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# Structure of infaunal communities in New Zealand submarine canyons is linked to origins of sediment organic matter

*Running title: Infauna of New Zealand submarine canyons*

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## Abstract

Submarine canyons can facilitate the transfer of land-derived organic matter to the deep sea. Here, we investigated links between variability in organic matter availability from land and marine sources and infauna communities in two contrasting canyon systems off New Zealand, and used stable isotope analyses to identify potential food sources of benthic invertebrates. Kaikōura Canyon, a steep, short canyon close to the shore, was characterised by high food availability and varying proportions of marine- and land-derived organic matter, whereas Hokitika Canyon, a narrow and lower-gradient canyon that extends further from the coast, was characterized by low food availability and mostly land-derived sediment organic matter throughout. Both macro- and meiofaunal abundance and biomass were greater in Kaikōura Canyon than in Hokitika Canyon. Correlation analyses suggested that land-derived organic matter may contribute to increased meiofaunal abundance in Kaikōura Canyon. Carbon and nitrogen isotopic analyses, however, did not provide unequivocal support for the uptake of land-derived material by large benthic invertebrates in Kaikōura Canyon. Infaunal abundance and biomass were low throughout Hokitika Canyon despite similar concentrations of land-derived organic matter in sediments of both canyons, which suggests that variations in marine-derived organic matter inputs is the main driver of community differences among canyons. Refractory vascular plant material by itself may not provide an adequate food supply to infaunal organisms, but may represent a complementary food resource when more labile marine phytodetritus is also readily available.

## Introduction

Submarine canyons that incise the continental shelf can facilitate the transfer of coastally-derived organic matter to the deep ocean (Puig et al. 2014). This organic matter provides a potentially important food resource to deep-sea benthic communities, including those in the canyons themselves which can exhibit elevated meio- and macro-infaunal abundance and biomass compared with adjacent slopes (Vetter 1994; Gage et al. 1995; Vetter and Dayton 1998; Vetter and Dayton 1999). Canyons are also often the locus for high biological primary productivity in surface waters, determined by physical processes of advective nutrient entrainment, oceanic stratification, tidal mixing and deep-water upwelling (Ryan et al. 2005). Accordingly, some canyons are recognised as hotspots of benthic biomass and activity; particularly Kaikōura Canyon, off New Zealand, which supports one of the highest biomass recorded to date at the deep seabed on a global scale (De Leo et al. 2010; Leduc et al. 2014). Nevertheless, other canyons do not seem to be significant conduits of organic matter from the coast and shelf, nor do they influence the structure of deep-sea benthic communities (Garcia et al. 2008; Duffy et al. 2014). Canyon morphology and distance from the land is considered to influence this variability in the degree of ecosystem connectivity (Romano et al. 2013; De Leo et al. 2014). Because the physical characteristics of canyons can vary considerably along continental margins (Harris and Whiteway 2011), it is difficult to ascertain how important canyons are for connecting coastal and deep-sea ecosystems at regional scales. Physical classifications of canyons may help in this regard (Huang et al. 2014), once the variable influence of canyon location and morphology on organic matter transport is understood. A better understanding of the relative importance of canyons for connecting ecosystems is crucial for informing the conservation of canyons, some of which face anthropogenic threats (Mordecai et al. 2011; Ramirez-Llodra et al. 2013; Fernandez-Arcaya et al. 2017).

Environmental heterogeneity within canyons has been clearly linked to variations in the abundance, biomass and community structure of benthic fauna (e.g., see studies conducted in Whittard Canyon, cited in Amaro et al. 2016). Within canyons, organic matter quantity and quality (with their spatial variability often coincident with water depth and canyon morphology) are among the most important factors influencing the distribution and abundance of infaunal sediment communities that rely on organic matter as a food source (e.g., Escobar Briones et al. 2008; Ingels et al. 2009). Differences in benthic fauna have also been observed among canyons (e.g., Schlacher et al. 2007). Nevertheless, the way in which environmental factors exert an influence on communities at this scale of variation is less well understood, primarily because the number of studies that compare discrete canyons is relatively small. Differences in the delivery of organic matter to the seafloor has been evoked to explain in-part the differences in infaunal benthic communities among canyons (Cunha et al. 2011; De Leo et al. 2014); however, other comparative studies provide no evidence that variation in organic matter quantity influences community differences among canyons (Bianchelli et al. 2008; 2010), and others suggest that the effect of food availability on canyon communities is modulated by hydrodynamic conditions

(Ingels et al. 2011b). For this reason, the question why organic matter delivery is important for structuring infaunal communities in some canyons and not in others, is poorly resolved.

Regional differences in phytoplankton productivity of the surface water overlying canyons likely play a significant role in determining differences in the organic matter that is delivered to the deep-sea. Since this organic matter is utilised by canyon infauna, variability in benthic secondary productivity, community structure and ecosystem functioning among canyons (Duineveld et al. 2001; Leduc et al. 2016) might be in-part explained by variation in surface productivity. Regional differences in macro-algal and seagrass productivity are also likely to effect organic matter supply (Vetter and Dayton 1998), with lateral contributions from nearshore and terrestrial environments enhanced during extreme riverine flooding and/or weather events (Lopez-Ferdinand et al. 2013; Kao et al. 2014). Nevertheless, variations in the sources of organic matter from the land could also be important in determining differences in infaunal communities among canyons. For example, greater amounts of organic matter may be received by canyons connected to rivers on steep and erosion-prone catchments with high rainfall regimes (Bao et al. 2015). Differences in land vegetation will also influence the relative accessibility of this organic matter for benthic organisms, in terms of the quality of the potential food source (Kiriakoulakis et al. 2011). Typically, land-derived organic matter is nitrogen-poor (C:N > 10, depending on the specific organic material; Smith and Epstein 1971; Wada et al. 1987; Middelburg and Nieuwenhuize1998) compared with organic matter derived from algal production (C:N

= 6-7; Redfield et al. 1963). Land-derived organic matter is, therefore, not as readily available to consumers but may enter the food web following bacterial degradation (Tenore et al. 1982; Harrison 1989). Overall, the quantity, lability and proportions of marine-, coastal- and land-derived organic matter will likely determine the relative standing stocks of benthic communities in canyons (Duineveld et al. 2001; Hunter et al. 2013).

The delivery of the marine, coastal and land organic matter to the seafloor and benthic organisms is likely to be modulated by the location and morphology of the canyon. For example, canyons that incise the shelf and are near the coast are likely to receive more land-derived organic matter than those more distant from land (Nazaré Canyon, Kiriakoulakis et al. 2011, cf. Wittard Canyon, Amaro et al. 2016). Once the organic matter has entered a canyon system, it is likely to be delivered to deeper depths and more widely if the floor of the canyon's main axis is steep (via down-canyon sediment gravity and current flows) compared to a gently-sloping canyon. However, the potential importance of canyon location and morphology for the delivery of organic matter by canyons to deep-sea communities, and how this aspect influences benthic standing stocks among canyons, has not been specifically examined at this time.

The present study contributes to an overall project that seeks to understand the variable influence of land-derived organic matter on deep-sea benthic communities, and how these relationships may be mediated by the physical characteristics of canyons. A companion study examined the quantity, quality and sources of the sediment organic matter (Gibbs et al. submitted), whereas the aim of the present study (using largely existing data and samples) was to investigate the relationships between sediment organic matter parameters and macro- and meiofaunal abundance, biomass and community structure of two contrasting canyons. The two study canyons were Kaikōura Canyon, which has a steep bathymetric gradient and is close to the east coast of South Island/Te Waipounamu of New Zealand/Aotearoa, and Hokitika Canyon, which is connected to the South Island west coast by a longer, narrow channel-like feature with a lower gradient. The overall project aimed to test the following hypotheses: (1) that the steep topography and proximity to the coast of Kaikōura Canyon results in higher organic matter enrichment from land sources relative to Hokitika Canyon (Gibbs et al. submitted), and (2) that within- and between-canyon variability in organic matter availability from land and marine sources is an important driver of infauna community parameters. Here, we test the second hypothesis by investigating relationships between environmental parameters (including concentrations of land- and marine-derived organic matter) and infaunal community parameters, including preliminary stable isotope analyses of benthic invertebrates from Kaikōura Canyon.

## Materials and methods

### *Study areas*

The two study areas are described in detail in Gibbs et al. (submitted). For completeness, the study area descriptions are repeated here. Kaikōura Canyon on the northeastern coast of South Island/Te Waipounamu, New Zealand/Aotearoa, cuts deeply into the narrow continental shelf, with the canyon head within only 500 m off the shore (Fig.1). Kaikōura Canyon is close to the highly productive Subtropical Front (STF), where warm subtropical surface waters to the north meet cold, high nutrient-low chlorophyll subantarctic surface waters to the south (Murphy et al., 2001; Chiswell et al. 2015). Episodic upwelling events may also contribute to the high primary productivity of the surface water above the canyon (Heath 1982; Chiswell and Schiel 2001), with annual gross productivity estimated to be in the order of 160 g carbon (C)/m$^2$/year and seasonal peaks of ~10 g C/m$^2$/day in spring (Bradford 1972), compared with high spring values of ~1 g C/m$^2$/day further offshore in the STF on Chatham Rise (Bradford-Grieve et al. 1997).

The North Canterbury region, located immediately south of Kaikōura Canyon, has several large river catchments that drain from the Marlborough mountains to the coast, which collectively transport 5.68 Mt/year of suspended sediment (Hicks et al. 2011). The Hurunui, Waiau and Conway rivers transport 0.53, 0.78, and 0.22 Mt/year of suspended sediments to the coast, respectively, and are the main contributors of terrigenous sediments in the region (Fig. 1; Hicks et al. 2011). The northeast littoral drift system transports sediments along the eastern South Island continental shelf, driven by the Southland Current along the shelf break (Chiswell 1996; Sutton 2003; Chiswell et al. 2015), and prevailing southeastward wind- and storm-waves (Carter and Heath 1975; Carter and Herzer 1979). Fine sands and mud transported in the littoral drift system along the eastern South Island coastline are eventually captured at the head of submarine canyons such as Kaikōura Canyon (Herzer 1979; Lewis and Barnes 1999), or dispersed across the continental slope as a mud drape (Carter and Herzer 1979; Bostock et al. 2018a). The accumulation of sediment in the head and on the steep sides of the canyon has the potential to fail under severe ground-shaking by earthquakes, which can lead to transport of sediments down the canyon into the deep-sea Hikurangi Channel as turbidity currents (Lewis and Pantin 2002). During the recent November 2016 Moment magnitude (Mw) 7.8 Kaikōura earthquake (Clark et al. 2017; Hamling et al. 2017; Kaiser et al. 2017), slope failures and substantial erosional scouring of geological materials within the canyon led to the generation of a turbidity current, the effects of which were extended over a 600 km distance from the Kaikōura Canyon source (Mountjoy et al. 2018).

Hokitika Canyon is one of several similar bathymetric features that incise the continental slope and outer shelf along the middle part of the west coast of South Island/Te Waipounamu (Fig. 2). The shelf narrows markedly southwards along the coast from 40–80 km width off northwest Nelson, to 30–35 km south of Hokitika Canyon, and to <5–10 km off south Westland further to the south (Zeldis et al. 2010). The canyons, most of which have high to moderate sinuosity, often coalesce to form deeply incised channels that continue out into the Tasman Sea to beyond 4000 m water depth, with evidence of small depositional fans on the Tasman Abyssal Plain (Mitchell et al. 2012). Hokitika Canyon is about 1250 km long and the northernmost feature, cutting across the southern flank of the Challenger Plateau. The canyon axis is incised 200–600 m into the seafloor from the shelf break down the continental slope, with up to 1000 m of incision on the lower slope and continental rise (H. Neil., NIWA, pers. comm.). The canyon head receives sediment from numerous distributary channels across the shelf-break, with the canyon becoming wider (from 10 to 20 km wide) and characterised by geomorphic features reminiscent of a braided river system (e.g., meanders, ox bows) in the upper and mid-slope area. Sediments in the canyon axis are dominated by micaceous silts and fine sands, with turbidite deposits on the abyssal plain levees outside of the incised channel (H. Neil., NIWA, pers. comm.; Bostock et al. 2018b).

The west coast of the South Island contributes the second highest annual suspended sediment yield in New Zealand (62.3 Mt/y), after East Cape, North Island/Te Ika a Māui (68.8 Mt/y; Hicks et al. 2011), driven by the high exhumation, erosion and rainfall rates in the rapidly uplifted Southern Alps/Kā Tiritiri o te Moana, which lie along the Alpine Fault plate boundary (Adams 1980; Jiao et al. 2017; Sutherland et al. 2000). The prevailing westerly winds lead to periodic coastal upwelling (Bradford-Grieve et al. 2006; Stanton and Moore 1992) cause storm-driven current flows and generate the northwards-directed Westland Current (Heath 1982; Zeldis et al. 2010; Chiswell et al. 2015). Biological productivity on the shelf is on the order of ~180 g C/m$^2$/year (Probert 1986; Zeldis et al. 2010), with seasonal productivity peaks of 0.2–0.7 g C/m$^2$/day likely in spring and summer (Bradford-Grieve et al. 1997). In the vicinity and south of Hokitika Canyon are several large rivers, including the Hokitika, Waitaha, Whataroa, Waiho, Haast and Arawhata rivers, contributing substantial annual suspended yields in the order of 3–7 Mt/year (; Griffiths and Glasby

1985; Hicks et al. 2011). Nevertheless, Radford (2012) suggests that Hokitika Canyon does not receive sediment directly from Hokitika River under modern sea-level conditions, but that a more direct connection occurred during the glacial lowstand, when the rivers debouched at or near the present-day shelf break. Terrestrial organic matter in the form of high proportions of lignin (Probert and Swanson 1985), low organic carbon contents (<0.5%) and high C:N ratios (9 to >15) in the shelf sediments (Stoffers et al. 1984) suggest that much of this organic material cannot be readily assimilated by the shelf benthos (Probert 1986; Zeldis et al. 2010).

### ***Sampling and sample processing***

Sediment core samples were collected using an Ocean Instruments MC-800A multicorer (internal core diameter = 9.52 cm). Core samples were obtained from 17 sites along the axis of Kaikōura Canyon (404–1485 m water depth; Fig. 1, Table 1) using *RV Tangaroa* in May 2010 and November 2006 (voyages TAN1006 and TAN0616, respectively) and in June 2007 using *RV Kaharoa* (KAH0706). Seven sites were sampled along the axis of Hokitika Canyon (191–1953 m water depth; Fig. 2) using *RV Tangaroa* in September 2017 and October 2013 (TAN1712 and TAN1311, respectively). To provide context for the stable isotope analyses conducted on selected benthic invertebrates from Kaikōura Canyon (see below), suspended particulate organic matter in surface waters in the Kaikōura Canyon region ($n$ = 33) was sampled from the underway system onboard RV *Tangaroa* (TAN1708) in September 2017. Approximately 1.5 to 2 litres were filtered through pre-combusted Whatman GF/F filters. The filters were acidified with 4 ml of 0.4 N $H_2SO_4$ acid to remove carbonates (Lorrain et al. 2003), rinsed with 0.2 µm filtered seawater and frozen (-20°C) prior to analysis for carbon and nitrogen stable isotopes.

One core per site was obtained for analyses of sediment parameters in Kaikōura (TAN1006) and Hokitika canyons (TAN1712 and TAN1311). The following sediment variables were quantified: total organic matter (%TOM), carbonate (%$CaCO_3$), nitrogen (%N), total organic carbon (%TOC), organic carbon to nitrogen molar ratio (C:N), chlorophyll *a* concentration (chl *a*; $\mu g\ g^{-1}$ dry weight $(DW)_{sediment}$), phaeopigment concentration (phaeo; $\mu g\ g^{-1} DW_{sediment}$), ratio of chlorophyll *a* to phaeopigment concentrations (chl *a*:phaeo), and proportions of sand, silt and clay particles (%sand, %silt, and %clay, respectively). Cores for sediment parameter analyses were sliced into 0.5 cm (Kaikōura Canyon) or 1.0 cm (Hokitika Canyon) sediment depth layers to five cm depth. Sediment parameter data (except for pigment data, which were obtained from the top one cm of sediment only) were averaged across the top five centimetres of sediment from each core. Limited sediment parameter data were obtained during TAN1712 (%TOM and %$CaCO_3$ only from top one cm of sediment). Laboratory methods are largely as described in Nodder et al. (2003), with %TOM determined by loss-on-ignition (500°C for 4 hours), %$CaCO_3$ by vacuum gasometry, and %TOC, %N and C:N by CHN analyser (CE Instruments NC2500) after acidifying with 8% sulphurous acid (Verardo et al. 1990). Phytopigments were determined by spectrofluorometric techniques after freeze-drying and extraction in 90% acetone, and grain-size determinations were made using

Beckman Coulter LS 13 320 Laser Diffraction Particle Size Analyzer (Nodder et al. 2003, 2011).

Two to three cores were obtained for meiofauna community analyses from each of 11 sites in Kaikōura Canyon (TAN1006) and six sites in Hokitika Canyon (TAN1311). In Kaikōura Canyon, meiofaunal cores were obtained from a single deployment per site (i.e., pseudo-replicates) whereas in Hokitika Canyon each meiofaunal core was obtained from a separate deployment (i.e., replicates). Each meiofaunal sample consisted of a subcore (internal diameter 26 or 29 mm) taken to a depth of five cm. All meiofauna samples were preserved in 10% buffered formalin. Samples were rinsed through a 1-mm mesh to remove macrofauna, and through a 45 μm mesh size to retain meiofauna. Meiofauna were extracted from the remaining sediment by Ludox flotation (Somerfield and Warwick 1996). Samples were then rinsed with a mixture of dilute ethanol and glycerol, transferred to a cavity block, and left under a fume hood for at least 48 h to allow water and ethanol to evaporate, leaving the sample material in pure glycerol (Somerfield and Warwick 1996). Samples were mounted on slides and sealed with paraffin wax. All meiofauna present in the sample were identified to major taxa (e.g., nematodes, annelids, harpacticoid copepods, kinorynchs; Supplement 1) and counted using a compound microscope (100× magnification). Meiofaunal body volumes were estimated from length and maximum body width measurements obtained by video image analysis (Nodder et al. 2003; Grove et al. 2006). Estimates of mean body weight were based on a minimum of 100 individuals (nematodes) or all individuals (other taxa).  Body volumes were converted to dry weight (DW) based on a relative density of 1.13 and a dry:wet weight ratio of 0.25 (Feller and Warwick 1988).

One to four cores were obtained for macrofaunal community analyses from each of 17 sites in Kaikōura Canyon (TAN1006, KAH0706 and TAN0616) and 7 sites in Hokitika Canyon (TAN1712 and TAN1311). In Kaikōura Canyon, macrofaunal cores were obtained from a single deployment per site (pseudo-replicates) whereas in Hokitika Canyon each macrofaunal core was obtained from a separate deployment (replicates, except for two deployments where two cores were analysed per deployment; Table 1). Each macrofauna core was sectioned into 0-5, 5-10 and 10-20 cm sediment depth layers. Each sample was sieved on a 300 μm mesh and fixed in buffered 10% formalin. In the laboratory, macrofaunal samples were identified to major taxa (e.g., polychaetes, amphipods, ophiuroids; Supplement 2) and counted and sorted into broad taxa (e.g., polychaetes, bivalves) using a dissecting microscope. For each specimen, any shell material was removed prior to being blotted dry and weighed.

Samples for invertebrate stable isotope analyses were obtained from six sites in Kaikōura Canyon during voyage TAN0616 (Table 1) at depths of 1014–1079 m using a 0.2 m$^2$ Van Veen grab, and a beam trawl. Animals were sorted at sea using a 2-mm mesh or by hand, and were stored in 80% ethanol until further processing in 2017. Analyses focused on two large deposit-feeding taxa common in Kaikōura Canyon, the echinoid *Brissopsis oldhami* and the holothuroid *Molpadia musculus*. Bivalves of the genus *Neilo* (family Malletidae) were also analysed from one site for comparison. One to seven samples of each species were obtained per site. Each sample consisted of 1–3 individuals; only individuals of similar size (± 10 mm) were pooled, as determined by measurements of test diameter (*B. oldhami*), body length (*M. musculus*) and shell length (*Neilo* sp.). Samples consisted of entire animal(s) (i.e., gonad and muscle tissue dissected from exoskeleton (*B. oldhami*), body wall (*M. musculus*), and muscle tissue (*Neilo* sp.). Tissue samples were dried at 60°C for 48 h and ground to a homogeneous powder using a mortar and pestle. Echinoid and holothurian tissue samples were subsequently acidified using 10% v/v hydrochloric acid to remove traces of carbonates, and then re-dried and ground again prior to analysis.

Stable isotope analyses of invertebrate samples were carried out on a DELTA V Plus (Thermo-Fisher Scientific, Bremen, Germany) continuous flow, isotope ratio mass spectrometer, with a Porapak Q chromatograph column and open split Conflo IV interface, connected to a Flash 2000 elemental analyser (EA) at the National Institute of Water and Atmospheric Research (NIWA) Environmental and Ecological Stable Isotope Analytical Facility in Wellington. Samples where nitrogen mass exceeded 20 µg were introduced to the EA using a MAS200 autosampler. For samples with less than 20 µg N, a zero blank autosampler was used to minimise the ingress of laboratory air and lower the N blank and a series of low nitrogen standards were run to correct low nitrogen $\delta^{15}N$ values. $CO_2$ (calibrated against NBS19-calcite referenced to Vienna Pee Dee Belemnite: VPDB) and $N_2$ (calibrated against atmospheric air) reference gas standards were introduced to the mass spectrometer with every sample analysis. Delta $^{15}$N and $\delta^{13}$C isotope values were normalized and corrected against National Institute of Standards and Technology (NIST) standards USGS40 L-glutamic acid (C and N), NIST 8548 IAEA-N2 ammonium sulphate (N) and NIST8542 sucrose (C). Percentage C and N values were calculated relative to a solid laboratory reference standard of DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $C_6H_{13}NO_2$, Lot 127H1084, Sigma, Australia) at the beginning of each run. Repeat analysis of NIST standards produced data accurate to within 0.3 ‰ for $\delta^{15}$N and $\delta^{13}$C and a precision of better than 0.2 ‰ for N and 0.1 ‰ C using the MAS200 autosampler. For samples with <20 µg N content analysed using the zeroblank autosampler precision was better than 0.5 ‰ for N and 0.2 ‰ for C. For % N and C content, data are accurate to within 0.4%, with a precision usually above 0.3% for N and 0.2% for C.

### *Data analyses*

Analyses of environmental parameters and infauna were conducted using statistical routines in the multivariate software package PRIMER v6 (Clarke and Gorley 2006). The principal components analysis (PCA) routine was used to compare sediment parameters between Kaikōura and Hokitika canyons (Anderson et al. 2008). The analysis was based on a resemblance matrix derived from normalized environmental data using Euclidean distance. Proportion of sand and organic matter content data were log-transformed prior to analyses to minimize the impact of outlier data. To show which variable(s) differed between and within the canyons, vectors showing the multiple partial correlations of each environmental variable were overlain onto the PCA plot. Proportions of silt particles and nitrogen content were highly correlated with the proportions of sand particles and carbon content, respectively ($r > 0.9$), and so for clarity were not shown on the PCA plot. Differences in environmental parameters between canyons were tested using the PERMANOVA+ routine (Anderson et al. 2008; one-way PERMANOVA with fixed factor Canyon).

Meiofaunal communities typically comprise both temporary meiofaunal taxa (i.e., juveniles of macrofaunal-sized taxa, such as most polychaetes and molluscs, which typically have a pelagic larval stage) and permanent meiofaunal taxa (e.g., nematodes and harpacticoid copepods, which spend their entire life cycle in the sediment) (Warwick 1989). Temporary meiofauna, which are larger, have a highly patchy distribution, and occur at low densities relative to permanent meiofauna, are not appropriately sampled due to the small size of subcores used to sample meiofauna (<10 cm$^2$). For the purpose of statistical analyses, only taxa that are considered to be permanent meiofauna were included in analyses of meiofaunal communities (i.e., nematodes, harpacticoid copepods, nauplii, ostracods, gastrotrichs, kinorynchs, loriciferans, mites, tardigrades). Conversely, macrofaunal samples often contain substantial numbers of specimens belonging to taxa typically classified as meiofauna (e.g., nematodes) due to the relatively fine mesh used for processing deep-sea core samples (i.e., 300 μm). This mesh size, however, only retains a small proportion of individuals belonging to these taxa and, therefore, provides a biased estimate of their abundance. For this reason, analyses of macrofaunal communities were based on data that excluded taxa typically considered as belonging to the meiofauna, such as nematodes.

The PERMANOVA routine in PRIMER was used to compare meio- and macrofaunal univariate parameters (abundance, biomass, mean individual biomass) between Kaikōura and Hokitika canyons based on similarity matrices built using the Euclidean similarity measure of untransformed data (Anderson et al. 2008). We also compared community structure of meio- and macrofauna, based on similarity matrices built using Bray-Curtis similarity of fourth-root (meiofauna) and square root-transformed (macrofauna) of multivariate taxon abundance data. Multivariate community structure data were visualised using two-dimensional multidimensional scaling (MDS) plots. P-values for individual predictor variables were obtained using 999 permutations. Because PERMANOVA is sensitive to differences in multivariate dispersion among groups, the PERMDISP routine in PRIMER was used to test for homogeneity of dispersion when significant factor effects were found (Anderson et al. 2008). The SIMPER routine in PRIMER was used to identify which taxa were responsible for differences in community structure between canyons.

Relationships between environmental predictor variables and meio- and macrofaunal community parameters (abundance, biomass, community structure) were investigated using Distance-based Linear Models (DistLMs) in PERMANOVA+ (Anderson et al. 2008). In addition to the sediment parameters described above, data from Gibbs et al. (submitted) on the relative proportions of marine- and land-derived organic carbon at the canyon sampling sites derived from bulk carbon stable isotopic mixing models were used to investigate potential relationships with infaunal parameters. Gibbs et al. (submitted) determined the proportional contribution of land- and marine-derived organic matter by comparing it to offshore (100% marine-derived organic matter) and riverbed (100% land-derived organic matter) sediments using a simple IsoError mixing model based on bulk stable isotope values of carbon (δ13C) (Phillips and Gregg 2001). Data from Gibbs et al. (submitted) were available from six of the Kaikōura Canyon sampling sites (TAN1006, see Table 1), and six of the Hokitika Canyon sampling sites (TAN1311). DistLM analyses were conducted for each canyon separately. DistLM analyses were conducted to investigate relationships between individual environmental predictors (water, depth, sediment and organic matter parameters) and infaunal community parameters in marginal tests.

Among-site differences in $\delta^{13}$C and $\delta^{15}$N values of *B. oldhami* and *M. musculus* were evaluated using PERMANOVA. The potential effect of body size on the isotopic values of *B. oldhami*, *M. musculus* and *Neilo* were investigated by correlation analyses using the DistLM routine in PRIMER. The relative contributions of marine- and land-derived food sources to deposit feeders in Kaikōura Canyon was investigated by comparing invertebrate $\delta^{13}$C and $\delta^{15}$N data from this study to published values of: (1) sediment organic matter off the east coast of New Zealand's South Island (offshore from Kaikōura Canyon) comprising only marine-derived organic detritus; and (2) riverbed sediment organic matter from catchments that likely contribute land-derived organic material to the canyon (Gibbs et al. submitted).

## Results

### *Sediment characteristics*

Considering grain-size distributions, Kaikōura and Hokitika canyons shared some similarities, with silt-sized particles dominating at all locations (80 to >95%), except the sandy shallowest site sampled at ~200 m water depth at the head of Hokitika Canyon (Table 2). Nevertheless, there were obvious differences in sediment parameters between the two canyons. Sites from each canyon formed clearly separated clusters on the two-dimensional PCA plot, with the first two axes combined explaining 69% of the variance (Fig. 3). Kaikōura Canyon was characterized by significantly higher values of most sediment parameters compared with Hokitika Canyon (PERMANOVA, $P < 0.05$), except for sediment C:N molar ratio, which were significantly greater in Hokitika Canyon than Kaikōura Canyon ($P < 0.01$). Total organic matter content, land-derived organic carbon content, sand content, and silt content did not differ significantly between the two canyons ($P > 0.1$).

Sediment organic carbon content showed a gradual and relatively steep increase with water depth in Kaikōura Canyon, which largely reflected the trend observed in marine-derived organic carbon content (Fig. 4). Land-derived organic carbon content was relatively low (0.15-0.43%) and decreased with depth, whereas marine-derived organic matter content was greater overall (0.45–1.04%), and increased with depth. Phaeopigment and carbonate concentrations showed a steep increase with water depth similar to that observed for total organic carbon content and marine-derived organic carbon content. Chlorophyll *a* to phaeopigment ratios were lowest at the shallowest and deepest sites. Carbon to nitrogen (C:N) molar ratios in Kaikōura Canyon ranged from 8–10 (Fig. 4). Sediments consisted of sandy silts throughout the canyon, with 8–20% sand and small amounts of clay particles (<5%; Table 2).

Organic carbon content in Hokitika Canyon showed relatively limited variability among sites except for an exceptionally high value at site H700, which reflected high land-derived organic carbon content at that location (Fig. 4). Marine-derived organic carbon content was low throughout the canyon (< 0.1%). Pigment concentrations were also low throughout the canyon but were elevated at the H700 site; chlorophyll *a* to phaeopigment ratios showed no obvious trend. C:N molar ratios in Hokitika Canyon were around 14 at the shallowest sites and 9–11 at the deeper sites. Carbonate content increased slightly with water depth, whereas sand content decreased from almost 50% at the shallowest site to ~5-9% at intermediate depths and ~3-4% at the deepest sites (Fig. 4). Sediments within the canyon comprised slightly sandy silts, with 4–9% sand and <2% clay, except at 200 m water depth, where sand and silt contents each comprised ~50% of the total grain-size distribution (Table 2).

### *Meiofauna*

Nematodes, nauplii and harpacticoid copepods were the most abundant meiofaunal taxa, together comprising an average of 98% of total meiofaunal abundance in both canyons (Supplement 1). Nematodes were particularly dominant in Kaikōura Canyon where they comprised on average 92% of total meiofauna abundance, compared with 80% in Hokitika Canyon. Meiofaunal biomass was dominated by nematodes, ostracods and harpacticoid copepods in both canyons, and together they comprised an average of 98% of total meiofauna biomass in Kaikōura Canyon and 96% of total meiofauna biomass in Hokitika Canyon. Nematodes comprised 87 and 54% of total biomass in Kaikōura and Hokitika canyons, respectively.

Total meiofauna abundance was approximately ten times greater in Kaikōura Canyon (mean = 1983 ind. 10 $cm^{-2}$) than in Hokitika Canyon (174 ind. 10 $cm^{-2}$). A similar difference was also observed for biomass (657 versus 38 μg DW 10 $cm^{-2}$). These differences in abundance and biomass between the canyons were both statistically significant (PERMANOVA, $P < 0.01$). Mean individual biomass ranged from 0.14 to 0.49 μg DW in Kaikōura Canyon and from 0.07 to 0.41 μg DW in Hokitika Canyon, and did not differ significantly between canyons ($P > 0.05$). Meiofaunal community structure differed significantly between the canyons ($P = 0.001$), due to the greater abundance of most taxa (except mites and tardigrades) in Kaikōura Canyon relative to Hokitika Canyon (SIMPER, Supplement 3). There was no significant difference in multivariate dispersion between the canyons (PERMDISP, $P > 0.05$). On the MDS plot, Kaikōura Canyon sites largely clustered well apart from the Hokitika Canyon sites, except for the two deepest Kaikōura Canyon sites (with low abundance) which were situated closer to the Hokitika Canyon sites (Fig. 5).

Meiofaunal abundance and biomass peaked at intermediate (~1000 m) depths in both canyons (Fig. 6). In Kaikōura Canyon, meiofaunal abundance was significantly and negatively correlated with calcium carbonate concentrations (DistLM, $P < 0.05$), and significantly and positively correlated with concentrations of land-derived organic matter ($P < 0.05$; Table 3). A significant negative correlation between meiofaunal biomass and concentrations of marine-derived organic matter was also observed in Kaikōura Canyon ($P < 0.05$), whereas community structure was significantly correlated with water depth and calcium carbonate concentration ($P < 0.05$). In Hokitika Canyon, meiofaunal abundance and biomass were not significantly correlated with any of the predictor variables ($P > 0.05$), although community structure was significantly correlated with calcium carbonate concentration ($P = 0.05$). No significant relationship was found between mean individual biomass of meiofauna and any of the environmental parameters at either Kaikōura or Hokitika Canyon ($P < 0.05$).

### *Macrofauna*

Polychaetes, bivalves, amphipods and tanaids were the most abundant taxa in both Kaikōura and Hokitika canyons and together comprised 78 and 80%, respectively, of total macrofaunal abundance (Supplement 3). Polychaetes were by markedly the most abundant taxon and accounted for 63 and 64% of all macrofauna in both canyons. Macrofaunal biomass in Kaikōura Canyon was dominated by holothurians (54% of total biomass), polychaetes (14%), echiurans (13%), and echinoids (9%). Macrofaunal biomass in Hokitika Canyon was characterised by two outlying sites (H700 and H1200B) with high biomass of scaphopod molluscs, which represented 94% of all macrofaunal biomass recorded from all study sites in the canyon. Polychaetes and bivalves were the only other taxa, making small biomass contributions (5 and 1% of the total, respectively).

Total macrofaunal abundance was approximately five times greater in Kaikōura Canyon (mean = 184 ind. core$^{-1}$) than in Hokitika Canyon (37 ind. core$^{-1}$). A similar but weaker contrast was observed for biomass (1.70 versus 0.98 g wet weight (WW) core$^{-1}$). When the scaphopod biomass data were excluded, mean macrofaunal biomass in Hokitika Canyon was substantially lower (0.06 g WW core$^{-1}$). Macrofaunal abundance was significantly greater in Kaikōura Canyon than Hokitika Canyon (PERMANOVA, $P < 0.01$). Mean individual biomass ranged from <0.001 to 0.06 g WW in Kaikōura Canyon and from <0.001 to 0.09 g WW in Hokitika Canyon, and did not differ significantly between canyons ($P > 0.05$). Macrofaunal biomass and mean individual biomass (with or without scaphopod biomass) did not differ significantly between the canyons ($P > 0.05$), likely due to the high variability in biomass values in Kaikōura Canyon. Macrofaunal community structure differed significantly between the canyons ($P = 0.001$, Fig. 5), mainly due to the greater abundance of polychaetes, bivalves, scaphopods, and aplacophorans in Kaikōura Canyon (SIMPER, Supplement 2). Most taxa, except ophiuroids, echinoids, pycnogonids and cirripeds were more abundant in Kaikōura Canyon than Hokitika Canyon. There was no difference in multivariate dispersion between the canyons (PERMDISP, $P > 0.05$).

Neither total nor mean individual macrofaunal biomass showed any significant trends with any of the predictor variables in either canyon (DistLM, $P > 0.05$, Fig. 7). In both canyons, macrofaunal abundance exhibited a significant negative trend with depth, and a significant positive trend with C:N ratio ($P < 0.05$, Table 3). Macrofaunal abundance was also significantly and negatively correlated with silt content and marine-derived organic matter content in Hokitika Canyon ($P < 0.05$, Fig. 7). Community structure in Kaikōura Canyon was significantly correlated with land-derived organic matter content ($P = 0.05$), whereas in Hokitika Canyon, community structure was significantly correlated with water depth and marine-derived organic matter content ($P < 0.05$).

*Stable isotopes*

The $\delta^{13}C$ isotopic values of *Brissopsis oldhami* (-20.3 to -17.8‰) were significantly more depleted than values of *Molpadia musculus* (-19.4 to -16.6‰) and *Neilo* sp. (-17.6 to -16.9‰; PERMANOVA, $P = 0.001$; Supplement 4). The $\delta^{15}N$ values of *B. oldhami* (9.8 to 11.8‰) and *Neilo* sp. (9.9–11.0‰) were significantly more depleted than *M. musculus* values (11.3 to 14.7‰; $P = 0.001$). There were significant among-site differences in $\delta^{13}C$ and $\delta^{15}N$ values of *B. oldhami* and *M. musculus* ($P < 0.05$; Fig. 8). There was a significant positive correlation between $\delta^{13}C$ and $\delta^{15}N$ values of *B. oldhami* ($P = 0.001$, $R^2 = 0.69$) and *M. musculus* ($P = 0.\ 03$, $R^2 = 0.21$), but not *Neilo* sp. ($P > 0.05$). There was significant positive correlation between body size and $\delta^{13}C$ isotopic values of *B. oldhami* (DistLM, $P = 0.001$, $R^2 = 0.47$), but not $\delta^{13}C$ values of *M.*

*musculus* or *Neilo* sp. ($P > 0.05$). There was no relationship between body size and $\delta^{15}$N values of any of the taxa we considered.

Mean invertebrate $\delta^{13}$C signatures were more enriched than the signatures of offshore sediment organic matter by 0.7–3.5‰, more enriched than Kaikōura Canyon sediment organic matter by 1.5–6.5‰, and more enriched than riverbed organic matter by 6.2–10.1‰ (Fig. 9). Mean invertebrate $\delta^{15}$N signatures were more enriched than the signatures of offshore sediment organic matter by 3.5–7.3‰, more enriched than Kaikōura Canyon sediment organic matter by 4.2–8.32‰, and more enriched than riverbed organic matter by 6.1–10.8‰.

## Discussion

### *Sediment characteristics*

The quantity, quality and origins of organic matter clearly differed between the two canyons (Fig. 10; see also detailed discussion in Gibbs et al. submitted). Kaikōura Canyon sediments were characterised by elevated organic matter concentrations relative to the Hokitika Canyon, which largely reflected greater input of marine-derived organic matter; concentrations of marine-derived organic matter, in turn, likely reflected the higher surface primary productivity on the east coast than on the west coast of New Zealand's South Island (Bradford-Grieve et al. 1997; Zeldis et al. 2010). In Kaikōura Canyon, the marine contribution of sediment was also reflected in the relatively high overall chlorophyll *a* to phaeopigment ratio (typically >20%). Concentrations of marine-derived organic matter increased with depth and distance from land in both canyons, although this aspect was most obvious in Kaikōura Canyon, where the proportions increased from ~0.3% in the head of the canyon to ~1% only 25 km down-canyon (Fig. 10, also Gibbs et al. submitted). In comparison, the proportion of marine-derived organic matter remained <0.1% throughout the ~400 km reach of Hokitika Canyon that was sampled, but did increase slightly with increasing water depth. This bathymetric down-canyon increase in marine-derived organic matter likely reflects the higher contribution made to organic carbon stocks due to increased nutrient transport and enhanced primary production in surface waters associated with canyon-related processes, such as upwelling, downwelling and tidal mixing (Skliris and Djenidi 2006; Allen and Durrieu de Madron 2009). Because deep currents within canyons are constrained to the canyon axis and independent of wind-driven flows above (She and Klinck 2000), marine organic matter that sinks to the benthos is subsequently incorporated into such flows and transported down-canyon (e.g., Lopez-Ferdinand et al. 2013). As these flows are also able to erode and transport sedimentary organic matter that has accumulated in marine sediments either on the canyon walls and/or canyon floor (Inman et al. 1976; Pantin 1979), the relative contribution of marine organic matter is also enhanced preferentially along the canyon axis. These transport processes must operate over sufficiently short timescales to prevent complete mineralization of marine organic matter by microorganisms and benthic fauna before reaching the deeper parts of the canyon; at this point it is likely that marine organic matter will be at least partially degraded and therefore of lower nutritional value (e.g., Nodder et al. 2016).

Nevertheless, the land-derived organic matter component may still be important in New Zealand canyons. For example, in Hokitika Canyon, the presence of terrestrial material in axial sediments is suggested by elevated C:N molar ratios and isotopically depleted $\delta^{13}C$ ratios that are similar to riverbed sediments (Gibbs et al. submitted). Similar interpretations have been made for other canyons, such as Nazaré Canyon/Atlantic Ocean (Masson et al. 2010), where strong terrestrial-ocean linkages are apparent across the continental margin via submarine canyons (see also Kiriakoulakis et al. 2011; Pasqual et al. 2013). The differences in organic matter composition as evidenced by the bulk isotope data, molar C:N ratios and pigments between Hokitika Canyon compared with Kaikōura Canyon suggest that the organic material in the former canyon is likely to be more refractory and, therefore, may not provide a high quality food source for the resident benthic communities.

The concentrations of calcium carbonate in the sediments of Kaikōura and Hokitika canyons were generally positively correlated with the concentrations of marine-derived organic matter derived from the isotopic analyses of Gibbs et al. (submitted) from the same sites (Fig. 11). This positive relationship was most evident for Kaikōura Canyon sites where variability in calcium carbonate concentrations was greater than in Hokitika Canyon. Although care should be taken in extrapolating from this limited range of concentrations (<10%), this relationship suggests that $CaCO_3$ concentrations may be used as a proxy of marine-derived organic matter inputs to the sediments at the study locations (Alt-Epping et al. 2007). These observations are, however, opposite to the relationship found by Kiriakoulakis et al. (2011), who showed a negative relationship between %$CaCO_3$ and %total organic carbon in submarine canyons on the Portuguese margin. These European data also covered a wider range of carbonate percentages (10–55%) than the present study, highlighting that caution is warranted in developing this extrapolation further for the New Zealand examples. Nevertheless, we also observed a negative relationship between the ratio of marine- to land-derived organic carbon and C:N ratios, which supports the use of the latter variable as an indicator of organic matter origins (Fig. 11), consistent with other continental margin and canyon studies (e.g., Kiriakoulakis et al. 2011; Brackley et al. 2010). Probert and Anderson (1986) showed that refractory, land-derived lignin was a conspicuous component of the organic matter constituents on the upper slope and shelf of Westland (South Island west coast, New Zealand), highlighting the importance of terrestrial systems as a subsidy source of organic matter to fuel benthic communities in this region (Probert 1986).

Calcium carbonate concentrations in Hokitika Canyon were low (<2%) compared with $CaCO_3$ concentrations from the adjacent continental slope; for example, $CaCO_3$ contents in open slope sediment samples taken in the vicinity of sites H2000, H1500 and H1200 were 54–68, 28–37 and 20–33%, respectively (S. Nodder unpublished data; also Stoffers et al. 1984; Probert and Swanson 1985; Bostock et al. 2018a). If we assume that sediment calcium carbonate originates solely from marine production, these substantially greater values on the open slope suggest that land-derived organic matter is largely restricted to the canyon, which supports the notion that Hokitika Canyon acts as an efficient conduit of land material to the deep sea. On the other hand, there appeared to be little if any differences in C:N values between Hokitika Canyon and adjacent slope samples, which could suggest that land-derived organic matter is also present outside the canyon (Stoffers et al. 1984; Probert and Anderson 1986; Zeldis et al. 2010). However, degraded and partially mineralised organic matter of marine origin can also be characterized by relatively elevated C:N ratio, as on the central Chatham Rise where surface sediment with marine carbon isotopic signatures have C:N ratios ranging from 8 to 16 (Leduc et al. 2015).

The calcium carbonate content on the Kaikōura shelf and slope grades from 0–20% to 40–60% $CaCO_3$ on the mid-outer shelf and around the canyon rim, down to 20–40% on the upper slope (Bostock et al. 2018a; b), compared with ~2% in the upper canyon and 5–8% in the lower canyon (Table 2). This pattern also reflected the relative dilution of carbonate material in the canyon by terrigenous material as observed on other New Zealand margins (e.g., west coast South Island – Stoffers et al. 1984; Probert and Swanson 1985, east coast North Island – Carter et al. 2002). There are no available data of C:N ratios from the continental slope sediments off the east coast South Island with which to corroborate these interpretations, although the C:N ratios throughout most of the Kaikōura Canyon were relatively low (~8–10), while most of the chlorophyll *a* to phaeopigment ratios were high (>0.2) (Fig. 4). These data suggest that more labile material is being deposited and transported down-canyon in Kaikōura Canyon compared with Hokitika Canyon.

It should be noted that sediment parameters from the two canyons were measured from samples obtained in different years and seasons (late autumn 2010 in

Kaikōura canyon and spring 2010 in Hokitika Canyon). Some of the differences we observed between the canyons may therefore be linked to factors such as temporal variation in surface primary productivity and river flows, as well as seismic activity. This may be particularly true for pigment data, which were obtained from the 1 cm of sediment (versus top 5 cm of sediment for all other sediment parameters), and which can degrade or be consumed relatively quickly by microorganisms and benthic fauna. Other parameters, such as calcium carbonate content and proportions of marine versus land-derived organic matter are less likely to have been affected by sampling years as they were obtained from the top 5 cm of sediment, which integrates several years to decades of sedimentation in the study areas (Probert and Swanson 1985; Gomez et al. 2004; Alexander et al. 2010, Radford 2012).

### *Meiofauna*

The structure of meiofaunal communities in Kaikōura and Hokitika canyons, which were dominated by nematodes, harpacticoid copepods and nauplii, is typical of deep-sea meiofaunal communities in general (Rosli et al. 2018). The current results support previous findings on nematodes, demonstrating that abundance and biomass of this taxon is higher in Kaikōura Canyon than in any other canyon for which nematode data are available (Leduc et al. 2014). The abundance of meiofauna in three canyons located along Hikurangi Margin, off the east coast of New Zealand's North Island, however, is only slightly lower than in Kaikōura Canyon (mean and maximum abundance = 1728 and 2702 ind. 10 $cm^{-2}$ *versus* 1983 and 3103 ind. 10 $cm^{-2}$, respectively; Rosli et al. 2016). Nevertheless, these results, together with the markedly elevated biomass of the larger macro-infauna and mega-epifauna (De Leo et al. 2010), suggest that Kaikōura Canyon sediments are characterized by high food availability. In contrast, the lower nematode and meiofaunal abundance and biomass we observed in Hokitika Canyon are similar to values from canyons with low standing stocks such as the Setubal and Whittard canyons (Atlantic Ocean) (Ingels et al. 2011a, b; Leduc et al. 2014). These differences in meiofaunal abundance and biomass in the New Zealand canyons are mainly consistent with the differences in total organic matter and pigment concentrations we observed between the canyons, which largely reflect differences in inputs of labile marine-derived material to the seabed. Absolute levels of land-derived organic material did not differ markedly between the canyons, which indicates that the high benthic standing stocks of Kaikōura Canyon relative to Hokitika Canyon may not be linked to inputs of land-derived material. It should also be noted that the contrast in meiofaunal standing stocks between the two canyons may partly be the result of the different sampling years and seasons in which each canyon was sampled. For example, Nodder et al. (2003) found generally elevated meiofaunal biomass at Chatham Rise sites in autumn 1997 compared to spring 1997 and summer 2000.

Although our results did not reveal an obvious difference in the range of land-derived organic matter concentrations between the study canyons, the result of DistLM analyses indicate that within-canyon variation in meiofaunal community parameters was linked to inputs of land- and marine-derived organic matter as well as calcium carbonate content. In Kaikōura Canyon, meiofaunal abundance and biomass were negatively correlated with marine-derived organic matter and calcium carbonate concentrations, respectively, whereas meiofaunal abundance was positively correlated with land-derived organic matter concentrations. Mean meiofaunal body mass, however, was not correlated with food availability, indicating that variability in biomass was largely due to variation in abundance. It is unclear why meiofaunal standing stocks should be negatively correlated with concentrations of marine-derived organic matter, which is typically considered a high-quality food source, and positively correlated with land-derived organic matter, a more refractory food source typically considered to be of lower nutritional value (Tenore et al. 1982; Middelburg and Nieuwenhuize1998). Studies of canyon meiofauna normally describe a positive relationship between food quality and meiofaunal abundance and biomass, with the strength of this relationship becoming greater in environments where hydrodynamic disturbance is greater (Bianchelli et al. 2008; Ingels et al. 2011a). In addition, effects of food quality on deep-sea meiofaunal communities have been shown to be stronger in areas that are oligotrophic or where food supply to the benthos is relatively constant and not highly variable temporally (Danovaro et al. 1995; Gambi and Danovaro 2006). It is, therefore, possible that the lack of a positive relationship between the supply of high-quality, marine-derived organic matter and meiofaunal abundance and biomass in Kaikōura Canyon is due to the highly abundant and potentially variable food supply to the benthos in this environment. The accumulation of large quantities of labile marine phytodetritus in the sediments could also have a negative impact on meiofaunal communities if low oxygen conditions were to develop, although low oxygen conditions tend to mainly impact diversity rather than abundance (Neira et al. 2018). The positive relationship between land-derived organic matter and meiofaunal abundance may reflect the concomitant decrease in both land-derived material concentrations and meiofaunal abundance with water depth. There was no relationship between macrofauna and meiofaunal abundance in either study canyon (DistLM, $P > 0.05$), suggesting that meiofauna are not negatively impacted by interactions with macrofauna (e.g., competition for food; Olafsson 2003). Alternatively, the relationship could indicate a positive impact of terrigenous material on meiofaunal abundance through the provision of an additional (though relatively low quality) food resource. Meiofauna may be better able to assimilate low-quality terrestrial organic matter when there is also an adequate supply of high-quality marine organic matter; for example, refractory vascular plant material low in nitrogen is more readily assimilated by consumers when a rich source of nitrogen (an otherwise limiting nutrient) is also present (Finlay and Tenore 1982). A better understanding of the effects of land-derived food inputs on deep-sea and canyon meiofauna requires further investigation.

The two shallowest Kaikōura Canyon sites, at ca. 400 and 700 m depths, were characterised by low meiofaunal abundance and biomass relative to sites at 1000–1300 m depths.  A high frequency of physical disturbance near canyon heads, which may result from greater tidal current velocities, heightened internal wave activity and/or slope instability relative to deeper parts of the canyons (Pratson et al. 1996; Allen et al. 2009; de Stigter et al. 2011), has previously been advocated as likely mechanisms leading to the relatively low infaunal densities sometimes observed in the upper part of canyons (Garcia et al. 2007; Liao et al. 2017). Although we did not directly test for relationships between disturbance and benthic communities, it seems likely that variation in the degree of physical disturbance among sites had an influence on the structure of meiofaunal communities in Kaikōura Canyon. During the November $M_W$7.8 Kaikōura earthquake, significant amounts of erosion in the upper parts of the canyon were a feature of this canyon-flushing event (Mountjoy et al. 2018).

*Macrofauna*

Polychaetes were the dominant macrofaunal taxon in both study canyons (~60% of all fauna), which is the typical pattern of dominance for macrofauna observed in deep-sea canyons elsewhere (e.g., for New Zealand, mean = 56%, range = 28-95%; Leduc et al. 2016; e.g., Whittard canyon, mean = 53%; Gunton et al. 2015). Nevertheless, macrofaunal community structures in Kaikōura and Hokitika canyons were significantly different, determined largely by differences in abundance for most taxa. Total macrofaunal abundance was approximately five times greater in Kaikōura Canyon compared with Hokitika Canyon. Particularly high abundances of macro-infauna have been recorded previously at the head of Kaikōura Canyon (51,500 ind. $m^{-2}$, De Leo et al. 2010), and similarly, the high abundances of macro-infauna observed in this study using additional samples (mean and maximum of 184 and 615 ind. $core^{-1}$, or 31,837 and 86,764 ind. $m^{-2}$) are among the highest recorded elsewhere in deep-sea sediments (excluding chemosynthetic environments; Rex et al. 2006). As for our results on sediment parameters and meiofauna, however, our findings on macrofauna may have been influenced by the different years and seasons in which the Kaikōura and Hokitika canyons were sampled. For example, if we compare sites which were sampled in different years in the same branch of upper Kaikoura Canyon (see lower half of Figure 1C), we observe that macrofaunal density was somewhat low in 2010 (81-194 ind. core-1, sites K4 and K5) compared to 2007 (312 ind. core-1, site K14) and 2006 (163-615 ind. core-1, sites K16-K19).

Macrofaunal abundance in both canyons exhibited a significant negative relationship with water depth, which is typical for many deep-sea environments and has been observed previously for shelf and slope macrobenthos off New Zealand's South Island (e.g., Probert and Anderson 1986). This negative relationship between depth and macroinfaunal abundance in the deep sea is generally thought to be related to decreasing food availability with increasing depth (e.g., Escobar Briones et al. 2008), but our study mainly found that food-related variables increased with depth in both study canyons (particularly marine-derived organic matter in Kaikōura Canyon). Nevertheless, the sediment C:N ratio decreased with increasing depth in both canyons, and was positively correlated with macroinfaunal abundance. Thus, it appears that the relative quality of this material (as indicated by the C:N ratio) is an important factor controlling the abundance of macrofauna along the canyon depth gradients. Unexpectedly, there was no statistical difference in macrofaunal biomass between the two canyons, despite marked variations in abundance and associated environmental factors (including depth). This finding is particularly unexpected given previous findings that Kaikōura Canyon is a hotspot of deep-sea megafaunal biomass (De Leo et al. 2010), and that negative relationships between macro-infaunal biomass and water depth have been observed off the west coast of South Island (Probert and Anderson 1986) and on Chatham Rise (east of New Zealand) (Berkenbusch et al. 2011). The reasons why these previous observations are not reflected in the biomass of canyon macro-infauna in the present study requires further investigation, especially given the relatively labile nature of the sediments in Kaikōura Canyon compared with Hokitika Canyon. One possible reason for the lack of difference in the macrofaunal biomass between the two canyons may be related to the sampling: samples in the earlier study by De Leo et al. (2010) were from only a limited area in the canyon (presumably the most productive area, possibly due to greater accumulation of phytodetritus), whereas samples from the present study were taken throughout the canyon and encompassed greater variation in sediment organic matter content. It is also possible that temporal variability in organic matter supply to the benthos drives changes in macrofaunal standing stocks.

The macrofaunal community structure (defined as the multivariate relative abundance of taxa) in Kaikōura Canyon was correlated with land-derived organic matter content of the sediment, and with marine-derived organic matter in Hokitika Canyon. The amount of land-derived organic matter decreased markedly with distance from land in Kaikōura Canyon (Fig. 10), likely because of its proximity to land and because of its steep and short axis. These characteristics likely explain the correlation between community structure and land-derived organic matter in Kaikōura Canyon. In contrast, Hokitika Canyon sediments showed an increase in land-derived organic matter with distance from land (if we omit the exceptionally high value observed at 700m; Fig. 10) , but this increase was gradual along the length of the canyon, and this sediment parameter was not significantly correlated with community structure in this canyon comparatively distant from land. The positive relationship observed between marine-derived organic matter concentration and macrofauna in Hokitika canyon may be related to the relatively low concentrations of this labile food source in this environment, meaning that marine organic matter is the main limiting factor shaping macrofaunal communities.

Differences in macrofaunal abundance, biomass and community structure among canyons have been observed elsewhere by previous studies, and in-part have been related to measured or inferred differences in the amount of organic matter available to the infauna in the different canyons (Cunha et al. 2011; De Leo et al. 2014; Paterson et al. 2011; Leduc et al. 2016). Nevertheless, there are only a limited number of studies to our knowledge that have examined differences in infaunal communities among canyons in relation to the source of the organic matter. For example, Cunha et al. (2011) observed spatial heterogeneity among macrofauna in three canyons on the Portuguese margin. Overall, these authors attributed the difference between Nazaré Canyon and the Setúbal and Cascais canyons to the higher amounts of sediment nitrogen and carbon in the former canyon. In addition, the quality of the organic matter was lower in Nazaré Canyon (indicated by a low C:N ratio), which the authors inferred to be mostly land-derived refractory carbon compared with the predominantly marine-derived carbon received by Setúbal and Cascais canyons. In a study of the organic geochemistry of the same samples, Kiriakoulakis et al. (2011), using a variety of biochemical tracer techniques, found that the sediments of Nazaré Canyon did possess a greater proportion of land-derived organic matter components than the other two canyons; the same study also found that organic matter preservation was enhanced in this canyon. Overall, the conclusion from these investigations was that organic loading probably was the major driver for structuring canyon benthic assemblages through a series of mechanisms that act on the availability of food and partitioning of resources by different species (Cunha et al. 2011).

Based on our findings, we suggest that the relative amounts of marine-derived organic matter in the sediment are at least partly responsible for the difference observed between the macrofaunal communities in Kaikōura and Hoikitika canyons. That is, benthic communities in Hokitika Canyon are more food-limited than at Kaikōura Canyon, with contributions to the canyon benthic environment from highly labile marine organic matter predominating in the latter canyon. In their *in situ* stable isotope labelling experiment at a single depth in Whittard Canyon (NE Atlantic), Hunter et al. (2013) found that, over the course of the experiment, the assemblage from the eastern branch of the canyon consumed greater quantities of marine- compared with land-derived organic matter than the assemblage of the western branch. The latter assemblage showed little difference in consumption between the sources of organic matter, and was significantly different from that of the eastern branch: the western assemblage had relatively lower abundances of crustaceans and tanaids than the eastern branch, which consisted of taxa occurring at higher abundances and dominated by polychaetes and large nematodes. Hunter et al. (2013) speculated that the different macrofaunal assemblages and their response to the experiment reflected differing regimes of disturbance and resource availability between the canyon branches. They considered that the higher abundances of disturbance-tolerant taxa (polychaetes and large nematodes) indicated a higher frequency of disturbance events and organic matter availability in the eastern branch of the canyon. Our study of among-canyon differences in macrofaunal communities seems to provide some support for these within-canyon observations. Marine-derived organic carbon was higher and more labile (as reflected in lower molar C:N ratios) in the sediments of Kaikōura Canyon, as were the abundances of polychaetes (and of nematodes). Kaikōura Canyon is also known to experience irregular geological disturbance events from turbidity flows (Mountjoy et al. 2018), which could also affect the quantity and quality of organic matter available to benthic fauna in this canyon compared to Hokitika Canyon. Nevertheless, the precise role of turbidity flows, triggered by storms or earthquakes, for the availability of organic matter, and their concomitant influence on the structuring of canyon macrofaunal communities have rarely been studied (Okey 1997; McClain and Barry 2010), and warrant further investigation.

### *Stable isotopes*

In Kaikōura Canyon, we observed a positive correlation between the $\delta^{13}$C and $\delta^{15}$N values of the burrowing urchin *Brissopsis oldhami* and of the holothurian *Molpadia musculus*, which suggests that variation in trophic level (and not carbon source) is the cause of the variability among samples and sampling sites in this canyon. This kind of relationship has been observed in several other studies of deep-sea communities, and is indicative of common primary source material (Polunin et al. 2001; Reid et al. 2012). These correlations result from the increase in both $\delta^{15}$N and $\delta^{13}$C values (1.4–3.4 and 0.5–1.0‰, respectively) with each trophic level (DeNiro and Epstein 1978; McCutchan et al. 2003). The slope of the relationship observed for *B. oldhami* and *M. musculus*, however, was low relative to the range of slopes expected based on the usual enrichment in carbon and nitrogen isotopic signatures (0.9 and 0.3, respectively, versus 1.4–6.8). A similar slope was observed by Iken et al. (2001) for a benthic community at the Porcupine Abyssal Plain. This discrepancy could be due to either relatively small trophic enrichment in $\delta^{15}$N values, or to the influence of different carbon sources. The lack of a relationship between body size and $\delta^{15}$N values indicated that body size is not a reliable predictor of trophic level for the species we studied. The isotopic separation between these two species also suggested that they are feeding on slightly different food sources in Kaikōura Canyon, with the holothurian consuming more enriched material. The enriched isotopic values of holothurians may reflect a diet comprised almost exclusively of highly refractory and frequently recycled organic matter, perhaps hosting high bacterial biomass (Iken et al. 2001; Roberts et al. 2001).

The preservation of invertebrate tissue samples in ethanol can lead to shifts in carbon and nitrogen isotopic signatures. These shifts are usually in the order of -1 to +2‰ for $\delta^{13}$C and -0.5 to +1‰ for $\delta^{15}$N (Kaehler and Pakhomov 2001; Sarakinos et al. 2002; Syvaranta et al. 2011; Hogsden and McHugh 2017), although there is evidence suggesting that ethanol preservation effects are similar to isotopic shifts associated with freezing, the most commonly used preservation method (Syvaranta et al. 2011). Effects of ethanol preservation on *Molpadia musculus* may be relatively pronounced, with a shift of +3.6‰ observed in $\delta^{13}$C values observed after 3 to 12 months, whereas $\delta^{15}$N values appeared to be unaffected (Fanelli et al. 2010). Overall, the use of ethanol generally leads to more enriched $\delta^{13}$C signatures probably because it acts as a solvent of isotopically lighter lipid compounds (DeNiro and Epstein 1976; Doucett et al. 1999) and few if any changes in $\delta^{15}$N signatures. Since all invertebrate samples analysed in the present study were preserved in ethanol, it is likely that consumer $\delta^{13}$C signatures were more enriched than samples analysed from frozen specimens, particularly for *M. musculus*. Overall, the main effect of using ethanol-preserved specimens in food web studies will be to underestimate the contribution of $^{13}$C-depleted food sources such as land-derived organic matter.

Interpreting food web dynamics in aquatic food webs, even in simple two end-member models, can be difficult because benthic primary consumers have $\delta^{13}$C values that are typically enriched by about 4 ‰ relative to suspended organic matter (Nadon and Himmelman 2006). Romero-Romero et al. (2016) suggested that this fractionation results from the presence of a distinct bacterial community in the gut of deep-sea benthic consumers. It has also been argued that slow deposition of particulate organic matter (POM) leads to enriched isotopic composition due to ongoing microbial degradation (Mintenbeck et al. 2007; Reid et al. 2012). However, Gibbs et al. (submitted) showed that the $\delta^{13}$C signature of organic matter in continental margin sediment is similar to the isotopic signature typical of suspended organic matter at the ocean's surface (see also Fig. 9). Therefore, the enrichment often observed between consumers and suspended organic matter in studies of deep-sea trophic dynamics (e.g., Leduc et al. 2015; Demopoulos et al. 2017) has unclear implications for the interpretation of food web relationships. To help address this limitation, Post (2002) suggested using bivalves (primary consumers of pelagic primary production) to determine the $\delta^{13}$C and $\delta^{15}$N isotopic baseline against which to compare other consumers. Assuming that *Neilo* sp. feeds solely on phytoplankton (either directly through suspension feeding or through feeding on fresh phytodetritus in the sediment, corresponding to a 3.6 and 4.7 ‰ enrichment relative to SPOM $\delta^{13}$C and $\delta^{15}$N values, respectively), then the relatively depleted $\delta^{13}$C values of *B. oldhami* and *M. musculus* likely reflect a diet comprising a mixture of marine- and land-derived organic carbon. *Neilo* spp. are infaunal bivalves that have been shown to preferentially occur (often in association with *Brissopsis oldhami*) in fine sediments with high input of terrigenous organic matter and low oxygen levels, which has led some authors to hypothesise this genus to be deposit-feeding with a diet of "bacteria associated with the breakdown of terrigenous matter" (Marshall 1978). In contrast, assuming that *Neilo* sp. feeds partly on land-derived material in the sediments would suggest an even greater contribution of land-organic matter to the diet of *B. oldhami* and *M. musculus* in Kaikōura Canyon, which would be consistent with the positive relationship we observed between meiofaunal abundance and concentrations of land-derived carbon in this canyon. However, given the uncertainty associated with the effect of ethanol on invertebrate isotopic values, the absence of samples from adjacent slope habitats, and the uncertainty about the feeding habits of *Neilo* sp., the contribution of land-derived organic matter of Kaikōura canyon remains far from clear. If we consider that invertebrate isotopic values were closest to SPOM and offshore sediment isotopic values, then the diets of *B. oldhami* and *M. musculus* may well consist mainly (if not exclusively) of marine-derived organic matter. Elucidating the diet of canyon benthic fauna will require the use of additional isotopic tracers (e.g., $\delta^{34}S$) or methods such as gut content analyses.

## Conclusions

Gradients of land- and marine-derived organic matter can differ widely within and among submarine canyons depending on factors such as their morphology, local physical oceanography (currents, tides, internal waves) and proximity of riverine sources. We hypothesised that this variability in relative organic matter availability is an important driver of infaunal community parameters in canyons. We found that the nature of relationships between infaunal communities and organic matter concentrations varied, depending on the origin of the latter from land or marine sources. It is, therefore, important to consider the origins and quality of sediment organic matter, in addition to its quantity. Correlation analyses and stable isotope data suggest that land-derived organic matter may contribute to infaunal standing stocks in Kaikōura Canyon. Nevertheless, infaunal abundance and biomass were low throughout Hokitika Canyon despite similar concentrations of land-derived organic matter in sediments of both canyons. This finding suggests that variation in marine-derived organic matter concentration is more important in determining community differences between canyons.

The results from this study will be used in the future to model, using a physical canyon classification (that includes parameters used in this study to characterise the two contrasting study canyons, e.g., river sediment load and flow rates; Rowden et al. in prep.), the wider regional influence of canyons to, for example, deliver land-derived organic matter to support deep-sea benthic communities around New Zealand. Thus, the model prediction could then be used to understand more broadly the connectivity of land and deep-sea ecosystems, thereby informing management measures taking into account this connectivity.

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## Figure captions

**Figure 1.** Map of New Zealand (A) and of Kaikōura Canyon (B) showing the location sampling sites, with detail of sites sampled near the head of the canyon (C). Orange symbols denote sites sampled for the quantification of meiofauna and/or macrofaunal community parameters, and white symbols indicate sites sampled for stable isotope analyses of invertebrates during voyages TAN1006 (circular symbols), KAH0706 (triangles) and TAN0616 (squares) (see Table 1 for details). Watershed areas sampled by Gibbs et al. (submitted) for the characterization and quantification of land-derived organic matter are shown in dark orange (Conway River), pale orange (Waiau River) and yellow shading (Hurunui River).

**Figure 2.** Map of New Zealand (A) and of Hokitika Canyon (B) showing the location sampling sites sampled during TAN1712 (diamond symbol) and TAN1311 (triangles) (see Table 1 for details). Watershed areas sampled by Gibbs et al. (submitted) for the characterisation and quantification of land-derived organic matter are shown in dark (Hokitika River), and light green shading (Whataroa River).

**Figure 3.** Principal components analysis (PCA) ordination based on environmental data from Kaikōura (black squares, sampled during voyage TAN1006 in 2010) and Hokitika canyons (empty triangles, sampled during voyage TAN1311 in 2013) with eigenfactors overlay corresponding to Pearson correlations of individual variables with the PCA axes.

**Figure 4.** Relationships between water depth and selected environmental variables in Kaikōura (black squares, sampled during voyage TAN1006 in 2010) and Hokitika canyons (empty triangles, sampled during voyage TAN1311 in 2013). (TOC, total organic content; C:N, carbon:nitrogen ratio; %OC = organic carbon content; %CaCO3, calcium carbonate content, Chl *a*:phaeo, chlorophyll *a* to phaeopigment ratio)

**Figure 5.** Two-dimensional multidimensional scaling ordination plot for (A) meiofaunal and (B) macrofaunal taxa from sites in Kaikōura (filled symbols) and Hokitika canyons (empty symbols). Labels refer to water depth. The shape of the symbols refer to the sampling voyages and sampling years: circles (TAN0616, 2006), inverted triangles (KAH0706, 2007), squares (TAN1006, 2010), diamonds (TAN1712, 2017) and triangles (TAN1311, 2013).

**Figure 6.** Relationship between selected environmental predictor variables and meiofaunal abundance (left-hand side graphs) and biomass (right-hand side graphs) in Kaikōura (black squares, sampled during voyage TAN1006 in 2010) and Hokitika canyons (empty triangles, sampled during voyage TAN1311 in 2013). Dotted lines indicate a significant relationship (DistLM, $P < 0.05$).

**Figure 7.** Relationship between selected environmental predictor variables and macrofaunal abundance (left-hand side graphs) and biomass (right-hand side graphs) in the Kaikōura (filled symbols) and Hokitika canyons (empty symbols). Dotted (Kaikōura) and broken lines (Hokitika) indicate a significant relationship (DistLM, $P < 0.05$). The shape of the symbols refer to the sampling voyages and sampling years:

circles (TAN0616, 2006), inverted triangles (KAH0706, 2007), squares (TAN1006, 2010), diamonds (TAN1712, 2017) and triangles (TAN1311, 2013).

**Figure 8.** Variability in $\delta^{13}C$ (top) and $\delta^{15}N$ values (bottom) of *Brissopsis oldhami*, *Molpadia musculus*, and *Neilo* sp. among Kaikōura Canyon sites. For each taxon, sites sharing the same lower case (*B. oldhami*) or upper case letter (*M. musculus*) indicate that the isotopic values are not significantly different (PERMANOVA pairwise comparisons, $P > 0.05$).

**Figure 9.** Dual isotopic plot showing $\delta^{13}C$ and $\delta^{15}N$ values of *Brissopsis oldhami*, *Molpadia musculus*, and *Neilo* sp. from Kaikōura Canyon sites in relation to sediment organic matter from locations within the canyon, offshore from the canyon and from riverbeds considered to contribute land-derived organic matter to the canyon (Gibbs et al. submitted) (SPOM = suspended particulate organic matter). (Data labels refer to sites listed in Table 1.)

**Figure 10.** Concentrations of land-derived (top graph) and marine-derived (bottom graph) organic carbon (OC) in sediments from Kaikōura (black squares) and Hokitika canyons (empty triangles) on the continental margin of New Zealand's South Island. (One outlier data point from Hokitika Canyon (site H700) was omitted for clarity; data from Gibbs et al. (submitted).)

**Figure 11.** Relationship between land-derived organic carbon and calcium carbonate concentrations (DistLM, $P < 0.01$, $R^2 = 0.86$; top graph), and between the ratio of land- to marine-derived organic carbon and molar carbon to nitrogen (C:N) ratio in

sediment from Kaikōura (black squares) and Hokitika canyons (empty triangles).

Organic carbon data from Gibbs et al. (submitted).

**Table 1.** Details of Kaikōura and Hokitika canyon study sites with number of cores analysed for macro- and meiofauna (abundance, biomass and community structure) and sediment parameters from each multicorer deployment (station).

| Canyon | Voyage | Date mm/YYYY | Station | Site | Water depth (m) | Latitude °S | Longitude °E | Sediment | Meiofauna | Macrofauna |
|---|---|---|---|---|---|---|---|---|---|---|
| Kaikōura | TAN1006 | 05/2010 | 6 | K13 | 404 | 42.4897 | 173.5510 | 1 core | 3 cores | 2 cores |
| | | | 5 | K9 | 706 | 42.4810 | 173.5582 | 1 | 2 | 3 |
| | | | 3 | K5 | 989 | 42.5243 | 173.6127 | 1 | 2 | 3 |
| | | | 4 | K1 | 1017 | 42.4838 | 173.6147 | 1 | 2 | 3 |
| | | | 14 | K3 | 1032 | 42.5039 | 173.6192 | 1 | 2 | 3 |
| | | | 7 | K4 | 1061 | 42.5082 | 173.6325 | 1 | 2 | 3 |
| | | | 8 | K2 | 1127 | 42.4922 | 173.6569 | 1 | 2 | 2 |
| | | | 2 | K6 | 1289 | 42.5203 | 173.7118 | - | 3 | 2 |
| | | | 11 | K7 | 1320 | 42.5237 | 173.7356 | 1 | 2 | 3 |
| | | | 9 | K8 | 1420 | 42.5692 | 173.7389 | 1 | 2 | 3 |
| | | | 1 | K12 | 1485 | 42.6230 | 173.7505 | 1 | 2 | 2 |
| | KAH0706 | 06/2007 | 6 | K14 | 1040 | 42.5192 | 173.6223 | - | - | 3* |
| | | | 3 | K15 | 1808 | 42.6880 | 173.9078 | - | - | 3* |
| | TAN0616 | 11/2006 | 105 | K16 | 1020 | 42.5228 | 173.6210 | - | - | 1* |
| | | | 103 | K17 | 1033 | 42.5187 | 173.6237 | - | - | 1* |
| | | | 101 | K18 | 1041 | 42.5150 | 173.6268 | - | - | 2* |
| | | | 98 | K19*** | 1061 | 42.5118 | 173.6325 | - | - | 1* |
| | | | 99 | K20*** | 1079 | 42.4850 | 173.6153 | - | - | - |
| | | | 106 | K21*** | 1020 | 42.5200 | 173.6197 | - | - | - |
| | | | 107 | K22*** | 1029 | 42.5177 | 173.6220 | - | - | - |
| | | | 108 | K23*** | 1014 | 42.5232 | 173.6190 | - | - | - |
| | | | 109 | K24*** | 1028 | 42.5163 | 173.6268 | - | - | - |
| Hokitika | TAN1712 | 09/2017 | 2 | H1200A | 1169 | 42.4063 | 169.8828 | 1** | - | 2 |
| | TAN1311 | 10/2013 | 63 | H200 | 191 | 42.7020 | 170.7270 | - | 1 | 1 |
| | | | 64 | H200 | 193 | 42.7020 | 170.7262 | 1 | 1 | 1 |
| | | | 66 | H200 | 190 | 42.7028 | 170.7277 | - | 1 | 1 |
| | | | 12 | H700 | 726 | 42.5766 | 170.3262 | 1 | 1 | 1 |
| | | | 13 | H700 | 726 | 42.5766 | 170.3262 | - | 1 | 1 |
| | | | 14 | H700 | 726 | 42.5766 | 170.3262 | - | 1 | 1 |
| | | | 7 | H1000 | 950 | 42.4619 | 170.0441 | 1 | 1 | 1 |
| | | | 8 | H1000 | 946 | 42.4619 | 170.0442 | - | 1 | 1 |
| | | | 11 | H1000 | 948 | 42.4618 | 170.0440 | - | 1 | 2 |
| | | | 23 | H1200B | 1239 | 42.4141 | 169.7914 | 1 | 1 | 1 |
| | | | 24 | H1200B | 1242 | 42.4141 | 169.7914 | - | 1 | 1 |
| | | | 18 | H1500 | 1504 | 42.1632 | 169.3648 | 1 | 1 | 1 |
| | | | 19 | H1500 | 1503 | 42.1637 | 169.3643 | - | 1 | 1 |
| | | | 20 | H1500 | 1503 | 42.1637 | 169.3645 | - | 1 | 1 |
| | | | 28 | H2000 | 1953 | 42.1958 | 168.6642 | 1 | 1 | 1 |
| | | | 29 | H2000 | 1952 | 42.1962 | 168.6638 | - | 1 | 1 |
| | | | 31 | H2000 | 1953 | 42.1962 | 168.6640 | - | 1 | 1 |

*abundance data only

**Total organic matter and calcium carbonate content data only

***sites sampled for invertebrate stable isotope analyses

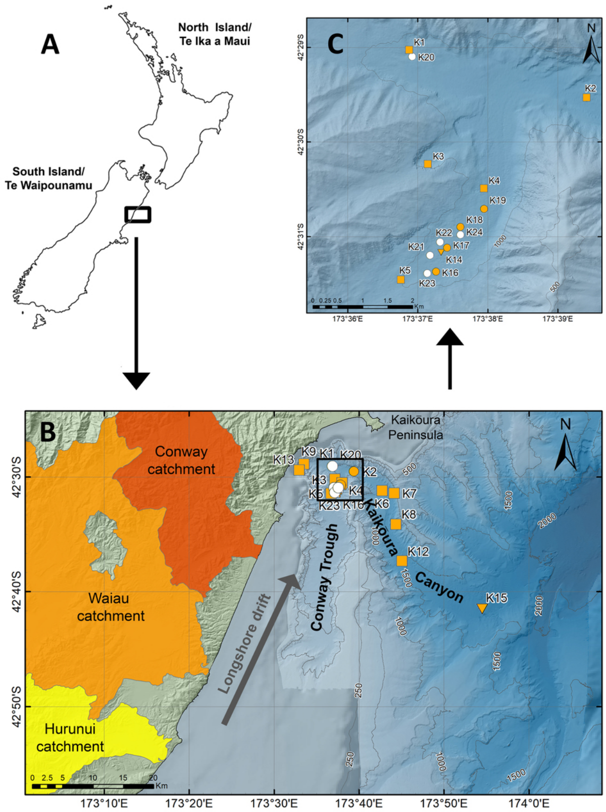
**Table 2.** Summary of sediment data from the Kaikōura and Hokitika Canyon sampling sites. $CaCO_3$ = inorganic calcium carbonate, Chl *a* = chlorophyll *a*, Phaeo = phaeopigments, TOC = total organic carbon, TOM = total organic matter, C:N = carbon:nitrogen ratio (molar), N = nitrogen, OC = organic carbon. ND = No data.

| **Canyon** | **Site** | **Distance from land (km)** | **Depth (m)** | **%sand** | **%silt** | **%clay** | **%$CaCO_3$** | **Chl *a* (*mg $g^{-1}$ sediment*)** | **Phaeo (mg $g^{-1}$ sediment)** | **Chl *a*:Phaeo** | **%TOM** | **C:N (molar)** | **%N** | **%TOC** | **%OC (land-derived)*** | **%OC (marine-derived)*** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Kaikōura | K13 | 5.2 | 404 | 10.9 | 87.2 | 1.9 | 2.3 | 0.3 | 3.2 | 0.08 | 3.59 | 10.0 | 0.07 | 0.64 | | |
| | K9 | 4.1 | 706 | 12.4 | 83.0 | 4.6 | 1.6 | 6.8 | 23.5 | 0.29 | 2.49 | 9.4 | 0.09 | 0.75 | | |
| | K5 | 8.7 | 989 | 20.5 | 76.2 | 3.3 | 1.6 | 4.5 | 14.2 | 0.32 | 2.19 | 9.0 | 0.08 | 0.63 | | |
| | K1 | 4.7 | 1017 | 8.0 | 87.3 | 4.7 | 1.8 | 7.2 | 24.9 | 0.29 | 3.09 | 9.3 | 0.11 | 0.88 | 0.43 | 0.45 |
| | K3 | 6.8 | 1032 | 11.2 | 84.4 | 4.4 | 4.9 | 6.2 | 28.6 | 0.22 | 2.78 | 9.0 | 0.10 | 0.77 | 0.36 | 0.41 |
| | K4 | 7.2 | 1061 | 11.5 | 84.0 | 4.5 | 2.0 | 3.4 | 15.3 | 0.22 | 2.60 | 8.5 | 0.10 | 0.73 | 0.36 | 0.36 |
| | K2 | 7.8 | 1127 | 19.1 | 76.8 | 4.1 | 1.6 | 4.3 | 17.6 | 0.25 | 2.11 | 8.9 | 0.10 | 0.73 | | |
| | K7 | 15.1 | 1320 | 6.3 | 89.8 | 3.9 | 4.1 | 9.4 | 36.2 | 0.26 | 3.56 | 8.6 | 0.13 | 0.96 | 0.32 | 0.64 |
| | K8 | 18.5 | 1417 | 8.0 | 88.0 | 4.0 | 4.9 | 6.8 | 24.8 | 0.27 | 3.64 | 8.8 | 0.12 | 0.90 | 0.28 | 0.62 |
| | K12 | 23.8 | 1485 | 8.0 | 88.5 | 3.5 | 7.9 | 4.0 | 28.3 | 0.11 | 4.38 | 8.2 | 0.17 | 1.19 | 0.15 | 1.04 |
| Hokitika | H200 | 18.4 | 193 | 48.2 | 51.8 | 0.3 | 0.2 | 0.6 | 3.6 | 0.16 | 1.73 | 14.0 | 0.02 | 0.24 | 0.21 | 0.03 |
| | H700 | 53.6 | 726 | 8.7 | 91.3 | 2.4 | 1.0 | 0.5 | 8.8 | 0.06 | 17.08 | 14.6 | 0.10 | 1.25 | 1.25 | 0.00 |
| | H1000 | 79.7 | 950 | 7.9 | 92.1 | 1.3 | 0.9 | 0.3 | 2.4 | 0.12 | 1.69 | 10.9 | 0.03 | 0.28 | 0.23 | 0.05 |
| | H1200A | 101 | 1169 | ND | ND | ND | 1.8 | ND | ND | ND | 1.05 | ND | ND | ND | ND | ND |
| | H1200B | 101 | 1239 | 5.2 | 94.8 | 2.1 | 1.1 | 0.4 | 2.5 | 0.17 | 1.91 | 9.0 | 0.04 | 0.31 | 0.23 | 0.07 |
| | H1500 | 144 | 1504 | 3.2 | 96.7 | 3.6 | 0.6 | 0.2 | 1.5 | 0.10 | 1.83 | 10.2 | 0.04 | 0.35 | 0.26 | 0.09 |
| | H2000 | 196.5 | 1953 | 3.6 | 96.3 | 4.8 | 1.6 | 0.4 | 3.1 | 0.12 | 2.22 | 10.5 | 0.04 | 0.36 | 0.28 | 0.08 |

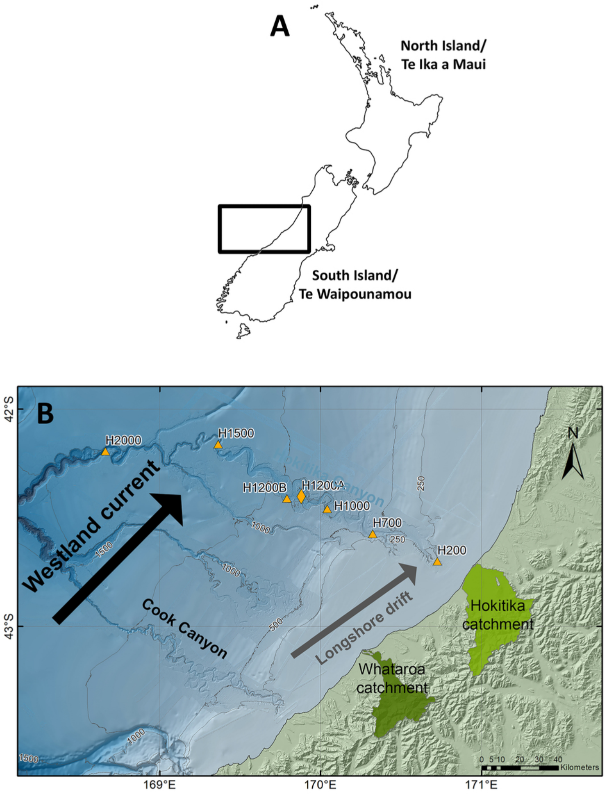
*Data from Gibbs et al. (submitted)

**Table 3.** Results of DistLM analyses investigating relationships between environmental predictor variables and meio- and macrofauna community parameters. Only variables that show significant correlations are shown. $CaCO_3$ = inorganic calcium carbonate, C:N = cabon to nitrogen ratio (molar), OC = organic carbon, N/A = not applicable.

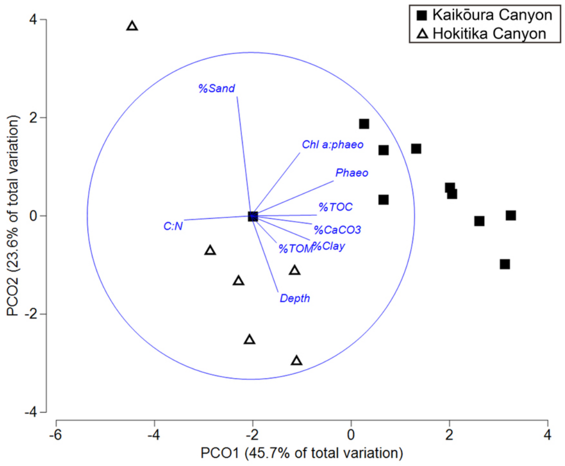
| Canyon/response variable | Predictor Variable | Pseudo-F | P | $R^2$ | res. df | Relationship |
|---|---|---|---|---|---|---|
| ***Kaikōura canyon*** | | | | | | |
| Meiofaunal abundance | %$CaCO_3$ | 7.22 | 0.034 | 0.47 | 8 | - |
| | %OC (land-derived) | 10.54 | 0.011 | 0.73 | 4 | + |
| Meiofaunal biomass | %OC (marine-derived) | 8.59 | 0.047 | 0.68 | 4 | - |
| Meiofaunal community structure | Depth | 3.06 | 0.039 | 0.28 | 8 | N/A |
| | %$CaCO_3$ | 2.91 | 0.033 | 0.27 | 8 | N/A |
| Macrofaunal abundance | Depth | 7.33 | 0.019 | 0.48 | 8 | - |
| | C:N | 5.96 | 0.004 | 0.43 | 8 | + |
| Macrofauna community structure | %OC (land-derived) | 2.14 | 0.050 | 0.35 | 4 | N/A |
| ***Hokitika Canyon*** | | | | | | |
| Meiofaunal community structure | %$CaCO_3$ | 3.16 | 0.050 | 0.44 | 4 | N/A |
| Macrofaunal abundance | Depth | 25.76 | 0.006 | 0.87 | 4 | - |
| | C:N | 9.97 | 0.047 | 0.71 | 4 | + |
| | %sand | 4.36 | 0.010 | 0.52 | 4 | + |
| | %silt | 4.36 | 0.008 | 0.52 | 4 | - |
| | %OC (marine-derived) | 13.29 | 0.016 | 0.77 | 4 | - |
| Macrofaunal community structure | Depth | 2.44 | 0.026 | 0.38 | 4 | N/A |
| | %OC (marine-derived) | 2.41 | 0.049 | 0.38 | 4 | N/A |



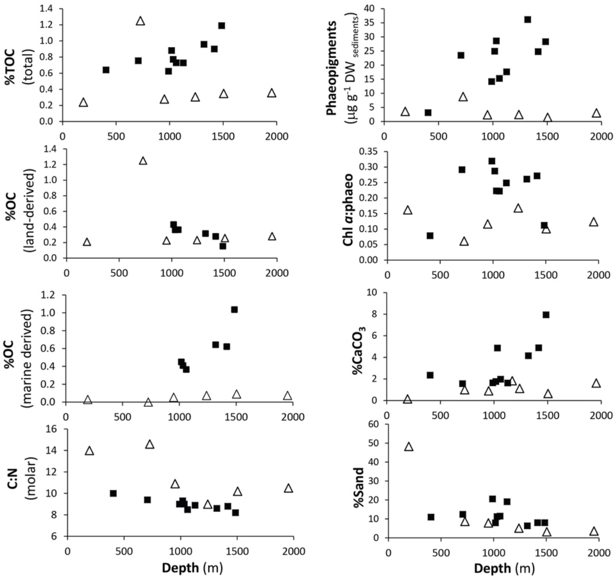
LNO_11454_Fig1 Kaikoura NEW_REVISED.jpg



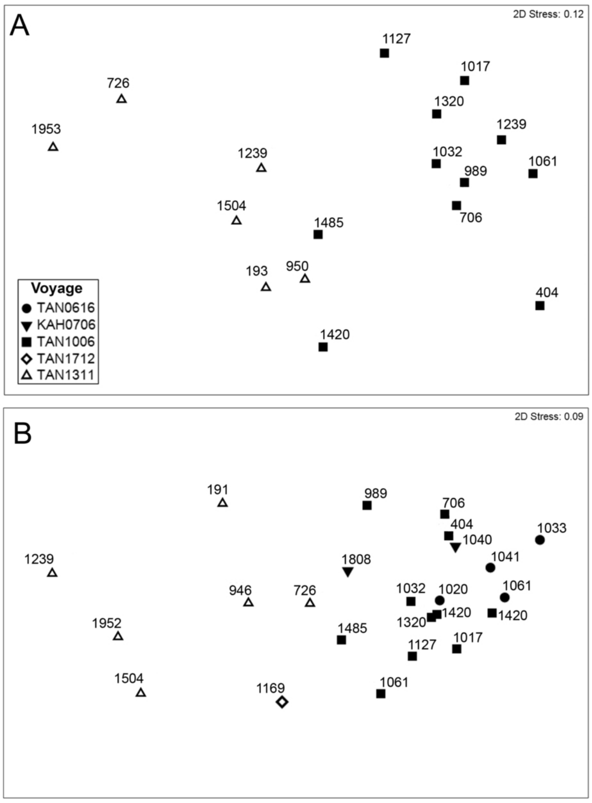
LNO_11454_Fig2 Hokitika NEW II.jpg



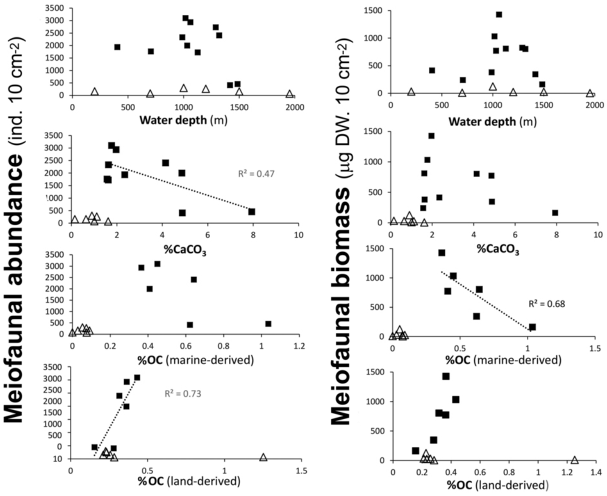
LNO_11454_Fig3_Environment PCA.jpg



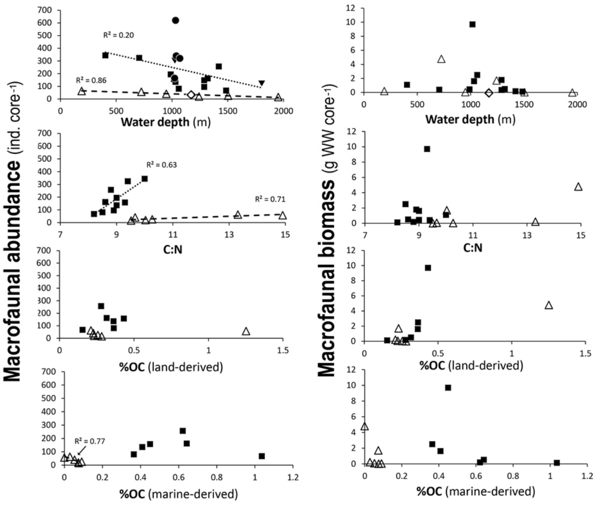
LNO_11454_Fig4_Environment graphs.jpg



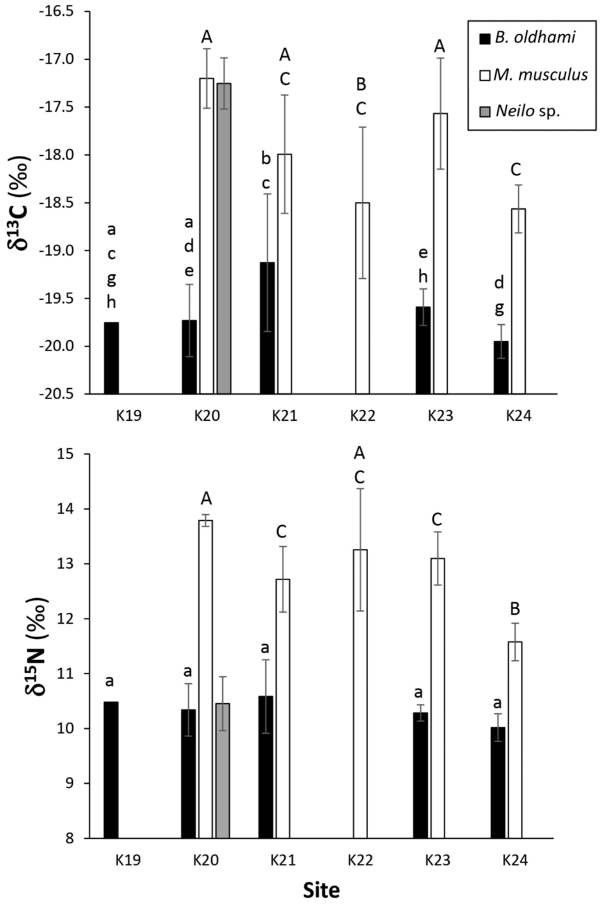
LNO_11454_Fig5_Meio & Macro MDS_REVISED.jpg



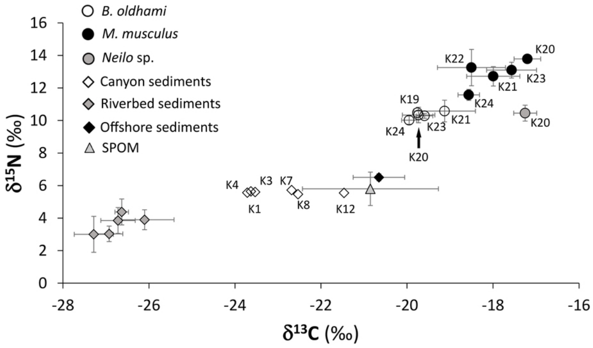
LNO_11454_Fig6_Meio plots REVISED.jpg



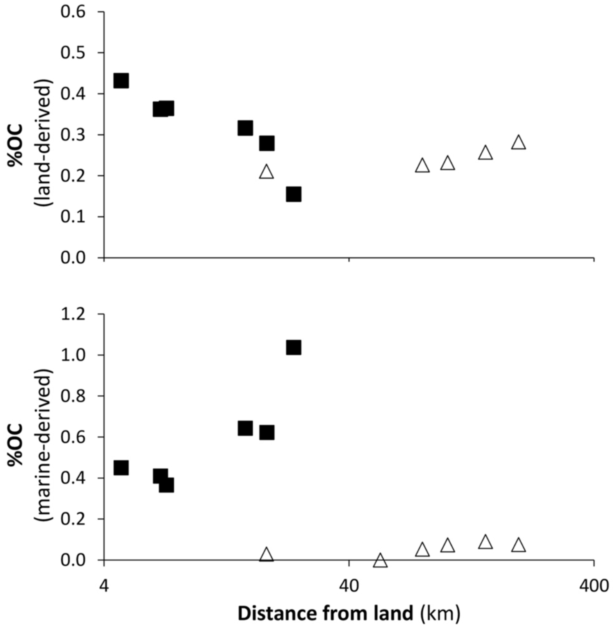
LNO_11454_Fig7_Macro plots_REVISED II.jpg



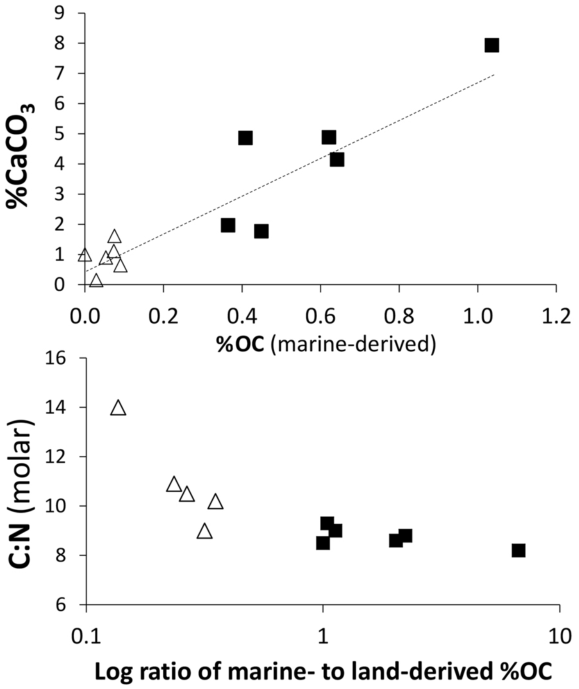
LNO_11454_Fig8_13C and 15N bar graphs.jpg



LNO_11454_Fig9_dual isotopic plot NEW.jpg



LNO_11454_Figure 10 land distance OM.jpg



LNO_11454_Figure 11 CaCO3 CN marine OM.jpg

**Table 1.** Details of Kaikōura and Hokitika canyon study sites with number of cores analysed for macro- and meiofauna (abundance, biomass and community structure) and sediment parameters from each multicorer deployment (station).

| Canyon | Voyage | Date mm/YYYY | Station | Site | Water depth (m) | Latitude °S | Longitude °E | Sediment | Meiofauna | Macrofauna |
|---|---|---|---|---|---|---|---|---|---|---|
| Kaikōura | TAN1006 | 05/2010 | 6 | K13 | 404 | 42.4897 | 173.5510 | 1 core | 3 cores | 2 cores |
| | | | 5 | K9 | 706 | 42.4810 | 173.5582 | 1 | 2 | 3 |
| | | | 3 | K5 | 989 | 42.5243 | 173.6127 | 1 | 2 | 3 |
| | | | 4 | K1 | 1017 | 42.4838 | 173.6147 | 1 | 2 | 3 |
| | | | 14 | K3 | 1032 | 42.5039 | 173.6192 | 1 | 2 | 3 |
| | | | 7 | K4 | 1061 | 42.5082 | 173.6325 | 1 | 2 | 3 |
| | | | 8 | K2 | 1127 | 42.4922 | 173.6569 | 1 | 2 | 2 |
| | | | 2 | K6 | 1289 | 42.5203 | 173.7118 | - | 3 | 2 |
| | | | 11 | K7 | 1320 | 42.5237 | 173.7356 | 1 | 2 | 3 |
| | | | 9 | K8 | 1420 | 42.5692 | 173.7389 | 1 | 2 | 3 |
| | | | 1 | K12 | 1485 | 42.6230 | 173.7505 | 1 | 2 | 2 |
| | KAH0706 | 06/2007 | 6 | K14 | 1040 | 42.5192 | 173.6223 | - | - | 3* |
| | | | 3 | K15 | 1808 | 42.6880 | 173.9078 | - | - | 3* |
| | TAN0616 | 11/2006 | 105 | K16 | 1020 | 42.5228 | 173.6210 | - | - | 1* |
| | | | 103 | K17 | 1033 | 42.5187 | 173.6237 | - | - | 1* |
| | | | 101 | K18 | 1041 | 42.5150 | 173.6268 | - | - | 2* |
| | | | 98 | K19*** | 1061 | 42.5118 | 173.6325 | - | - | 1* |
| | | | 99 | K20*** | 1079 | 42.4850 | 173.6153 | - | - | - |
| | | | 106 | K21*** | 1020 | 42.5200 | 173.6197 | - | - | - |
| | | | 107 | K22*** | 1029 | 42.5177 | 173.6220 | - | - | - |
| | | | 108 | K23*** | 1014 | 42.5232 | 173.6190 | - | - | - |
| | | | 109 | K24*** | 1028 | 42.5163 | 173.6268 | - | - | - |
| Hokitika | TAN1712 | 09/2017 | 2 | H1200A | 1169 | 42.4063 | 169.8828 | 1** | - | 2 |
| | TAN1311 | 10/2013 | 63 | H200 | 191 | 42.7020 | 170.7270 | - | 1 | 1 |
| | | | 64 | H200 | 193 | 42.7020 | 170.7262 | 1 | 1 | 1 |
| | | | 66 | H200 | 190 | 42.7028 | 170.7277 | - | 1 | 1 |
| | | | 12 | H700 | 726 | 42.5766 | 170.3262 | 1 | 1 | 1 |
| | | | 13 | H700 | 726 | 42.5766 | 170.3262 | - | 1 | 1 |
| | | | 14 | H700 | 726 | 42.5766 | 170.3262 | - | 1 | 1 |
| | | | 7 | H1000 | 950 | 42.4619 | 170.0441 | 1 | 1 | 1 |
| | | | 8 | H1000 | 946 | 42.4619 | 170.0442 | - | 1 | 1 |
| | | | 11 | H1000 | 948 | 42.4618 | 170.0440 | - | 1 | 2 |
| | | | 23 | H1200B | 1239 | 42.4141 | 169.7914 | 1 | 1 | 1 |
| | | | 24 | H1200B | 1242 | 42.4141 | 169.7914 | - | 1 | 1 |
| | | | 18 | H1500 | 1504 | 42.1632 | 169.3648 | 1 | 1 | 1 |
| | | | 19 | H1500 | 1503 | 42.1637 | 169.3643 | - | 1 | 1 |
| | | | 20 | H1500 | 1503 | 42.1637 | 169.3645 | - | 1 | 1 |
| | | | 28 | H2000 | 1953 | 42.1958 | 168.6642 | 1 | 1 | 1 |
| | | | 29 | H2000 | 1952 | 42.1962 | 168.6638 | - | 1 | 1 |
| | | | 31 | H2000 | 1953 | 42.1962 | 168.6640 | - | 1 | 1 |

*abundance data only

**Total organic matter and calcium carbonate content data only

***sites sampled for invertebrate stable isotope analyses

**Table 2.** Summary of sediment data from the Kaikōura and Hokitika Canyon sampling sites. $CaCO_3$ = inorganic calcium carbonate, Chl *a* = chlorophyll *a*, Phaeo = phaeopigments, TOC = total organic carbon, TOM = total organic matter, C:N = carbon:nitrogen ratio (molar), N = nitrogen, OC = organic carbon. ND = No data.

| **Canyon** | **Site** | **Distance from land (km)** | **Depth (m)** | **%sand** | **%silt** | **%clay** | **%$CaCO_3$** | **Chl *a* (*mg g$^{-1}$ sediment*)** | **Phaeo (mg g$^{-1}$ sediment)** | **Chl *a*:Phaeo** | **%TOM** | **C:N (molar)** | **%N** | **%TOC** | **%OC (land-derived)*** | **%OC (marine-derived)*** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Kaikōura | K13 | 5.2 | 404 | 10.9 | 87.2 | 1.9 | 2.3 | 0.3 | 3.2 | 0.08 | 3.59 | 10.0 | 0.07 | 0.64 | | |
| | K9 | 4.1 | 706 | 12.4 | 83.0 | 4.6 | 1.6 | 6.8 | 23.5 | 0.29 | 2.49 | 9.4 | 0.09 | 0.75 | | |
| | K5 | 8.7 | 989 | 20.5 | 76.2 | 3.3 | 1.6 | 4.5 | 14.2 | 0.32 | 2.19 | 9.0 | 0.08 | 0.63 | | |
| | K1 | 4.7 | 1017 | 8.0 | 87.3 | 4.7 | 1.8 | 7.2 | 24.9 | 0.29 | 3.09 | 9.3 | 0.11 | 0.88 | 0.43 | 0.45 |
| | K3 | 6.8 | 1032 | 11.2 | 84.4 | 4.4 | 4.9 | 6.2 | 28.6 | 0.22 | 2.78 | 9.0 | 0.10 | 0.77 | 0.36 | 0.41 |
| | K4 | 7.2 | 1061 | 11.5 | 84.0 | 4.5 | 2.0 | 3.4 | 15.3 | 0.22 | 2.60 | 8.5 | 0.10 | 0.73 | 0.36 | 0.36 |
| | K2 | 7.8 | 1127 | 19.1 | 76.8 | 4.1 | 1.6 | 4.3 | 17.6 | 0.25 | 2.11 | 8.9 | 0.10 | 0.73 | | |
| | K7 | 15.1 | 1320 | 6.3 | 89.8 | 3.9 | 4.1 | 9.4 | 36.2 | 0.26 | 3.56 | 8.6 | 0.13 | 0.96 | 0.32 | 0.64 |
| | K8 | 18.5 | 1417 | 8.0 | 88.0 | 4.0 | 4.9 | 6.8 | 24.8 | 0.27 | 3.64 | 8.8 | 0.12 | 0.90 | 0.28 | 0.62 |
| | K12 | 23.8 | 1485 | 8.0 | 88.5 | 3.5 | 7.9 | 4.0 | 28.3 | 0.11 | 4.38 | 8.2 | 0.17 | 1.19 | 0.15 | 1.04 |
| Hokitika | H200 | 18.4 | 193 | 48.2 | 51.8 | 0.3 | 0.2 | 0.6 | 3.6 | 0.16 | 1.73 | 14.0 | 0.02 | 0.24 | 0.21 | 0.03 |
| | H700 | 53.6 | 726 | 8.7 | 91.3 | 2.4 | 1.0 | 0.5 | 8.8 | 0.06 | 17.08 | 14.6 | 0.10 | 1.25 | 1.25 | 0.00 |
| | H1000 | 79.7 | 950 | 7.9 | 92.1 | 1.3 | 0.9 | 0.3 | 2.4 | 0.12 | 1.69 | 10.9 | 0.03 | 0.28 | 0.23 | 0.05 |
| | H1200A | 101 | 1169 | ND | ND | ND | 1.8 | ND | ND | ND | 1.05 | ND | ND | ND | ND | ND |
| | H1200B | 101 | 1239 | 5.2 | 94.8 | 2.1 | 1.1 | 0.4 | 2.5 | 0.17 | 1.91 | 9.0 | 0.04 | 0.31 | 0.23 | 0.07 |
| | H1500 | 144 | 1504 | 3.2 | 96.7 | 3.6 | 0.6 | 0.2 | 1.5 | 0.10 | 1.83 | 10.2 | 0.04 | 0.35 | 0.26 | 0.09 |
| | H2000 | 196.5 | 1953 | 3.6 | 96.3 | 4.8 | 1.6 | 0.4 | 3.1 | 0.12 | 2.22 | 10.5 | 0.04 | 0.36 | 0.28 | 0.08 |

*Data from Gibbs et al. (submitted)

**Table 3.** Results of DistLM analyses investigating relationships between environmental predictor variables and meio- and macrofauna community parameters. Only variables that show significant correlations are shown. $CaCO_3$ = inorganic calcium carbonate, C:N = cabon to nitrogen ratio (molar), OC = organic carbon, N/A = not applicable.

| Canyon/response variable | Predictor Variable | Pseudo-F | P | $R^2$ | res. df | Relationship |
|---|---|---|---|---|---|---|
| ***Kaikōura canyon*** | | | | | | |
| Meiofaunal abundance | %$CaCO_3$ | 7.22 | 0.034 | 0.47 | 8 | - |
| | %OC (land-derived) | 10.54 | 0.011 | 0.73 | 4 | + |
| Meiofaunal biomass | %OC (marine-derived) | 8.59 | 0.047 | 0.68 | 4 | - |
| Meiofaunal community structure | Depth | 3.06 | 0.039 | 0.28 | 8 | N/A |
| | %$CaCO_3$ | 2.91 | 0.033 | 0.27 | 8 | N/A |
| Macrofaunal abundance | Depth | 7.33 | 0.019 | 0.48 | 8 | - |
| | C:N | 5.96 | 0.004 | 0.43 | 8 | + |
| Macrofauna community structure | %OC (land-derived) | 2.14 | 0.050 | 0.35 | 4 | N/A |
| ***Hokitika Canyon*** | | | | | | |
| Meiofaunal community structure | %$CaCO_3$ | 3.16 | 0.050 | 0.44 | 4 | N/A |
| Macrofaunal abundance | Depth | 25.76 | 0.006 | 0.87 | 4 | - |
| | C:N | 9.97 | 0.047 | 0.71 | 4 | + |
| | %sand | 4.36 | 0.010 | 0.52 | 4 | + |
| | %silt | 4.36 | 0.008 | 0.52 | 4 | - |
| | %OC (marine-derived) | 13.29 | 0.016 | 0.77 | 4 | - |
| Macrofaunal community structure | Depth | 2.44 | 0.026 | 0.38 | 4 | N/A |
| | %OC (marine-derived) | 2.41 | 0.049 | 0.38 | 4 | N/A |