

# Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons

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**Abstract.** Habitat heterogeneity is a major structuring agent of ecological assemblages promoting beta diversity and ultimately contributing to overall higher global diversity. The exact processes by which heterogeneity increases diversity are scale dependent and encompass variation in other well-known processes, e.g., productivity, disturbance, and temperature. Thus, habitat heterogeneity likely triggers multiple and cascading diversity effects through ecological assemblages. Submarine canyons, a pervasive feature of the world's oceans, likely increase habitat heterogeneity at multiple spatial scales similar to their terrestrial analogues. However, our understanding of how processes regulating diversity, and the potential for cascading effects within these important topographic features, remains incomplete. Utilizing remote-operated vehicles (ROVs) for coring and video transects, we quantified faunal turnover in the deep-sea benthos at a rarely examined scale (1 m–1 km). Macrofaunal community structure, megafaunal density, carbon flux, and sediment characteristics were analyzed for the soft-bottom benthos at the base of cliff faces in Monterey Canyon (northeast Pacific Ocean) at three depths. We documented a remarkable degree of faunal turnover and changes in overall community structure at scales <100 m, and often <10 m, related to geographic features of a canyon complex. Ultimately, our findings indicated that multiple linked processes related to habitat heterogeneity, ecosystem engineering, and bottom-up dynamics are important to deep-sea biodiversity.

**Key words:** *benthic; biodiversity; bioturbation; bottom-up; canyon; deep sea; disturbance; ecosystem engineering; habitat heterogeneity; productivity.*

## INTRODUCTION

Heterogeneous environments are predicted to support more complex and diverse biological assemblages (Pianka 1966, Ricklefs and Schluter 1993, Tews et al. 2004). At regional and global levels, turnover in major habitat types may promote genetic isolation leading to speciation (Pianka 1966). At local scales, microscale variation in factors such as sediment type, vegetative complexity, topography, temperature, moisture, and wave exposure appear to provide multiple niches and/or contribute to local coexistence of species (Menge 1976, Leviten and Kohn 1980, Thistle 1983, Shmida and Wilson 1985, Etter and Grassle 1992, Weckstrom and Korhola 2001, Holz et al. 2002, Hurlbert and Haskell 2003). Heterogeneous environments may regulate diversity through patch variation in a suite of other well-examined processes, e.g., productivity (Vetter and Dayton 1999), disturbance regimes (Roxburgh et al. 2004), connectivity (Chase and Ryberg 2004), and temperature (Flieshman et al. 2000). Of course, none of these processes occur in isolation but rather interact to yield

intricate responses in biological communities (Ricklefs and Schluter 1993, Jetz and Rahbek 2002, Chase and Ryberg 2004). Thus, habitat heterogeneity likely triggers multiple and cascading diversity effects through ecological assemblages.

On land, canyons and ridge topography are known to increase diversity by offering a multitude of habitat types over small spatial scales and by isolating populations geographically (Nevo 1995, Flieshman et al. 2000). In the deep sea, canyons are a pervasive feature of the ocean floor incising over 20% of the northeast Pacific shelf and reaching 50% at latitudes north of 45° (Kuhnze et al. 2002). Submarine canyons are important globally as potential sinks of carbon (Vetter and Dayton 1999) and in understanding the influences of climate change on the deep sea (Company et al. 2008). Yet, our understanding of their influence on biodiversity remains limited. With regard to habitat heterogeneity, submarine canyons through their control of current regimes are likely to promote gradients in the type, quality, and quantity of food resources (Vetter and Dayton 1999). Material transport from turbidity flows through the canyon, raining of material off cliff faces, and sediment slides on steep slopes are also expected to create disturbance regimes. Thus the factors regulating biological communities within submarine canyons are likely a complex interplay of multiple factors.

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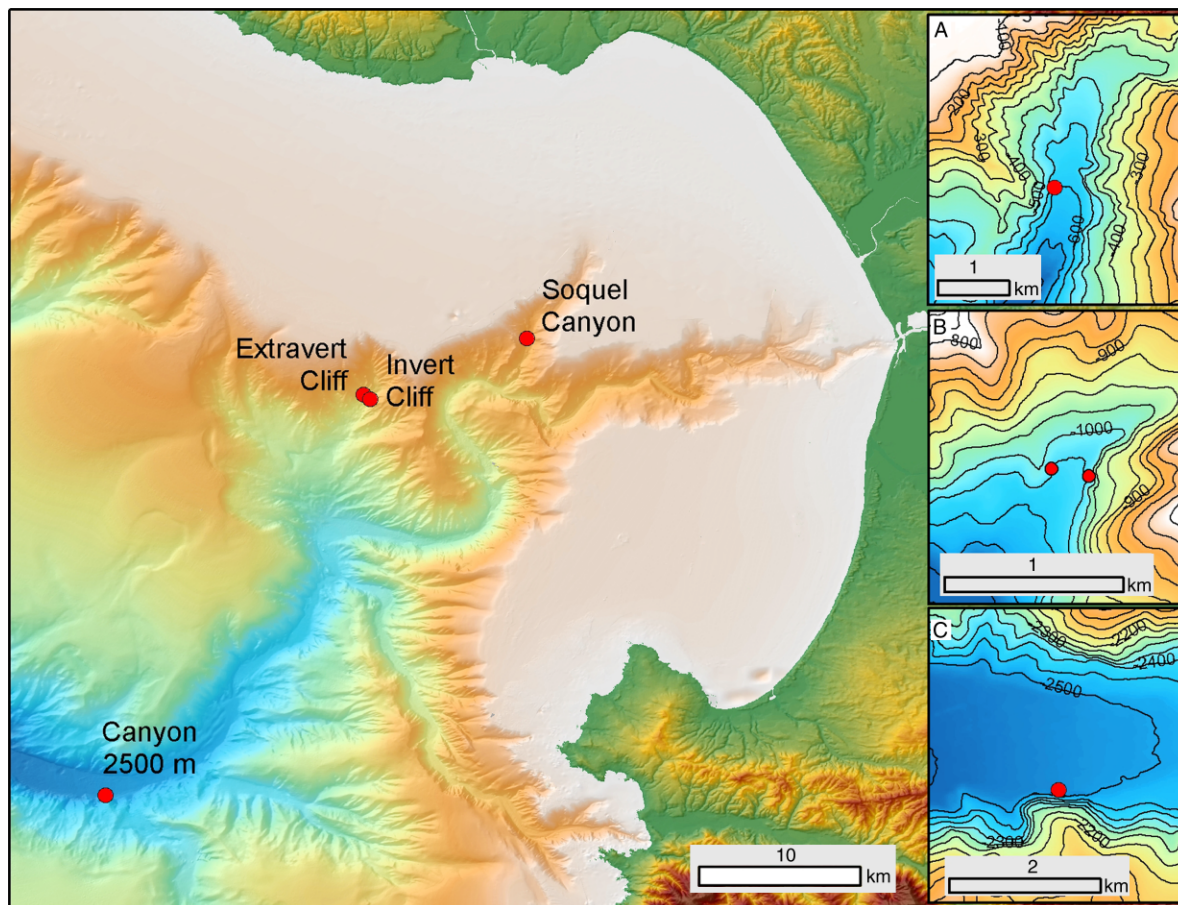


FIG. 1. Map of study sites in Monterey Canyon off the central California coast, USA. Insets display detailed bathymetry for the four sites: (A) Soquel Canyon (595 m); (B) Extravert Cliff (1004 m) and Invertebrate Cliff (1010 m); and (C) Canyon 2500 (2500 m).

Many deep-sea studies concentrate on scales of less than a few meters or greater than a kilometer, reflecting the sample size of individual gear and precision associated with gear typically available to study these environments. Previous studies on submarine canyons focused primarily on the abundance and variation of megafauna (e.g., corals, sponges, and fish) and how it varies at larger spatial scales, such as between adjacent canyons or canyons and slopes (Schlacher et al. 2007). The few studies addressing diversity quantify inter- and intra-canyon variation at scales  $>1$ – $2$  km (Vetter and Dayton 1998, 1999, Schlacher et al. 2007). The biodiversity of the deep sea, however, reflects not only global, regional, and landscape drivers, but processes operating at spatial scales less than a few meters (Jumars 1975, Rex 1981, Grassle 1989, Snelgrove et al. 1992, Levin et al. 2001).

With the advent of new technologies, e.g., remote-operated vehicles, we are able to quantify and explore pattern and processes at a poorly studied range of spatial scales in deep-sea studies. We examine the role of topographic heterogeneity related to cliff faces in

Monterey Canyon on the soft-bottom benthos. We hypothesize that canyon topography greatly alters delivery of food to the seafloor, thereby triggering other processes, leading to ecological reorganization over small spatial scales. Ultimately, we hope to uncover how these processes affect alpha- and beta-diversity in submarine canyons and ultimately contribute to both large-scale geographic variation and high global species diversity in the deep sea.

## MATERIALS AND METHODS

### *Sampling locations*

Three locations (Fig. 1) were sampled in Monterey Canyon between 2006 and 2007 with the remote-operated vehicles (ROVs) *Ventana* and *Tiburón* of the Monterey Bay Aquarium Research Institute, Moss Landing, California, USA. The goal of the project was to quantify both biological and environmental changes in soft-sediment habitats across the canyon floor as distance from cliff faces increased. Monterey Canyon was chosen for its proximity to the facilities, research vessels, and resources of the Monterey Bay Aquarium

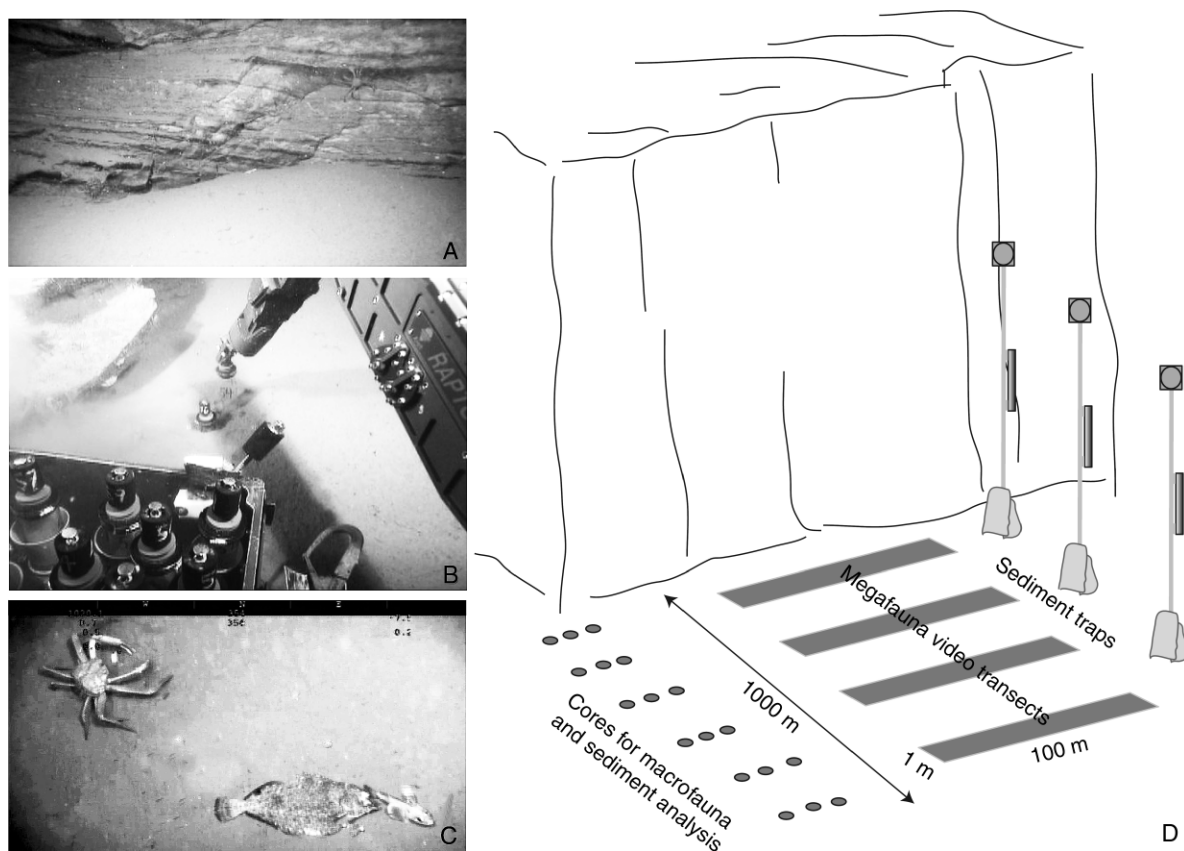


FIG. 2. (A) Photograph of cliff face and adjacent soft-bottom seafloor at Canyon 2500 m. (B) Photograph of sediment cores taken near the cliff face at Canyon 2500 m with the remote-operated vehicle (ROV) *Tiburon*. (C) Photograph from a megafauna video transect at Invertebrate Cliff showing typical species encountered: *Chionectes tanneri*, *Sebastolobus altivelis*, and *Embassichythes bathybius*. (D) Illustration of sampling program. Sediment and macrofaunal cores were taken with an ROV (see panel B) in 100-m transects away from the cliff face. Video transects (100 × 1 m) were conducted with the ROV to quantify megafauna densities. Small tubular sediment traps were also deployed in a transect away from the cliff face to quantify variation in flux. Traps were suspended between a float and bags of gravel serving as anchors. See *Methods* and Table 1 for details.

Research Institute, allowing for maximization of sampling under time and financial constraints. A general diagram of the sampling program is given in Fig. 2. Sampling sites included: Canyon 2500 (2500 m), Invertebrate Cliff (1010 m)/Extravert Cliff (1004 m), and Soquel Canyon (595 m). Three localities were chosen to maximize our depth coverage, where currents and topography allowed for ROV accessibility, and areas where prominent cliff faces were detected based on bathymetric data. Invertebrate Cliff and Extravert Cliff occupy opposite sides of the same 200-m canyon area and when combined represent a continuum from cliff face to canyon floor to cliff face allowing a unique opportunity to examine clines where productivity, flow regimes, oxygen, temperature, disturbance, and other factors are constant. Temperature decreases with depth among the sites (Soquel, 5.2°C; Invertebrate/Extravert Cliff, 3.9°C; Canyon 2500, 1.8°C). Soquel Canyon lies in the middle of the oxygen minimum zone (0.25 ml/L) with oxygen concentrations only slightly higher at Invertebrate/Extravert Cliff (0.50 ml/L). Canyon 2500

has considerably higher oxygen concentrations than the other sites (2.0 ml/L).

#### Macrofauna

At all the sites sediment cores (diameter: 7 cm) were taken with the ROV. Core transects were conducted perpendicular to the four cliff faces with 1–3 cores taken at each distance along the transect (see Table 1 for details and Fig. 2 for illustration). The top 1–5 cm of each core were sieved for macrofauna on a standard 250- $\mu$ m mesh and preserved in 10% formalin. Fractions of 5–10 cm were also sieved but often yielded no or few individuals and were not included in the analyses and discussions here. All individuals were identified to morphospecies and assigned Latin binomials when possible. Taxonomic experts were consulted with for polychaetes and amphipods. A representative individual for each species was photographed using a digital image analysis system connected to a dissecting microscope. A single estimate of biovolume for each species was calculated using length, width, and height measure-

TABLE 1. Summary of the sampling program in Monterey Canyon, off the coast near Moss Landing, California, USA.

Site, depth, and sample type	Date	No.	Distances from cliff face (m)
Soquel Canyon, 595 m			
Macrofauna cores	Aug 2007	18	1, 1, 1, 3.5, 3.5, 3.5, 6, 6, 6, 15, 15, 15, 25, 25, 25, 50, 50, 50
Invertebrate/Extravert Cliff, 1010, 1004 m			
Macrofauna cores	Jul 2006	11	3, 3, 6, 6, 12, 24, 48, 75, 75, 100, 100
	Aug 2006	12	1, 1, 3, 3, 7, 7, 11, 11, 35, 35, 75, 75
	Nov 2006	13	1, 1, 10, 20, 20, 30, 30, 40, 40, 50, 50, 60, 60
	Dec 2006	20	1, 1, 1, 1, 50, 50, 50, 50, 100, 100, 100, 100, 150, 150, 150, 150, 200, 200, 200, 200
	Feb 2007	14	1, 1, 1, 50, 50, 50, 100, 100, 150, 150, 150, 200, 200, 200
Megafauna video transects	Jul 2007	4	1.5, 10, 25, 50
	Aug 2007	4	5, 10, 15, 30
Sediment traps		5	1, 12, 25, 50, 75
Sediment cores C:H:N	Jul 2006	7	3, 6, 12, 24, 48, 75, 100
	Sep 2006	6	1, 1, 50, 50, 100, 100
Sediment cores grain size	Sep 2006	10	1, 1, 3, 12, 24, 48, 50, 75, 100, 100
	Aug 2007	10	1, 1, 3.5, 3.5, 7, 7, 12, 12, 24, 24
Canyon 2500 m			
Macrofauna cores	Aug 2007	21	1, 1, 1, 3, 3, 3, 6, 6, 6, 12, 12, 12, 25, 25, 25, 50, 50, 50, 100, 100, 100
Megafauna video transects	Aug 2007	5	1, 12, 25, 50, 75

ments. As interspecific biovolume variation will be significantly greater than intraspecific variation, a single body size estimate for each species provides a useful tool for examining community size clines for the studied fauna here (McClain 2004).

#### *Megafauna*

At Invertebrate Cliff and Canyon 2500, video transects across the soft sediment of the canyon floor were conducted parallel to the cliff face (see Table 1 for details and Fig. 2 for illustration). No megafaunal video transects were conducted at Soquel Canyon due to technical problems that arose during the ROV dive. Transects were 100 m in length by 1 m wide, the latter determined by two parallel lasers 29 cm apart. Video observations were recorded using high-resolution video equipment. Video transects were annotated in detail using MBARI's Video Annotation and Reference System, VARS (Schlining and Jacobsen-Stout 2006). The density of megafauna per square meter per transect was calculated. No significant changes occurred in measures of megafaunal species composition or diversity with distance from the cliff face at either Invertebrate Cliff or Canyon 2500 and thus are not further discussed here. Significant changes were detected in megafaunal abundance and described in the results.

#### *Environmental parameters*

Small sediment traps were deployed at varying distances from the cliff base at Invertebrate Cliff by the ROV Ventana in July 2006 to estimate the pattern of material flux at Invertebrate Cliff. Each trap was a 1 m long PVC tube with a 15.25 cm diameter opening at the top (covered by a 2-cm mesh to prevent swimming mobile megafauna to enter the trap). Traps were filled with seawater containing a mercuric chloride solution

for preservation of organic debris. The sediment trap openings were positioned 15 m off the bottom and deployed at multiple distances from the cliff face (see Table 1 for details and Fig. 2 for illustration). Traps were collected after 41 days and their contents were dried and weighed. All analyses of C:H:N composition and stable isotopes of carbon and nitrogen, both for the sediment traps and sediment cores, were performed in the laboratory of R. Dunbar (Stanford University, Stanford, California, USA) on a Finnigan mass spectrometer (Thermo Electron, San Jose, California, USA).

Cores of surficial sediments were also taken at Invertebrate/Extravert Cliff to assess the grain size distribution, C:H:N composition, and stable isotopic composition (C, N) of the upper 1 cm of sediments. Sediment texture and composition in the various treatments was quantified with the combined use of a laser particle sizer and visual verification with optical petrography by I. Aiello at Moss Landing Marine Laboratory. Particle size analyses were carried out with a Beckman-Coulter LS 13 320 laser particle size analyzer attached to an aqueous module equipped with a pump and a built-in ultrasound unit. Verification of grain types and visual calibration of grain sizes were carried out with petrographic microscopy analysis of smear slides.

#### *Statistical analyses*

Species accumulation curves for macrofauna were quantified with Mao's Tau in Estimate S (Colwell 2005) for each site. For each macrofaunal core, species richness ( $S$ ), Shannon's diversity index ( $H'$ ), Pielou's evenness ( $J'$ ), and abundance were calculated using Primer version 6 (Clarke 1993, Clarke and Warwick 2001, Clarke and Gorley 2006). Changes in overall

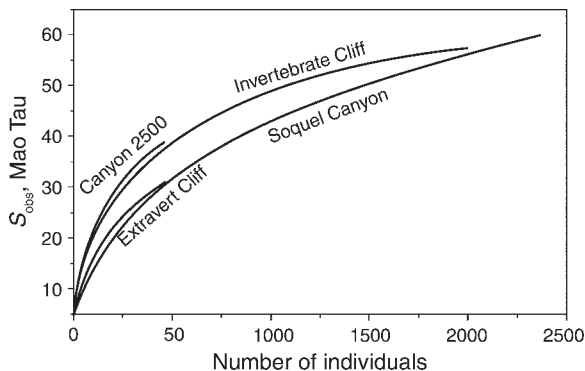


FIG. 3. Species accumulation curves (measured as Mao's Tau) for all four sampling sites.

community body size were assessed using the mean body size across species for each core. Each of the biotic and abiotic variables was regressed against distance from the cliff face using general linear models in JMP statistical software (SAS Institute 1989–2007). ANCOVA was utilized to test for differences in slope and intercept among dives (i.e., variation with sampling time) at Invertebrate/Extravert Cliff between measures of diversity, abundance, size, and distance decay and distance to cliff base. Because no significant differences were found between slope or intercept among the dives in any of the analyses, we report only the overall relationships with all dives grouped. As multiple analyses were conducted, we modified alpha levels using Bonferroni corrections such that  $\alpha = 0.01$  for Soquel and Canyon 2500 m with five faunal analyses each,  $\alpha = 0.005$  for Invertebrate and Extravert Cliff with 10 faunal analyses,  $\alpha = 0.0125$  for the four CHN analyses at Invertebrate Cliff, and  $\alpha = 0.025$  for flux analyses at Invertebrate Cliff.

To examine how similarity among assemblages changes with distance from the cliff face at each of the locations, we employed the distance decay of similarity method as described by Nekola and White (1999). Similarity between samples was quantified as Bray-Curtis similarity on presence/absence data. Decay was measured as change in similarity from the macrofaunal core closest to the cliff face, typically 1 m, and chosen at random when several replicates were available.

Several multivariate analyses were conducted using PRIMER version 6 (Clarke 1993, Clarke and Warwick 2001, Clarke and Gorley 2006). Bray-Curtis similarity was calculated between cores using both presence/absence and log-transformed data. Utilizing both presence/absence and log-transformed abundances allows us to explore variation in both species composition and the relative abundances among species. Nonmetric multidimensional scaling (MDS) was used to explore turnover between cores in a reduced multivariate space. MDSs were conducted with a standard 25 restarts and allowing dissimilarities, which are equal, to be represented in the final ordination by distances, which are not. Using the RELATE function in PRIMER, we

tested the correlation between the faunal similarity matrices and a model similarity matrix based solely on differences in distances between samples. We set up model matrices based on seriated samples (i.e., similarity decreases with increasing distance among cores), assuming faunal similarity changes significantly away from the cliff face. Additionally, for transects that span from Invertebrate Cliff, across the canyon floor, to Extravert Cliff we set up cyclical model matrices (i.e., similarity decreases with increasing distance but the ends of the transect are assumed to be similar), assuming that faunal similarity changes away from the cliff face but that cores the same distance from either cliff will be similar.

## RESULTS

### Macrofauna

In total 5280 individuals from 197 species were identified from the sampled sites (Soquel Canyon, 2366 individuals from 60 species; Invertebrate Cliff, 1993 individuals from 65 species; Extravert Cliff, 462 individuals from 33 species; and Canyon 2500, 459 individuals from 39 species). The species accumulation curve for Invertebrate Cliff is near asymptotic and at Soquel Canyon the addition of new species with increased sampling has slowed suggesting these sites have been reasonably well sampled (Fig. 3). The sampling curves for the remaining two sites, although clearly not asymptotic, do indicate that future sampling will likely return new species at a slower rate.

Macrofaunal abundance at Soquel Canyon is highly dominated by polychaetes (93%). The species composition is more equitable with 19 polychaetes, 21 crustaceans, 10 mollusks, and 10 species from other groups. At all the remaining sites polychaetes were also numerically dominant but ranged from 42% to 46% and from 23% to 52% of the total species. Crustaceans, including amphipods, isopods, and cumaceans were well represented in the samples both in terms of species richness (15–41%) and abundance (19–36%). Mollusks, primarily bivalves with a lesser contribution of gastropods, scaphopods, and aplousobranchs, ranged in representation from 27% to 31% of the species and 17% to 38% of the individuals.

The abundance of macrofauna per core did not change significantly across the canyon floor as distance increased from cliff faces, except potentially at Soquel Canyon where density was slightly suppressed near the cliff face (Table 2, Fig. 4O–Q). Species richness did not vary across the gradient at either Soquel Canyon or Canyon 2500, and was only marginally significant (and not so after Bonferroni adjustment) at Extravert Cliff (Table 2, Fig. 4L–N). However, species richness was reduced significantly near the cliff face at Invertebrate Cliff (Table 2, Fig. 4L–N). Shannon's diversity index ( $H'$ ) and Pielou's evenness ( $J'$ ) both increased with increasing distance from the cliff face at Canyon 2500, Invertebrate Cliff, and Extravert Cliff (Table 2, Fig. 4F–K). However, Soquel Canyon exhibited the opposite

TABLE 2. Regression statistics of environmental and biological variables measured as a function of distance ( $D$ ) from the cliff base.

Location, no. of samples	Analysis	Equation	$R^2$	$P$
<b>Soquel Canyon</b>				
18	no. individuals	$92.7 + 40.7D$	0.291	0.0253
18	no. species	$12.5 + 0.4D$	0.009	0.7144
18	$H'$	$1.6 - 0.2D$	0.550	<b>0.0007</b>
18	$J'$	$0.6 - 0.1D$	0.563	<b>0.0005</b>
17	distance decay	$72.7 - 19.1D$	0.557	<b>0.0006</b>
<b>Invertebrate Cliff</b>				
33	no. individuals	$27.9 + 1.7D$	0.012	0.5482
33	no. species	$8.9 + 2.8D$	0.382	<b>0.0001</b>
33	$H'$	$1.5 + 0.4D$	0.425	<b>0.0001</b>
33	$J'$	$0.7 + 0.1D$	0.296	<b>0.0011</b>
32	distance decay	$68.9 - 13.3D$	0.574	<b>0.0001</b>
33	biovolume	$0.3 + 0.3D$	0.157	<b>0.0044</b>
7	carbon mass in sediment at 0–1 cm (%), Jul 2006	$1.6 + 0.3D$	0.844	<b>0.0034</b>
7	carbon mass in sediment at 1–2 cm (%), Jul 2006	$1.8 + 0.3D$	0.531	0.0631
7	carbon mass in sediment at 2–3 cm (%), Jul 2006	$2.10 + 0.02D$	0.011	0.8238
6	carbon mass in sediment at 0–1 cm, Sep 2006	$1.6 + 0.4D$	0.710	<b>0.0081</b>
10	skewness of sediment grain size, Sep 2006	$-0.6 - 0.1D$	0.544	<b>0.0150</b>
10	skewness of sediment grain size, Aug 2007	$-0.3 - 0.1D$	0.496	<b>0.0105</b>
10	mass flux ( $\text{g}\cdot\text{d}^{-1}\cdot\text{m}^{-2}$ ) at 15 m off bottom	$5.8 - 0.5D$	0.882	<b>0.0001</b>
10	carbon flux ( $\text{g}\cdot\text{C}\cdot\text{d}^{-1}\cdot\text{m}^{-2}$ ) at 15 m off bottom	$0.2 - 0.01D$	0.807	<b>0.0004</b>
<b>Extravert Cliff</b>				
26	no. individuals	$24.4 + 1.7D$	0.016	0.5345
26	no. species	$6.9 + 1.6D$	0.217	0.0165
26	$H'$	$1.4 + 0.2D$	0.453	<b>0.0002</b>
26	$J'$	$0.8 + 0.1D$	0.280	0.0054
25	distance decay	$77.5 - 18.4D$	0.757	<b>0.0001</b>
26	biovolume	$0.3 + 0.3D$	0.39439	<b>0.0002</b>
<b>Canyon 2500</b>				
20	no. individuals	$25.9 - 2.9D$	0.068	0.2658
20	no. species	$8.1 + 1.5D$	0.174	0.0671
20	$H'$	$1.7 + 0.24D$	0.424	<b>0.0019</b>
20	$J'$	$0.8 + 0.1D$	0.505	<b>0.0004</b>
19	distance decay from base sample 1	$64.7 - 12.2D$	0.660	<b>0.0001</b>

Notes: Bold indicates significance with Bonferroni corrections; see *Methods* for explanation.  $H'$  is Shannon-Wiener index;  $J'$  is Pielou's evenness; distance decay is the faunal similarity change over distance; and biovolume is the average size ( $\text{mm}^3$ ) across species for a sample.

pattern with both  $H'$  and  $J'$  greatest near the cliff face (Table 2, Fig. 4F, I). At both Invertebrate and Extravert Cliff, species in the communities near the cliff face were significantly smaller in body size than compared to the rest of the transect (Fig. 5A, Table 2).

At all sites, a turnover of  $\sim 40\%$  in species was observed over the sample gradient (Fig. 4C–E, Table 2). At Canyon 2500, Invertebrate Cliff, and Extravert Cliff this occurred over 100 m and at Soquel Canyon  $< 50$  m. This pattern of change was also apparent in multivariate space with the distribution of individuals among species and species composition changing over the gradient (Fig. 6, Table 3). In general, the highest rate of faunal turnover was observed closest to the cliff face. Species turnover within the first 15–30 m adjacent to the cliff face exceeded that over the rest of the transect. In the MDS plots (Fig. 6) this results in a relatively large distance in multivariate space between individual samples  $< 30$  m compared to those occurring at  $> 30$  m. For example at Soquel Canyon, Canyon 2500, and Invertebrate Cliff (September 2006), samples  $< 15$  m from the cliff base occupied a large percentage of the

multivariate space (Fig. 6). Samples  $> 15$  m occupied relatively smaller areas considering the amount of physical distance separating those samples.

The model matrices and faunal similarity matrices based on presence/absence and abundances were significantly correlated across all sites, implying that continuous changes in assemblages are related to distance from the cliff (Table 3). The pattern also remained regardless of seasonal changes or location along the cliff face at a single site. Macrofaunal assemblages at Invertebrate Cliff were sampled in December, September, November, and July 2006 as well as February 2007. In each the strong gradient in community structure remains. Interestingly, samples from the middle of the canyon displayed little seasonal variation (Fig. 6, lower panel). However, samples adjacent to the cliff face ( $> 12$  m) exhibited variation over the course of the sampling period. Invertebrate and Extravert Cliff occupy opposite sides of the same 200-m canyon, and thus represent a continuum from cliff face to canyon floor to cliff face. Nevertheless, the assemblages near the cliff base on either side of the canyon axis at this site were more

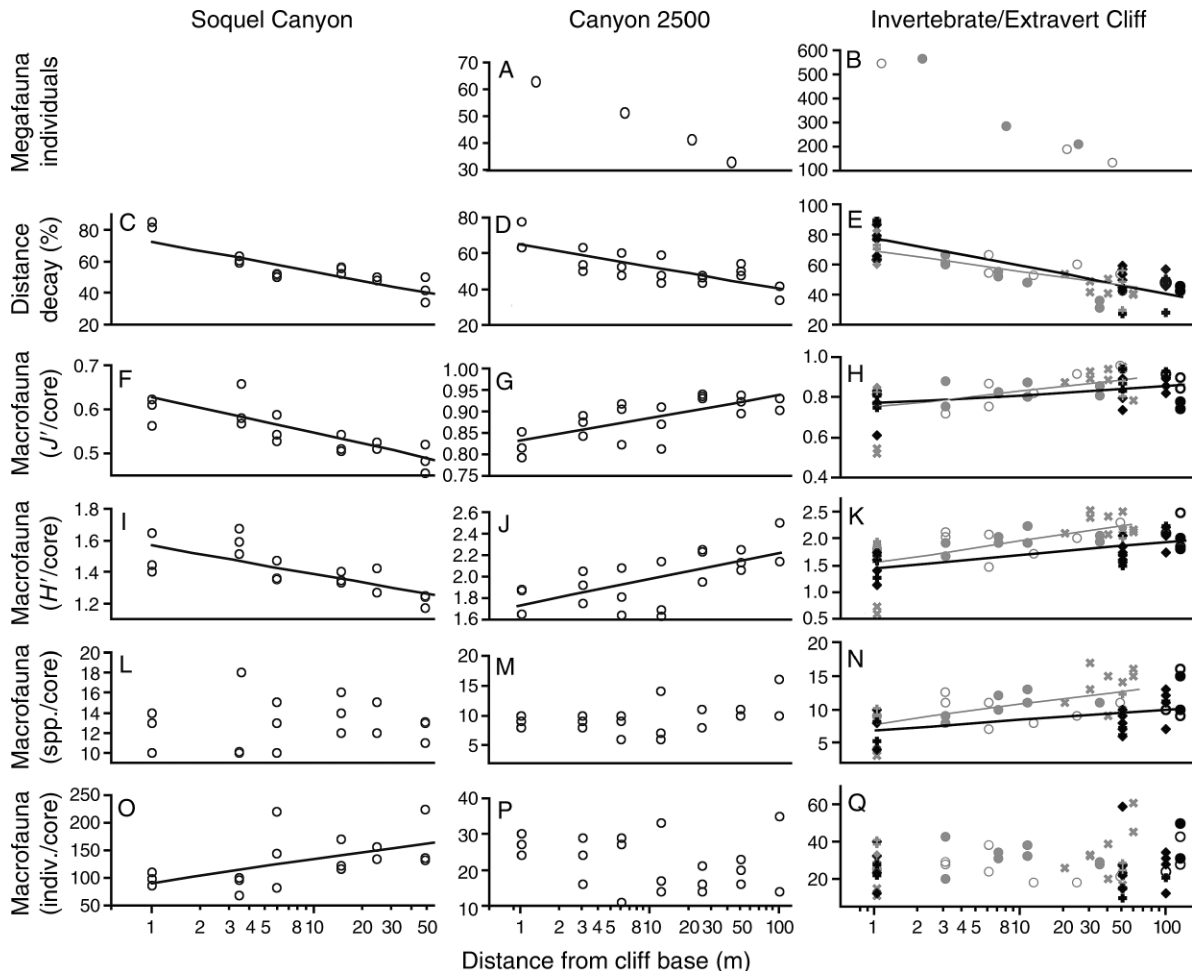


FIG. 4. Biological attributes of soft-bottom benthic macrofaunal and megafaunal communities at Soquel Canyon, Canyon 2500, and Invertebrate/Extravert Cliff as a function of distance from the cliff base, plotted on a log scale. At Invertebrate/Extravert Cliff, Invertebrate Cliff is denoted by gray symbols and Extravert Cliff by black with varying symbol type denoting different seasons and ROV dives. Regression statistics are given in Table 2. (A, B) The number of megafaunal individuals seen on 100-m video transects parallel to the cliff face. (C–E) Distance decay of similarity based on Bray-Curtis similarity matrix of presence/absence (see *Methods* for details). (F–H) Pielou's evenness ( $J'$ ) per macrofaunal core. (I–K) Shannon's diversity index ( $H'$ ) per macrofaunal core. (L–N) The number of macrofaunal species per core. (O–Q) The number of macrofaunal individuals per core.

similar than assemblages just 50 m away from the cliff base. MDS plots for Invertebrate/Extravert Cliff (Fig. 6) demonstrate this clearly, with assemblages at 1 m and 200 m from Invertebrate Cliff (the latter being samples at the base of Extravert Cliff), forming a distinct cluster in multivariate space compared to those assemblages in the middle of the canyon. Formally testing this hypothesis using a model of similarity based on distances from the cliff faces, assuming samples at the ends of the transect were more similar, yields a significant correlation between the model and faunal similarity matrices (Table 3).

#### *Megafauna and environmental variation*

Megafaunal densities were greatest near the cliff face both at Canyon 2500 and Invertebrate Cliff (Fig. 4A, B). An ANOVA including location (Canyon 2500, Inverte-

brate Cliff 1 and 2), wall distance (near, mid, far), and interaction effects produced significant relationships with all three effects (total model,  $df = 9$ , within,  $df = 6$ ,  $R^2 = 0.99$ , model,  $SS = 243363$ , error,  $SS = 9$ ,  $F = 3208.6$ ,  $P > 0.0125$ ; distance group,  $df = 2$ ,  $SS = 59232$ ,  $P > 0.0116$ ; location,  $df = 2$ ,  $SS = 9729$ ,  $P > 0.0072$ ; interaction,  $df = 4$ ,  $SS = 36317$ ,  $P > 0.0223$ ). The amount of material arriving at the seafloor both overall and in terms of carbon also was significantly higher at the cliff face at Invertebrate Cliff (Fig. 5B, C, Table 2). Proto-branch bivalves of the genus *Yoldiella* were found in sediment traps near the cliff face. Because byssus are unknown in both adult and juvenile proto-branches, a thread drifting behavior is highly unlikely, indicating that higher flux near the wall resulted from material raining off the cliff face (Gustafson and Reid 1988). The sediment grain size distribution at Invertebrate and

Extravert Cliff, with larger particles occurring near the cliff face (Fig. 5D, Table 2), also supports this scenario. The sediment near the cliff face possesses both a greater frequency of coarse granitic material, the composition of the cliff, and large fecal pellets attributable to the increased densities of megafauna. The percentage carbon of the sediment in the top 1 cm is greatly reduced at both Invertebrate and Extravert Cliff (Fig. 5E, Table 2).

#### DISCUSSION

##### *Patterns of diversity and standing stock in submarine canyons*

Here we report a significant shift in macrofaunal assemblages across <100 m mirroring a stark environmental gradient produced by cliff faces in a deep-sea submarine canyon. This ecological reorganization reflects significant changes in species composition and richness, relative abundances, and average body size. At all sites, a faunal change of ~40% was exhibited over <100 m and at one site <50 m (Fig. 4C–E). Near cliff face communities were typically numerically dominated by a few species (Fig. 4G, H). At the best-sampled site, Invertebrate Cliff, macrofaunal diversity was significantly lower near the cliff face, with cores containing 1–11 species compared to 5–17 species found mid-canyon (Fig. 4N). The average body size of macrofaunal species was fourfold greater away from cliff faces. Combined with lack of pattern in abundance, the results suggest that overall macrofaunal biomass may be suppressed near cliff faces. To summarize, soft-sediment macrofaunal communities near cliff walls in Monterey Canyon were compositionally different, in some cases species poor, extremely uneven, and typically of smaller body size and biomass than their mid-canyon counterparts. With all these metrics, the greatest change in ecological structuring occurred in the 15 m closest to the cliff face. This evidence suggests that cliff faces through their control of either biotic or abiotic features significantly alter deep-sea assemblages.

##### *Processes regulating diversity in submarine canyons*

Like their terrestrial counterparts, submarine canyons possess considerable habitat heterogeneity. Across scales, stark environmental gradients and physical barriers related to topography may lead to genetic isolating mechanisms (Nevo 1995) or produce novel microhabitats and communities (Chikatunov et al. 1997, Larson et al. 2005). For submarine canyons, many of these processes are similar. Differing canyons or sections of a single canyon may vary significantly in their topography and hydrodynamic regimes (Inman et al. 1976, Yoklavich et al. 2000, Allen et al. 2001). Changes in bathymetry, some abrupt, within canyons correlate to changes in abiotic factors such as oxygen, temperature, and resource availability (Vetter and Dayton 1999). Flow dynamics within canyons may create patches that vary in sedimentation, larval recruitment, and flow-

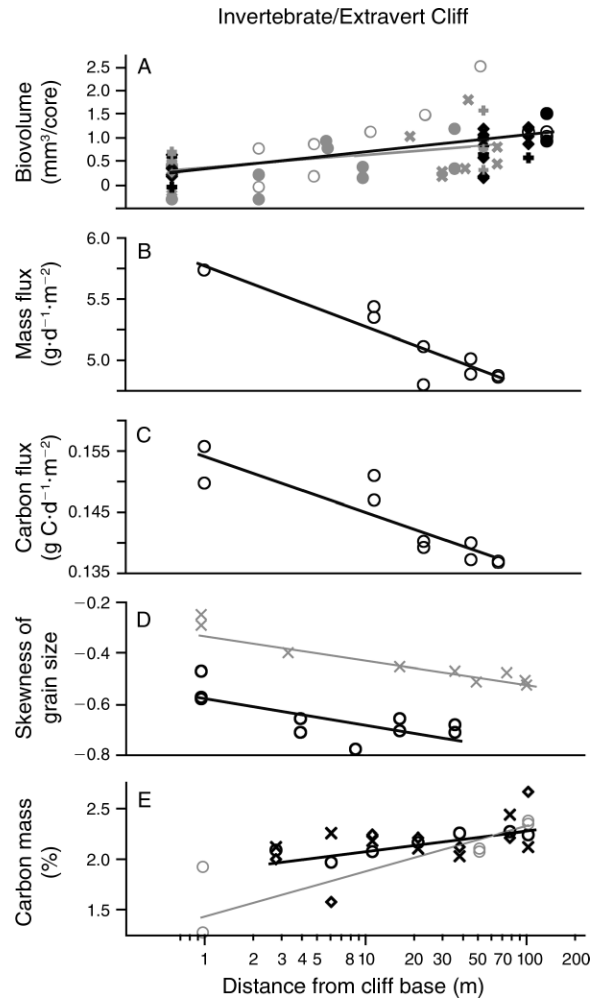


FIG. 5. Biological and environmental attributes at Invertebrate/Extravert Cliff in relation to distance from the cliff base, plotted on a log scale. Invertebrate Cliff is denoted by gray symbols, and Extravert Cliff by black with varying symbol type denoting different seasons and ROV dives. Regression statistics are given in Table 2. (A) Average biovolume across all species per core, (B) mass flux in sediment traps deployed 15 m off the bottom, (C) carbon flux in sediment traps deployed 15 m off the bottom, (D) skewness of sediment grain size distribution from cores, and (E) percentage of the total mass of carbon in the sediment from cores.

related disturbance (Allen et al. 2001, Kuhnze et al. 2002). Turbidity flows, a flow of dense, muddy water moving down a slope due to currents, can create a significant disturbance regime that varies along both the main canyon axis and between the main canyon axis and ancillary canyons (Kneller and Buckee 2002, Xu et al. 2002).

For deep-sea submarine canyons, one of the largest influences of habitat heterogeneity may be the alteration of food quantity and quality available to the benthos (Vetter and Dayton 1998, 1999, Okey 2003). With the exception of chemosynthetic communities, deep-sea



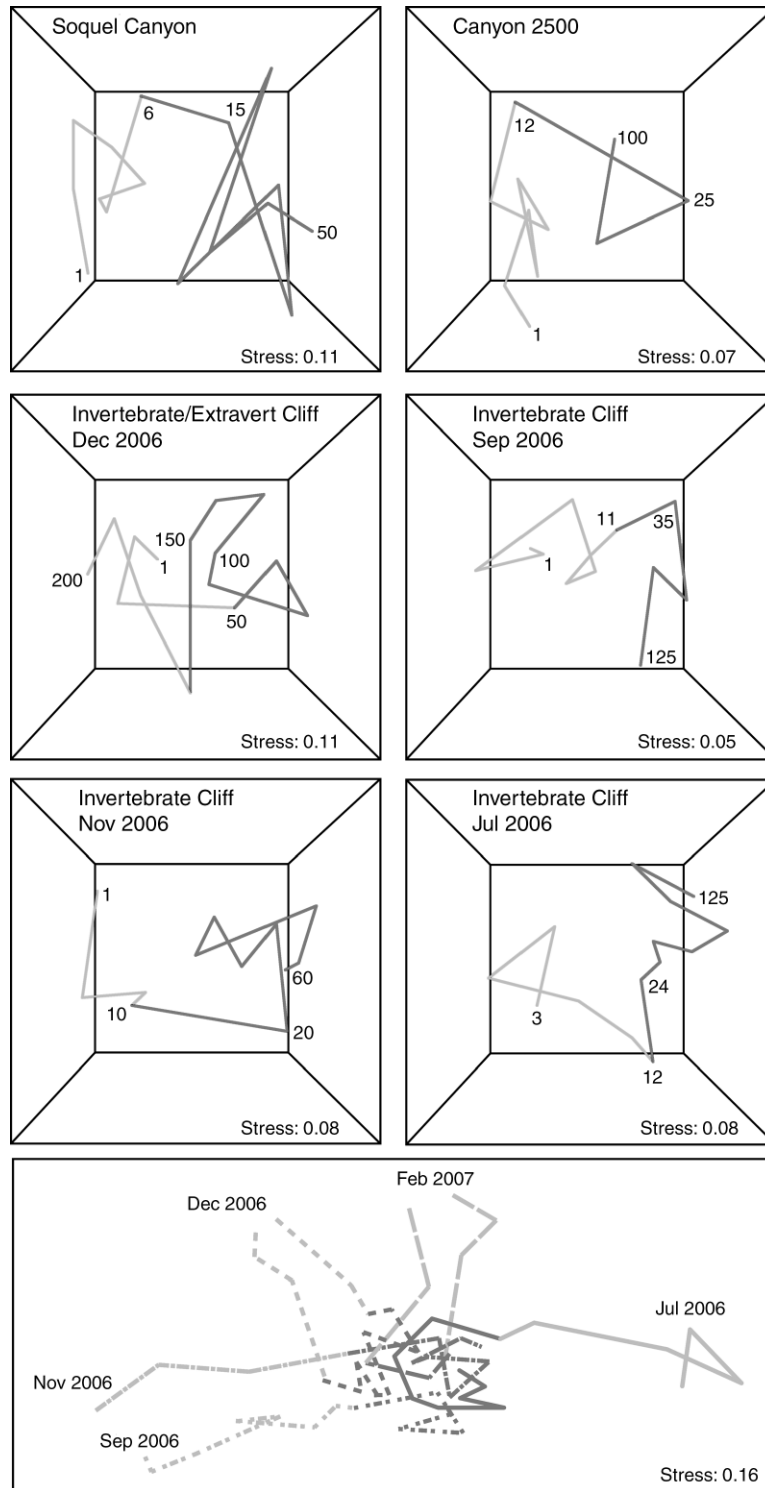


FIG. 6. Multidimensional scaling plots of Bray-Curtis similarity matrices based on  $\log(x + 1)$  abundance data for each site. Statistics are given in Table 3. Lines connect adjacent cores in transects away from the cliff base. Numbers denote distance from cliff face (in meters) at each site. For clarity, not all distances or cores are labeled. Distances  $<12$  m are denoted in light gray, and those  $>12$  m are in dark gray. The bottom panel shows changes in structure over varying seasons and dives (denoted by different line styles).

TABLE 3. Results of a RELATE test of correlations between a model matrix of seriation or cyclicity based on distances to cliff face and a matrix based on Bray-Curtis similarities of macrofaunal assemblages for both presence/absence and  $\log(x + 1)$  abundance data.

Site	Dive	Date	Model matrix	Log( $x + 1$ )		Presence/absence	
				Rho	<i>P</i>	Rho	<i>P</i>
Invertebrate Cliff	V2856	Jul 2006	seriation	0.32	0.0342	0.26	0.0418
Invertebrate Cliff	V2880	Sep 2006	seriation	0.53	0.0002	0.45	0.0008
Invertebrate Cliff	V2928	Nov 2006	seriation	0.37	0.0062	0.29	0.0097
Invertebrate/Extravert Cliff	V2932	Dec 2006	cyclicity	0.27	0.0170	0.24	0.0330
Invertebrate/Extravert Cliff	V2979	Feb 2007	cyclicity	0.45	0.0050	0.41	0.0072
Soquel Canyon	V3058	Aug 2007	seriation	0.22	0.0370	0.20	0.0534
Canyon 2500	T1125	Aug 2007	seriation	0.33	0.0403	0.27	0.0501

communities are dependent upon the sinking flux of organic debris derived from primary production near the sea surface (Smith 1985, Levin et al. 2001). From local to global spatial scales and ecological to evolutionary time scales, a host of deep-sea phenomena are related to variation in carbon input (Smith 1986, Gooday et al. 1990, Smith et al. 1997, Levin et al. 2001, Gooday 2002, Ruhl and Smith 2004, McClain et al. 2005, 2006, Rex et al. 2006). Submarine canyons serve as conduits for the transport of organic material from nearshore and terrestrial sources to the deep sea, leading to increased megafaunal and macrofaunal biomass (Vetter and Dayton 1998, 1999) compared to non-canyon habitats. We hypothesize that canyon topography also affects this process greatly, thereby increasing patchiness in food availability, a long-predicted structuring agent of deep-sea communities (Snelgrove et al. 1992, Snelgrove and Smith 2002), within the canyon. Here, we show that the input of organic debris to the canyon floor is enhanced near cliff bases (Fig. 5B, C) either due to the channeling of sinking material down the cliff face and/or potential variation in flow across the canyon ultimately creating different patches with contrasting assemblages.

Increases in megafaunal density near the cliff face suggest that biogenic interactions between different faunal components and biogenic disturbance may underlie the observed patterns. Globally, megafauna biomass and abundance reflect variation in food availability at depth (Rex et al. 2006). Temporally, standing stock and activity of megafauna, especially echinoderms, can radically increase with pulses of detrital material to the seafloor (Bett et al. 2001, Ruhl and Smith 2004). The megafauna response, both in terms of colonization and population response, to increase food availability can be rapid (Gooday et al. 1990, Wigham et al. 2003). Megafauna can account for near-half to near-total removal of this flux (Miller et al. 2000, Bett et al. 2001). The increase in megafaunal density (Fig. 4A, B), decreased carbon content of the sediment (Fig. 5E), and potentially lower macrofaunal biomass support the notion that megafauna are dominating the consumption of increased carbon flux near the cliff face.

The large, mobile deposit feeders and scavengers of the deep-sea floor and their effects on the surrounding

seafloor can be viewed as an analogue to terrestrial vertebrates and their regulation of ecosystem structure and function (Du Toit and Cumming 1999). Large megaherbivores can both increase and decrease the availability of resources to other faunal components through the domination of a food resource (Pianka 1973), altering vegetative complexity (Janzen 1976, Pringle 2008), or by serving as ecosystem engineers through production of biogenic structures (Jones et al. 1994, Wright et al. 2004, Davidson and Lightfoot 2008). In marine systems, megafauna alter the soft sediment benthos through burrowing, tube-building, feeding, defecating, and simply moving along the sediment surface. These activities can alter vertical distribution of sediment grain sizes, destabilize or facilitate resuspension of sediments, and alter sediment oxygen profiles by physically reworking the sediment (Rhodes and Young 1970, Wilson 1981, 1991, Mann 1982). Increases in individual activity levels and density afforded by increased energy availability lead to greater bioturbation intensity, e.g., a 50% increase in carbon flux leads to 2–4-fold increase in bioturbation (Smith et al. 2008). Thus bioturbation by megafauna represents a form of disturbance for infaunal communities.

Given the dynamic nature of canyon environments and the near-doubling of megafaunal densities near the cliff face, we hypothesize that the macrofaunal benthos near the cliff face is likely experiencing high levels of disturbance. The changes we observe, e.g., changes in evenness and richness, at high (near the cliff face) and intermediate disturbance levels (mid-canyon) are largely in agreement with intermediate-disturbance theory (Connell 1978, Huston 1979) and empirical work for shallow water systems (Thrush 1988, Wilson 1991, Widdicombe and Austen 1998, 1999, Ellis et al. 2000, Widdicombe et al. 2000). The reduction in body size at the cliff face might be expected if small “weedy” species are quicker to colonize and reproduce compared to larger-sized species. Additionally, we observed an absence of tube-building polychaetes and amphipods in near cliff face communities consistent with findings that the removal of mobile deposit feeders leads to increases in the density of tube-building species (Wilson 1991). Experiments in the deep sea on nekton falls, hypothesized to replicate low levels of disturbance

(Smith 1985, 1986), provide some evidence that megabenthic disturbance reduces richness, evenness, and the total density of macrofauna, but with no significant change in the taxa present. Reducing disturbance by using deep-sea caging experiments that excluded large, mobile megafauna led to increases in nematode abundance (Gallucci et al. 2008) but decreases in polychaetes and copepods (Thistle et al. 2008). However the lack of changes in one of these studies, combined with equivocal results of others, led one study to conclude that megafauna were unimportant in accounting for high species coexistence in the deep sea (Gallucci et al. 2008). Our results, and work from previous studies focusing on the diversity impacts of biogenically produced structures (Thistle 1979, 1983, Smith et al. 1986), suggest megafauna are important habitat modifiers in the deep sea with measurable effects on macrofaunal biodiversity.

Macrofaunal community response varies with both depth and season (Figs. 4 and 6), potentially reflecting spatial and temporal variation in carbon flux. While Soquel Canyon, our shallowest site, displayed a similar compositional change away from the cliff face, the gradients in richness, diversity, and abundance, contrasted to the deeper sites (Figs. 4 and 6). The higher overall quantity and quality of carbon availability at this site, due to its shallower depth and proximity to shore, could produce a stronger gradient in flux or conversely overwhelm a trend produced by the presence of the cliff face. Our results suggest the former might be the most likely scenario. The lower density of macrofauna and higher evenness near the cliff face at Soquel Canyon under potentially greater megafaunal density is consistent with intermediate disturbance theory prediction of preferential effects on the most numerically dominant species. Seasonal fluctuations were also detectable at Invertebrate/Extravert Cliff (Fig. 6). Seasonality in composition of species at the cliff face, echoing the seasonality in overall surface production in Monterey Bay (Pennington and Chavez 2000), supports the hypothesis that the gradient in carbon flux is underlying these community level changes.

#### CONCLUSIONS

Utilizing precision spatial coring with a remote-operated vehicle, we are able to quantify a gradient in diversity over an often-ignored spatial scale in deep-sea studies. At spatial scales >1 m and <100 m, we find an astounding degree of ecological reorganization in a submarine canyon related to microhabitat heterogeneity. Large changes (~40%) in species composition were detected over <100 m across all sites despite variation in depth, overall resource availability, and oxygen concentration. Our work, combined with previous studies, demonstrates that submarine canyons, a pervasive feature of the world's oceans, may enhance both  $\beta$ - and  $\gamma$ -diversity (Vetter and Dayton 1998, 1999, Schlacher et al. 2007) and ultimately lead to greater diversity at landscape and global scales in the deep sea.

We also begin to link the regulation of diversity to potentially cascading processes (habitat heterogeneity in submarine canyons  $\Rightarrow$  patchiness in food resources  $\Rightarrow$  gradients in megafaunal density and bioturbation  $\Rightarrow$  varying disturbance patches) demonstrating that multiple linked processes related to habitat heterogeneity, ecosystem engineering, and bottom-up dynamics maybe important to deep-sea biodiversity. Decreases in macrofaunal diversity at higher flux levels, demonstrated in some instances here, may also explain the decline of macrofaunal diversity with increased food availability seen at larger spatial scales in the deep sea, such as with depth (Rex 1973). Overall more work will be required to fully understand these linkages. However, our preliminary findings present several testable hypotheses about ecological dynamics on the seafloor that may serve to guide future research and refine our understanding of deep-sea processes.

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