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Unusually high food availability in Kaikoura Canyon linked to distinct deep-sea nematode community

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ABSTRACT

Kaikoura Canyon, on the eastern New Zealand continental margin, is the most productive, non-chemosynthetic deep-sea habitat described to date, with megafaunal biomass 100-fold higher than those of other deep-sea habitats. The present study, which focused on free-living nematodes, provides the first comparison of faunal community structure and diversity between Kaikoura Canyon and nearby open slope habitats. Results show substantially higher food availability in the canyon relative to open slope sediments, which probably reflects greater levels of primary productivity above the canyon, coupled with downwelling and/or topographically-induced channelling, which serves to concentrate surface-derived organic matter along the canyon axis. This high food availability appears to be responsible for the elevated nematode biomass in Kaikoura Canyon, with values exceeding all published nematode biomass data from canyons elsewhere. There was also markedly lower local species diversity of nematodes inside the canyon relative to the open slope habitat, as well as a distinct community structure. The canyon community was dominated by species, such as *Sabateria pulchra*, which were absent from the open slope and are typically associated with highly eutrophic and/or disturbed environments. The presence of these taxa, as well as the low observed diversity, is likely to reflect the high food availability, and potentially the high levels of physically and biologically induced disturbance within the canyon. Kaikoura Canyon is a relatively small habitat characterised by different environmental conditions that makes a disproportionate contribution to deep-sea diversity in the region, despite its low species richness.

1. Introduction

Canyons are conspicuous and widespread topographic features of continental margins worldwide, and contribute to the high macro-habitat heterogeneity typical of slope environments (Levin and Sibuet, 2012). Canyons exhibit a wide range of geomorphological, hydrological and sedimentological characteristics (e.g., Guerreiro et al., 2009; Pusceddu et al., 2010). The majority of canyons, many of which are considered inactive, cut into only the outer edge of continental shelves and are remote from abundant near-shore supplies of sediments, whereas active canyons typically cut deeper into the continental shelf and retain their abundant supply of coastal sediment (Harris and Whiteway, 2011). Active canyons constitute major conduits for the transport of sediment and organic matter from shallow to deep waters through processes such as tidally-driven downslope currents (e.g., Mulder et al., 2012), or sediment gravity flows and turbidity currents generated by storms or fault ruptures (e.g., Martín et al., 2011; Jobe et al., 2011). Active canyons are typically characterised by high productivity and high levels of physical disturbance associated with more intense hydrological regimes relative to the adjacent slope (Xu, 2009), whereas these parameters often do not differ markedly between inactive canyons and surrounding slope environments (Pusceddu et al., 2010). As such, the environmental conditions within canyons can have a strong influence on the functional and structural attributes of benthic communities, and how these communities may or may not differ from those on the open continental slope.

Many studies have found greater faunal standing stocks in canyons relative to the adjacent slope (e.g., Vetter, 1994; Vetter and Dayton, 1998; Baguley et al., 2006; Ingels et al., 2009; Vetter et al., 2010). However, higher standing stock in the canyon may be restricted to particular depth strata (e.g. De Leo et al., 2012), or there may be little or no difference between the two habitats (e.g., Houston and Haedrich, 1984; Soltwedel et al., 2005; Bianchelli et al., 2010), and in some cases higher abundances have been found on slopes compared to adjacent canyons (e.g., Van Gaever et al., 2009; Vetter et al., 2010). Studies reporting the largest differences in faunal standing stocks between canyon and slope habitats, and which often refer to canyons as abundance or

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biomass hotspots, were conducted at highly productive or organically-rich sites (e.g., Vetter, 1994; Baguley et al., 2006; De Leo et al., 2010; van Oevelen et al., 2011). Likewise, canyons with high levels of organic matter, relative to the adjacent slope, harbour distinct sediment communities, whilst canyons without organic matter enrichment usually show no such pattern (Danovaro et al., 2009; Pusceddu et al., 2010).

When present, the effect of canyon environmental conditions on faunal communities differs between taxa and functional groups. For example, the abundance and diversity of scavenging mobile megafauna (e.g., fish, crustaceans) may increase inside canyons due to the ability of large mobile organisms to exploit food-falls under strong hydrodynamic conditions, while less mobile or sessile megafauna may be adversely affected by strong currents and/or sediment transport (Vetter et al., 2010). Standing stocks of smaller meio- and macrofauna usually reflect the quantity and quality of sediment organic matter (Soetaert and Heip, 1995; Vetter and Dayton, 1998; Grémare et al., 2002; Ingels et al., 2009; Cunha et al., 2011; De Leo et al., 2014), but disturbance by strong hydrodynamic conditions may counteract the positive effects of high food availability for some components of this fauna (e.g., Garcia et al., 2007).

To date, almost all studies of the fauna of deep-sea canyons have focused on the macro- and mega-benthos, with species-level investigations of the meiofauna being rare (but see Danovaro et al., 2009). Nevertheless, meiofauna and the dominant nematodes in particular, offer a useful model fauna to help understand the role that individual drivers play in shaping the differences between the benthic communities of canyons and slopes. In a recent review of the effect of macrohabitat heterogeneity on deep-sea nematode genus distribution, Vanreusel et al. (2010) showed considerable overlap between canyon and slope assemblages, but noted high levels of variability between canyons. Where a canyon habitat broadly resembles that of the open slope (e.g., the soft sediment of the canyon axis), macrohabitat heterogeneity is unlikely to influence greatly any differences in the structure of nematode communities between these two habitats.

It has been suggested that nematodes recover more quickly than macrofauna following physical disturbance (Lambshead et al., 2001, Schratzberger and Jennings, 2002; Whomersley et al., 2009) and sediment resuspension (Leduc and Pilditch, 2013), because they are less likely to suffer direct mortality from the disturbance event and have fast turnover rates. Nematode standing stocks and community structure may thus be less affected than the larger fauna by the episodic natural disturbances that occur in canyons. With macrohabitat heterogeneity and disturbance less likely to operate as primary drivers of community attributes, it is possible to investigate, through observational study, the extent of the influence of other factors, such as productivity and food availability, on nematode canyon communities.

Benthic communities of canyons are vulnerable to direct disturbance from fishing activity that targets fish or invertebrates that are concentrated along continental margins and show a particular affinity for canyon habitats (e.g., Stefanescu et al., 1994; Sarda et al., 1994). Furthermore, bottom trawling has been shown to increase sediment resuspension and sedimentation, which may eventually trigger sediment gravity flows in canyons that may also impact benthic communities (Palanques et al., 2006; Martín et al., 2008, 2014). The natural cycle of dense shelf water that "cascades" or "flushes" through canyons on continental margins can be affected by climate change (Canals et al., 2006; Herrmann et al., 2008), with subsequent effects for invertebrate populations (Company et al., 2008). Thus, it is of critical importance to better describe faunal communities in canyons, how they may differ from slope communities, and the factors driving these differences, so that potential impacts of human activities may be predicted (Schlacher et al., 2007).

The aim of the present study off New Zealand was to compare nematode community attributes (i.e., abundance, biomass, species diversity, and community structure) between sites in the axis of Kaikoura Canyon and sites on the nearby open slope, Chatham Rise. Because Kaikoura Canyon is an active, highly productive canyon (Lewis and Barnes, 1999; De Leo et al., 2010), we hypothesised a canyon community characterised by high standing stocks, low diversity and distinct community structure relative to the bathyal environments of the Chatham Rise. We also examined whether the nematode community of Kaikoura Canyon displayed some of the exceptional characteristics (e.g., extremely high biomass), as previously described for benthic mega-faunal communities (De Leo et al., 2010).

2. Methods

The study was conducted in Kaikoura Canyon on the northeastern coast of South Island, New Zealand (Fig. 1). Kaikoura Canyon cuts deeply into the narrow continental shelf (the canyon head is within 500 m of the shore) and is thought to serve as a conduit for the downslope transport of coastal sediments and organic debris originating from rivers south of the canyon (Carter and Herzer, 1979; Carter et al., 1982; Lewis and Barnes, 1999). Kaikoura Canyon is also near the highly productive Subtropical Front (STF), where warm subtropical surface water to the north meets cold, high nutrient-low chlorophyll subantarctic surface water to the south (Bradford-Grieve et al., 1997; Boyd et al., 1999; Murphy et al., 2001). Episodic upwelling events may also contribute to the high productivity above the canyon (Heath, 1972; Chiswell and Schiel, 2001). Semi-diurnal flows are aligned along the canyon axis and reach up to 0.25 m s^{-1} with a net drift down the canyon (Lewis and Barnes, 1999). This tidally-induced flow and the steep topography of the canyon may help channel organic matter along its axis. Data from open slope sites on Chatham Rise were used for comparative purposes (Leduc et al., 2012b). Chatham Rise is a submarine ridge extending eastwards adjacent to Kaikoura Canyon. It encompasses water depths from ca. 250 to 3000 m and lies beneath the STF (Nodder et al., 2012). Productivity is the highest on the southern flank of the rise where the STF appears to be bathymetrically locked (Uddstrom and Oien, 1999; Sutton, 2001).

Samples were collected from 11 locations between 404 and 1417 m water depth on the axis of Kaikoura Canyon in May 2010, during National Institute of Water and Atmospheric Research (NIWA) cruise TAN1006. Samples were taken using an Ocean Instruments MC-800A multicorer (MUC; core i.d. = 9.52 cm). One to three pseudo-replicates (i.e., samples from the same MUC deployment) per site were obtained. Each sample consisted of a subcore (i.d. = 2.6 cm) taken to a sediment depth of 5 cm. All samples were preserved in 10% buffered formalin and stained with Rose Bengal. Similar sampling and processing methods were used for the Chatham Rise samples (e.g., Nodder et al., 2003; Grove et al., 2006; Leduc et al., 2012a, b, c).

Samples were rinsed through a 1-mm mesh to remove macrofauna, and through a 45 μm mesh size to retain nematodes. Nematodes (and other 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 up to four slides (depending on the amount of material in the sample) and sealed with paraffin wax. All nematodes present in the sample were counted using a compound microscope (100 × magnification). Nematode body volumes were estimated from length and maximum body width measurements obtained by video image analysis (Nodder et al., 2003; Grove et al., 2006). Body

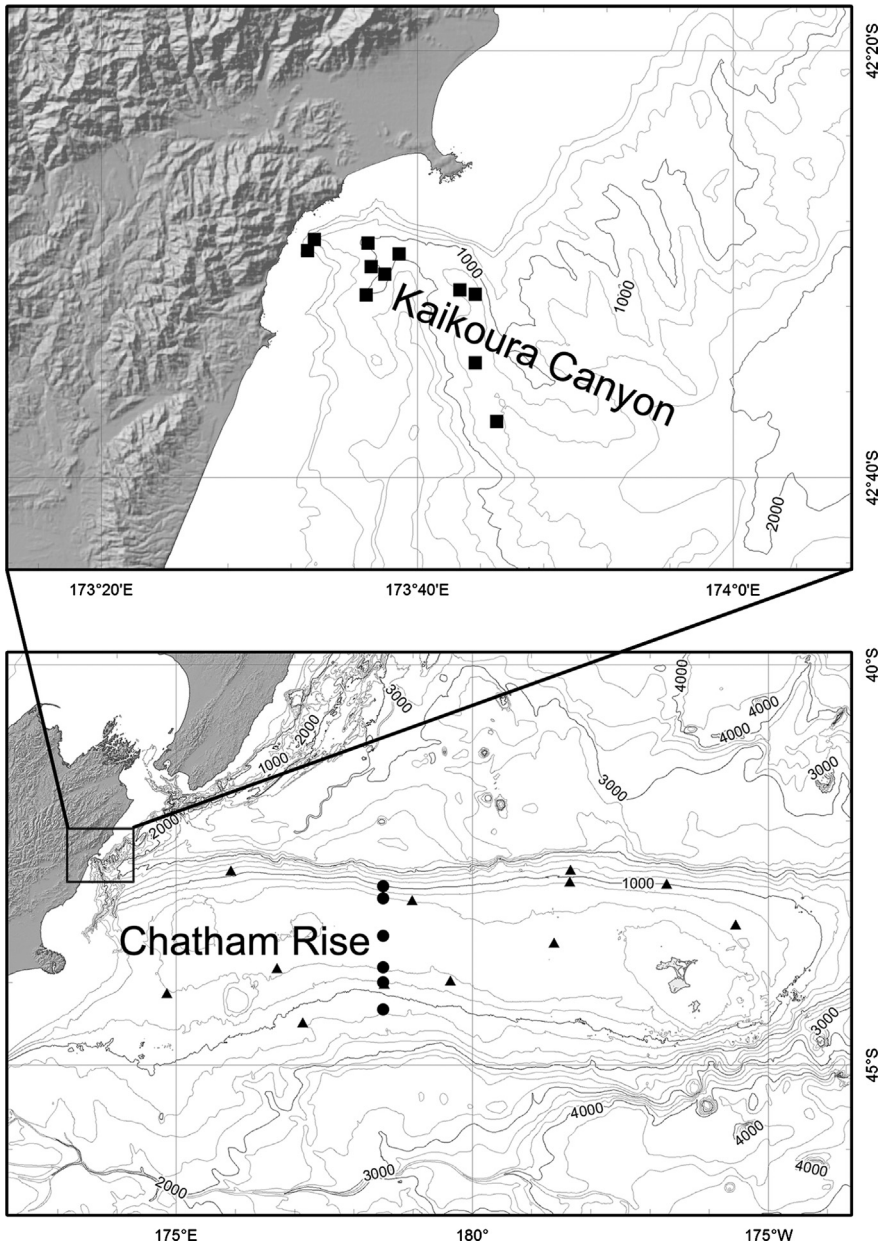

Fig. 1. Map of study area showing location of Kaikoura Canyon (top) and Chatham Rise study sites (bottom).

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). Estimates of mean and median body weight were based on a minimum of 100 nematodes (or all individuals if fewer were present).

Between 125 and 135 randomly chosen nematodes were identified to genus and putative species using the descriptions in Warwick et al. (1998), as well as the primary literature. *Monhystrella* and *Thalassomonhystera* were treated as one genus ("Monhysteridae") because they are sometimes difficult to distinguish based on morphology (Fonseca and Decraemer, 2008). Nematode diversity was quantified using the Shannon diversity index (H'), Pielou's evenness (J'), and Hurlbert's (1971) rarefaction method for estimating the expected number of species for a sample of 51 individuals (ES(51)).

Physical and biogeochemical sediment parameters at each site (except for two sites at 404 (K13) and 1289 m water depth (K6) where samples for sediment analyses were not recovered) were measured from one core of the same MUC deployment. These parameters were total organic matter (%TOM), chloroplastic pigment equivalents (CPE; $\mu g\ g^{-1}\ DW_{sediment}$, sum of chlorophyll *a* and phaeopigments), proportion of chlorophyll *a* relative to chloroplastic pigment equivalents (%chl *a*), water content ($\%H_2O$), carbonate content ($\%CaCO_3$), sum of silt and clay particles (%silt/clay) and sediment particle size diversity (SED). The latter was calculated from the percentage dry weight of 5 size classes (i.e., <63, 63–125, 125–250, 250–500, and >500 μm) using the Shannon–Wiener diversity index (Etter and Grassle, 1992; Leduc et al., 2012a). All parameters were determined from the 0–5 mm sediment depth layer, except for %silt/clay and SED, which were determined from the 0–5 cm sediment depth layer. CPE and %TOM were used as measures of food availability, whereas %chl *a* provided a proxy for food quality (e.g., Ingels et al., 2009). The sediment parameters $\%H_2O$, $\%CaCO_3$, and %silt/clay provided measures of sediment physicochemical characteristics, and SED was used as a proxy for microhabitat heterogeneity (Leduc et al., 2012a). Methods for the determination of environmental parameters are given in Nodder et al. (2003) and Grove et al. (2006). Briefly, %silt/clay was determined by analysing the <63-μm fraction using an X-ray Sedigraph for Chatham Rise samples, or the whole sample by laser diffraction

Coulter counter techniques for Kaikoura Canyon samples. CPE and %chl *a* were estimated using standard spectrophotometric techniques after freeze-drying and extraction in 90% acetone (Sartory, 1982), $\%CaCO_3$ was measured by a CO_2 vacuum-gasometric method with +1% accuracy, and %TOM content was determined by loss-on-ignition (500 °C for 4 h) (Eleftheriou and Moore, 2005).

Net primary production (NPP; mg C m^{-2} d^{-1}) was estimated in order to compare productivity levels above Kaikoura Canyon and Chatham Rise sites, and to account for the potential effect of this variable on nematode community attributes. NPP was estimated from data downloaded from the Ocean Productivity web site (http://www.science.oregonstate.edu/ocean.productivity/). The specific dataset chosen was the Standard product, which implements the Vertically Generalised Production Model (VGPM) of Behrenfeld and Falkowski (1997) using MODIS chlorophyll and temperature data, SeaWiFS PAR, and estimates of euphotic zone depth from a model developed by Morel and Berthon (1989) and based on chlorophyll concentration. Time-mean NPP for the years 2003–2011 was calculated from monthly data at 4 km resolution and interpolated to each site.

Data on environmental parameters, and on nematode abundance, biomass, species diversity, and community structure from 18 sites on the open slope of Chatham Rise adjacent to Kaikoura Canyon were obtained from Leduc et al. (2012b). Only sites within a similar water depth range to those of Kaikoura Canyon sites were included in the analyses (350–1238 m). Nematode and sediment data from the Chatham Rise sites were obtained using the same methodology as described above, except for samples obtained in 2001 (NIWA cruise TAN0116), which were processed using a 425 μm upper mesh instead of a 1 mm mesh. Nematodes were identified by the same person (D. Leduc), allowing direct comparisons of putative species records.

Comparisons of environmental parameters (%silt/clay, $\%H_20$, $\%CaCO_3$, SED, %TOM, CPE, %chl *a*, NPP) and nematode community attributes (abundance, biomass, diversity, and community structure) were conducted using PERMANOVA, a semi-parametric, permutation-based routine for analysis of variance based on any similarity measure (e.g., Euclidean, Bray–Curtis) (Anderson et al., 2008). Similarity matrices for univariate variables were built using Euclidean distance of log-transformed environmental data and untransformed diversity data, and similarity matrices for multivariate data (nematode community structure) were built using the Bray–Curtis similarity measure of fourth root-transformed data (Anderson et al., 2008). *P*-values for individual predictor variables were obtained using 9999 permutations (Anderson et al., 2008). 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 differences were found (Anderson et al., 2008). The SIMPER routine in PRIMER was used to identify: (1) sediment parameters contributing most to dissimilarity between Kaikoura Canyon and Chatham Rise (Euclidean distance of normalised data), and (2) species contributing most to within-group similarity and between-group dissimilarity (Bray–Curtis similarity of fourth-root transformed data; Clarke and Warwick, 2001). SIMPER was also used to quantify Bray–Curtis dissimilarity of nematode communities between Kaikoura Canyon and Chatham Rise, to provide a basis for comparisons with other studies of nematode species turnover (e.g., Danovaro et al., 2009), and to identify those taxa responsible for any observed dissimilarity.

3. Results

The range of environmental parameter values at Chatham Rise and Kaikoura Canyon sites overlapped to a large extent, except for CPE, %chl *a* and NPP (Table 1). There was a significant difference in multivariate sediment characteristics between Kaikoura Canyon and Chatham Rise (PERMANOVA, $P<0.001$), mainly driven by pigment concentrations (CPE, %chl *a*), net surface primary production, and sediment water content (SIMPER; Table 2). Mean net primary production (NPP) and pigment concentrations (CPE and chl *a*) were approximately two and ten times greater at Kaikoura Canyon sites relative to Chatham Rise sites, respectively (PERMANOVA, $P<0.001$). Sediment particle size diversity (SED) was two times higher at the Chatham Rise sites than at the Kaikoura Canyon sites ($P<0.001$). Silt/clay and water contents were highest at Kaikoura Canyon sites, whereas the opposite trend was observed for carbonate content ($P<0.001$). Sediment organic matter content (%TOM) did not differ significantly between the two habitats.

Mean nematode abundance was about 1.5 times higher at Kaikoura Canyon sites relative to Chatham Rise sites (1935 vs 1278 ind. 10 cm^{-2}; $P<0.05$), and nematode biomass was almost five times higher (641 vs 131 μgDW 10 cm^{-2}; $P<0.001$). Nematode diversity values (ES(51), *H′*, *J′*) did not overlap between the two areas, and were markedly lower at Kaikoura Canyon sites relative to Chatham Rise sites ($P<0.001$; Table 1).

Table 1
Comparison of environmental and nematode community parameters between Chatham Rise and Kaikoura Canyon sites (mean (range), $n=11$ and 17, respectively). Asterisks indicate significant differences between the two habitats (PERMANOVA, * $P<0.05$; ** $P<0.001$).

	Chatham Rise[a]	Kaikoura Canyon
Environmental parameters		
%Silt/clay*	57 (23–94)	89 (80–95)
SED**	0.42 (0.13–0.59)	0.17 (0.10–0.26)
$\%CaCO_3$**	38.7 (9.7–72.4)	4.5 (0.5–13.2)
$\%H_2O$**	43.4 (35.0–53.8)	60.4 (49.3–69.9)
%TOM	3.43 (1.44–5.67)	3.76 (2.18–6.80)
CPE (ng gDW^{-1} sediment)**	4308 (2063–8348)	32,812 (18,200–45700)
%chl *a***	3.23 (< 0.1–13.9)	35.4 (10.7–33.8)
NPP** (mgC m^{-2} d^{-1})	787 (582–956)	1317 (1192–1381)
Nematode community parameters		
Abundance 10 cm^{-2}*	1278 (475–2828)	1935 (507–3315)
Biomass μgDW 10 cm^{-2}**	131 (20–323)	641 (128–1353)
ES(51)**	37.1 (32.7–41.5)	17.7 (10.8–25.6)
*H′***	3.99 (3.70–4.32)	2.54 (1.45–3.26)
*J′***	0.94 (0.91–0.97)	0.77 (0.49–0.88)

SED = sediment particle size diversity; $\%CaCO_3$ = sediment carbonate content; %TOM = sediment total organic matter content; CPE = sediment chloroplastic pigment content; %chl *a* = proportion of chlorophyll *a* relative to chloroplastic pigment equivalents; NPP = net primary production; ES(51) expected number of species for a sample of 51 individuals; *H′* = Shannon's diversity index, *J′* = Pielou's evenness.

[a] Data from Leduc et al. (2012b).

Table 2
Results of SIMPER analysis showing percentage dissimilarity contribution of environmental parameters between Kaikoura Canyon and Chatham Rise sites (Euclidean distance of normalised data).

Sediment parameter	Cumulative % dissimilarity
CPE	14.3
NPP	28.3
%chl *a*	42.1
$\%H_2O$	54.3
$\%CaCO_3$	64.8
SED	74.9
%silt/clay	83.9
Water depth	92.6
%TOM	100.0

CPE = sediment chloroplastic pigment content; NPP = net primary production; %chl *a* = proportion of chlorophyll *a* relative to chloroplastic pigment equivalents; $\%CaCO_3$ = sediment carbonate content; SED = sediment particle size diversity; %TOM = sediment total organic matter content.

A total of 2149 nematodes belonging to 113 species and 67 genera were identified from Kaikoura Canyon. The five most dominant species were *Daptonema* sp. 1 (20% of all individuals), *Microlaimus* sp. 1 (11%), *Sabatieria pulchra* (8%), *Cervonema kaikouraensis* (7%), and *Retrotheristus* sp. 1 (5%). There was a significant difference in nematode community structure between canyon and slope habitats (PERMANOVA, $P<0.001$), which was due to a difference in both location and dispersion (PERMDISP, $P<0.001$) of multivariate data; variability in nematode community structure was much less pronounced in Kaikoura Canyon relative to Chatham Rise (Fig. 2). Mean Bray–Curtis dissimilarity between Kaikoura Canyon and Chatham Rise sites was very high (93%). The five most abundant species at Kaikoura Canyon sites (see above) were absent from Chatham Rise sites and accounted for much of the dissimilarity between the two habitats (Table 3). Total species richness at Kaikoura Canyon was four times lower than at Chatham Rise (113 vs 488 species), even though roughly similar numbers of individuals were identified from each region

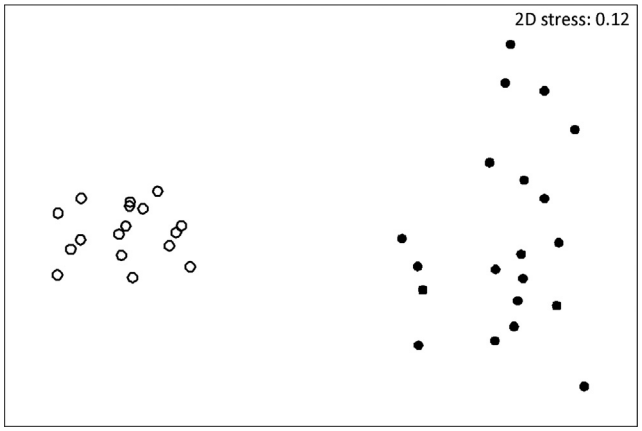

Fig. 2. Two-dimensional multidimensional scaling configuration for nematode species abundance at Kaikoura Canyon (empty circles) and Chatham Rise sites (filled circles).

Table 3
Nematode species contributing most to dissimilarity between Kaikoura Canyon and Chatham Rise sites (New Zealand) based on SIMPER analysis of fourth root-transformed species abundance data.

Species	Mean abundance		Cumulative % dissimilarity
	Chatham Rise	Kaikoura Canyon	
Daptonema sp. 1	0.0	2.1	2.0
Retrotheristus sp. 1	0.0	1.5	3.5
Sabatieria pulchra	0.0	1.4	4.9
Microlaimus sp. 1	0.0	1.4	6.2
Cervonema kaikouraensis	0.0	1.4	7.5
Campylaimus sp. 1	0.6	1.2	8.5
Paramonohystera sp. 1	1.3	0.5	8.5
Sabatieria sp.1	0.1	1.0	10.4
Leptolaimus sp. 1	1.0	0.1	11.3
Sabatieria bitumen	0.9	0.0	12.2
Sabatieria sp. 2	0.9	0.0	13.1
Hapalomus sp. 1	0.9	0.1	13.9
Desmoscolex sp. 1	0.9	0.2	14.7
Dichromadora sp. 1	0.8	0.0	15.5
Vasostoma aurata	0.8	0.0	16.3
Endeolophos sp. 1	0.8	0.0	17.0
Daptonema sp. 2	0.4	1.0	17.8
Leptolaimus sp. 2	0.0	0.8	18.5
Daptonema sp. 3	0.0	0.8	19.3
Sabatieria sp. 3	0.0	0.8	20.0

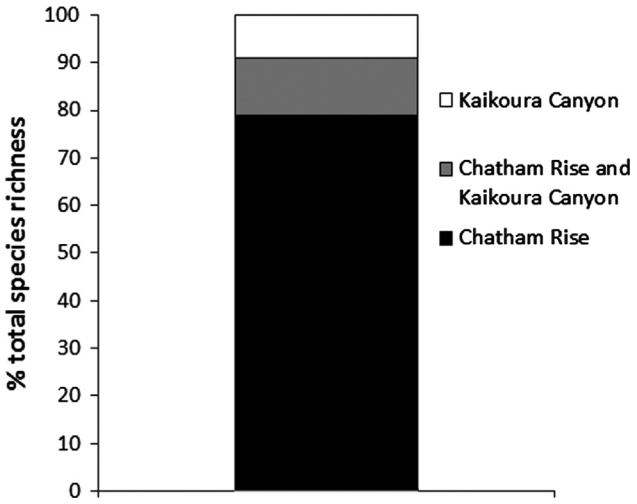

Fig. 3. Contribution of Kaikoura Canyon and Chatham Rise study sites to total observed species richness.

(2149 vs 2583, respectively); 79% of all species were from Chatham Rise, 9% from Kaikoura Canyon, and 12% were present in both habitats (Fig. 3).

4. Discussion

There were some major differences in environmental parameters between Kaikoura Canyon and Chatham Rise, and the most obvious was the considerably higher sediment pigment concentrations at the canyon sites, suggesting markedly higher food availability than at slope sites. This finding is consistent with the greater nematode standing stocks observed in Kaikoura Canyon. High food availability in the canyon could be due to a variety of factors, such as input of terrestrial organic matter, greater surface primary productivity above the canyon, and/or topographically-induced focusing of primary production. Whilst several studies have shown enhanced localised supply of organic material from terrestrial or shallow water habitats inside canyons (e.g., macrophyte detritus; e.g., Vetter, 1998; Vetter and Dayton, 1999), the lack of a pattern in total organic matter content (TOM) of the sediments between Kaikoura Canyon and Chatham Rise suggests no or limited influence of terrestrial material to food availability. Relatively low C:N ratios of sediment organic matter (mean = 7.6; range = 6.3–9.6) inside the canyon also suggest low input of refractory macrophyte material (S. Nodder, unpublished data). In contrast, estimates of net primary productivity (NPP) were two times greater at the canyon sites relative to sites outside the canyon, which may explain some of the differences in food availability between the two habitats. In addition, other factors are likely to be involved, because between-habitat differences in sediment pigment concentrations were five times higher than differences in net primary productivity; that is, sediment pigment concentrations inside the canyon were greater than expected if NPP was assumed to be the sole driver of food availability (Fig. 4). Water depth also influences how much of the surface productivity reaches the seabed and becomes available for consumption by the benthic community. As the sites sampled spanned a similar depth range in Kaikoura Canyon and Chatham Rise, it is likely that processes that facilitate the transport of surface primary productivity to the seabed inside the canyon are involved. Lewis and Barnes (1999) have shown that tidally-driven currents in Kaikoura Canyon have a net downslope component, thereby leading to downwelling of surface waters into the canyon. The observations from previous studies, and the results of the present study, suggest that high food availability at canyon sites is likely to result from high surface primary productivity above

the canyon in addition to the concentration of surface organic matter along the canyon axis by downwelling and/or topographically-induced channelling. De Leo et al. (2010) found that photographic surveys of the seabed along the axis of Kaikoura Canyon showed no evidence of sediment transport (e.g., ripples), and, together with the unusually high megafaunal biomass recorded there, led them to describe the canyon as a low-energy depocentre for organic matter derived from surface waters.

Nematode standing stocks in Kaikoura Canyon are among the highest recorded in the deep sea (Leduc et al., 2012c). Comparison with published data from other canyons showed that the maximum values of nematode abundance and biomass recorded in Kaikoura Canyon exceeds previous values by a factor of two or more (Table 4; Fig. 5). Although this difference is not as pronounced as the 100-fold difference in megafaunal biomass observed by De Leo et al. (2010) between Kaikoura Canyon and other non-chemosynthetic deep-sea habitats, the present findings support the latter authors' description of Kaikoura Canyon as one of the most productive deep-sea habitats described to date. Nematode biomass represents ~0.2% of megafaunal biomass in Kaikoura Canyon (assuming a 1:4 dry to wet weight ratio; De Leo et al., 2010), but its contribution to secondary production is likely to be substantially greater since turnover rates are typically larger for small organisms (Heip et al., 1985). High densities of both mega- and macrofaunal organisms inside the canyon are likely to lead to high predation and competitive pressures on small meiofaunal organisms (e.g., Debenham et al., 2004), which may explain why differences in nematode standing stocks between Kaikoura Canyon and open slope habitats are not as pronounced as for the larger fauna.

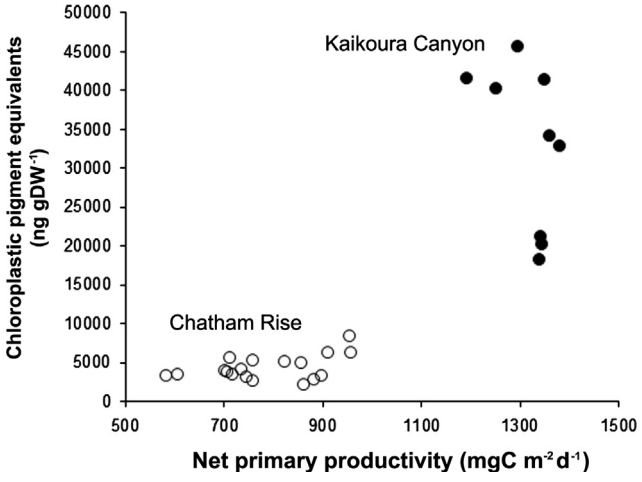

Fig. 4. Plot of sediment chloroplastic pigment equivalents (CPE) against values of estimated surface net primary productivity in overlying waters at Kaikoura Canyon sites (filled circles) and Chatham Rise (empty circles).

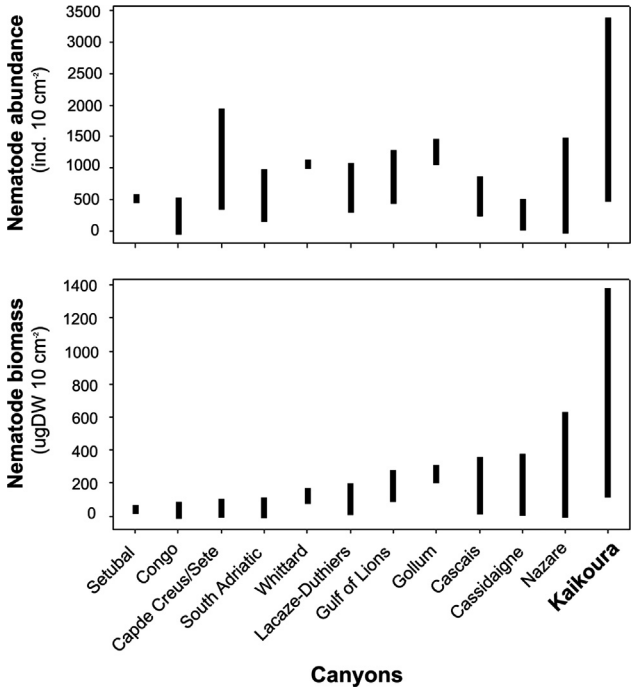

Fig. 5. Range of nematode abundance (top) and biomass (bottom) recorded from canyons worldwide. See Table 4 for details of study sites and literature sources.

Table 4
Nematode abundance and biomass in canyon and adjacent slope habitats. Data are from the Northeast Atlantic (Gollum Channel, and Whittard, Nazaré, Cascais, and Setúbal Canyons), Mediterranean (Lacaze-Duthiers, Cap de Creus/Sete, South Adriatic, Cassidaigne, and Gulf of Lions Canyons), Central East Atlantic (Congo Channel), Northeast Pacific (Monterey Canyon), and Southwest Pacific (Kaikoura Canyon).

Region	Water depth		Abundance (ind. 10cm^{-2})		Biomass (μg DW 10 cm^{-2})		Source
	Canyon	Slope	Canyon	Slope	Canyon	Slope	
Gollum Channel	755–1090	N/A	1110–1400[a]	N/A	210–280[a]	N/A	Ingels et al. (2011a)
Whittard Canyon	762–1160	N/A	1030–1070[a]	N/A	90–130[a]	N/A	Ingels et al. (2011a)
Nazaré Canyon	354–4969	300–4798	10–160[a]	20–120[a]	4–44[a,b]	4–38[a,b]	Garcia et al. (2007)
Nazaré Canyon	458–4363	416–4902	242–1336[a]	158–744[a]	57–607[a,b]	17–112[a,b]	Bianchelli et al. (2010)
Nazaré Canyon	3425–4340	3400–4277	800–1180[a]	410–490[a]	93–343	30–54	Ingels et al. (2009)
Nazaré Canyon	344–4323	N/A	586–1414	N/A	37–256	N/A	Soetaert et al. (2002)
Nazaré Canyon	3500	N/A	1261	N/A	161	N/A	Ingels et al. (2010)
Cascais Canyon	445–4689	1002–4987	285–810[a]	320–723[a]	43–329[a,b]	191–235[a,b]	Bianchelli et al. (2010)
Cascais Canyon	3209–4244	N/A	467–711	N/A	24–37[a]	N/A	Ingels et al. (2011b)
Setúbal Canyon	3224–4485	N/A	491–515	N/A	25–40[a]	N/A	Ingels et al. (2011b)
Lacaze-Duthiers Canyon	434–1497	334–1022	189–1196[a]	434–1420[a]	23–170[a,b]	25–124[a,b]	Bianchelli et al. (2010)
Cap de Creus/Sete Canyon	960–2342	398–1887	134–567[a]	274–667[a]	9–75[a,b]	37–90[a,b]	Bianchelli et al. (2010)
South Adriatic Margin Canyons B and C	341–721	196–908	21–483[a]	140–309[a]	3–84[a,b]	14–64[a,b]	Bianchelli et al. (2010)
Cassidaigne Canyon	168–580	N/A	72–441	N/A	20–352	N/A	Vivier (1978)
Gulf of Lions Canyon system	240–1380	340–830	472–1234	648–1533	99–250	148–255	Grémare et al. (2002)
Monterey Canyon	3262	3607	450	854	N/A	N/A	Fleeger et al. (2010)
Congo Channel	3964–4788	1304–3994	2.5–466	917–1182	< 1–62[a]	34–85[a]	Van Gaever et al. (2009)
Kaikoura Canyon	404–1417	350–1238	507–3315	475–2828	128–1353	20–323	Present study

[a] Estimated from figure.
[b] Assuming dry weight:wet weight ratio of 0.25.

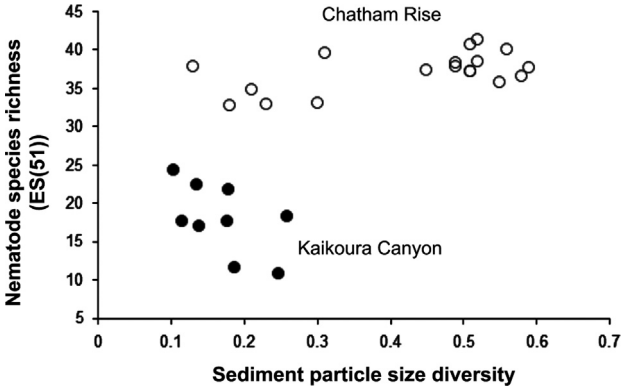

Fig. 6. Plot of nematode species richness against sediment particle size diversity at Kaikoura Canyon (filled circles) and Chatham Rise sites (empty circles).

Nematode diversity inside the canyon was markedly lower than at open slope sites on Chatham Rise. This difference could be the result of contrasting sediment physical characteristics between the two habitats, i.e., higher silt/clay content and lower sediment particle size diversity (SED) inside the canyon compared with the slope habitat. For example, SED is positively correlated with local nematode diversity (Leduc et al., 2012a), and could account for the contrast observed here. Values of SED, however, overlapped to a large extent between the two habitats, and Kaikoura Canyon sites with SED values similar to Chatham Rise sites were characterised by much lower diversity (Fig. 6). This finding suggests that factors other than SED are responsible for differences in diversity between the two habitats; this suggestion seems to be valid also for other sediment parameters, such as %silt/clay and $\%H_2O$, as their values overlapped between the Kaikoura Canyon and Chatham Rise sites.

Differences in the diversity of sediment fauna between canyon and slope habitats are commonly ascribed to food availability (e.g., Vetter and Dayton, 1998; Ingels et al., 2009; De Leo et al., 2014). As food availability was markedly higher inside the canyon habitat it may therefore account for the difference in diversity observed here. A study based on data from around the globe showed a unimodal relationship between nematode biomass (a proxy for productivity) and local nematode diversity in the deep sea, with Chatham Rise and Kaikoura Canyon sites located at the intermediate and most productive portions of the curve, respectively (Leduc et al., 2012c). Low nematode diversity at highly productive sites may be due to factors such as elevated competitive exclusion rates (Rex, 1983) and challenging biogeochemical conditions (e.g., low oxygen and high sulphide levels; Bagarinao, 1992; Levin, 2003) permitting only a few species to persist. Some of the dominant taxa at Kaikoura Canyon sites, such as *S. pulchra* and the genus *Daptonema*, are regularly encountered in hypoxic subsurface layers of organic rich sediments (e.g., Jensen, 1984; Olafsson, 1992; Wetzel et al., 2002). *S. pulchra* is among the few nematode species known to survive periods of hypoxia or anoxia (Steyaert et al., 2007); it is most commonly found in eutrophic coastal sediments and, to our knowledge, this is the first record of this species in the deep sea (Miljutin et al., 2010). The presence of this species at our study sites suggests that conditions similar to those present in shallow-water eutrophic habitats (and atypical of most deep-sea environments) may be present in Kaikoura Canyon.

Our findings agree well with previous studies that have found a link between high food input and altered nematode community structure inside canyons (e.g., Ingels et al., 2009; 2011a, b). Sediment depth often explains a greater amount of the variability in nematode community structure than horizontal distance (100s of km) and water depth, which suggest that small-scale vertical biogeochemical gradients have an overriding influence on their distribution (Ingels et al., 2011a, b). Biogeochemical gradients are largely driven by bacterial processes associated with organic matter decomposition in the sediments, which in turn depend on the availability of food. In addition, high abundance of the genus *Sabatieria* has been observed in several North Atlantic and Mediterranean canyons subject to elevated organic matter input (Soetaert and Heip, 1995; Ingels et al., 2009; 2011a, b).

Disturbance is another factor that may affect benthic communities in canyon habitats, but quantifying disturbance is a considerably more challenging task than (for example) quantifying food availability. Lewis and Barnes (1999) suggested that turbidity currents in Kaikoura Canyon may operate on time scales of centuries, rather than millennia. Repeated physical disturbance following sediment resuspension and deposition events along the canyon axis could help explain the low diversity levels observed in Kaikoura Canyon (for example, see Garcia et al., 2007). The genus *Microlaimus*, which was common in some of the Kaikoura Canyon samples, is usually considered to be an opportunistic coloniser, and is often among the first taxon to recolonise physically disturbed patches (e.g., Lee et al., 2001; Raes et al., 2010). Biologically-induced disturbance by predation is also likely to be intense due to the high densities of macro- and megafauna within the canyon (De Leo et al., 2010), and may contribute to the low nematode diversity. However, the role of disturbance in maintaining diversity patterns in Kaikoura Canyon remains unknown.

Variability in community structure was substantially lower inside the canyon than outside, and may reflect the constraints imposed on the nematode community by the relatively challenging environmental conditions found at the study sites. This low beta (or turnover) diversity may also be the result of low variability in sediment physico-chemical characteristics (see Table 1), and/or the small size of the canyon relative to Chatham Rise. This lack of variability between sites also contributed to the low regional diversity in the canyon.

The Kaikoura Canyon nematode community was characterised by low diversity, both at the local and regional scale, and by a high degree of dominance by a few species/taxa typically associated with environmental conditions not typical of the deep sea (i.e., high food availability, potentially high levels of disturbance). The community was also highly distinct from open slope communities: of the 538 nematode morphospecies identified from Chatham Rise and Kaikoura Canyon, only 12% were shared between the two habitats, and 50 species (or 9%) were found only within the canyon. The distinct nature of the community could make it vulnerable to the effects of disturbance from activities such as fishing (e.g., De Leo et al., 2010). Kaikoura Canyon is a relatively small habitat characterised by different environmental conditions that makes a disproportionate contribution to deep-sea diversity in the region despite its low species richness. The importance of this habitat, and potentially other deep-sea canyons on the New Zealand margin, suggests that this type of habitat should be considered separately from other continental slope habitats for management purposes.

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