

Submarine canyons: hotspots of benthic biomass and productivity in the deep sea

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Submarine canyons are dramatic and widespread topographic features crossing continental and island margins in all oceans. Canyons can be sites of enhanced organic-matter flux and deposition through entrainment of coastal detrital export, dense shelf-water cascade, channelling of resuspended particulate material and focusing of sediment deposition. Despite their unusual ecological characteristics and global distribution along oceanic continental margins, only scattered information is available about the influence of submarine canyons on deep-sea ecosystem structure and productivity. Here, we show that deep-sea canyons such as the Kaikoura Canyon on the eastern New Zealand margin (42°01' S, 173°03' E) can sustain enormous biomasses of infaunal megabenthic invertebrates over large areas. Our reported biomass values are 100-fold higher than those previously reported for deep-sea (non-chemosynthetic) habitats below 500 m in the ocean. We also present evidence from deep-sea-towed camera images that areas in the canyon that have the extraordinary benthic biomass also harbour high abundances of macrourid (rattail) fishes likely to be feeding on the macro- and megabenthos. Bottom-trawl catch data also indicate that the Kaikoura Canyon has dramatically higher abundances of benthic-feeding fishes than adjacent slopes. Our results demonstrate that the Kaikoura Canyon is one of the most productive habitats described so far in the deep sea. A new global inventory suggests there are at least 660 submarine canyons worldwide, approximately 100 of which could be biomass hotspots similar to the Kaikoura Canyon. The importance of such deep-sea canyons as potential hotspots of production and commercial fisheries yields merits substantial further study.

Keywords: submarine canyons; benthic biomass hotspots; molpadiid holothurians; macrourid fishes; eastern New Zealand margin

1. INTRODUCTION

Continental margins are considered major reservoirs of marine biodiversity and productivity (Sanders & Hessler 1969; Rex 1983; Snelgrove *et al.* 1992; Levin *et al.* 2001; Brandt *et al.* 2007) and have been, albeit controversially, compared with the most diverse terrestrial and shallow-water marine habitats (Rex 1983; Etter & Grassle 1992). Submarine canyons are abundant and ubiquitous features along continental and oceanic island margins that connect continental shelves to deep ocean basins (Shepard & Dill 1966). Roughly, 20 per cent of the northeast Pacific shelf edge between Alaska and the equator is interrupted by steep, narrow and abrupt submarine canyons (Hickey 1997). The single global review available on canyon distribution, origin, geology and sedimentation patterns dates from 1966 and mapped 96 major canyons around the world (Shepard & Dill 1966). Today's more detailed, readily available bathymetric data (still far from being comprehensive, and compiled in the present paper for the first time, to our knowledge) show at least 660 canyons crossing continental margins globally (figure 1).

Patterns of benthic community structure and productivity have been studied in relatively few submarine

canyons (e.g. Vetter 1994; Vetter & Dayton 1999; Hargrave *et al.* 2004; Schlacher *et al.* 2007). Some findings suggest that increased habitat heterogeneity in canyons is responsible for enhancing benthic biodiversity and creating biomass hotspots (Rowe *et al.* 1982; Vetter 1994; Vetter *et al.* 2010). Enhanced local fishery production in canyons, when contrasted to regular slope environments, has also been reported and attributed to the channelling and concentrating of detrital organic matter and pelagic animal populations (Yoklavich *et al.* 2000; Brodeur 2001; Tudela *et al.* 2003; Company *et al.* 2008). Many other unusual ecological and physical characteristics have been attributed to canyons such as concentrating diel vertical migrators (Greene *et al.* 1988), displacing deep-water species to coastal zones (King 1987), promoting topographically induced upwelling (Klinck 1996; Hickey 1997; Sobarzo *et al.* 2001), enhancing dyapical mixing via internal wave generation (Kunze *et al.* 2002) and focusing of internal tidal bores (Vetter & Dayton 1999).

Canyons are complex topographic features often characterized by complicated patterns of hydrography, flow and sediment transport and accumulation (Shepard *et al.* 1974; Oliveira *et al.* 2007; Garcia *et al.* 2008). Unusual physical oceanographic conditions inside canyons, such as accelerated currents and dense-water cascades, can be caused by topographic and climate forcing, increasing suspended particulate matter concentrations and transport

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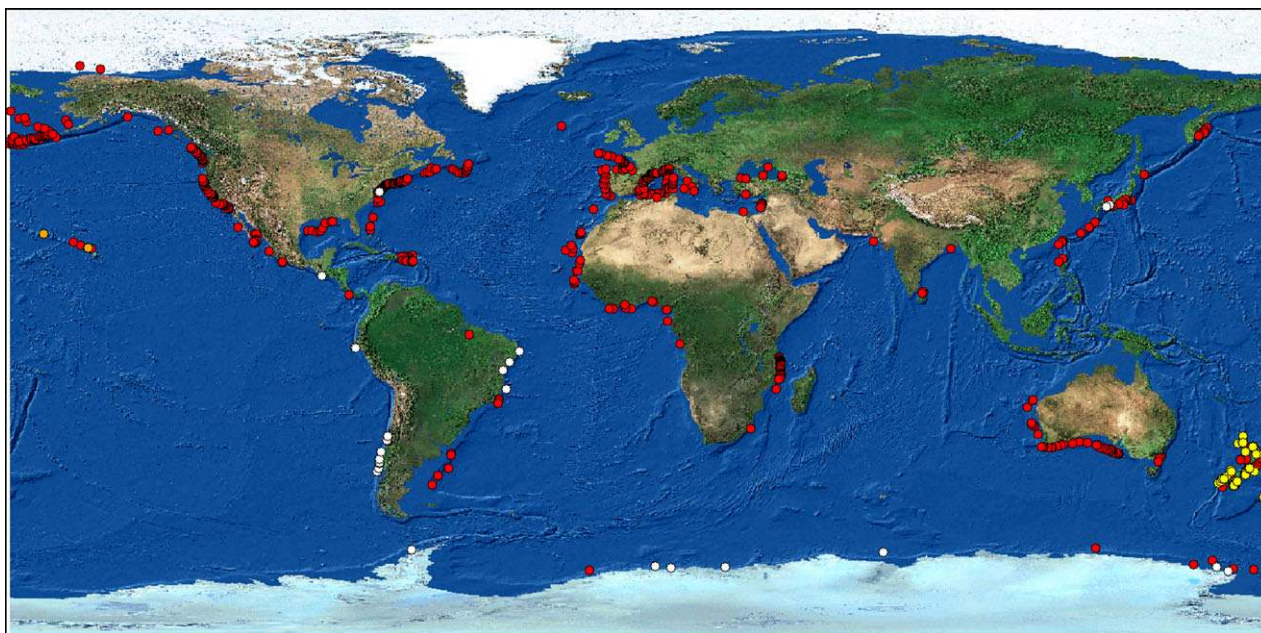


Figure 1. Global distribution of submarine canyons counted in this study (total of 660 canyons, see table S1 for a complete listing). Three datasets were used. (i) Red circles (named) and white (unnamed) canyons from the Google-Earth (SIO, NOAA, US Navy, NGA, GEBCO) databases, (ii) light yellow circles from an unpublished report of New Zealand canyons (Thompson 2001), and (iii) orange circles from Vetter *et al.* (2010). For methods, see §2f.

of organic matter from coastal zones to the deep ocean (Bosley *et al.* 2004; Genin 2004; Billett *et al.* 2006; Canals *et al.* 2006; Company *et al.* 2008). These phenomena can be responsible for enhancing both pelagic and benthic productivity inside canyon habitats as well as biodiversity of many benthic faunal groups (Rowe *et al.* 1982; Schlacher *et al.* 2007; Vetter *et al.* 2010).

Here, we study the deep-sea Kaikoura submarine canyon on the eastern New Zealand margin ($42^{\circ}01' S$, $173^{\circ}03' E$) as part of the RENEWZ (Exploration of Chemosynthetic Habitats of the New Zealand Region) and National Institute of Water and Atmospheric Research's (NIWAs) 'Impact of resource use on vulnerable deep-sea communities' research projects. Our quantitative samples and photographic surveys from the sediment-covered canyon floor indicate one of the most productive benthic habitats described so far in the deep sea. Trawl data also show evidence of elevated demersal fish abundances associated with the canyon floor, especially of benthic-feeding species. We hypothesize that the high benthic invertebrate biomass and the estimated productivity, as well as the higher benthic-feeding fish abundance, are produced by a combination of high pelagic productivity (i.e. export of phytodetrital material from the Subtropical Front System; Nodder *et al.* 2007) and high macrophyte detrital export from shallow coastal areas, channelled and deposited onto flat, low-energy areas of the Kaikoura Canyon.

2. MATERIAL AND METHODS

(a) Sampling of macro- and megafauna

During the research cruise TAN0616 aboard NIWA's *R/V Tangaroa* (1–20 November 2006), a framed, 0.2 m^2 Van Veen grab was used to collect four quantitative samples (Eleftheriou & McIntyre 2005) for infaunal megabenthos at depths of 1000–1040 m inside the Kaikoura Canyon (figure 2 and table 1). On shipboard, sediment samples

were washed on a 2 mm mesh-sized sieve (mega-infauna) and the residue stored in 80 per cent ethanol for quantitative analysis of abundance and biomass. Standard protocols for wet weight biomass were used (Van der Meer *et al.* 2005). Briefly, animals were blotted dry on Whatman glass microfibre filter grade GF/F and weighed individually on a 0.001 g precision balance after removing excess ethanol by strong suction using a peristaltic pump. Wet weights in grams of wet tissue were converted to grams of carbon using the conversion factor of 4.3 per cent (Rowe 1983). Four multiple-core deployments, each collecting three tubes 10 cm in diameter by 40 cm in depth, provided quantitative samples of infaunal macrobenthos in the Kaikoura Canyon at depths of approximately 1000 m (figure 2 and table 1). Samples were sieved on a $300 \mu\text{m}$ mesh and residues stored in 4 per cent buffered formaldehyde–sea water solution. Macrofauna were sorted using a dissecting microscope. During a second cruise (KAH0706) aboard NIWA's *R/V Kaharoa*, similar multiple-core samples were collected in a control area on the Wairarapa slope ($41^{\circ}46' S$; $175^{\circ} E$) at two depths, 1000 and 1600 m (figure 2 and table 1). A deeper station (approx. 1600 m) located inside the Kaikoura Canyon was also sampled. A beam trawl was used to provide qualitative information on megafaunal community structure (e.g. species lists and material for taxonomic identification).

(b) Seafloor photographic surveys

A towed camera platform (NIWA's 'deep-towed imaging system' or DTIS) took digital photographs oriented perpendicular to the seafloor every 20 s along transects that varied from 0.65 to 1.6 km in length (11 transects, 464 total photographs analysed; table 1). A total of eight transects were positioned inside the Kaikoura Canyon in two depth zones (900–1100 m and 1200–1300 m), and three transects positioned in a control area on the Wairarapa slope at depths ranging from 1027 to 1064 m (figure 2 and table 1). Photographs with frames covering an area between 1.6 and 2.5 m^2 of the seafloor were analysed. Frames with

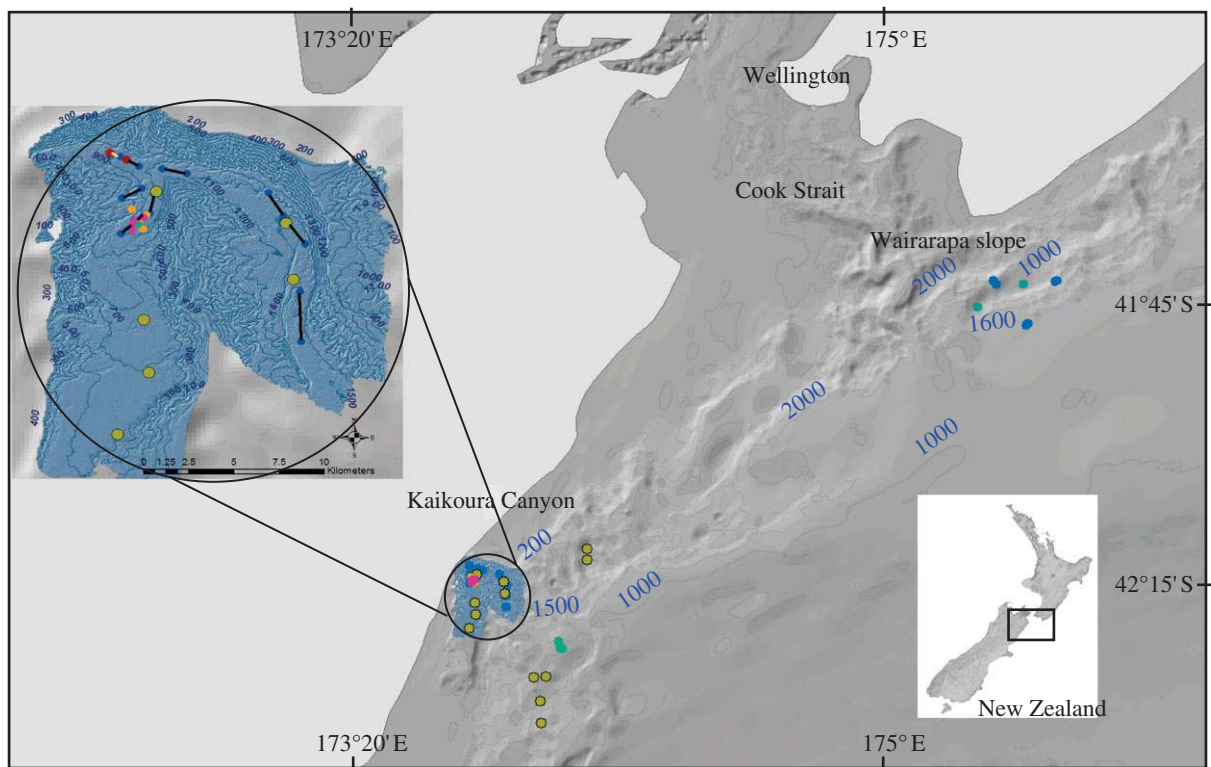


Figure 2. Map showing the areas sampled in the eastern New Zealand margin. Coloured symbols show positions of grab, multi-cores, DTIS photo-transects and bottom-trawl samples in the Kaikoura Canyon and the Wairarapa slope. Pink, grab samples; orange, multi-core TAN0616; cyan, multi-core KAH0706; blue, photo transects; yellow, bottom trawling; red, beam trawl.

areas outside of this range (when the camera was either too close or too far from the seafloor) were excluded from the analysis. The total area of the seafloor analysed in the photographs was 920.4 m² in the canyon and 280.8 m² in slope transects. We employed image analysis software (IMAGEJ; Rasband 2009) to determine the abundance of megafauna (invertebrate and fish) as well as of bioturbation features (*lebensspuren*) from the images. Seafloor images were scaled with two parallel laser beams 20 cm apart. Animal and bioturbation feature densities measured from each frame were then normalized to 1 m² of the seafloor and plotted along the transect length. Transects performed within similar depth ranges and in close proximity were pooled (transects 92, 100 and 104; 94 and 97; 90 and 102; 75–77; table 1).

(c) Multi-beam data and Geographical Information System (GIS) analysis

A digital terrain map of the Kaikoura Canyon floor was produced using bathymetric data collected during the TAN0616 cruise by a multi-beam echo sounder (EM300). We used the high-resolution bathymetry to estimate the total area of the canyon that could be considered the invertebrate infaunal megabenthos biomass hotspot. We based this estimate on biomass measurements from grab samples collected in the upper arm of the canyon and from the abundances of invertebrate and bioturbation features observed in photographic transects. We assumed that the high-biomass assemblages were restricted to depositional canyon-floor regions with gentle slopes of 10° or less, similar to the sites where infauna were sampled, and within the depth range where the greatest concentration of animal feeding and moving traces were observed in photographs, i.e. 900–1100 m. The areal calculation was then performed using the functions ‘reclassify’ and

‘sum raster’ of the *Spatial Analyst* tool kit of ArcGIS 9 as follows: the original bathymetry grid data file (20 × 20 m cell size) was first used to create another grid with the average slope of each cell (> spatial analyst > surface analysis > slope). This new grid file was then reclassified to provide only the cells in which slopes were 10° or less. The next reclassification step used the original bathymetry grid to produce a new layer with only cells filled by depths between 900 and 1100 m. The two new layers generated, i.e. (i) depths of 900–1000 m and (ii) slopes of 10° or less, were then overlaid. The total number of 20 × 20 m cells in the overlaid layer were counted (74 297) and multiplied by the area of a single cell (0.0004 km²) to reach a total area of 29.719 or approximately 30 km².

(d) Bottom-fish trawl data

Research trawl survey data from the area of 42°00′–43°00′ S, 173°20′–174°00′ E were extracted from the New Zealand Ministry of Fisheries database *Trawl*. Several bottom-trawl surveys for orange roughy were carried out in the 1980s and 1990s, and trawls were taken on cruise TAN0616 (RENEWZ I). All cruises employed the standard NIWA rough-bottom orange roughy trawl net and gear set-up. Data from a total of 12 trawls from the canyon and the nearby continental slope met the criteria of similarities in depth, slope and apparent bottom type. Six trawls came from the canyon; three from the upper, western side of the canyon head at about 700 m depth, and three from 1300–1400 m on the northern and eastern sides of the canyon head. Six tows were available from similar depths away from the canyon to the south and east on the adjacent slope (figure 2 and table S2). The catch composition of the 12 trawls included 66 fish and squid species, which were considered demersal rather than pelagic, and to be sufficiently

Table 1. Detailed information about oceanographic stations where macro- and megabenthic communities were sampled in the Kaikoura Canyon and on the Wairarapa slope (DTIS, deep-towed imaging system).

cruise code	station no.	date	area	gear	deployment duration (min)	latitude south	longitude east	depth gear start (m)	depth gear end (m)	distance covered (km)	no. photos analysed/cores sorted	
Kaikoura Canyon sampling												
TAN0616	106	17 Nov 2006	canyon	grab	—	42°31.20'	173°37.18'	1020	—	—	—	
TAN0616	107	17 Nov 2006	canyon	grab	—	42°31.06'	173°37.32'	1029	—	—	—	
TAN0616	108	17 Nov 2006	canyon	grab	—	42°31.39'	173°37.14'	1014	—	—	—	
TAN0616	109	17 Nov 2006	canyon	grab	—	42°30.98'	173°37.61'	1028	—	—	—	
TAN0616	92	16 Nov 2006	canyon	DTIS	58	42°30.85'	173°37.86'	1055	1087	0.64	42	
TAN0616	100	16 Nov 2006	canyon	DTIS	66	42°30.91'	173°37.62'	1044	993	0.9	40	
TAN0616	104	17 Nov 2006	canyon	DTIS	62	42°30.35'	173°36.76'	899	1035	0.65	51	
TAN0616	94	16 Nov 2006	canyon	DTIS	57	42°29.41'	173°38.34'	1039	1185	0.74	31	
TAN0616	97	16 Nov 2006	canyon	DTIS	60	42°29.32'	173°37.46'	1076	1015	0.65	30	
TAN0616	90	15 Nov 2006	canyon	DTIS	54	42°30.93'	173°43.13'	1296	1200	0.86	55	
TAN0616	102	17 Nov 2006	canyon	DTIS	62	42°31.84'	173°43.97'	1348	1300	0.91	60	
TAN0616	95	16 Nov 2006	canyon	DTIS	48	42°35.01'	173°43.82'	1376	1390	1.63	45	
TAN0616	98	16 Nov 2006	canyon	multi-core	—	42°30.71'	173°37.95'	1061	—	—	1	
TAN0616	101	17 Nov 2006	canyon	multi-core	—	42°30.90'	173°37.61'	1041	—	—	2	
TAN0616	103	17 Nov 2006	canyon	multi-core	—	42°31.12'	173°37.42'	1033	—	—	1	
TAN0616	105	17 Nov 2006	canyon	multi-core	—	42°31.37'	173°37.26'	1020	—	—	1	
KAH0706	3	11 June 2007	canyon	multi-core	—	42°41.27'	173°54.46'	1808	—	—	4	
KAH0706	6	12 June 2007	canyon	multi-core	—	42°31.15'	173°37.33'	1040	—	—	5	
TAN0616	99	16 Nov 2006	canyon	beam trawl	15	42°29.10	173°36.92	1079	1023	0.51	—	
Wairarapa slope sampling												
TAN0616	75	13 Nov 2006	slope	DTIS	16	41°46.82'	175°23.85'	1027	1058	0.8	38	
TAN0616	76	13 Nov 2006	slope	DTIS	45	41°47.03'	175°23.79'	1041	1055	0.33	34	
TAN0616	77	13 Nov 2006	slope	DTIS	35	41°47.22'	175°24.63'	1051	1064	0.36	36	
KAH0706	12	13 Jun 2007	slope	multi-core	—	41°50.82'	175°14.79'	1628	—	—	4	
KAH0706	14	13 Jun 2007	slope	multi-core	—	41°47.40'	175°23.65'	1077	—	—	4	

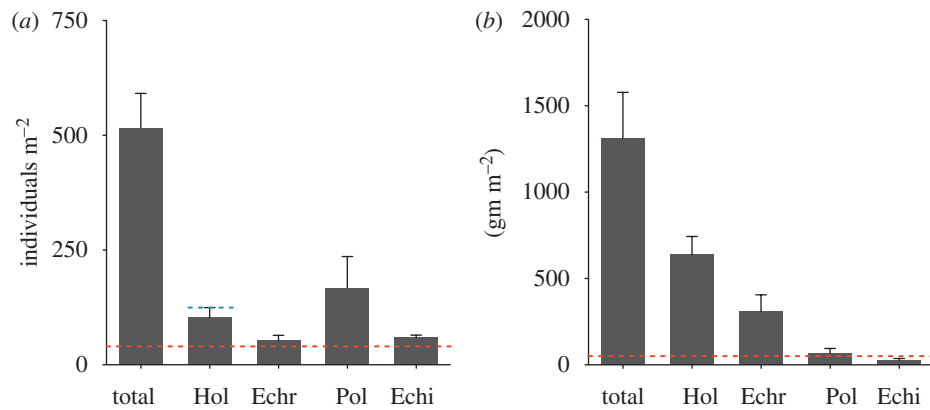


Figure 3. Kaikoura Canyon megafaunal abundance and biomass from Van Veen grab samples (Hol, holothurians; Echr, echiurans; Pol, polychaetes; Echi, echinoids). (a) Average abundance (+s.e.). (b) Average wet weight biomass (+s.e.). Dashed red lines represent the maximum total megafaunal abundance and biomass previously reported in the scientific literature primarily for non-canyon habitats at depths greater than 500 m (Rex *et al.* 2006). Dashed green line represents holothurian densities at 3500 m in Nazare Canyon (Portugal), from Weaver (2005) cited in Amaro *et al.* (2009).

large-bodied to be fully captured and retained by the trawl gear for valid comparison. These were then categorized as benthic feeders (22 species) or benthopelagic feeders (44 species) based on a combination of dietary data from NIWA gut-content studies and the morphology of the fish species (e.g. mouth position). Catch rate analyses were carried out on the species combined into the two ecological feeding groups (table S2).

(e) Data analysis and statistics

Analysis of variance was employed to verify significant differences between faunal parameters (invertebrate megafauna, fishes and bioturbation-feature abundances) between all sites sampled. The groups of photographic transects compared were: (i) Kaikoura Canyon head, transects 92, 94, 97, 100 and 104 ($n = 90$ photographs), (ii) deep Kaikoura Canyon, transects 90, 95 and 102 ($n = 160$ photographs) and (iii) Wairarapa slope control site, transects 75, 76 and 77 ($n = 108$ photographs). Normality and homoscedasticity of variances were tested prior to analysis using parametric one-way ANOVA. The alpha-level was corrected with Holm's modification of the sequential Bonferroni correction to an experiment-wise $p = 0.05$ to avoid inflation of type-I error from multiple testing. Student's t -test was used to compare the log-transformed mean total catch and catch rates between bottom trawls inside the Kaikoura Canyon ($n = 6$) versus in slope reference areas ($n = 6$).

(f) Worldwide inventory of submarine canyons

To estimate the number of submarine canyons potentially harbouring biomass hotspots such as Kaikoura, we include a worldwide inventory of submarine canyons. To the best of our knowledge, this is the first such inventory in the scientific literature. Using the online available databases for seafloor bathymetry in Google-Earth (data sources: SIO, NOAA, US Navy, NGA, GEBCO), currently mapped submarine canyons can be viewed when activating the layer 'Boarders and Labels' in the 'layers' panel of the Google-Earth applicative. Spatial coordinates can be then extracted. We employed a fly-through over continental margins globally, using an 'eye altitude' distance of a maximum of 25 miles, enabling discernment of the smallest canyon features mapped. Available names and geographical coordinates for all canyons observed are provided in electronic supplementary material, table S1. A smaller proportion of

geo-referenced submarine canyons were identified from unpublished databases cited in the scientific literature, such as the canyons in New Zealand (Thompson 2001) and the Hawaiian Archipelago (e.g. Vetter *et al.* 2010). It is clear that the online bathymetric data still fail to provide a comprehensive global inventory of submarine canyons because of the extremely patchy distribution (figure 1). For example, the eastern and western continental margins of South America lack detailed bathymetry data; however, the lower resolution bathymetry data available still reveal major canyons in those areas. In addition, major gaps occur along the margins of Africa, India and Southeast Asia. Therefore, our current inventory should be considered a conservative estimate.

3. RESULTS AND DISCUSSION

The multiple remote sampling devices (grab samples, multi-cores, beam trawls and photographic transects) employed on the sediment-covered Kaikoura Canyon floor revealed extremely dense populations of large burrowing holothuroids, echiurans, polychaete worms and irregular urchins at depths of 900–1100 m. The mean (\pm s.e.) abundance of infaunal megabenthos (animals retained on a 2 mm sieve) was 516 ± 75.2 individuals per square metre (figure 3a), i.e. roughly 10-fold higher than ever measured in detritus-based (i.e. non-chemosynthetic) habitats deeper than 500 m in the ocean (Rex *et al.* 2006). Megafaunal biomass, measured as wet weight, ranged from 0.8 to 2.1 kg m^{-2} , averaging $1.31 \pm 0.26 \text{ kg m}^{-2}$ (figure 3b). Biomass dominants included the mound-building, conveyor-belt deposit-feeding (Wheatcroft *et al.* 1989) holothuroid *Molpadia musculus* (50% of biomass), the mound-building, deposit-feeding echiuran *Alomasoma nordpacificum* (24%) and the conveyor-belt deposit-feeding polychaete, *Maldane theodori* (5%). When converted to grams of carbon, the average megabenthic biomass ($89 \pm 18 \text{ g C m}^{-2}$) in the Kaikoura Canyon is extraordinary for detritus-based habitats in the deep sea, exceeding by 100-fold the highest megabenthic biomass previously recorded at depths below 500 m (Rex *et al.* 2006).

The physical setting (low relief with muddy sediments) of the main study area in the canyon head (900–1100 m depths) appears suitable for trapping particulate organic

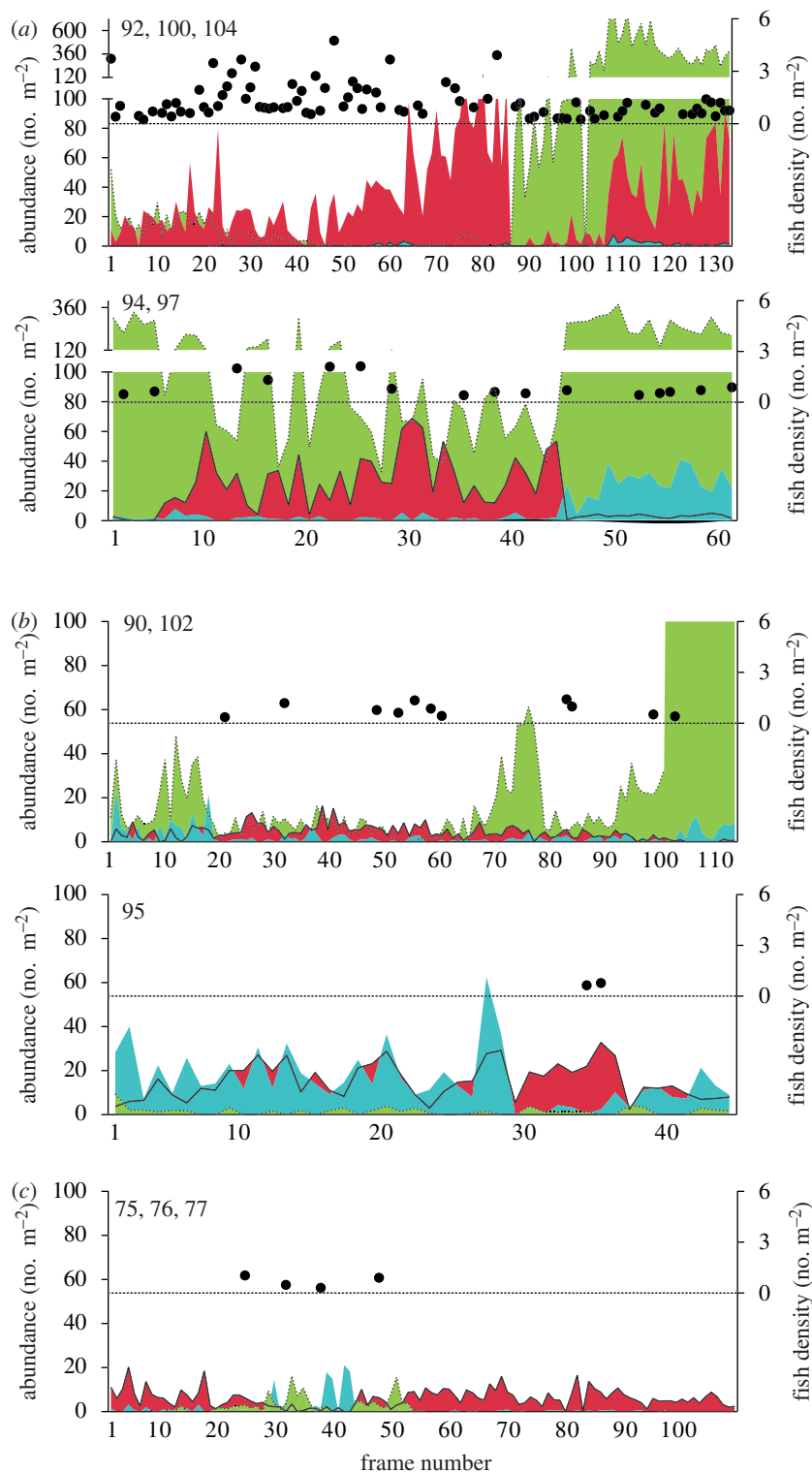


Figure 4. Abundance of epibenthic megafauna, bioturbation features and the foraminiferan *Bathysiphon* sp. (left *y*-axis), and demersal fishes (four macrourid species, right *y*-axis). Epifaunal invertebrate megabenthos (blue shading), bioturbation features characteristic of infaunal megabenthos (red shading), demersal fishes (black dots) and *Bathysiphon* sp. (green shading) from photographic transects (with station numbers for the 11 transects indicated at top left of charts). (a) Canyon head (900–1100 m; $n = 195$). (b) Main canyon axis (1100–1300 m; $n = 160$). (c) Wairarapa open slope site (900–1100 m; $n = 108$). Frame numbers represent individual photographs and indicate the total taken in each depth zone. Transects performed in close proximity within the same depth zones were pooled (e.g. transects 92, 100 and 104 were all conducted within one branch of the canyon head; figure 5). Note the change in scale in the *y*-axis in the upper (canyon head) panels.

matter (POM) derived from pelagic production and coastal detrital export. The overall biomass and organic loading patterns suggest that the Kaikoura Canyon is a low-energy depocentre for POM derived from the

Subtropical Front System (Nodder *et al.* 2003, 2007) as well as from riverine and terrestrial inputs (Lewis & Barnes 1999). These conclusions from previous studies are corroborated by observations from the present study

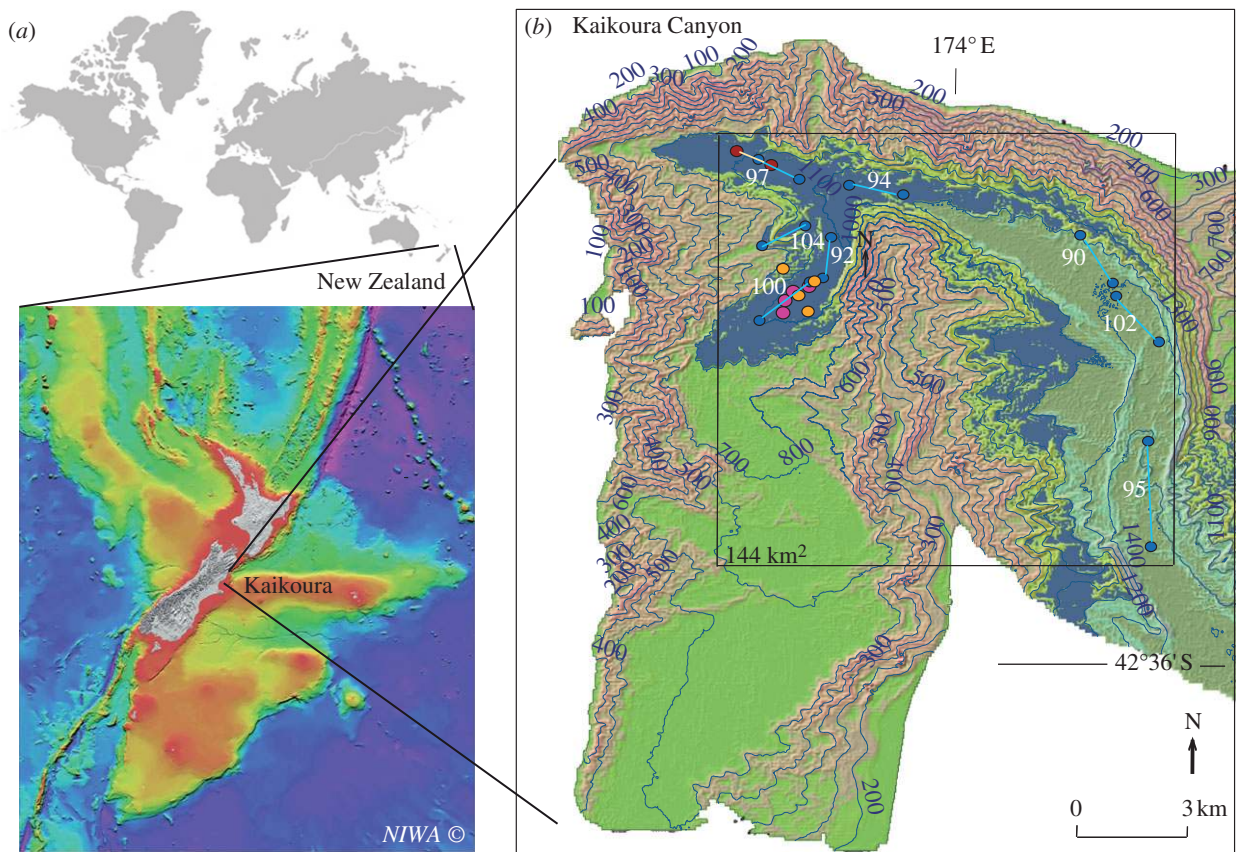


Figure 5. Kaikoura Canyon ($42^{\circ}01' S$, $173^{\circ}03' E$), eastern New Zealand margin. (a) World map and topographic altimetry map showing bathymetry of New Zealand continental margins and highlighting the surveyed area. (b) Detailed multi-beam bathymetry map of the canyon seafloor showing sampling sites and highlighting the estimated extent of the megafaunal biomass hotspot obtained from the GIS analysis. Green shaded area, slope 10° or less; blue shaded area, biomass hotspot; blue circles, photo transects; brown circles, Agassiz trawl; pink circles, grab samples; orange circles, multi-cores.

of macroalgal detritus in the shallowest photographic transects near the canyon head (900 m) and the absence of sediment ripples or other evidence of sediment transport in all canyon photographs from 900 to 1100 m.

Our benthic biomass measurements were concentrated in one arm of the Kaikoura Canyon head (figure 2), but analysis of seafloor photographic transects indicates that this high-biomass community was widespread throughout canyon-floor sediments at depths of 900–1100 m. The eight seafloor photographic transects conducted in the canyon, extending over approximately 7 linear km and covering an area of $11\,200\text{ m}^2$, revealed in all images analysed (920.4 m^2 of the seafloor) high densities ($33 \pm 2.5\text{ m}^{-2}$) of bioturbation features characteristic of the biomass dominants *M. musculus* and *A. nordpacificum*, including faecal mounds, feeding traces and burrows (figure 4). Feeding and mobility traces of megafauna in this part of the canyon are an order of magnitude more abundant (significant one-way ANOVA, $p = 0.001$) than at similar depths on the nearby slope ($6\text{ m}^{-2} \pm 0.4\text{ s.e.m.}$, $n = 108$), and at greater depths (1200–1400 m) within the canyon ($7.2\text{ m}^{-2} \pm 0.5\text{ s.e.m.}$, $n = 160$) (figure 3; see also electronic supplementary material, figure S1, for more details on the abundance and types of bioturbation features). The bioturbation features formed by megafauna in the Kaikoura Canyon head area are also strikingly abundant when compared with general deep-sea depositional habitats, where biogenic structures such as feeding traces, faecal

mounds and animal tracks are common features on the ocean floor (Gage & Tyler 1996). Our mean value (33 m^{-2}) is at least seven times higher than that reported from North Atlantic non-canyon habitats (mean $4.5\text{ m}^{-2} \pm 0.25\text{ CI}$) where a similar towed camera platform was employed over similar depth ranges and spatial scales (Jones *et al.* 2007). In addition, the remarkable densities observed for the foraminiferan *Bathysiphon* sp. ($127\text{ m}^{-2} \pm 12\text{ s.e.}$, $n = 195$) in the canyon head (threefold higher than at deeper areas in the canyon and 50-fold higher than at the open slope control site; figure 4) also indicate organic-rich, bioturbated sediments, as observed elsewhere in continental margin depositional environments (Goody *et al.* 1992).

GIS spatial analysis of the Kaikoura Canyon revealed a total area of approximately 30 km^2 of the canyon floor between depths of 900 and 1100 m with gentle slopes of less than 10° in which we expect the high-biomass megafaunal assemblages to be found (figure 5; refer to §2c). Assuming an average infaunal biomass of 1.31 kg m^{-2} (based on grab samples) for this 30 km^2 , we estimate total infaunal megabenthic biomass for this 'biomass hotspot' in the Kaikoura Canyon to be approximately 3.9×10^4 tonnes wet weight. Assuming conservatively that this megafaunal biomass in the Kaikoura Canyon turns over once approximately every 20 years (Gage & Tyler 1996), the biomass hotspot is likely to produce on the order of 2.0×10^3 tonnes of megafaunal biomass per year. To place this production estimate in

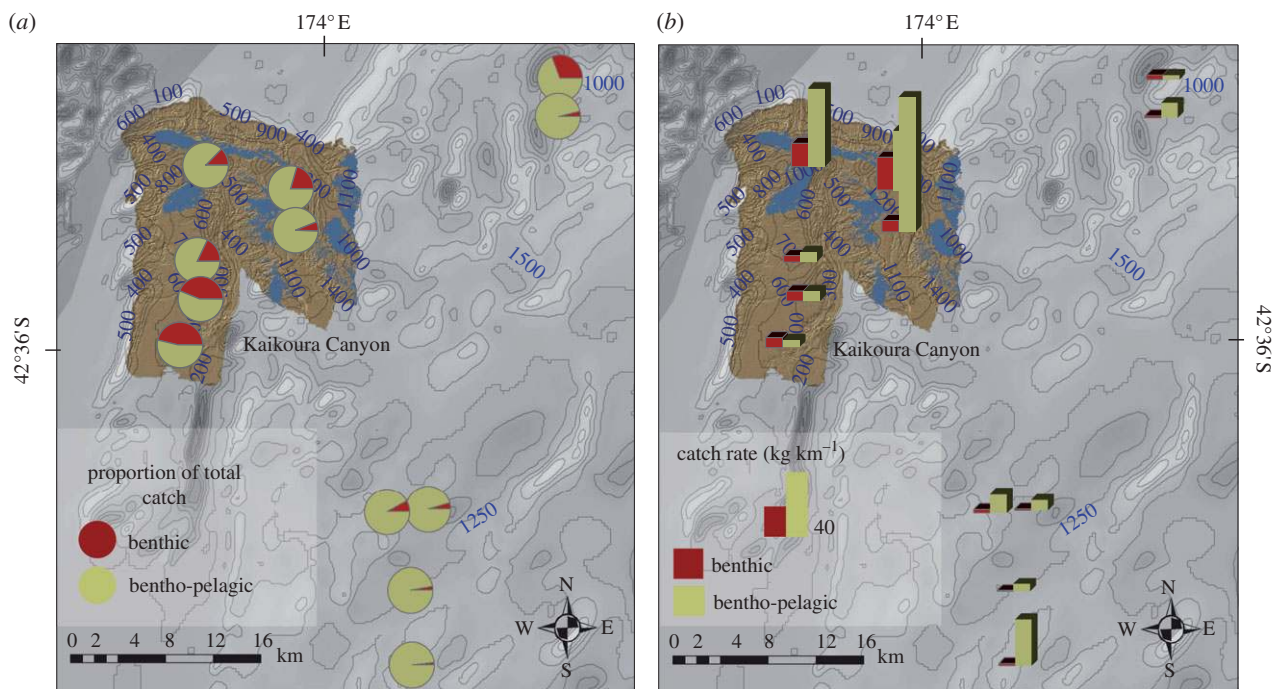


Figure 6. Total catch and catch rates of benthic and benthic-pelagic fishes trawled in the Kaikoura Canyon and adjacent slopes. (a) Proportion of benthic-feeding fishes (red fill) relative to benthic-pelagic-feeding fishes (beige fill) in trawl catches in the areas indicated. (b) Catch rates (kg km^{-1}) of combined benthic (red) and benthic-pelagic (beige) fish species (see table S2 for catch and catch-rate values). Blue shaded areas represent megafaunal biomass hotspots calculated from the GIS analysis (§2c, figure 4).

a regional fishery context, the estimated annual production of Kaikoura megabenthic invertebrates exceeds a recent estimate of the production of orange roughy (*Hoplostetetus atlanticus*) for the entire Mid-East Coast stock of the New Zealand fishery, which is derived from an area of greater than 10^5 km^2 (New Zealand Ministry of Fisheries Report 2009).

Higher local benthic invertebrate biomasses have been recorded at depths of 10–60 m in submarine canyons; e.g. a maximum of approximately $10 \text{ kg wet weight m}^{-2}$ in detrital mats in the Scripps Canyon on the Californian margin (Vetter 1994). However, these high-biomass detrital mats extended over relatively small areas (approx. 0.01 km^2) and, therefore, the total invertebrate biomass concentrated in detrital mats in the Scripps Canyon (approx. 100 tonnes wet weight) is roughly two orders of magnitude lower than that estimated at 900–1100 m in Kaikoura Canyon head. In addition, very high abundances of infaunal megabenthic holothuroids similar to those in the Kaikoura Canyon have been reported at 3500 m depths in the Nazare Canyon off the coast of Portugal, although the biomass and areal extend of these holothuroid populations have not been documented (Amaro *et al.* 2009).

Other evidence of community enrichment at depths around 1000 m in the Kaikoura Canyon comes from the data on infaunal macrobenthos obtained from the multiple-core samples. Densities in the canyon ($n = 10$) are twice as high (significant one-way ANOVA, $p = 0.0085$) as on the slope ($n = 4$), with the average of 51 500 m^{-2} ($n = 10$; s.e. = 5500) being 10-fold higher than average macrofaunal abundances at the same depths (obtained from a global-scale analysis of macrobenthic standing stock (Rex *et al.* 2006)).

The abundant macro- and megafaunal taxa in the Kaikoura Canyon play well-documented roles in sediment reworking and carbon burial (e.g. Smith *et al.* 1986; Wheatcroft *et al.* 1990) and can also serve as important prey for demersal fishes (Issacs & Schwartzlose 1975; Drazen 2002; Jones 2008). Research trawls from similar depth ranges inside the canyon and on the adjacent slope reveal that benthic-feeding fishes constitute a much higher proportion of the fish catch in the canyon (21%) than on the open slope (5%) (figure 6a). In addition, total catch rates of demersal (bottom-associated) fish species in Kaikoura are sevenfold higher than at comparable depths on the open slope (figure 6b)—this difference is highly statistically significant ($t = -5.033$, $p = 0.001$, d.f. = 10). Among the most abundant demersal fish trawled inside the canyon, the rattails (macrourids) *Coelorrinchus bollonsi*, *C. innotabilis*, *Trachyrinchus* spp. and *Coryphaenoides subserrulatus* were consistently present in our bottom photographs, and particularly abundant at 900–1100 m depths (figure 4). Rattail densities from photographic transects at 900–1100 m depths in the canyon head are very high, with 141 specimens observed over 273 m^2 of seafloor, i.e. a density of 5000 ha^{-1} . This exceeds by one order of magnitude total fish abundance estimated for well-studied bathyal slopes in the Northeast Atlantic (Bailey *et al.* 2009) (approx. $120\text{--}220 \text{ ha}^{-1}$) and off central California (approx. $50\text{--}500 \text{ ha}^{-1}$) (Cailliet *et al.* 1999). Frequently, our photographs revealed multiple rattails in a single frame in head-down positions consistent with feeding on sediment infauna and/or epifauna (electronic supplementary material, figure S2). These observations suggest that the high invertebrate macro- and megabenthic abundance/biomass is exploited by

bottom-feeding fishes in the Kaikoura Canyon, which historically has been an important area of major deepwater fishery catch off New Zealand (Clark *et al.* 2003).

Our findings suggest that the Kaikoura Canyon is one of the most productive benthic habitats known for the deep sea and may contribute significantly to deep-sea ecosystem production in the immediate canyon vicinity, which includes deep commercial fisheries for hoki (*Macruronus novaezelandiae*) and orange roughy (*H. atlanticus*) (Clark *et al.* 2003). Whether Kaikoura Canyon production is important for fishes residing temporarily in the canyon but commercially exploited more broadly remains to be ascertained.

Submarine canyons are globally numerous but very poorly sampled, which may explain why biomasses similar to those in the Kaikoura Canyon have not been previously recorded for the deep sea. How common are biomass hotspots such as the Kaikoura Canyon likely to be on ocean margins? Approximately 15 per cent of the 96 submarine canyons whose physical and geological features have been reviewed in detail (Shepard & Dill 1966) exhibit characteristics similar to those of the Kaikoura Canyon (and the Nazare Canyon off Portugal margin, as potentially another example; Amaro *et al.* 2009) including: (i) heads positioned in coastal embayments with high loads of terrestrial material, (ii) U-shaped canyon cross sections, and (iii) substantial inputs of coastal sediments (Lewis & Barnes 1999; Oliveira *et al.* 2007). Thus, on the order of 15 per cent of submarine canyons globally may support intense deep-sea biomass hotspots. Recent global bathymetry data made available on Google-Earth (refer to §2f) indicate that there are 660 or more submarine canyons cutting across the world's continental margins, excluding Antarctica (which exports little terrestrial organic material to the ocean) (figure 1 shows the first available map with submarine canyon distribution on continental and island margins worldwide; see electronic supplementary material, table S1, for canyon geographical coordinates). This suggests that globally there could be on the order of $0.15 \times 660 = 99$ deep-sea canyons harbouring biomass hotspots like the Kaikoura Canyon. Clearly, the role of submarine canyons as hotspots of benthic biomass and potential fisheries production in the deep sea merits further investigation, especially owing to the steadily increasing human footprint on deep-sea ecosystems (Smith *et al.* 2008).

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