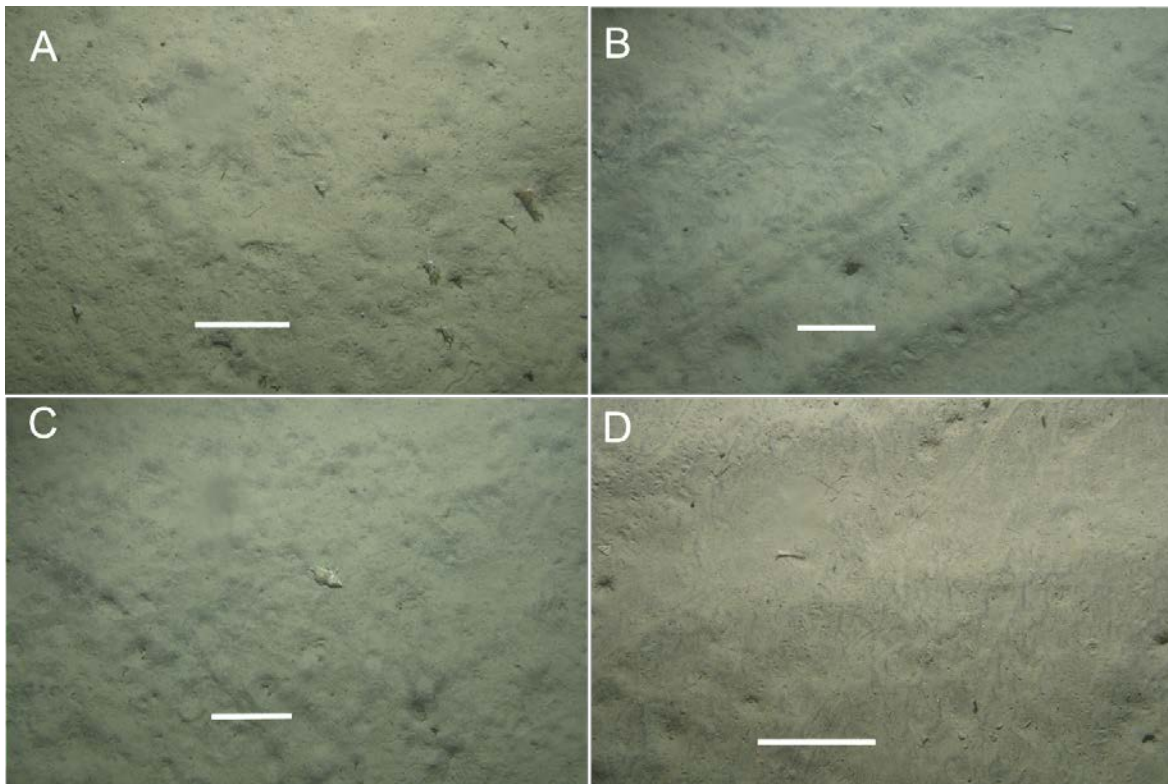


Figure 12: Box I (SOUTH region, highest trawl intensity), seabed photographs showing muddy sediments with trawl marks and (A) *Kophobelemnon* sp. sea pens and *Taiaroa tauhou*, (B) *T. tauhou*, (C) pagurid crab, and (D) *T. tauhou*.

Macro-infauna

Macro-infaunal communities were characterised by large numbers of taxa occurring at low densities (mean±sd, 71.5±26.7 individuals site⁻¹), with just a few numerically dominant ones; primarily nematode worms, the polychaete worm *Prionospio* spp., and foraminiferans. nMDS ordinations showed greater within-box variability of community structure than for mega-epifauna, and greater overlap between boxes (Figure 13) with consequently high 2-dimensional stress, which limited their usefulness for interpretation of pattern. Comparison of the range of data transformations, however, indicated that a broad dissimilarity between the two study regions resulted from differences in overall abundance rather than taxonomic composition; this distinction only being clear in the ordination of the untransformed data (Figure 13). An outlying site (Box I, extreme right in Figure 13 ordinations), consisted of a single core with the lowest abundance of all the study sites (37 ind.). Within-box similarities were in the range 42–53 % in both regions and dissimilarity between boxes ranged from 44 to 46 % in MERNOO and from 52 to 60 % in SOUTH (SIMPER, Table A 6).

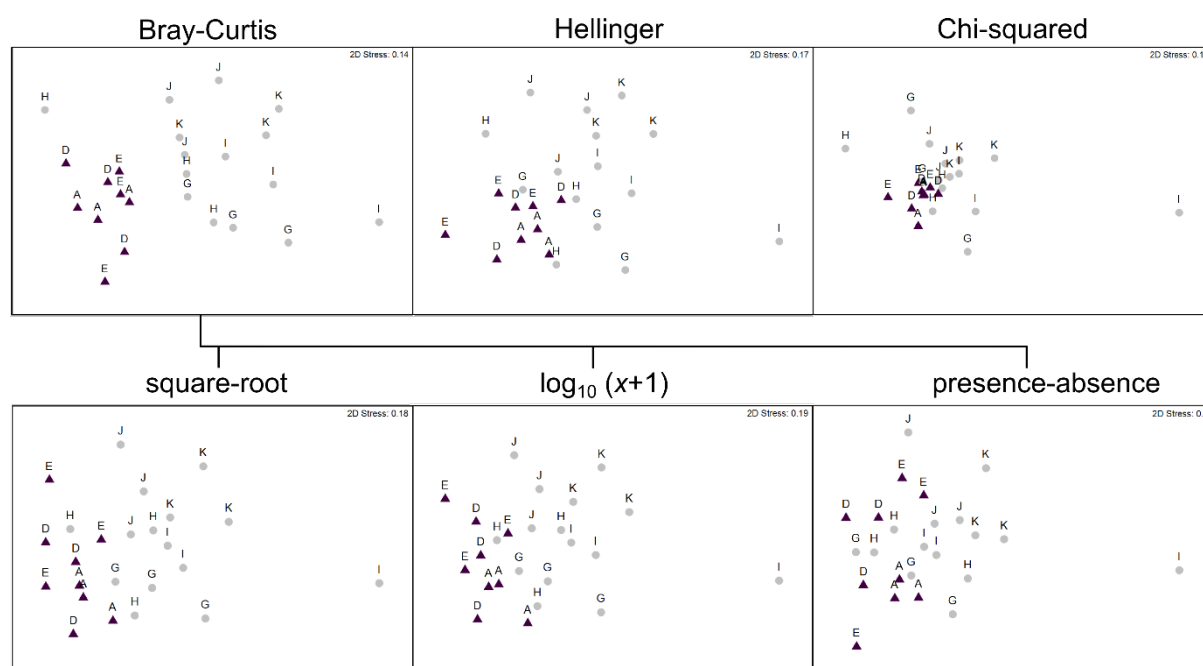


Figure 13: Macro-infaunal communities recorded from multicorer samples: nMDS ordinations of Bray-Curtis similarities among sites (in boxes A to K, labelled) in both regions (MERNOO, black triangles; SOUTH, grey circles) from untransformed, square-root transformed, and presence-absence data.

Ordinations of box centroids showed no obvious relationship between box-level community similarity and trawl history in either region. For example, communities in the least-trawled box in the SOUTH region (G) were more similar to those in the two most trawled boxes (H and I) than to those with intermediate trawling (Figure 14). Because these analyses showed that community composition was broadly similar across the study regions, with no obvious spatial or trawl-associated patterns, differences in taxonomic composition

among survey boxes were not investigated further but results of SIMPER analyses identifying the characteristic taxa in each survey box are shown in Table A 6.

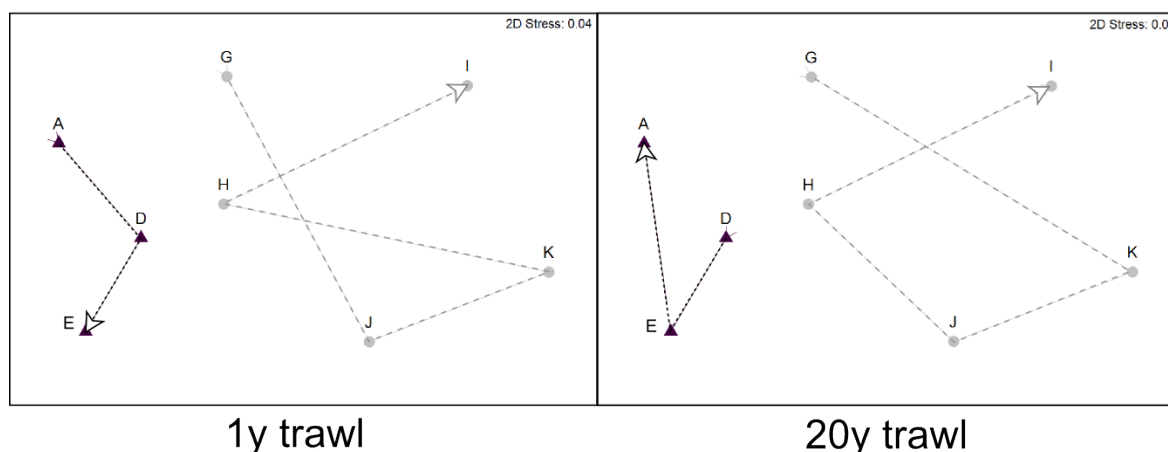


Figure 14: Macro-infauna community change in relation to cumulative trawl disturbance; nMDS ordination of Hellinger distances among box centroids for survey boxes in the MERNOO (A–E, black triangles) and SOUTH (G–K, grey circles) regions, using untransformed abundance data. Superimposed lines with directional arrows show the gradients of increasing average cumulative trawled area over the full 20 years of records (1989 to 2010, '20 y trawl') and the latest year of records (2009–2010, '1 y trawl') per site in each survey box. Ordinations in the left and right panels are identical, with only the trawl gradient trajectories changing.

Bioturbation marks

The bioturbation data were dominated by four types of mark: burrows; the feeding impressions of rat-tail fishes ('rat-tail bite marks', Figure 15); pits, and tracks. Trial nMDS ordinations and SIMPER analyses based on untransformed and log-transformed bioturbation data indicated that distinctions among sites were primarily the result of differences in the relative abundances of these four mark types. The nMDS based on untransformed abundance data (Figure 16) showed a distribution of sites broadly similar to that seen for mega-epifauna, in that sites in the least-trawled boxes (G and D) grouped together away from those in the most trawled boxes (A, H, I, J). Pits occurred at highest density in boxes I, K, and J, burrows occurred at highest densities in boxes I, J, K, and A, and both of these mark types were at lowest density in boxes G and D. Rat-tail bite mark densities were highest in boxes D, G, and H, and lowest in boxes A and I. The ordination of box centroids overlaid with trajectories of increasing cumulative trawled area also showed similar patterns to those seen for the mega-epifauna, with the least-trawled boxes in both regions (D and G) close to each other at one extreme of the ordination space, and the most-trawled boxes (A and I) together at the other extreme (Figure 17).



Figure 15: Rat-tail feeding marks (three ‘bite marks’ made by the snout and mouth of the fish show clearly in the centre of the image) in muddy sediments in the MERNOO region.

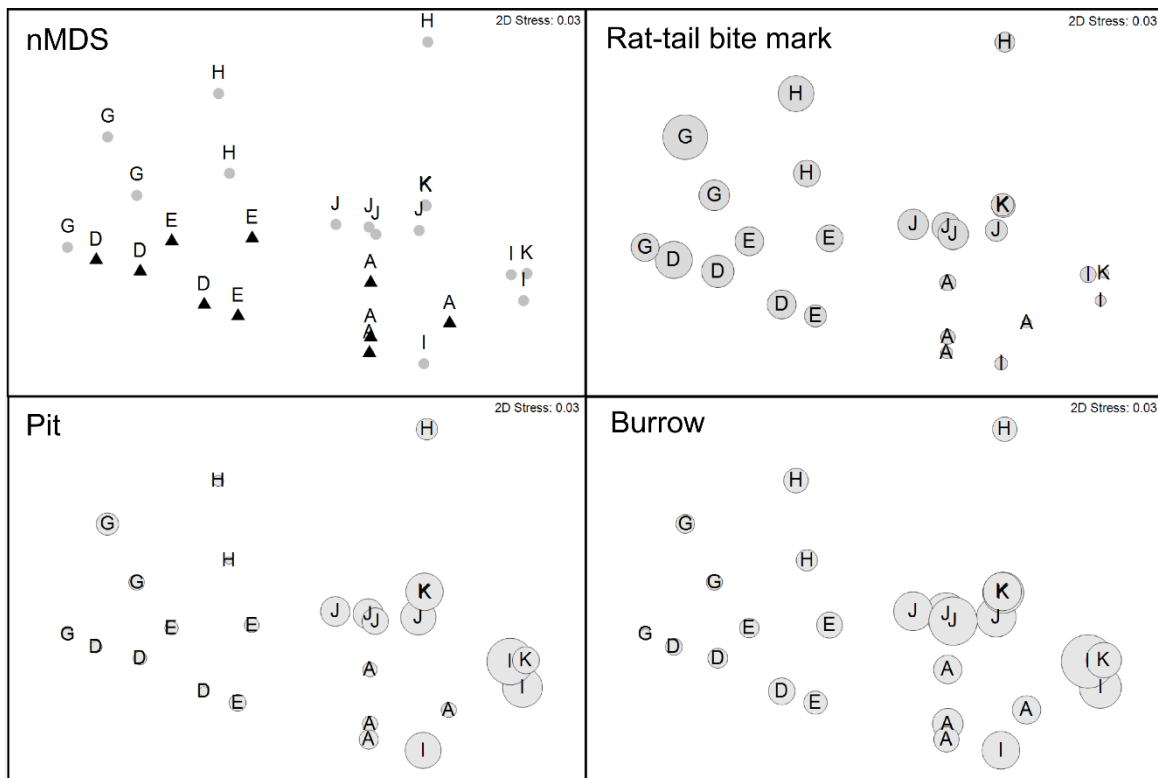


Figure 16: Bioturbation marks recorded from video transects: nMDS ordination based on Hellinger distances calculated from untransformed abundance data, with superimposed bubble plots showing the relative abundances of the three most frequently recorded bioturbation mark types: rat-tail bite marks; burrows, and pits.

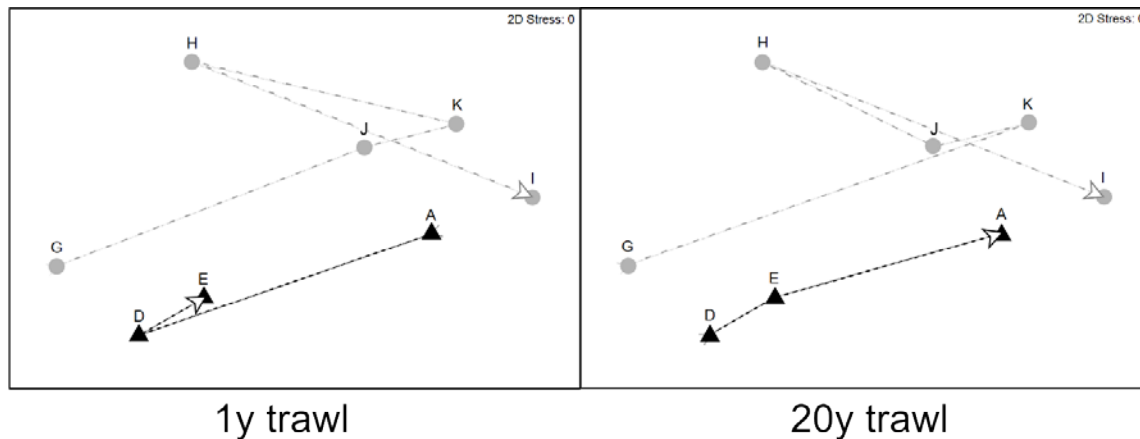


Figure 17: Bioturbation change in relation to cumulative trawl disturbance; nMDS ordination of Hellinger distances among box centroids for survey boxes in the MERNOO (A–E, black triangles) and SOUTH (G–K, grey circles) regions, using untransformed abundance data. Superimposed lines with directional arrows show the gradients of increasing average cumulative trawled area over the full 20 years of records (1989 to 2010, '20 y trawl') and the latest year of records (2009–2010, '1 y trawl') per site in each survey box. Ordinations in the left and right panels are identical, with only the trawl gradient trajectories changing.

3.2 Relationships between community and environment

For each of the main data sets (mega-epifauna, macro-infauna, and bioturbation marks, all using transect-level data), DistLM models were run on both Bray-Curtis similarities and Hellinger distances calculated from untransformed abundance data, and on Bray-Curtis similarities calculated from $\log(x+1)$ transformed data. Models based on \log -transformed data and Bray-Curtis similarity explained the least amount of variance in the data, with none of the three cumulative trawl summaries explaining more than 2–3% of total variance. Models based on Bray-Curtis similarities and Hellinger distances using untransformed data were comparable to each other, particularly with respect to the first explanatory variables selected, but with differences in the amount of total variance explained and the sequence of subsequent variables selected. Below, we show results only from the Bray-Curtis and Hellinger models of untransformed data for each data set.

Mega-epifauna

In marginal tests, spatial and surface productivity variables explained the greatest amount of variance, the greatest individual explanatory power coming from latitude (up to 50 %) in the MERNOO region and surface chlorophyll concentration (up to 18 %) in the SOUTH region, but the 20 y trawl summary explained 41–43 % of total variance (R^2 , based on Bray-Curtis and Hellinger resemblances, respectively) in the MERNOO region and the 1 y trawl summary explained 15–18 % in the SOUTH region. The full DistLM models (sequential tests, Table 3) explained 63–65 % (Adj. R^2) of total community variance in the MERNOO region, with spatial variables explaining 60–61 % and trawling accounting for only 3 %. In the SOUTH region, by contrast, models explained 55–65 % of community variance but spatial variables explained only 30–37 % and the 1 y trawl summary had a statistically significant influence in both Bray-Curtis and Hellinger based models ($P \leq 0.01$), accounting for 8–17 % of total variance.

Table 3: Distance-based linear model (DistLM) sequential test results for relationships between mega-epifaunal community structure and environmental variables, including trawling. Results are shown for models of the MERNOO and SOUTH regions, separately. Each model was run using two resemblance metrics: Bray-Curtis similarity and Hellinger distance, calculated from untransformed abundance data. Spatial variables (latitude, longitude, and depth) were included as starting terms, and the models used stepwise selection with the Adjusted R² criterion. See Table 2 for details of environmental variables). Bold font indicates variables that explain ≥ 10 % of total variance (R²) and have significant influence on the model (P<0.05).

Region	Resemblance	variable	Adj. R ²	SS(trace)	Pseudo-F	P	R ²	Cumul. R ²	res.df
MERNOO	Bray-Curtis	Spatial	0.612				0.741		
		+ 20y_trawl	0.649	858.8	1.6319	0.171	0.064	0.805	5
		+ curvature	0.690	589.5	1.2660	0.344	0.044	0.897	3
		+ 1y_trawl	0.695	482.6	1.0555	0.435	0.036	0.932	2
		+ chla_surf	0.703	469.0	1.0530	0.480	0.035	0.967	1
	Hellinger	Spatial	0.592				0.728		
		+ 20y_trawl	0.621	0.1533	1.4503	0.186	0.061	0.789	5
		+ curvature	0.629	0.1146	1.1069	0.409	0.046	0.835	4
		+ chla_surf	0.629	0.1039	1.0053	0.464	0.041	0.876	3
		SOUTH	Bray-Curtis	Spatial	0.302				0.441
+ 1y_trawl	0.407			3793	3.1301	0.012	0.124	0.565	11
+ curvature	0.417			1410	1.1829	0.286	0.046	0.611	10
+ Range	0.466			2091	1.9150	0.113	0.068	0.679	9
+ vrm	0.546			2402	2.5884	0.042	0.078	0.757	8
+ chla_surf	0.552			1020	1.1144	0.363	0.033	0.791	7
Hellinger	Spatial		0.373				0.498		
	+ 1y_trawl		0.540	0.7512	5.3598	0.005	0.164	0.663	11
	+ chla_surf		0.590	0.2923	2.3398	0.042	0.064	0.727	10
	+ vrm		0.609	0.1782	1.4970	0.185	0.039	0.766	9
		+ Range	0.645	0.2057	1.9013	0.087	0.045	0.811	8

Macro-infauna

In marginal tests, spatial, sediment, and productivity variables explained the highest proportions of variance in both regions (up to 15 % for both surface chlorophyll concentration and depth). The trawl summary periods individually explained 11–13 % of total community variance in the MERNOO region and 8 % in the SOUTH region. The full DistLM models explained 40–56 % of infaunal community variance in the MERNOO region but only 23–27 % in the SOUTH region, and trawl variables were not selected by any of the models in which sediment property variables were available. When sediment variables were excluded, the 1 y and 20 y trawl summaries were the first selected variables in SOUTH region models, each explaining 6–8 % of variance but the total variance explained by the models was only 14–22 %.

Table 4: Distance-based linear model (DistLM) results for relationships between macro-infauna (from multicorer data) and environmental variables, including trawling. Results are shown for Bray-Curtis similarity and Hellinger distance on untransformed taxon density data. Details as for Table 3. Bold font indicates variables that explain ≥ 10 % of total variance (R^2) and have significant influence on the model ($P < 0.05$)

Region		variable	Adj R^2	SS(trace)	Pseudo-F	P	R^2	Cumul. R^2	res.df	
MERNOO	Bray-Curtis	Spatial	0.148				0.467			
		+ Sorting	0.275	1036	1.8757	0.1092	0.170	0.637	4	
		+ Range	0.388	812	1.7432	0.1567	0.133	0.771	3	
		+ Phaeo	0.513	655	1.7668	0.2297	0.108	0.878	2	
		+ Curvature	0.566	412	1.2448	0.4446	0.068	0.946	1	
	Hellinger	Spatial	0.077				0.423			
		+ Sorting	0.167	0.2278	1.5459	0.155	0.161	0.584	4	
		+ vrm	0.231	0.1811	1.3303	0.302	0.128	0.712	3	
		+ curvature	0.335	0.1730	1.4694	0.302	0.122	0.834	2	
		+ Phaeo	0.394	0.1282	1.1952	0.446	0.091	0.924	1	
	SOUTH	Bray-Curtis	Spatial	0.113				0.303		
			+ Sorting	0.206	2145	2.2867	0.010	0.130	0.433	10
			+ MEAN_grain	0.234	1238	1.3688	0.180	0.075	0.508	9
+ PN			0.242	975	1.0887	0.394	0.059	0.567	8	
+ POC			0.268	1111	1.285	0.264	0.067	0.634	7	
Hellinger		Spatial	0.088				0.284			
		+ Sorting	0.166	0.4330	2.0308	0.013	0.121	0.405	10	
		+ MEAN_grain	0.180	0.2440	1.1631	0.315	0.068	0.473	9	
		+ PN	0.187	0.2254	1.0846	0.389	0.063	0.536	8	
		+ POC	0.219	0.2649	1.3267	0.226	0.074	0.610	7	
		+ curvature	0.229	0.2147	1.0888	0.402	0.060	0.670	6	
		+ chla_surf	0.231	0.1997	1.0152	0.460	0.056	0.725	5	

Bioturbation marks

In marginal tests, the 1y trawl summary explained 20 % of variation in bioturbation marks in the SOUTH region, whereas in the MERNOO region, trawl variables each explained only 4–5 % of variance. Full models explained 56–98 % of variance in the data. In the MERNOO region, spatial variables explained 74–77 % of total variance and 20 y trawl was the most influential additional variable, explaining 6 %. In the SOUTH region, spatial variables explained 35–36 % of variance and 1 y trawl was the most important additional variable, explaining an additional 10–17 % of variance and having a statistically significant influence in both the Bray-Curtis and Hellinger models ($P=0.01$, Table 5).

Table 5: Distance-based linear model (DistLM) results for relationships between bioturbation marks (from DTIS video transect data) and environmental variables, including trawling. Bray-Curtis similarities on untransformed density data, with step-wise selection using the Adjusted R² criterion. Bold font indicates variables contributing ≥10 % of explained variance (R²).

Region		variable	Adj R ²	SS(trace)	Pseudo-F	P	R ²	Cumul. R ²	res.df
MERNOO	Bray-Curtis	Spatial	0.769				0.846		
		+ 20y_trawl	0.828	257.4	3.0623	0.079	0.059	0.904	5
		+ curvature	0.860	145.8	2.1234	0.169	0.033	0.938	4
		+ 1y_trawl	0.864	75.1	1.1303	0.402	0.017	0.955	3
		+ aspect	0.882	84.5	1.4690	0.313	0.019	0.974	2
	Hellinger	Spatial	0.745				0.830		
		+ 20y_trawl	0.800	0.0254	2.6530	0.075	0.059	0.889	5
		+ curvature	0.818	0.0130	1.4921	0.253	0.030	0.919	4
		+ chla_surf	0.843	0.0122	1.6231	0.233	0.028	0.948	3
SOUTH	Bray-Curtis	Spatial	0.347				0.478		
		+ 1y_trawl	0.515	1802	5.1496	0.0090	0.167	0.644	11
		+ Range	0.558	657	2.0582	0.1211	0.061	0.705	10
	Hellinger	Spatial	0.563				0.650		
		+ 1y_trawl	0.652	0.1139	4.0994	0.013	0.095	0.745	11
		+ Range	0.671	0.0426	1.6205	0.207	0.036	0.781	10
		+ curvature	0.692	0.0414	1.6831	0.185	0.035	0.815	9

3.3 Influence of trawling

Because the DistLM analyses showed no significant correlation between macro-infauna and trawl history, we concentrated on the mega-epifauna and bioturbation mark data sets for the third stage of the analyses, in which we examined univariate metrics of community structure and the occurrence of functional types, sensitivities, and individual taxa and bioturbation mark types in relation to trawl history. We did, however, first calculate univariate indices of community structure for macro-infauna and found that none were correlated with any of the trawl history metrics in either region.

Mega-epifauna

Univariate community metrics

When averaged by survey box, the number of megafaunal individuals (N) was highest, and community evenness (J') and diversity (1-λ') were lowest, at the highest intensity of trawling (Box I in the SOUTH region) (Figure 18), while evenness was highest at the lowest intensity of trawling (Box G, SOUTH region). Largely because of the differences between these two survey boxes (I and G), increasing trawl intensity in the SOUTH region was associated with trends of increasing numbers of individuals (R²=0.120, regression based on individual sites), and declining community evenness (0.237) and diversity (0.170). These trends were strongest for the most recent year of trawl data in both regions but were not statistically significant (P>0.05). Total numbers of taxa (S) showed no clear trend in either region.

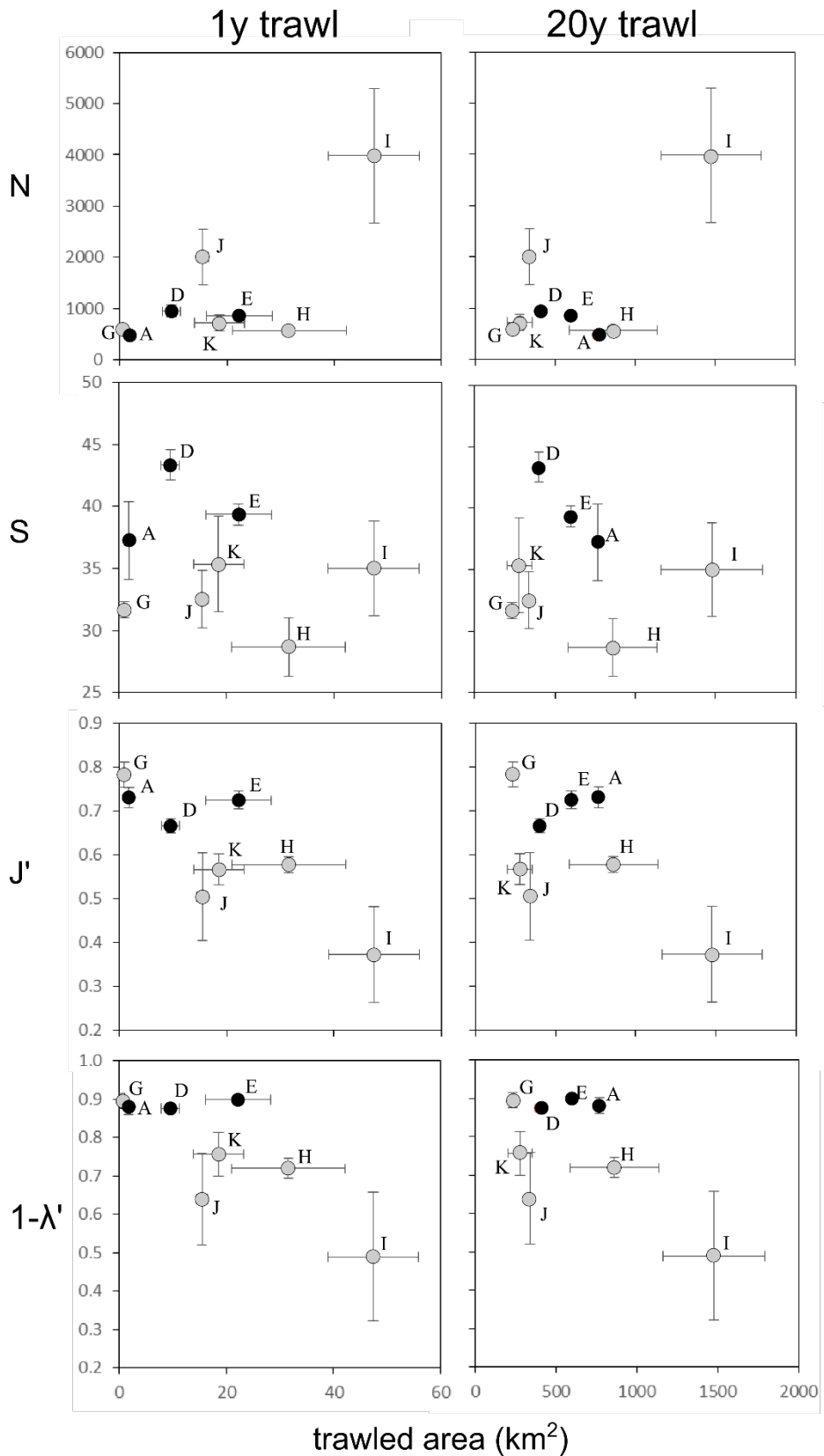


Figure 18: Mega-epifauna: univariate metrics of community structure in the MERNOO (black symbols) and SOUTH (grey symbols) regions, plotted as box means ($\pm 1se$) against cumulative trawled area (box mean $\pm 1se$) in the year 2009–10 (1 y trawl) and over the period 1989–2010 (20 y trawl). N; total number of individuals, S; total number of taxa, J' ; Pielou's Evenness, $1-\lambda'$; Simpson's diversity. Letters identify survey boxes. Trawled area is taken as the total seabed swept area in 5×5 km grid cells in which each sample site is located.

Functional trait classes

The traits associated with each of the six k-means traits classes (K1-K6, derived without assigning sensitivity rankings to traits) were identified by SIMPER (Table A 7) and summarised as: *mobile deposit-feeders* (K1); *sessile suspension-feeders* (K2); *large predator/scavengers* (K3); *small predator scavengers* (K4); *sedentary predators* (K5), and *sessile filter-feeders* (K6). The characteristic taxa represented by each of these classes are shown in Table A 8, ranked by the number of sites at which each was recorded and with their corresponding sensitivity group membership. Total abundances in each of these traits classes were then examined in relation to trawl intensity gradients. Because relationships with all three trawl summary time periods were very similar, only the most recent year of trawling (1 y trawl) is shown for illustration (Figure 19).

Mobile deposit-feeders (K1) and sessile suspension-feeders (K2) were the most abundant taxa overall, the numerically dominant taxa in these classes being the quill worm *Hyalinoecia longibranchiata* in K1, and the solitary soft coral *Taiaroa tauhou* and the pennatulacean *Kophobelemnion* sp. in K2. Small predator-scavengers (K4; predominantly pagurid crabs, whelks [Buccinidae], and indeterminate errant worms) and sedentary predators (K5; anemones, onuphid worms, *Flabellum* spp. solitary corals and others) occurred at intermediate abundances across all sites. Large predator-scavengers (K3; asteroids, *Epizoanthus* sp. and its associated crab host, octopods, and others) and sessile filter-feeders (K6; sponges and ascidians) occurred at lowest abundances across all sites. Across all sites combined, there was a weak trend (OLS regression, Adj. $R^2=0.11$, $P=0.06$; DistLM, Adj. $R^2=0.13$, $P=0.04$) for increasing abundance of sessile suspension-feeders (K2) with increasing trawl intensity (Figure 19), which was driven largely by very high abundances of *T. tauhou* and *Kophobelemnion* sp. in survey boxes I and J, respectively, and absence of these taxa in box A (Figure 20, Table A 4). Small predator-scavengers (K4; primarily pagurid crabs) were also at highest abundance at sites in boxes I and J (Figure 20, Table A 4). Within regions, however, there were no obvious relationships between trait class abundances and trawl intensity gradients.

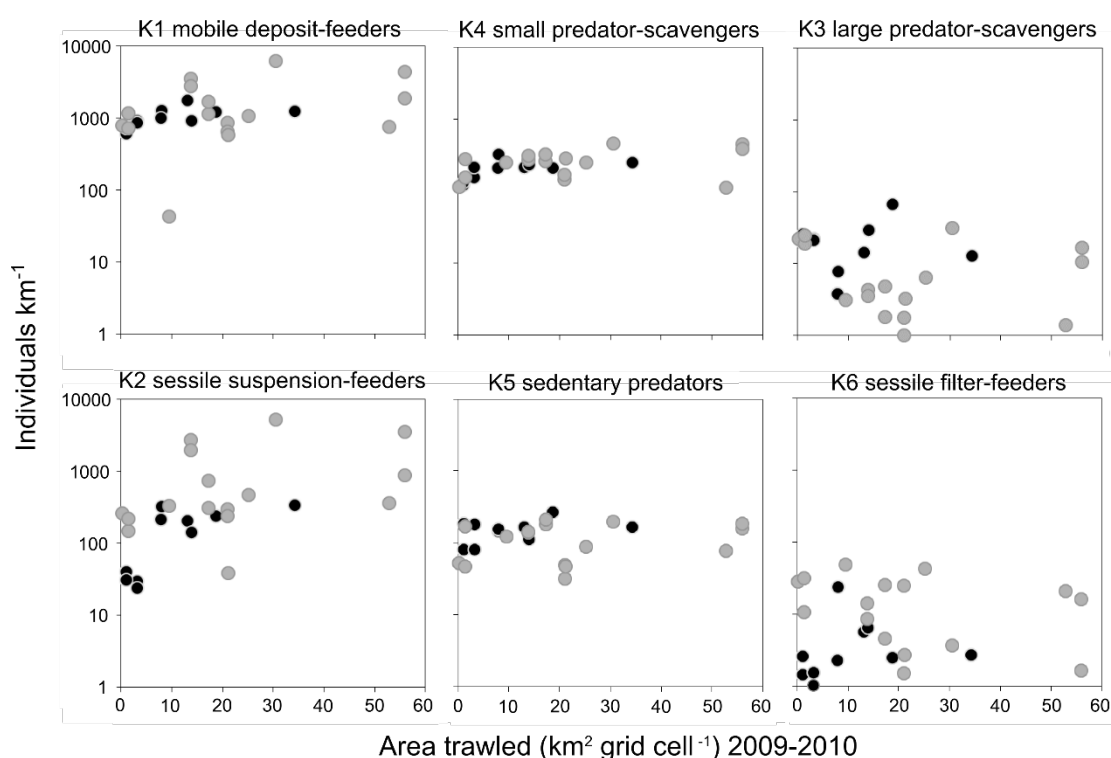


Figure 19: Mega-epifaunal functional traits classes: abundance per site in relation to total trawled area for the year 2009–2010. Plots are organised into mobile taxa (upper panels) and sessile and sedentary taxa (lower panels) and show values from individual sites differentiated by region (MERNOO black, SOUTH grey). Log y scales for all plots.

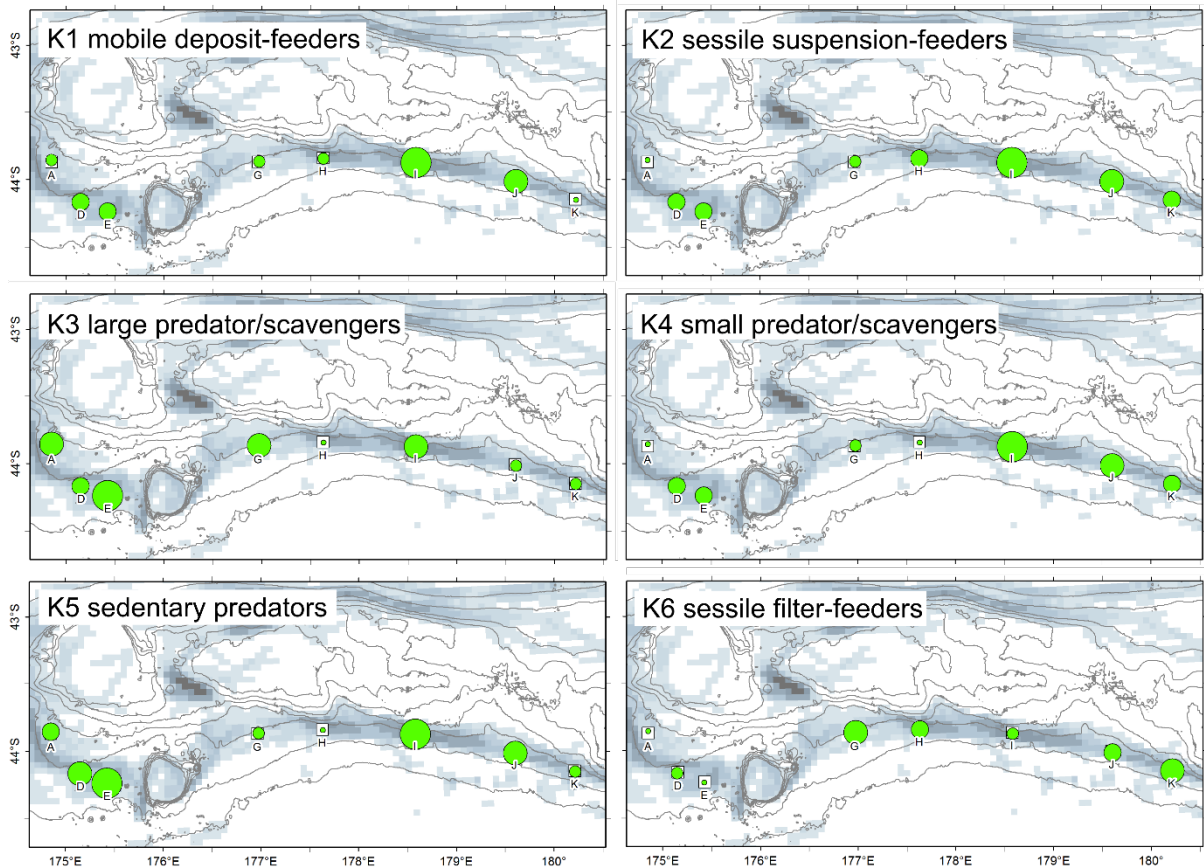


Figure 20: Relative occurrence of mega-epifaunal taxa in six biological traits-based classes in relation to trawl history. Blue gradient fill indicates relative intensity of trawling for the 2009–2010 fishing year (most trawling in darkest shading), green expanding symbols indicate relative mean abundances of each traits class within each survey box (labelled A–K). Note, symbols are scaled to the same maximum diameter in each map, thus, abundance comparisons are valid within but not between maps.

Sensitivity groups

The functional traits associated with each of the five sensitivity classes (classes G1–G5, derived by weighting traits with putative sensitivity rankings, G1 being least sensitive and G5 most sensitive) were identified by SIMPER analysis and summarised as: G1, *small predator/scavengers*; G2, *large predator/scavengers and deposit-feeders*; G3, *small sessile suspension-feeders and sedentary predators*; G4, *medium-sized sessile suspension- and filter-feeders*, and G5, *large sessile suspension- and filter-feeders*. When plotted against each of the trawl summary periods, variations in the abundance of the most sensitive groups (G4 and G5) conformed to the hypothesised threshold decline response (e.g. for 20 years of trawling, Figure 21, top right), whereas the numbers (and proportional representation; results not shown) of taxa in these groups did not (e.g. for 20 years of trawling, Figure 21, lower right). These analyses also showed that the most taxon-rich groups across all sites were those representing the least sensitive taxa (G1 and G2), and that intermediate sensitivity taxa (G3) were the most abundant. The G3 intermediate sensitivity taxa also showed a trend of increasing abundance with increased trawl disturbance. These points are clearer when the data for all groups are plotted on the same graph as mean values per survey box (e.g. for most recent year of trawling, Figure 22).

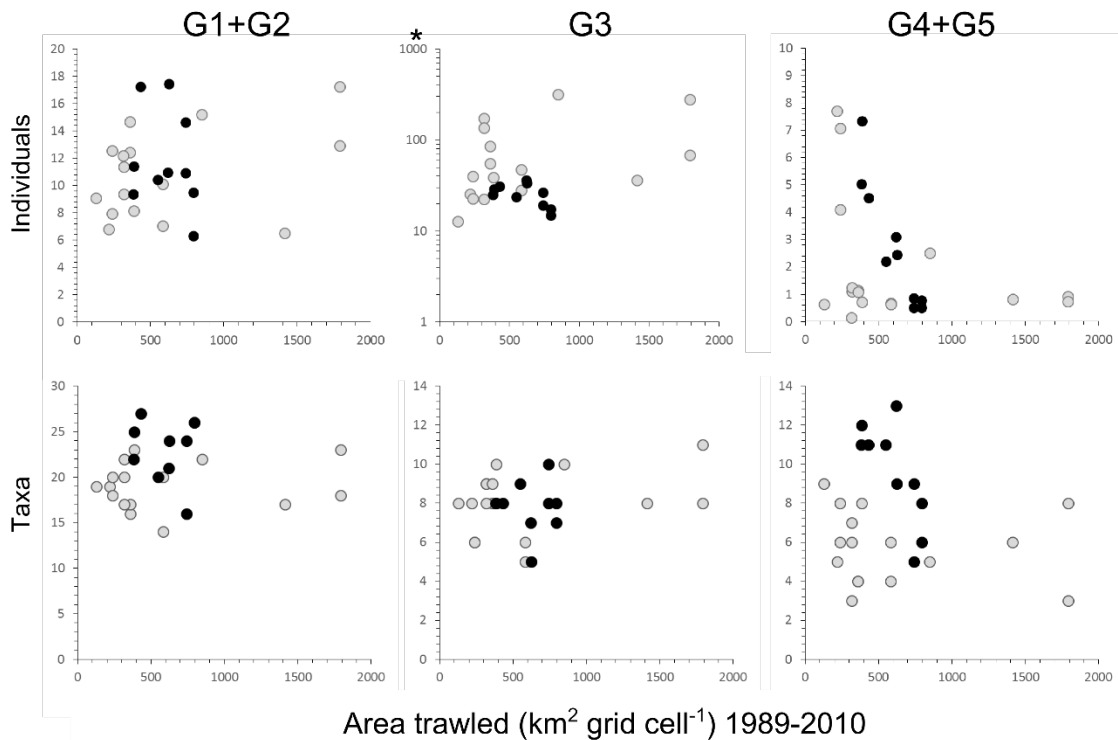


Figure 21: Occurrence of mega-epifaunal taxa in five sensitivity classes (G1, least sensitive, to G5, most sensitive) in relation to cumulative trawled area per 5×5 grid cell for the period 1989–90 to 2009–2010 (20 y trawl). The top row of graphs shows the abundance of each sensitivity group at each site (number of individuals km^{-1} standardised by the number of taxa at each site), while the bottom row shows the number of taxa per sensitivity group per site. *Note log scale for G3 abundance.

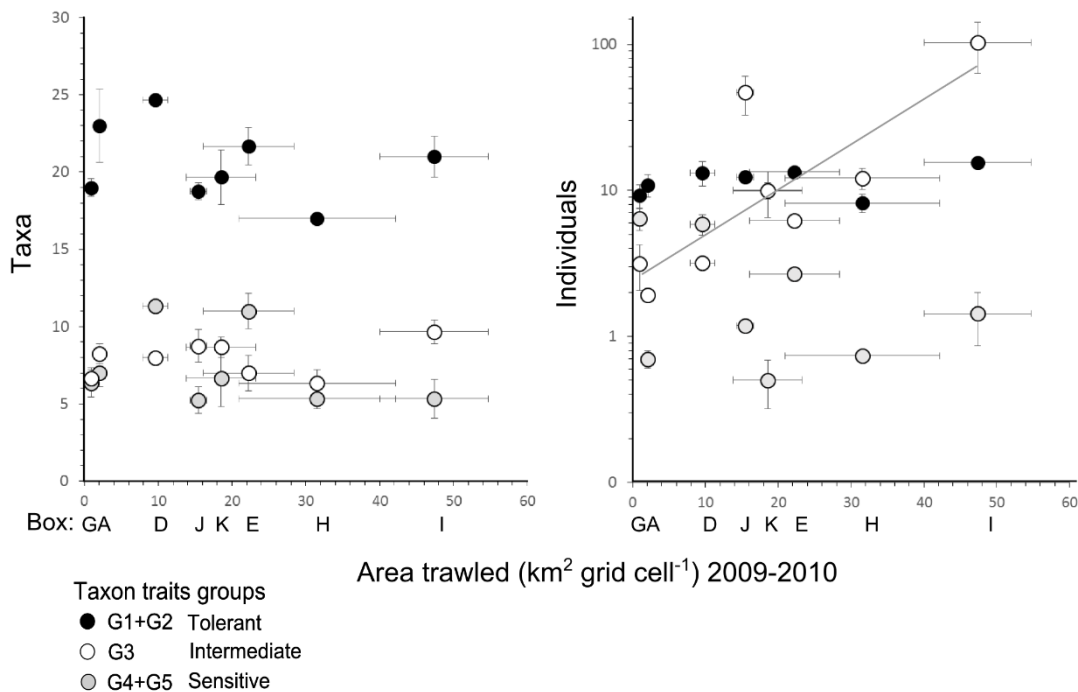


Figure 22: Occurrence of taxa in five sensitivity classes (G1, least sensitive, to G5, most sensitive, see symbol key) in relation to cumulative trawled area during the most recent year of trawl data ('1 y trawl', 2009–2010), with both variables summarised as mean values ($\pm 1\text{se}$) in each of the 8 survey boxes (A to K, labelled along the x-axis) across the entire study. The regression line in the Individuals plot is for log-transformed abundances of G3 intermediate sensitivity taxa and is significant at $P=0.03$ (Adj $R^2=0.5$).

Bioturbation marks

Because bioturbation marks are likely to be ephemeral over short time periods, we examined relationships between each of the four most common mark types and cumulative trawled area in the most recent year of trawl records (Figure 23). The density of rat-tail feeding marks decreased with increasing cumulative trawled area in the SOUTH region (OLS, Adj. $R^2=0.45$, $P<0.01$; DistLM, Adj. $R^2=0.41$, $P=0.005$) (Figure 14), while the density of large burrows increased (Adj. $R^2=0.3$, $P=0.016$; DistLM, Adj. $R^2=0.13$, $P=0.029$). Small burrows, pits, and mounds showed weak trends of increase in density with increased trawling in the SOUTH region, but none of these were supported in regressions (Adj. $R^2 <0.1$, $P>0.1$ for all) (Figure 14).

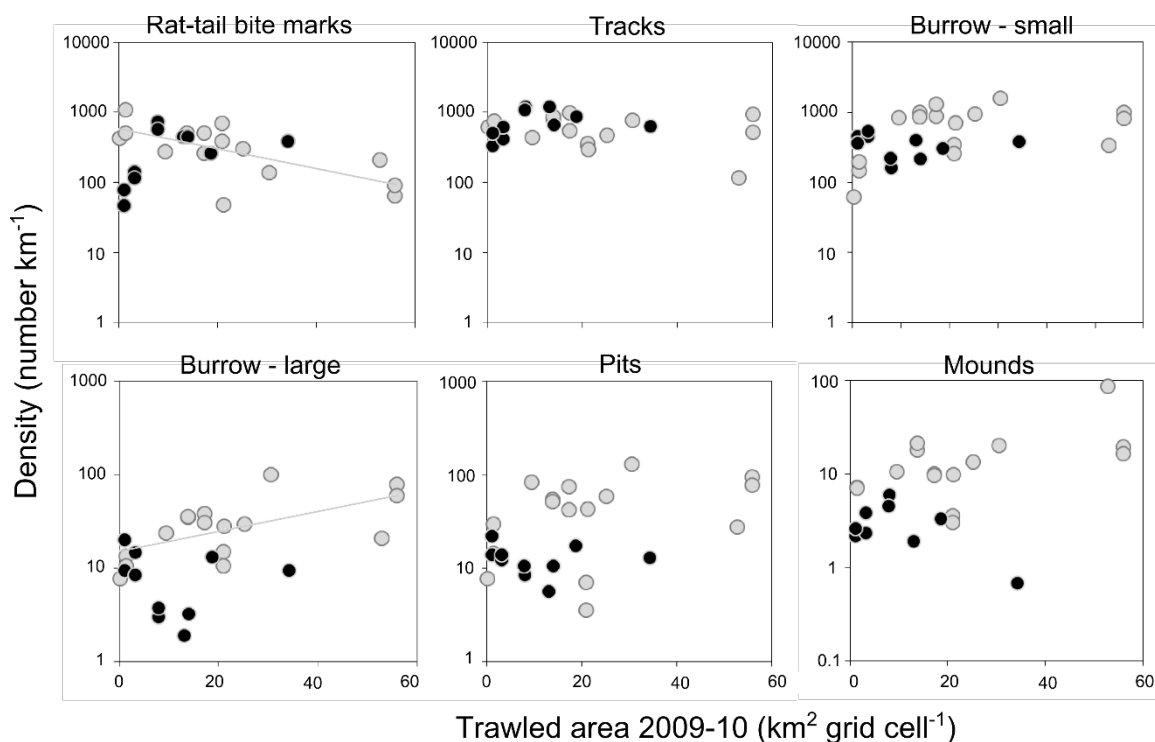


Figure 23: Densities of bioturbation mark types observed in video transects in relation to cumulative trawled area per 5×5 km grid cell in the fishing year 2009-10. Plots represent individual transects from survey boxes in the MERNOO (black symbols) and SOUTH (grey symbols) regions. Note log y scales for all plots. Regression lines are shown for statistically significant relationships ($P<0.05$) for rat-tail bite marks and large burrows in the SOUTH region.

4. DISCUSSION

As far as we are aware, this is only the second study to explore benthic community change along gradients of chronic trawl disturbance in the deep-sea beyond continental shelf depths. Our study differs from the first such study by Cryer et al. (2002) through using a purpose-designed sampling strategy with methods appropriate for sampling both mega-epibenthic and macro-infaunal communities, and by examining effects within a single fishery; the Chatham Rise hoki fishery. Through use of acoustic and photographic imaging of the seafloor, we were also able to ensure that all samples included in our analyses were taken from open muddy sediments and thus a single type of habitat. This was done to avoid potential confounding factors associated with changes in environmental heterogeneity but an important consequence is that all sites in our study will have been trawled to a greater or lesser extent during the previous twenty years of the fishery.

Thus, our data represent a chronically disturbed ecosystem and include no undisturbed reference sites or previously trawled areas that have been closed to fishing.

As noted in prior studies of trawling effects on benthos (Dayton et al. 1995, Jennings & Kaiser 1998, Cryer et al. 2002), the likelihood of failing to detect an effect of fishing where one actually exists (Type II error) is high in mensurative studies such as this, which necessarily span broad spatial and temporal scales because these are the scales at which the fisheries operate. Because our study was designed to sample entirely within the established hoki trawl fishery footprint and within a single habitat, it might be anticipated that the likelihood of detecting clear effects of trawling would be further reduced. We also took a conservative approach at all stages of the analyses, for instance, in selecting only muddy sediment sites, which reduced the number of samples in the MERNOO region to a bare minimum (whereas it would have been simple to have included heterogeneous substrata from boxes C, B, and F and thus shown a pronounced 'effect' of trawled versus un-trawled, simply through inclusion of other habitats), restricting the sampled depth range, and by forcing inclusion of spatial variables as starting terms in regression analyses. Furthermore, given that the most recent trawl history data available when the study was designed and executed were from 2004–05, eight years before sampling for this study took place, it is also likely that the survey sites could have been better placed to span recent trawl gradients than they were. Despite this, we found correlations between trawl history and community structure and function that correspond to predicted effects of trawling.

Through the three stages of our analyses, we have shown: first, that there are patterns in the spatial variability of epibenthic communities that are not explained by location, depth, or any of the other environmental variables; second that these patterns are correlated with gradients of cumulative trawl disturbance, and third, that the community-level effects of trawling are manifested more as changes in the densities of taxa than in the taxonomic composition of communities. Increased trawling was associated with decreased evenness, and hence diversity, of epifaunal communities. Declines in these community-level indices were a consequence of decreased densities of taxa with functional traits most sensitive to disturbance (primarily sessile filter- or suspension-feeders including the soft coral *Anthomastus* sp., *Flabellum* spp. scleractinian corals, sponges, and ascidians), and increased densities of taxa with intermediate or low sensitivity to trawling (notably the solitary octocoral *Taiaroa tauhou*, the sea-pen *Kophobelemnon* sp., and pagurid crabs). Increased trawling, in the SOUTH region at least, was also correlated with a decrease in the density of rat-tail feeding marks and an increase in the density of burrows.

These observations conform broadly with the results of studies of trawling effects on soft sediment benthos in other regions, particularly with respect to the declines in diversity and the densities of sensitive epifaunal taxa, and the increases in the densities of less-sensitive traits and infaunal activity (as indicated by large burrows). That the functional groups occurring in highest density throughout our study area were primarily small mobile deposit feeders, particularly the quill worm *Hyalinoecia longibranchiata* and small shrimps, the small sessile suspension-feeders *T. tauhou* and *Kophobelemnon* sp., and small predator scavengers, also matches predictions from studies of trawled areas elsewhere (summarised in Thrush & Dayton 2002) and seems likely to be a symptom of the chronically disturbed nature of seabed habitats at these depths on the flanks of Chatham Rise. Comparing our results with those of Cryer et al. (2002), statistical models in both studies explained up to 70 % of total community variance and after excluding the influence of depth and location, trawling explained more than 10 %. Both studies also found declines in mega-epifaunal diversity with increased trawling but whereas in the present study this decline was mainly the result of reduced evenness, Cryer et al (2002) also detected reduced species richness. That we found no evidence of reduced species richness, in terms of simple counts of taxa present, might be a reflection of the lower taxonomic resolution achievable with video sampling compared with scampi trawls and the smaller seabed area sampled by video transects (about 2000 m² versus 140 000 m²). It is also possible, however, that it is a consequence of the habitat criteria applied here. That is, because our samples are all constrained to be from a single habitat within the trawl footprint, we are effectively sampling towards one end of a disturbance gradient where we might expect the local species pool to be reduced.

The relationships with trawl gradients were only for mega-epifaunal communities and bioturbation marks recorded in camera transects; no comparable relationships with trawl disturbance gradients were detected

in parallel analyses of macro-infaunal communities. There are practical and ecological reasons why this may not be surprising. First, the camera transects integrate over spatial scales of approximately 1 km and thus approximate more closely to the spatial scale of the trawl data (5 × 5 km grid), than do the point-sampled multicorer data. Within even the most highly trawled areas, trawling is likely to generate a fine-scale patchwork of seabed areas representing a range of times since disturbance. Thus, as the size of the sampling unit decreases, fewer such patches will be spanned, and it becomes more likely that a given sample will come from an ‘atypical’ patch at the extremes of the disturbance scale (Andrew & Mapstone 1987). Second, because of their infaunal habit and small size, it is likely that macro-infaunal taxa are less susceptible to disturbance than larger epifaunal taxa. To determine whether the lack of trawl effects on macro-infaunal communities seen in our results is a consequence of either sampling scale or lower sensitivity of macro-infauna to trawl disturbance would require either increased replication of sampling within survey boxes (Thrush et al. 1998, for instance collected n=15 replicate cores per site), or finer-scale spatial resolution of the trawl history data, neither of which would have been an achievable option in this project. Because smaller faunal size classes (macro- and meio-fauna) dominate biomass in deep-sea sediments and their activities account for much of the cycling of nutrients and minerals (Leduc et al. 2016), any future evaluation of the effects of deep-sea trawl fisheries on ecosystem-level processes and services is likely to be dependent on provision of trawl event data at much finer spatial resolution than is presently available.

It is perhaps surprising that the two taxa occurring at highest densities in the most trawled sites, *T. tauhou* and *Kophobelemnion* sp., should be sessile suspension-feeders. The traits of emergent sessile habit and suspension-feeding are usually associated with sensitivity to disturbance, and both soft corals and sea-pens are usually ranked highly in terms of sensitivity (e.g., de Juan & Demestre 2012). However, seabed images and recovered specimens show that both of these taxa are not only small in terms of height above the seabed (less than about 5 cm) but are also anchored to a depth of some centimetres within the sediment by a pronounced foot or peduncle. These characteristics resulted in both taxa being placed in the ‘G3’ intermediate sensitivity class here, yet still images show both of these taxa at high densities at sites that, from the presence of well-defined trawl marks in the sediment, had clearly been impacted directly and recently by trawling (Figure 24). This suggests that these two taxa are actually either highly resistant to trawl disturbance, or are able to recruit rapidly following trawl disturbance. Individuals of *T. tauhou* at these sites were similar in appearance to those at all other sites, including those with least trawl disturbance, but *Kophobelemnion* sp. individuals were much shorter than sea pens recorded at sites in the un-trawled survey boxes B, C, and F, which were measured at up to 35 cm in length. Because all fauna were identified from photographs and video, rather than physical specimens, it is possible that these are separate species with different growth forms, and that the small form, *Kophobelemnion* sp., is resistant to trawl impacts because it is not tall enough to be impacted by the gear. Alternative explanations, however, are that either the short individuals seen in the highly trawled boxes have been truncated by trawl impact, or that these are relatively new recruits at an early growth stage. With the present data we cannot distinguish between these explanations but if the truncation hypothesis were to be correct, it would suggest the need for some assessment of physical condition or developmental stage to be incorporated into assessments of community status.

In summary, this study has demonstrated quantifiable effects of variations in seabed trawling intensity on benthic epifaunal, but not infaunal, communities on the southern flank of Chatham Rise. These effects are manifested as decreases in the evenness and diversity of communities, and in the densities of taxa with functional traits sensitive to disturbance, and increases in the densities of some smaller taxa that are presumably either highly resistant to trawl disturbance or are able to recolonise rapidly following disturbance. Reductions in epifaunal diversity and the loss of functional types may have wider effects on the ecosystem, perhaps the most direct of which would be reduction in the availability of prey items for benthic-feeding demersal fishes. The reduced density of rat-tail feeding marks at higher trawling intensities observed here has several potential explanations, including that there are fewer of these fishes in the most-trawled areas because they are caught in trawls, that their feeding marks are erased more rapidly by trawling, and that trawling reduces benthic prey availability. If the latter explanation were correct, it would have wider implications for ecosystem effects of fishing.

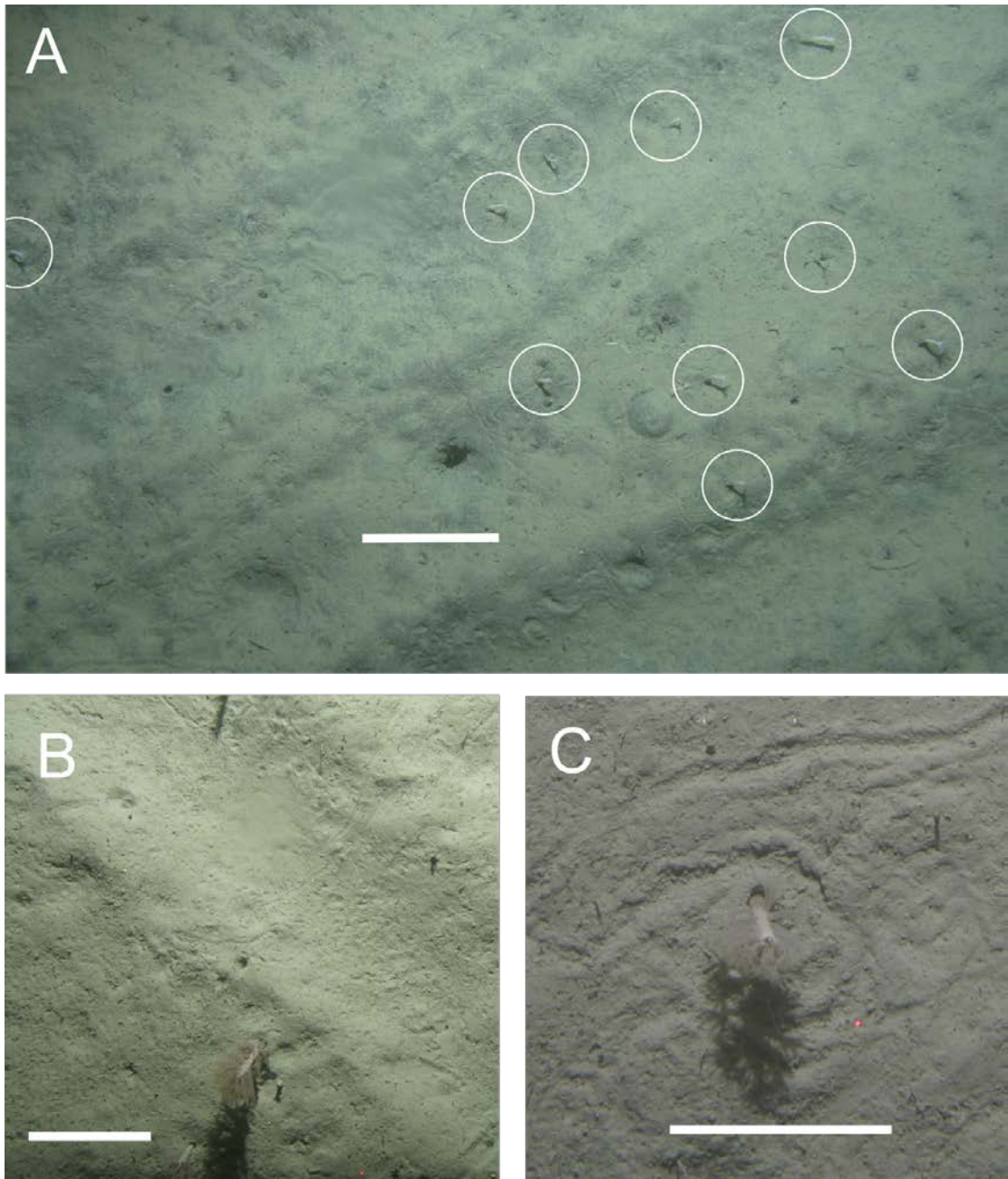


Figure 24: Seabed images from survey box I (A) showing *Taiaroa tauhou* solitary soft corals (circled) on muddy sediments with diagonal striations from trawl gear (DTIS image: TAN1306_070_010), and survey box J (B and C) showing the pennatulacean *Kophobelemnion* sp., with proximity to trawl bobbin furrow clear in (B). Scale bars: (A) 20 cm, (B and C) 10 cm.

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7. APPENDIX 1 – Maps

MERNOO bathymetric maps

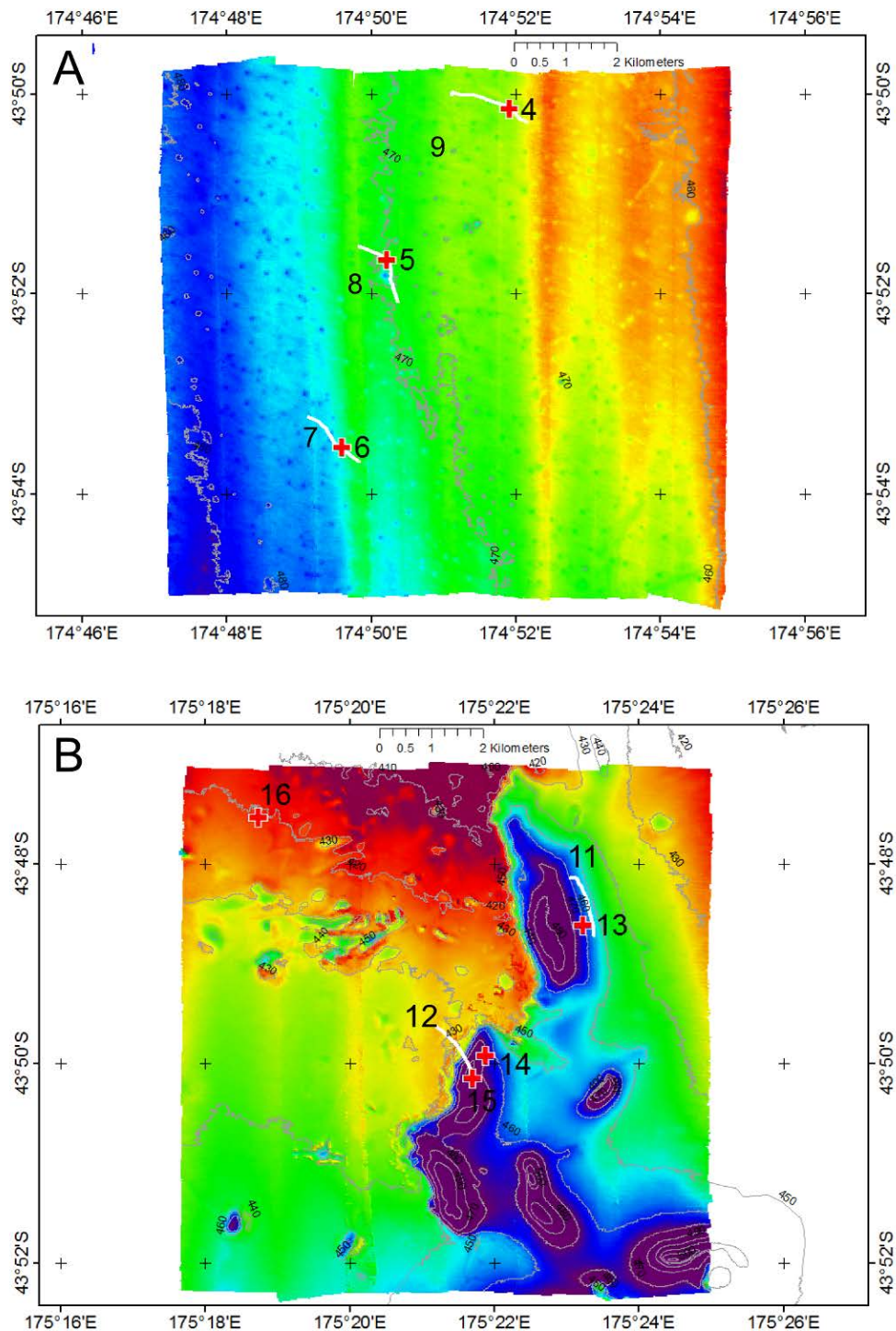


Figure 25: Survey Boxes A and B in the MERNOO study region, showing multibeam bathymetry and location of DTIS transects (white lines) and multicorer deployments (red crosses). See Figure 2 for context. Large black numerals are sequential station numbers for gear deployments (see Station Record table for details), small black numerals show depths in metres.

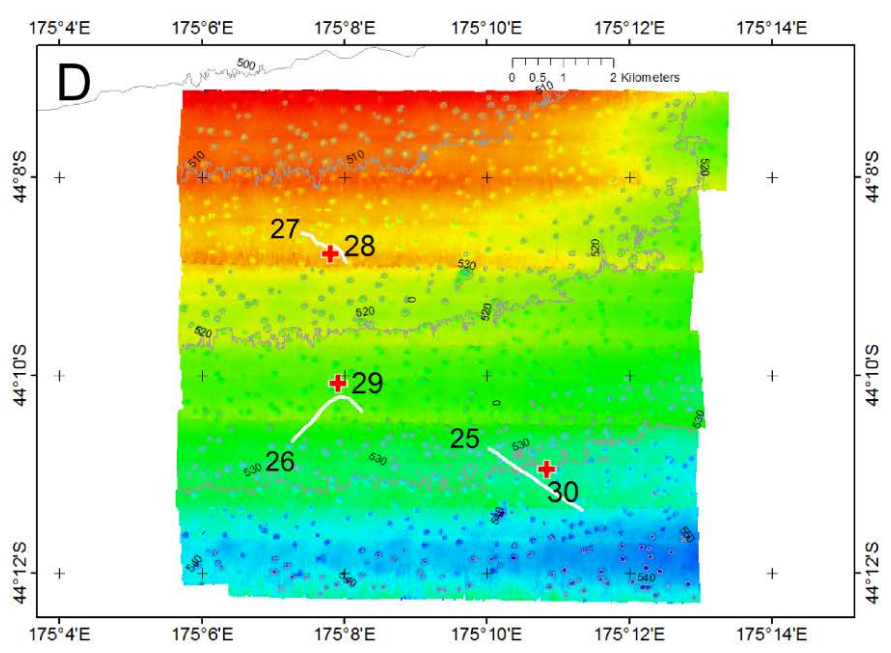
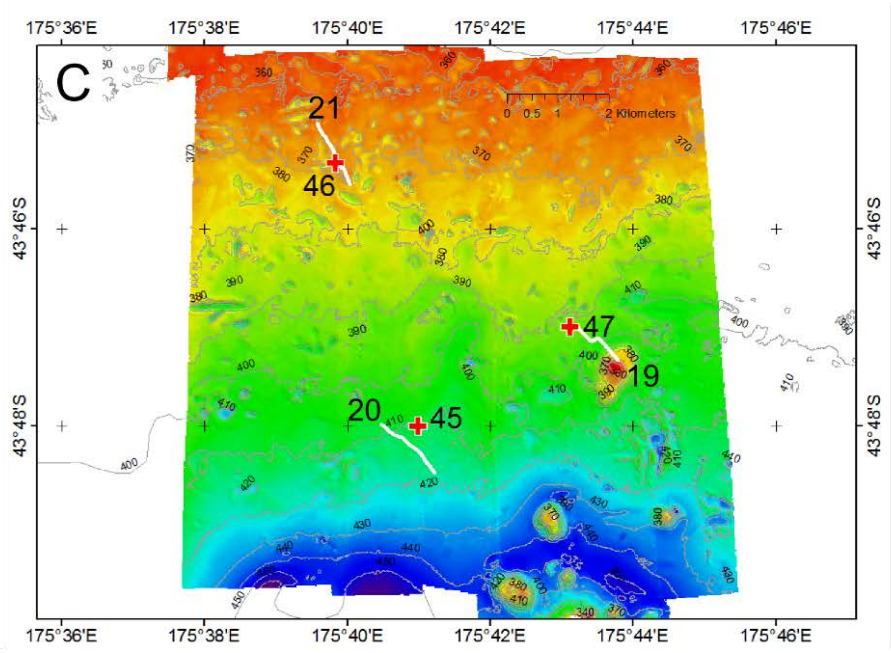


Figure 26. Survey Boxes C and D in the MERNOO study region, details as for Figure 3.

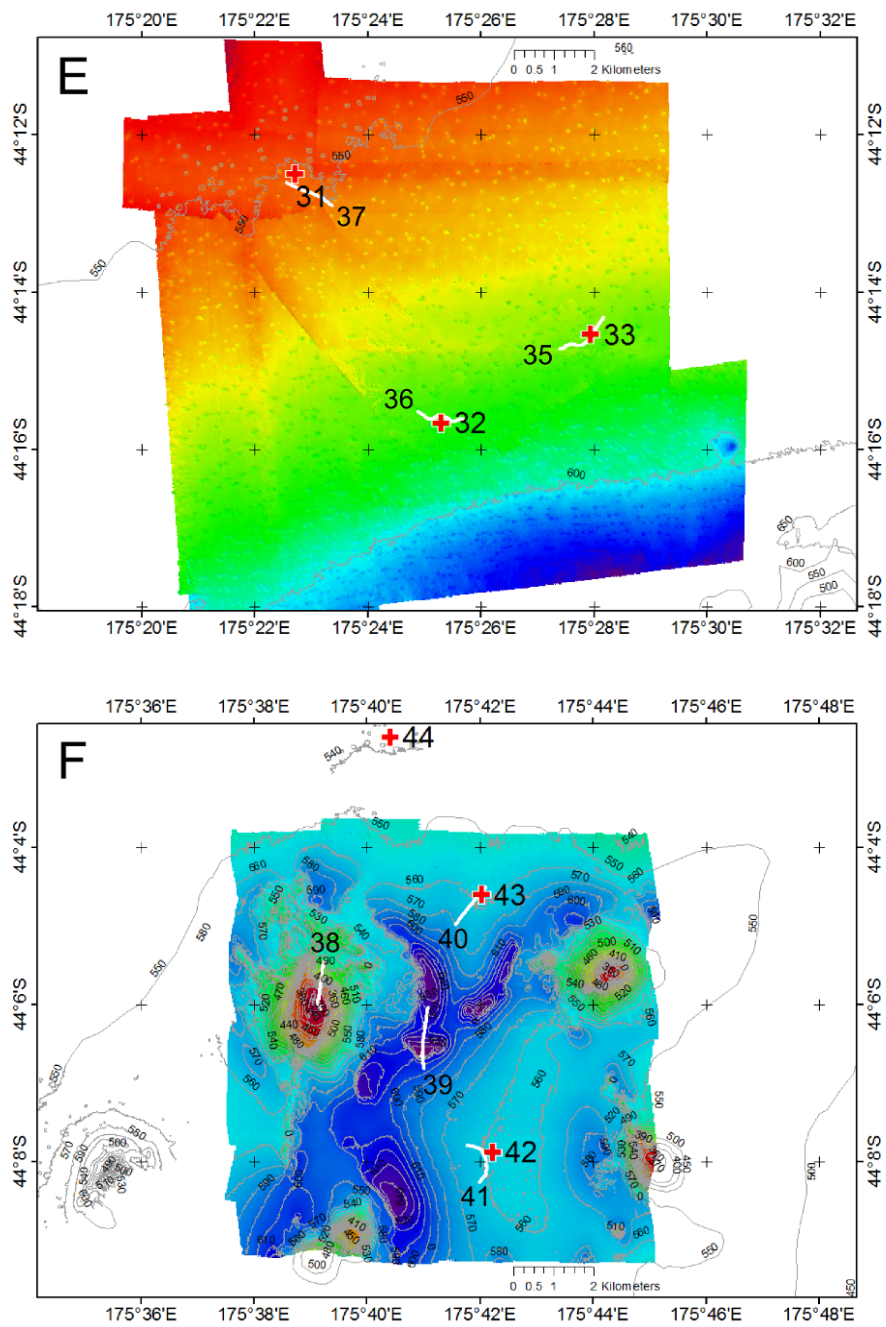


Figure 27: Survey Boxes E and F in the MERNOO study region, details as for Figure 3. (Note, Box F map is shown at a smaller scale to include multicorer station #44).

SOUTH bathymetric maps

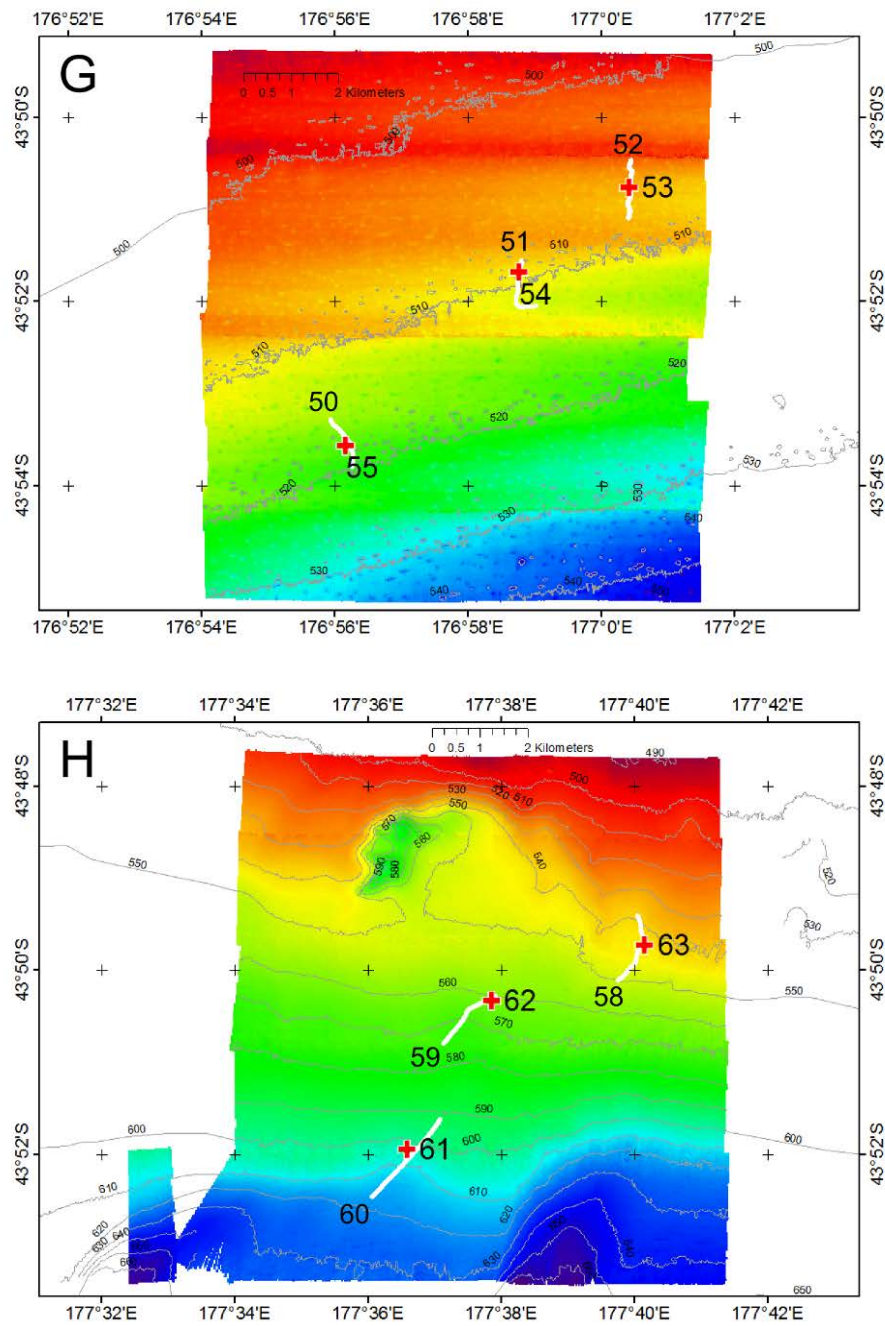


Figure 28: Survey Boxes G and H in the SOUTH study region, details as for Figure 3.

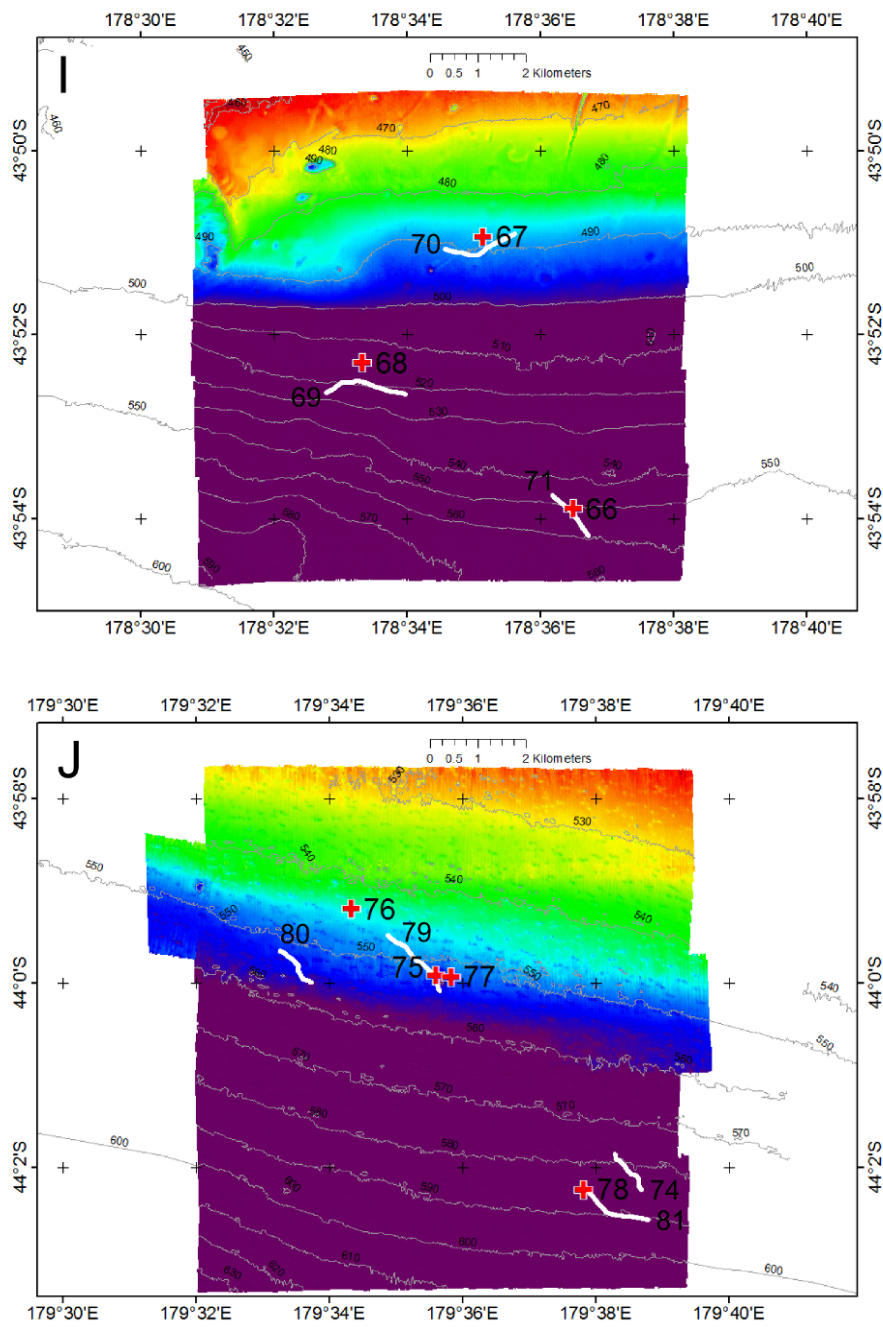


Figure 29: Survey Boxes I and J in the SOUTH study region, details as for Figure 3.

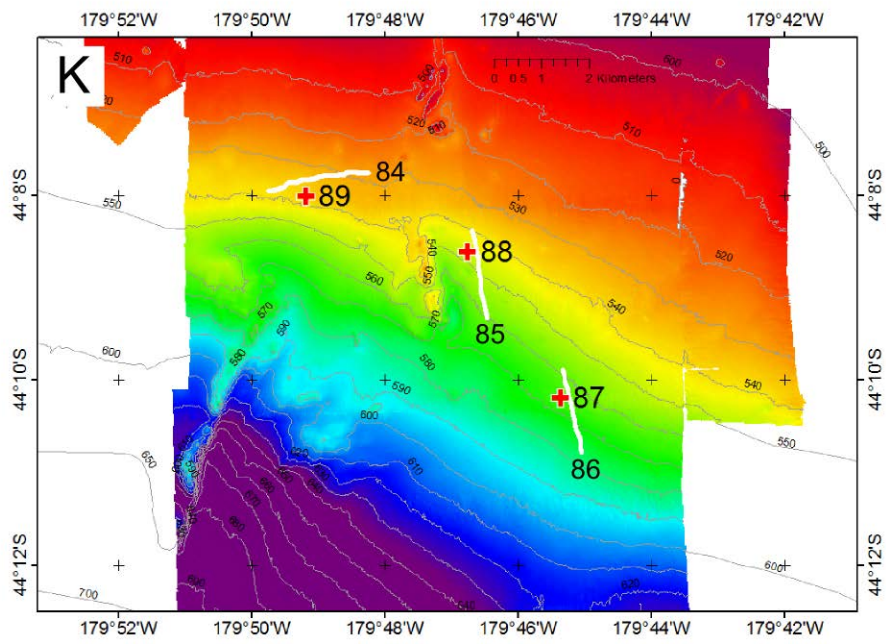


Figure 30: Survey Box K in the SOUTH study region, details as for Figure 3.

8. APPENDIX 2 – Tables

Table A 1: Samples collected during voyage TAN1306 and used in the study of fishing gradient effects on the benthos. DTIS; Deep Towed Imaging System, MUC; multicorer. Depths in metres.

station	method	region	box	site	date_start	time_s	lat_start	Lon_start	E-W	lat_end	lon_end	E-W	depth_start	depth_end
3	DTIS	MERNOO	A	1	6-Jun-13	11:39	-45.8383	174.8632	E	-43.8373	174.8827	E	459	458
4	MUC	MERNOO	A	1	6-Jun-13	15:17	-43.8358	174.8652	E				460	
5	MUC	MERNOO	A	2	6-Jun-13	16:07	-43.8610	174.8370	E				464	
6	MUC	MERNOO	A	3	6-Jun-13	16:51	-43.8923	174.8267	E				470	
7	DTIS	MERNOO	A	3	6-Jun-13	18:33	-43.8937	174.8167	E	-43.8865	174.8167		468	
8	DTIS	MERNOO	A	2	6-Jun-13	21:01	-43.8667	174.8388	E	-43.8585	174.8290	E	464	467
9	DTIS	MERNOO	A	1	6-Jun-13	22:59	-43.8377	174.8680	E	-43.8337	174.8522	E	459	463
25	DTIS	MERNOO	D	1	9-Jun-13	04:36	-44.1890	175.1875	E	-44.1782	175.1647	E	527	520
26	DTIS	MERNOO	D	2	9-Jun-13	06:51	-44.1718	175.1358	E	-44.1793	175.1193	E	520	522
27	DTIS	MERNOO	D	3	9-Jun-13	09:04	-44.1472	175.1330	E	-44.1432	175.1223	E	510	508
28	MUC	MERNOO	D	3	9-Jun-13	11:13	-44.1462	175.1302	E				510	
29	MUC	MERNOO	D	2	9-Jun-13	11:52	-44.1680	175.1320	E				517	
30	MUC	MERNOO	D	1	9-Jun-13	12:47	-44.1825	175.1807	E				527	
31	MUC	MERNOO	E	3	9-Jun-13	14:18	-44.2082	175.3787	E				547	
32	MUC	MERNOO	E	2	9-Jun-13	15:14	-44.2610	175.4218	E				580	
33	MUC	MERNOO	E	1	9-Jun-13	16:04	-44.2423	175.4658	E				573	
34	MBES	MERNOO	E	NA	9-Jun-13	16:50	-44.2547	175.4870	E	-44.1997	175.4907	E	585	
35	DTIS	MERNOO	E	1	9-Jun-13	20:17	-44.2395	175.4692	E	-44.2452	175.4557	E	571	574
36	DTIS	MERNOO	E	2	9-Jun-13	22:35	-44.2602	175.4278	E	-44.2580	175.4137	E	582	576
37	DTIS	MERNOO	E	3	10-Jun-13	01:05	-44.2647	175.3885	E	-44.2100	175.3750	E	550	548
50	DTIS	SOUTH	G	1	11-Jun-13	07:32	-43.8962	176.9377	E	-43.8887	176.9307	E	513	512
51	DTIS	SOUTH	G	2	11-Jun-13	09:57	-43.8675	176.9832	E	-43.8590	176.9800	E	507	503

station	method	region	box	site	date_start	time_s	lat_start	Lon_start	E-W	lat_end	lon_end	E-W	depth_start	depth_end
52	DTIS	SOUTH	G	3	11-Jun-13	12:20	-43.8498	177.0070	E	-43.8408	177.0077	E	501	499
53	MUC	SOUTH	G	3	11-Jun-13	14:10	-43.8460	177.0070	E				502	
54	MUC	SOUTH	G	2	11-Jun-13	14:55	-43.8613	176.9795	E				504	
55	MUC	SOUTH	G	1	11-Jun-13	15:37	-43.8927	176.9362	E				513	
58	DTIS	SOUTH	H	1	12-Jun-13	01:08	-43.8235	177.6673	E	-43.8353	177.6622	E	535	547
59	DTIS	SOUTH	H	2	12-Jun-13	03:24	-43.8380	177.6313	E	-43.8467	177.6197	E	558	558
60	DTIS	SOUTH	H	3	12-Jun-13	05:56	-43.8740	177.6010	E	-43.8600	177.6180	E	614	587
61	MUC	SOUTH	H	3	12-Jun-13	08:04	-43.8657	177.6097	E				600	
62	MUC	SOUTH	H	2	12-Jun-13	08:51	-43.8388	177.6308	E				557	
63	MUC	SOUTH	H	1	12-Jun-13	09:34	-43.8288	177.6692	E				538	
66	MUC	SOUTH	I	1	12-Jun-13	19:28	-43.8982	178.6083	E				548	
67	MUC	SOUTH	I	2	12-Jun-13	20:57	-43.8490	178.5858	E				487	
68	MUC	SOUTH	I	3	12-Jun-13	20:18	-43.8718	178.5557	E				515	
69	DTIS	SOUTH	I	3	12-Jun-13	22:37	-43.8512	178.5763	E	-43.8483	178.5938	E	488	484
70	DTIS	SOUTH	I	2	13-Jun-13	01:06	-43.8770	178.5467	E	-43.8775	178.5665	E	525	520
71	DTIS	SOUTH	I	1	13-Jun-13	03:41	-43.8958	178.6032	E	-43.9032	178.6122	E	545	554
74	DTIS	SOUTH	J	1	13-Jun-13	14:50	-44.0362	179.6302	E	-44.0427	179.6465	E	580	590
75	MUC	SOUTH	J	3	13-Jun-13	18:35	-43.9987	179.5935	E				554	
76	MUC	SOUTH	J	2	13-Jun-13	17:50	-43.9867	179.5723	E				542	
77	MUC	SOUTH	J	2	13-Jun-13	19:11	-43.9990	179.5972	E				550	
78	MUC	SOUTH	J	1	13-Jun-13	20:08	-44.0373	179.6305	E				582	
79	DTIS	SOUTH	J	3	13-Jun-13	21:17	-44.0010	179.5940	E	-43.9913	179.5812	E	551	544
80	DTIS	SOUTH	J	2	13-Jun-13	23:10	-43.9998	179.5618	E	-43.9940	179.5542	E	554	550
81	DTIS	SOUTH	J	1	14-Jun-13	01:32	-44.0372	179.6445	E	-44.0307	179.6380	E	580	574
84	DTIS	SOUTH	K	1	14-Jun-13	12:59	-44.1325	179.8287	W	-44.1292	179.8037	W	537	525

station	method	region	box	site	date_start	time_s	lat_start	Lon_start	E-W	lat_end	lon_end	E-W	depth_start	depth_end
85	DTIS	SOUTH	K	2	14-Jun-13	16:25	-44.1552	179.7745	W	-44.1393	179.7783	W	556	534
86	DTIS	SOUTH	K	3	14-Jun-13	19:08	-44.1793	179.7508	W	-44.1645	179.7557	W	574	555
87	MUC	SOUTH	K	3	14-Jun-13	20:56	-44.1698	179.7560	W				564	
88	MUC	SOUTH	K	2	14-Jun-13	21:37	-44.1435	179.7792	W				544	
89	MUC	SOUTH	K	1	14-Jun-13	22:21	-44.1335	179.8197	W				538	

Table A 2: Mega-epifaunal invertebrate taxa identified from towed camera video transects

Phylum	Sub-phylum	Class	Sub class	Order	Family	Taxon
Annelida		Polychaeta	Aciculata	Eunicida	Onuphidae	Worm (indeterminate)
						Onuphidae
						Quill worm
						Tube worms
						Sabellidae (fan worm)
Arthropoda	Crustacea	Malacostraca	Eumalacostraca	Decapoda		Crustacean (crab)
						<i>Campylonotus rathbunae</i>
						Crustacean (shrimp)
						Crustacean (galatheid/Chirostylidae)
						Goneplacidae
						<i>Munida gracilis</i>
						<i>Metanephrops challengerii</i>
						Pagurid crab
						<i>Notopandalus magnoculus</i>
						<i>Trichopeltarion fantasticum</i>
Arthropoda	Chelicerata	Pycnogonida		Isopoda		Isopoda
						Pycnogonid
Bryozoa		Gymnolaemata		Cheilostomata		Bryozoans
						<i>Bitectipora retepora</i>
Chordata	Tunicata	Ascidiacea				Ascidians (clonal)
						Ascidians (solitary)
						Didemnid
						<i>Diplosoma</i>
						<i>Synicum otagoensis</i>
		Thaliacea				Salp
Cnidaria		Anthozoa	Hexacorallia	Actiniaria		Anemones
						Anenome uni 2
						Anenome uni 3

Phylum	Sub-phylum	Class	Sub class	Order	Family	Taxon
Cnidaria		Anthozoa	Hexacorallia	Actiniaria	Actinostolidae	Anenome uni 4
					Hormathiidae	Actinostolidae
				Ceriantharia	Ceriantharia	Hormathiidae
					Corallimorpharia	Ceriantharia
				Scleractinia	Corallimorpharia	Corallimorpharia
					Caryophylliidae	<i>Goniocorella dumosa</i>
					Caryophylliidae	<i>Desmophyllum/ Caryophyllia</i>
					Flabellidae	<i>Flabellum</i> sp.
				Zoantharia	Flabellidae	<i>Flabellum</i> 1
					Flabellidae	<i>Flabellum rubrum</i>
			Epizoanthidae		<i>Epizoanthus</i> sp.	
					Zoantharia	
			Octocorallia	Alcyonacea	Alcyonacea	Alcyonacea
					Alcyoniidae	<i>Anthomastus</i> sp.
					Clavulariidae	<i>Telesto</i> sp.
				Gorgonacea	Taiaroidea	<i>Taiaroa tauhou</i>
					Gorgonacea	Gorgonacea
				Pennatulacea	Chrysogorgiidae	<i>Radicipes</i> sp.
					Pennatulacea	Pennatulacea
					Anthoptilidae	Anthoptilidae
Kophobelemnidae	<i>Kophobelemn</i> sp.					
Protoptilidae	Protoptilidae					
Echinodermata	Asteroidea	Brisingida	Brisingida	Asteroid		
			Forcipulatida	Brisingida		
				Asteriidae		
				<i>Sclerasterias mollis</i>		
				<i>Pseudechinaster rubens</i>		
				<i>Zoroaster</i> sp		
		Paxillosida	Stichasteridae	Zoroasteridae/Asteriidae	Zoroasteridae/Asteriidae	
			Astopectinidae	Astropectinidae		
				Astromesites/Psilaster/Proserpinaster		
		Spinulosida		<i>Dipsacaster magnificus</i>		
				<i>Plutonaster/Dytaster</i>		
				Echinasteridae		
Valvatida	Echinasteridae	<i>Pillsburiaster</i> sp.				
	Goniasteridae					

Phylum	Sub-phylum	Class	Sub class	Order	Family	Taxon			
Echinodermata		Asteroidea		Valvatida	Goniasteridae	Plinthaster/Ceramaster Lithosoma/Pseudarchaster <i>Hippasteria</i> sp. <i>Mediaster</i> sp. <i>Lithosoma novazealandiae</i> <i>Solaster torulatus</i> <i>Crossaster multispinus</i>			
					Solasteridae	<i>Solaster torulatus</i> <i>Crossaster multispinus</i>			
					Echinoidea	Camarodonta	Echinidae	<i>Gracilechinus multidentatus</i>	
						Cidaroida	Cidaridae	Cidaridae <i>Goniocidaris parasol</i>	
					Euechinoidea	Echinoida		Echinoid	
						Echinothurioida	Echinothuriidae/Phormosomatidae	Echinothuriidae/Phormosomatidae <i>Phormosoma bursarium</i>	
		Holothuroidea				Spatangoida	Eurypatagidae Spatangidae	<i>Paramaretia peloria</i> Spatangidae	
						Aspidochirotida	Synallactidae	<i>Bathyploetes</i> sp.	
						Elasipodida		Elasipoda	
						Aspidochirotacea	Elasipodida	Laetmogonidae	Laetmogonidae
							Ophiuroidea	Chilophiurina	Ophiodermatidae
		Hydrozoa		Hydrozoa	Hydroidolina	Leptothecata		Hydroids	
						Anthoathecata	Stylasteridae	Stylasteridae	
Mollusca		Bivalvia		Pteriomorpha	Limidae	<i>Acesta maui</i>			
				Cephalopoda	Octopoda		Mollusc (octopod)		
					Octopoda	Octopodidae	<i>Graneledone</i> sp.		
		Gastropoda	Prosobranchia	Neogastropoda		Mollusc (gastropod)			
				Neogastropoda	Buccinidae	Buccinidae			
					Buccinidae	<i>Penion</i> sp.			
					Muricidae	Muricidae			
					Olividae	Olividae			
					Turbinellidae	Turbinellidae			
					Turridae	Turridae			
	Volutidae	Volutidae							
	Neotaenioglossa	Cassidae	Cassidae						

Phylum	Sub-phylum	Class	Sub class	Order	Family	Taxon	
Porifera		Demospongiae		Vetigastropoda	Ranellidae	Ranellidae	
					Trochidae	<i>Calliostoma</i>	
						Sponge (demospongiae)	
						Encrusting sponges	
						<i>Poecillastra laminaris</i>	
				Astrophorida			
				Poecilosclerida	Cladorhizidae	Cladorhizidae	
				Suberitida			<i>Suberites</i>
				Tetractinellida	Corallistidae		<i>Awhiowhio sepulchrum</i>
					Geodiidae		Geodia vestigifera
	Hexactinellida		Lyssacinosa	Rossellidae	<i>Hyalascus</i> n. sp		
					<i>Rossellidae Acanthascus (Rhabdocalyptus)</i> sp. 1		

Table A 3: Macro-infaunal invertebrate taxa identified from multicorer samples.

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon
Annelida	Clitellata	Oligochaeta	Haplotaxida	Naididae	Naididae	Naididae
		Polychaeta	Errantia	Amphinomida	Amphinomidae	<i>Linopherus minuta</i>
	Aphroditiformia			Polynoidae	Polynoidae	Polynoidae
			Sigalionidae		<i>Labiothenolepis laevis</i>	Sigalionidae
		Sigalionidae	Sigalionidae		Sigalionidae	
		Eunicida	Dorvilleidae	Dorvilleidae	Dorvilleidae	Dorvilleidae
				Lumbrineridae	Lumbrinerid-unknown	Lumbrineridae
				Onuphidae	<i>Hyalinoecia longibranchiata</i>	Onuphidae
			<i>Kinbergonuphis proalopus</i>		Onuphidae	
			<i>Leptoecia oxyrhincha</i>		Onuphidae	
			Onuphidae		Onuphidae	
			Phyllodocida	Aphroditidae	Aphroditidae	<i>Aphrodita talpa</i>
	Chrysopetalidae	Chrysopetalidae			Chrysopetalidae	
		Glyceridae			<i>Glycera knoxi</i>	Glyceridae
	<i>Glycera</i> sp.			Glyceridae		
	Goniadidae			Goniada	Goniadidae	
		Goniadidae		Goniadidae		
	Hesionidae	Hesionidae		Hesionidae		
		Nephtyidae		<i>Aglaophamus</i>	Nephtyidae	
	Nephtys			Nephtyidae		
	Nereididae			Nereidae		
	Phyllodocidae	Phyllodocidae				
	Pilargidae	Ancistrosyllis ancistrosyllis-A		Pilargidae		
	Sphaerodoridae	Sphaerodoridae				
	Syllidae Eusyllinae/Syllinae	Odontosyllis		Syllidae Eusyllinae/Syllinae		
		Syllidae Eusyllinae/Syllinae		Syllidae Eusyllinae/Syllinae		
	Sedentaria	Sabellida	Syllidae Exogoninae	Syllidae Exogoninae		
			Oweniidae	Myriochele	Oweniidae	
			Sabellidae	Euchone	Sabellidae	
		Sabellidae		Sabellidae		
		Serpulidae	<i>Serpula tiwhana</i>	Serpulidae		
			Siboglinidae	Siboglinidae		
		Siboglinidae	Siboglinum	Siboglinidae		
Siboglinidae	Siboglinidae					
Scolecida	Capitellidae	Notomastus	Capitellidae			

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon
				Cossuridae	<i>Cossura consimilis</i>	Cossuridae
				Maldanidae	<i>Asychis asychis-B</i>	Maldanidae
					<i>Asychis trifilosus</i>	Maldanidae
					<i>Euclymene euclymene-A</i>	Maldanidae
					Euclymenin	Maldanidae
					<i>Lumbriclymene cf. cylindricauda</i>	Maldanidae
					<i>Maldane theodori</i>	Maldanidae
					<i>Metasychis metasychis-A</i>	Maldanidae
					Maldanidae	Maldanidae
					Notoproctus	Maldanidae
					<i>Rhodine intermedia</i>	Maldanidae
				Opheliidae	<i>Ophelina ophelina-B</i>	Opheliidae
				Orbiniidae	Orbiniid-unknown	Orbiniidae
					Scoloplos	Orbiniidae
				Paraonidae	Aricidea	Paraonidae
					<i>Levinsenia gracilis</i>	Paraonidae
					Paraonidae	Paraonidae
				Scalibregmatidae	Scalibregmatidae	Scalibregmatidae
			Spionida	Chaetopteridae	<i>Spiochaetopterus</i>	Chaetopteridae
			Spionida	Poecilochaetidae	<i>Poecilochaetus sp.</i>	Poecilochaetidae
					<i>Poecilochaetus trachyderma</i>	Poecilochaetidae
				Spionidae	<i>Dipolydora socialis</i>	Spionidae
					<i>Laonice laonice-A</i>	Spionidae
					Laonice	Spionidae
					<i>Paraprionospio coora</i>	Spionidae
					<i>Prionospio ehlersi</i>	Spionidae
					<i>Prionospio sp.</i>	Spionidae
					<i>Scolecoplepides scolecoplepides-A</i>	Spionidae
					<i>Spiophanes japonicum</i>	Spionidae
					<i>Spiophanes modestus</i>	Spionidae
					<i>Spiophanes</i>	Spionidae
					<i>Spiophanes wigleyi</i>	Spionidae
				Uncispionidae	<i>Uncopherusa uncopherusa-A</i>	Uncispionidae
			Terebellida	Acrocirridae	<i>Macrochaeta macrochaeta_A</i>	Acrocirridae
				Ampharetidae	<i>Ampharete kerguelensis</i>	Ampharetidae
					<i>Melinna armandi</i>	Ampharetidae

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon
					Ampharetidae sp.	Ampharetidae
				Cirratulidae	Aphelochaeta	Cirratulidae
					Chaetozone	Cirratulidae
				Chrysopetalidae	Chrysopetalidae	Chrysopetalidae
				Fauveliopsidae	<i>Fauveliopsis</i>	Fauveliopsidae
				Flabelligeridae	Flabelligeridae	Flabelligeridae
				Terebellidae	Artacama artacama-A	Terebellidae
					Terebellidae	Terebellidae
					<i>Pista</i>	Terebellidae
					Terebellidae Polycirrinae	Terebellidae
Arthropoda	Cephalocarida	-			Cephalocarida n .gen n. sp.	Terebellidae
	Malacostraca	Eumalacostraca	Amphipoda	Ampeliscidae	Ampelisca sp. A	Ampeliscidae
				Aoridae	<i>Meridiolembos</i>	Aoridae
				Caprellidae	<i>Pseudoprotomima hurleyi</i>	Caprellidae
				Colomastigidae	Colomastigidae indet.	Colomastigidae
				Eusiridae	<i>Regalia</i> sp. A	Eusiridae
					<i>Harpinioides</i> Sp.	Eusiridae
				Iphimedidae	Iphimedidae indet.	Iphimedidae
				Isaeidae	<i>Gammaropsis</i>	Isaeidae
				Ischyroceridae	<i>Cerapus fallohidius</i>	Ischyroceridae
					<i>Ischyrocerus</i>	Ischyroceridae
				Liljeborgiidae	<i>Liljeborgia</i>	Liljeborgiidae
				Lysianassidae	<i>Tryphosites</i> sp. cf. <i>T. coxalis</i>	Lysianassidae
					<i>Figorella</i>	Lysianassidae
					<i>Hippomedon</i> Sp. B	Lysianassidae
					Lysianassidae indet.	Lysianassidae
					<i>Parawaldeckia</i> sp. A	Lysianassidae
					<i>Parawaldeckia</i> Sp. B	Lysianassidae
					<i>Uristes</i>	Lysianassidae
				Oedicerotidae	Oedicerotidae indet.	Oedicerotidae
					<i>Oedicerotid</i> sp. A	Oedicerotidae
					<i>Oedicerotid</i> sp. small rostrum	Oedicerotidae
					<i>Oedicerotid</i> sp. large rostrum	Oedicerotidae
				Photidae	<i>Photis</i>	Photidae
				Phoxocephalidae	<i>Cephalophoxus regium</i>	Phoxocephalidae
					<i>Harpiniopsis nadania</i>	Phoxocephalidae

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon
					<i>Palabriophoxus palabria</i>	Phoxocephalidae
					<i>Paraphoxus pyripes</i>	Phoxocephalidae
					<i>Protophoxus australis</i>	Phoxocephalidae
					<i>Torridoharpinia hurleyi</i>	Phoxocephalidae
					<i>Waipirophoxus</i> sp.	Phoxocephalidae
				Ischyroceridae	<i>Runanga</i>	Ischyroceridae
				Sebidae	<i>Seba</i>	Sebidae
				Stenothoidae	Stenothoidae indet.	Stenothoidae
				Urothoidae	Urothoidae indet.	Urothoidae
				[amphipods]	Amphipoda indet.	[amphipods]
				Caprellidae	Caprellidae	Caprellidae
			Cumacea		Cumacea indet.	Cumacea
			Decapoda		Paguroidea sp.	Paguroidea
			Decapoda		Decapoda sp. squat lobster	Galatheidae
			Isopoda	Hyssuridae	<i>Kupellonura proberti</i>	Isopoda
				Leptanthuridae	<i>Bullowanthurra crebrui</i>	Isopoda
				Leptanthuridae	<i>Leptanthura</i> spp.	Isopoda
					<i>Asellota</i> spp.	Isopoda
					<i>Valvifera</i> sp.	Isopoda
					Isopoda indet.	Isopoda
			Mysida	Family indet.	Mysida indet.	Mysida
			Tanaidacea	incertae cedis	<i>Arintheus truncus</i>	Tanaidacea
				Apseudidae	<i>Apseudes larseni</i>	Tanaidacea
				Anarthruridae	anarthrurid D NZ#1	Tanaidacea
				Colletteidae	<i>Pseudoarthrura</i> NZ#1	Tanaidacea
					colletteid A	Tanaidacea
				Nototanaididae	<i>Nototanais</i> sp.	Tanaidacea
				incertae cedis	<i>Libanius</i>	Tanaidacea
					Tanaidacea indet.	Tanaidacea
	Maxillopoda	Copepoda	Calanoida	Aetideidae	<i>Bradyidius</i> sp.	Aetideidae
			Calanoida	Tharybidae	<i>Neoscolecithix</i> sp.	Tharybidae
			Cyclopoida	Cyclopoida	Cyclopoida sp. 1	Cyclopoida
					Cyclopoida sp. 4	Cyclopoida
			Harpacticoida	Harpacticoida	Harpacticoida sp. 1	Harpacticoida
					Harpacticoida sp. 2	Harpacticoida
					Harpacticoida sp. 3	Harpacticoida

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon
					Harpacticoida sp. 4	Harpacticoida
					Harpacticoida sp. 5	Harpacticoida
					Harpacticoida sp. 6	Harpacticoida
					Harpacticoida sp. 8	Harpacticoida
					Harpacticoida sp. 10	Harpacticoida
					Harpacticoida sp. 11	Harpacticoida
					Harpacticoida sp. 12	Harpacticoida
					Harpacticoida sp. 13	Harpacticoida
					Harpacticoida sp. 14	Harpacticoida
					Harpacticoida sp. 16	Harpacticoida
			Misophrioida	Misophrioida	Misophrioida sp. 1	Misophrioida
	Ostracoda	Myodocopa			Myodocopa Indet punctate sp.	Ostracoda
					Myodocopa Indet acuminate sp.	Ostracoda
					Myodocopa Indet translucent sp.	Ostracoda
					Myodocopa indet thin translucent sp.	Ostracoda
					Myodocopa Indet elongate sp.	Ostracoda
					Myodocopa Indet sighted sp.	Ostracoda
			Halocyprida	Polycopidae	Polycope sp.	Ostracoda
				Halocyprididae	Conchoecia sp.	Ostracoda
				Cypridinidae	<i>Vargula</i> sp.	Ostracoda
					<i>Vargula</i> Sp. A	Ostracoda
					<i>Vargula</i> Sp. B	Ostracoda
					<i>Metavargula</i> sp.	Ostracoda
				Philomedidae	<i>Philomedes</i> sp.	Ostracoda
					<i>Harbansus</i> sp.	Ostracoda
				Cylindroleberididae	<i>Xenoleberis</i> sp.	Ostracoda
					<i>Xenoleberis</i> sp.	Ostracoda
				Sarsiellidae	<i>Neomuelleriella</i> sp.	Ostracoda
					<i>Spinacopia</i> sp. A	Ostracoda
					<i>Spinacopia</i> sp. B	Ostracoda
		Podocopa			Podocopa indet.	Ostracoda
			Platycopida	Cytherellidae	<i>Cytherella</i> sp.aff. Intonsa	Ostracoda
				Cytherellidae	<i>Cytherella</i> sp. (punctate).	Ostracoda
				Cytherelloidea	Cytherelloidea sp.aff. Praeauricula	Ostracoda
			Podocopida	Bairdiidae	<i>Bairdia</i> sp.	Ostracoda
				Macrocyprididae	<i>Macromackenzia</i> sp.	Ostracoda

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon
					<i>Macropyxis</i> sp.aff. Andreseni	Ostracoda
					<i>Macropyxis</i> sp.aff sonneae	Ostracoda
					<i>Macropyxis</i> sp.aff. Thiedeii	Ostracoda
					<i>Macropyxis</i> indet.sp.	Ostracoda
					<i>Macropyxis</i> indet. Sp.2	Ostracoda
					<i>Macrocypriina</i> sp.	Ostracoda
				Hemicytheridae	<i>Bradleya silentium</i>	Ostracoda
				Cytheruridae	<i>Cytheropteron</i> sp.aff. Testudo	Ostracoda
				Leptocytheridae	<i>Bisulcocythere novaezealandiae</i>	Ostracoda
				Cytheridae	<i>Javanella</i> sp.	Ostracoda
				Krithidae	<i>Kritha</i> sp.	Ostracoda
	Pycnogonida				Pycnogonida indet.	Pycnogonida
Bryozoa	Gymnolaemata		Cheilostomata	Conescharellinidae	<i>Trochosodon</i> sp.	Cheilostomata
				Candidae	<i>Caberea</i> sp.	Cheilostomata
				Bitectiporidae	<i>Parkermavella</i> sp.	Cheilostomata
				Celleporidae	<i>Osthimosia</i> sp.	Cheilostomata
				Arachnidiidae	<i>Arachnidium</i> sp.	Ctenostomata
Chordata	Asciacea		[Asciacea]	ascidians	Asciacea sp.	[Asciacea]
Ciliophora	Heterotrichea		Heterotrichida	Folliculinidae	Folliculinidae sp.	Heterotrichida
Cnidaria	Anthozoa		Alcyonacea	Taiarooidae	<i>Taiaroa</i> sp.	Alcyonacea
					Alcyonacea sp.	Alcyonacea
	Hydrozoa		Leptothecata		Leptothecata sp. 1	Leptothecata
					Leptothecata sp. 2	Leptothecata
	Scyphozoa		Coronatae	Nausithoidae	Nausithoidae sp.	Coronatae
Echinodermata	Echinoidea	Cidaroida	Cidaroida	Cidaridae	Cidaridae	Cidaroida
		Euechinoidea	Spatangoida	Brissidae	Brissidae	Spatangoida
					<i>Brissopsis oldhami</i>	Spatangoida
				Spatangidae	Spatangidae	Spatangoida
	Holothuroidea		Molpadida	Caudinidae	Caudinidae sp.	Holothuroidea
	Holothuroidea				Holothuroidea indet.	Holothuroidea
		Ophiurida	Ophiurida		Ophiurida indet.	Ophiurida
				Amphiuridae	Amphiura	Ophiurida
					Amphiuridae	Ophiurida
					<i>Amphiura dikellacantha</i>	Ophiurida
					<i>Amphiura cf. micra</i>	Ophiurida
				Amphiuridae	Amphioplus	Ophiurida

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon				
Foraminifera Mollusca	Bivalvia	Heterodonta	Anomalodesmata	Ophiacanthidae	Ophiolimna	Ophiurida				
					<i>Ophiozonella stellamaris</i>	Ophiurida				
					Ophiuridae	<i>Ophiomisidium irene</i>	Ophiurida			
						Formanifera spp.	Foraminifera			
						<i>Cuspidaraia fairchildi</i>	Cuspidariidae			
						Thraciidae	<i>Parvithracia suteri</i>	Thraciidae		
						Lucinoidea	Thyasiridae	Thyasiridae sp. A	Thyasiridae	
							Thyasiridae	Thyasiridae sp. B	Thyasiridae	
							Thyasiridae	Thyasiridae sp. C	Thyasiridae	
							Thyasira neozelanica	Thyasiridae		
						Veneroidea	Neoleptonidae	<i>Neolepton antipodum</i>	Neoleptonidae	
							Kelliidae	<i>Kaneoha minima</i>	Kelliidae	
						Anomalodesmata	Cuspidariidae	<i>Pseudoneaera wellmani</i>	Cuspidariidae	
					Protobranchia	Nuculanoida	Neilonellidae	<i>Pseudotindaria flemingi</i>	Neilonellidae	
							Yoldiidae	<i>Yoldiella</i> sp. A	Yoldiidae	
								<i>Yoldiella</i> sp. B	Yoldiidae	
						Nuculida	Nuculidae	<i>Linucula recens</i>	Nuculidae	
							Sareptidae	<i>Pristigloma</i> sp.	Sareptidae	
							Nuculidae	<i>Nucula nitidula</i>	Nuculidae	
								<i>Ennucula strangeiformis</i>	Nuculidae	
						Solemyoidea	Nucinellidae	<i>Nucinella maoriana</i>	Nucinellidae	
					Pteriomorphia	Arcoidea	Arcidae	<i>Bathyarca caebaea</i>	Arcidae	
						Pectinoidea	Cyclochlamydidae	<i>Cyclochlams delli</i>	Cyclochlamydidae	
					Gastropoda	Caenogastropoda	-	Eulimidae	<i>Melanella puhana</i>	Eulimidae
							Littorinimorpha	Naticidae	<i>Uberella denticulifera</i>	Naticidae
								Tornidae	<i>Scrupus uniliratus</i>	Tornidae
								Naticidae	<i>Falsilunatia powelli</i>	Naticidae
		Retusidae	<i>Retusa oruanensis</i>	Retusidae						
			<i>Retusa</i> sp. A	Retusidae						
			<i>Retusa</i> sp. B	Retusidae						
			<i>Retusa</i> sp. C	Retusidae						
		Vetigastropoda		<i>Lissotesta</i> sp. A		Seguenzioidea				
				<i>Lissotesta</i> sp. B		Seguenzioidea				
			Skeneidae	<i>Liotella rotula</i>	Skeneidae					
		Cephalaspidea	Philinidae	<i>Philine</i>	Philinidae					
	Scaphopoda		Dentaliida	Dentaliidae	Dentaliidae					

Phylum	Class	Subclass	Order	Family	Taxon	Aggregated taxon
		-	Gadilida	Gadilidae	<i>Cadulus teliger</i>	Gadilidae
		-			<i>Cadulus delicatulus</i>	Gadilidae
Mollusca [Aplacophora]	Caudofoveata	-	Chaetodermatida		<i>Caudofoveata</i> sp.	Aplacophorans
		-		Chaetodermatidae	<i>Falcidens</i> sp. nov.	Aplacophorans
		-			<i>Falcidens macrafrondis</i>	Aplacophorans
		-			<i>Falcidens</i>	Aplacophorans
		-			<i>Chaetoderma</i> sp.	Aplacophorans
		-		Prochaetodermatidae	<i>Prochaetoderma</i> sp. nov.	Aplacophorans
		-		Limifossoridae	<i>Limifossor</i> sp. nov. “big”	Aplacophorans
		-			<i>Limifossor</i> sp. nov. “medium”	Aplacophorans
		-			<i>Limifossor</i> sp. nov. “pangolin”	Aplacophorans
		-			<i>Scutopus</i> sp. nov.	Aplacophorans
	Solenogastres	-	Cavibelonia		<i>Cavibelonia</i> spp.	Aplacophorans
		-	Pholidoskepia		<i>Pholidoskepia</i> spp.	Aplacophorans
				Aplacophorans	Aplacophora indet.	Aplacophorans
Nematoda					Nematoda spp.	Nematoda
Nemertea				micronemerteans	Nemertea spp. Micronemerteans	Nemertea
				nemertea	Nemertea spp.	Nemertea
Platyhelminthes	Turbellaria		Polycladida	['polyclads']	Polycladida spp.	Platyhelminthes
Sipuncula				sipunculans	Sipuncula spp.	Sipuncula

Table A 4: Mega-epifaunal taxa (video transect analyses) characterising each survey box; SIMPER analysis using Bray-Curtis similarity on untransformed taxon abundance data with cut-off at 90 %. [Av. Sim = Average similarity, Sim/SD = Similarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum% = % cumulative similarity.]

Box (Av. Sim)	Species	Av.Abund	Av.Sim	Sim/SD	Contrib.%	Cum.%
A (63.78)	Onuphidae	105.55	14.53	2.72	22.79	22.79
	Buccinidae	56.76	10.36	5.54	16.24	39.03
	<i>Munida gracilis</i>	37.56	7.06	11.76	11.06	50.09
	Quill worm	38.3	5.35	2.45	8.38	58.47
	Spatangidae	53.51	4.68	2.54	7.34	65.82
	<i>Phormosoma bursarium</i>	28.16	4.4	1.8	6.9	72.72
	Pagurid crab	21.39	2.83	2.52	4.44	77.16
	<i>Crossaster multispinus</i>	15.01	2.32	4.35	3.64	80.8
	<i>Flabellum</i> spp.	16.17	1.72	2.06	2.7	83.5
	Bryozoans	8.95	1.67	7.55	2.62	86.12
	<i>Radicipes</i> spp.	8.26	1.34	3.28	2.1	88.22
	Isopoda	16.62	1.27	1.23	1.99	90.21
D (68.47)	<i>Anthomastus</i> sp.	173.7	15.71	4.08	22.95	22.95
	Quill worm	183	12.35	8.36	18.04	40.99
	<i>Flabellum</i> spp.	92.76	9.54	7.68	13.93	54.91
	Pagurid crab	74.45	7.03	6.3	10.27	65.18
	Buccinidae	59.97	5.43	18.93	7.94	73.12
	<i>Munida gracilis</i>	32.96	2.96	4.75	4.32	77.44
	Onuphidae	33.18	2.72	3.58	3.97	81.4
	Bryozoans	30.79	2.19	3.2	3.21	84.61
	Worm (indeterminate)	65.59	2.15	1.56	3.14	87.75
	Anemones	21.51	1.86	3.36	2.72	90.47
E (66.92)	Quill worm	109.65	10.41	6.86	15.56	15.56
	Pagurid crab	107.74	9.74	5.96	14.55	30.11
	<i>Taiaroa tauhou</i>	134.63	9.43	1.72	14.09	44.2
	Buccinidae	91.1	8.91	3.1	13.31	57.52
	Bryozoans	44.07	4.93	27.99	7.37	64.89
	<i>Flabellum</i> spp.	48.12	4.54	7.67	6.78	71.67
	Anemone indet.	45.55	4.19	5.5	6.26	77.92
	<i>Goniocidaris parasol</i>	31.8	3.25	8.17	4.86	82.78
	Onuphidae	81.07	2.83	25.39	4.23	87.01
	<i>Munida gracilis</i>	14.07	1.14	3.38	1.7	88.71
	<i>Crossaster multispinus</i>	13.06	1.07	14.45	1.6	90.31
G (62.10)	<i>Anthomastus</i> sp.	115.84	10.51	1.01	16.93	16.93
	Pagurid crab	75.82	9.38	3.96	15.11	32.03
	<i>Telesto</i> sp.	47.26	6.42	1.36	10.34	42.37
	Quill worm	37.95	6.18	5.63	9.95	52.32
	Buccinidae	26.32	3.72	4.12	6	58.32
	Worm (indeterminate)	46.23	3.66	4.52	5.89	64.2
	<i>Crossaster multispinus</i>	20.65	3.15	8.28	5.07	69.28
	<i>Munida gracilis</i>	23.12	3.04	8.22	4.9	74.17
	<i>Taiaroa tauhou</i>	21.9	2.91	5.68	4.69	78.86
	Hormathiidae	10.7	1.54	7.89	2.48	81.34
	Onuphidae	15.82	1.52	1.67	2.44	83.78
	<i>Ceriantharia</i> spp.	11.03	1.42	1.2	2.29	86.08
	Anemone indet.	13.52	1.36	3.75	2.18	88.26
	<i>Flabellum</i> spp.	41.55	1.15	0.9	1.85	90.12

Box (Av. Sim)	Species	Av.Abund	Av.Sim	Sim/SD	Contrib.%	Cum.%
H (75.52)	<i>Taiaroa tauhou</i>	285.95	42.59	10.8	56.4	56.4
	Pagurid crab	64.08	8.99	4.28	11.91	68.31
	Quill worm	45.71	5.43	5.51	7.19	75.49
	Worm (indeterminate)	35.74	4.42	12.75	5.85	81.35
	Buccinidae	17.85	2.58	2.59	3.41	84.76
	Anemone indet.	13.78	2.03	5.51	2.69	87.45
	Anemone uni 2	13.98	1.76	3.67	2.33	89.78
	Hormathiidae	11.63	1.53	2.71	2.03	91.81
I (49.20)	<i>Taiaroa tauhou</i>	2970.75	31.49	0.99	63.99	63.99
	Pagurid crab	219.45	4.97	3.98	10.1	74.1
	<i>Kophobelemnon</i> sp.	261.98	3.47	0.83	7.06	81.15
	Worm (indeterminate)	90.57	2.14	2.79	4.34	85.49
	Anemone uni 2	60.21	1.37	1.6	2.78	88.27
	Anemone indet.	78.78	1.26	6.64	2.57	90.84
	J (56.83)	<i>Kophobelemnon</i> sp.	1244.31	23.64	1.17	41.6
Pagurid crab		189.19	9.87	2.66	17.37	58.97
<i>Taiaroa tauhou</i>		172.59	6.84	3.24	12.04	71.01
Anemone uni 2		68.12	2.97	1.65	5.23	76.24
Anemone indet.		59.58	2.92	1.76	5.14	81.38
Worm (indeterminate)		53.84	2.51	1.54	4.41	85.79
Quill worm		40.19	1.96	2.46	3.44	89.23
Hormathiidae		25.82	1.28	2.52	2.25	91.48
K (59.14)		Pagurid crab	205.16	25.99	5.15	43.94
	<i>Taiaroa tauhou</i>	174.68	10.48	0.96	17.72	61.66
	Anemone indet.	56.49	6.18	12.71	10.45	72.11
	Quill worm	34.5	3.68	3.47	6.23	78.34
	Worm (indeterminate)	23.75	2.61	6.5	4.42	82.76
	Cladorhizidae	27.59	1.61	0.79	2.72	85.48
	<i>Kophobelemnon</i> sp.	93.67	1.5	2.82	2.54	88.02
	<i>Munida gracilis</i>	12.8	1.19	2.74	2.01	90.03

Table A 5: Mega-epifaunal taxa (video transect analyses) contributing to community dissimilarity between survey boxes; SIMPER analysis using Bray-Curtis similarity on untransformed taxon abundance data with cut-off at 90 %. [Av. Diss = Average dissimilarity, Dis/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum% = % cumulative dissimilarity.]

Comparison (ave. dissim.) A vs D (63.59)	Taxon	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
		Box A	Box D				
	<i>Anthomastus</i> sp.	0	173.7	12.47	3.96	19.62	19.62
	Quill worm	38.3	183	9.82	1.7	15.45	35.06
	<i>Flabellum</i> spp.	16.17	92.76	5.54	3.66	8.72	43.78
	Onuphidae	105.55	33.18	5.13	1.36	8.06	51.85
	Spatangidae	53.51	73.08	4.95	1.14	7.78	59.63
	Worm (indeterminate)	0	65.59	4.62	1.07	7.26	66.89
	Pagurid crab	21.39	74.45	3.88	2.47	6.1	73
	<i>Phormosoma bursarium</i>	28.16	0	2.05	2.06	3.22	76.22
	<i>Telesto</i> sp.	0.38	22.62	1.52	3.19	2.4	78.61
	Bryozoans	8.95	30.79	1.49	1.83	2.34	80.95
	Anemone indet.	8.57	21.51	0.95	1.73	1.49	82.44
	Buccinidae	56.76	59.97	0.91	1.39	1.43	83.87
	Isopoda	16.62	7.29	0.89	0.95	1.4	85.27
	<i>Crossaster multispinus</i>	15.01	3.41	0.83	1.77	1.31	86.58
	<i>Taiaroa tauhou</i>	0.33	10.98	0.77	2.32	1.22	87.8
	<i>Munida gracilis</i>	37.56	32.96	0.55	1.41	0.86	88.66
	<i>Radicipes</i> spp	8.26	0.66	0.55	2.37	0.86	89.52
A vs E (63.06)		Box A	Box E				
	<i>Taiaroa tauhou</i>	0.33	134.63	9.74	2.25	15.45	15.45
	Pagurid crab	21.39	107.74	6.55	2.46	10.38	25.83
	Onuphidae	105.55	81.07	6.28	1.57	9.95	35.78
	Quill worm	38.3	109.65	5.28	2.47	8.38	44.16
	Spatangidae	53.51	4.33	3.69	1.01	5.85	50.01
	Anemones	8.57	45.55	2.81	2.62	4.45	54.46
	Buccinidae	56.76	91.1	2.8	1.29	4.43	58.9
	Bryozoans	8.95	44.07	2.66	10.28	4.22	63.11
	<i>Flabellum</i> spp.	16.17	48.12	2.45	1.8	3.88	66.99
	<i>Goniocidaris parasol</i>	1.31	31.8	2.38	2.95	3.78	70.77
	<i>Phormosoma bursarium</i>	28.16	0	2.19	2.05	3.47	74.24
	<i>Munida gracilis</i>	37.56	14.07	1.79	2.76	2.84	77.08
	<i>Epizoanthus</i> sp.	0	22.61	1.7	1.25	2.69	79.77
	Isopoda	16.62	2.06	1.08	1	1.71	81.48
	<i>Telesto</i> sp.	0.38	13.77	0.98	1.44	1.56	83.04
	<i>Kophobelemnon</i> sp.	0	9.75	0.76	1.3	1.2	84.25
	Anthoptilidae	0	9.7	0.75	1.26	1.19	85.43
	Protoptilidae	0	8.88	0.69	1.46	1.1	86.54
	<i>Radicipes</i> spp	8.26	0	0.64	2.52	1.01	87.54
	<i>Ceriantharia</i> spp	1.31	9	0.59	5.17	0.93	88.47
	Pennatulacea	0.38	7.74	0.54	0.84	0.85	89.32
G vs H (59.87)		Box G	Box H				
	<i>Taiaroa tauhou</i>	21.9	285.95	22.88	5.02	38.21	38.21
	<i>Anthomastus</i> sp.	115.84	0.24	9.69	1.65	16.19	54.41
	<i>Telesto</i> sp.	47.26	2.94	4.05	2.11	6.76	61.17
	<i>Flabellum</i> spp.	41.55	0.24	3.17	0.91	5.3	66.47
	Worm (indeterminate)	46.23	35.74	2.31	1.19	3.86	70.33
	Pagurid crab	75.82	64.08	2.17	1.54	3.63	73.97
	<i>Crossaster multispinus</i>	20.65	0	1.78	13.13	2.98	76.94

**Comparison
(ave. dissim.)**

	Taxon	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
	Onuphidae	15.82	17.83	1.42	1.42	2.36	79.31
	Quill worm	37.95	45.71	1.34	1.05	2.24	81.55
	<i>Munida gracilis</i>	23.12	8.43	1.24	1.97	2.07	83.61
	Cladorhizidae	12.7	14.2	1.14	1.32	1.91	85.52
	Ascidians (solitary)	10.88	1.42	0.84	1.29	1.41	86.93
	Buccinidae	26.32	17.85	0.83	1.52	1.39	88.33
	Hydroids	8.4	0.71	0.69	1.25	1.16	89.48
		Box G	Box I				
G vs I (83.39)	<i>Taiaroa tauhou</i>	21.9	2970.75	55.04	2.03	66	66
	<i>Kophobelemnon</i> sp.	0	261.98	8.42	0.97	10.09	76.09
	Pagurid crab	75.82	219.45	3.53	2.36	4.23	80.32
	<i>Anthomastus</i> sp.	115.84	0	3.1	1.19	3.72	84.04
	<i>Munida gracilis</i>	23.12	72.66	1.91	0.81	2.29	86.33
	Anenome uni 2	7.33	60.21	1.55	1.48	1.86	88.19
G vs J (74.47)	Kophobelemnon	0	1244.31	39.99	1.7	53.7	53.7
	<i>Taiaroa tauhou</i>	21.9	172.59	6.41	2.02	8.61	62.31
	Pagurid crab	75.82	189.19	5.14	1.97	6.91	69.22
	<i>Anthomastus</i> sp.	115.84	0	5.08	1.33	6.82	76.04
	Anenome uni 2	7.33	68.12	2.98	1.54	4	80.03
	Anemone indet.	13.52	59.58	2.24	1.55	3	83.03
	<i>Telesto</i> sp.	47.26	4.31	2.04	1.45	2.74	85.77
	Worm (indeterminate)	46.23	53.84	1.55	1.58	2.09	87.86
	<i>Flabellum</i> spp.	41.55	16.21	1.47	0.79	1.97	89.83
		Box G	Box K				
G vs K (63.32)	Pagurid crab	75.82	205.16	10.89	1.87	17.19	17.19
	<i>Taiaroa tauhou</i>	21.9	174.68	10.79	1.28	17.04	34.24
	<i>Anthomastus</i> sp.	115.84	0.99	8.78	1.55	13.86	48.1
	<i>Kophobelemnon</i> sp.	0	93.67	6.35	0.79	10.03	58.13
	<i>Telesto</i> sp.	47.26	1.62	3.78	1.95	5.97	64.1
	Anemone indet.	13.52	56.49	3.35	2.37	5.3	69.4
	<i>Flabellum</i> spp.	41.55	1.37	2.83	0.87	4.48	73.87
	Worm (indeterminate)	46.23	23.75	1.93	0.86	3.04	76.91
	Cladorhizidae	12.7	27.59	1.67	1.44	2.64	79.56
	<i>Crossaster multispinus</i>	20.65	0	1.62	5.01	2.56	82.11
	Buccinidae	26.32	9.27	1.32	2.39	2.08	84.19
	Onuphidae	15.82	6.72	0.86	1.41	1.36	85.56
	<i>Munida gracilis</i>	23.12	12.8	0.85	1.22	1.34	86.9
	Quill worm	37.95	34.5	0.85	1.98	1.34	88.24
	Ascidians (solitary)	10.88	0.21	0.8	1.18	1.26	89.5

Table A 6: Macro-infaunal taxa (multicorer samples) characterising each survey box; SIMPER analysis using Bray-Curtis similarity on untransformed taxon abundance data with cut-off at 80 %. [Av. Sim = Average similarity, Sim/SD = Similarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum% = % cumulative similarity.]

Box (Av. Sim)	Species	Av.Abund	Av.Sim	Sim/SD	Contrib.%	Cum.%
A (57.17)	Nematoda spp.	23.33	13.33	4.61	23.31	23.31
	<i>Prionospio</i>	20.17	12.79	9.49	22.37	45.68
	Foraminifera spp.	18	8.85	1.7	15.48	61.16
	Lumbrinerid-unknown	4	2.73	5.52	4.77	65.93
	<i>Gammaropsis</i>	2.5	1.48	9.37	2.59	68.52
	Aricidea	2.83	1.29	1.46	2.26	70.78
	<i>Linucula recens</i>	2.33	1.18	1.7	2.06	72.84
	Paraonidae	1.83	1.01	1.87	1.77	74.61
	Ampharetidae	2.17	0.99	2.26	1.73	76.34
	Chrysopetalidae	2	0.96	3.06	1.68	78.02
	Nemertea spp. Micronemerteans	1.83	0.96	3.06	1.68	79.7
	Syllidae Exogoninae	2.67	0.74	9.37	1.29	80.99
D (53.71)	Nematoda spp.	28.83	20.13	5.69	37.48	37.48
	Foraminifera spp.	12	8.13	5.34	15.15	52.63
	<i>Prionospio</i>	12.5	3.79	3.45	7.06	59.69
	Lumbrinerid-unknown	5	2.54	2.65	4.74	64.42
	<i>Fauveliopsis</i>	2.33	1.3	2.45	2.41	66.83
	<i>Notomastus</i>	2.17	1.14	4.48	2.12	68.95
	Terebellidae	2.17	1.08	2.2	2.02	70.97
	Thyasiridae sp. A	2	1.08	1.5	2	72.97
	<i>Linopherus minuta</i>	1.83	0.92	2.07	1.71	74.67
	Nemertea spp. Micronemerteans	1.33	0.92	2.07	1.71	76.38
	Maldanidae	2.5	0.7	1.35	1.31	77.69
	Syllidae Exogoninae	3.83	0.6	1.77	1.11	78.8
	<i>Linucula recens</i>	1.83	0.56	0.58	1.04	79.84
	<i>Thyasira neozelanica</i>	1.17	0.54	1.5	1	80.84
E (55.65)	Nematoda spp.	20.33	16.84	7.06	30.25	30.25
	Foraminifera spp.	16.33	11.13	2.68	19.99	50.24
	<i>Prionospio</i>	8.83	4.78	0.84	8.59	58.83
	Syllidae Exogoninae	6.67	2.51	1.43	4.51	63.34
	Prochaetoderma sp. nov.	2.5	1.77	3.2	3.19	66.53
	Syllidae Eusyllinae/Syllinae	2.17	1.63	4.14	2.92	69.46
	<i>Linopherus minuta</i>	2.5	1.61	5.66	2.9	72.36
	<i>Notomastus</i>	2	1.49	1.55	2.67	75.03
	<i>Cephalophoxus regium?</i>	2.17	1.45	1.75	2.61	77.64
	Lumbrinerid-unknown	1.83	1.27	2.7	2.28	79.92
	<i>Fauveliopsis</i>	2.5	0.94	1.24	1.69	81.61
G (53.76)	<i>Prionospio</i>	5	4.79	1.69	8.91	8.91
	Nematoda spp.	6	4.6	1.77	8.56	17.48
	Maldanidae	3.33	3.9	2.46	7.26	24.74
	Foraminifera spp.	3.17	3.82	3.34	7.1	31.84
	Syllidae Exogoninae	3	3.29	2.06	6.12	37.96
	Lumbrinerid-unknown	3.17	3.01	1.22	5.59	43.55
	Thyasiridae sp. C	2.33	2.57	5.94	4.77	48.32
	Chrysopetalidae	2.33	2.36	1.57	4.39	52.71
	<i>Torridoharpinia hurleyi?</i>	1.83	2.09	2.02	3.88	56.6
	<i>Fauveliopsis</i>	1.5	1.82	3.25	3.38	59.97
	Paraonidae	1.5	1.8	4.18	3.34	63.31

Box (Av. Sim)	Species	Av.Abund	Av.Sim	Sim/SD	Contrib.%	Cum.%
	<i>Prochaetoderma</i> sp. nov.	1.17	1.54	17.34	2.87	66.18
	Nemertea spp. Micronemerteans	1.17	1.54	17.34	2.87	69.05
	Thyasiridae sp. A	1.17	1.04	2.02	1.94	70.99
	Syllidae Eusyllinae/Syllinae	1	1.02	2.37	1.91	72.9
	Ampharetidae	0.83	1.02	2.37	1.91	74.8
	Terebellidae	1	1.02	2.6	1.89	76.69
	Polynoidea	0.5	0.77	17.34	1.43	78.12
	<i>Ophelina ophelina</i> -B	0.83	0.77	17.34	1.43	79.56
	Aricidea	0.67	0.77	17.34	1.43	80.99
H (42.43)	Nematoda spp.	17.33	9.89	4.19	23.3	23.3
	<i>Prionospio</i>	8.33	5.06	3.82	11.93	35.24
	Foraminifera spp.	6	5.05	3.93	11.91	47.15
	Syllidae Exogoninae	5	2.43	3.2	5.74	52.89
	Urothoidae indet.	2.67	1.87	1.57	4.41	57.3
	Lumbrinerid-unknown	21.33	1.7	3.98	4	61.3
	Terebellidae	3	1.35	2.37	3.17	64.47
	Thyasiridae sp. A	2.67	1.01	1.17	2.39	66.86
	<i>Torridoharpinia hurleyi</i> ?	1	0.96	3.26	2.26	69.12
	Ampharetidae	1.5	0.87	1.43	2.04	71.17
	Syllidae Eusyllinae/Syllinae	1.33	0.75	1.79	1.76	72.93
	Maldanidae	2.17	0.75	1.79	1.76	74.69
	Nemertea spp. Micronemerteans	1.17	0.75	1.79	1.76	76.45
	<i>Scoloplos</i>	1.67	0.74	1.9	1.74	78.19
	<i>Gammaropsis</i>	0.83	0.7	1.33	1.64	79.83
	<i>Parawaldeckia</i> sp. A	0.83	0.7	1.33	1.64	81.47
I (42.76)	Nematoda spp.	7.5	8.21	3.29	19.19	19.19
	<i>Prionospio</i>	4.5	4.66	1.77	10.9	30.1
	Chrysopetalidae	2.67	3.57	7.99	8.34	38.44
	Paraonidae	3	2.43	1.92	5.68	44.12
	Maldanidae	2	1.78	7.99	4.17	48.29
	Orbiniid-unknown	1.17	1.57	5.22	3.67	51.96
	<i>Parawaldeckia</i> sp. A	1.5	1.57	5.22	3.67	55.62
	Urothoidae indet.	1.33	1.29	1.48	3.02	58.65
	Nemertea spp.	1.33	1.29	1.48	3.02	61.67
	<i>Labiothenolepis laevis</i>	0.83	1.1	1.6	2.57	64.24
	<i>Notomastus</i>	0.83	1.1	1.6	2.57	66.81
	<i>Macrochaeta macrochaeta</i> _A	1	1.1	1.6	2.57	69.38
	<i>Fauveliopsis</i>	3.5	1.08	0.58	2.51	71.89
	<i>Chaetozone</i>	1.17	1.04	2.32	2.43	74.32
	<i>Ophelina ophelina</i> -B	0.67	0.78	5.22	1.83	76.15
	<i>Harpinioides</i> ? Sp.	1	0.78	5.22	1.83	77.99
	<i>Harpiniopsis nadania</i>	1	0.78	5.22	1.83	79.82
	Naididae	1.67	0.65	0.58	1.51	81.33
J (49.27)	<i>Prionospio</i>	9.22	7.02	3.6	14.24	14.24
	Nematoda spp.	7.22	6.23	2.38	12.64	26.88
	Syllidae Exogoninae	5.67	5.4	3.01	10.96	37.84
	Terebellidae	4.11	4.06	8.72	8.23	46.08
	Syllidae Eusyllinae/Syllinae	4.11	3.78	8.27	7.68	53.76
	Lumbrinerid-unknown	4	3.4	1.79	6.91	60.66
	<i>Notomastus</i>	3.22	2.03	8.72	4.12	64.78
	<i>Fauveliopsis</i>	2.89	2	0.94	4.07	68.85
	Maldanidae	2.11	1.62	2.14	3.28	72.13
	Orbiniid-unknown	2.44	1.37	0.8	2.79	74.91

Box	Species	Av.Abund	Av.Sim	Sim/SD	Contrib.%	Cum.%
(Av. Sim)	<i>Linopherus minuta</i>	1.44	1.28	3.89	2.6	77.51
	Naididae	2.67	1.14	12.39	2.32	79.83
	Aricidea	1.11	1.14	12.39	2.32	82.15
K (52.93)	Nematoda spp.	11	11.54	3.06	21.8	21.8
	Syllidae Eusyllinae/Syllinae	3.83	4.55	19.54	8.6	30.4
	Naididae	3.17	3.87	4.95	7.32	37.72
	<i>Fauveliopsis</i>	3	3.15	4.4	5.96	43.67
	<i>Prionospio</i>	4.67	2.64	3.15	5	48.67
	Aricidea	2.33	2.6	4.37	4.92	53.59
	Urothoidae indet.	2	2.43	3.74	4.59	58.18
	Syllidae Exogoninae	2.67	1.88	2.91	3.55	61.74
	Paraonidae	2	1.71	2.92	3.23	64.96
	Orbiniid-unknown	1.33	1.44	10.45	2.73	67.69
	Maldanidae	1.83	1.25	1.28	2.36	70.06
	Lumbrinerid-unknown	1.5	1.2	1.45	2.27	72.32
	<i>Notomastus</i>	1.33	0.96	2.32	1.82	74.14
	Onuphidae	1	0.94	2.91	1.78	75.92
	Phyllodocidae	1	0.94	2.91	1.78	77.69
	Nemertea spp.	0.83	0.94	2.91	1.78	79.47
	<i>Ophelina ophelina</i> -B	0.83	0.72	10.45	1.36	80.84

Table A 7: Traits-based faunal classes derived using k-means clustering of the biological traits matrix. These classes do not include any estimation of sensitivity to disturbance and are a means of generalising functional types across multiple taxa. The contributions of each trait to class definitions were calculated using SIMPER analysis on the untransformed traits allocation matrix and are shown at 95% contribution cut-off. Labels are simplified summaries of the trait composition of each class ('Sedentary predator/scavengers' are organisms such as anemones, corallimorpharians, and flabellum corals). [Av. Sim = Average similarity, Sim/SD = Similarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum% = % cumulative similarity.]

k-means class	Label	Trait	Av. Trait score	Av.Sim	Sim/SD	Contrib%	Cum.%
K6_1	Mobile deposit feeders	crawling	0.98	23.79	6.31	32.13	32.13
		surface	0.95	22.6	4.54	30.53	62.65
		deposit	0.70	14.36	3.24	19.4	82.05
		medium	0.49	7.3	1.09	9.85	91.9
		large	0.29	2.89	0.6	3.9	95.8
K6_2	Sessile suspension feeders	suspension	0.96	23.18	5.26	33.49	33.49
		sessile	0.94	22.26	3.15	32.15	65.64
		erect	0.72	13.28	1.35	19.19	84.83
		small	0.41	4.24	0.55	6.12	90.95
		medium	0.28	2.81	0.53	4.06	95.01
K6_3	Large predator/scavengers	surface	0.98	24	7.07	28.88	28.88
		crawling	0.92	21.13	2.76	25.42	54.31
		predscav	0.86	18.88	3.02	22.72	77.03
		large	0.83	17.55	2.12	21.12	98.15
K6_4	Small predator/scavengers	small	0.9	20.6	3.44	26.19	26.19
		crawling	0.9	20.6	3.44	26.19	52.38
		predscav	0.86	18.45	2.22	23.46	75.84
		surface	0.68	13.76	3	17.5	93.34
		top	0.3	4.4	0.76	5.6	98.94
K6_5	Sedentary predator/scavengers	sedentary	1	25.21	123.43	32.82	32.82
		surface	0.92	21.22	3.56	27.62	60.43
		suspension	0.63	11.65	1.84	15.16	75.6
		small	0.52	8.47	1.56	11.02	86.62
		medium	0.31	4.89	1.02	6.37	92.99
		predscav	0.29	4.04	0.68	5.25	98.24
K6_6	Sessile filter feeders	sessile	0.97	23.61	5.99	33.96	33.96
		filter	0.97	23.61	5.99	33.96	67.92
		medium	0.47	6.86	0.96	9.87	77.79
		erect	0.5	5.96	0.61	8.58	86.37
		surface	0.44	4.9	0.59	7.05	93.42
		small	0.33	3.76	0.63	5.41	98.82

Table A 8: Mega-epifaunal taxa recorded in video transects grouped by six functional traits classes (K1 to K6) derived by k-means classification of the raw functional traits attribution matrix and showing sensitivity group allocation (G1-G5), total number of individuals recorded (Inds.; sum of transect-length standardized densities across entire study), and the number of sites at which each was recorded. [Inds = number of individuals].

Traits class	Label	Taxon	Sensitivity group	Inds.	Site occurrence
K1	mobile deposit-feeders	Quill worm	G2	1 839	28
		Calliostoma	G2	75	22
		Ophiuroid	G3	59	21
		Spatangidae	G2	517	21
		<i>Goniocidaris parasol</i>	G2	186	18
		Cidaridae	G2	70	16
		<i>Gracilechinus multidentatus</i>	G2	17	9
		Crustacean (crab)	G2	7	7
		<i>Bathyplores</i> sp.	G2	14	7
		Astromesites/Psilaster/Proserpinaster	G2	12	6
		Echinoid	G2	6	5
		Laetmogonidae	G2	30	5
		<i>Notopandalus magnoculus</i>	G2	5	4
		<i>Phormosoma bursarium</i>	G3	113	4
		<i>Paramaretia peloria</i>	G2	8	4
		K2	sessile suspension-feeders	<i>Taiaroa tauhou</i>	G3
<i>Telesto</i> sp.	G4			473	25
Bryozoans	G4			373	22
Protoptilidae	G4			70	17
Hydroids	G4			76	16
<i>Kophobelemon</i> sp.	G3			6 075	13
<i>Anthomastus</i> sp.	G4			891	13
Anthoptilidae	G5			80	11
Pennatulacea	G4			28	9
<i>Radicipes</i> sp.	G5			39	7
Tube worms	G3			27	5
Alcyonacea	G4			7	5
Desmophyllum/ Caryophyllia	G4			3	3
Brisingida	G5			4	3
Zoanthidea	G5			18	2
K3	large predator/scavengers	<i>Crossaster multispinus</i>	G2	204	18
		Asteroid	G2	38	17
		<i>Dipsacaster magnificus</i>	G2	17	12
		Zoroasteridae/Asteriidae	G2	11	10
		Goneplacidae	G2	11	8
		Asteriidae	G2	14	6
		Mollusc (octopod)	G2	6	5
		<i>Epizoanthus</i> sp.	G2	72	5
		Plinthaster/Ceramaster	G2	10	5
		<i>Solaster torulatus</i>	G2	6	4
		<i>Metanephrops challengeri</i>	G2	4	4
		<i>Zoroaster</i> sp.	G2	3	3
		Lithosoma/Pseudarchaster	G2	4	3
		<i>Trichopeltarion fantasticum</i>	G2	6	3
Echinasteridae	G2	3	2		
K4	Small predator/scavengers	Pagurid crab	G2	3 251	28
		<i>Campylonotus rathbunae</i>	G1	168	28
		<i>Munida gracilis</i>	G1	709	28

Traits class	Label	Taxon	Sensitivity group	Inds.	Site occurrence
		Buccinidae	G1	1 176	28
		Isopoda	G2	175	26
		Worm (indeterminate)	G2	1 118	24
		Volutidae	G1	45	22
		Crustacean (shrimp)	G2	80	19
		Ranellidae	G1	43	13
		Mollusc (gastropod)	G2	27	12
		Turbinellidae	G1	8	7
		Pycnogonid	G2	5	4
		<i>Penion</i> sp.	G1	7	4
		Turridae	G1	9	3
		Cassidae	G1	3	3
K5	sedentary predators	Anemones	G3	1 000	28
		Onuphidae	G2	1 003	28
		Hormathiidae	G4	344	27
		<i>Ceriantharia</i> sp.	G2	240	27
		Flabellum	G3	806	26
		Anenome uni 2	G3	556	21
		Anenome uni 3	G3	41	12
		Actinostolidae	G3	8	4
		Anenome uni 4	G3	7	4
		<i>Flabellum</i> 1	G3	13	2
		<i>Flabellum rubrum</i>	G3	3	2
K6	sessile filter-feeders	Cladorhizidae	G3	239	17
		Suberites	G5	10	11
		Ascidians (solitary)	G4	70	9
		<i>Geodia vestigifera</i>	G5	11	7
		Didemnid	G4	3	3