

Organic enrichment by macrophyte detritus, and abundance patterns of megafaunal populations in submarine canyons

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ABSTRACT: Submarine canyons can provide large quantities of food in aggregated form on the deep-sea floor by acting as conduits for marine macrophyte production produced in the intertidal and shallow subtidal zone. Longshore transport delivers substantial quantities of macrophyte detritus from surfgrass *Phyllospadix torreyi*, kelps *Macrocystis pyrifera* and *Egregia menziesii*, and other macroalgae to the heads of Scripps and La Jolla Submarine Canyons. Strong tidal and gravity currents distribute this material throughout much of the canyon system, where it is utilized as food and habitat by benthic fauna. Video data taken from remotely operated vehicles and submarines were used to evaluate differences in detrital cover and megafaunal abundance in the canyons, and at nearby reference stations. Within the canyons dense mats of detritus were common down to 550 m, and *M. pyrifera* holdfasts were observed at 700 and 900 m. Virtually no drift material was observed out of the canyons. Comparisons of megafaunal invertebrates in and out of the canyons revealed generally higher densities at non-canyon sites due to large numbers of urchins. Species richness of all megafauna and abundance of non-urchin megafauna were greater in the canyons than out. It is likely that urchin abundance in canyons is reduced through disturbance by currents and detrital flows in the canyons. Species richness and abundance of fishes were greater in the canyons at all depths for which comparative data were available (100 to 500 m). From 150 to 200 m in Scripps Canyon, juvenile Pacific hake *Merluccius productus* were so abundant at times that their bodies obscured visibility. Turbot *Pleuronichthys* sp. and zoarcids *Lycodes pacifica* were also abundant in Scripps Canyon from 100 to 300 m. Data from this study support the hypotheses that macrophyte detritus covers large areas of the La Jolla and Scripps Canyon axis, and that megafaunal abundance is associated with detritus at both large and small spatial scales.

KEY WORDS: Submarine canyon · Detritus · Megafauna · Organic enrichment · Community · Physical disturbance · Surfgrass · Kelp

INTRODUCTION

Community composition and respiration in some regions of the sea floor are strongly influenced by food falls in the form of nekton carcasses (Stockton & DeLaca 1982, Smith 1985, 1986, Vetter 1996), macrophyte detritus (Wolff 1976, 1979, Thrush 1986, Lawson et al. 1993, Vetter & Dayton 1998), and pulsed inputs of phytodetritus (Billett et al. 1983, Lampitt 1985, Thiel et al. 1988/1989, Smith et al. 1992). Most studies

of this issue have been carried out in the deep sea where a background of low productivity amplifies the effect of food falls, especially on local diversity (Grassle & Morse-Porteous 1987). The greater productivity of waters overlying the continental shelf and slope, however, support a greater abundance and biomass of nekton and therefore a greater incidence of food falls. Regions near substantial marine macrophyte communities, or that receive detritus-rich outflows from estuaries, are probably most heavily impacted by food falls. Detritus with relatively low specific gravity, such as fine particulate and plant matter, will have greatest effect where physical condi-

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tions allow it to accumulate and persist long enough to be exploited by detritivores. On small scales, such conditions exist in the lee of rocks and other debris, in and around biogenic structures such as pits and mounds (VanBlaricom 1982, Thiel et al. 1988/1989), and on larger scales in depressions such as small basins, and submarine canyons and troughs (Josselyn et al. 1983, Okey 1993, Vetter 1995a, Harrold et al. 1998).

Submarine canyons receive macrophyte detritus and other bedload debris originally deposited on wide areas of the coastline by intercepting material transported along the shore by wave energy (Inman & Frautschy 1965, Shepard & Dill 1966, Inman & Brush 1973). This is especially true for canyons with shallow heads; however, large accumulations of kelp detritus have also been reported from offshore canyons (BBA & ROS 1986). Canyons located near macrophyte communities, such as forests of the giant kelp *Macrocystis pyrifera*, are likely to be highly organically enriched because of the high productivity of this species (Foster

& Schiel 1985) and the large proportion of that production which is exported (Zobell 1959, 1971, Gerard 1976). Once in canyons, detritus is transported deeper by continuous processes, such as periodic resuspension by tidal flows, and by violent episodic events, such as slumps and turbidity currents (Shepard 1973, Inman et al. 1976, Gardner 1989). Organic aggregates channeled to the deep-sea through submarine canyons may provide habitat for fishes and increase their invertebrate prey populations through elevated benthic secondary production.

Suspension feeders may benefit from enhanced currents and behavior of their prey within canyons. Several studies have found higher than background abundances of plankton and micronekton in and around canyons (Koslow & Ota 1981, Greene et al. 1988, Heckler et al. 1988, Cartes et al. 1993, Macquart-Moulin & Patriiti 1993). This may result from concentration of these pelagic animals at the base of canyons as they migrate down during the day, or through aggregation around physical structures associated with the

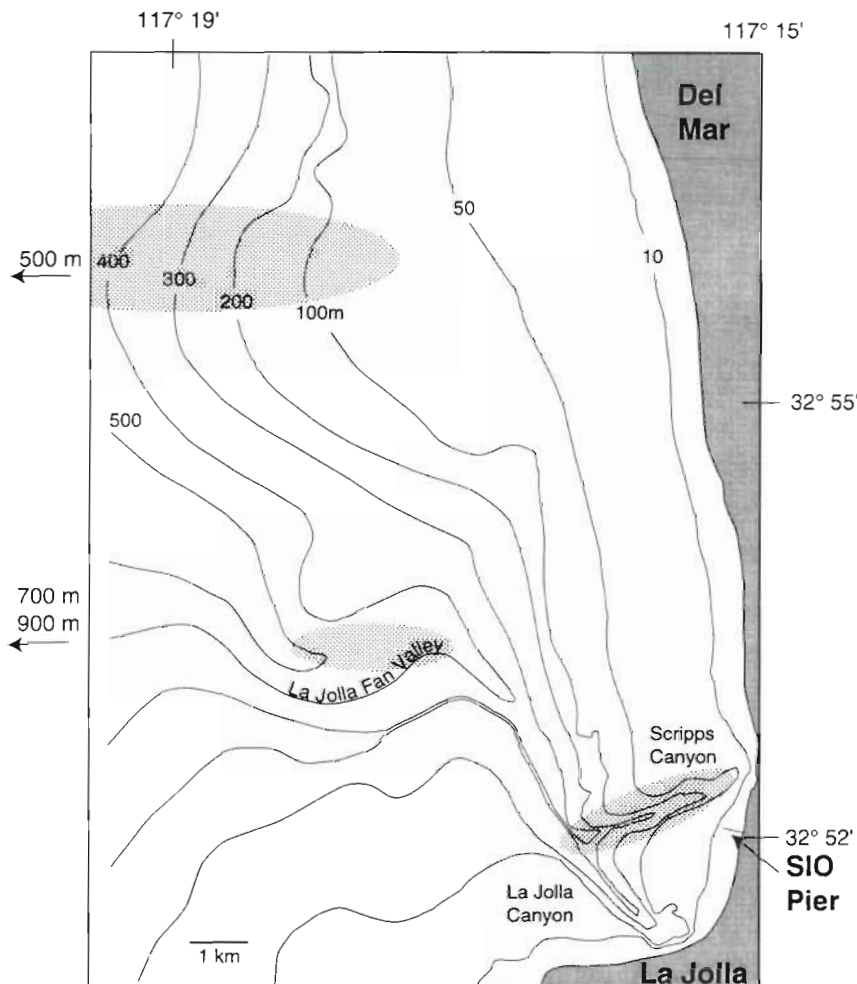


Fig. 1. Southern California coastline from Del Mar to Pt. La Jolla. Shaded regions show areas sampled. The Del Mar 500 m, and La Jolla Canyon 700 and 900 m areas are not shown. The approximate location of Scripps Institution of Oceanography pier is shown

canyons. Even in the absence of increased density of plankton and other food items, suspension feeders probably benefit from enhanced currents commonly found in canyons (Shepard et al. 1979).

Studies of infaunal patterns in canyons have found both increased biomass or density (Gage et al. 1995) and decreased biomass or density (Houston & Haedrich 1984, Maurer et al. 1994). Rowe et al. (1982) found that macrofaunal biomass was greater within the Hudson Canyon only at depths where the canyon was geologically inactive and was accumulating organic-rich, fine-grained sediments. Scripps and La Jolla Canyons are active throughout their length, have coarse-grained sediments and yet still house increased density and biomass of macrofauna (Vetter & Dayton 1998). Most studies of canyon megafauna have reported increased megafaunal density or biomass in canyons (Rowe 1971, Haedrich et al. 1975, 1980, Hecker et al. 1988, Cartes et al. 1994).

Large accumulations of detrital kelp *Macrocystis pyrifera* and *Egregia menziesii* and surfgrass *Phyllospadix torreyi* at the heads of Scripps and La Jolla Submarine Canyons were found to support enormous populations of macrofaunal crustaceans, which in turn supported large numbers of fishes (Vetter 1995b). Detritus arrived at the heads of these canyons at all times of the year, while export of that material appeared to be largely confined to periods of strong wave action, primarily during winter and spring storms (Vetter 1998). Those observations led us to hypothesize that large portions of the floor of La Jolla and Scripps Canyons are regularly covered with macrophyte detritus, and that megafaunal abundance is positively correlated with detritus and its associated macrofauna at large and small scales.

For the purposes of this study, detritus refers to large, identifiable pieces or entire plants of drift algae and surfgrass. Particulate detritus was abundant, but was not easily quantifiable except as parts of organic aggregates. Here, megafauna refers to animals large enough to be seen by eye on video, for the most part, animals larger than about 2 cm.

MATERIALS AND METHODS

Video data were taken in July and August 1995 from submersibles in Scripps and La Jolla submarine canyons (32° 52' to 32° 54' N, 117° 15' to 117° 19' W), and a nearby control area (32° 49' to 32° 51' N, 117° 21' to 117° 23' W) at depths between 100 and 550 m. Data were also collected from La Jolla Canyon at 700 m (32° 55' N, 117° 26' W) and 900 m (32° 51' N, 117° 34' W) (Fig. 1, Table 1). La Jolla Canyon follows a sinuous path from its head, which is visible at a depth of 20 m,

to the San Diego Trough, 39 km to the west at a depth of 900 m. Scripps Canyon branches off La Jolla Canyon at a depth of 290 m and continues as a straight rock gorge for about 2.7 km inshore to a depth of 15 m.

Strong currents (Shepard et al. 1979) and a source of beach sand at the head of the canyons result in well-sorted sandy sediments in the canyons to a depth of at least 700 m (Vetter & Dayton 1998). Between 700 and 900 m canyon sediments transform into poorly sorted mud with a high silt content. Organic carbon in canyon sediments was significantly lower than in non-canyon sediments at 300 and 500 m (Vetter & Dayton 1998). This may be due to strong canyon currents that winnow away much of the fine particulate matter, which includes much of the organic material.

Relative abundances of megafaunal invertebrates and fishes were estimated from video taken by a starboard-directed Hi-8 camera system mounted on the submersible 'Delta' (100 to 300 m depth range), and from a forward-directed Hi-8 camera on the advanced tethered vehicle (ATV, a remotely operated vehicle, used for depths from 310 to 900 m). Transect data were collected on 32 dives. Transects at the control area were run along isobaths; within La Jolla Canyon they were run using a serpentine down-canyon pattern. The narrow floor of Scripps Canyon forced us to run transects straight up and down the gorge. Transects were run along both sides and down the center of the Scripps Canyon axis.

Megafaunal invertebrates and fishes in the lower $\frac{2}{3}$ of each video frame were counted. This constrained our sampled area to within about 0.8 to 2 m of the submersibles. The upper $\frac{1}{3}$ of the frame usually recorded a much greater area of the sea floor than the lower $\frac{2}{3}$, and could not be reliably sampled. Frames were advanced by selecting a feature on the sea floor at the leading edge of the monitor and advancing the tape until it disappeared from view at the trailing edge of

Table 1. Number of video frames used for relative abundance estimates by depth and location (DM: Del Mar, non-canyon; CYN: canyon, 100 to 280 Scripps Canyon, 310 to 700 La Jolla Canyon)

| Station | Depth sampled (m) | No. of frames |
|---------|-------------------|---------------|
| DM 100 | 90–120 | 595 |
| DM 200 | 190–215 | 290 |
| DM 300 | 280–310 | 385 |
| DM 500 | 495–510 | 820 |
| CYN 100 | 90–125 | 307 |
| CYN 200 | 160–230 | 121 |
| CYN 280 | 260–290 | 80 |
| CYN 310 | 300–320 | 59 |
| CYN 500 | 490–550 | 993 |
| CYN 700 | 695–705 | 280 |

the monitor. All of the video in which the vehicles were swimming level and just skimming the bottom was used. This criteria constrained the area sampled by each frame and disqualified more than half of the video. It also prevented us from sampling from video when the vehicles were stationary. Frame area (lower $\frac{2}{3}$ of monitor) varied between about 0.8 to 1.5 m² with the Delta's video system, and from about 1.5 to 3 m² with the ATV's camera. Cross depth and platform megafaunal comparisons were not made. For example, data collected from the canyon at or near 100 m with Delta were only compared with data taken at the reference station at the same depth also using Delta. The relatively low spatial variability between frames and the large number of frames evaluated (Table 1) minimized errors in abundance estimation. On occasion the vehicles were stopped so that close-up video of animals and detritus could be taken to help with identification.

Percent cover of organic aggregates within Scripps and La Jolla Submarine Canyons was quantified over depths from 20 to 900 m, and at the non-canyon control station from 100 to 500 m. At scuba depths (20 to 65 m) percent cover of detrital patches was estimated by laying a 50 m tape measure along the canyon axis and recording the width of the canyon, detrital patches and clear spaces every 3 m. Percent cover of detritus below 60 m was estimated from video data. For video analysis of detrital cover a uniform grid of 100 dots was placed on the lower $\frac{2}{3}$ of the monitor. Percent cover per frame was recorded as the number of dots which fell on part of an organic aggregate. Species composition of the detritus could not be reliably determined from the video.

Statistical comparisons (ANOVA) were made with the Macintosh statistical package SYSTAT (V. 5.2.1, SPSS Inc., Chicago, IL, USA).

RESULTS

Detritus cover within the canyon ranged from 90 to 100% between 30 and 65 m, to 5% at 500 m, and was sparse at 700 (0.2%) and 900 m (<0.1%) (Fig. 2). Estimates of cover at 500 m were likely biased downward by data taken from the sloping substrate near the base of the canyon walls rather than the canyon floor. Along the non-canyon transects off of Del Mar, the only detritus observed were 2 freshly deposited *Macrocystis pyrifera* fronds at 100 m. Within the canyon *M. pyrifera* debris was found at all depths (to 900 m), but at 500 m detrital patches were strongly dominated by surfgrass (*Phyllospadix* spp.). Most of the detritus in the canyon was aggregated into dense mats which commonly exceeded 10 cm in thickness and could easily conceal megafaunal fishes and invertebrates.

A small tree branch (about 1 m long) found at 700 m within the canyon was inhabited by large numbers of snails (25 to 50) and amphipods (100 to >300). A small log found at 500 m hosted at least 7 large crabs *Glyptolithodes cristatipes* which were grazing on what appeared to be filamentous bacteria extending out from the log. Close-up video revealed that the portion of the log behind the crabs had been scraped clean, and the rest of the log was covered with thin filaments of a white substance which gave it a furry appearance. The filaments looked much like the bacterium *Beggiatoa* sp. which was identified from detritus collected at 50 m in the canyon (Vetter unpubl. data). At depths between 300 and 500 m patches of *Phyllospadix* spp. detritus were frequently observed with large aggregations (100s to 1000s over ~10 to 200 cm² of detritus) of amphipods on the surface of the detrital aggregates.

Relative megafaunal abundance data cannot be compared across platforms because the video system on the ATV tended to sample a slightly larger area (1.5 to 3 m²)

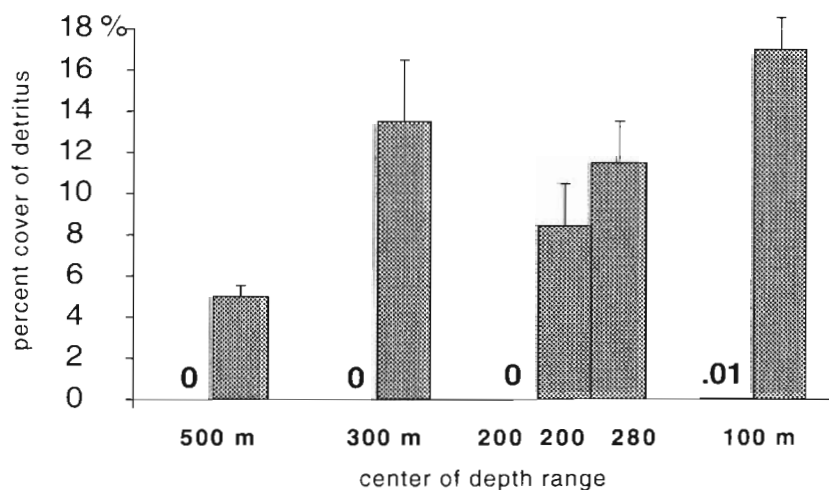


Fig. 2. Percent cover of detritus on the sea floor by depth and location. Columns represent canyon data and numbers non-canyon (Del Mar) data. Error bars are 1 standard error

Table 2. Summary of ANOVA results comparing invertebrate megafaunal abundances between canyon and non-canyon sites. *F*-ratio and *p*-values in parentheses are for data excluding urchins

| | df | Mean square | <i>F</i> -ratio | <i>p</i> |
|-------|------|-------------|-----------------|----------|
| 500 m | 1 | 209.8 | 26.78 | <0.001 |
| Error | 1888 | 7.9 | (31.17) | (<0.001) |
| 300 m | 1 | 0.3 | 0.13 | 0.722 |
| Error | 442 | 2.3 | (89.77) | (<0.001) |
| 200 m | 3 | 48.7 | 8.67 | <0.001 |
| Error | 670 | 5.6 | (41.46) | (<0.001) |
| 100 m | 1 | 52.7 | 16.19 | <0.001 |
| Error | 900 | 3.3 | (11.51) | (<0.002) |

than the one on Delta (0.8 to 1.5 m²). Likely differences in the measurement uncertainty associated with each vehicle would have also made direct comparisons inappropriate. Abundance of megafaunal invertebrates was significantly greater out of the canyon at 500 and 200 m (Table 2), there was no difference at 300 m, and the difference was greater in the canyon at 100 m (Figs. 3 & 4, Table 2). At 500 m the non-canyon sites were dominated by the heart-urchin *Brissopsis pacifica*, but the regular urchin *Allocentrotus fragilis*, asteroids (mostly *Mixoderma platyacanthum*), and the holothurian *Pannychia moseleyi* were also common. The canyon differed by having relatively few *B. pacifica*, no *A. fragilis*, and the benthic siphonophore *Dromalia alexandri* (Tables 3 & 4) was common. At 300 m, non-canyon transects were strongly dominated by *A. fragilis* with relatively few *B. pacifica*. The canyon was also dominated by *A. fragilis* (most within 1 m of the walls), and holothurians, benthic siphonophores and octopus were common (Table 3). Non-canyon sites at 200 and 300 m were similar in megafaunal composition. Within the canyon at 200 m the urchin *Lytechinus pictus* and large prawns appeared, *Parastichopus californicus* replaced *Pannychia moseleyi*, and the benthic siphonophores became less common. At 100 m *Parastichopus californicus* were observed at non-canyon sites and *A. fragilis* virtually disappeared from the canyon. When urchins are excluded from the analysis, megafaunal abundances are significantly greater in the canyons at all depths (Figs. 3 & 4, Table 2).

Megafaunal invertebrates were strongly associated with detrital aggregates at

500 m in the canyon, averaging 2.7 individuals per frame where detritus covered more than 5% of the frame, and 1.6 in other frames (ANOVA, *p* < 0.001). At 300 m the association of megafaunal invertebrates was even stronger, with a mean of 2.9 individuals in frames with detrital aggregates and 0.2 in frames without aggregates (ANOVA, *p* < 0.001). In Scripps Canyon (100 to 290 m) an average of 1.4 animals were observed in frames with detrital aggregates and 0.7 in frames without (ANOVA, *p* = 0.002). Below 200 m some animals, especially the holothurian *Pannychia moseleyi* and the crab *Glyptolithodes cristatipes*, were common within the detrital mats and may have been severely under-counted. On several occasions when the ATV was stopped at detrital patches to collect samples, the wash from the propellers disturbed the detritus revealing crabs that had been completely obscured. Counts of *P. moseleyi* could have been improved if we had stopped at each detritus patch and carefully panned the camera to cover the portion of the patches within the transect area, but this would have violated our transect sampling protocol.

The pattern of increased megafaunal abundance near detrital aggregates held for fishes at 500 m (0.8 fish frame⁻¹ near detritus, 0.3 away, ANOVA, *p* < 0.001) but not at 300 m (0.6 fish frame⁻¹ near detritus, 0.3 away, ANOVA, *p* = 0.19), and it was barely significant at depths

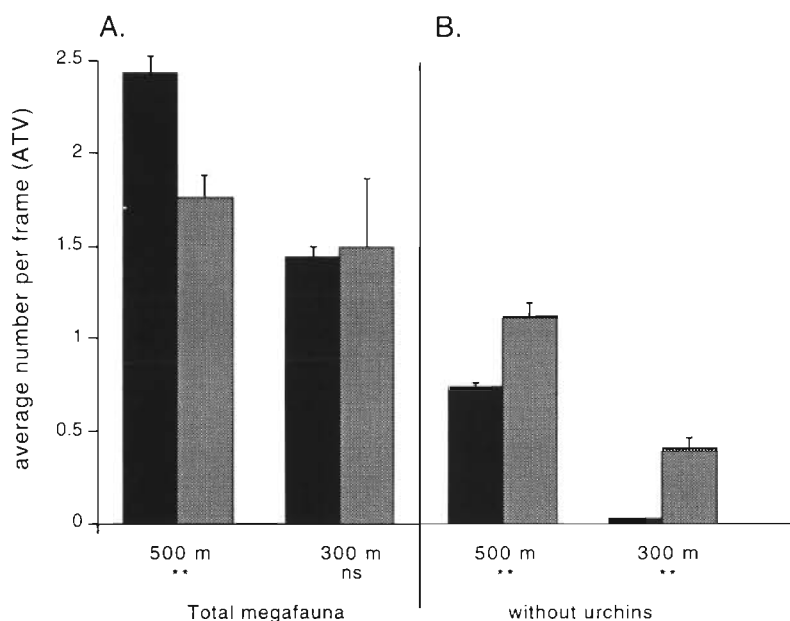


Fig. 3. Relative abundance of megafaunal invertebrates at 300 and 500 m. Solid columns show non-canyon data and shaded columns data from canyon stations. (A) All invertebrate megafauna. (B) All invertebrate megafauna except for sea urchins. Video data from the advanced tethered vehicle (ATV), frame size approximately 2 m². Error bars are 1 standard error. Asterisks indicate significant differences in megafaunal abundances within the given depth range, ***p* < 0.001, ns = not significant (ANOVA, Table 2)

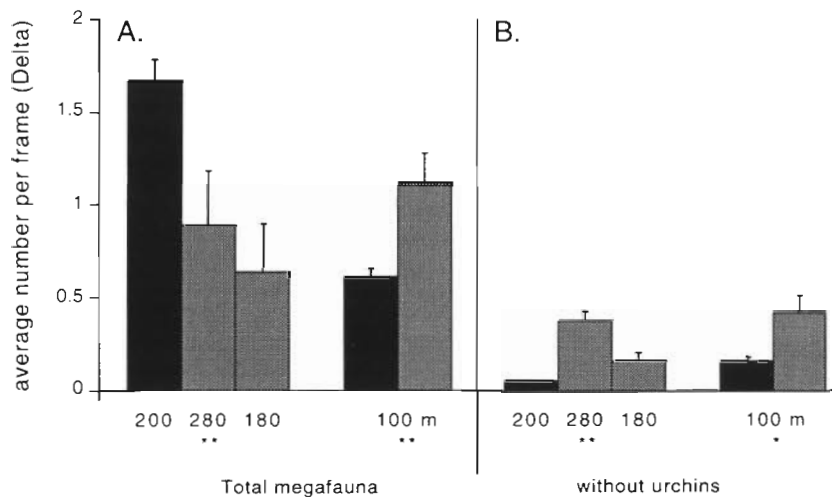


Fig. 4. Relative abundance of megafaunal invertebrates at 100 and 200 m. Solid columns show non-canyon data and shaded columns data from canyon stations. (A) All invertebrate megafauna. (B) All invertebrate megafauna except for sea urchins. Video data from the submersible 'Delta', frame size approximately 1 m². Error bars are 1 standard error. Asterisks indicate significant differences in megafaunal abundances within the given depth range, *p < 0.002, **p < 0.001 (ANOVA, Table 2)

Table 3. Relative abundance of fishes and invertebrate megafauna. Values are individuals per 100 frames (about 200 to 300 m²). Holothurians change from exclusively *Parastichopus* sp. at 100 m to exclusively *Pannychia moseleyi* at 500 m. Zeros indicate an average density of <0.2 individuals per 100 frames

| Platform: Location: Depth: | ATV | | | | DELTA | | | |
|---|-----------|------------|-----------|------------|-----------|------------|-----------|------------|
| | DM 500 | CYN 500 | DM 300 | CYN 310 | DM 200 | CYN 200 | DM 100 | CYN 100 |
| Invertebrates | | | | | | | | |
| <i>Brissopsis pacifica</i> | 170 | 9 | 13 | 0 | 24 | 0 | 5 | 0 |
| <i>Alloctenotus fragilis</i> | 52 | 0 | 126 | 95 | 139 | 26 | 41 | 1 |
| <i>Lytechinus pictus</i> | 0 | 0 | 0 | 0 | 1 | 24 | 0 | 28 |
| Asteroids (spp.) | 46 | 43 | 0 | 0 | 0 | 0 | 4 | 0 |
| <i>Pannychia moseleyi</i> | 17 | 43 | 0 | 15 | 0 | 0 | 0 | 0 |
| <i>Parastichopus</i> sp. | 0 | 0 | 0 | 0 | 0 | 12 | 7 | 9 |
| <i>Dromalia alexandri</i> | 0.1 | 16 | 1 | 12 | 1 | 1 | 0 | 0 |
| Decapods (spp.) | 0 | 0 | 0 | 0 | 0 | 7 | 0 | 24 |
| <i>Octopus</i> sp. | 0 | 0 | 0 | 5 | 0 | 2 | 0 | 0 |
| Fishes | | | | | | | | |
| Juv. <i>Merluccius productus</i> , | 4 | 8 | 0 | 5 | 0.4 | 900 | 0 | 69 |
| Adult <i>M. productus</i> , hake | 2 | 2 | 0.3 | 7 | 0 | 2 | 0 | 0 |
| <i>Sebastes</i> sp., thornyhead | 0.2 | 5 | 3 | 0 | 0 | 0 | 0 | 0 |
| <i>Anoplopoma fimbria</i> , sablefish | 6 | 11 | 2 | 12 | 0 | 0 | 0 | 0 |
| <i>Facciolella gilberti</i> , witch eel | 0 | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Microstomus pacificus</i> , sole | 0 | 48 | 4 | 0 | 0 | 0 | 0 | 0 |
| <i>Pleuronichthys</i> sp., turbot | 0 | 0 | 0 | 0 | 0 | 118 | 4 | 208 |
| <i>Lycodes pacifica</i> | 0 | 0 | 0 | 0 | 0 | 36 | 0 | 38 |
| <i>Scorpaena guttata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |

shallower than 300 m (Scripps Canyon, 5.7 fish frame⁻¹ near detritus, 3.8 away, ANOVA, p = 0.04).

Canyon stations had more fish than non-canyon stations at all depths (Table 5, Fig. 5). Within La Jolla Canyon sole *Microstomus pacificus* were largely responsible for this difference at 500 m, and relatively large numbers of sablefish *Anoplopoma fimbria* and hake *Merluccius productus* were important at 300 m. Inshore of 300 m (in Scripps Canyon) the difference was even more pronounced, with large numbers of

hake, turbot *Pleuronichthys* sp., and zoarcids *Lycodes pacifica* in the canyon (Table 3). From about 150 to 230 m juvenile hake were exceptionally abundant (often obscuring view of the bottom) within 2 m of the canyon floor. Dense aggregations of juvenile hake from 150 to 200 m prevented us from recording data in the regions where fishes were most abundant, severely biasing our estimates of fish abundance downward at those depths in the canyon (transect data were only recorded when the bottom was clearly visible).

Table 4. Summary of ANOVA results comparing *Dromalia alexandri* abundance between canyon and non-canyon sites

| | df | Mean square | F-ratio | p |
|-------|------|-------------|---------|--------|
| 500 m | 1 | 12.09 | 106.34 | <0.001 |
| Error | 1888 | 0.11 | | |
| 300 m | 1 | 0.57 | 19.26 | <0.001 |
| Error | 442 | 0.03 | | |
| 200 m | 3 | 0.01 | 1.18 | 0.315 |
| Error | 670 | 0.01 | | |

Table 5. Summary of ANOVA results comparing abundance of fishes between canyon and non-canyon sites

| | df | Mean square | F-ratio | p |
|-------|------|-------------|---------|--------|
| 500 m | 1 | 37.3 | 93.0 | <0.001 |
| Error | 1888 | 0.4 | | |
| 300 m | 1 | 5.9 | 31.1 | <0.001 |
| Error | 442 | 0.2 | | |
| 200 m | 3 | 13 363.5 | 52.4 | <0.001 |
| Error | 670 | 255.2 | | |
| 100 m | 1 | 2 113.0 | 276.8 | <0.001 |
| Error | 900 | 7.6 | | |

DISCUSSION

There have been numerous reports of sea grasses, macroalgae and other plant debris aggregates in the deep sea and submarine canyons (Schoener & Rowe 1970, Josselyn et al. 1983, Suchanek et al. 1985, Bach 1986, Alongi 1990, McHugh et al. 1992, Rice & Lamshead 1994, Gage et al. 1995); however little is known about the ecological effects of this material. Existing evidence suggests that the presence of detrital aggregates leads to higher growth rates and/or higher abundance of benthic animals (Rowe & Staresinic 1979, Wolff 1976, 1979, Duntun & Schell 1987, Grassle & Morse-Porteous 1987, Duggins et al. 1989, Lawson et al. 1993, Rice & Lamshead 1994, Snelgrove et al. 1994). Within Scripps and La Jolla Canyons the increased megafaunal abundance near detrital aggregates appeared to be due to utilization of detritus as food (urchins, holothurians) or for both food and shelter/habitat (decapods). Infaunal abundance and biomass were significantly greater at all depths within both Scripps and La Jolla Canyons than at the non-canyon sites (Vetter & Dayton 1998).

In addition to providing organic carbon to ocean sediments, macrophyte detritus can be exploited by metazoans either directly or following microbial processing (Fenchel & Jørgensen 1977, Lopez et al. 1977, Levinton 1982, Kemp 1986, Peterson et al. 1986, Lopez & Levinton 1987, Harrison 1989). It also provides habitat and/or refuge for animals (Lawson et al. 1993, Vetter 1994, 1995a). Concentration of such material within submarine canyons and relatively rapid transport of detritus to slope and bathyal depths through canyons results in ecologically important patches of ele-

vated benthic production (Vetter 1995b), and possibly elevated fisheries production (Stefanescu et al. 1994, Vetter & Dayton unpubl. data). Globally, the overall importance of macrophyte detritus to the metabolism of the benthos may be small (Menzies et al. 1967, Menzies & Rowe 1969, Schoener & Rowe 1970); however locally important enhanced benthic production can occur in regions likely to accumulate macro-detritus, such as some submarine canyons (Josselyn et al. 1983, Gage et al. 1995, Vetter 1995a, Okey 1997, Harrold

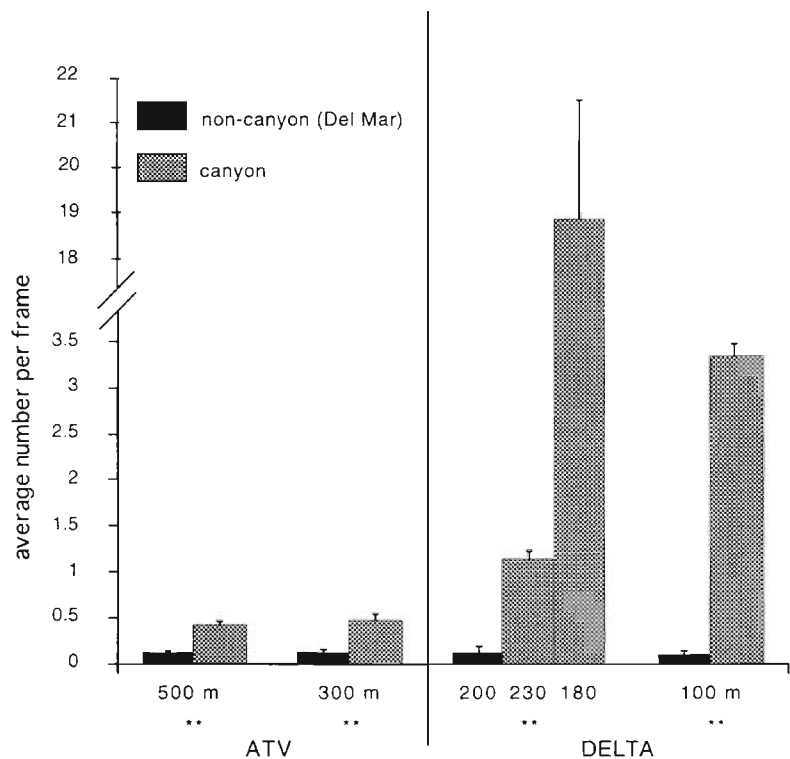


Fig. 5. Relative abundance of fishes at non-canyon (solid columns) and canyon (shaded columns) stations. Frame size approximately 1 m² with Delta, and 2 m² with video from ATV. Note change in scale. Error bars are 1 standard error. Asterisks indicate significant differences in fish abundances within the given depth range, **p < 0.001 (ANOVA, Table 5)

1998). In the absence of canyons the only major pathway for the delivery of giant kelp to great depths is the diffuse sinking of kelp paddies (Smith 1983).

The near absence of detritus at 700 m (0.2% cover) may have been primarily a result of decreased delivery of material to that depth; however, rapid consumption of macro-algal detritus by urchins probably also played a role. Nearly all fresh *Macrocystis pyrifera* fronds and stipes observed on the sea floor were covered by urchins. If most detritus is delivered to the deep portions of the canyons following winter and spring storms (see Josselyn et al. 1983, Vetter 1995a), much of the drift kelp transported to our study sites would have been consumed prior to our cruises in August. At 900 m in La Jolla Canyon we did find a kelp holdfast, but the sediments were muddy (Vetter & Dayton 1998) suggesting that the strong currents responsible for transporting material down the canyons might be rare at this depth. Moore (1965), however, found a channel at 900 m in La Jolla Canyon which may have been formed by turbidity currents, suggesting that physical disturbance is periodically important in the canyon at all depths.

In an investigation of benthic detrital abundance in and around Carmel Canyon (central California) Harold et al. (1998) also found large amounts of detritus on the canyon floor, and essentially none on the continental shelf and slope away from the canyon. Large mats of detritus (*Macrocystis pyrifera*, *Egregia menziesii*, *Pterygophora californica*, *Gigartina* spp., etc.) have been observed at 100 m in an offshore canyon near Pt. Conception (California), and detritus was seen moving down a second nearby canyon (BBA & ROS 1986). Dume Canyon in northern Santa Monica Bay (Southern California) contained large accumulations of *M. pyrifera* holdfasts and surfgrass blades, which were absent at a nearby control site (Vetter & Dayton unpubl. data). It is clear that canyons near kelp forests are important sites of drift algal and surfgrass accumulation along the California coast.

The distribution of total megabenthos in and out of the canyon did not present a clear pattern; however, when urchins are removed from the analysis, megafauna were significantly more abundant in the canyon at all depths examined (Figs. 3 & 4). Urchins were relatively rare in the canyon in contrast to recent observations in Dume Submarine Canyon where enormous numbers of urchins (especially the urchins *Allocentrotus fragilis* and *Strongylocentrotus purpuratus*) were observed from 100 to 350 m in July 1996 (Vetter & Dayton unpubl. data). This difference may be due to the disturbance regimes in the 2 canyons. Judging by fine sediment accumulation on beer and soft-drink cans (with recent designs), and large amounts of rubbish observed there, Dume Canyon has a more

benign physical environment than Scripps and La Jolla Canyons. Intense tidal currents, turbidity currents and detrital flows within the Scripps–La Jolla canyon system (Inman et al. 1976) may be unfavorable to invertebrate megafauna, especially urchins. Ross (1968) made the same suggestion based on observations of abundant fishes but sparse sessile invertebrates and rapid currents within Corsair Canyon (USA east coast). Rowe (1972) theorized that high incidence of disturbance by sediment movements in the canyon would favor more motile species. This is consistent with our observations of fewer urchins, animals that may be relatively susceptible to disturbance, and more octopuses and crabs in the canyons (Table 3, Figs. 3 & 4).

Our estimates of megafaunal (fish and invertebrates) abundance were biased downwards by our inability to effectively count animals in and under detrital aggregates. Some species, including the zoarcid *Eucryptophycus californica*, were only found in clumps of detritus taken with the submersibles' manipulator. These fishes were surprisingly abundant in some samples (up to 5 fish in about 1 l of detritus), and have been reported in large numbers from detrital aggregates in Monterey Submarine Canyon (Cailliet & Lea 1977). Because of their cryptic habit, none of these fishes were recorded from the video data. Crabs *Glyptolithodes cristatipes* were frequently seen under patches of detritus when wash from the submersibles' thrusters disturbed the detritus; however, this only occurred while the vehicle was stopped to collect physical samples, so those observations were not included in our video transect data. One of the few instances when the presence of *G. cristatipes* was recorded in our megafauna data was mentioned above for 7 large crabs grazing on a log.

Megafaunal invertebrates (especially echinoderms and decapods) in La Merenguera Canyon (western Mediterranean) were found at higher density and biomass than at nearby non-canyon stations (Cartes et al. 1994, Sardà et al. 1994). Species richness was also higher in the canyon and was presumed to stem from greater variability in physical factors such as sedimentation, currents, and supply of organic matter (Cartes et al. 1994). In a study of the community structure of continental slope epibenthic populations south of New England, Haedrich et al. (1975) reported greater trawl catch rates in the canyon (228 specimens h^{-1} and 3.4 kg h^{-1} at slope stations, versus 368 specimens h^{-1} and 5.7 kg h^{-1} at canyon stations). Hecker et al. (1988) found that megafaunal densities were higher in Hendrickson and Lydonia Canyons than at comparable depths on the surrounding shelf and slope. High densities of filter feeders (anemones, corals and sponges) appeared to benefit from the greater availability of hard substrate and the enhanced currents within the canyons.

Increased abundance of fishes in canyons have also been observed in other studies. Stefanescu et al. (1994) found similar species of fishes in and out of a canyon (350 to 650 m, Catalan Sea, northwestern Mediterranean), but much higher abundance and biomass in the canyon. The fishes were slightly smaller in the canyon, and the size distributions of common species led to the conclusion that the canyon acts as a nursery ground for some species. This may well be the case for juvenile Pacific hake within southern Californian submarine canyons. In an ongoing investigation, large numbers of juvenile hake were also observed in Carlsbad and Redondo Canyons (southern California) in July 1996 (Vetter unpubl. data). Stefanescu et al. (1994) surmised, as do we, that the increased abundance of fishes in the canyons is at least partially due to higher food availability there. It is also likely that physical structures such as rock walls, boulders and detritus patches in the canyon are attractive to fishes. Hecker et al. (1988) did not find any clear pattern of abundance for fishes in and out of canyons, but did consider the grenadier *Coryphaenoides rupestris* to be a canyon indicator species on the mid- and north-Atlantic coast of the USA. In the present study fishes that were relatively common in the canyons and rare or absent on the shelf and slope included turbot *Pleuronichthys* sp., the zoarcid *Lycodes pacifica* and juvenile hake *Merluccius productus* (Table 3).

The greater abundance of the benthic siphonophore *Dromalia alexandri* in the canyon may be related to canyon effects on currents. This species and other rhodaliid siphonophores, such as *Thermopalia taraxaca*, the 'dandelion' described from the 'Rose Garden' hydrothermal vent in the Galápagos Rift region (Pugh 1983), are buoyed up by a large pneumatophore, and are typically found anchored to the sea floor with their tentacles. This arrangement allows the animals to benefit from currents flowing past their feeding zooids without having to grow out of, or even having significant structures in the benthic boundary layer. We observed a *D. alexandri* float slowly to the bottom and anchor itself in the canyon, so these animals appear to have some influence over where they will reside. If they behave like 'optimal foragers', it is reasonable to presume that they will remain longer in places with high food density or where currents are strong enough to increase the flux of food past their gastrozooids, without being so strong that they cause the animals to lose their purchase on the substrate. *T. taraxaca* is found in abundance on the periphery of some hydrothermal vents (Galápagos, 13°N East Pacific Rise) (Hessler & Smithey 1983, Tunnichliffe 1991) where, in addition to high particle concentrations in the water, convective water motion generated

by the vent fields should result in current speeds elevated above background levels (Enright et al. 1981); however *T. taraxaca* is also very common in some regions of the southern East Pacific Rise away from vents (C. van Dover pers. comm.). The relatively high abundance of *D. alexandri* in the canyon may reflect a preference for regions with relatively strong currents. Several studies have reported enhanced current flows in submarine canyons (Shepard et al. 1964, 1979, Shepard & Marshall 1973, Gordon & Marshall 1976, Inman et al. 1976) which may result from along-shore pile up of water by strong onshore winds, down-canyon pulses resulting from high incident waves, standing waves producing down-canyon oscillations, or turbidity currents (Inman et al. 1976). Tidal flows, internal waves, and spin-off eddies from large current systems are more likely to drive canyon currents in deep-water (also see Freeland & Denman 1982, Noble & Butman 1989, Durrieu De Madron 1994, Alvarez et al. 1996).

CONCLUSIONS

It is clear that physical conditions in canyons are often distinct from the surrounding shelf and slope, and can affect the structure of canyon communities. We feel the following generalizations are warranted:

- (1) Submarine canyons in the vicinity of populations of macroalgae or surfgrass receive extensive inputs of macrophyte detritus and will probably be organically enriched by that material.

- (2) Organic enrichment in canyons may lead to greater than background densities of megafaunal invertebrates; however, even in canyons where detritus is abundant, some megafauna such as echinoderms may actually be present at lower than background density because of higher disturbance rates in canyons.

- (3) Detrital patches attract megafauna and on small scales their density is enhanced in the immediate vicinity of organic aggregates.

- (4) Fish abundance is enhanced in canyons, and canyons may serve as important nursery grounds for fishes; explanations may include increased availability of benthic or planktonic prey and the increased structural diversity found in canyons.

When compared to regions on the surrounding continental shelf and slope, submarine canyons are responsible for substantial accumulation of organic material. Canyons provide conduits for the rapid transport and deposition of macroalgal and seagrass detritus to great depths. In the absence of canyons much of the macro-detritus would be consumed or simply buried on the shallow portions of the shelf.

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