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Contrasting effects of substrate mobility on infaunal assemblages inhabiting two high-energy settings on Fieberling Guyot

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ABSTRACT

The influence of seamount-intensified flows on the structure of infaunal assemblages was examined at two sand-covered sites located 2.3 km apart atop the summit plain of Fieberling Guyot (32°27.6'N 127° 48.0'W). Both sites experience strong, tidal bottom currents with flows exceeding 20 cm/s on a daily basis (4 mab). Estimates of shear velocity (u_*) did not differ significantly between the two sites. However, differences in sediment composition and density produced different sediment transport regimes at the two sites. At Sea Pen Rim (SPR), located on the NW perimeter (635 m), sedimentary particles were composed primarily of basaltic sands that experienced negligible transport during the study period. At White Sand Swale (WSS, 580 m), a narrow valley enclosed on three sides by basalt outcrops, sediments were composed almost entirely of foraminiferal sands that moved daily. Sediment organic content and microbial abundances were similar at the two sites. Infauna (> 300 μm) had higher densities at WSS ($1870/m^2$) than SPR ($1489/m^2$), but lower expected species richness. Although the 2 sites shared nearly 50% of identified species, peracarid crustaceans, echinoderms, sponges, and bryozoans were proportionally more important in the stable substrates of SPR, while turbellarians, bivalves, and aplacophorans were better represented in the shifting sands of WSS. The infauna of WSS lived deeper in the sediment column ($> 50\%$ below 2 cm) than that of SPR ($> 50\%$ in the upper 1 cm), at least partly because the majority (83%) at WSS were subsurface burrowers with motile lifestyles. Tube-building and epifaunal lifestyles were more common at SPR than WSS, as were surface-deposit and filter-feeding modes.

Fences and weirs were deployed at the study sites for 6.5-wk and 6-mo periods to manipulate bottom stress. Changes in faunal patterns within weirs at WSS reinforced our conjecture that contrasting sediment transport regimes explain between-site differences in community structure. Fence effects varied with deployment period and site.

Topographic features on Fieberling Guyot produce heterogeneous sedimentary settings characterized by different transport regimes. Our results suggest that substrate mobility exerts primary control over infaunal community structure at the two high-energy sites.

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1. Introduction

The interaction of seamounts with ambient flow fields has numerous implications for geological and biological properties and processes on seamounts (Keating *et al.,* 1987; Smith and Schwab, 1989). Current intensification is commonly observed over seamounts in the form of eddies (Roden, 1987), internal tides (Noble *et al.,* 1988), trapped waves (Brink, 1989), or freely propagating currents from internal waves (Eriksen, 1982). Biological effects of this intensification can include enhanced productivity of plankton due to elevated local production and retention or entrainment of organisms (Boehlert and Genin, 1987; Boehlert *et al.,* 1992), increased size and density of suspension-feeding taxa on hard substrates (Genin *et al.,* 1986; Grigg *et al.,* 1987), as well as reduced faunal abundances and altered community structure in sediments (Levin and Thomas, 1989).

Studies of Pacific seamounts have documented several important mechanisms by which flow influences the geology and biology of the benthic boundary layer. Strong currents affect the seabed, locally molding loose sediments into bedforms such as ripples and dunes, sweeping sediment from and exposing bedrock surfaces, or eroding previously deposited sediment and truncating bedding horizons (Lonsdale *et al.,* 1972; Noble and Mullineaux, 1989; Cacchione *et al.,* 1988). Boundary layer flows resuspend, aggregate, and transport floc which concentrates in seafloor depressions of biogenic or physical origin (Reimers and Wakefield, 1989). On central Pacific seamounts, bottom current intensity was inversely related to the presence of fine sediments, sediment stability, organic content, and microbial abundance (Levin and Thomas, 1989). Abundance, species composition, and lifestyles of sediment-dwelling fauna exhibit variations in response to heterogeneity of both flow and sediment characteristics on seamounts (Kaufmann *et al.,* 1989; Levin and Thomas, 1989; Levin *et al.,* 1991a).

Much of the evidence for these associations is correlative and has been derived without detailed characterization of benthic boundary layer flow regimes. The HEBBLE (High Energy Benthic Boundary Layer Experiment) study, carried out at 4850 m on the Nova Scotia Rise (Gross and Williams, 1991; Aller, 1989; Thistle *et al.,* 1991) is one of the few investigations to integrate bottom-boundary layer (BBL) flow, sediment dynamics, and biological responses of deep-water faunas. Much of what is known about communities inhabiting high-energy regimes in the deep sea is based on the fine-grained HEBBLE region where episodic, storm-related events frequently transport sediments.

High-energy settings on seamounts differ from the HEBBLE environment in that above 2500 m, the sediments are commonly coarse-grained sands composed of autochthonous volcanic material or foraminifera tests (Levin and Nittrouer, 1987). These are often subject to periodic (e.g., diurnal), strong currents which are intensified by the interaction of the seamount with the ambient flow (Noble *et al.,* 1988; Genin *et al.,* 1989; Brink, 1989).

2. Program objectives

This investigation employed the high-energy sedimentary settings found atop Fieberling Guyot to examine hypotheses concerning control of infaunal community structure by bottom stress, sediment motion, and substrate characteristics. When the study was designed, we had intended to compare two sites with different bottom stress and sediment transport regimes. Our general working hypothesis was that topographically-induced heterogeneity in BBL flow fields would generate spatial variation in the structure of sediment-dwelling faunal assemblages. Before visiting Fieberling Guyot, we predicted that sediments at the NW Guyot perimeter (a) periodically experience stronger boundary shear stress and more frequent and intense suspended and bedload sediment transport than at the summit interior, (b) have slower rates of sediment accumulation than on the interior summit plain, and (c) have sediment that contains a smaller proportion of fine grains and organic matter than do interior sediments. Expecting the perimeter region to experience higher bottom stresses than more interior sites, we hypothesized that the perimeter sediments should exhibit reduced microbial and infaunal abundances and that the infauna should exhibit greater mobility, more surface feeding activity, deeper vertical distributions, and reduced species richness.

As current data became available, it became clear that we could not distinguish differences in bottom stress between our two study sites during the period of study. However, because there were dramatic differences in substrate composition and thus particle density, the two sites represented two very different sediment transport regimes with much more frequent sediment motion at the interior site. Thus, while some of our hypotheses regarding the effects of sediment motion on benthos were correct, most of our site-specific predictions were not.

3. Study site

Fieberling Guyot is a large, conical seamount located 992 km west of San Diego, California. It rises from a base at 4300 m water depth to a flat-topped summit plain which is oval in shape and has an approximate area of 9 km². Most of the summit plain lies between 500 m and 700 m water depth (Fig. 1), then drops sharply onto steep flanks. The summit is composed of basalt and lithified ash beds. Much of the summit plain is free of sediment and supports large populations of epifaunal suspension feeders (antipatharians, sponges, anemones, corals). These attain extraordinarily high densities near a shallow (438 m) pinnacle (Levin, pers. obs.). Sediments cover the seamount floor in small patches (<0.5 km²) between 500 and 600 m, and over much of the NW and western rim of the summit, between 600 and 700 m (Lonsdale, pers. comm.; Levin, pers. obs.). The eastern side of the summit plain has not been explored in detail.

Mesoscale circulation in the region surrounding Fieberling Guyot has been described by Roden (1991). The peak of Fieberling Guyot is located in the eastern,
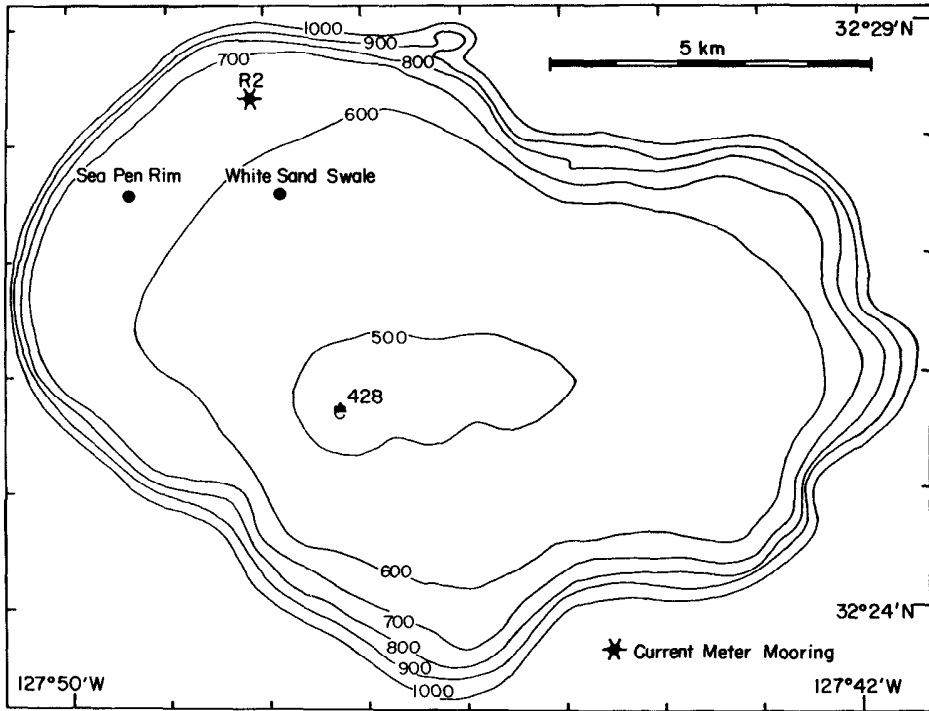
Figure 1. Location of sampling sites, Sea Pen Rim (SPR) and White Sand Swale (WSS) on the summit plain of Fieberling Guyot. The Guyot base occurs at a depth of approximately 4300 m. The mooring R2 contained a bottom-moored, upward looking acoustic doppler current meter, deployed from 9/15/90 to 10/9/91.

southward moving part of the subtropical Pacific gyre, near the outer boundary of the California current (Roden, 1991). Deep flow is generally in the opposite direction near the bottom. Currents atop Fieberling Guyot are dominated by diurnal fluctuations, driven by diurnal tides with amplitudes of 0.2 to 0.4 m/s or more (Eriksen, 1991). The current oscillations have characteristics of seamount-trapped waves (sensu Brink, 1989) which produce anticyclonically directed, low-frequency currents in the vicinity of the seamount summit. Waters overlying the seamount exhibit variable biological properties influenced by both the oligotrophic Pacific central gyre and the eutrophic California current. Primary production measured in September 1989 was 250 mg C m^{-2} da^{-1}, a value typical of the waters surrounding Fieberling Guyot (L. Haury, pers. comm.).

4. Materials and methods

a. Sample collection

Sampling was carried out at two sediment-covered locations, approximately 2.3 km apart atop the relatively flat summit of Fieberling Guyot (Fig. 1). The outer site,

referred to as Sea Pen Rim (SPR) (Fig. 2a, 32° 27.631'N, 127° 49.489'W), is located on the NW rim of the summit plain (Fig. 1) at a water depth of 630–640 m. Sediment cover by basaltic and calcareous sand in this area is extensive. The area is relatively flat (~ 5°), though steeper than the interior, but is within a few hundred meters of the rim and the steep flanks of the seamount.

The inner site, referred to as White Sand Swale (WSS) (Fig. 2b, 32° 27.581'N, 127° 47.839'W) is located about 3.7 km from the center of the summit plain. This site, situated in water depths of 580 to 585 m, is a narrow valley or swale that is 30–40 m wide, 300 m long, and is surrounded on 3 sides by 4 to 5-m high basalt cliffs. The swale floor is covered with a > 1-m thick carpet of nearly white, calcareous sand (Fig. 2b). The orientation of bedforms within the swale suggests that the currents are locally steered along its axis.

Sediments and infauna were sampled by the submersible *Alvin* during 3 cruises with the RV *Atlantis* II. These took place on Oct. 7–27 and Dec. 2–19 in 1990, and on June 20–27 in 1991. Faunal samples were collected by careful placement of spring-loaded, Ekman-style box corers (15 × 15 cm). Some larger Ekman-style box corers (16.2 × 16.2 cm) were used during the latter two cruises. Core samples were subdivided into quarters on board ship. Three quarters of each core were processed for infauna by sectioning sediments vertically at 0–1, 1–2, 2–5, and 5–10 cm intervals and preserving the unsieved sediments in 10% buffered formalin. The fourth quarter was sampled for bacterial counts and characterization of sediment properties as described below.

Sediments collected in boxcores or cylindrical tube cores (7 cm diameter × 10 cm depth) were analyzed for texture and composition. Grain size samples were sectioned from cores on board ship at 1 cm intervals to a 5 cm depth, and at 3 cm intervals at deeper levels. The samples were stored wet in Whirl-Pak bags until analysis. Cylindrical subcores (2 cm diameter × 10 cm depth) were taken for analysis of organic C, N, and $CaCO_3$ content and stored frozen until analysis. Bacterial counts were carried out on sediments collected in sterile 1-cm diameter glass tubes. One cc fractions from the 0–1, 2–3, 5–6, and 9–10 cm depth horizons were preserved in 9 ml of 2% glutaraldehyde and 0.2-μm filtered seawater. Samples were stored refrigerated until analysis 1–5 wk later.

b. *BASS tripod and least squares logarithmic profiles*

The turbulent bottom boundary layer was characterized by near-bed profiles of velocity. With the time series of velocity vectors, the mean horizontal speed profile is obtained from a logarithmic profile fit which gives estimates of the shear stress velocity scale, u_*, and bottom roughness scale z_o, (Gross *et al.*, 1992).

A Benthic Acoustic Stress Sensor (BASS) tripod was used to obtain the velocity data (Williams *et al.*, 1987). The BASS tripod consists of six current meters arrayed at 0.325, 0.675, 1.275, 2.125, 2.725 and 4.375 meters above the bed (mab). The 3-dimensional velocity vector is measured instantaneously by each current meter.
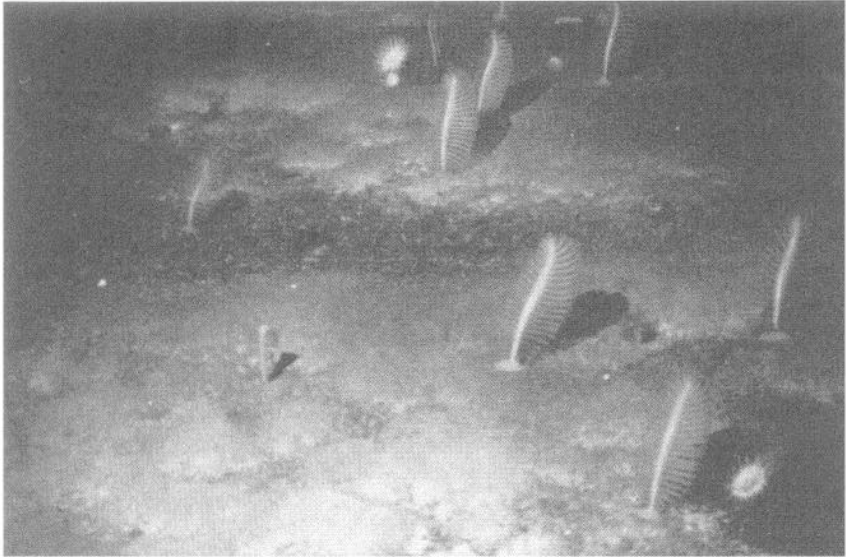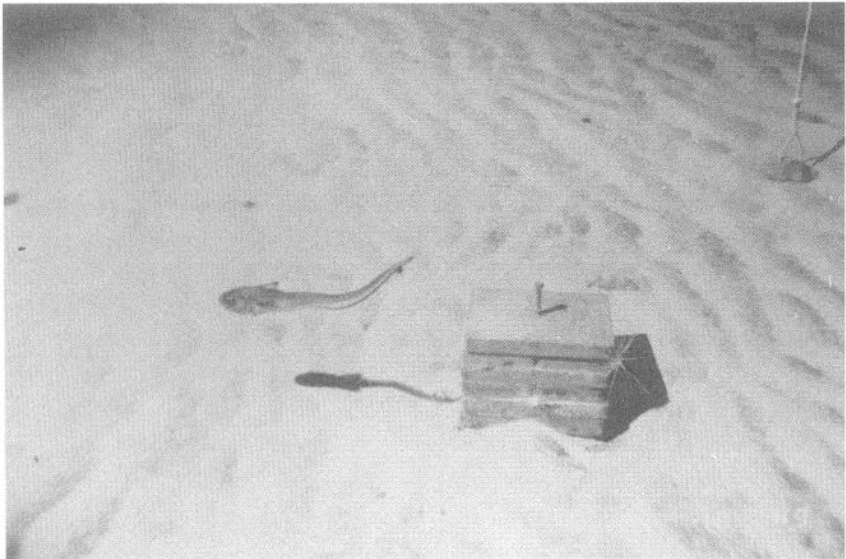
a

b

Figure 2. (a) Sea Pen Rim, located at 630–640 m on the northwest rim of the Fieberling summit plain (32° 27.631′N 127° 49.489′W). Seapens (*Pennatula* sp.) (~ 15 cm high) are the dominant epifaunal form on the predominantly basalt-sand substrate. (b) White Sand Swale, located at 580–585 m in a narrow valley in the Fieberling summit plain interior (32° 27.581′N 127° 47.389′W). Sediments are rippled foraminiferal sands. *Alvin* weights and a rattail fish appear in the foreground.

Average velocity and cross covariances are made of 10 minutes of data at the top of every hour. The BASS current meters have a resolution of ±0.03 cm/s and an accuracy of ±0.2 cm/s (Williams *et al.*, 1987).

The BASS tripod was deployed once at each site. Bottom velocity profiles were measured from Oct. 21–25, 1990, approximately 100 m north of WSS on cobbly sand (581 m, 32°26.631′N 127°48.049′W), and from Dec. 7–15, 1990, approximately 100 m west of SPR on coarse basaltic sand (635 m, 32°27.625′N 127°49.514′W). BASS was relocated upon the bottom by picking it up and moving between sites with the *Alvin* submersible. Regrettably, the sampling times at the WSS and SPR locations were cut short by a problem with the data recorder. Additional details regarding BASS measurements at these and several other sites atop Fieberling Guyot are reported by Gross (in prep.).

When a boundary layer forms over a uniformly rough bed in an unstratified, stationary flow, a logarithmic velocity profile is usually observed:

$$\overline{U}(z) = \frac{u_*}{\kappa} \log \frac{z}{z_o}$$

where u_* is the shear velocity scale and z_o represents the bed roughness length scale. The logarithmic profile is fit with least squares regression to the averaged data every hour. The average error in estimates of u_* and z_o are calculated from the overall distribution of regression coefficients (Gross *et al.*, 1992). Errors in estimates of roughness z_o are expressed as multiplicative, as the normal error estimate is for $\log(z_o)$. For WSS the estimated expected value of the regression coefficient was found to be $R = 0.96$ giving 95% error bands for $u_* \pm 0.36u_*$ and $z_o*/5.4$. For SPR the estimated expected value of the regression coefficient was found to be $R = 0.94$ giving 95% error bands for $u_* \pm 0.46u_*$ and $z_o*/8.5$. The boundary layer was not uniform-and regression coefficients were found to be lower than normally expected. However, the distribution of ½ atanh(R) was appropriately Gaussian.

c. Flow manipulation experiments

Cylindrical fences (50-cm diameter and 22-cm high) (Fig. 3a) formed of aluminum supports and plastic netting (2 cm × 1.5 cm mesh) were deployed by *Alvin* at each site to reduce bottom stress and enhance sediment deposition inside fences. Deployments were for 6.5 wk (Oct. to Dec. 1990) or 6 mo (Dec. 1990 to June 1991). Fences were held in place with T-handles that penetrated 32 cm into the seabed and protruded 26 cm above the fence mesh. Fenced sediments were sampled from the center of the fenced areas by box coring for evaluation of sediments and infauna. In Dec. 1990, 10 fences were sampled successfully, 6 at WSS and 4 at SPR. In June 1990, 9 fences were sampled, 5 at WSS and 4 at SPR.

Four weirs (Fig. 3b), designed to elevate bottom stress, were deployed by *Alvin* at WSS for 6.5 wk between Oct. and Dec. 1990. These were placed perpendicular to the
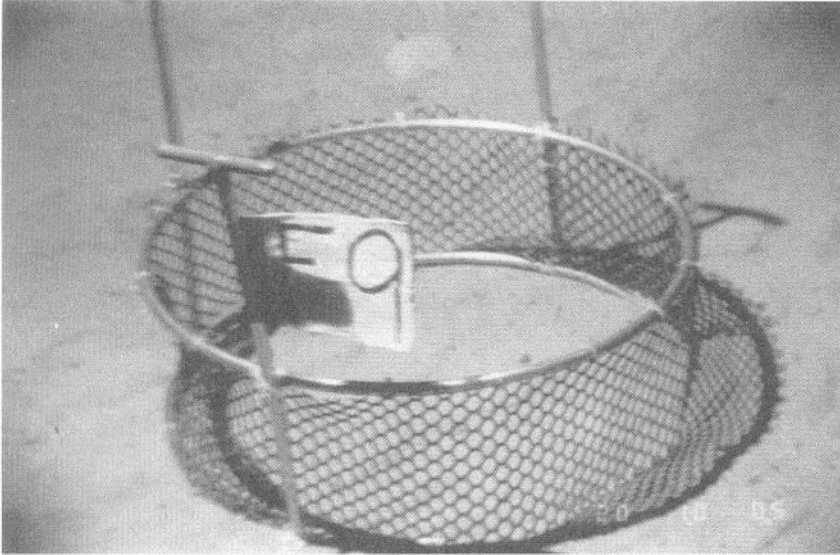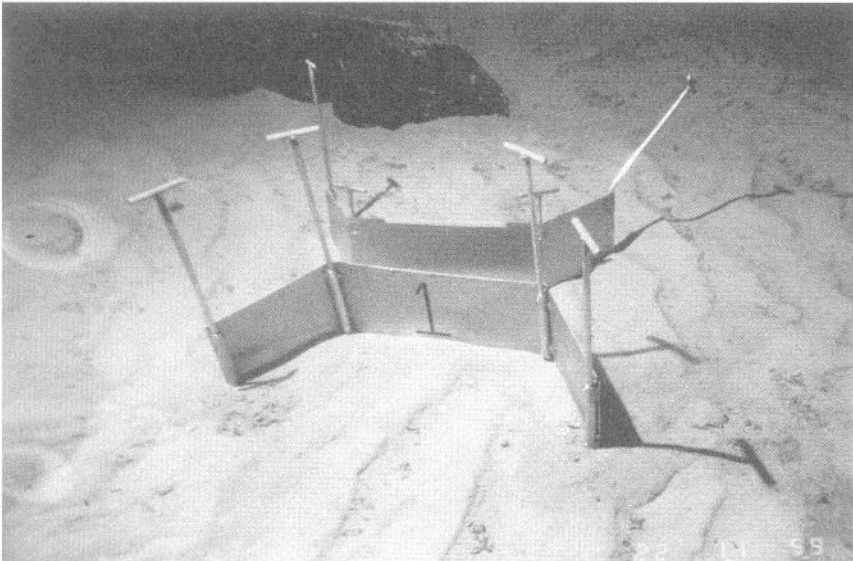
a

b

Figure 3. Flow-manipulation apparatus deployed on Fieberling Guyot. T-handles permitted *Alvin*'s mechanical arm to deploy the apparatus with as little disturbance as possible. (a) Cylindrical mesh fences, 50 cm diameter and 22 cm high, were designed to reduce bottom stress and enhance sediment deposition inside the fence. (b) Aluminum weirs, 20 cm-high with a 30 cm-wide and 48 cm-long corridor were designed to elevate bottom stress.

sand ripples. Three of these were sampled successfully. The weirs were made of ⅛″ thick aluminum and were 20 cm high. The interior corridor was 48 cm long and about 30 cm wide. Flanges 30 cm long were splayed from the corridor at 120° angles. Weirs were held in place with stakes as described above for fences. Weir sediments were sampled by box core in the central corridor.

d. Tracer particle experiments

Tracers were employed to make qualitative comparisons of sediment transport and burial at WSS and SPR. During Oct. 1990, colored particles of various size and composition were distributed with a shaker apparatus on the sediment surface in several (30 × 50 cm) patches at each site. We used blue aquarium gravel (1–2.5 mm diameter), SPR basaltic sand painted green (0.8–1.2 mm), orange-dyed quartz sand (0.2–0.5 mm) and WSS foraminiferal sands (0.25–0.50 mm) dyed with alizarin red. Tracer patches were marked with small posts and sediments were sampled by boxcore approximately 8 mo later in June, 1991. On board ship, sediments containing tracers were sectioned vertically at 1 cm intervals and stored wet in 60 ml vials.

e. Laboratory procedures

In the laboratory fauna were sieved, sorted, counted and identified for half of the sediments (2 quarters) from each boxcore. Infaunal samples were washed through nested 300-μm and 63-μm screens. Those taxa retained on the larger screen are reported here. While the majority of the individuals retained on the 300-μm screen belonged to traditional macrofaunal taxa, some, such as the turbellarians and oligochaetes, were meiofauna whose populations may not have been sampled as thoroughly.

The grain-size distribution of sediments was analyzed by standard sieve and pipette techniques. The sediments were first rinsed to remove salts, then sieved through a 64 μm (4 phi) screen to separate the sand and mud fractions. The dried sand fraction was sieved at half phi intervals (where phi = $-\log_2 D$, and D = nominal grain diameter in mm) using a Ro-Tap shaker. Dispersant was added to the mud fraction to prevent flocculation and pipette analysis was conducted to determine the proportions of silt and clay in the sample. The mean and modal grain size and sorting of each sample was determined by graphical techniques (Folk and Ward, 1957).

The composition of sand-sized particles in six surface samples was determined by visual examination under a microscope. Grains in each half-phi size class were examined separately. The relative proportions of basalt grains and foraminifera tests, the two most prevalent particles, and minor components such as sponge spicules, were tabulated. Following Cacchione *et al.* (1988), who conducted settling velocity experiments on sand-sized planktonic foraminiferal tests from Horizon Guyot, we assumed a density of 1.8 g/cc for similar tests in our samples. A torsion

density balance was used to determine an average density of 2.7 g/cc for basalt grains.

Carbonate content of surface sediments (0–2 cm) was determined by weight after leaching with 0.1 N HCl as described in Levin and Nittrouer (1987). Organic carbon and nitrogen content were determined for homogenized surface sediments (0–2 cm), following the removal of inorganic C, using a Carlo-Erba CNS analyzer. Direct counts of bacteria were made using acridine orange staining and epifluorescence microscopy as described in Levin and Thomas (1989). Sediments containing tracer particles were examined qualitatively under a dissecting microscope at 12× magnification to determine the depth of penetration and generalized vertical profiles of each tracer type.

f. Statistical analyses

Statistical analyses were performed on sediment and faunal data using General Linear Model procedures. Statistical significance was assumed for $P \leq 0.05$. However, P values > 0.05 and < 0.10 are discussed in light of small sample sizes resulting from logistical difficulties in collecting samples. ANOVA assumptions of symmetry, homogeneity of variance, and heteroscedasticity were checked for untransformed data by examining residual plots. When the assumptions were not met, square root, log or arcsine transformations were applied, and residuals were reexamined. The most suitable transformation was applied. Square root transformations ($\sqrt{x + 0.5}$) were applied to bacterial counts, all infaunal categories, and C:N ratios. Arcsine transformations were applied to all percentage data. When ANOVA results were significant, differences among means were evaluated with an *a posteriori* LSD test.

Nonexperimental (background) samples were examined for cruise (sampling date) and site (SPR vs. WSS) effects. When differences among cruises were not detected, data were combined to examine between-site variation. Treatment effects (background, fence, and weir) were examined within sites for each cruise. Interactions between site and vertical distribution of infauna in sediments were evaluated using a repeated measures analysis (where depth in the sediment was the repeated measures factor) followed by pair-wise comparisons of the adjusted means for data within a vertical fraction using an appropriate error term. Estimates of species richness, $E(S_n)$, as a function of sample size (rarefaction analyses) were made using the following equation:

$$E(S_n) = \sum_{i=1}^{S} \left[1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right]$$

where S is the number of species, N is the number of individuals, N_i is the number of individuals of species i, and n is the total target population (Hurlbert, 1971). Infaunal

taxonomic representation, lifestyles and vertical distributions were compared between sites using *t*-tests for each cruise separately and for all three sampling dates combined. Faunal feeding mode, dwelling habits, and mobility patterns were assigned based on information in Fauchald and Jumars (1979) and on personal observations of animal morphologies, distributions, and dwelling structures. Turbellarians were all assumed to feed as carnivores or scavengers.

5. Results

a. Bedform and epifaunal descriptions

i. Sea Pen Rim. Sea Pen Rim was located on a large expanse of sediment covering the northwestern summit rim. Over a relatively large area explored (1 × 3 km), at least two scales of bedforms were present. Low amplitude dunes, in excess of 5 m in wavelength and tens of cm high, were the largest bedforms observed. The dunes were composed of dark brown basaltic gravel, chocolate brown basaltic sand and silt, and white foraminiferal sand. The dune crests were rounded and did not appear to be actively migrating. Their rounded, degraded appearance suggests a relatively long period of immobility.

Smaller-scale bedforms were observed in the area, and included both two-dimensional, asymmetric, sinuous-crested ripples and three-dimensional ripples with wavelengths of 10–30 cm and heights of a few cm. In some cases the ripples were superimposed on the larger dunes, while in other cases the ripples formed on light-colored patches of sand overlying flat surfaces covered with dark, basaltic gravel. The small-scale ripples were commonly sharp-crested, suggesting that they were recently active, but no sediment transport was observed during the dives.

Sediment cover was over 90%, with pebbles, rocks and boulders distributed throughout the area. Many individuals (0.5 to 1/m²) of the sea pen *Pennatula* sp. were present on sediments (Fig. 2a). Basalt surfaces supported numerous filter-feeding organisms including antipatharians (*Stichopathes* sp.), gorgonians, sponges, crinoids, bamboo corals, anemones, solitary corals and holothurians. Rattail fishes were also common.

ii. White Sand Swale. Sediment cover was primarily white, rippled, foraminiferal sands (Fig. 2b). Basaltic boulders were sparsely distributed in the swale and were surrounded by rippled sand. In several cases, evidence for scour of the sand on the southern, upcurrent side of the boulders was observed. The ripples were asymmetric toward the south, although in some places subdued remnants of older sets of ripples oriented in almost perpendicular directions were observed in the ripple troughs. The southward-directed ripples were sinuous-crested, 2-dimensional forms in some places, and 3-dimensional forms in other places. Typical wavelengths were 10–20 cm, and typical heights were a few cm. The ripple crests were sharp during each dive, suggesting active sediment transport.

Table 1. Characteristics of sediments at Sea Pen Rim (SPR, 635 m) and White Sand Swale (WSS, 580 m) on the summit plain of Fieberling Guyot.

| | SEA PEN RIM | | WHITE SAND SWALE | | ANOVA (P) | |
	mean	(SD)	mean	(SD)	Site	Cruise (within site) SPR/WSS
Grain Size	n = 6		n = 7			
% Gravel	2.66	(3.01)	0.05	(0.05)		
% Sand	93.09	(2.11)	96.02	(2.95)	NS	NA
% Silt	3.60	(2.79)	1.56	(1.60)	NS	NA
% Clay	0.93	(0.66)	2.38	(2.18)	0.06	NA
Mean (phi)	1.17	(0.62)	1.36	(0.41)	NS	NA
Sorting	1.23	(0.35)	0.82	(0.35)	0.06	NA
Organic Composition	n = 9		n = 13			
% Organic C	0.134	(0.028)	0.119	(0.034)	NS	NS/NS
% Organic N	0.016	(0.002)	0.014	(0.004)	0.08	NS/NS
C:N Ratio	8.16	(1.39)	8.31	(0.64)	NS	NS/NS
CaCO$_3$ (%)	n = 8		n = 11			
	19.9	(9.6)	82.4	(6.7)	<0.001	NS/NS
Bacterial Counts						
(0–1 cm)	n = 11		n = 21			
(no. × 10^8/ml)	2.06	(0.98)	1.91	(0.66)	NS	NS/0.07 (Oct. < June)

NS = Not Significant, NA = Not Available.

Rattail fishes were very abundant (often ~0.5 to 1/m^2) in bottom waters and on the sea floor. Other mobile epifauna included large (0.5 m-diameter) spider crabs, and small (5 cm-diameter) white sea urchins (*Caenopedina diomedeae*). An attached fauna similar to that at Sea Pen Rim was present on the basalt walls surrounding the swale and on rocks or boulders distributed on the rippled sands.

b. Sediment texture and composition

Surficial (0–1 cm) sediments (unmanipulated) were examined for 6 cores from SPR and 7 from WSS. Surface samples at both sites were composed primarily of sand-sized sediments (>64 μm or 4 phi) with small proportions of silt and clay (Table 1, Fig. 4). Gravel-sized particles (>2 mm or −1 phi) were significantly more abundant in the SPR samples compared to WSS samples (Table 1).

Sediments from SPR had a mean grain size of 1.17 ± 0.25 phi (0.37–0.53 mm) and were poorly sorted (Table 1). Modal grain sizes were in the coarse and medium sand classes, ranging from 0.5 to 1.5 phi (0.71 to 0.35 mm). The modal class and most of the particles larger than 1 phi (>0.5 mm) were composed of basalt fragments (Fig. 4a). The nonbasaltic grains were composed almost entirely of calcium carbonate (foraminiferan tests) with minor amounts of siliceous sponge spicules.

A.

SEA PEN RIM
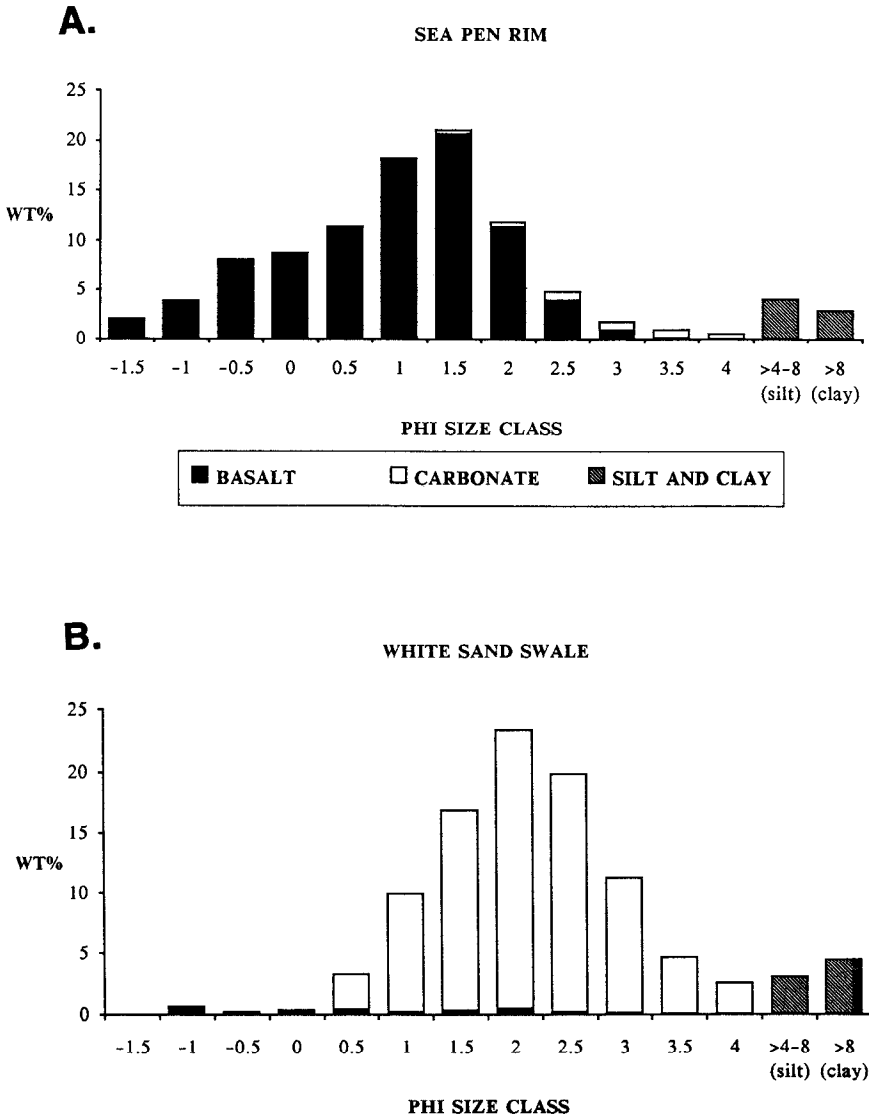

B.

WHITE SAND SWALE

Figure 4. Frequency histograms showing the size distribution and composition of grains in representative samples of unmanipulated surface sediments. The composition of silt- and clay-sized grains has not been determined. Note that the size distribution of sedimentary grains at White Sand Swale and Sea Pen Rim exhibit only minor differences. Sand-sized grains at White Sand Swale, however, are composed almost entirely of calcium carbonate (foraminiferal tests) whereas sand-sized grains are composed chiefly of basalt at Sea Pen Rim.

At WSS, sediments had a mean grain size of 1.36 ± 0.16 phi (0.34–0.43 mm) and were moderately sorted (Table 1). Modal grain sizes were in the coarse and medium sand class, ranging from 0.5 to 2.0 phi (0.71 to 0.25 mm). The sediments were composed primarily of globigerinacean foraminiferan tests, with minor basalt fragments and sponge spicules (Fig. 4b). Accordingly, percent $CaCO_3$ was consistently higher at WSS than SPR (Table 1).

Vertical distributions of grain size were examined in one core each from SPR and WSS. In a 5 cm-long core from SPR, grain size was relatively uniform in the upper 3 cm of the core (mean ~ 1 phi [0.5 mm]). Below 4 cm the sediment was substantially coarser, with a mean grain size of 0.2 phi (0.87 mm). At WSS, an 11 cm-long core showed very gradual downcore fining, from a mean of 1.4 phi (0.37 mm) at the surface to a mean of 1.67 phi (0.31 mm) at the base. Sediment percent organic carbon, organic nitrogen, and C:N ratios did not differ significantly between sites and did not exhibit temporal (between-cruise) variation within sites. Percent organic carbon and nitrogen were extremely low at both SPR and WSS (Table 1), while C:N ratios were near 8 at both sites.

c. Bottom currents and stress

Long-term records of currents were made with a bottom moored, upward looking acoustic doppler current meter during the period of Sept. 1990 to Oct. 1991 at a site between and 2 km north of our two study sites (R2 mooring, 32° 28.27'N 127° 48.57'W; Wichman *et al.*, 1993). The R2 mooring measured currents of 2 cm/s to 40 cm/s 18 mab during the periods of Oct. 14–30, 1990 (Fig. 5a) and speeds of 2 cm/s to 47 cm/s during the period Dec. 4–20, 1990 (Fig. 5c). The October currents were typical of those observed for the whole year (25, 50, and 75 percentile speeds were the same to within 0.5 cm/s) [$U25\% = 7.3$ cm/s, $U50\% = 11.2$ cm/s, $U75\% = 16.7$ cm/s]). The December currents were faster than the yearly average [$U25\% = 7.8$ cm/s, $U50\% = 12.2$ cm/s, $U75\% = 19.2$ cm/s]. Currents greater than 45 cm/s were observed during the year only 0.05% of the time.

BASS current meter records taken 4 mab from SPR and WSS are juxtaposed with the R2 speeds in Figure 5b and d, respectively. The BASS currents (4.4 mab) were usually about half the R2 currents at 18 mab. This is a larger gradient than expected for an unstratified turbulent boundary layer. However, temperature stratification has been observed and could account for this shear. The boundary shear stress velocity measured by BASS is summarized by the time series and cumulative frequency plots of Figure 6. The shear velocity, u_*, exceeded 0.5 cm/s and 1.0 cm/s 40% and 4% of the time, respectively at SPR (Fig. 6a) and 45% and 10% of the time, respectively at WSS (Fig. 6b). The differences in occurrence of large stress between SPR and WSS are not significant. By comparing the shear stress velocity cumulative plots to current speed cumulative plots of BASS and R2, we can infer that stress larger than 1.5 cm/s may occur only 0.1%, or less, of the time throughout the year.
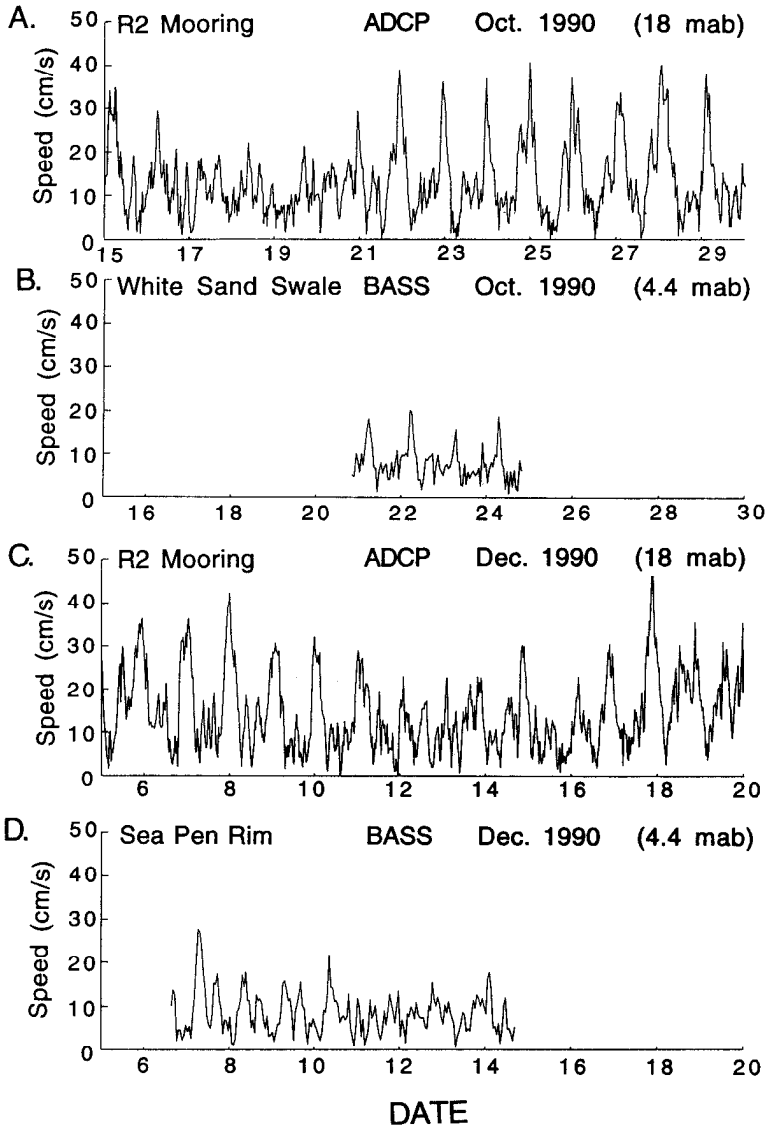
Figure 5. (a) Current speed measured 18 mab with the R2 mooring between October 15–29, 1990 (See Fig. 1 for mooring location). (b) Current speed measured 4.4 mab near White Sand Swale with the BASS tripod from Oct. 20 to Oct. 25, 1991. (c) Current speed measured 18 mab at the R2 mooring between December 6–20, 1990. (d) Current speed measured 4.4 mab near Sea Pen Rim with the BASS tripod from Dec. 6–15, 1990.

d. Sediment transport

Sediment transport calculations, based on measured grain size and grain density distribution of surface sediments and on BASS current records, were used to evaluate the relative frequency of sediment motion at WSS and at SPR. Because the
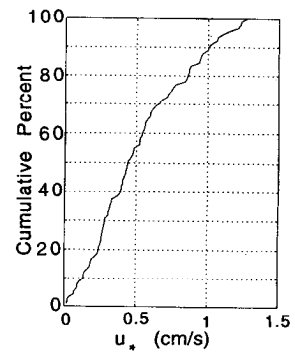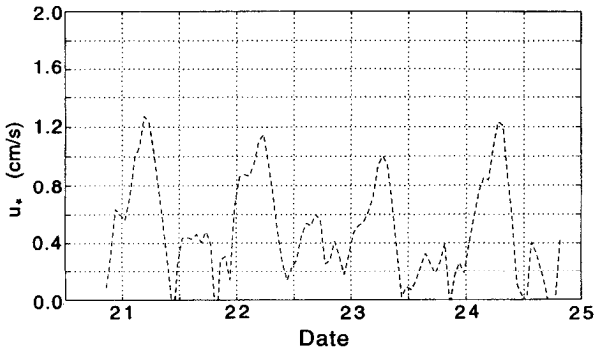
A. Sea Pen Rim
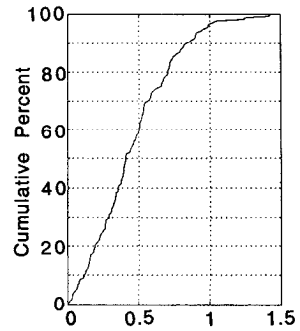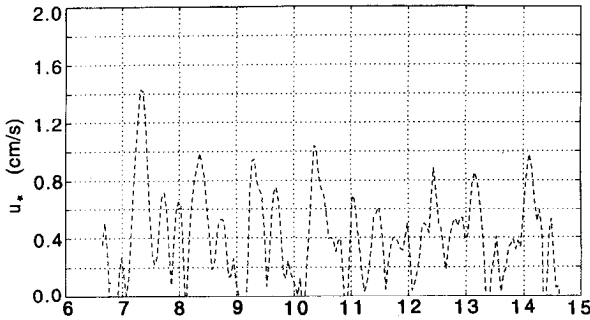
B. White Sand Swale

Figure 6. Bottom stress calculated from BASS data. (a) Time series of u_* obtained from least
squares fit to logarithmic velocity profiles with BASS at White Sand Swale (Oct. 20–Oct. 25,
1990), shown with the cumulative probability of u_* at White Sand Swale for that same
period. (b) Time series of u_* obtained from least squares fit to logarithmic velocity profiles
with BASS at Sea Pen Rim (Dec. 6–15, 1990), shown with the cumulative probability of u_*
at Sea Pen Rim for that same period.

distribution of dunes and ripples at the sites is patchy, we did not attempt to account
for extraction of momentum from the flow by bedforms in our calculations (e.g.,
Smith and McLean, 1977). We similarly did not account for the contribution of
sediment transport to the total boundary shear stress. Thus it is possible that our
estimates of the frequency of sediment transport are slightly elevated.

At WSS, a typical sediment sample had a modal grain size of about 2 phi (0.25 mm)
(Fig. 4b). Particles of this size are composed almost entirely of calcareous foraminif-
eral tests (density of 1.8 g/cc). The critical shear velocity (u_*) required to move such
particles was calculated using a modified Shield's curve (Smith, 1977) and assuming
transport in seawater at about 5°C. The calculations indicated that transport of the
modal size class would be initiated at shear velocities of about 1.0 cm/s (critical shear
stress 1.06 dyne/cm^2). Examination of BASS records (Fig. 6) indicates that this
condition was met on a daily basis about 10 percent of the recorded time during the 4

days that currents were measured at WSS. Further, the maximum shear velocity recorded at WSS was about 1.3 cm/s (shear stress 1.74 dyne/cm^2) during the period over which measurements were made. Sediment transport calculations indicate that under these conditions carbonate grains as large as coarse-sand size (0.5 phi, 0.65 mm) would have been moved. These results indicate that during the strongest current flows we measured, up to 95% of the grains in a typical WSS sediment sample would have been in motion.

At SPR, the modal grain size (1.5 phi, 0.35 mm) is composed entirely of basalt (Fig. 4a). These grains are estimated to have a critical shear velocity of about 1.53 cm/s (critical shear stress of about 2.4 dyne/cm^2). During the time that currents were recorded by BASS at SPR (about 8 da), this shear velocity was never achieved. The maximum shear velocity recorded at this site was about 1.4 cm/s. Under these conditions basaltic particles in the fine sand range (about 2.1 phi or 0.24 mm) may theoretically have been mobilized. This result suggests that during the strongest current flows at SPR, up to 15% of the grains in a typical surface sample could have been transported. It is likely however, that armoring of the sea bed by the coarser basaltic grains would have inhibited transport of the finer fraction.

Results of the tracer particle experiments supported the above interpretations of substrate mobility. At SPR much of the largest tracer (blue gravel) remained visible at the sediment surface more than 8 months after being deposited and rarely penetrated below the top cm of sediment. At WSS no tracer particles were visible on the sediment surface at the time of sampling. Instead the blue gravel was concentrated in the 1–2 cm fraction (except for 1 sample where it was present throughout the top cm). Green basaltic and orange quartz sands (both with similar densities) had similar distributions indicative of redistribution by bioturbation. At SPR they were distributed throughout the upper 2–3 cm of sediment, but in one boxcore some particles penetrated to 5–6 cm. At WSS they either exhibited abundance maxima at 3–4 cm depth or were most abundant in the top 1 cm and declined downcore, penetrating to a depth of 6 m. No dyed foraminiferan sands were observed in samples after 8 mo at either SPR or WSS. We assume they were transported away from the tracer plots by bottom currents, since some red-dyed foraminifera tests were recovered in faunal cores at WSS taken within 10 m of the original sites of deposition.

e. Bacterial abundance

Surface sediments (0–1 cm) at the two study sites exhibited no difference in bacterial abundance during any of the three sampling periods. Mean counts were around 2×10^8 bacteria per ml (Table 1). No temporal variation was observed at SPR. However, Oct. 1990 counts were somewhat higher than June 1991 counts at WSS, with Dec. 1990 counts being intermediate, and not significantly different from the others (Table 1). The vertical distribution of bacteria did not differ between study
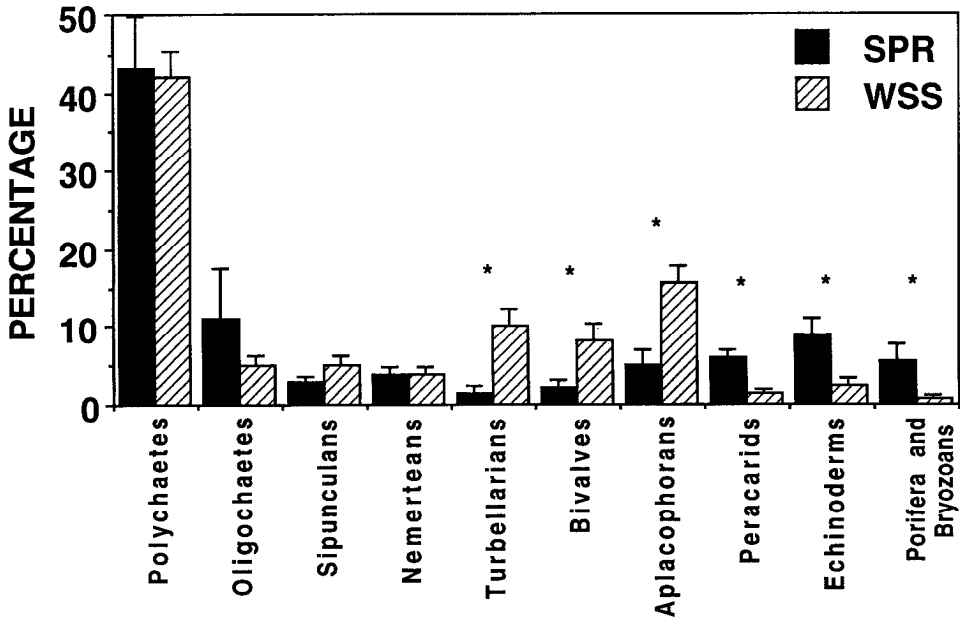
Figure 7. Percent composition of major infaunal taxa (retained on a 300-μm screen) in samples from Sea Pen Rim and White Sand Swale. Asterisks indicate statistically significant differences between sites (*t*-tests, α = 0.05). Data represent all cruises combined.

sites. At both WSS and SPR bacterial counts 5–6 cm below the sediment surface $(0.5 - 1.0 \times 10^8 / \text{ml})$ were about ¼ to ½ those found in the surface fraction.

f. Infauna

i. Composition. Polychaetes were the most common taxon at both sites, comprising on average 43.2% of the individuals at SPR and 42.1% at WSS (Fig. 7). The two sites had many of the same polychaete species present, but with different rank abundances. The pilargid *Synelmis dineti* (26.5%) and 4 species of ampharetid (25.6%) accounted for over half of the polychaetes at SPR. At WSS over three quarters of the polychaetes collected belonged to the families Dorvilleidae (23%), Pilargidae (19%), Cirratulidae (14%), Hessionidae (12%), and Ampharetidae (10%). The SPR sediment community consisted of a greater proportion of peracarids ($P < 0.001$), echinoderms (mostly ophiuroids and crinoids) ($P = 0.003$), porifera and bryozoans ($P = 0.037$) than WSS (Fig. 7). The WSS sediment community contained higher proportions of turbellarians ($P = 0.003$), bivalves ($P = 0.056$), and aplacophorans ($P = 0.003$) than SPR (Fig. 7).

ii. Abundance. Densities of infauna did not differ between SPR and WSS in Dec. 1990 and June 1991, and no temporal differences were detected within each site

(Table 2). However, densities were 59% higher at WSS than SPR in Oct. 1990 ($F_{1,18}$ = 5.17, P = 0.035). Averaged over the entire study, mean infaunal densities (± 1 SE) were 1489 $\pm$ 267/m^2 at SPR and 1870 $\pm$ 153/m^2 at WSS ($F_{1,36}$ = 3.42; P = 0.072).

Several taxa were significantly more abundant at one site or the other. Densities were significantly greater at WSS than SPR for aplacophorans in Oct. 1990 and Dec. 1990, and for predatory vermes (nemerteans and turbellarians) in Oct. 1990 (Table 2). Densities were significantly greater at SPR than WSS for peracarid crustaceans in Dec. 1990 and June 1991, echinoderms in Dec. 1990, and bryozoans in Oct. 1990 (Table 2).

iii. Vertical distributions. The position of infauna within the sediment column varied between sites ($F_{3,147}$ = 9.02, P = 0.002) (Fig. 8). Infauna at SPR were concentrated largely in the uppermost cm of sediment (53.0 $\pm$ 7.2%), with less than 25% found below 2 cm. In contrast, at WSS only 30% ($\pm 3.1\%$) of the animals were present in the top 1 cm, whereas over 53% were found below 2 cm (Fig. 8). The proportion of infauna in the 0–1 cm fraction was higher at SPR than WSS (P = 0.032), comparable between sites in the 1–2 cm fraction (P = 0.736), and higher at WSS than SPR in the 2–5 cm (P = 0.018) and 5–10 cm (P = 0.021) fractions.

Between-site differences in the vertical distribution of infauna resulted both from taxonomic differences between sites and from site-specific shifts in vertical distributions within taxa (Fig. 9). The deepest dwelling taxa were vermiform, burrowing animals. These included the oligochaeta, found primarily in the 5–10 cm fraction, and nemerteans and turbellarians, which were concentrated in the 2–5 cm fraction (Fig. 9). Aplacophorans, bivalves, peracarid crustaceans, echinoderms, and poriferans were largely concentrated in the upper 2 cm of sediment. Significantly deeper vertical distributions were observed for polychaetes (P < 0.001), oligochaetes (P = 0.054), and nemerteans (P = 0.050) at WSS relative to SPR (Fig. 9). Similar trends were observed in the sipunculans and echinoderms (Fig. 9), but were not statistically significant.

iv. Lifestyles. Significant differences in faunal lifestyles were observed between SPR and WSS (Fig. 10a). Both filter feeding (P = 0.003) and surface-deposit feeding (P = 0.050) forms were more common at SPR than WSS. Together they accounted for 47.0% of the infauna at SPR, but only 24.3% at WSS. In contrast, subsurface-deposit feeding was more common at WSS (30.4%) than SPR (17.3%) (P = 0.042) (Fig. 10). No significant difference was observed in representation of carnivorous and scavenging feeding modes, which accounted for 35.6% of the fauna at SPR and 45.4% of the fauna at WSS.

Between-site differences in faunal dwelling habits were observed for tube builders, epifaunal forms, and subsurface burrowers (all P < 0.001). Nearly 83% of the

Table 2. Comparison of faunal abundances (no./m²) at White Sand Swale (WSS) and Sea Pen Rim (SPR) for animals retained on a 300-μm screen. n = number of cores from which 2 subcores (98 cm² total surface area) were examined. Nos. per core were converted to numbers per square meter using a conversion factor of 102. P values are for comparisons between WSS and SPR unless otherwise noted, and are given in bold face when values are <0.10.

| | Oct 1990 | | | | | Dec 1990 | | | | |
| | SPR (n = 9) | | WSS (n = 11) | | | SPR (n = 4) | | WSS (n = 6) | | |
	x̄	(SE)	x̄	(SE)	P	x̄	(SE)	x̄	(SE)	P
Total Infauna	1303.7	(466.8)	2076.8	(174.6)	**0.035**	1600.00	(130.8)	1619.1	(207.1)	0.975
Annelids										
Polychaetes	563.0	(192.0)	832.3	(79.8)	**0.060**	711.1	(72.6)	613.8	(114.3)	0.483
Oligochaetes	39.5	(15.6)	88.9	(20.8)	0.127	111.1	(22.2)	44.4	(30.4)	**0.070**
Molluscs										
Bivalves	39.5	(21.5)	121.2	(46.8)	0.206	66.7	(42.6)	169.3	(177.7)	0.413
Aplacophorans	29.6	(14.8)	307.1	(82.5)	**0.001**	133.3	(57.4)	364.0	(174.8)	**0.043**
Gastropods	0.0	(0.0)	8.1	(8.1)	0.380	0.0	(0.0)	14.8	(14.8)	0.447
Sipunculans	39.5	(15.6)	72.7	(31.3)	0.494	44.4	(25.7)	171.4	(54.5)	0.134
Turbellarians	19.8	(19.8)	274.7	(55.5)	**0.001**	66.7	(42.6)	103.7	(74.1)	0.994
Nemerteans	69.1	(28.8)	97.0	(25.3)	0.536	44.5	(25.7)	57.2	(18.2)	0.667
Peracarids	108.6	(43.9)	40.4	(14.0)	0.274	111.1	(42.6)	12.7	(12.7)	**0.040**
Amphipods	9.9	(9.9)	8.1	(8.1)	0.889	0.0	(0.0)	0.0	(0.0)	—
Isopods	59.3	(25.7)	32.3	(13.5)	0.512	44.5	(25.7)	0.0	(0.0)	**0.059**
Tanaids	39.5	(30.0)	0.0	(0.0)	0.125	66.7	(42.6)	12.7	(17.7)	0.227
Echinoderms	187.7	(101.0)	40.4	(27.8)	0.115	177.8	(0.0)	38.1	(26.0)	**0.009**
Holothurians	29.6	(14.8)	24.2	(24.2)	0.455	0.0	(0.0)	25.4	(16.1)	0.242
Sea urchins	0.0	(0.0)	0.0	(0.0)	—	44.5	(25.7)	12.7	(17.7)	0.281
Ophiuroids	79.0	(50.1)	24.2	(17.3)	0.336	88.9	(0.0)	0.0	(0.0)	—
Crinoids	79.0	(54.3)	0.0	(0.0)	0.113	44.5	(25.7)	0.0	(0.0)	**0.059**
Other Taxa	158.0	(82.2)	121.2	(32.3)	0.849	88.9	(88.9)	14.8	(14.8)	0.478
Poriferans	39.5	(30.0)	40.4	(18.4)	0.720	44.5	(44.5)	14.8	(14.8)	0.607
Anemones	59.3	(49.1)	56.6	(18.1)	0.468	44.5	(44.5)	0.0	(0.0)	0.242
Bryozoans	29.6	(14.8)	0.0	(0.0)	**0.039**	44.5	(44.5)	0.0	(0.0)	0.242
Pycnogonids	9.9	(9.9)	0.0	(0.0)	0.281	0.0	(0.0)	0.0	(0.0)	—
Chaetognaths	0.0	(0.0)	16.2	(10.8)	0.196	0.0	(0.0)	0.0	(0.0)	—

|	June 1991					Combined cruise					Between-cruise comparisons	
	SPR (n = 3)		WSS (n = 5)			SPR (n = 16)		WSS (n = 22)				
	$\bar{x}$	(SE)	$\bar{x}$	(SE)	P	$\bar{x}$	(SE)	$\bar{x}$	(SE)	P	SPR	WSS
Total Infauna	1896.3	(258.3)	1717.0	(513.9)	0.672	1488.9	(267.3)	1870.2	(153.5)	**0.072**	0.402	0.338
Annelids												
Polychaetes	977.8	(271.6)	703.6	(152.9)	0.402	677.8	(121.7)	743.5	(61.6)	0.203	0.325	0.303
Oligochaetes	148.1	(59.3)	101.6	(41.7)	0.424	77.8	(17.9)	79.7	(16.2)	0.837	**0.025**	0.375
Molluscs												
Bivalves	0.0	(0.0)	129.5	(65.5)	0.143	38.9	(16.2)	136.2	(32.7)	**0.033**	0.408	0.849
Aplacophorans	177.8	(135.8)	363.2	(247.2)	0.780	83.3	(30.9)	335.4	(68.1)	**0.001**	0.156	0.644
Gastropods	29.6	(29.6)	15.2	(15.2)	0.684	5.6	(5.6)	11.5	(6.4)	0.490	0.109	0.857
Sipunculans	59.3	(29.6)	63.5	(44.7)	0.783	44.0	(11.5)	97.6	(24.7)	0.213	0.833	0.199
Turbellarians	0.0	(0.0)	215.9	(102.6)	**0.069**	27.8	(15.7)	214.7	(42.3)	**0.001**	0.261	**0.093**
Nemerteans	118.5	(78.4)	45.7	(45.7)	0.335	72.2	(21.8)	74.5	(17.0)	0.841	0.727	0.368
Peracarids	118.5	(29.6)	0.0	(0.0)	**<0.001**	111.1	(26.3)	23.7	(8.5)	**0.002**	0.766	0.132
Amphipods	0.0	(0.0)	0.0	(0.0)	—	5.6	(5.6)	4.1	(4.1)	0.790	0.707	0.629
Isopods	118.5	(29.6)	0.0	(0.0)	**<0.001**	66.7	(17.2)	16.2	(7.5)	**0.011**	0.301	**0.092**
Tanaids	0.0	(0.0)	0.0	(0.0)	—	38.9	(19.8)	3.5	(3.5)	**0.051**	0.442	0.275
Echinoderms	118.5	(118.5)	48.3	(19.8)	0.873	172.2	(58.8)	41.7	(15.7)	**0.016**	0.618	0.688
Holothurians	0.0	(0.0)	15.2	(19.7)	0.482	16.7	(9.0)	22.5	(12.9)	0.876	0.276	0.828
Sea urchins	0.0	(0.0)	0.0	(0.0)	—	11.1	(7.6)	3.5	(3.5)	0.343	**0.026**	0.275
Ophiuroids	29.6	(29.6)	33.0	(20.3)	0.901	72.2	(28.4)	19.6	(9.8)	**0.043**	0.412	0.353
Crinoids	88.9	(88.9)	0.0	(0.0)	0.220	72.2	(33.7)	0.0	(0.0)	**0.008**	0.970	—
Other Taxa	148.1	(78.4)	0.0	(0.0)	**0.036**	138.9	(51.3)	64.6	(20.4)	0.302	0.780	**0.012**
Poriferans	0.0	(0.0)	0.0	(0.0)	—	61.1	(25.3)	24.2	(10.4)	0.319	0.298	0.267
Anemones	0.0	(0.0)	0.0	(0.0)	—	44.4	(29.3)	28.3	(10.8)	0.949	0.732	**0.014**
Bryozoans	0.0	(0.0)	0.0	(0.0)	—	27.8	(13.4)	0.0	(0.0)	**0.015**	0.604	—
Pycnogonids	0.0	(0.0)	0.0	(0.0)	—	5.6	(5.6)	0.0	(0.0)	0.214	0.707	—
Chaetognaths	148.2	(78.4)	0.0	(0.0)	**0.036**	0.0	(0.0)	8.1	(5.6)	0.246	—	0.368

VERTICAL DISTRIBUTION OF INFAUNA
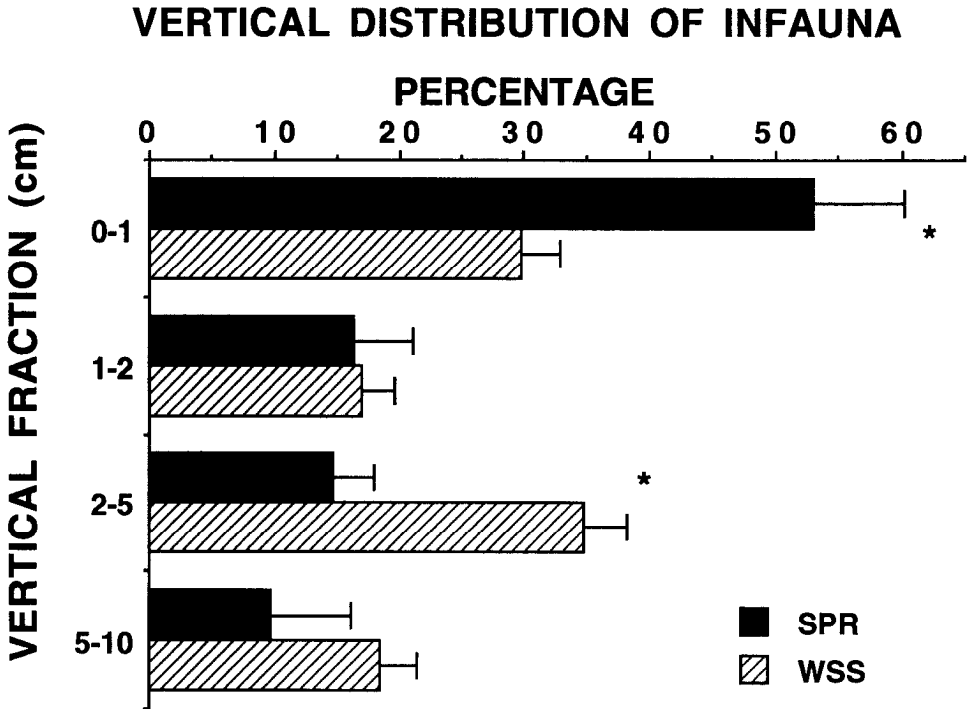
Figure 8. Vertical distribution of major infaunal taxa (300 μm) within the sediment column at Sea Pen Rim and White Sand Swale, shown as percent of the total infauna for each site. Asterisks indicate significant differences between sites within a vertical fraction (repeated measures analysis followed by pairwise comparisons of the adjusted means for data within a vertical fraction, α = 0.05). Data represent all cruises combined.

infauna at WSS were subsurface burrowers, while at SPR almost 50% had tube-building or epifaunal lifestyles (Fig. 10b). Motile lifestyles were more common at WSS (82.9%) than SPR (58.7%) ($P < 0.001$). Sessile lifestyles were more prevalent at SPR (28.2%) than WSS (3%) ($P < 0.001$) (Fig. 10c).

v. Diversity. A minimum of 67 species were recorded from the 203 individuals identified at SPR, and 71 species were recorded from the 406 individuals identified at WSS. Of the 94 total species found on Fieberling Guyot, approximately 46% were found at both SPR and WSS. About 38% of the polychaetes and 52% of the other infauna occurred at both sites. Rarefaction curves (Fig. 11a) indicate that many more species probably exist than were sampled, and that when normalized to sample size, species richness is expected to be higher at SPR. Information indices (H') were similar at SPR (3.57) and WSS (3.44). Cumulative rank abundance curves for infauna were similar for the two sites, though common species made slightly higher contributions to total abundance at WSS (Fig. 11b).
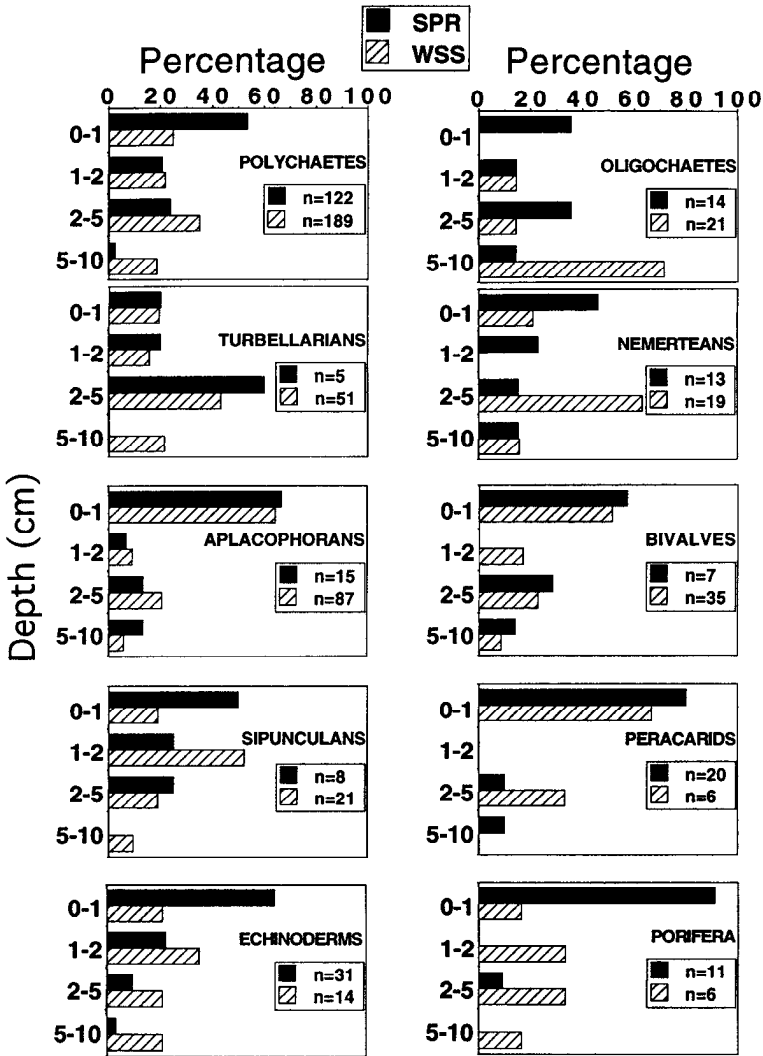
Figure 9. Vertical distribution of major infaunal taxa (300 μm) within the sediment column at Sea Pen Rim and White Sand Swale, shown as the percent of the total taxon for each site. n = the number of individuals in a taxon sampled at each site. Data represent all cruises combined.

g. Flow manipulations

At the time of sample recovery, sediments within weirs appeared heavily scoured. No significant differences in sediment grain size, organic content or carbonate content were observed, however, between WSS weir and background samples. Fences deployed for 6.5-wk produced no visible changes in surface topography at either site, but sediment mounding and scouring was observed inside some fences

A.
FEEDING HABIT

B.
DWELLING MODE

C.
MOTILITY

WSS

SPR

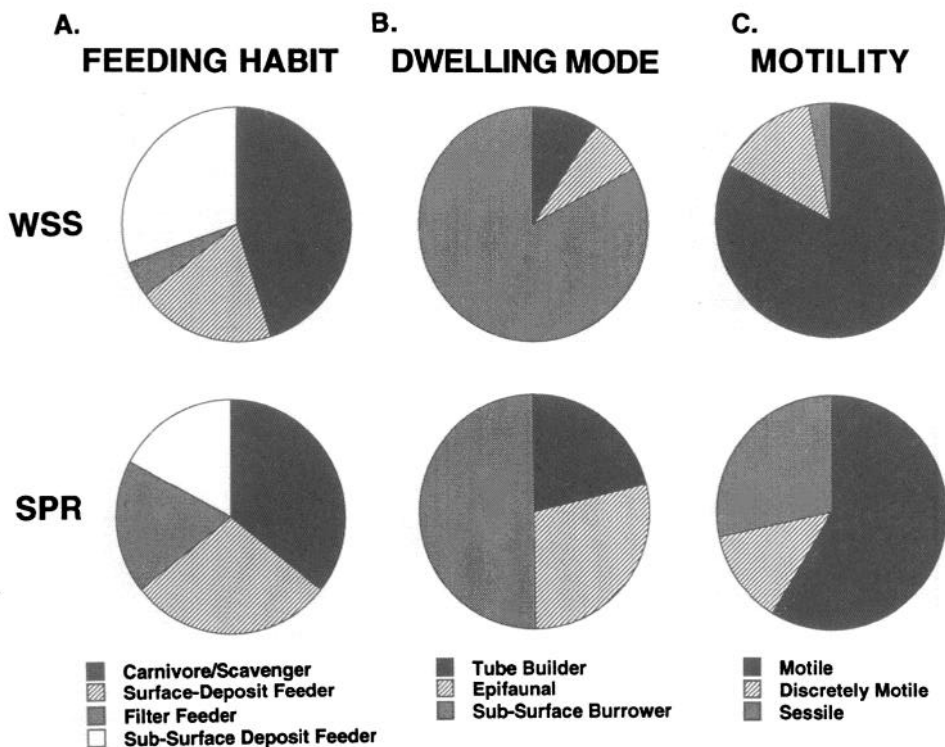|		
■ Carnivore/Scavenger	■ Tube Builder	■ Motile
▨ Surface-Deposit Feeder	▨ Epifaunal	▨ Discretely Motile
■ Filter Feeder	■ Sub-Surface Burrower	■ Sessile
☐ Sub-Surface Deposit Feeder		

Figure 10. Proportional representation of infaunal lifestyles observed at Sea Pen Rim and White Sand Swale. (a) feeding mode, (b) dwelling habit, (c) mobility.

deployed for 6 mo at WSS. Fences did not alter sediment organic C and N content, C:N ratio, carbonate content, or bacterial counts in surface sediments at either site during either deployment. The 6.5-wk fence deployments led to significantly higher clay content of surface sediments at SPR (3.5% in fences vs 0.9% background; $F_{1,4} = 13.412$, $P = 0.022$) but not at WSS. Insufficient grain size sample numbers prevented analyses of fence effects on granulometry during longer deployments.

Bacterial abundances in weir surface sediments (0–1 cm) were 20% below those in background sediments and 25% below those in fence sediments, but were statistically different only from the latter ($F_{2,13} = 3.98$, $P = 0.045$). Bacterial counts in fenced sediments did not differ from those in unmanipulated (background) sediments.

Flow manipulations had only minor effects on infaunal abundance and composition. Weir samples contained fewer infauna than Dec. 1990 fence samples but were only marginally different from Dec. 1990 background samples ($F_{2,12} = 3.25$, $P = 0.074$). Following the 6.5-wk fence deployments, the only infaunal response was enhancement of oligochaete abundances in fences over background sediments at both SPR ($F_{1,6} = 113.57$, $P < 0.001$) and WSS ($F_{2,12} = 6.77$, $P = 0.011$). Oligochaetes were
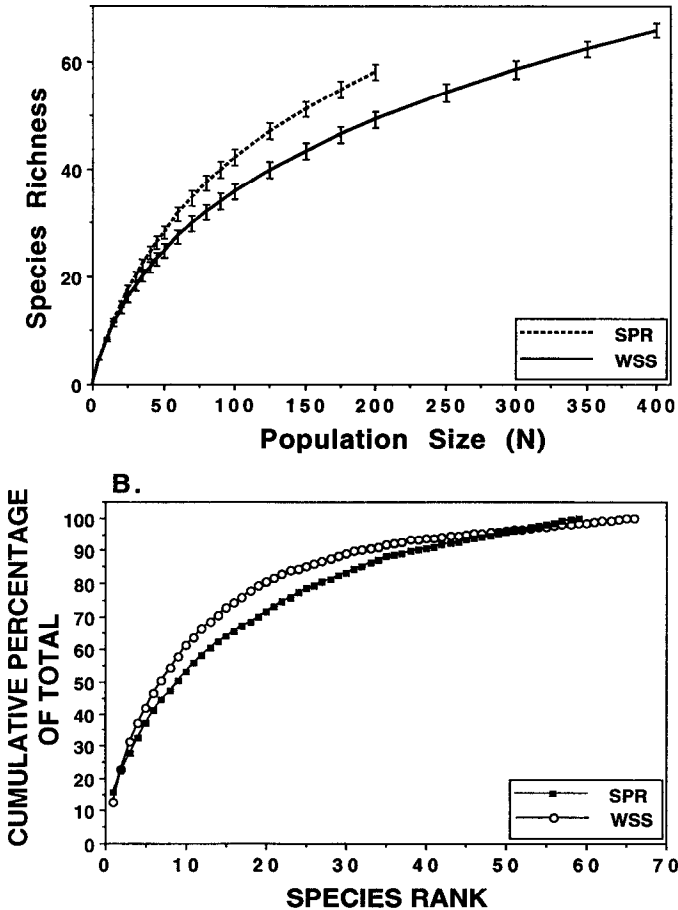
Figure 11. Diversity of infauna (> 300 μm) in Sea Pen Rim and White Sand Swale sediments
on Fieberling Guyot. Approximately 150 individuals, representing about 25% of the total
fauna, could not be identified as distinct species (usually because they were juveniles or
heavily fragmented). These were excluded from the diversity analyses. (a) Rarefaction
curves for each site, indicating expected species richness as a function of sample size. Error
bars are 95% confidence intervals. (b) Cumulative rank abundance curves indicating degree
of dominance.

absent in weir samples at WSS. Six-month fence deployments did not affect total
infaunal abundance at either site. Isopods at WSS were significantly more abundant
inside than outside fences in June 91 ($F_{1,6} = 7.47$, $P = 0.034$), but no other taxa
responded to fences.

Vertical distributions of infauna within the sediment column were examined in
flow treatments. At SPR, the 6.5-wk fence deployments (Fig. 12a) had no effect on
vertical distribution. However, the 6-mo fences (Fig. 12c) produced a trend toward
deepening of the fauna in the sediment column, with a 40% reduction in the mean
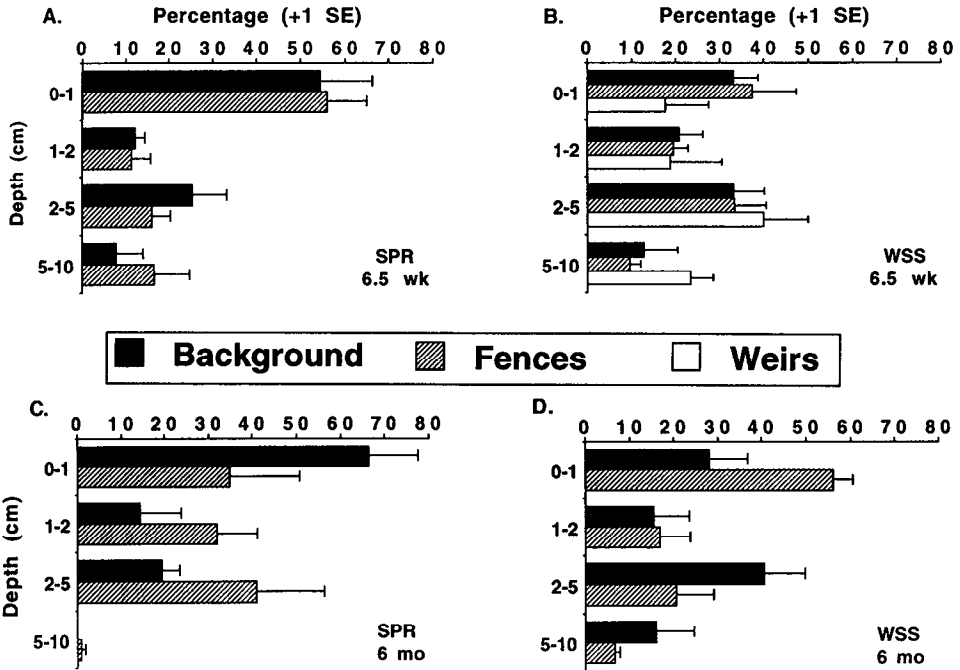
Figure 12. Vertical distribution of infauna (> 300 μm) in background and flow-manipulation sediments. (a) Dec. 1990 background vs sediments in fences deployed for 6.5 wk at Sea Pen Rim (Oct.–Dec., 1990). (b) Dec. 1990 background vs sediments in fences and weirs deployed at White Sand Swale for 6.5 wk (Oct.–Dec., 1990). (c,d) June 1991 background vs sediments in fences deployed for 6 mo (Dec. 1990–June 1991) at Sea Pen Rim (c) and White Sand Swale (d).

proportion of fauna in the top cm ($P = 0.090$). At WSS, weirs led to an apparent deepening of vertical distributions relative to unmanipulated sediments (Fig. 12b), though the small sample sizes ($n = 3$ weirs) precluded detection of statistically significant differences. In contrast, the 6-mo fence deployments led to a shallowing of vertical distributions (Fig. 12d) with a 28% increase in the mean proportion of fauna inhabiting the upper 1 cm ($P = 0.063$).

Significant effects of flow manipulations on animal life habits were detected at WSS but not at SPR. Weir samples contained exclusively mobile, subsurface burrowing forms: polychaetes, nemerteans, turbellarians, sipunculans and aplacophorans. Weir sediments contained significantly fewer surface-deposit feeders (6.3%) than background sediments (34.9%) ($F_{2,12} = 8.67$, $P = 0.005$) and more subsurface-deposit feeders (59.0%) than background sediments (12.6%) ($F_{2,12} = 16.08$, $P < 0.001$). Fence sediments at WSS contained proportionally more subsurface-deposit feeders in Dec. 1990 (49.4%) ($P < 0.001$) and June 1991 (48.6%) ($P = 0.030$) than background samples (12.6% in Dec. 1990 and 18.3% in June 1991), fewer

surface-deposit feeders than background sediments in Dec. 1990 ($P = 0.005$), and fewer carnivores in June 1991 ($P = 0.007$).

6. Discussion

a. Causes and consequences of habitat heterogeneity on the Fieberling summit

Sediments atop the most current-swept portions of the Fieberling Guyot summit are patchily distributed and sediment composition of patches varies, as on many other eastern Pacific seamounts (Levin and Nittrouer, 1987; Levin, unpubl. obs.). Irregularities in summit topography allow foraminiferal sands to accumulate in some places, but not in others. Patches are generally ≤ 0.5 km^2 in area. The distribution of less mobile basaltic sands, which are autochthonous in origin, may be governed by the eruptive events that form them. Habitats dominated by basaltic particles appear larger in area and more contiguous than the foraminiferal sand patches, but are still limited in extent compared to other environments. The consequences of patchy habitats are of growing interest (Levin *et al.*, 1993). Issues concerning effects of patch dispersion, dispersal between patches, and patch persistence are beyond the scope of this paper. However, seamount settings like those on Fieberling Guyot are ideal for the study of such questions.

A primary result that emerges from this investigation is that there is no single set of traits that characterizes the faunas inhabiting high-energy sedimentary settings in the ocean. On Fieberling Guyot, topography-induced variations in sediment composition lead to different sediment-transport regimes (under conditions of similar bottom currents and shear velocities) that govern the taxonomic composition, diversity, vertical distributions, and lifestyles of infauna. Stable, coarse-grained sediments support relatively sessile assemblages whose feeding activities are focused at the sediment-water interface. Unstable, coarse-grained sediments that move daily support a highly mobile assemblage with well-developed burrowing abilities. Although polychaetes dominate in both regimes on Fieberling Guyot, peracarids and suspension feeders such as ophiuroids, crinoids, sponges, and bryozoans were more prevalent in the stable system (SPR), and turbellarians, bivalves and aplacophorans were better represented in unstable sediments (WSS).

We acknowledge that the sediment regimes we compare are unreplicated, and therefore caution is required in making broad generalizations. However, the results of our flow manipulation experiments at WSS reinforce the likelihood that we are correct in attributing faunal differences between WSS and SPR to substrate mobility.

b. Comparisons with other high-energy settings

i. Seamounts. High-energy, sedimentary settings have been sampled by the authors on several seamounts in the central and eastern Pacific Ocean (Levin *et al.*, 1986; Levin and Thomas, 1989; Levin *et al.*, 1991a,b). The summit perimeter of Horizon

Guyot (1800 m) in the central Pacific Ocean resembles WSS in the presence of rippled foraminiferal sands and high $CaCO_3$ content, but the ripples appeared old and sediment transport was not studied at this site. Horizon perimeter sediments exhibited lower organic content, higher C:N ratios, comparable bacterial counts, but much lower infaunal densities than those on the Fieberling summit. Community structure at WSS was similar to that of the Horizon perimeter in percent representation of polychaetes, the scarcity of peracarid crustaceans, and the common occurrence of aplacophoran and bivalve molluscs (Table 3). Animals inhabiting Horizon perimeter sediments had deeper vertical distributions than in lower-energy settings on Horizon Guyot. However, polychaete lifestyles in Horizon perimeter sediments bore stronger resemblance to the SPR infauna than to WSS infauna (Levin and Thomas, 1989). Differences among lifestyles in the rippled foram sands of WSS and Horizon Guyot probably reflect frequencies and intensities of sediment motion, and lability of organic matter present.

Comparisons of Fieberling infauna with that of coarse-grained sites (>75% sand) on the flanks of 6 eastern Pacific seamounts at 10N, 13N and 32N revealed comparable average densities (Table 3). Polychaetes were a smaller component of the infaunal assemblage on Fieberling Guyot than on the other eastern Pacific seamounts (Table 3). WSS sediments contained many more molluscs and fewer peracarids, while SPR sediments contained more echinoderms than the other eastern Pacific seamounts (Table 3). The deposit-feeding polychaete family Paraonidae accounted for 28% of polychaetes collected from eastern Pacific seamount sands (Levin *et al.,* 1991b), but less than 4% of the Fieberling polychaetes.

ii. HEBBLE. The HEBBLE region is the only high-energy, deep-sea setting whose boundary-layer flow and sediment transport regimes have been characterized in relation to the benthic fauna (Gross and Williams, 1991; Thistle *et al.,* 1985, 1991; Aller, 1989). This area experiences periodic erosion and redeposition of sediment by near bottom currents that exceed 15–23 cm/s for periods of 2 or more days (Aller, 1989). These storm currents are comparable to those measured by BASS on Fieberling Guyot, but do not exhibit the diurnal fluctuations typically associated with seamounts (e.g., Fig. 5) and do not occur daily throughout the year. Thus intense bottom stress at the HEBBLE site is more intermittent than on Fieberling Guyot. Sediments at the HEBBLE site contain approximately 5× the organic carbon and nitrogen of Fieberling summit sediments and support infaunal densities that are somewhat higher than those of Fieberling (Table 1). Densities of polychaetes and bivalves at the HEBBLE site are roughly twice those of WSS sediments, while peracarid crustaceans are many times more abundant than on Fieberling Guyot (Thistle *et al.,* 1991).

The HEBBLE macrofauna is a low-diversity assemblage, dominated (>50%) by ampharetid polychaetes (Thistle *et al.,* 1985). Ampharetids were well-represented on

Table 3. Summary of infaunal characteristics in high-energy, coarse-grained settings. NA = not available.

| | SHALLOW BEACHES | | SEAMOUNTS | | | | HEBBLE*** |
| | Exposed† | Semi-Exposed† | Fieberling Guyot†† | | Horizon Guyot††† | Eastern Pacific*** | (Nova Scotia Rise) |
			SPR	WSS	Perimeter		
Depth (m)	<50	<50	635	580	1850	788–3353	4820
Particle Composition	Quartz	Quartz	Basalt	Forams	Forams	Forams	Silts/Forams
Macrofaunal density (mean #/m²)	1575	1791	1489	1870	255	1350	2254
% Macrofauna in top 2 cm	NA	NA	69%	47%	57%	61%	NA
Species richness	11.5	24.0	67	71	NA	NA	NA
H'	1.7	1.9	3.6	3.4	NA	NA	NA
Taxonomic composition							
% Polychaetes	7.5	19.5	45	40	47	57	70.4
% Crustaceans	82.3	64.6	7.4	1.3	0	10	17.8
% Molluscs	2.6	5.7	8.5	26.2	27	8.7	11.1
% Echinoderms	NA	NA	11.5	2.9	3.4	4.5	0.1
Dominant polychaete families	NA	NA	Pilargidae Ampharetidae	Dorvilleidae Pilargidae Cirratulidae Hessionidae	Ampharetidae Dorvilleidae Flabelligeridae Paraonidae	Paraonidae Cirratulidae	Ampharetidae
Feeding mode							
% Surface feeders (filter, deposit)	NA	NA	47	24	59	40α	NA
% Subsurface-deposit feeders	NA	NA	17	30	9	35α	NA

References †Dexter, 1992; ††This paper; †††Levin & Thomas, 1989; *Levin, 1988; **Levin *et al.*, 1991b; ***Thistle *et al.*, 1991; αPolychaetes only.

Fieberling Guyot, especially at SPR, (14.3% of total). However, the pattern of high dominance by 2 species of ampharetids at the HEBBLE site was not observed on the Fieberling summit, where the two most abundant taxa at each site together comprised about 22% of the total individuals (Fig. 11b).

iii. Shallow water. The ecology of shallow-water sandy beaches has been well described from many parts of the world (Brown and McLachlan, 1990). A recent review of 248 beaches by Dexter (1992) indicates that macrofaunal density, H', and species richness all decline with increasing exposure. Mean grain sizes of WSS and SPR sediments were comparable to those shallow beaches categorized by Dexter as most exposed. Mean infaunal densities atop Fieberling Guyot were comparable to those of shallow, semi-exposed (mean $\pm$ 1 SD = 1575 $\pm$ 311/m^2), and protected sandy beaches (1791 $\pm$ 282/m^2), but much higher than in shallow, exposed beaches (312 $\pm$ 82/m^2) (Table 3). Diversity, expressed in terms of species richness or the Shannon-Weiner information index (H'), was considerably higher on Fieberling than on all sandy beaches (Table 3; Dexter, 1992). Shallow-water sands subject to wave, or mass-wasting disturbance are consistently dominated by crustaceans, whereas polychaetes and molluscs become proportionally more important in more stable sediments (Oliver *et al.,* 1980; Brown and McLaughlin, 1990). Based on Dexter's (1992) review, the Fieberling infauna contained proportionally many fewer crustaceans and more molluscs and polychaetes than exposed and semiexposed sandy beaches. Polychaetes that withstand wave disturbance in shallow water are generally burrowing spionids, orbiniids and nephtyids (Tamaki, 1987), but these families were rare on Fieberling. Thus, densities of infauna on the Fieberling summit resemble shallow, coarse-grained systems, but composition and diversity do not.

c. Vertical distributions

Concentration of infauna in near-surface sediments has been documented in intertidal flats (Whitlatch, 1980), on the continental shelf (Hayashi, 1988) and in the deep sea (Shirayama and Horikoshi, 1982). Variations in vertical distribution of infauna occur in association with body size (Jumars *et al.,* 1990), water depth (Shirayama and Horikoshi, 1982), distance from shore, and particle size (Hayashi, 1988), and inferred hydrodynamic regime (Levin and Thomas, 1989). Hayashi (1988) found that total macrofauna and polychaetes inhabiting coarse-grained sediments in the Sea of Japan exhibited shallower vertical distributions (> 66% above 2 cm) than those inhabiting muddy sediments (~ 20% above 2 cm) and that crustaceans had shallower vertical distributions than polychaetes.

Our investigations on Fieberling Guyot suggest that vertical distribution of animals in the sediment column is strongly affected by substrate motility, and shifts rapidly (within wk to mo) in response to changing conditions. Over 80% of the WSS fauna are burrowers, many of which have maximum abundances occurring below 2 cm depth in sediments (Fig. 9). Burrowing ability should be highly adaptive in

substrates that shift daily for extended periods. This hypothesis is supported by the deepening of infaunal vertical distributions observed in stress-intensifying weirs (Fig. 12). We acknowledge that the vertical distributions recorded from submersible-collected cores are likely to represent the deepest achieved by each taxon due to disturbance during sampling and sample recovery, but site and treatment comparisons remain valid.

Several alternative hypotheses could explain varying vertical distributions of infauna. Basaltic sands may be less desirable as food for deposit feeders, although organic matter content and bacterial counts do not support this (Table 1). Basaltic sands also may be more difficult to burrow through than foraminiferal sands. Either situation would promote surface-feeding lifestyles. Alternatively, predation could favor forms that burrow deeply into sediments if the high densities of rattail fishes, sea urchins and spider crabs observed at WSS (Levin, unpubl. obs.) consume the shallowest-dwelling taxa. Predator exclusion is unlikely to account for the shallowing of fauna reported in WSS fences, as most epifaunal predators were observed to swim or crawl readily in and out of the cages, which were all topless.

d. Concluding remarks

Past studies reveal that community structure of faunal assemblages inhabiting seamount sediments can be influenced by oxygen concentration (Wishner *et al.,* 1990; Levin *et al.,* 1991a), organic matter availability (Levin *et al.,* 1991a; Levin *et al.,* 1994), flow regime, and water depth (Levin and Thomas, 1989), and by large, agglutinating protozoans in the Class Xenophyophorea (Levin *et al.,* 1986; Levin and Thomas, 1988). This study suggests another factor for this list. On the current-swept summit of Fieberling Guyot, variability in sediment transport regime, mediated by sediment composition, appears to be the primary determinant of infaunal community structure. This forcing agent is viewed as distinct from forcing by bottom currents because the two settings being compared did not exhibit different flow regimes.

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