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Vertical distribution of microbial and meiofaunal populations in sediments of a natural coastal hydrocarbon seep

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ABSTRACT

We studied the vertical distribution of microbes and meiofauna in natural hydrocarbon seep sediments to determine if there was a relationship between profiles of benthic trophic structure and the unique biogeochemical conditions present at the seep. Three stations in the Santa Barbara Channel represented a gradient of natural petroleum seepage, from very active, to moderate, to none. Seasonal differences were examined by sampling in the three major oceanographic seasons, upwelling (April), mixed (July), and Davidson (December). Densities of microbes and meiofauna were highest in July, and decreased in winter. All population sizes decreased with increasing depth in the sediment. Harpacticoids and Chl *a* were practically restricted to the surface sediments. Harpacticoids and Chl *a* were more dense (number per unit volume or strata of sediment) and abundant (number per unit area of sediment or sum of the strata) at the comparison site than at the seep sites. Density and abundance of nematodes, bacteria cell counts, and bacterial biomass were greater at the station with the most active seepage rates. Bacterial biovolumes appeared constant among sediment depths and stations, but cell biovolumes were larger in July. The data are consistent with the hypothesis that organic enrichment via petroleum utilization is responsible for increased abundances of bacteria and nematodes at the seep. There were strong correlations between densities of harpacticoids and microalgae, and densities of nematodes and bacteria. These links indicate that seeping petroleum might have an enhanced effect on the detrital (bacterial based) food web, but a toxic effect on the grazing (microalgal based) food web.

1. Introduction

The Isla Vista hydrocarbon seep, offshore of Coal Oil Point in the Santa Barbara Channel, has recently been the subject of several benthic investigations. Surprisingly, there is a robust benthic community at the seep. The macroinfauna, which are dominated by deposit-feeders, are more dense at the seep than at a nearby nonseep station (Spies and Davis, 1979; Davis and Spies, 1980). Concentrations of ATP are

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also greater in sediments where fresh petroleum is actively seeping (Spies *et al.*, 1980). Mats of the sulfide-oxidizing bacteria *Beggiatoa* spp. are a common feature of the oil seep and contain large quantities of chlorophyll and meiobenthos (Montagna and Spies, 1985). Densities of nematodes and bacteria are also greater at the seep than at a nonseep site (Montagna *et al.*, 1987).

Although, density (i.e., the number of organisms per unit volume at a given depth within the sediment) is greater at the seep, total abundance (i.e., the total number of organisms integrated over several sediment depth ranges) may not be greater at the seep. If the benthos are concentrated in the surface sediments at the seep, but distributed more deeply away from the seep, then the total abundance would be greater away from the seep. The oxic zone is only a thin veneer at the seep. The annual average depth of the visual redox-potential-discontinuity (RPD) layer was 1 cm at the seep and 4.5 cm away from the seep, and the average depth at which Eh decreased to 0 mV was 0.5 cm at the seep and 7 cm deep away from the seep (Montagna *et al.*, 1987). Oxygen concentration and Eh are very important in controlling the vertical distribution and abundance of meiofauna (McLachlan, 1978). Therefore, differences in physical factors and biogeochemical profiles could be responsible for the higher densities of benthos in seep sediments.

Alternatively, trophic relationships can control densities of benthic organisms. In South Carolina twice as many meiofauna were found in the top 1 cm of muddy sediments than were found in the top 10–15 cm of sandy sediments (Coull and Bell, 1979). Thus, the oxic zone of the organically enriched mud site can support 20 times more biomass per volume of sediment than the oxic zone of the sand site. Predation pressure of fish on meiofauna is also greater at the mud site (Smith and Coull, 1987).

In this study we investigated the physical and biological factors related to the vertical distribution of meiofauna at the seep. The seep site has higher densities of animals in the surface sediments. Could the total abundance be the same as nonseep sites? Is the distribution of potential food sources (bacteria and microphytobenthos) related to meiofaunal distributions? The seep is a natural experiment. By gaining an understanding of the factors that control the vertical distribution of meiofauna in this unusual environment, we will gain knowledge of the underlying generic processes.

2. Materials and methods

a. Study area. The hydrocarbon seep studied is in the Santa Barbara Channel between Coal Oil Point and Goleta Point about 800 m offshore of Isla Vista, California, USA. We sampled three stations with different rates of petroleum seepage. A map of the study area has been previously published (Montagna *et al.*, 1987; Bauer *et al.*, 1988). A companion study examining the biogeochemical relationships within vertical profiles of sediments was performed at the same time as this study (Bauer *et al.*, 1988).

Station A is within the Isla Vista seep and in the center of large quantities of fresh oil and natural gas seeping from the sediments. In our previous studies, we sampled at the fringe of station A, where there was less fresh petroleum in the samples (Montagna *et al.*, 1986; 1987). In the current study we sampled the center of the seep with concentrations of total extractable hydrocarbons (TEH) averaging 2.2 mg · cm^{-3} at the surface and increasing to 25 mg · cm^{-3} 7 cm below the surface (Bauer *et al.*, 1988). Station B, about 20 m north of A, has much less fresh oil seepage but has large quantities of weathered asphalt-like tar 4–12 cm below the sediment surface. The average TEH concentration of sediments at station B was 0.4 mg · cm^{-3} at the surface and increased to 3.5 mg · cm^{-3} (Bauer *et al.*, 1988) at 5 cm depth. Station C is about 1.4 km east of the Isla Vista seep and has about 4.8 times less weathered tar than station B (Stuermer *et al.*, 1982). Station C averaged only about 0.1 mg · cm^{-3} over the entire top 7 cm of sediment (Bauer *et al.*, 1988). Stations B and C were previously studied in great detail and have similar granulometry with a median grain size of about 160 μm (Spies and Davis, 1979; Palmer *et al.*, 1988). Stations A and B are within the Isla Vista seep but station C is not. All stations were at a depth of 18 m in fine-sand sediments.

b. Sampling periods and profiles. Three sampling periods during 1986 were chosen based on biological and physical data from a previous study (Montagna *et al.*, 1987). There was one period in each of the three major oceanographic seasons defined for the California continental shelf: upwelling (February–July), mixed (August–November), and Davidson (December–January). April was chosen to represent the upwelling season, because we recorded the lowest bottom temperatures in that month of the previous year. July was chosen for the mixed period, because we had the highest chlorophyll and meiofaunal densities in that month of the previous year. December was chosen for the Davidson period, because chlorophyll and meiofaunal densities were lowest in that month of the previous year.

The average bottom water temperatures during April, July and December 1986 were 13.5°C, 14.6°C, and 17.0°C respectively. During the December sampling period there was a very unusual storm. Although the skies were very clear, wave height was around 3 m and there was a great deal of storm surge at the bottom of the sampling sites. Sand ripples were also greatly pronounced relative to other times.

Vertical samples were taken at depth intervals of 0–1 cm, 1–2 cm, 2–4 cm, 4–6 cm, and 6–8 cm. These intervals were chosen so that oxic and anoxic zones would be sampled and distinguished at all stations. In the previous year the RPD layer was at 0–1 cm in station A, 1–2 cm in station B, and 4–6 cm in station C (Montagna *et al.*, 1987). All samples were taken by divers using hand-held corers. During each sampling period similar vertical profiles of pore water (Eh, alkalinity, oxygen, sulfate, and sulfide), and microbial activity (sulfate reduction, and hydrocarbon degradation) were measured and are reported elsewhere (Bauer *et al.*, 1988). Triplicate samples were taken for all measurements.

c. Microbes and meiofauna. Meiofaunal samples were taken with 60 cm^3 syringe barrels with the bottoms cut off (area = 5.5 cm^2). One-cm^3 subsamples for enumeration of bacteria were taken from the larger cores. Bacterial samples were preserved in 4% buffered formalin that had been filtered through a 0.2 μm filter and were refrigerated until they were analyzed. Bacterial cell counts were measured using the acridine orange direct count (AODC) technique (Daley and Hobbie, 1975) as modified by Montagna (1982). Direct count techniques, which use light microscopy, can lead to systematic errors in estimating bacterial abundance (Brock, 1984). However, they are also the easiest techniques that measure only bacterial-sized organisms and will yield relative results which allow for station comparisons (Montagna, 1982). Photographs of bacteria were used to estimate cell biovolumes (Fuhrman, 1981) and the frequency of dividing cells (FDC) (Hagstrom *et al.*, 1979). Biovolumes are converted to biomass assuming 0.38 g carbon · cm^{-3} cell volume (Lee and Fuhrman, 1987).

Turnover times of bacteria were estimated from the FDC data using the formula given in Newell and Christian (1981): where $\mu = e^{(0.299FDC - 4.961)}$, and is the growth rate in h^{-1}. In other studies, growth rates obtained by FDC are at least an order of magnitude higher than rates obtained using oxygen consumption or thymidine incorporation into DNA (Newell and Fallon, 1982; Fallon *et al.*, 1983; Riemann and Sondergaard, 1984; Riemann *et al.*, 1984). However, we present the FDC growth rates to compare the depth distributions at three stations in a relative sense, not to estimate absolute values for bacterial productivity. The only assumption made is that any errors occur with equal probability in all samples, making our results relative and allowing us to test for depth and site differences (Montagna *et al.*, 1987).

Photosynthetic pigments were used as indicators of microphytobenthos biomass. Sediment samples for pigment analysis were frozen immediately after collection. Chlorophyll *a* (Chl *a*) and phaeophytin *a* (Phae *a*) concentrations were measured spectrophotometrically by the acidification technique (Lorenzen, 1967) as modified by Montagna and Spies (1985) for sediment samples containing oil.

Meiofaunal samples were taken with 60-cm^3 syringe barrels that had the bottoms removed (area = 5.5 cm^2). Animals were relaxed with magnesium sulfate and were preserved with 10% buffered formalin containing rose bengal. Meiofauna were extracted from the sediments by a decantation and elutriation technique and collected on a 63 μm sieve. All harpacticoid copepods were removed and identified, and nematodes were counted by the dish-subsampling technique (Sherman *et al.*, 1984).

d. Statistical analysis. Since cores were sectioned to obtain vertical distributions, depth zonation is a nested-random effect, not a crossed-fixed effect. That is, the vertical depth-interval samples from each core have a relationship with one another that must be accounted for. Therefore, all variables counted from vertical profiles were analyzed by the following partially hierarchical model (Kirk, 1982):

$$Y_{ijklm} = \mu + \alpha_j + \beta_k + \alpha\beta_{jk} + \gamma_{l(jk)} + \delta_m + \alpha\delta_{jm} + \beta\delta_{km} + \alpha\beta\delta_{jkm} + \epsilon_{i(jklm)},$$

where: μ = overall sample mean, α_j = main effect of month, β_k = main effect of stations, $\gamma_{l(jk)}$ = nested effect for replicate core, δ_m = main effect for depth, $\epsilon_{i(jklm)}$ = random error, and combined terms are interaction effects. The expected mean squares were calculated for each term, and the proper F-test was derived (Kirk, 1982). All analysis of variance (ANOVA) tables indicate which terms were used in the F-tests. The most interesting test is for the station-month interaction term. The null hypothesis for this term is that there is no difference between the patterns of the vertical distributions among stations.

The independent variable in this study is density, i.e., the number of individuals (or cells) per unit volume of sediment at the depth horizon sampled. Analyses were performed with both log transformed and untransformed data, and the residuals were analyzed for departures from normality. In general log transformed data yielded residuals with fewer departures from normality, and with less of a dependency of the variance on the mean, so the analyses on log transformed data are reported here. Tukey multiple comparison procedures were used to find *a posteriori* differences among sample means. Mean values throughout the text and tables that were not significantly different at the 0.05 level are underlined. All analyses were performed using SAS software (SAS Institute, 1985). All figures have mean densities plotted at the center of the sampling horizon level without error bars.

The biovolume and FDC data were handled slightly differently. Since biovolume was randomly sampled from photographs, the replicate core effect was dropped and the problem reduced to a 3-way ANOVA. The FDC data have a binomial distribution, i.e., cells are dividing or they are not. The mean of a binomial distribution is given by np, where, p is the probability of finding a dividing cell among n cells. The variance is given by $np(1 - p)$. Since the mean and variance are a function of all cells counted, the number of dividing and nondividing cells in each treatment were summed before calculating the FDC. This problem reduces to a 3-way ANOVA, and the triple interaction is used as the mean square error.

Finally, to examine if deeper dwelling organisms changed our interpretations based on density, total abundances were computed. Abundances were calculated by summing the products of the density and volume of sediment over the entire sampling range. Whereas, density is reported in units per volume of sediment at a specific depth interval, abundance is reported in units per area to a depth of 8 cm.

3. Results

a. Microphytobenthos. The pattern of the vertical distribution of pigments was the same in all stations (Table 1, $P = 0.4237$). On average 63% of the Chl *a* was found in the top 1 cm of the sediment. There were differences in sediment Chl *a* concentrations

Table 1. Results from ANOVAs on sediment pigment data. Probabilities (P) are that there were no differences in chlorophyll *a* (Chl *a*), phaeophytin *a* (Phae *a*), and total pigment (Chl *a* + Phae *a*) concentrations between months, stations and vertical distributions and interactions. The following abbreviations are used throughout all tables to identify sources of variation: M = month, S = station, MS = month-station interaction, R(MS) = replicate core (nested within month-station interaction), D = depth interval, MD = month-depth interaction, SD = station-depth interaction, MSD = month-station-depth interaction. The F column finds the numerator and denominator used in the F-test. In addition to the abbreviations used in the Source-column the following abbreviations are used throughout in the F-column: ms(X) = mean square of X, ms(E) = mean square error.

Source	F	Chl *a* P	Phae *a* P	Total P
M	ms(M)/ms(MSD)	0.0003	0.0024	0.0001
S	ms(S)/ms(MSD)	0.0007	0.0187	0.3595
MS	ms(MS)/ms(E)	0.0077	0.0418	0.0009
R(MS)	ms(R)/ms(E)	0.7030	0.5305	0.0001
D	ms(D)/ms(MSD)	0.0006	0.0319	0.0001
MD	ms(MD)/ms(MSD)	0.0853	0.2675	0.2684
SD	ms(SD)/ms(MSD)	0.4237	0.2627	0.0954
MSD	ms(MSD)/ms(E)	0.3043	0.5903	0.2015

between stations, months, and depth intervals (Table 1). Over all months and stations, Chl *a* decreased with depth: the concentration in the top 1 cm was 1.382 $\mu g \cdot cm^{-3}$, 1–2 cm was 0.450 $\mu g \cdot cm^{-3}$, 2–4 cm was 0.179 $\mu g \cdot cm^{-3}$, 4–6 cm was 0.158 $\mu g \cdot cm^{-3}$, and 6–8 cm was 0.141 $\mu g \cdot cm^{-3}$. There was a significant interaction between month and station indicating that the depth distribution was changing seasonally (Table 1, Fig. 1). In April all Chl *a* concentrations were very low and uniform among stations, and depths. In July and December there was a large amount of Chl *a* in the surface 2 cm of the sediments (Fig. 1). Station C had the highest overall average concentration (0.777 $\mu g \cdot cm^{-3}$), which was higher than stations B and A (0.259 and 0.137 $\mu g \cdot cm^{-3}$) which were the same. December and July had the highest concentrations (0.517 and 0.529 $\mu g \cdot cm^{-3}$ respectively), and were higher than April (0.099 $mg \cdot cm^{-2}$).

There were also significant differences in Phae *a* concentrations along the sediment depth intervals (Table 1, $P = 0.0319$). The concentration in the top 1 cm was 0.359 $\mu g \cdot cm^{-3}$, 1–2 cm was 0.325 $\mu g \cdot cm^{-3}$, 2–4 cm was 0.147 $\mu g \cdot cm^{-3}$, 4–6 cm was 0.156 $\mu g \cdot cm^{-3}$, and 6–8 cm was 0.067 $\mu g \cdot cm^{-3}$. Phae *a* concentrations were different among months and stations (Table 1, $P = 0.0418$). Phae *a* concentrations averaged 0.180 $\mu g \cdot cm^{-3}$ overall. Stations A and B had the highest overall average concentration (0.318 $\mu g \cdot cm^{-3}$ and 0.201 respectively), which was higher than station C (0.090). Phae *a* was higher in April (0.381 $\mu g \cdot cm^{-3}$) than July (0.208 $\mu g \cdot cm^{-3}$) and December (0.071 $\mu g \cdot cm^{-3}$) which were the same.

The Chl *a* to Phae *a* ratio was much higher at the comparison site, C (77) than at the

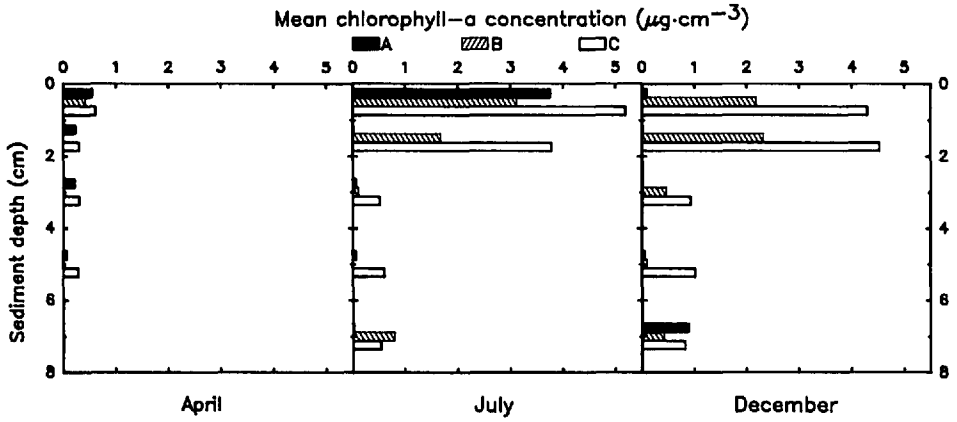

Figure 1. Mean chlorophyll concentrations in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The coefficient of variation for the data is 132%, and the overall mean was 0.304 $\mu g \cdot cm^{-3}$.

seep stations A and B (22 and 19 respectively). This indicates that much of the pigment at the seep was degrading, either through the grazing activities of seep animals or through toxic effects of the hydrocarbons.

b. Bacteria. There were significant differences in cell density between depths, stations, and seasons, and all interactions. However, there were general trends. Densities decreased with depth, averaging over all dates and stations $2.16 \times 10^8 \cdot cm^{-3}$ in the top 0–1 cm, $2.15 \times 10^8 \cdot cm^{-3}$ in the 1–2 cm section, $1.92 \times 10^8 \cdot cm^{-3}$ in 2–4 cm, $1.56 \times 10^8 \cdot cm^{-3}$ in 4–6 cm, and $1.25 \times 10^8 \cdot cm^{-3}$ in 6–8 cm. The exception to this trend was stations A and C in December, when densities were relatively uniform throughout the sediment (Fig. 2). Station A had higher densities ($2.36 \times 10^8 \cdot cm^{-3}$) than station B ($1.60 \times 10^8 \cdot cm^{-3}$) and C ($1.56 \times 10^8 \cdot cm^{-3}$) which were statistically the same. Densities in December ($2.19 \times 10^8 \cdot cm^{-3}$) and July ($1.92 \times 10^8 \cdot cm^{-3}$) were higher than in April ($1.62 \times 10^8 \cdot cm^{-3}$).

Biovolumes were generally uniform in size with respect to depth (Fig. 3, Table 2). The exception was the 6–8 cm section from station A in July when the biovolume averaged 0.048 μm^3, compared to an overall mean of 0.014 μm^3. This one extremely large value was also responsible for significant month, depth, and month-depth interaction effects (Table 2). Bacteria biovolumes were not different among stations (Table 2). Photographs of cells from deep sediments in December did not turn out well, so those data are missing.

Bacteria biomass was calculated as a function of cell density, biovolume, and conversion factors. The average biovolume for December in the top 2 sections among all stations (0.026 μm^3) was used to calculate biomass for the deeper sediments. Since there were strong station and depth effects for cell density and no differences overall

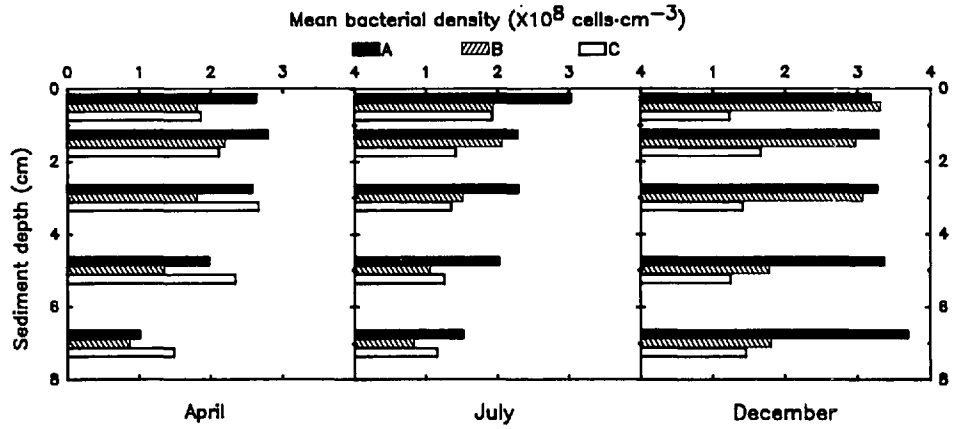

Figure 2. Mean bacteria cell densities in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The coefficient of variation for the data is 1.6%, and the overall mean was 1.80×10^8 cells · cm^{-3}.

for biovolume, differences among biomass estimates were driven by the density component (Fig. 4). The biomass in the top 2 cm (1.13 μg C · cm^{-3}) was higher than the lower 2–8 cm sections (0.81 μg C · cm^{-3}). Biomass in December (1.25 μg C · cm^{-3}) and July (1.20 μg C · cm^{-3}) was twice as high as in April (0.62 μg C · cm^{-3}). Station A (1.22 μg C · cm^{-3}) had a higher biomass than B (0.85 μg C · cm^{-3}) and C (0.80 μg C · cm^{-3}) which were the same.

The vertical distribution of the frequency of dividing cells (FDC) was the same in all stations (Table 2, $P = 0.3057$). Although there was a tendency for FDC to increase down to 4 cm, and then decrease from 4–8 cm (Fig. 5), the trend was not significant.

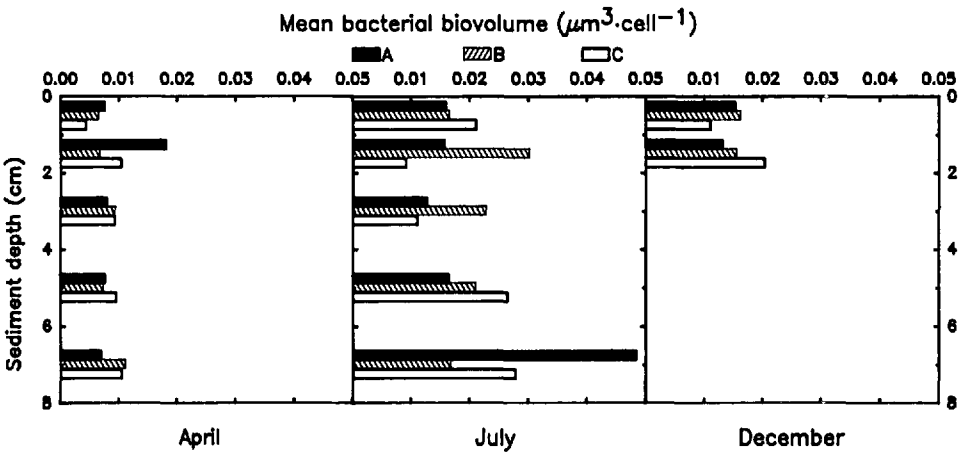

Figure 3. Mean bacteria biovolume in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The coefficient of variation for the data is 184%, and the overall mean was 0.0324 μm^3 per cell.

Table 2. Results from ANOVAs on bacterial biovolume and frequency of dividing cell (FDC) data. Probabilities are that there were no differences in cell density between months, stations and vertical distributions and interactions. For biovolumes, measurements of 40 cells were made from the samples for each month-station-depth combination, thus, the problem reduces to a 3-way ANOVA. For FDC, the sum of all dividing and nondividing cells was used to calculate the percent dividing, thus, there is no replication for FDC and the triple interaction is used as the error term. Abbreviations as in Table 1.

	Biovolume		FDC	
Source	F	*P*	F	*P*
M	ms(M)/ms(E)	0.0001	ms(M)/ms(MSD)	0.0004
S	ms(S)/ms(E)	0.8382	ms(S)/ms(MSD)	0.2254
MS	ms(MS)/ms(E)	0.1718	ms(MS)/ms(MSD)	0.1880
D	ms(D)/ms(E)	0.0008	ms(D)/ms(MSD)	0.0370
MD	ms(MD)/ms(E)	0.0056	ms(MD)/ms(MSD)	0.7456
SD	ms(SD)/ms(E)	0.0553	ms(SD)/ms(MSD)	0.3057
MSD	ms(MSD)/ms(E)	0.0001		

The FDC was different among months and stations (Table 3). FDC in December (17.7%) and April (15.1%) was higher than in July (11.1%). Stations B and C had higher FDC in April and December, but station A had the highest FDC in July. Growth rates (μ) were calculated from the FDC data, and averaged 0.417 h^{-1}. Growth rates were higher in December (1.427 h^{-1}) than April (0.637 h^{-1}) and July (0.196 h^{-1}).

Bacterial productivity is calculated by the product of the biomass (i.e., cell counts, biovolumes, and conversion factors) and growth rate (i.e., FDC and conversion factors). Estimates of productivity are determined by cell counts, biovolume and FDC.

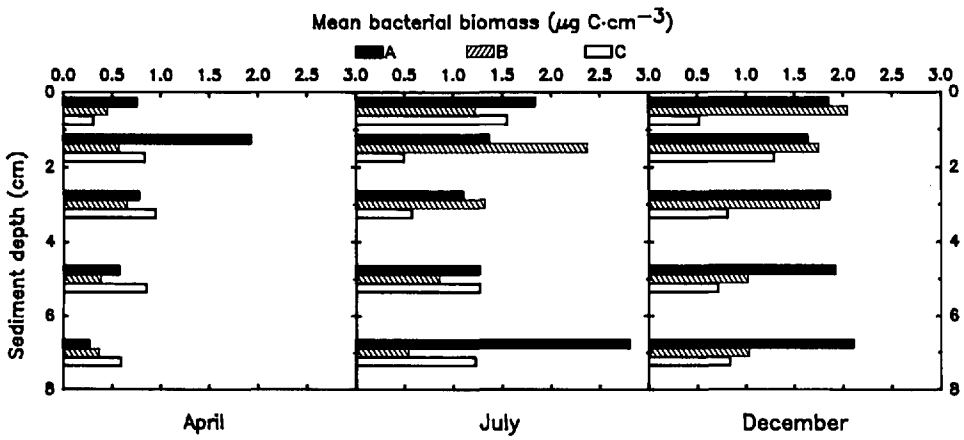

Figure 4. Mean bacteria biomass in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The overall mean was 0.934 $\mu g \cdot cm^{-3}$.

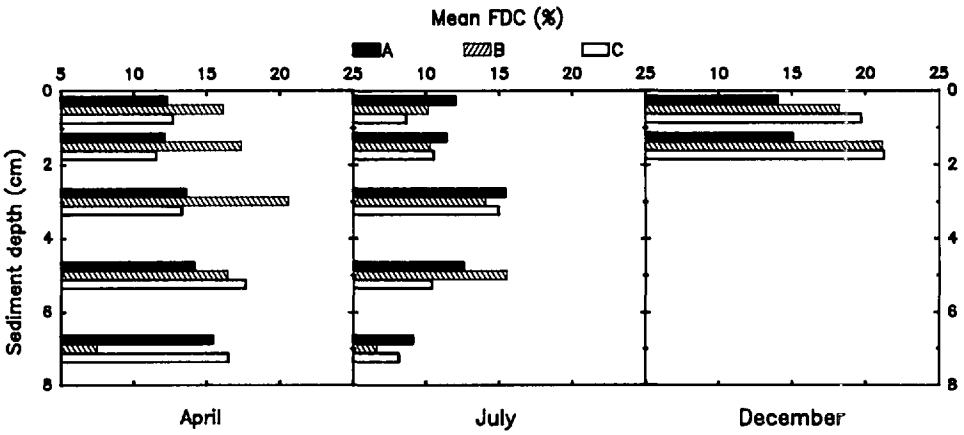

Figure 5. Mean frequency of dividing cells for bacteria in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The coefficient of variation for the data is 17.7%, and the overall mean was 13.8%.

Since the largest differences were found among depth intervals for cell densities, and months for FDC, there are differences among the station-month combinations (Fig. 6). The overall mean bacterial productivity was 20.5 μg C · cm^{-3} · d^{-1}. Productivity ranged over three orders of magnitude (Fig. 6). Productivity increased from 18.5 μg C · cm^{-3} · d^{-1} in the top 1 cm, to 40.2 μg C · cm^{-3} · d^{-1} at 4 cm, and then decreased to 4.87 μg C · cm^{-3} · d^{-1} at 8 cm.

The total productivity in the top 2 cm in December (1474 mg C · m^{-2} · d^{-1}) was much higher than in April (167 mg C · m^{-2} · d^{-1}) or July (68.9 mg C · m^{-2} · d^{-1}).

Table 3. Results from ANOVAs on meiofauna data. Probabilities that there were no differences in Nematoda, Harpacticoida, other meiofauna densities between months, stations and vertical distributions and interactions. The other category represented 13.2% of the total meiofauna, and included 13 taxa (in order of dominance: Ciliata 8.8%, Turbellaria 1.6%, Foraminifera 1.0%, Gastrotricha 1.02%, Polychaeta 0.36%, Oligochaeta 0.094%, juvenile bivalvia 0.075%, Ostracoda 0.072%, Kinoryncha 0.053%, juvenile Amphipoda 0.038%, juvenile Cumacea 0.034%, Isopoda 0.0057%, and Tanaidacea 0.0019%). Abbreviation as in Table 1.

Source	F	Nematoda *P*	Harpacticoida *P*	Others *P*
M	ms(M)/ms(MSD)	0.3178	0.0443	0.1253
S	ms(S)/ms(MSD)	0.4122	0.3572	0.0988
MS	ms(MS)/ms(E)	0.6209	0.0067	0.0490
R(MS)	ms(R)/ms(E)	0.0008	0.0026	0.0912
D	ms(D)/ms(MSD)	0.0001	0.0001	0.0001
MD	ms(MD)/ms(MSD)	0.0010	0.1672	0.5152
SD	ms(SD)/ms(MSD)	0.0012	0.5960	0.0641
MSD	ms(MSD)/ms(E)	0.8249	0.1499	0.1426

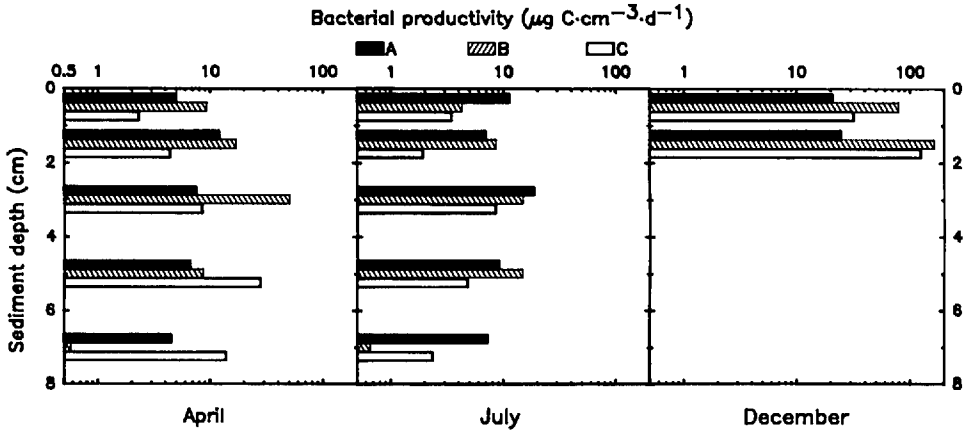

Figure 6. Mean bacteria productivity in sediment profile during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The overall mean was 20.5 μg C · cm^{-3} · d^{-1}.

The productivity in the top 8 cm at station B averaged 1824 mg C · m^{-2} · d^{-1}, at C 1222 mg C · m^{-2} · d^{-1}, and at A 807 mg C · m^{-2} · d^{-1}.

c. Meiobenthos. Nematodes dominated the meiofauna taxa composition, averaging 85.0% overall. Harpacticoids comprised 1.8% of the community overall. The remaining 13.2% was comprised of 13 other taxa (in order of dominance): Ciliata, 8.8%; Turbellaria, 1.6%; Foraminifera, 1.0%; Gastrotricha, 1.02%; Polychaeta, 0.36%; Oligochaeta, 0.094%; juvenile bivalvia, 0.075%; Ostracoda, 0.072%; Kinoryncha, 0.053%; juvenile Amphipoda, 0.038%; juvenile Cumacea, 0.034%; Isopoda, 0.0057%; and Tanaidacea, 0.0019%. If protozoans are excluded, then nematodes represent 94.4% of the metazoans, harpacticoids represent 1.9%, and the remaining 11 taxa comprise 3.7%. Nematodes were the only group exhibiting different depth distributional patterns among stations, harpacticoids and other meiofauna taxa did not (Table 3).

Nematode densities were not different among stations and months, but there were differences between depth intervals, and the vertical distribution changed among months and stations (Table 3). There were more nematodes in the top 2 cm at station A (2058 · 10 cm^{-3}) in all months than stations C (860 · 10 cm^{-3}) or B (695 · 10 cm^{-3}). In contrast, in deeper sediments (6–8 cm) nematode densities were the lowest (24 · 10 cm^{-3}) at station A, compared to 54 · 10 cm^{-3} at B, and 59 · 10 cm^{-3} at C. There was less depth stratification in April than in July and December (Fig. 7).

Harpacticoids were virtually limited to the top 1 cm of the sediment (Fig. 8), where 84.5% of all individuals were found. There was no significant difference in vertical distributions among stations, (Table 3, $P = 0.5960$). This was because harpacticoids were restricted to the surface. There were differences in harpacticoid density among

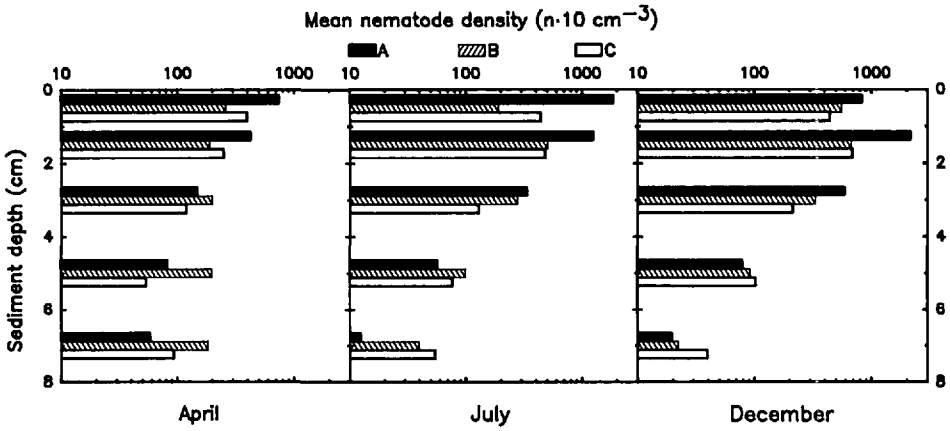

Figure 7. Mean density of Nematoda in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The coefficient of variation for the data is 15.2%, and the overall mean was 193 individuals · 10 cm^{-3}.

stations and months (Table 3, $P = 0.0067$), but this was due to the few harpacticoids found at deeper depths (Fig. 8). In the top 1 cm there were on average 61.0 · 10 cm^{-3} harpacticoids at station C, 26.1 · 10 cm^{-3} at B and 4.2 · 10 cm^{-3} at station A. There were 4.6 times as many harpacticoids in December and July than there were in April.

Like nematodes and harpacticoids, other taxa were more abundant in the surface sediments than in deeper sediments (Fig. 9). The vertical distribution was barely the same among stations (Table 3, $P = 0.0641$) indicating that the decrease at A in deeper sediments in April and December may be significant. There were no differences among

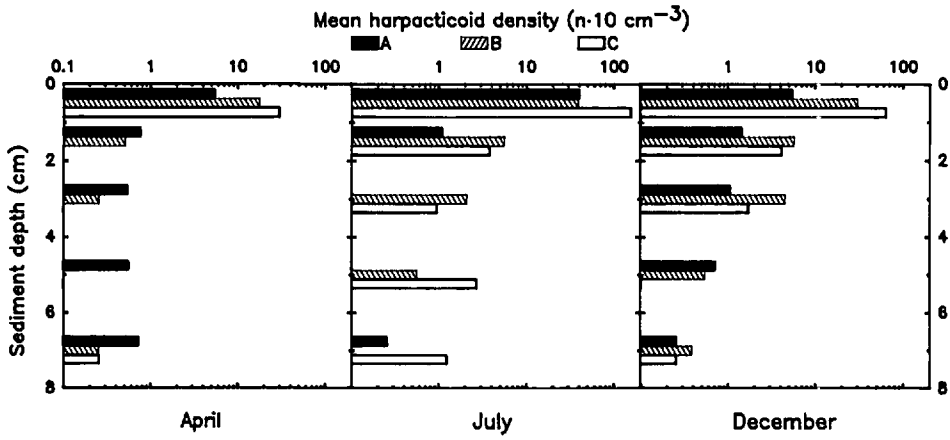

Figure 8. Mean density of Harpacticoida in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. 0.1 was added to all harpacticoid densities, and thus values falling on the ordinate represent 0. The coefficient of variation for the data is 278%, and the overall mean was 0.456 individuals · 10 cm^{-3}.

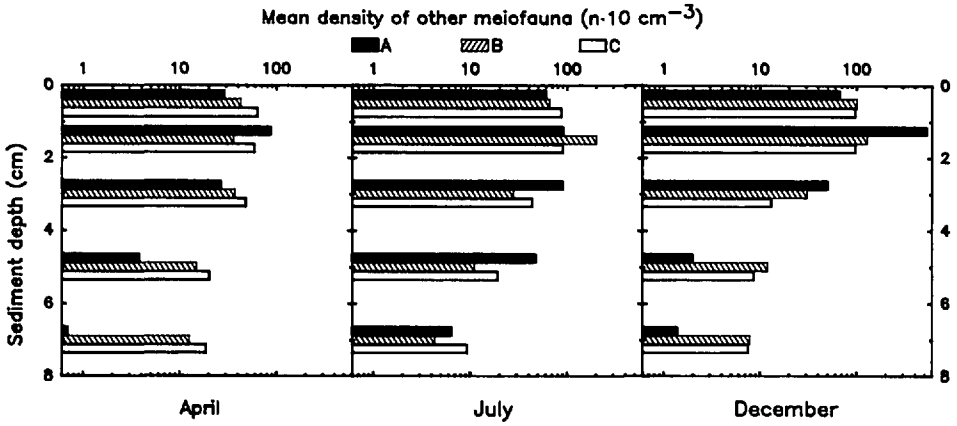

Figure 9. Mean density of meiofauna taxa other than Nematoda and Harpacticoida in sediment profiles during three months (1986) at the three stations. Scale on the abscissa is the same for all three months. The coefficient of variation for the data is 39.5%, and the overall mean is 24.6 individuals · 10 cm^{-3}.

months for the other meiofaunal taxa (Table 3). In December there was an unusually large number of ciliates present in the 2–4 cm section, resulting in a subsurface peak in that month (Fig. 9). Ciliates (76%) were predominantly found in the 2–6 cm depth intervals. Foraminiferans increased in abundance from the surface through to the 4–6 cm interval, and then decreased with depth. Oligochaetes, polychaetes, turbellaria, ostracods, bivalves, amphipods, tanaids, isopods, cumaceans, and kinorynchs were all most abundant at the surface and decreased with depth. There were differences in density of other meiofaunal taxa among stations (Table 3). The average density at station A was 16.1 · 10 cm^{-3}, for station B 28.7 · 10 cm^{-3}, and for C 32.1 · 10 cm^{-3}. This result was largely due to ciliates which favored station A. Foraminifera and ostracods favored station B, and all other taxa were more abundant at station C.

d. Harpacticoida species. Most harpacticoid species (87.8%) were distributed in the top 1 cm of the sediment. However, half of the 33 species could be found deeper (Table 4). Only three species were exclusively subsurface dwellers (Table 4). Five species were found only at the seep sites (stations A and B), and only 3 species were found exclusively at the comparison site (station C) (Table 4). Thus, 76% of the species were common to all three stations. Station C had more harpacticoids than stations A and B combined, but this was largely due to *Zausodes sextus,* which represented 29% of all station C harpacticoids, and was mostly absent at stations A and B. There were more harpacticoids in July than in April or December in 64% of the species.

Factor analyses were performed on the species distributions. When sediment depth is included, it is overwhelmingly the most important factor. Repeating the analysis using only the top 1 cm surface section of the sediment revealed that 48% of the

Table 4. Vertical distribution of harpacticoid copepods. Average density (individuals·m^{-2}) from three stations and three months. Taxonomic order follows Bodin (1979).

		Depth (cm)					Station			Month		
Family	Species	0–1	1–2	2–4	4–6	6–8	A	B	C	APR	JUL	DEC
Longipediidae	*Longipedia* (cf.) *minor*	780	0	0	0	0	39	39	430	150	320	40
Ectinosomatidae	*Ectinosoma paranormani*	2880	333	267	0	0	117	1213	900	600	1000	600
	Ectinosoma melaniceps	120	0	0	0	0	0	0	78	38	40	0
	Halectinosoma kunzi	900	0	133	0	0	78	235	352	262	320	80
	Microsetella norvegica	180	67	0	67	0	0	78	117	38	80	80
	Pseudobradya cornuta	60	67	0	0	0	0	0	78	0	40	40
	Pseudobradya crassipes	240	0	0	0	0	0	78	78	0	120	40
	Pseudobradya pectinifera	120	0	0	0	0	0	0	78	75	0	0
Harpacticidae	*Zausodes sextus*	9840	333	67	0	67	117	1213	5361	2062	1840	2800
Tisbidae	*Tachidiella parva*	240	0	0	0	0	78	39	39	75	80	0
Thalestridae	*Dactylopodia paratisboides*	1260	200	67	0	0	235	235	509	75	840	80
	Diarthrodes dissimilis	840	67	0	0	0	157	78	352	75	520	0
Diosaccidae	*Amphiascoides lancisetiger*	3300	0	67	0	0	78	743	1370	75	1560	600
	Amphiascoides petkovskii	960	0	0	0	0	39	157	430	38	320	280
	Robertgurneya diversa	5040	267	133	67	0	196	704	2661	338	2000	1280
	Robertsonia propinqua	240	67	0	0	0	0	39	157	75	120	0
	Stenhelia (S.) proxima	540	0	0	0	0	0	39	313	38	280	40
	Typhlamphiascus sp.	1020	0	0	0	0	0	78	587	488	40	120
	Pseudoamphiascopsis sp.	1980	0	0	0	0	1057	78	157	0	1320	0

Ameiridae	*Ameira parvuloides*	120	67	133	0	0	39	157	0	0	120	80
	Unknown genus	0	67	133	67	67	0	117	78	0	80	120
	Leptomesochra sp.	0	0	67	333	133	157	78	78	150	80	80
Paramesochridae	*Apodopsyllus vermiculiformis*	0	0	267	0	133	0	235	0	0	40	200
Canthocamptidae	*Mesochra pygmaea*	5820	533	533	200	67	2035	117	2426	0	3400	1280
	Orthopsyllus illgi	360	200	0	0	0	0	157	196	38	240	80
Cletodidae	*Acrenhydrosoma karlinga*	360	67	0	0	0	78	196	0	75	120	80
	Cletodes hartmannae	480	0	0	0	0	78	117	117	38	40	240
	Enhydrosoma hopkinsi	420	0	67	0	0	39	274	0	0	120	200
	Enhydrosoma propinquum	180	0	0	0	0	39	78	0	0	120	0
	Stylicletodes verisimilis	180	0	0	0	0	0	39	78	75	0	40
Laophontidae	*Normanella bolini*	2100	200	0	0	67	313	430	783	600	560	360
	Normanella confluens	1200	133	0	0	0	78	157	626	38	680	160
	Paralaophonte asellopsiformis	540	0	0	0	0	0	78	274	38	0	320
Percent within group (depth, station, month)		87.8	5.5	4.0	1.5	1.1	16.3	23.5	60.3	17.7	52.4	29.9

variability in the distributions could be explained by three factors. The first factor (27% of the variability) was due to high abundances of 8 species at station C in July. These 8 species were (ranked in loading order): *Normanella confluens, Robertgurnea diversa, Amphiascoides lancisetiger, Longipedia minor, Mesochra pymaea, Robertsonia propinquum, Diarthrodes dissimilis,* and *Dactylopodia paratisboides.* The second and third factors (11% and 10% of the total variance, respectively) separated stations and months. Within each month, the seep stations (A and B) were always separable from the comparison station (C). The seep stations were characterized by 4 species (ranked by the second factor loadings): *Enhydrosoma propinquum, Pseudoamphiascus* sp., *Ameira parvuloides,* and *Acrenhydrosoma karlinga.* The comparison station was characterized by 5 species (ranked by negative second factor loadings): *Paralaophonte asellopsiformis, Z. sextus, Typhlamphiascus* sp., *Amphiascoides petkovskii,* and *D. dissimilis.*

e. Interannual variability. The temporal variability of benthic microbial and meiofaunal populations of the Isla Vista petroleum seep was also studied in 1985 (Montagna *et al.,* 1987). Only sediment above the RPD layer was used in that study. Therefore only the top 1 cm section is comparable between years for microbes. For meiofauna, the top two sections (0–2 cm) from the present study would be an appropriate comparison for stations A and B, and the top 3 sections (0–4 cm) for stations C. When the subset from the first study (December 1984, April and July 1985) is compared to data from the present study interannual differences are noted in many variables (Table 5). Some of the differences may be due to factors other than interannual variability. Because of sampling location differences, station A had more fresh petroleum in the sediment in the present study than in the previous year. There was also a great deal of bottom surge during December 1986.

The annual mean Chl *a* concentration was not different between years. In both years, chlorophyll was highest in July, with April and December being similar. In the first year, Chl *a* was similar among stations, but in the second year there were very low values at station A.

Measures of bacterial growth and abundance were very similar over the two years. The best example of this is productivity because it is the product of cell counts, volumes, and FDC. Productivity was not statistically different between years, but for different reasons. In the first year there were slightly fewer cells, but they were larger, and dividing at a greater rate. The net result is that there was no real change in productivity between years. In both years there were greater densities and larger cells in July than in the other two months, resulting in highest biomasses in July. In the second year FDC was very high in December. Productivity at station C was lowest in both years. Biomass and FDC were both lower at station C in both years.

Densities of meiofauna were almost twice as high in the first year as in the second. Nematodes decreased by 65% from the first year to the second year, but harpacticoids

Table 5. Interannual variability in the density of microbes and meiofauna and bacterial growth above the RPD zone (i.e., in aerobic sediments). Data for 1984–85 are from Montagna *et al.* (1987). Since sampling in that study was biweekly, data from two sampling trips per month were combined. Data for 1986 are from the present study. To compare the present data with past sampling regimes the 0–1 cm section was used for the microbial parameters, the 0–2 cm sections were summed for the meiofaunal parameters at stations A and B, and the top 0–4 cm sections were summed for the meiofaunal parameters at station C. Key and units: Chlorophyll *a* (Chl *a*) = $mg \cdot m^{-2}$, bacterial cell density (Bc) = $cells \cdot cm^{-3}$, bacterial biovolume (Bv) = μm^3, bacterial biomass (Bm) = $\mu g\ C \cdot cm^{-3}$, frequency of dividing bacterial cells (FDC) = %, bacterial secondary production (2°) = $mg\ C \cdot m^{-2} \cdot d^{-1}$, and nematode (Nem), harpacticoid (Har), and other meiofauna (Oth) density = individuals $\times\ 10^3 \cdot m^{-2}$

Year	Month	Sta	Chl *a*	Bc	Bv	Bm	FDC	2°	Nem	Har	Oth
84–5	·	·	14.5	1.95	0.028	2.14	13.6	211	1767	326	136
84	Dec	·	6.6	1.80	0.017	1.21	15.1	188	1219	409	62
85	Apr	·	13.0	2.01	0.049	3.74	12.3	247	2308	205	293
85	Jul	·	23.6	2.05	0.024	2.00	13.0	163	1955	324	104
·	·	A	16.3	2.50	0.029	2.93	16.3	638	2309	166	118
·	·	B	13.8	1.88	0.024	1.78	12.3	119	1406	188	120
·	·	C	13.6	1.46	0.030	1.71	12.3	112	1587	625	170
86	·	·	12.7	2.16	0.013	1.05	12.5	185	1069	27	170
86	Apr	·	5.2	2.05	0.006	0.47	13.8	55	696	15	100
86	Jul	·	39.4	2.27	0.018	1.56	10.0	64	1211	65	189
86	Dec	·	9.7	2.07	0.014	1.13	16.7	437	1588	26	275
·	·	A	5.9	2.93	0.014	1.51	12.7	123	2058	11	208
·	·	B	14.3	2.08	0.013	1.02	13.9	307	696	30	162
·	·	C	24.0	1.69	0.012	0.75	11.4	125	860	64	160

decreased by 1100%. The changes were due to decreases at stations B and C. The density of nematodes and other meiofauna were similar at station A in both years. Nematode densities were highest in both years at station A, and decreased concomitantly at stations B and C from the first to the second year. Harpacticoid densities were lowest at A in both years. There are generally more meiofauna in July.

The present data from 1986 generally substantiate the conclusions drawn from the data in 1985. Nematode and bacterial densities and bacterial productivity are greater at the seep relative to the comparison station. Chl *a* concentrations were not different among stations, and harpacticoid densities were not distinguishable between stations A and B during the first year (Montagna *et al.*, 1987). However, harpacticoid and Chl *a* density was greater at the comparison site (station C) in 1986, when more fresh petroleum was found in station A.

4. Discussion

a. Physical factors. In marine sediments physical factors affect the vertical distribution of benthic organisms. Advective currents and wave action control grain size and

bedform structures. Organic matter is deposited from the water column above. The interaction between organic matter decomposition, mineral chemistry and porosity of the sediment control concentrations of pore water nutrients. The petroleum seep is different in that there is a large inverted flux of organic matter which stimulates microbial activity (Bauer *et al.*, 1988). Thus, we should find large differences in the vertical distribution patterns of microbes and meiofauna in the seep and comparison stations.

Microphytobenthic pigment (Chl *a*) is found predominantly in the surface sediments (Fig. 1). Since 1% of the surface light penetration in sand is to a depth of only 2–4 mm (Fenchel and Straaup, 1971; Haardt and Nielsen, 1980) most benthic primary production and growth must be taking place in the surface sediments. The higher concentration of Chl *a* in the 1–2 cm section during December is undoubtedly due to sediment reworking by the storm surge (Fig. 1). Chl *a* is apparently buried in the sediment because it can be found in abundance to a depth of 4 cm throughout the year. It would be interesting to know if the buried Chl *a* is photosynthetically competent. If it is, the sediment could represent a large pool of high quality food during resuspension events. Benthic diatom films stabilize sediments (Holland *et al.*, 1974) and affect transfer of organic matter between the sediment and water column (Grant *et al.*, 1986). Resuspension of diatoms occurs at current velocities as low as 10 cm $\cdot$ s^{-1} (de Jonge and van den Bergs, 1987). In contrast, intertidal microalgae migrate to deeper sediments (1–2 mm) during high water, indicating that they may be trying to avoid resuspension (Joint *et al.*, 1982). There were generally very low levels of Chl *a* at the seep station (A) below 2 cm. There are two possible explanations. Either there are toxic effects of fresh seeping petroleum on benthic microalgae, or there is no burial because of an interaction between freshly oiled sediments, wave action and diatom films.

Bacteria densities decrease with sediment depth (Fig. 2). The same result has been reported for a wide range of sediments ranging from salt marshes (Rublee and Dornseif, 1978; Rublee, 1982), to silty subtidal sediments (Aller and Yingst, 1980), and sandy subtidal sediments (Moriarty, 1980). Typically, this decrease in microbial biomass may be due to organic matter available for decomposition (Aller and Yingst, 1980). Bacteria densities are correlated with carbon content in sediments (Dale, 1974; Rublee and Dornseif, 1978). Total organic carbon (TOC) content at the comparison site (station C) was uniform at 0.2% to a depth of 8 cm (Bauer *et al.*, 1988). At station B TOC was similar to station C at the surface but increased to 2.8% at a depth of 4–6 cm (Bauer *et al.*, 1988). At station A TOC was 1.5% at the surface and increased to 2.8% at a depth of 6–8 cm (Bauer *et al.*, 1988). Because of the petroleum in seep sediments, bacteria density is (atypically) inversely correlated with carbon content of the sediment.

Bacterial production (as measured by the microscopical technique) increased with depth to a depth of 3 cm, and then decreased. Rates of sulfate reduction also increased to the depth of 1.5 – 3 cm and then decreased (Bauer *et al.*, 1988). In contrast, dark

uptake of bicarbonate was relatively uniform with respect to depth, except at station A in July when uptake was very high in the surface sample (Bauer *et al.*, 1988). If we assume the top 2 cm of sediments represent the aerobic portion of the microbial community, then the total bacterial production rate (measured by FDC) in this study ($A = 269$ mg $C \cdot m^{-2} \cdot d^{-1}$, $B = 931$ mg $C \cdot m^{-2} \cdot d^{-1}$, and $C = 562$ mg $C \cdot m^{-2} \cdot d^{-1}$) was in the same range as aerobic respiration (measured by oxygen uptake) as reported by Bauer *et al.* (1988) ($A = 1500$ mg $C \cdot m^{-2} \cdot d^{-1}$, $B = 300$ mg $C \cdot m^{-2} \cdot d^{-1}$, and $C = 900$ mg $C \cdot m^{-2} \cdot d^{-1}$). This indicates that the FDC technique was giving us production values in the correct range, and that bacterial metabolism accounted for about two-thirds of total aerobic benthic metabolism. However, the rankings for stations were reversed. This is probably due to very low FDC rates at Station A in December 1986, which yielded low turnover times of bacterial and thus lower productivity.

Vertical distributions of ATP concentrations were also measured during this study (Bauer *et al.*, 1988). ATP probably measures the sum of bacterial, microphytal, and meiofaunal biomass (Sikora *et al.*, 1977; Stevenson *et al.*, 1979; Wilson *et al.*, 1981). Accordingly, we would expect that ATP concentrations be highest in surficial sediments (because Chl *a*, bacterial biomass, and meiofauna are all highest in surficial sediments). However, ATP concentrations followed that pattern in April 1986 only. ATP was also highest in July, correlating with higher Chl *a* and bacterial biomass in July. However, meiofaunal densities were highest in December. ATP data were also considerably more variable than Chl *a*, bacterial biomass, or meiofaunal density. Whereas the biological measurements only varied by as much as four-fold, ATP varied by as much as 200×.

Meiofauna densities decreased with sediment depth (Figs. 7–9). This pattern is well established for all meiofaunal communities (Coull and Bell, 1979). Meiofaunal biomass dominates in the top 1 cm and the top 2 cm contain 71% of all meiofauna (Yingst, 1978). The vertical distribution of meiofauna is probably the result of many factors, but trophic interactions and behavior related to currents seem important. Nematodes apparently migrate downward when water flows to avoid erosion, while copepods do not (Palmer and Molloy, 1986). Surface dwelling meiofauna must also contend with increased pressure from predators. For example, in South Carolina juvenile spot (*Leiostomus xanthurus*) prefer feeding in muddy sediments where meiofaunal abundance is 1.8 times higher in the top 1 cm than that of the top 10 cm of sandy sediments (Smith and Coull, 1987).

Chemical as well as biological factors control vertical distributions of meiofauna. Aerobic organisms prefer the surface sediments because oxygen diffusion into sediments is limited. The vertical distribution of metazoans can be explained by many chemical profiles, but they are all related to the concentration of oxygen in pore water (McLachlan, 1978). For example, as the concentration of oxygen decreases, Eh decreases, and sulfide increases. In general, oxidized forms of nutrients decrease, and

reduced forms increase (Fenchel and Riedl, 1970). Although, the existence of an exclusive thiobiotic community has been questioned (Reise and Ax, 1979), there are definitely some taxa that can live where there is no measureable oxygen (Meyers *et al.*, 1987). Biogenic structures are also very important in increasing the depth distribution of meiofauna into anoxic sediments by providing microxygenated halos within burrow walls (Reise, 1981a, b; Meyers *et al.*, 1987).

b. Trophic factors. Based on Eh and sulfide concentration alone, we would have hypothesized *a priori* that meiofauna densities would be very low at station A. Eh was generally lower at station A than B than C, and sulfide was always higher at A than B and C (Bauer *et al.*, 1988). The vertical profiles of Eh at stations A and B were similar, but very different from station C (Bauer *et al.*, 1988). The seep stations generally dropped off dramatically past the 1.5 cm horizon, whereas at station C the decline in Eh was more gradual. In contrast, the vertical profiles at stations B and C were similar, with gradual increases in sulfide concentration; and distinct from station A, where sulfide increased greatly to about 3 cm (Bauer *et al.*, 1988). This difference in the patterns of these two factors allows us to differentiate the effects of these two variables. Nematode (and to a lesser extent other meiofauna) distribution patterns resembled sulfide patterns: highest at A, and increasing density to the 3 cm horizon. Harpacticoid distribution patterns resembled Eh patterns: lowest at A, decreasing rapidly within the top cm. These patterns are consistent with a suggestion by Sikora and Sikora (1982) that nematodes are adapted to anaerobic soils, and represent a link between anaerobic decomposition of organic matter (sulfate reduction) and transfer of energy to higher trophic levels. Harpacticoids seem to be strictly limited by available oxygen, as indicated by Eh (the sum of all potential reducing agents).

Microalgal-feeding nematodes are usually distributed closer to the surface than nonselective deposit-feeding nematodes (Joint *et al.*, 1982; Jensen, 1983). In the present study, harpacticoids and Chl *a* decreased rapidly with depth, and were both most abundant in July. Nematodes and bacteria were both most abundant at station A and decreased less rapidly with depth. The link between nematodes and bacteria versus harpacticoids and microalgae has been noted previously at the seep (Montagna *et al.*, 1987) and in other locations (Montagna *et al.*, 1983). It is tempting to speculate that harpacticoids are more closely linked to the grazing (primary production) based food web, and the nematodes are more closely linked to the detrital (heterotrophic production) based food web.

Unlike many marine sediments, seep sediments do not appear to be carbon limited. One manifestation of this may be the higher cell densities, biomasses and productivity of bacteria at the seep which can result from the microbial utilization of selected hydrocarbon components (unpublished data). Nematodes seem to be more dense at the seep. On the other hand, microalgae and harpacticoids may be negatively affected by the presence of oil or simply lower Eh values, because their densities are lower in seep

Table 6. Variability in microbial and meiofaunal density and abundance. Mean density is given for the month-station-depth interval interaction, and the key and units are: Chlorophyll *a* (Chl *a*) = $\mu g \cdot m^{-3}$, bacterial cell density (Bc) = 10^8 cells$\cdot cm^{-3}$, bacterial biomass (Bm) = μg C$\cdot cm^{-3}$, bacterial secondary production (2°) = μg C$\cdot cm^{-3} \cdot d^{-1}$, and nematodes (Nem), harpacticoids (Har), and other meiofauna (Oth) density = individuas$\cdot 10$ cm^{-3}. Mean abundance is the sum of the densities to a depth of 8 cm, and the units are: Cl *a* = $mg \cdot m^{-2}$, Bc = 10^8 cells$\cdot cm^{-2}$, Bm = mg C$\cdot cm^{-2}$, 2° = mg C$\cdot m^{-2} \cdot d^{-1}$, and Nem, Har, and Oth = individuals $\times$ $10^3 \cdot m^{-2}$.

Mean	Sta	Chl *a*	Bc	Bm	2°	Nem	Har	Oth
Density	A	0.14	2.4	1.2	11.2	230	0.25	16
	B	0.26	1.6	0.8	30.7	184	0.55	27
	C	0.78	1.6	0.8	19.6	168	0.65	32
Abundance	A	8.2	18.3	93.6	807	2866	13.3	326
	B	24.7	12.1	63.7	1824	1573	33.2	267
	C	65.5	12.3	64.9	1221	1426	66.6	272

sediments. There seems to be selection for and against the seep by certain harpacticoid species.

c. Density vs abundance. There appear to be differences in microbial and meiofaunal densities between the seep and comparison stations in the aerobic zone. If there are fewer organisms living in the deeper anoxic zones of the seep then the total abundance may not be different. There does appear to be fewer deep dwelling organisms at the seep for all meiofauna taxa (Figs. 7–9). There were no differences in meiofauna density between stations (Table 3), but when abundances are computed station differences appear. For example, the overall mean density of harpacticoids is only 1.2 times higher at station C than B, but the total abundance to a depth of 8 cm is 2.0 times higher (Table 6). Nematode density is 1.4 times greater at station A than C, but abundance (to 8 cm) is 2.0 times greater. Other meiofauna taxa (save harpacticoids and nematodes) are half as dense at the seep relative to the comparison site, but actually more abundant at the seep than the comparison site. Bacterial cell counts, biomass, and production changes little or the difference decreases, indicating more deeper dwelling microorganisms at the seep. Chl *a* is only 5.5 times as dense at C than A, but is 8.0 times more abundant at C than at A. The net affect is that trends suggested by density become stronger for abundance.

5. Conclusion

Populations of microbes and meiofauna were highest in July, and decreased in winter. All populations decreased with increasing depth.

Harpacticoids and Chl *a* densities decreased with depth at the greatest rates. Harpacticoids and Chl *a* are more dense and abundant at the comparison site than at the seep sites. Strong links between harpacticoids and microalgae and decreases in

both populations with increasing seepage indicate that seeping petroleum may have a deleterious effect on the grazing (microalgal based) food chain.

Nematode density and abundance, bacteria cell counts, and bacterial biomass were greater at the station with the most active seepage rates. Bacterial biovolumes appeared constant with depth, and stations, but cell biovolumes were largest in July. Strong links between nematodes and bacteria indicate that seeping petroleum has an enhanced effect on the detrital (bacteria based) food web. We hypothesize that organic enrichment via petroleum utilization is responsible for increased abundances of bacteria and nematodes at the seep.

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