Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system

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Abstract

Macrofaunal abundance, biomass, diversity and species assemblages within Scripps and La Jolla Submarine Canyons are compared with those on the nearby continental shelf and slope. Our primary objective was to examine the effect of detrital aggregates on infaunal communities within canyons. Two submarines, a remotely operated vehicle (ROV), and a Soutar box-corer were used to collect samples. Within the canyons, organic enrichment by macrophyte detritus was evident from canyon heads down to 550 m, and evidence of strong currents (coarse sediment) was found down to 700 m. Infaunal density and biomass were higher in the canyons than outside at all depths where comparative data were available (100–500 m). Infaunal assemblages in canyons were distinct from those at reference stations. Both the canyon and non-canyons samples showed community differentiation with depth. Species diversity was generally high, but decreased with depth outside of canyons and increased with depth within the canyons. Low diversity at shallow depths within the canyon is attributed to a combination of organic enrichment and physical disturbance. Submarine canyons are commonly found to contain distinct species assemblages or higher faunal densities and/or biomass than nearby non-canyon regions at similar depths. Canyons are regular features along most ocean margins and appear to be important as sites of enhanced secondary production, provide diverse habitats, and act as conduits of coastal detritus to the deep-sea. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

Studies of natural organic enrichment of the sea floor have typically focused on the effects of small, discrete patches or large regions of high productivity. On scales

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< 1 m, patches enriched with macroalgae or phytodetritus have been shown to contain different species assemblages (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1992; Smith, 1994) and sometimes higher densities than the surrounding sediments (Snelgrove et al., 1994). Carcasses of oceanic nekton are detected and quickly consumed by widely foraging scavengers (Stockton and DeLaca, 1982) including peracarids, decapods, echinoderms, and fishes (Dayton and Hessler, 1972; Hessler et al., 1978; Lampitt et al., 1983; Priede et al., 1991). Rapid consumption of carcasses may prevent significant local enrichment (Rice and Lambshead, 1994), but these food-falls can still disturb macrofaunal invertebrates (Smith, 1986) and may be important sources of carbon for the benthos (Smith, 1985). Taken together, small-scale patches of organic enrichment apparently help maintain high diversity in the deep-sea benthos (Stockton and DeLaca, 1982; Grassle and Morse-Porteous, 1987; Lambshead and Gooday, 1990; Rice and Lambshead, 1994; Gage, 1996).

On scales of hundreds of kilometers, studies have focused on the effects of high primary productivity on the benthos (Dayton and Oliver, 1977; Rosenberg et al., 1983; Tarazona et al., 1988; Schaff et al., 1992), while at intermediate scales (kms to tens of kms) enrichment through increased local deposition of particulate organic matter has been demonstrated (Levin et al., 1994). Our interest is in regions of the sea floor likely to be enriched on scales of kms to tens of kms through the horizontal advection of detritus along the sea floor. Numerous studies of isolated detrital parcels demonstrate that these patches can be sites of elevated biological activity (Turner, 1973, 1977; Wolff, 1976, 1979; Rowe and Staresinic, 1979; Lawson et al., 1993; Young et al., 1993; Vetter and Dayton, submitted). Here we investigate submarine canyons as regions with unusually large concentrations of macrophyte-detritus (Josselyn et al., 1983; Okey, 1993; Vetter, 1995a; Harrold et al., in press) and provide evidence that conditions in canyons can lead to widespread organic enrichment.

Submarine canyons are among the most spectacular features found along continental shelves and slopes, and play an important role in the transport of sediments and organic matter from the shore to deep basins (Shepard, 1951, 1961; Heezen et al., 1955). Once in canyons, materials are transported deeper through resuspension by tidal currents and by violent episodic events including slumps and turbidity flows (Bouma, 1965; Shepard, 1973; Gardner, 1989), which have been measured with sustained speeds of 1.9 m s^{-1} in Scripps Canyon (Inman, 1970; Inman et al., 1976). Disturbances from periodically intense currents, debris transport, sediment slumps and turbidity flows (Inman et al., 1976) are more likely to affect animals in canyons than in typical shelf and slope environments. Canyons may also accumulate and transport detritus; therefore, much of the organic carbon available to canyon benthos may arrive as flow along the sea floor rather than from the "rain of detritus" (Agassiz, 1888) from surface waters.

Canyon consumers potentially experience enhanced food supply through several mechanisms: suspension feeders may benefit from accelerated currents (Rowe, 1971; Shepard et al., 1974); demersal planktivores may exploit dense layers of krill and zooplankton that become concentrated in canyons during downward vertical migrations (Greene et al., 1988), and food for detritivores may be increased by high sedimentation rates in canyons not actively transporting sediment (Rowe et al., 1982)

or through accumulation of macrophyte-detritus (Okey, 1993; Vetter, 1994, 1995b; Harrold et al., in press).

In this study, we focused on enrichment within the La Jolla Submarine Canyon and its major tributary, Scripps Canyon (Southern California). The floor of Scripps Canyon from 15 m to beyond 60 m is typically covered with a persistent mat of kelp (*Macrocystis pyrifera*) and surfgrass (*Phyllospadix* spp., *Zostera marina*) detritus (since at least 1952; Dill, 1964). The mat can support enormous densities, biomass and production of amphipod and leptostracan crustaceans, which at times achieve densities of over 3 million individuals per square meter, and with biomass exceeding 1 kg m^{-2} (dry weight) (Vetter, 1995a,b). Large numbers of fishes, many of which typically prey on plankton, mega-invertebrates and other fish, appear to routinely exploit the detritus-associated crustaceans (Vetter, in press).

Based on these observations and reports from other canyon systems, we hypothesized that: (1) large portions of the La Jolla and Scripps Canyon axis below 60 m are regularly covered with macrophyte detritus; (2) dense macroinvertebrate assemblages similar to those found above 60 m are present within detritus throughout the canyon; (3) even where there is not a persistent cover of detritus, canyon sediments are organically enriched relative to slope stations at equivalent depth and/or distance from shore, and support a high density and biomass of infauna, and (4) fish abundance is positively correlated with detritus and its associated macrofauna, suggesting that the high secondary production within the canyon results in increased fish production. The presence of large amounts of macrophyte detritus, and increased abundance of megafauna and their relationship to detritus within the canyon are discussed in another paper (Vetter and Dayton, submitted). Here we are primarily concerned with the macrobenthos and sediments on the canyon floor.

We compared the density, biomass, and species composition and diversity of macrofauna from the canyon and reference stations at depths between 100 and 500 m. The reference (non-canyon) stations were located off the coast of Del Mar, 5–10 km north of the canyon. This study provides clear, though circumstantial, evidence that enhanced macrophyte deposition in submarine canyons leads to significantly increased production of macrofaunal invertebrates. Differences in macrofaunal communities found here are probably attributable to enrichment by macrophyte detritus, increased incidence and intensity of disturbance, and sandy sediments in the canyon.

2. Study site

The La Jolla submarine canyon system rises from a water depth of 1000 to 20 m over a distance of ∼ 40 km. It has steeply sloping, sediment-covered sides with rocky outcrops down to about 100 m, and steep rock walls from 100 to 350 m. At greater depths the sediment-covered walls have few exposed rocks, and it is more appropriately called the La Jolla Fan Valley. At 290 m, Scripps Canyon branches off La Jolla Canyon and ascends to the northeast into the surf-zone over ∼ 2.7 km. Because of sand-fill Scripps Canyon is usually first visible at a depth of 15 m. Scripps Canyon

possesses vertical walls for its entire length (see Crowell, 1952; Chamberlain, 1964; Shepard et al., 1964; Shepard and Dill, 1966).

3. Materials and methods

Infauna samples were collected in July and August 1995 from the La Jolla submarine canyon system (117°15′–117°19′W, 32°52′–32°54′N) and a nearby reference site located about 5 km to the north of the canyon (117°21′–117°23′W, 32°54′–32°57′N) at depths ranging between 100 and 550 m (Fig. 1). Samples also were collected from the canyon at 700 m (117°26′W, 32°55′N) and 900 m (117°34′W, 32°51′N). Four types of sediment samplers were used. On 12 July the reference site at 300 and 500 m was sampled from the R/V R. G. Sproul with a Soutar box-corer (subcores 100 cm^2). From 10–16th August the submersibles *Sea Cliff* and the *Advanced Tethered Vehicle* (ATV,
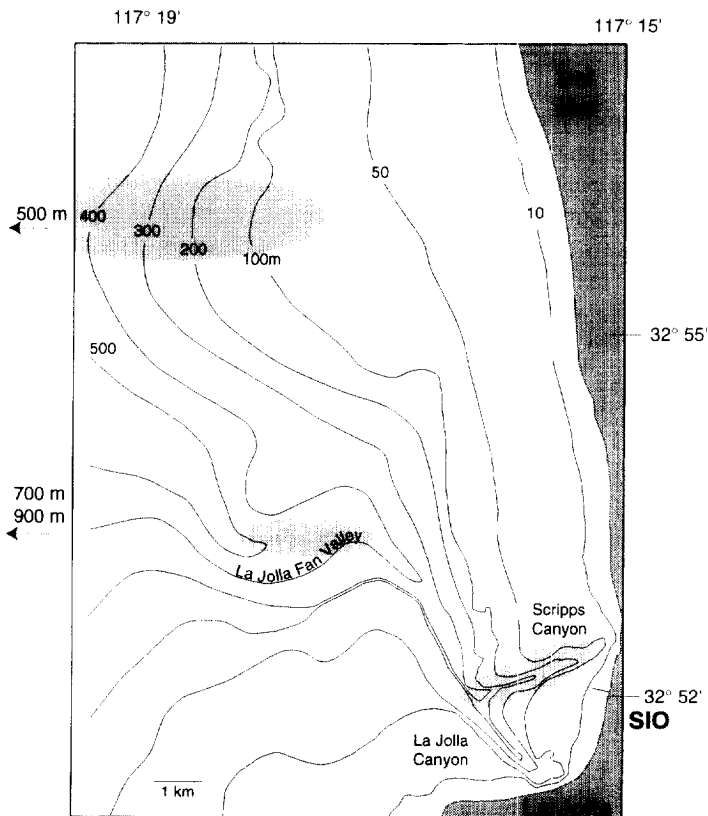

Fig. 1. Southern California coastline from Del Mar to Pt. La Jolla. Shaded regions indicate study areas. The Del Mar 500 m, and La Jolla Canyon 700 and 900 m sites are not shown. The approximate location of Scripps Institution of Oceanography and the SIO pier are shown.

Table 1
Type and number of cores collected at each site

Location	Depth (m)	Soutar cores	Eckman cores	Tube cores	Delta samples
Del Mar	100				4
	200				5
	300	5	3	11	1
	500	5	3	12	
Canyon	100				8
	200				7
	280				4
	310		7	24	
	500		17	45	
	700		2	5	
	900		2	5	

a remotely operated vehicle) were used to collect Ekman cores (20.3 × 20.3 cm) and cylindrical tube cores (7 cm diam.) from canyon and reference sites at depths between 300 and 900 m (Table 1). Coarse sediment within the canyon often limited penetration of the box cores to 5–6 cm.

Tube cores were taken within 2 m of each Ekman core site for CHN and sediment grain size analyses. A 5 l Niskin bottle carried on the submersibles and the Soutar box-corer collected bottom water samples for oxygen analyses. Water samples were taken upon arrival at the sea floor and were preserved on deck for Winkler titration. Macrophyte detritus was collected with the submersible's manipulator arm and placed in a PVC box.

The submersible *Delta* was used to sample sediments at canyon and reference sites from 100 to 280 m (28–31 August 95). Sediments were sampled using a suction device (slurp-gun) to remove the first 4 cm of material from circular 0.1 m² quadrats. The suction device emptied into a 300 μm mesh bag suspended from the submersible.

See Fig. 2 for sample sizes, and area sampled for infaunal analysis.

3.1. Sample processing and preservation

Subcores (100 cm²) from Soutar and Ekman-style box cores were sectioned vertically for infaunal analyses, yielding 0–2, 3–4, 5–6, and 7–11 cm fractions. Only the top 4 cm was preserved from the Ekman cores that penetrated ⩽ 6 cm into the sediment. All samples were live-sieved through a 300 μm screen on board ship, preserved in 10% buffered formalin, and stained with Rose Bengal to aid sorting. Samples were transferred to 70% ethanol within two weeks of collection. Infauna were sorted from the top 4 cm of core samples at 12–50 × magnification using a dissecting microscope.

Biomass of samples sorted to phylum were weighed using a Sartorius analytical balance. The ethanol-preserved animals were spread out on a GF/C glass fiber filter, blotted dry and left on the filter with strong suction for 1 min before weighing. This
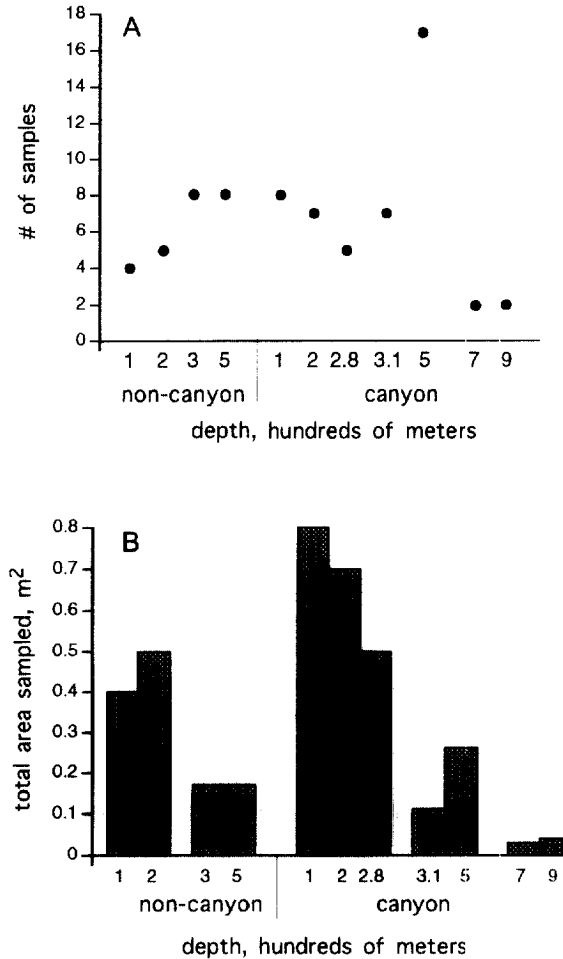
Fig. 2. Number of samples taken (A), and area sampled (B) at each station.

method removed nearly all ethanol from the surface of the animals and the filter prior to weighing. Filter weight was determined after the animals were removed.

CHN analyses were performed on the top 4 cm of sediment from canyon and non-canyon stations at 300 and 500 m. Prior to CHN analysis (Perkin–Elmer 2400 CHN elemental analyzer) sediments were dried for 2 days at 50°C, homogenized by grinding, and acidified with HCl to remove carbonates. Samples were frozen ($\leqslant -20$°C) prior to processing.

Sediment grain size analysis was performed on samples from 300 and 500 m both in and out of the canyon, and from 700 and 900 m in the canyon. The top 4 cm of sediment from each sample was dried for 72 h at 60°C and mechanically shaken for 20 min through a series of 12 geological sieves, each fraction was then weighed using an analytical balance.

3.2. Statistical analysis

Statistical comparisons for infaunal biomass and density (ANOVA) were carried out using SYSTAT (V 5.1). Because different samplers were used at shallow (100–280 m) and deep (300–900 m) stations, separate tests were used to compare values from each depth. Community analysis (classification and ordination) and diversity indices were run using PRIMER (Warwick and Clarke, 1991). Species present in 10 or more cores were used in the hierarchical cluster analysis, producing a Bray–Curtis similarity matrix (Bray and Curtis, 1957). Prior to analysis, data were fourth-root-transformed to allow all species to contribute to similarity, while still giving the most common species greater weight (Warwick, 1993). Non-metric multi-dimensional scaling (MDS, stress = 0.17, Kruskal and Wish, 1978; Clarke, 1993) was used for sample ordination.

The Shannon–Wiener diversity index (H') and Pielou's evenness index (J') were calculated. Rarefaction data were obtained using Hurlbert's (1971) modification of Sanders (1968) technique.

4. Results

4.1. Physical features

4.1.1. Scripps Canyon
The floor of the canyon from 90 m to its base at 290 m was flat and covered with sand, detritus, and occasionally rocks and boulders. In some areas it descended in steps up to 1.5 m high. From 240 to 250 m, evidence of rapid down-canyon currents was observed: the canyon floor consisted of coarse sand with few ripples, the sand sloped up slightly towards the walls, and the bottom was littered with highly friable sedimentary rocks with trails of darker sediment (matching the rocks) extending down-canyon. The canyon width varied from ~ 7 to 20 m. From 100 to 250 m, the width of the floor frequently narrowed dramatically, although on horizontal scales larger than 100 m, the canyon widened as it descended. Vertical rock walls with overhangs and deep crevices were present throughout the canyon, and the walls often extended upward > 80 m before grading into a steep sandy slope. Scripps Canyon has been described in detail by Shepard et al. (1964).

4.1.2. La Jolla Canyon
The walls near the canyon floor often had gentle slopes; however, they eventually steepened, in places having slopes exceeding 70°. Rock walls were not observed, and rocky outcrops were rare below 450 m. From 450 to 550 m the canyon floor was flat and at times exceeded 300 m in width. The canyon axis was difficult to locate at times owing to the presence of terraces with troughs and levies. Large crevasses (up to 2 m wide) in semi-consolidated sediments were seen on several terraces. Evidence of some canyon properties may have been biased by samples collected from gently sloping regions at the base of the walls and terraces, which apparently experienced less intense

currents and enrichment by macrophyte detritus. Detritus patches were usually common on the sea floor when we were confident that we were near the canyon axis. Fewer small-scale sediment features (especially urchin tracks) were seen in the canyon than at the Del Mar reference sites. This may have been due to more rapid sediment erosion by strong canyon currents.

4.1.3. Del Mar reference area

The shelf and slope floors at our non-canyon area off Del Mar were largely devoid of physical features at scales greater than 10 cm. Two exceptions were encountered; a patch of cobbles from 95 to 105 m, and a series of sediment ripples at a depth of 200 m. The ripples covered a distance of ~ 40 m, had an amplitude of ~ 1 m, a wavelength of ~ 6 m, and were oriented with crests normal to the 200 m isobath. At smaller scales, biogenic sedimentary features were abundant, with tracks of the heart urchin *Brissopsis pacifica* the most conspicuous; centimeter-scale mounds, depressions and holes were also common. Urchins were much more abundant at the Del Mar reference area than in the canyons at all depths (Vetter and Dayton, submitted).

4.1.4. Sediment grain size

Silt made up only about 4% of the canyon floor sediments at 300, 500 and 700 m (Fig. 3). Off Del Mar, deep in La Jolla Canyon, and at the base of the sloping canyon walls ("canyon edge") the sediments were composed of nearly 40% silt and clay.
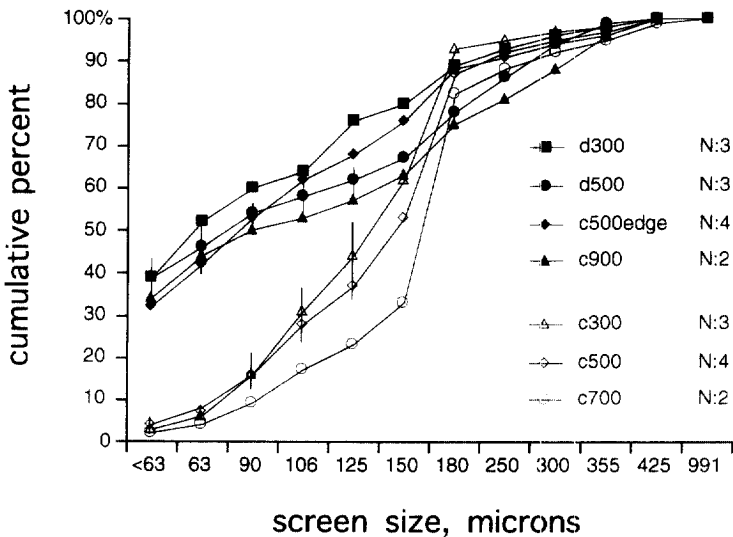

Fig. 3. Sediment grain size. Average percentage of sediments retained on each of 12 screen sizes. Legend identifies location (d = Del Mar, non-canyon; c = La Jolla Canyon), depth in meters, and sample size. Vertical bars show the range in values for the coarsest non-canyon sample (d500) and the least course sample from the lower group (c300). Those ranges show typical variability, others are not shown to avoid clutter.

Canyon sediments from 900 m were very similar to those found outside of the canyons.

4.1.5. Sedimentary CHN

The lowest value for sediment organic carbon (0.4%) was found in the canyon at 300 m. At 500 m, canyon organic carbon increased to just over 2%. Outside the canyons, carbon values increased from 2.6% at 300 m to 3.5% at 500 m. Nitrogen and C–N ratios did not vary consistently between canyon and non-canyon stations (Table 2).

4.1.6. Oxygen

Oxygen concentration was lowest at the non-canyon 500 m (0.74 ml/l, $n = 7$, S.D. $= 0.17$) and the Canyon 900 m (0.45 ml/l, $n = 1$) stations. At 300 m, values were similar in (1.39 ml/l, $n = 2$, S.D. $= 0.07$) and out (1.15, $n = 6$, S.D. $= 0.09$) of the canyon. Oxygen concentrations were highly variable at the canyon 500 m station, averaging 1.37 ml/l, but ranging between 0.5 and 2.1 ml/l ($n = 7$, S.D. $= 0.62$), probably resulting from tidal oscillations of the oxygen minimum zone within the canyon.

4.1.7. Infauna

Of the 435 resolvable species 68% were to identified species, 20% to genus, and 8% to family (many were undescribed). Nearly half of the species identified were found both in the canyon and off Del Mar (Table 3).

From 100 to 280 m, a circular quadrate and slurp-gun were used and from 300 to 900 m, Eckman and Soutar Box corers were used. We believe that all of these devices took excellent samples that can be compared across platform; however, we provide the following caveats. When using the slurp gun we may have lost some of the smallest polychaetes (*Cossura* sp., *Nephtys cornuta*, and juveniles of several species including *Capitella* cf. *capitata*) as samples emptied into 300 μm mesh bags on the outside of the submarine. This may have resulted in an underestimation of infaunal density from 100 to 280 m. Loss of some of the smallest individuals would have had an imperceptible effect on biomass. Area sampled also varied slightly between samplers. In the worst case, the larger area sampled with the slurp gun (1000 cm^2) may have resulted in more

Table 2
Mean sediment organic carbon, hydrogen and nitrogen. CYN: La Jolla Canyon. DM: Del Mar (non-canyon). Standard error (SE) is provided for C and N values. N = number of replicates

	DM 300	DM 500	CYN 300	CYN 500
%carbon	2.55	3.53	0.41	2.141
%hydrogen	0.96	1.17	0.053	0.779
%nitrogen	0.27	0.373	0.05	0.209
C-SE	0.12	0.216	0.04	0.183
N-SE	0.02	0.023	0.006	0.019
C/N ratio	9.4	9.5	8.2	10.3
N	8	4	3	3

Table 3
Numbers of macrofauna taxa found exclusively in or out of the canyons

	Exclusively in canyons	Exclusively off Del Mar	Total
Species	168	67	435
Genera	112	36	294

Table 4
Summary of ANOVA results for macrofaunal biomass with canyon and non-canyon biomass (log transformed) as factors. Canyon data from 280 and 310 m are combined to form the 300 m value. Significance level is unaffected when the 280 m data are excluded

	DF	Mean square	F-ratio	P
500 m	1	1.21	12.83	0.002
Error	20	0.09		
300 m	1	3.72	49.88	< 0.000
Error	18	1.34		
200 m	1	2.08	15.24	0.004
Error	9	0.14		
100 m	1	0.86	7.93	0.017
Error	11	0.11		

effective sampling of rare species, potentially influencing estimates of diversity; however, this would not have affected the community analysis because only species that were found in at least 10 samples were included. Statistical tests were only evaluated between canyon and non-canyon samples at like depths.

Infaunal biomass (wet, alcohol preserved) was significantly greater inside than outside canyons at all depths examined (Table 4, Fig. 4). Biomass was strongly dominated by polychaete worms except in a few canyon cores at (a) 100 m where amphipod and leptostracans were abundant, and (b) 200 and 310 m in which echiurans contributed substantial biomass. The highest biomass was found at the 310 m canyon station where the polychaetes *Pectinaria californiensis, Capitella* cf. *capitata, Chloeia pinnata*, and the echiuran *Listriolobus pelodes* contributed most of the biomass. Biomass did not vary significantly with depth at the non-canyon stations, with larger average size of the animals at the nearshore sites offsetting the higher density at offshore sites (Fig. 5).

Infaunal density was significantly higher inside than outside canyons at all depth comparisons (Table 5, Fig. 5). Outside canyons, density peaked at 300 m (it is possible that some of the small polychaetes collected at the 100 and 200 slipped through the mesh bags, see above). From 100 to 310 m within the canyon, density declined but biomass increased (Figs. 4 and 5). The exceptionally high density at the 100 m canyon station was due in part to four samples containing small amounts of macrophyte detritus and harboring numerous amphipods and leptostracans. Crustaceans (mostly peracarids) were the dominant group both in and out of the canyon at 100 m;
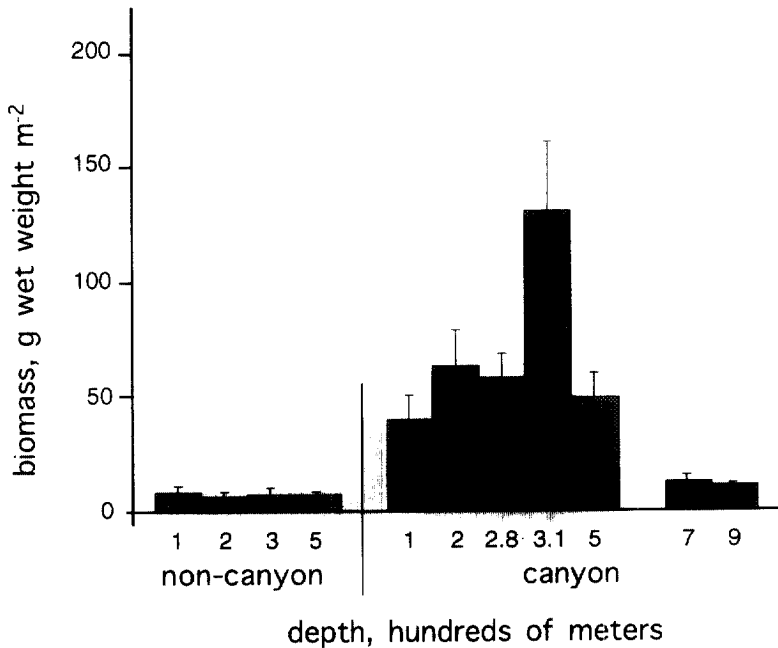
Fig. 4. Mean macrofaunal biomass (wet, ethanol preserved) in Scripps Canyon from 100 to 280 m, La Jolla Canyon from 300 to 900 m, and outside of the canyons from 100 to 500 m. Bars = 1 standard error.

polychaetes dominated at all other depths (Fig. 6). Molluscs, especially the scaphopod *Polyschides* sp. and the bivalves *Saturnia* sp. and *Thyasira flexuosa*, were abundant at 300 and 500 m in La Jolla Canyon. The bivalves *Saxicavella pacifica* and *Tellina carpenteri* were also abundant at 300 m, as were the gastropod *Astyris permodesta* and the bivalve *Dacrydium* sp. at 500 m.

Cluster analysis generally separated canyon from non-canyon stations after which stations clustered by depth (Fig. 7). There were three exceptions to these trends; (1) 100 m canyon samples containing some detritus and large numbers of crustaceans clustered apart from all others; (2) canyon 700 and 900 m cores clustered with the non-canyon cores; (3) canyon samples above 500 m clustering with samples from other (mostly adjacent) canyon depths. These patterns are more easily visualized using multi-dimensional scaling (MDS, Fig. 8). Values on the dendrogram (Fig. 7) can be used to identify clusters at a higher or lower Bray–Curtis similarity level on the MDS plot. For example, all of the non-canyon 100 and 200 m stations clustered at the 40% similarity level, and all of the canyon 280 m stations clustered at the 60% level.

The average densities by location and depth of some of the most important species responsible for these patterns (determined by the PRIMER subprogram SIMPER) are shown in Figs. 9 and 10. *Nebalia* sp. and *Orchomene limodes* (Fig. 9a) also were abundant in non-quantitative samples of detritus from scuba depths to ~ 170 m in
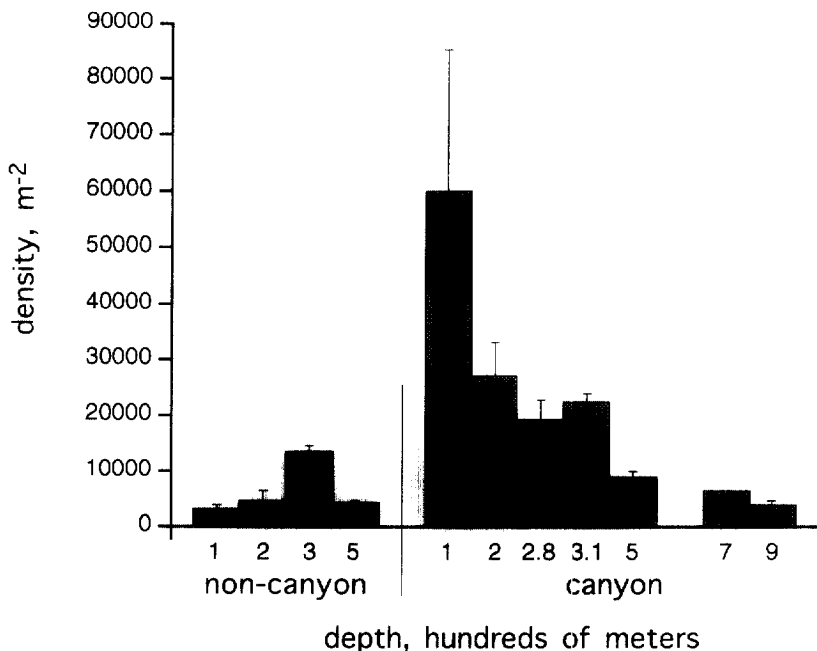
Fig. 5. Mean macrofaunal density in Scripps Canyon from 100 to 280 m. La Jolla Canyon from 300 to 900 m, and outside of the canyons from 100 to 500 m. Bars = 1 standard error.

Table 5
Summary of ANOVA results for macrofaunal density with canyon and non-canyon abundance (log transformed) as factors. Canyon data from 280 and 310 m are combined to form the 300 m value. Significance level is unaffected when the 280 m data are excluded

	DF	Mean square	F-ratio	P
500 m	1	0.409	7.69	0.011
Error	22	0.05		
300 m	1	0.13	10.47	0.005
Error	18	0.01		
200 m	1	1.92	10.84	0.008
Error	10	0.18		
100 m	1	3.22	22.40	< 0.000
Error	12	0.14		

Scripps Canyon. Other general patterns included greater abundances of tanaids (crustaceans), and maldanid, paraonid and cirratulid polychaetes off Del Mar, and more phyllodocid polychaetes in the canyons.

The total number of species at a given depth varied little between canyon and non-canyon stations (Fig. 11A); however, the Shannon–Wiener diversity index (H')
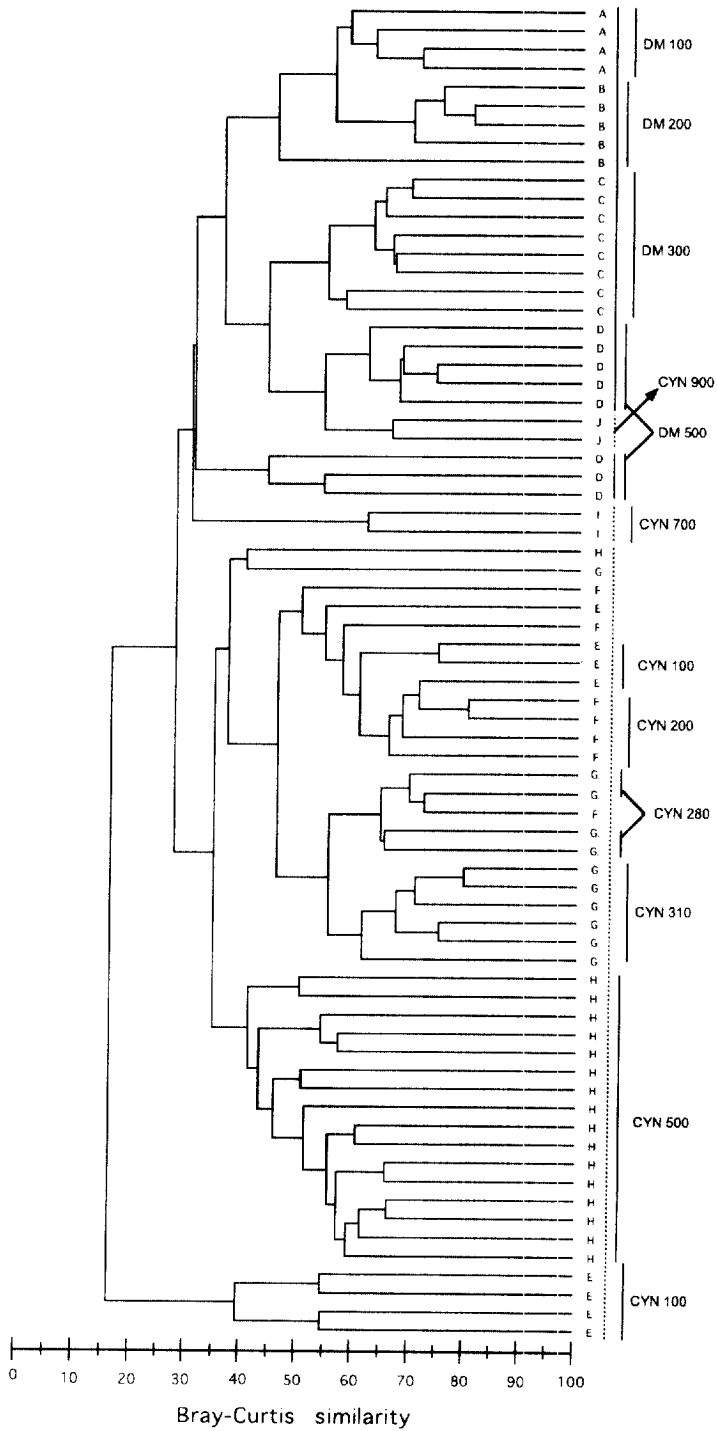
Non-Canyon   Canyon

density (m²)
Del Mar/
Canyon

100 m   3,200
59,900

200 m   4,400
27,000

300 m   13,600
21,200

500 m   4,000
8,900

Canyon 700 m   Canyon 900 m

polychaete
crustacean
mollusc
other

6,300   4,000
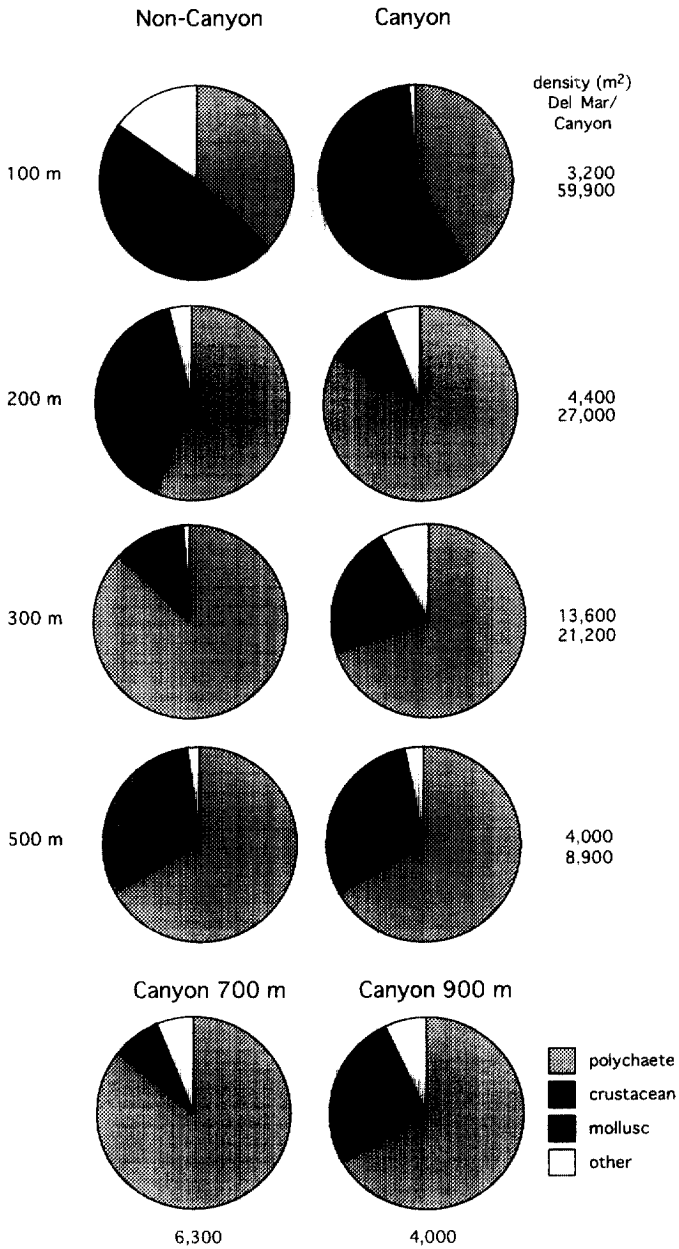
Fig. 6. Mean proportions of polychaete worms, crustaceans, molluscs and other taxa at each station. The canyon 280 and 310 m stations are combined to form the canyon 300 m chart. Macrofaunal densities (m²) are provided to the right (100–500 m) or below (700, 900 m) the charts.

Bray-Curtis similarity
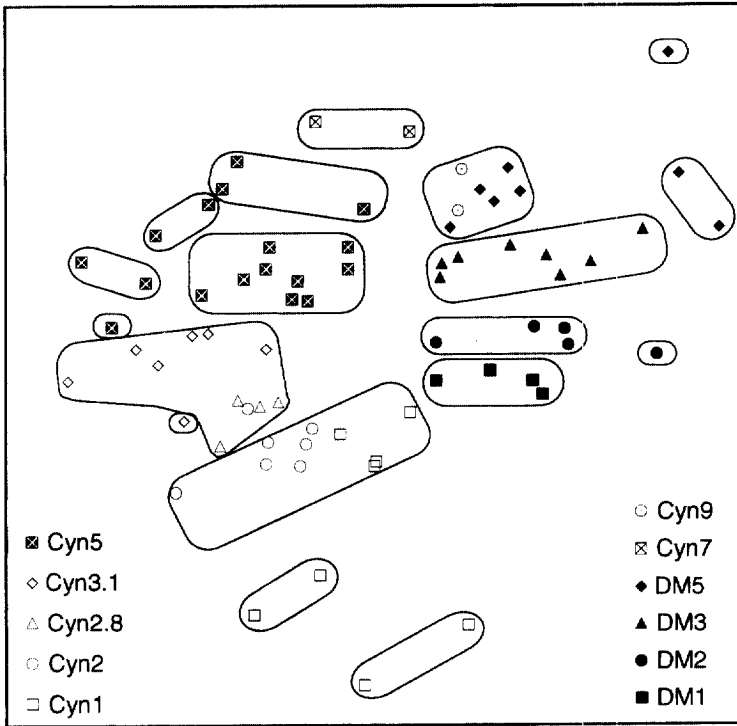
Fig. 8. Multi-dimensional scaling (MDS) ordination. Symbols represent individual cores. Lines enclose cores that cluster at the Bray–Curtis 50% similarity index or higher. Symbol identification: Cyn = canyon, DM = Del Mar. # = depth in hundreds of meters.

was significantly higher ($P < 0.001$) for the inshore non-canyon sites (100–200 m, Fig. 11B). This difference was driven by high dominance by *Capitella* cf. *capitata* and other species at the inshore canyon stations (Fig. 11C). These comparisons may be confounded by the variability in number of samples and area sampled between stations (Fig. 2). Rarefaction curves (Sanders, 1968; Hurlbert, 1971) were developed to deal with this problem; however, they may overestimate the number of species present when species distributions deviate strongly from random (Fager, 1972; Simberloff, 1979) as is true for this study. Two rarefaction plots are provided because of the large number of individuals sampled at 100, 200 and 280 m in the canyon. The rarefaction patterns are in general agreement with the H' values, with the non-canyon 100 m

Fig. 7. Dendrogram for hierarchical clustering of cores from all stations based on Bray–Curtis similarities. Non-canyon (DM) samples have a solid line next to them. Stations are indicated by letters. Letters indicate station locations: A–D Non-canyon 100, 200, 300 and 500 m. E canyon 100 m, F canyon 200 m, G. canyon 280 m, G canyon 310 m, H–J canyon 500, 700 and 900 m. Cyn = canyon, DM (Del Mar) = non-canyon.
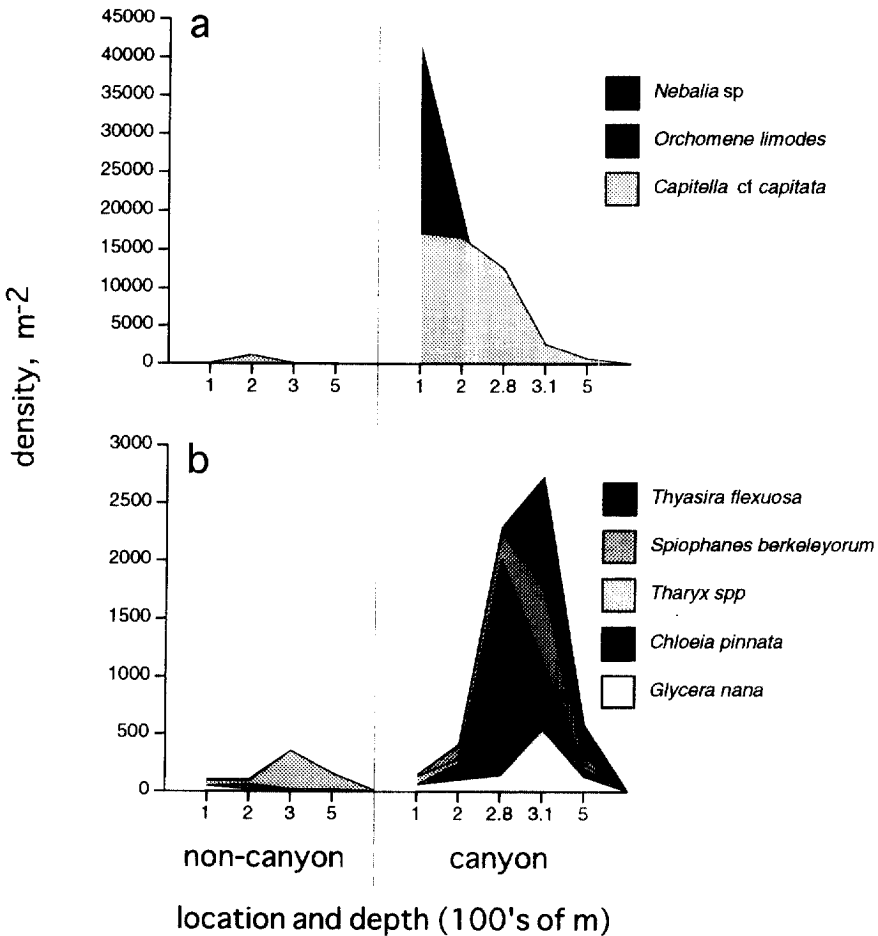
Fig. 9. Average density (cumulative) of various taxa at non-canyon (Del Mar) depths of 100, 200, 300 and 500 m, and canyon depths of 100, 200, 280, 310, and 500 m. *Nebalia* spp. – leptostracan crustacean, *Orchomene limodes* – amphipod, *Thyasira flexuosa* – bivalve (with bacterial symbionts), the remainder are polychaete worms.

station rising most abruptly, followed by non-canyon 200 and 500 m and canyon 500 m stations (Figs. 12 and 13). The estimated number of species at 100 individuals, $(E)100$, was higher than expected based on H' values for the 200, 280, and 700 m canyon stations, and it was lower than expected for the 310 m canyon station (Fig. 14). Even though the 100 m canyon rarefaction curve has the shallowest slope, the large area sampled and large number of individuals collected led to the second highest species count (Fig. 13).

We observed some inhabitants of detrital patches with video and collections made with the submersibles' manipulator. The video revealed large numbers of amphipods
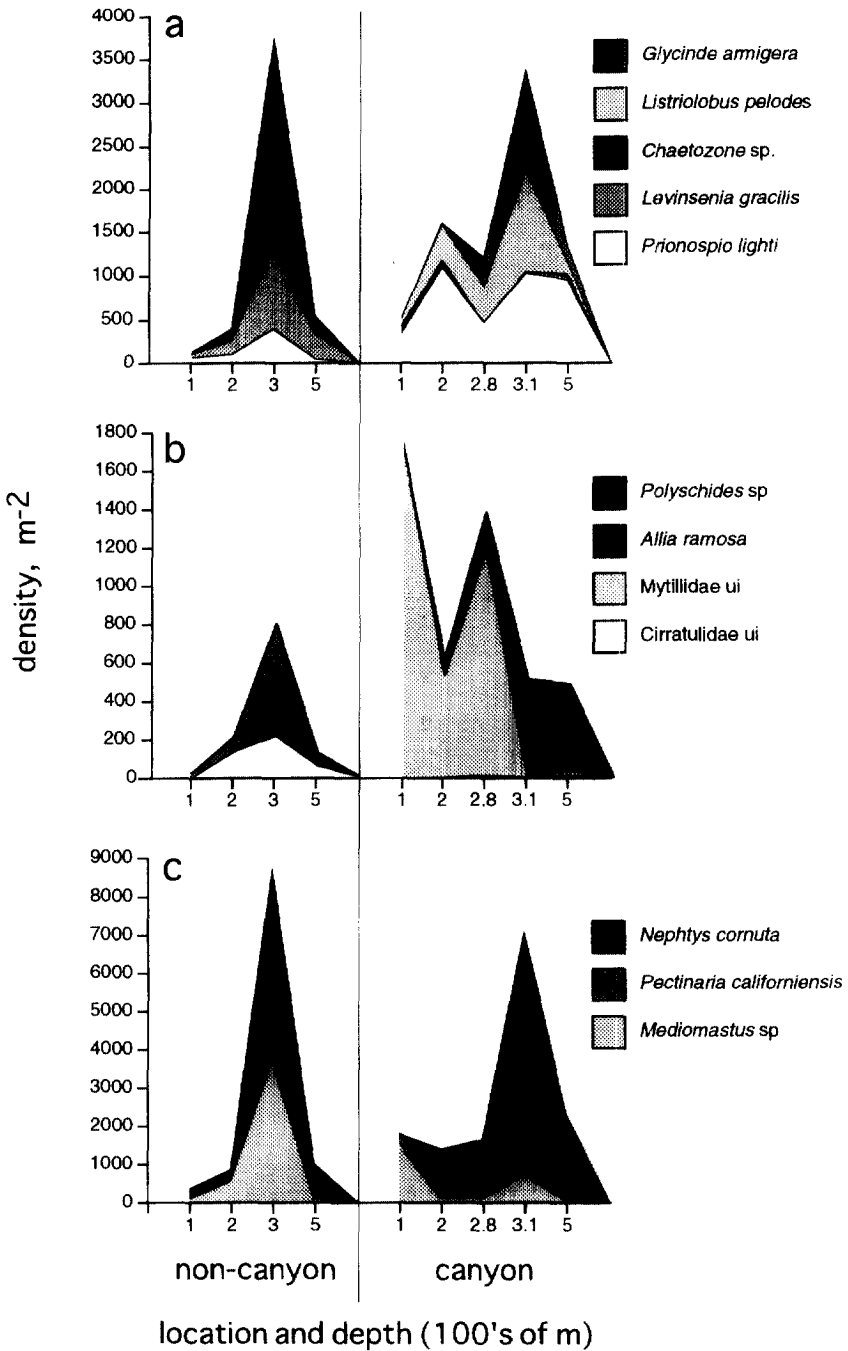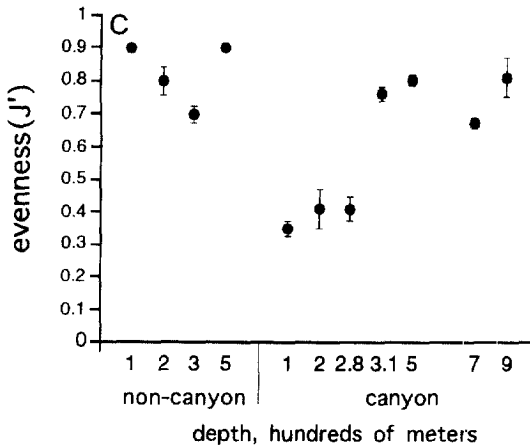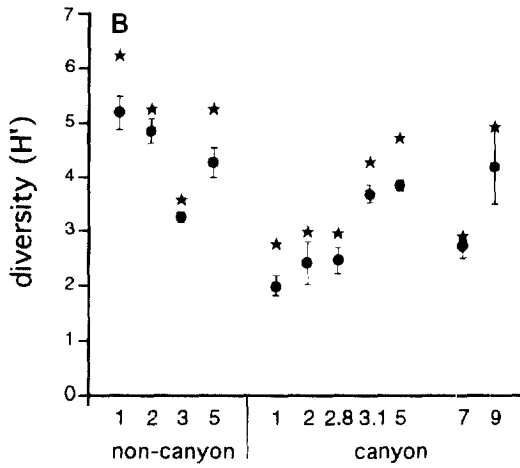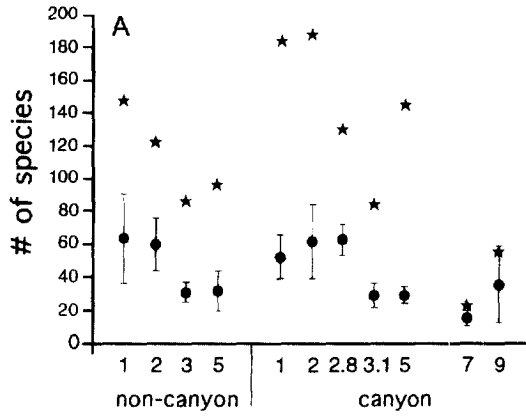
Fig. 10. Average density (cumulative) of various taxa at non-canyon (Del Mar) depths of 100, 200, 300 and 500 m, and canyon depths of 100, 200, 280, 310 and 500 m. *Listriolobus pelodes* – echiuran, *Polyschides* sp. – scaphopod, Mytillidae – bivalve, the remainder are polychaete worms.
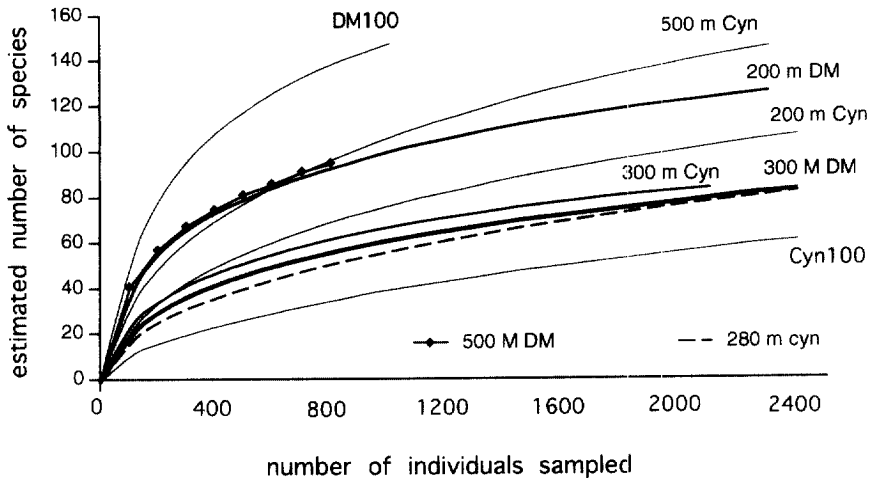
depth, hundreds of meters

Fig. 12. Rarefaction estimates of species richness of all fauna, all stations. The three shallow canyon stations (100, 200, and 280 m) extend beyond the maximum number of individuals on this figure. Cyn = canyon stations, DM (Del Mar) = non-canyon stations.

on the surface of some detrital aggregates, which were sometimes so numerous that they obscured the detritus with their bodies. Examination of detritus revealed consistently large numbers of polychaetes (especially scale worms and *Chloeia pinnata*) and occasionally amphipods and bivalves. One manipulator grab of detritus contained over 300 scale worms (mostly polynoid polychaetes) and probably represented a sample of less than 1/50 m².

5. Discussion

In a concurrent investigation we found large areas of the axis of the Scripps/La Jolla Canyon system covered by kelp and surfgrass detritus (Vetter and Dayton, submitted). The mats of macrophyte detritus were commonly 7–15 cm thick and ranged in size from < 1 to > 30 m² in area. Detrital cover on the canyons floor decreased with depth from 100% (65 m) to 11% (280 m) in Scripps canyon, and from 13% (300 m) to 5% (500 m) in La Jolla Canyon. Macrophyte detritus was virtually absent at our non-canyon sites. It is inappropriate to refer to these detrital aggregates as "food-falls"

Fig. 11. (A) Average per core and total (stars) number of resolvable taxa (most identified to genus or species) at each station. (B) Average and pooled (stars) Shannon–Wiener diversity at each station. (C) Average of Pielou's evenness index at each station. Error bars are one standard error. Core size: 100–280 m stations – 0.1 m², 300–900 m stations – 0.01 m². Average values are for 1000 cm² samples from 100 to 280 m and 100 cm² samples from 300 to 900 m. For areas sampled for pooled data see Fig 2.
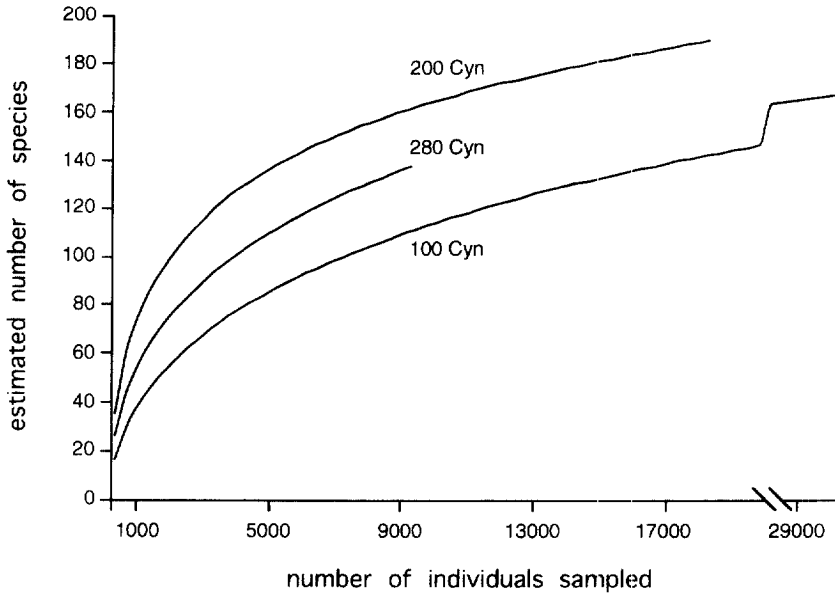
Fig. 13. Rarefaction estimates of diversity of all fauna for canyon stations with high infaunal density and large area sampled. Note the change in scale.
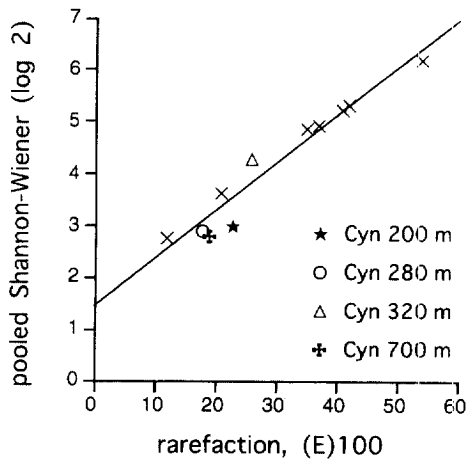

Fig. 14. Relationship of Shannon Wiener diversity (Log base 2) to estimated species number at 100 individuals, $(E)100$, by rarefaction. $R^2 = 93.5$. Cyn = canyon.

because they arrive predominantly by horizontal movement along the sea floor rather than by sinking through the water column.

The increased density and biomass of infaunal invertebrates within the canyons provide good circumstantial evidence for organic enrichment. The low organic carbon

values in canyon sediments (Table 2) suggest that the enrichment is not by particulate matter in the sediment, but by the abundant macro-detritus on the sediment surface. Stable carbon isotope analysis provided direct evidence of the importance of the macrophyte detritus in the diet of canyon macrofauna. The $\delta^{13}C$ of canyon infauna resembled that of detrital kelp and surfgrass, while animals from non-canyon samples more closely resembled carbon from particulate organic matter collected from surface waters (Vetter and Dayton, unpublished data). Incorporation of organic matter into the sediment may be reduced by winnowing of fine, organic-rich materials by strong currents (Bouma, 1965).

The intensity of organic enrichment within Scripps and La Jolla canyons was demonstrated by large numbers of two species that have been reported from heavily polluted sediments in Southern California. The echiuran *Listriolobus pelodes*, found at all canyon stations from 100 to 500 m and absent outside of canyons (Fig. 10a), has been periodically abundant off the Palos Verdes peninsula in sediments impacted by discharge from the Whites Point outfall (Stull et al., 1986; Maurer and Haydock, 1990). Even more significantly, the classic pollution indicator species, *Capitella* cf. *capitata* (Pearson and Rosenberg, 1978), attained high densities in the canyons (77,000 m^{-2} at 100 m, 27,000 m^{-2} at 200 m, 17,000 m^{-2} at 300 m and 3800 m^{-2} at 500 m). Further evidence of enrichment (or disturbance) was the low faunal diversity and evenness at several canyon depth stations (Fig. 11).

Large numbers of the bivalve *Thyasira flexuosa* in the canyons from 280 to 500 m in the canyons indicate the presence of hydrogen sulfide. Species of *Thyasira* contain endosymbiotic sulfur-oxidizing bacteria and are known from organic-rich sediments and cold seeps (Hartley, 1984; Schmaljohann et al., 1990; Dando et al., 1991, 1994). Within the canyons, the source of H$_2$S may be convergence of sedimentary pore-water flow-lines in the axis of the canyons bases (Orange and Breen, 1992) or anaerobic decomposition of buried detritus (Limbaugh and Shepard, 1957).

Macrofaunal densities in the canyon, though large (single sample maximum density of 240,000 m^{-2}), are not unprecedented. At slope depths, macrofaunal density of 55,482 m^{-2} (Schaff et al., 1992) and 53,000 (Blake et al., 1987) have been reported, and on the Santa Maria Basin shelf (California) macrofaunal densities sometimes exceed 30,000 m^{-2} (Hyland et al., 1991). Rowe et al. (1982) found elevated macrofaunal density and biomass from 200 to 570 m in Hudson Canyon and, as in the present study, found that the species composition of the slope surrounding the canyon was similar to canyon communities found much deeper. The Gulf of Maine deep-basin fauna at 300 m resembled the Hudson canyon fauna at 1100–1400 m (Rowe et al., 1982), and off Southern California, the Del Mar (non-canyon) fauna at 500 m closely resembled the La Jolla Canyon fauna at 900 m (Fig. 8).

Other investigations of deep-sea valleys, channels and trenches have reported enrichment by macrophyte detritus or land runoff, and higher than expected biomass or density of macrobenthos (Bruun, 1957; Vinogradova et al., 1974; Gage and Tyler, 1991; Gage et al., 1995). Griggs et al. (1969) reported that the benthic fauna in the Cascadia Channel (NW United States) was four times more abundant than on the adjacent Cascadia Abyssal plain, and concluded that terrestrial plant detritus was the likely cause. Large quantities of terrestrial and marine plant detritus also have been

recovered from trawl samples taken at hadal depths in the Puerto Rican trench (George and Higgins, 1979). Not all investigations have found enhanced density or biomass within canyons. Houston and Haedrich (1984) found no significant differences between abundance and biomass of macrofauna in and out of Carson Canyon (Grand Banks, Canada), and Maurer et al. (1994, 1995) found fewer macrofaunal invertebrates in Newport Canyon (Southern California) than in shelf stations at 60 m.

Local macrofaunal diversity was high at our non-canyon sites, with samples from depths of 100 m ($H' = 6.2$) approaching or exceeding the high diversity found by Grassle and Maciolek (1992) in the Western Atlantic (H': 6.6, 1500–2500 m), Hyland et al. (1991) in the Santa Maria Basin (H': 5.6, California, 90 m), Levin et al. (1991) in the East Pacific (H': 5.9, Volcano 7, 1500–3000 m), and Jumars (1974) in the San Diego Trough (H': 6.4, 1230 m, calculated by Levin and Gage, submitted). Within the canyon, high evenness (J') resulted in relatively high diversity (H') values at some stations, despite the presence of relatively few species (Fig. 11).

Pooling all cores by location and depth leads to an increase in diversity; however, the close agreement between H' and species richness (rarefaction) suggests that not all of the difference can be explained by simply increasing the area sampled (Fig. 14). Combining canyon and non-canyon samples has a less regular effect on H' and J', depressing them at shallow depths and sometimes increasing them at the deeper stations (Fig. 15). This depression of diversity at 100 and 200 m was due to strong dominance of species such as *Nebalia hessleri*, *N.* sp., *Orchomene limodes*, *Capitella* cf. *capitata*, *Pectinaria californiensis* and *Chloeia pinnata* at the canyon stations (Figs. 9 and 10), combined with the larger area sampled in the canyon (Fig. 12). *Pectinaria californiensis* and *C. pinnata* were also among the four most common taxa found by Hartman (1963) in a survey of 11 southern California submarine canyons (nine of which were reported to contain macrophyte detritus).

The increase of diversity with depth within the canyons is probably attributable to the concurrent decrease in detritus cover. At 500 m in La Jolla Canyon, the relatively high diversity was probably facilitated by the presence of relatively few, but highly discrete, enriched patches (Grassle and Morse-Porteous, 1987). However, at that same depth, physical disturbance (strong currents, turbidity currents, detritus transport, etc.) may have kept diversity from being even higher (Gage et al., 1995). The depression of diversity at 700 m may be attributed to disturbance by strong currents (inferred by coarse sediments) in the virtual absence of patches of organic enrichment (Vetter and Dayton, submitted).

High macrofaunal density and dominance by opportunistic species have been observed in both naturally and artificially enriched plots on cm to m scales (Pearson and Rosenberg, 1978; Levin, 1986; Grassle and Morse-Porteous, 1987; Ritz et al., 1989; Weston, 1990; Snelgrove et al., 1992; also see Gooday and Turley, 1990), and from tens to hundreds of km in regions which experience high organic C flux to the sea

Fig. 15. Diversity indices as a function of depth for pooled canyon and non-canyon samples (open circles) and non-canyon samples alone (stars): (A) total number of species; (B) Shannon–Wiener diversity; (C) Pielou's evenness index.
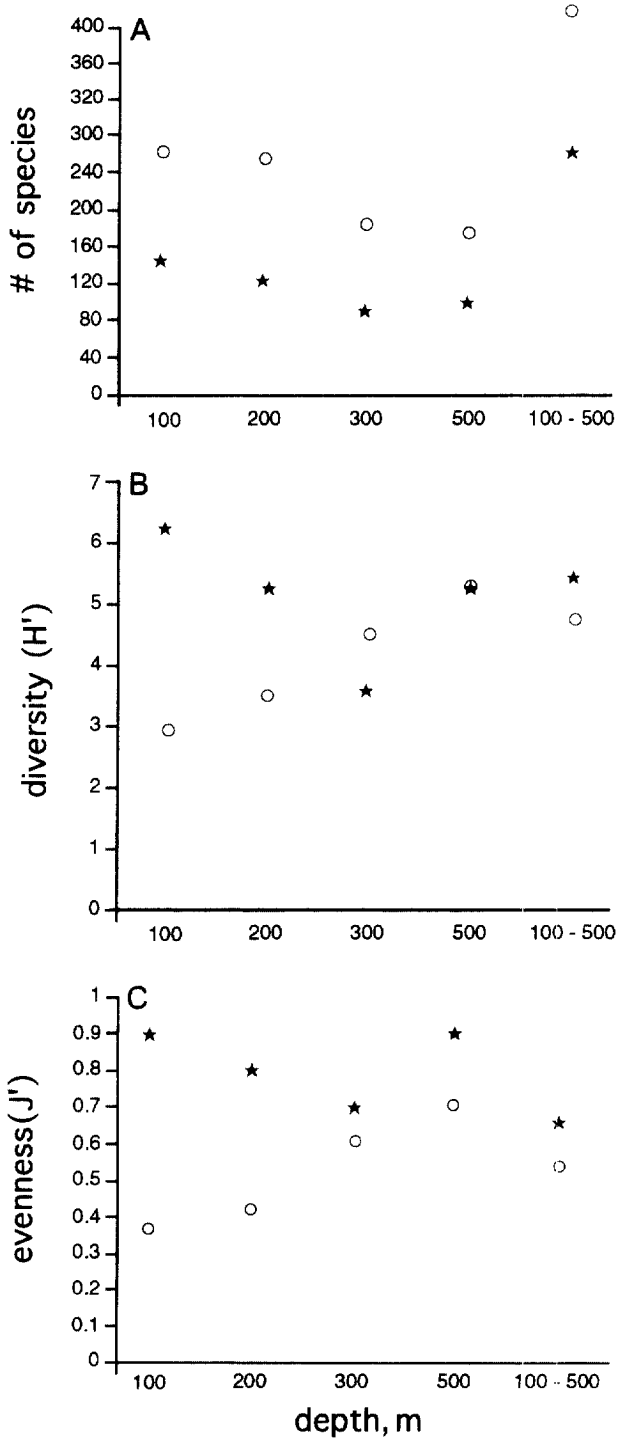
floor (Schaff et al., 1992; Levin et al., 1994). Despite low diversity within enriched patches, the presence of enriched or otherwise disturbed patches on a background of low productivity may be an important contributor to deep-sea β diversity (Dayton and Hessler, 1972; Grassle and Morse-Porteous, 1987).

The reduction of H' and J' when samples from the canyon are included with those from Del Mar (at 100 and 200 m, Fig. 15) reveals a potential problem with these indices. Relatively few samples are generally taken in deep-sea studies, and if an enriched patch is sampled, large numbers of opportunistic species in a single core could drive H' and $E(100)$ values down precipitously, as the total number of species increases.

Canyons originating in shallow water will accumulate and transport more bedload material from longshore transport than offshore canyons (Monaco et al., 1990). Furthermore, the organic content of that material should be greater in productive nearshore waters. However, even canyons receiving large amounts of POM may contain organically impoverished sediments if strong currents prevent the settlement of fine particulate matter. The most likely canyons to experience high levels of organic loading are those near marine macrophyte communities such as kelp forests, seagrass beds and estuaries. La Jolla and Scripps Canyons contain coarse grain sediments with low organic input, but this is offset by the large input of macrophyte detritus.

The intensity of sediment disturbance and enrichment is likely to vary with depth in canyons. Disturbance generally decreases with depth, but attenuation of enrichment should be greater because of consumption and decomposition of detritus, and widening of the canyon floor. Thus, it is not surprising that Gage et al. (1995) were particularly concerned with disturbance in their investigation of the macrobenthic community at the lower end of Setubal Canyon (Portugal, 3400 m), while we focused on enrichment effects in relatively shallow water (100–500 m).

Gage et al. (1995) found that the macrobenthos within Setubal Canyon was strikingly different from that on the Tagus Abyssal Plain (~ 150 km east of the canyon sites). Like the present study, they found the macrobenthos to be much more abundant in the canyon, and found higher species diversity and evenness at the non-canyon site. They reported the frequent presence of seagrass fragments in their canyon cores, and suggested that enhanced detrital input from shallow water may be at least partially responsible for the abundance of macrobenthos in the canyon. They concluded that physical disturbance was largely responsible for low diversity and high dominance of the macrobenthos within Setubal Canyon, and asserted that large-scale, diffuse sources of disturbance such as those operating in the canyon and at the High Energy Benthic Boundary Layer (HEBBLE) site (Richardson et al., 1981) are important determinants of species diversity.

We were unable to separate the effects of physical disturbance and enrichment on the macrofaunal communities in Scripps and La Jolla canyons; however, it is probable that the impact of disturbance increases relative to enrichment with depth. This is evident in the virtual absence of detritus, and the presence of coarse sediments (Fig. 3), unremarkable biomass (Fig. 4) and low diversity (Fig. 11B) at 700 m within the canyon, which suggests physical disturbance but not enrichment. Further, at 900 m in the canyon, muddy sediments (Table 2), high diversity (Fig. 11B), and modest biomass

(Fig. 4) suggest calm conditions and an absence of enrichment. In addition to similar physical conditions (currents, sediments, oxygen) the density (Fig. 5), biomass (Fig. 4), and species composition of the benthos (Figs. 7 and 8) were similar at 900 m in La Jolla Canyon and at 500 m outside the canyon.

Other investigations have shown that thick detrital aggregates can smother and largely defaunate the underlying sediments (Thrush and Townsend, 1986; Norkko and Bonsdorff, 1995, 1996). There are few studies of the epifaunal organisms dwelling within patches of detritus, but studies shallow in Scripps Canyon have shown the potential for extremely high biomass and secondary production within macrophyte detritus aggregates (Vetter, 1994, 1995b). Non-quantitative samples of detritus demonstrated that amphipods and polychaetes densely inhabit some detrital patches. Attraction of deep-sea amphipods to (experimental) macrophyte detritus was also observed by Lawson et al. (1993).

Community analysis of all samples taken during this study reveal marked differences between the canyon and the shelf and slope off Del Mar (Figs. 6–8). Our examination of macrofauna from non-quantitative samples of detrital aggregates, and the four (quantitative) detritus-containing samples from the canyon at 100 m (bottom-four samples in dendrogram, Fig. 7) suggest that the detritus supports yet another species assemblage. The clustering of samples from 100 to 200 and 200 to 310 m in the canyon (Fig. 8) is probably due to the relatively small distance between these stations and down-canyon transport of animals along with sediment and detritus. The relatively large variability in the macrofaunal community at 500 m in the canyon (Fig. 8) may result from periodic displacement of the oxygen minimum zone and greater spatial variability in the degree of enrichment. Patches of the canyon floor separated by 10–20 m could have very different exposures to detrital aggregates on time scales relevant to infauna, but they probably experience similar disturbance regimes. Differences in food availability, substrate type, and disturbance frequency and intensity are all probably responsible for the difference in community structure between canyon and non-canyon stations.

5.1. Disposition of hypothesis and conclusions

Elements of the shallow detritus assemblage (leptostracan and amphipod crustaceans) were only found in samples down to 180 m, falsifying the hypothesis that they are present in the detritus throughout the canyon; however, the detrital aggregates in the canyon continued to provide habitat and food resources that were unavailable out of the canyon.

The hypothesis that canyon sediments are generally organically enriched was also falsified, but the hypothesis that canyon sediments would support higher infaunal density and biomass than sediments on the surrounding shelf and slope was supported. Furthermore, at least at depths from 100 to 500 m, canyon sediments supported macrofaunal communities that diverged strongly from sediments at similar depths at the non-canyon stations.

Canyon communities are more likely to experience organic enrichment and physical disturbance than communities on the surrounding shelf or slope. The canyon

enrichment effect, where it occurs, appears to decrease with depth, perhaps because most detritus enters the canyon near its head, and is consumed during transport downslope. The canyon disturbance effect also may diminish with depth, though probably not as dramatically as the enrichment effect. Hence, the relative importance of enrichment should decrease with depth in canyons, compared with disturbance effects.

Acknowledgements

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