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Temporal variability and the relationship between benthic meiofaunal and microbial populations of a natural coastal petroleum seep

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ABSTRACT

Previous studies of the Isla Vista petroleum seep in the Santa Barbara Channel found much higher abundances of macrofauna and concentrations of adenosine triphosphate (ATP) in sediments near petroleum seepage compared to those from nonseep areas. To further assess the possible effect of petroleum on organisms at the base of benthic food webs, population abundances of meiobenthos and their suspected microbial food (bacteria and diatoms) were measured biweekly for one year at three stations with differing petroleum exposure. Determinations of suspended particulate matter and the abundance and gut contents of juvenile fishes were also made at seep and nonseep stations.

Nematodes and bacteria had higher abundances in areas of active petroleum seepage than in areas of moderate seepage (within 20 m) or no seepage (1.4 km away). Bacterial productivity (based on the frequency of dividing cells) was 340% greater in sediments from areas of active seepage compared to those from a nonseep station. Sediments within the seep, but away from active seepage, had rates of bacterial productivity 15 times greater than a nonseep comparison site. Densities of harpacticoid copepods and their probable principal food, diatoms, were not affected by petroleum seepage. Suspended organic matter caught in settling traps was not different between seep and nonseep stations. In addition, there was no evidence that predation pressure by juvenile fish on meiofauna was different between stations.

The higher bacterial biomass and productivity in areas of petroleum seepage are consistent with the hypothesis that petroleum carbon is available for assimilation by sediment bacteria. The enhanced level of microbial carbon associated with the petroleum seep is available for consumption by benthic invertebrates and could explain the higher abundances of macrofauna and meiofauna found there.

1. Introduction

Approximately 250,000 metric tons of petroleum hydrocarbons enter the marine environment each year from natural seeps and erosion of river sediments (Kvenvolden

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and Harbaugh, 1983). The distribution of hydrocarbons in nearshore marine sediments is very patchy. Therefore, studies of oil seeps not only can provide information about new petroleum reserves (Anderson *et al.*, 1983) but also on possible effects of chronic hydrocarbon exposure on marine life (Spies *et al.*, 1980).

The Isla Vista seep, offshore of Coal Oil Point in the Santa Barbara Channel, has recently been the subject of several benthic investigations. The macroinfauna, which are dominated by deposit-feeders, are more abundant at the seep than at a nearby nonseep station (Spies and Davis, 1979; Davis and Spies, 1980). Concentrations of ATP are 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). Organic enrichment, via heterotrophic hydrocarbon degrading bacteria and chemoautotrophic sulfide-oxidizing bacteria, has been hypothesized to explain the high densities of macroinfauna at the Isla Vista seep (Spies and DesMarais, 1983). Before the present study, it was not known whether meiofauna abundances are higher at the seep like those of macrofauna and microorganisms (as measured by ATP). Meiofauna, being much smaller, are generally thought to be more closely linked trophically to microbes than to macrofauna (Coull, 1973; Gerlach, 1971, 1978; Tietjen, 1980; Schwinghamer, 1981; Montagna *et al.*, 1983; Gerlach *et al.*, 1985).

In this study we investigated mechanisms that control meiofaunal population size as a function of distance from active petroleum seepage. Meiofaunal populations were followed over an annual cycle to determine if they were responding to fluctuations in the abundance of bacterial food. Microalgal populations were also followed over an annual cycle because meiofaunal populations are known to respond to microautotrophs, which are sometimes preferred over bacteria (Admiraal *et al.*, 1983; Montagna *et al.*, 1983; Montagna, 1984). Alternate forms of carbon input, other than petroleum, might also produce the apparent pattern of organic enrichment, so particulate material in the water column was also measured. In addition to being limited from below by food, population abundances are also controlled from above by predation. Since predators may be differentially affected by petroleum exposure, fish predation on meiofauna was also measured. By studying factors that may influence meiofaunal population abundances in a petroleum seep, we hope to understand how long-term hydrocarbon exposure affects meiofaunal populations.

2. Materials and methods

a. Study site characterization. The Isla Vista petroleum seep study area is located in the Santa Barbara Channel between Coal Oil Point and Goleta Point about 300 m offshore of Santa Barbara, CA (Fig. 1). Three stations with different amounts of petroleum seepage were chosen for study. Station A is within the Isla Vista seep and at the margin of where large quantities of fresh oil and natural gas are seeping from the

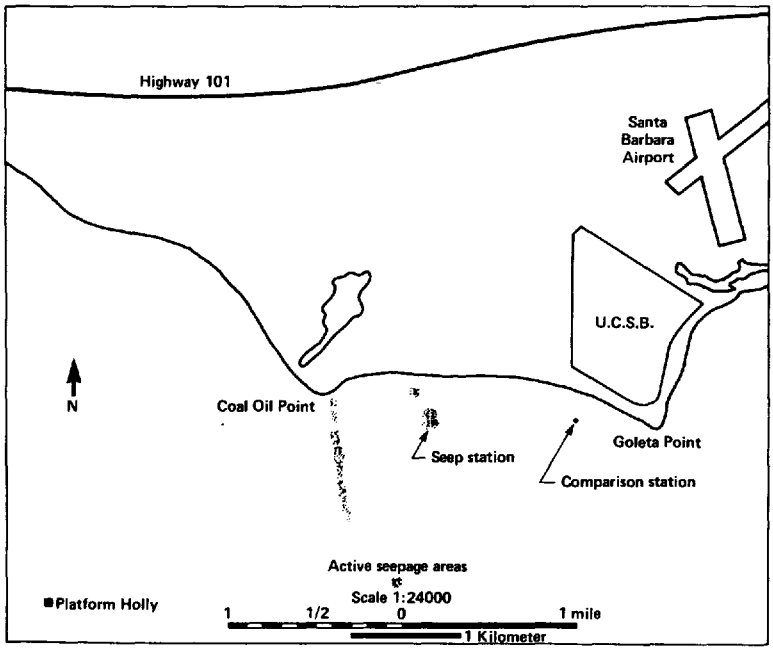

Figure 1. Map of Santa Barbara Channel indicating relative locations of the three stations. There are two stations within the oil seep, one (A) where there is active seepage, the other (B) 10 m away from active seepage. The comparison site (C) is east of the seep where the predominant current moves westerly. The stations are near the University of California, Santa Barbara (UCSB) campus.

sediments. 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. 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). Stations B and C were previously studied in great detail and have similar granulometry (Spies and Davis, 1979). 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. During the summer there were extensive kelp beds about midway between the shore and all stations.

Sampling began on November 18, 1984 and continued for one year. All samples were taken by divers with hand-held corers. At two week intervals, benthic samples were taken for enumeration of meiofauna, bacteria, and microalgae. Bi-weekly sampling was performed to measure short-term changes in population abundances (Montagna *et al.*, 1983). During each sampling period, vertical profiles of Eh in the sediments were measured using a polarographic probe. Every 4 weeks, particle traps were retrieved and the trapped material was measured to determine suspended organic matter in the water column at the seep (at station B only) and nonseep stations. Every

16 weeks, samples were taken for analyses of sediment hydrocarbon content. Triplicate samples were taken for all measurements.

Seawater temperature was recorded continuously with a Ryan-Peabody thermograph, model J. The instrument has a reported accuracy of ± 0.6°C. The thermograph was anchored within 0.5 m of the seabed at station B because this location was assumed to characterize the bottom temperature within the study area. The mean daily temperature was determined by averaging the temperatures at 0600, 1200, 1800, and 2400 h.

Suspended organic matter in the water column was measured to estimate the availability of organic matter to the benthos. The particle traps were constructed of clear butyrate cylinders 33 cm long and 2.2 cm i.d. This length-to-diameter ratio prevents resuspension of material from the bottom of the trap by even the most severe water movement (Weaver, 1977). The traps were filled with 2.5 cm of rock salt and 10% buffered formalin to prevent oxidation of organic matter by bacteria during the collection period. Three traps were deployed at each of stations B and C within 8 m of each other, 1 m above the sea floor. Traps were only deployed at B because it was only 20 m away from station A. After the 4-week collection period, the traps were capped and replaced with new ones. A strong formalin smell was always present, indicating that formalin remained in the traps during deployment and that organic matter samples were preserved. The traps were refrigerated until laboratory processing. The material caught in the traps was collected on tared and washed glass-fiber filters (Whatman, 1.2 μm) and was then dried and weighed. The filtered material was washed with distilled water and dried at 110°C for 10 h. Dry weight was measured after cooling in a desiccator. Samples were placed in a muffle furnace at 550°C for 75 min, then cooled in a desiccator and gravimetrically analyzed for ash weight. Total organic matter (TOM) was calculated as the difference between dry and ash weights. The matter caught represents the sum of fluxes driven by three forces: gravity, advection, and benthic resuspension.

Total hydrocarbon concentrations were measured in core samples which were taken to a depth of 4 cm with a 60-cm^3 syringe barrel with bottoms removed and frozen immediately after sampling. Sediment samples were Soxhlet-extracted with a 3:1 methanol/toluene solution for 24 h. Extracts were dried with anhydrous Na_2SO_4, reduced by vacuum and brought to 4 ml with hexane. A subsample (100–20 μl) was pipetted onto a tared weigh-boat and was air-dried. The total extractable material was then measured gravimetrically using a Cahn electrobalance.

b. Meiofauna and microbes. Meiofaunal samples were taken to the depth of the visual redox-potential-discontinuity layer (RPD), where sediment color turns from grey to black, 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 preserved in a solution of 50% glycerin and 50% ethanol, and nematodes were counted by the dish-subsampling technique (Sherman *et al.*, 1984). The harpacticoid copepods collected in this study are being used in a related study of petroleum effects on reproduction.

Samples for bacterial enumeration were taken to a depth of 2.7 cm with 5-cm^3 syringe barrels with the bottoms cut off (area = 1.1 cm^2) and yielded 3 cm^3 samples. Samples were preserved in 4% buffered formalin that had been filtered through a 0.2 μm filter and refrigerated until processing. 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 to use that measure only bacterial-sized organisms and will yield relative results which will allow for station comparison (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 were converted to biomass assuming 0.87×10^{-13} g carbon · μm^{-3} cell volume (Ferguson and Rublee, 1976). Estimates and variances of bacterial biomass were calculated by formulas given in Montagna (1984).

Turnover times and measures of bacterial productivity were estimated from the FDC data using the formula given in Newell and Christian (1981): where $\mu = e^{(0.299FDC - 4.961)}$, and μ is the growth rate in h^{-1}. There are several methods available for measuring bacterial growth rates. Each yields varying results and depends upon different assumptions regarding the growth state of the bacteria (Christian *et al.*, 1982). Most authors report that 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). When the FDC technique is used in water-column studies there are difficulties in identifying dividing cells. Furthermore, information is limited concerning the relationship between FDC, specific growth rate, and temperature. The standing stock or pool size of the bacterial assemblage is also difficult to estimate, and FDC assumes that all cells are metabolically active (Riemann *et al.*, 1984). The FDC technique is even more difficult to use in sediments because bacteria are attached to sediments and extraction techniques using homogenization may separate bacteria from sediments but not from each other, yielding false identifications of dividing cells (Fallon *et al.*, 1983). However, we present the FDC growth rates to compare the three stations in a relative sense, not to estimate absolute values for bacterial productivity. The only assumption made is that any errors or problems occur with equal probability in all samples, making our results relative and allowing us to test for site differences.

Microphytobenthos samples were taken to a depth of 10 cm with 60-cm^3 syringe

barrels that had the bottoms removed (area = 5.5 cm^2) and were frozen immediately after collection. Chlorophyll was measured spectrophotometrically by the acidification technique (Lorenzen, 1967) as modified by Montagna and Spies (1985) for sediment samples containing oil.

c. Fish predation. Juvenile fish may be active predators on meiofauna (Sibert *et al.*, 1977; Coull and Bell, 1979; Alheit and Scheibel, 1982; La Roche, 1982). Recruitment of most juvenile fish in the Santa Barbara Channel occurs during spring and summer (A.W. Ebeling, personal communication). Therefore, we conducted a study in May 1985 to determine if differences in predation pressure exist at the seep and nonseep sites. Sampling was performed on both May 6 and May 24, 1985. Ten-minute otter trawls (2 m) were taken, and the juvenile fish were sorted out and their stomachs injected with formalin (Alheit and Scheibel, 1982). Fish in the trawls were enumerated and their stomach contents were subsequently analyzed.

d. Statistical analysis. Two-way analysis of variance (ANOVA) models were used to analyze all data where the observations were a function of station, sampling time and the station*time interaction. Data are usually transformed to ensure additivity of main effects and homogeneity of cell variances. However, log transformations of the meiofaunal, chlorophyll, and bacterial count data actually led to a deterioration of the assumptions of additivity of main effects and homogeneity of cell variances as indicated by increased variance in the station*time interaction term, so analyses of untransformed data are presented. Arcsine transformation of the FDC (percentage) data would have resulted in a 76% decrease in growth rates, and not improve the validity of the ANOVA, so it was not used. 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. The potential for dependent relationships between meiofauna and their suspected food sources, bacteria and microphytobenthos, were analyzed by using a phase-shift correlation technique described in Montagna *et al.*, (1983). If meiofaunal populations are responding to microbes, then peak abundances of meiofauna should lag behind peak abundances of microbes.

3. Results

a. Physical and chemical parameters. Bottom (17.5 m) temperature at station B decreased in winter (December to March) from 15 to 11°C and remained near 11°C through the spring and early summer (Fig. 2). During the late summer and fall temperatures again rose to about 16°C. This is approximately the same pattern that has occurred at nearby Naples Reef most years since 1977 (Ebeling *et al.*, 1985); but, warmer than usual temperature was measured during 1982–84 during a strong El Niño episode (Ebeling and Laur, 1987).

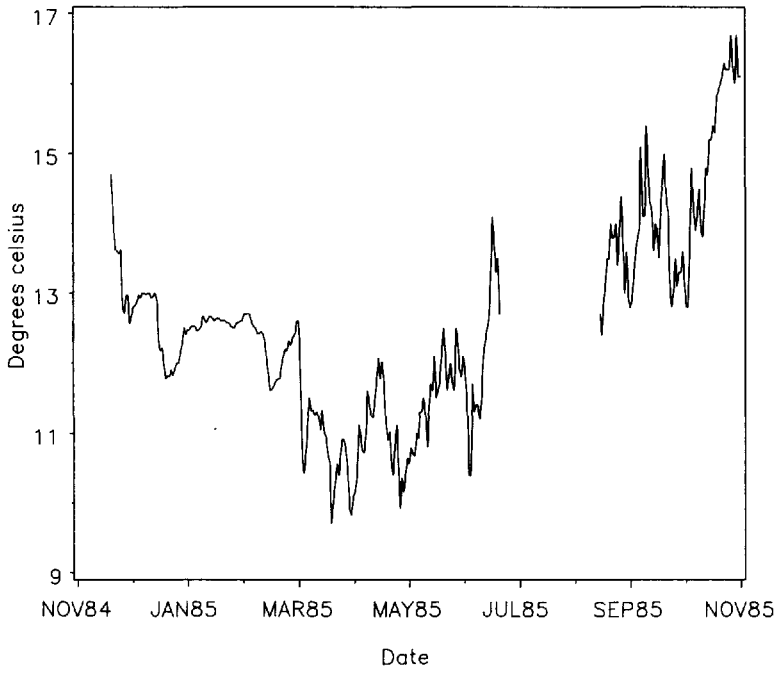

Figure 2. Time series of average daily water temperatures at station B (within the seep). A continuous recording temperature meter was anchored near the bottom at a depth of 18 m.

The RPD layer did not exhibit seasonal changes. There were, however, distinct differences between the three stations. The visual RPD (which was the depth to which meiofaunal cores were taken) was deepest at station C (4.5 cm), followed by station B (1.9 cm) and station A was the shallowest (1.0 cm). Eh is a measure of the electronegative potential in the sediments. The shape of the annual-average Eh profiles was very similar for the two seep stations, but with station A sediments being more electronegative with depth than those of station B (Fig. 3). The difference between the two stations was evident in Eh values of the surface sediments, 66 meV at A and 146 meV at B, and was maintained in a parallel fashion throughout the profile. The profile at station C was steeper and shifted to the right of those of stations A and B. Eh was 208 meV at the surface and decreased gradually and in a more linear fashion (Fig. 3). The trend in RPD and sediment Eh reflects the gradient of active petroleum seepage, with more electronegative sediments occurring in areas of active seepage.

During winter storms (the January–March period) there was more total organic matter (TOM) deposited at station C than B, but during the remainder of the year values were the same at both sites. This resulted in a significant interaction ($P = 0.0001$) between sampling dates and sites for the mean amount of TOM caught in particle traps (Fig. 4). Although there was strong seasonal variability in the amount of TOM caught in traps, there was no apparent difference in the annual average TOM

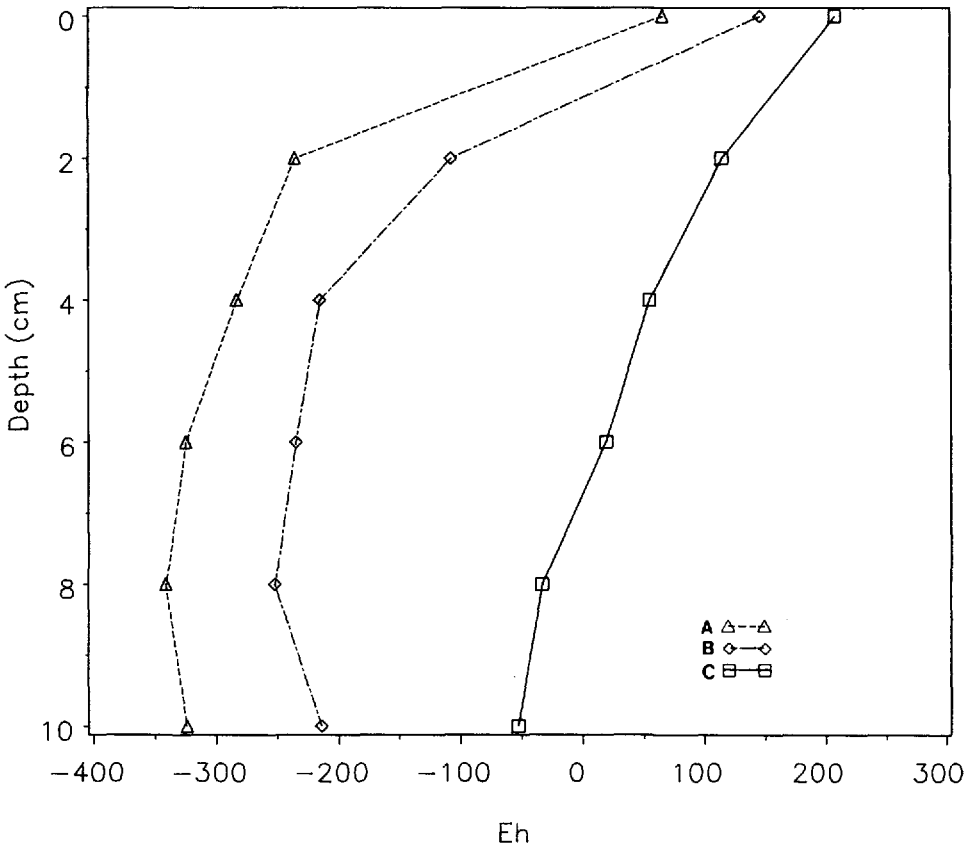

Figure 3. Average annual Eh profiles of sediments at three stations. Eh was measured at 2 cm intervals at three sites, 27 times (biweekly) for one year.

caught in particle traps at either the seep or comparison stations during 9 of the 12 sample periods (Fig. 4). The pattern in the amount of total inorganic matter (TIM) caught in the traps was identical to that of TOM in Figure 4. There was no proportional difference in the amount of TOM relative to TIM between the two sites (ANCOVA; $P = 0.15$). Therefore, during most of the year (spring–fall) the amount of suspended organic matter available to the benthos at the seep and comparison sites appears to be similar.

There were no significant differences among the four 16-week sampling dates (19 Nov. 1984, 11 Mar. 1985, 1 Jul. 1985, and 21 Oct. 1985) in the amounts of total solvent-extractable material in sediments of any station ($P = 0.42$). Station B sediments contained the highest concentration of total hydrocarbons (4.79 mg $\cdot$ g^{-1}), and was significantly different from stations A (2.11 mg $\cdot$ g^{-1}) and C (1.05 mg $\cdot$ g^{-1}) which were the same (Tukey test). These concentrations did not reflect the gradient of

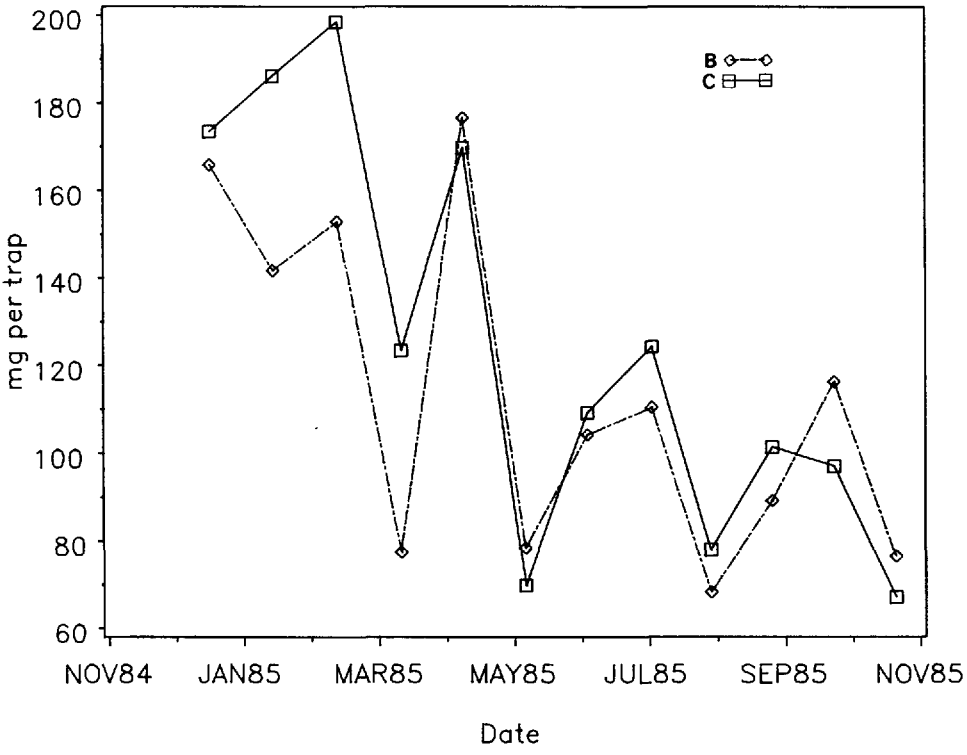

Figure 4. Average total organic matter (ash-free dry weight) caught in particle traps at monthly intervals. Traps were deployed 1 m above sediment surface at the seep (station B) and nonseep (station C) sites. Overall mean was 120 mg · trap^{-1} · month^{-1}, coefficient of variation was 9.5%.

fresh oil seepage that was evident to divers working with the sediments. As previously described, station A is on the margin of an area that has copious quantities of fresh oil seeping into the water column. Station B has only occasional seepage and is 20 m away from active seepage but has a substratum of asphaltic material beneath the sediment surface. Station B had 4.7 times more extractable hydrocarbons than station C, which is essentially the same as the 4.8-fold difference previously reported for stations B and C by Stuermer *et al.* (1982). Apparently hydrocarbon concentrations are not good measures of seep activity.

b. Microbial parameters. Station A almost always had the greatest density of bacterial cells in the upper 2.7 cm of sediment, followed by stations B and C (Fig. 5). This is similar to the trend of increasing ATP with increasing petroleum exposure found by Spies *et al.* (1980). There was a significant interaction (Table 1, $P = 0.0001$) among the means of direct bacterial cell counts for sampling dates and stations

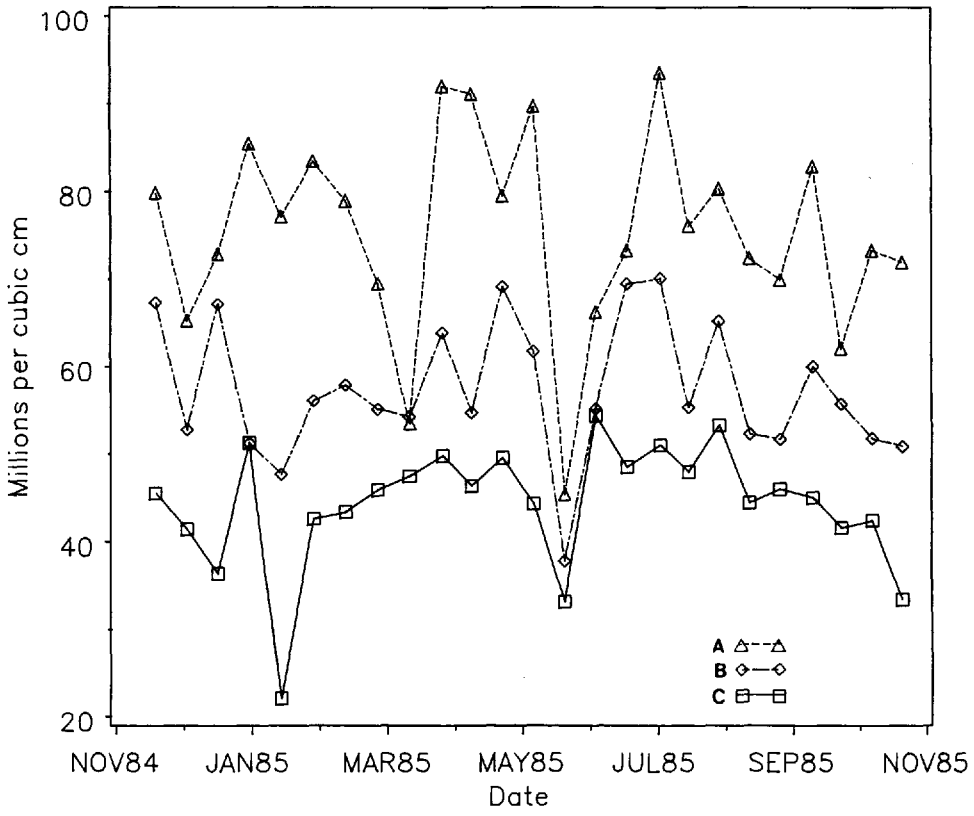

Figure 5. Average abundance of bacterial cells (0–2.7 cm depth) at three sites measured at biweekly intervals. Overall mean was 5.8×10^7 cells · cm^{-3}, coefficient of variation was 29%.

(Fig. 5). Although the response is not exactly parallel, there do not appear to be seasonal differences in cell abundances. The average annual densities of bacterial cells at stations A (7.5×10^8 · cm^{-3}), B (5.6×10^8 · cm^{-3}), and C (4.4×10^8 · cm^{-3}) are about half that reported for estuarine sediments in a review by Rublee (1981) but similar to those of sandy sediments in the Kiel Bight (Weise and Rheinheimer, 1978).

Table 1. Probabilities for sources of variability calculated from two-way ANOVAs for different data evolved from acridine orange direct count microscopy. DS = date*site interaction. Biomass was calculated as a function of abundance and biovolume for each DS combination, so no interaction term exists.

Source	Density	Biovolume	Biomass	FDC
Date	<0.00005	<0.00005	0.0001	0.0977
Site	<0.00005	0.1216	0.0001	0.0132
DS	0.0001	0.0001	—	0.6198

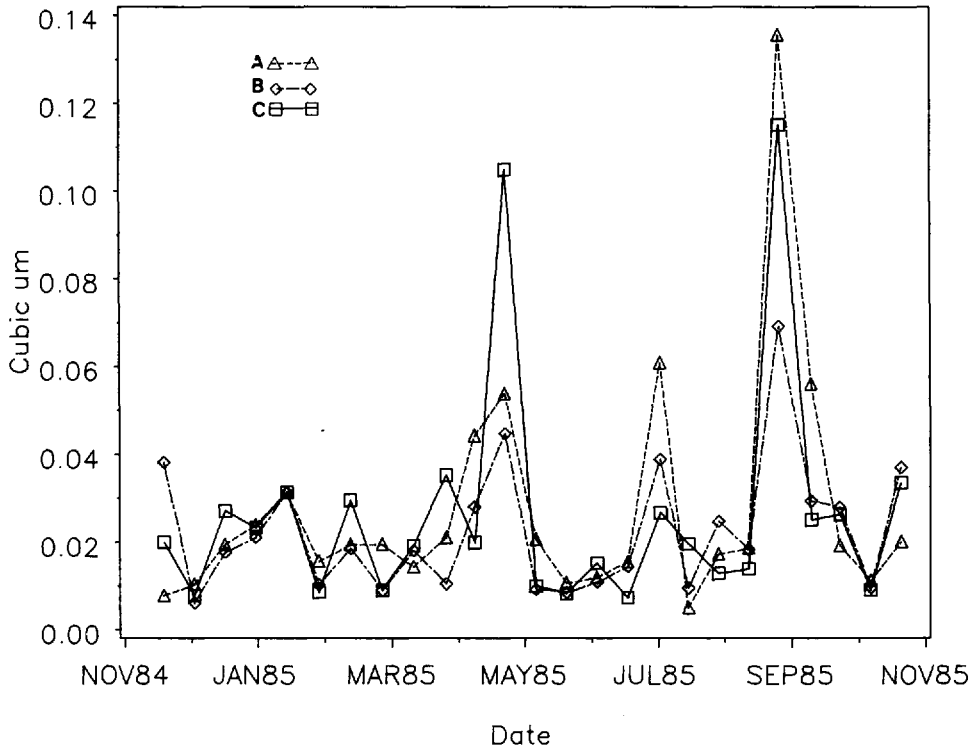

Figure 6. Average bacterial cell volume at three sites measured at biweekly intervals. Overall mean was 0.03 μm^3, coefficient of variation was 249%.

The biovolumes for 5,254 bacterial cells were calculated (Fig. 6). A significant interaction between means for stations and sampling dates (Table 1, $P = 0.0001$) indicates that responses were not parallel among date-station combinations. Bacterial biovolumes were the same at all three stations, but they appeared to undergo cyclical changes (Fig. 6). Peaks in cell sizes occurred in April, July, and September, 1985. The overall mean biovolume, 0.031 μm^3, was an order of magnitude smaller than that reported for estuarine sediment (mud) bacteria (Rublee, 1981).

Bacterial biomass is a function of abundance, biovolume, and a conversion factor. Because there was no seasonal trend in cell numbers (Fig. 5), the seasonal trend in bacterial biomass (Fig. 7) was strongly influenced by the seasonal trend of cell biovolumes (Fig. 6). Peaks of bacterial biomass occurred in January, April, July, and September, 1985 in an ever-increasing fashion. A two-way ANOVA using dates as blocks indicated that station differences existed in bacterial biomass (Table 1, $P = 0.0001$). The average biomass was significantly greater for station A (1.9 $\mu g\ C \cdot cm^{-3}$) than for station B (1.1 $\mu g\ C \cdot cm^{-3}$) and station C (0.98 $\mu g\ C \cdot cm^{-3}$) which were the same (Tukey test). However, this test assumes that there is no interaction between

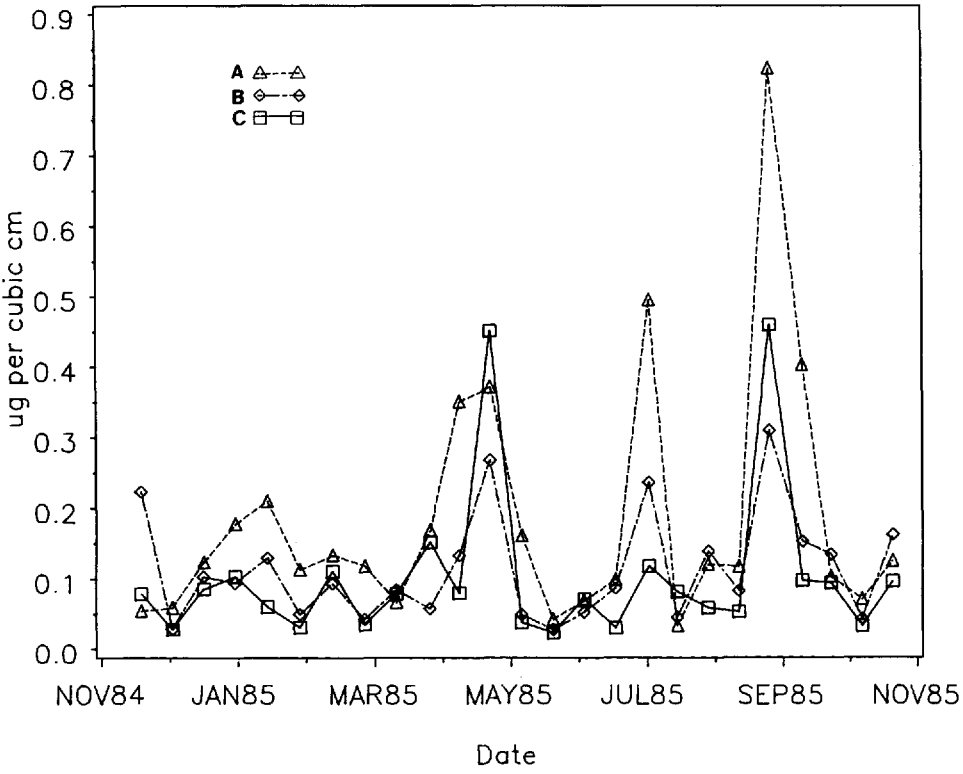

Figure 7. Average bacterial biomass at three sites calculated at biweekly intervals. Biomass was a function of cell abundance, biovolumes, and a conversion factor. Overall mean biomass was 0.13 $\mu g \cdot cm^{-3}$, coefficient of variation was 58%.

dates and stations, which does not appear to be a reasonable assumption since there are interactions for both cell density and biovolume. The overall mean biomass for the top 2.7 cm of sediment (the depth of sampling) was 36 $\mu g\ C \cdot cm^{-2}$, which is about the same as (59 $\mu g\ C \cdot cm^{-2}$) reported by Dale (1974) for intertidal sandy sediments, but 15 times lower than that reported by Rublee (1981) for estuarine marsh sediments. The lower biomass estimates for these subtidal stations are a function of finding both smaller cells and having fewer cell counts than reported in the other sediments.

Frequencies of dividing cells were quite high, averaging 14.0% overall (Fig. 8). There was no interaction between date and station ($P = 0.62$). Although there were no significant seasonal differences ($P = 0.09$), the low P value suggests that seasonality might exist (Table 1). Station A had a greater FDC (15.6%) than station C (12.8%), and station B (13.7%) was not significantly different from A or C (Tukey test). The trend suggests that there is higher bacterial productivity at the seep relative to the comparison station. The FDC values at the seep are about double the range for sediment bacteria in other coastal zones, which average about 6% (Newell and Fallon,

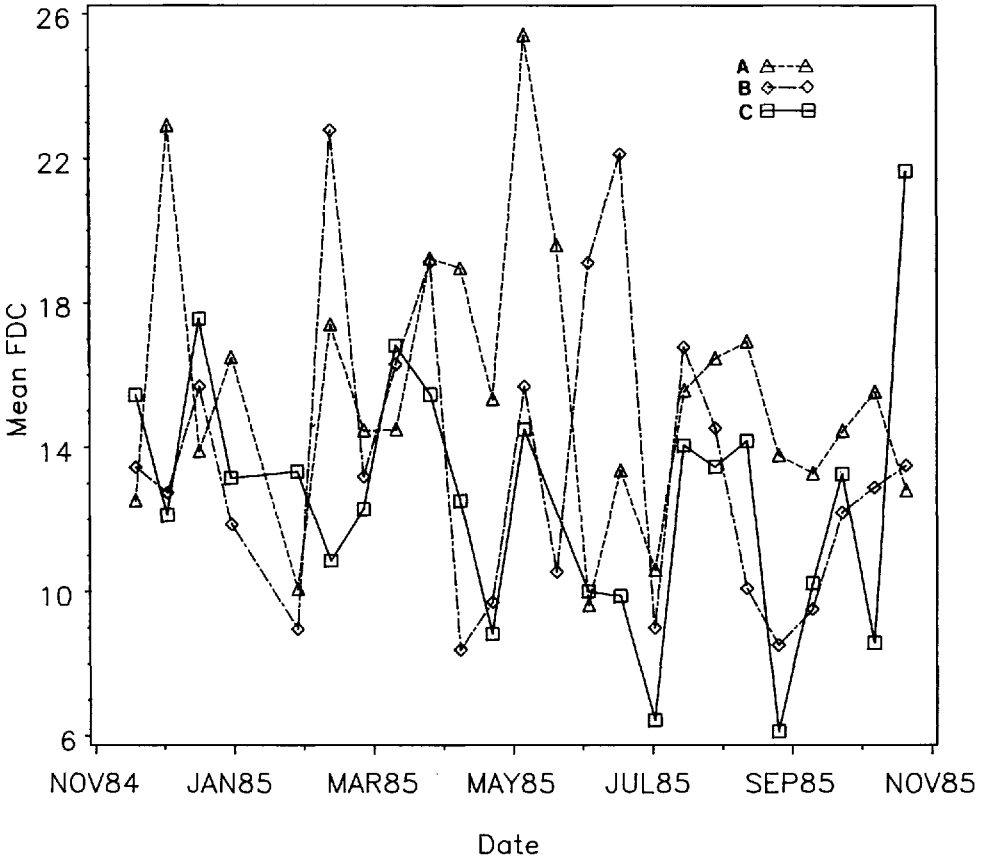

Figure 8. Average frequency of dividing bacterial cells (FDC) at three sites measured at biweekly intervals. Overall mean was 14%, coefficient of variation was 74%.

1982; Fallon *et al.*, 1983; Riemann *et al.*, 1984). Using the formula given by Newell and Christian (1981) to convert FDC to instantaneous growth rates, we calculated that the growth rate at station A was 0.74 (h^{-1}), 0.42 (h^{-1}) at station B, and 0.32 (h^{-1}) at station C. Multiplying these average growth rates by the average biomass indicates that bacterial productivity in the surface 3 cm of sediment is 1010 mg C · m^{-2} · d^{-1} at station A, 330 mg C · m^{-2} · d^{-1} at station B, and 230 mg C · m^{-2} · d^{-1} at station C.

Fallon *et al.*, (1983) reported productivity based on FDC for the coastal zone of Georgia (USA) to be in the range of 4,500–45,000 mg C · m^{-2} · d^{-1}. However, productivity estimates were an order of magnitude lower based on oxygen consumption or thymidine incorporation. Moriarty and Pollard (1982) reported bacterial productivity in Australian seagrass bed sediments of 43 mg C · m^{-2} · d^{-1} based on thymidine incorporation. Craven and Karl (1984) reported a range of bacterial productivity from 500 mg C · m^{-2} · d^{-1} in deep sediments (880 m) to 195,000 mg C · m^{-2} · d^{-1} in

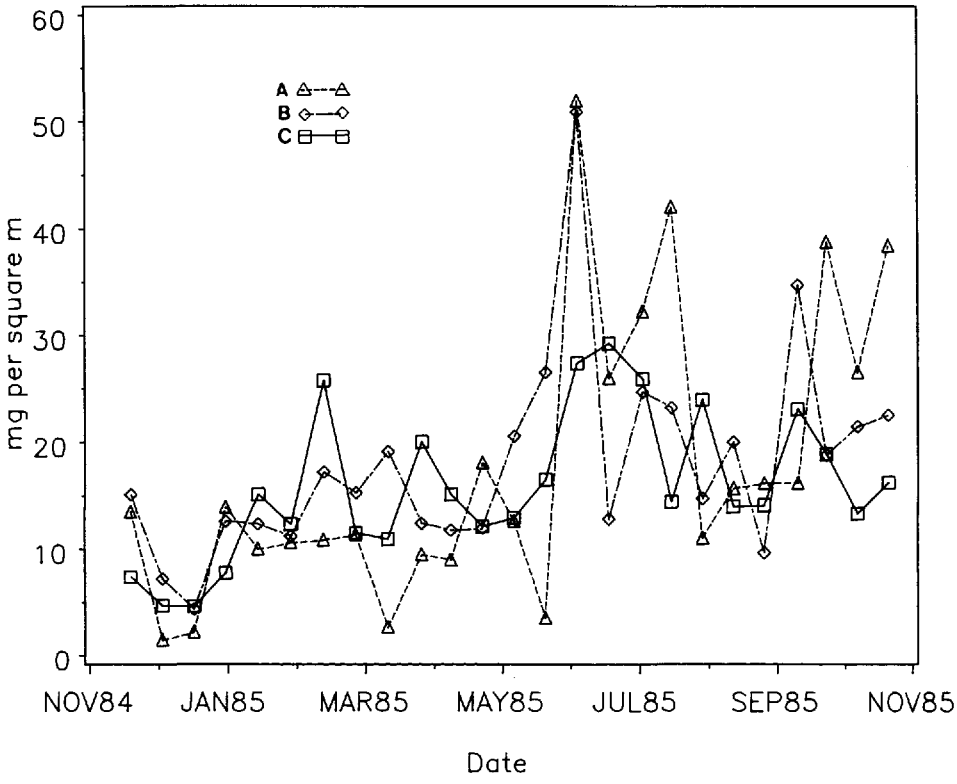

Figure 9. Average concentration of chlorophyll *a* at three sites measured at biweekly intervals. Overall mean was 18 mg · m^{-2}, coefficient of variation was 45%.

Hawaiian coral reef sediments (based on the uptake of adenine). Estimates of bacterial productivity at the seep and comparison sites, based on cell biovolumes and FDC, appear to be in the lower end of the range reported for other coastal sediments.

Chlorophyll *a* underwent clear seasonal trends which corresponded with day length, exhibiting lowest sediment concentrations (4 mg · m^{-2}) in December and highest values (43 mg · m^{-2}) in June (Fig. 9). There was a significant interaction between sampling dates and stations ($P = 0.0001$), but there were no apparent differences

Table 2. Chlorophyll *a* and phaeophytin *a* concentrations in sediments from the Santa Barbara Channel. Samples were taken to a depth of 2 cm. Mean values for one year, units = mg · m^{-2}.

Site	Chlorophyll *a*	Phaeophytin *a*
A	18.8	40.1
B	18.4	37.1
C	16.5	18.3

Table 3. Probabilities for sources of variability calculated from two-way ANOVAs for each meiofaunal taxa. The probability is for the null hypothesis that the mean values for each level of the main effect are all the same. Abbreviations: DS = date*site interaction, N/C = nematode to copepod ratio, and "others" include all other meiofaunal taxa found except nematodes and copepods (see text for description).

Source	Nematodes	Nauplii	Copepodites	Others	N/C
Date	0.0019	0.0001	0.0001	0.0001	0.4698
Site	0.0001	0.0856	0.0212	0.0001	0.0161
DS	0.1750	0.0054	0.1335	0.3528	0.5256

between the mean chlorophyll *a* values at any of the three stations. A trend previously noted for greater amounts of phaeophytin relative to chlorophyll at the seep (Montagna and Spies, 1985) was again found (Table 2). These chlorophyll values are about 5 times lower than those reported for estuarine sediments (Rublee, 1981) and an 18.3 m subtidal station off La Jolla, CA (USA) (Hartwig, 1978).

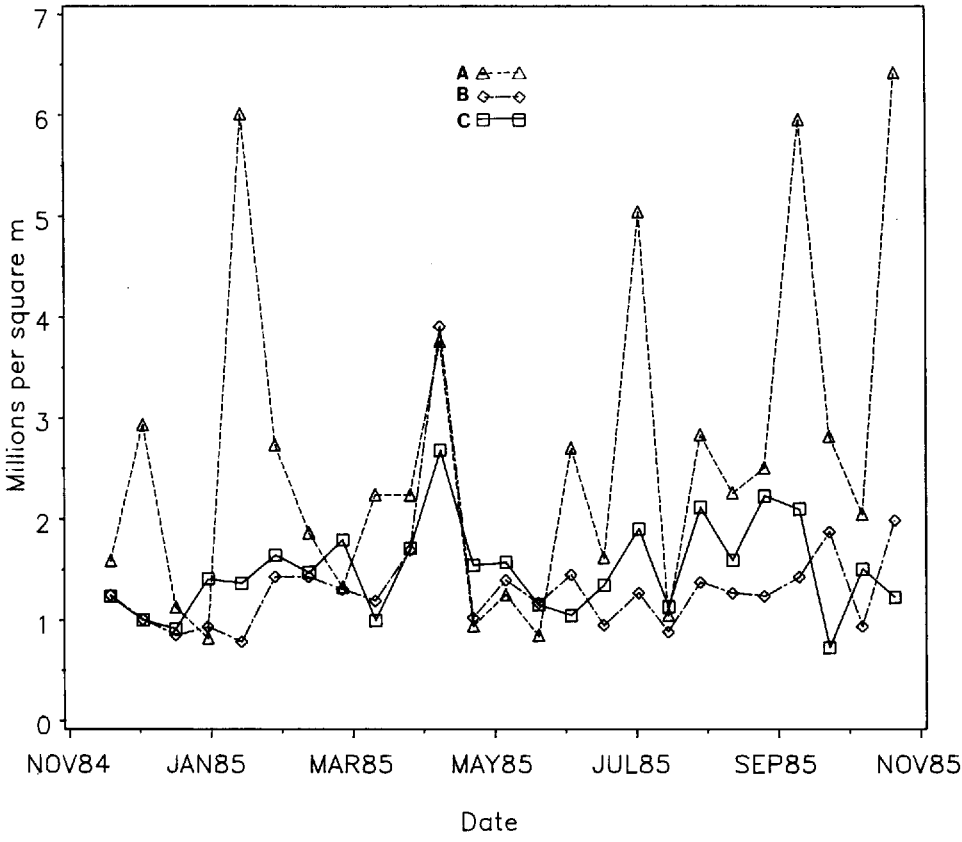

Figure 10. Average abundances of nematodes at three sites measured at biweekly intervals. Overall mean was $1.7 \times 10^6 \cdot m^{-2}$, coefficient of variation was 86%.

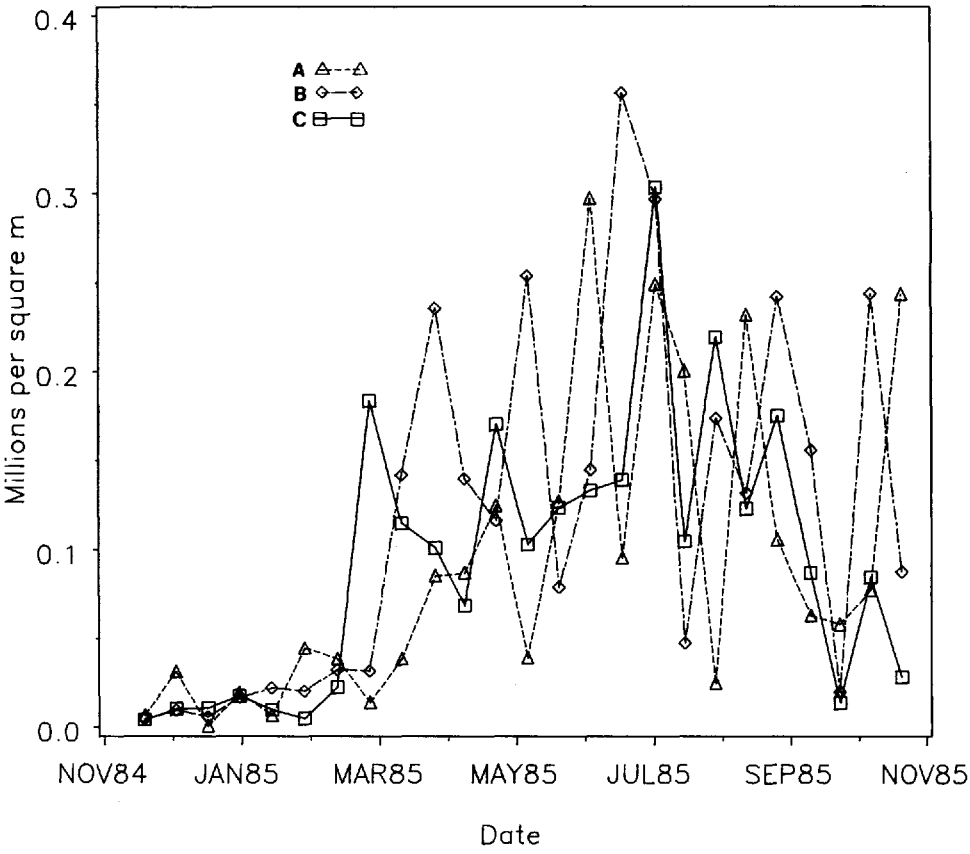

Figure 11. Average abundance of harpacticoid nauplii at three sites measured at biweekly intervals. Overall mean was $0.098 \times 10^6 \cdot m^{-2}$, coefficient of variation was 87%.

c. Meiofaunal populations. Nematode abundances exhibited significant seasonal and station fluctuations (Table 3, Fig. 10). Station A contained significantly greater numbers of nematodes ($2.42 \times 10^6 \cdot m^{-2}$) than stations B ($1.31 \times 10^6 \cdot m^{-2}$) and C ($1.41 \times 10^6 \cdot m^{-2}$) which were the same (Tukey test). Nematodes comprised a higher proportion of the meiofauna community at station A (88%) than at either stations B (76%) or C (78%). Extremes in nematode densities occurred at station A, ranging from 0.5×10^6 to $6.5 \times 10^6 \cdot m^{-2}$.

Benthic copepod nauplii abundances exhibited a strong seasonal trend (Fig. 11). Abundances were lowest in winter and peaked at about $0.3 \times 10^6 \cdot m^{-2}$ in June. The strong interaction between dates and stations and the lack of significance between stations (Table 3) indicates that there were no significant differences among mean abundances between stations. The overall annual abundance was $0.98 \times 10^6 \cdot m^{-2}$. Nauplii comprised an average of 3.3% of the harpacticoid copepod population at station A, 6.7% at B, and 4.9% at C.

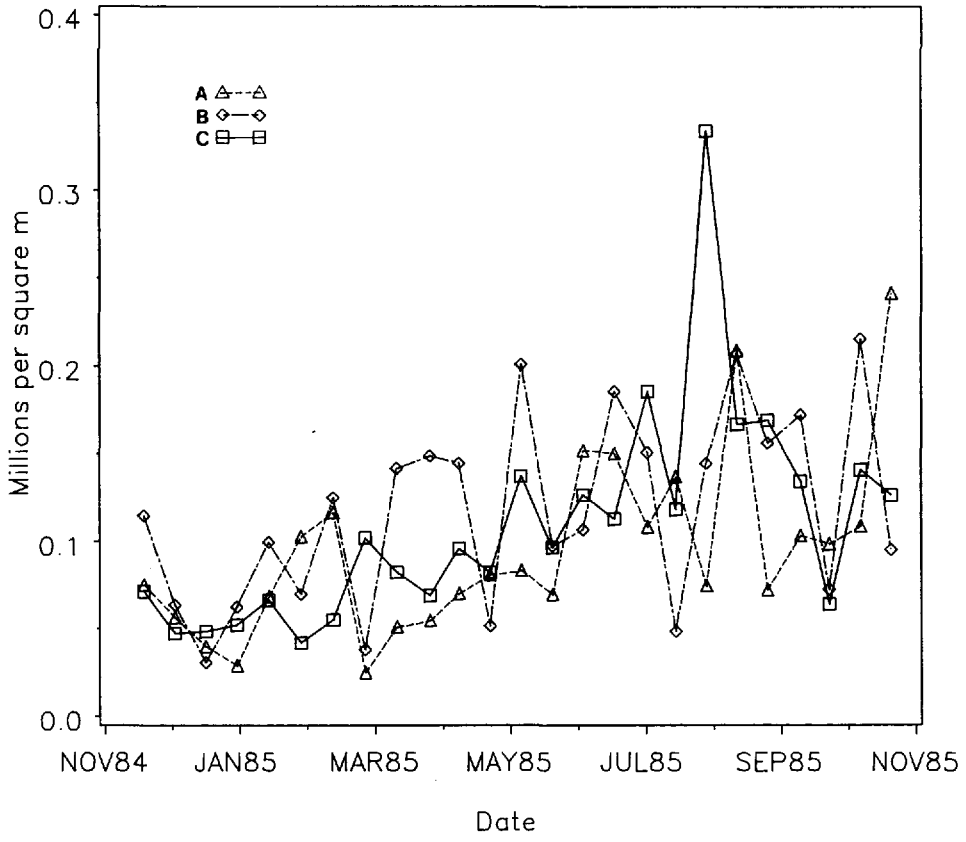

Figure 12. Average abundance of harpacticoid copepodites (including adults) at three sites measured at biweekly intervals. Overall mean was $0.11 \times 10^6 \cdot m^{-2}$, coefficient of variation was 58%.

Benthic harpacticoid copepodite (juveniles and adults) abundances also exhibited a strong seasonal cycle (Fig. 12, Table 3). Population abundances were lowest in early winter and rose continuously throughout the spring and summer, peaking at about $0.2 \times 10^6 \cdot m^{-2}$ in August. Station B had a significantly higher density of copepodites ($1.17 \times 10^6 \cdot m^{-2}$) than station A ($0.996 \times 10^6 \cdot m^{-2}$), but station C ($1.08 \times 10^6 \cdot m^{-2}$) was not different from either of the other two sites (Tukey test). Station B had the highest proportion of copepodites in its meiofaunal population (6.8%), followed by station C (4.9%) and station A (3.3%).

High nematode-to-copepod (N/C) ratios have been suggested by Rafaelli and Mason (1981) to indicate organic pollution. We found significantly greater N/C ratios at station A (40.1) than station C (12.5) and B (9.68) which were the same (Table 3, Tukey test). Coull *et al.* (1981) cautioned against the use of N/C ratios where seasonal data were lacking, but we found no seasonal differences in N/C over one year (Table

3). The proportion of total harpacticoids (copepodites + nauplii) relative to total meiofauna found at station A was much lower (6.9%) than either station B (13.5%) or station C (10.9%).

Nematodes and copepods accounted for 96% of the total meiofauna at station A but only 92% of the organisms at both stations B and C. A total of 19 other groups of organisms comprised the remaining 4% of taxa at A and 8% at B and C. These other taxa (with their average annual percent contribution for all sites in parentheses) were: Ciliata (2.84), Gastrotricha (0.98), Turbellaria (0.57), Polychaeta (0.53), Foraminifera (0.46), Bivalvia juveniles (0.36), Ostracoda (0.17), Amphipoda juveniles (0.14), Kinoryncha (0.04), Cumacea (0.04), Gastropoda (0.02), Ophiuroidea juveniles (0.02), Nemertinea (0.01), Cnidaria juveniles (0.01), cyprid larvae (0.01), Isopoda juveniles (0.01), Halacarida (<0.01), Leptostraca (<0.01), and Tanaidacea (<0.01). The overall mean abundance for all these other taxa at all three sites was $0.17 \times 10^6 \cdot m^{-2}$, similar to the abundance of total harpacticoids at all three sites of $0.21 \times 10^6 \cdot m^{-2}$. There were more of these other meiofauna at station C ($0.196 \times 10^6 \cdot m^{-2}$) and B ($0.181 \times 10^6 \cdot m^{-2}$), which were the same, than at station A ($0.134 \times 10^6 \cdot m^{-2}$) (Table 3, Tukey test). There were also strong fluctuations in abundance of these other taxa through time (Table 3, Fig. 13). The peaks in February, April, and July, 1985 were due to large increases in the abundance of gastrotrichs. The smaller but more enduring peak in late summer through early fall 1985 was due to increases in the number of ciliates.

d. Fish predation. The average number of total fish (27) and fish species (3.8) taken at the seep (stations A and B) was the same as at comparison station C (59 and 4.8, respectively) (*t*-test, Table 4). The size classes of the dominant fish, *Citharichthys stigmaeus,* were not the same in both station areas (χ^2, $P = 0.025$; Fig. 14). There were more larger fish (≥7 cm) at the comparison station than at the seep station, but the number of juvenile fish that would eat meiofauna were the same (Fig. 14). The juvenile fish of the seep and the comparison stations were not eating meiofauna (Table 5). Meiofauna comprised only 2% of the gut contents at the comparison station and <1% at the seep area. The numerically dominant food taxon (excluding one large fish that contained large numbers of mysids) was amphipods at both sites (Table 5). Because the average abundance, distribution, and diversity of fish were similar at both sites, there is no evidence that fish predation on meiofauna is greater at one site than another.

e. Relationships between parameters. If meiofauna abundances are dependent on abundances of their microbial food, then peaks of meiofaunal abundance should follow peaks of microbial abundance (Montagna *et al.,* 1983). There were no significant correlations between any meiofauna abundances and bacterial biomass, nor between nematode abundance and microalgal biomass (Table 6). Peaks of harpacticoid abundance were significantly correlated with peaks of microalgal biomass, but the

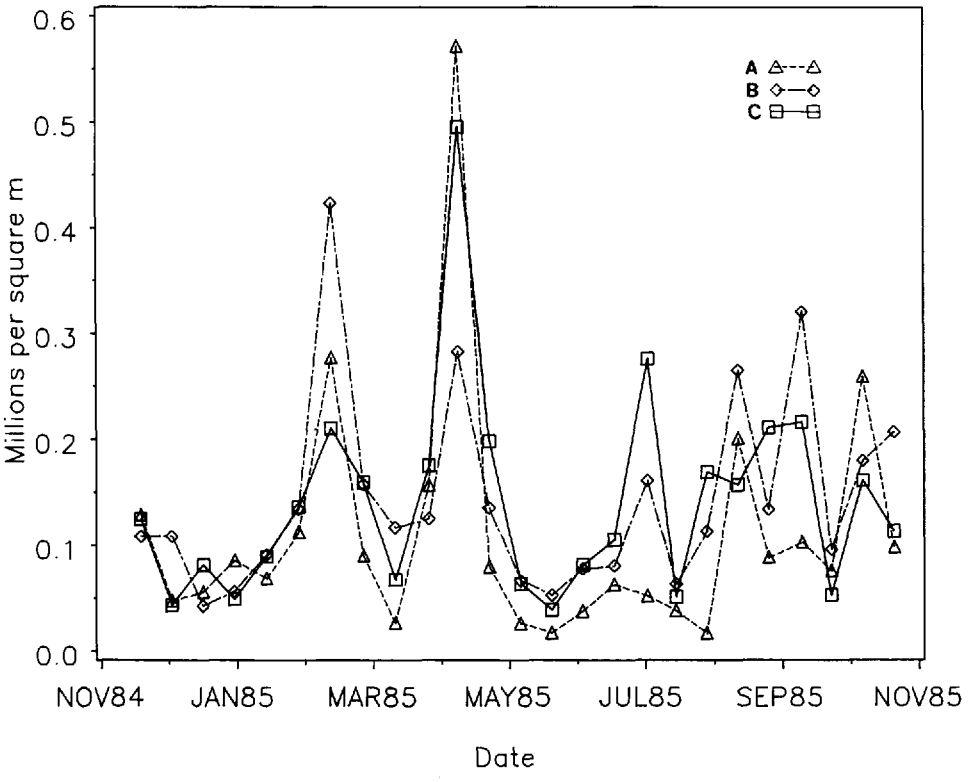

Figure 13. Average abundance of all meoifauna taxa other than nematodes and harpacticoids at three sites, measured at biweekly intervals. Overall mean was $0.17 \times 10^6 \cdot m^{-2}$, coefficient of variation was 59%. Meiofauna groups represented include: Polychaeta, Ciliata, Foraminifera, Gastrotricha, Turbellaria, Ostracoda, Bivalvia, Nemertinea, Amphipoda, Cnidaria, Cumacea, Cyprid larvae, Gastropoda, Halicaridae, Isopoda, Kinorincha, Leptostraca, Ophiuroidea, Tanadacea.

Table 4. Mean abundances (and standard deviations in parentheses) of fishes captured in five 10-minute trawls in the vicinity of the Isla Vista petroleum seep in May 1985.

Comparison		Seep	
Species	Mean	Species	Mean
Citharichthys stigmaeus	29.4 (37)	*Citharicthys stigmaeus*	12.8 (10)
Sebastes spp. (juvenile)	9.6 (11.7)	*Lepidogobius lepidus*	12.2 (10)
Icelinus quadriseriatus	8.4 (16)	*Sebastes* spp.	0.8 (0.84)
Lepidogobius lepidus	8.2 (3.7)	*C. sordidus*	0.2 (0.45)
Pleuronichthys verticalis	1.4 (1.5)	*Pleuronichthys verticalis*	0.2 (0.45)
		Synodus lucioceps	0.2 (0.45)
		Heterostichus rostratus	0.2 (0.45)
		Paralabrax nebulifer	0.2 (0.45)

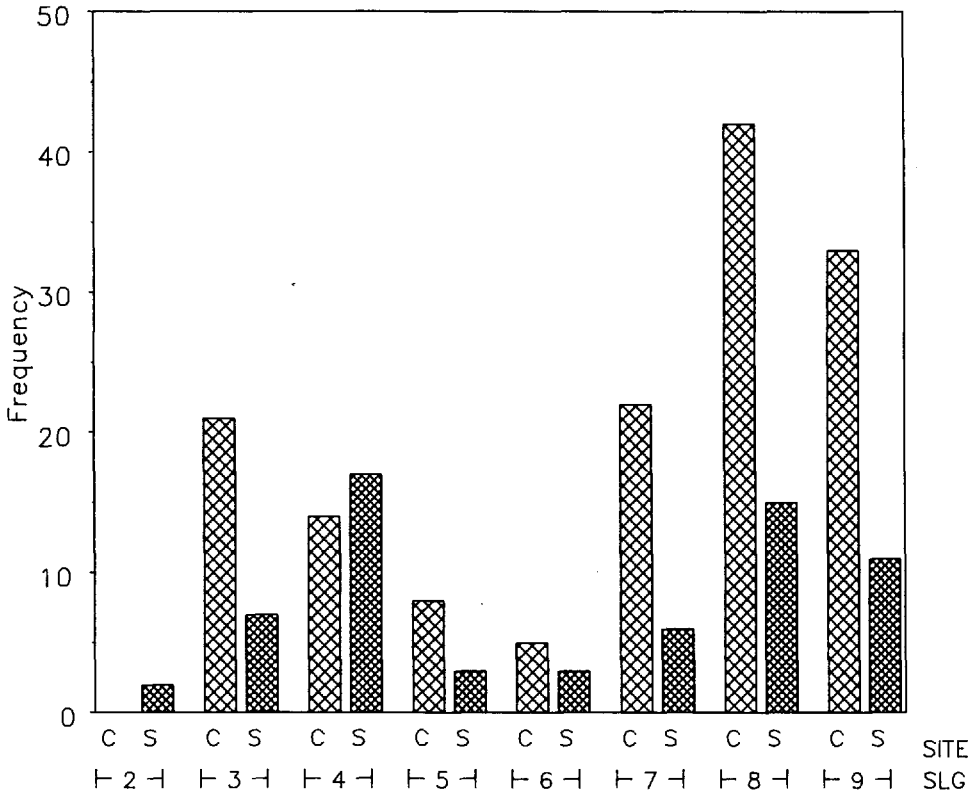

Figure 14. Size distribution of *Citharichthys stigmaeus* at the seep and comparison sites.

patterns were different at each station. At station A, harpacticoids were correlated with microalgae on the day of sampling and at 4-week lags. At station B, a peak of meiofaunal abundance occurred 2 weeks after peaks of microalgae occurred. At station C, copepodites correlated with algae at 0, 4, and 6 wk, whereas nauplii correlated with algae at lags of 2 and 4 wk. Overall, peaks of copepodite abundance (Fig. 12) followed peaks of nauplii abundance (Fig. 11) by about 4 weeks.

4. Discussion

Coastal petroleum seeps are unique, naturally occurring marine systems. This study was undertaken to determine the effect of chronic hydrocarbon exposure on marine communities and to investigate the effects of a unique carbon source for benthic food webs. Petroleum seeps provide us with a "natural laboratory" where organisms may have adapted to the persistent presence of varying amounts of petroleum hydrocarbons. We were specifically interested in determining if meiofaunal populations responded to the presence of petroleum seepage, as had been observed for macrofauna (Spies and

Table 5. Stomach contents (mean and standard deviation in parentheses) of juvenile fishes collected in the Isla Vista petroleum seep and the comparison station.

Species (*n*)	SL[α]	Calanoids	Polychaetes	Amphipods	Cumaceans	Mysids	Nematodes	Harpacti-coids
COMPARISON STATION								
Citharichthys stigmaeus (6)	3.5 (0.5)	0.2 (0.4)	1.5 (3.7)	5.8 (7.4)	1.0 (0.9)	1.0 (1.3)	0	0
C. sordidus (3)	7.0 (2.5)	0.7 (1.2)	1.3 (0.6)	6.3 (5.1)	1.0 (1.0)	3.0 (1.0)	0.7 (1.2)	0
Lepidogobius lepidus (2)	2.3	2	0	0	0	0	0	0
Sebastes (?) *babcocki* (3)	3.2 (0.2)	20 (15)	0	2.0 (1.7)	0	0.3 (0.6)	0	0
Sebastes sp. or spp. (6)	4.1 (0.5)	15 (19)	0	0	0	0.4 (0.6)	0	0.4 (0.9)[β]
Synodus Lucioceps (1)	6.6	0	0	0	0	0	0	0
SEEP STATIONS								
Citharichthuys stigmaeus (7)	3.4 (0.2)	0.1 (0.4)	0.4 (0.5)	3.1 (2.8)	0.7 (0.9)	0.4 (0.5)	0	1.4 (1.8)
Heterostichus rostratus (1)	13.4	0	0	6	0	28	0	0
Paralabrax nubilifer (1)	14.1	0	0	0	0	160	0	0
Sebastes (?) *babcocki*	3.3	15	0	0	0	0	0	0
Sebastes sp. or spp. (1)	3.2	4	0	0	0	0	0	0
Lepidogobius lepidus (2)	2.4	2 (0)	0	0	0	0	0	0

[α]SL = standard length in cm.

[β]One juvenile rockfish had 2 harpactcioid copepods, *Zausodes* sp.

Table 6. Correlations between microbial biomass and lag weeks in meiofauna taxa abundances at lags of 0, 2, 4, and 6 weeks. Table finds Pearson correlation coefficients. Abbreviations: nema = nematodes, naup = nauplii, cope = copepodites, ns = not significant.

		Site * Taxa								
		A			B			C		
Microbe	Lag	Nema	Naup	Cope	Nema	Naup	Cope	Nema	Naup	Cope
Bacteria	0–6	ns	ns	ns	ns	ns	ns	ns	ns	ns
Diatoms	0	ns	0.70$^{\alpha}$	0.62$^{\beta}$	ns	ns	ns	ns	ns	0.39$^{\delta}$
Diatoms	2	ns	ns	ns	ns	0.63$^{\beta}$	0.51$^{\gamma}$	ns	0.48$^{\delta}$	ns
Diatoms	4	ns	0.58$^{\gamma}$	0.59$^{\gamma}$	ns	ns	ns	ns	0.62$^{\beta}$	0.61$^{\gamma}$
Diatoms	6	ns	ns	ns	ns	ns	ns	ns	ns	0.61$^{\gamma}$

$^{\alpha}0.0001 \leq P$
$^{\beta}0.001 \leq P < 0.0001$
$^{\gamma}0.01 \leq P < 0.001$
$^{\delta}0.05 \leq P < 0.01$

Davis, 1979; Davis and Spies, 1980). Since many factors control the fluctuation and absolute abundance of natural populations, we also wished to assess what other parameters might be important in controlling meiofaunal population abundances at the petroleum seep. The three stations were chosen to represent a gradient in the magnitude of natural petroleum seepage.

Station A is at the margin of an area of intense and active seepage. Petroleum intrudes into the sediments and oil fingers rise from the sediments. Oil droplets pinch off from these fingers and then float to the surface forming the oil slicks which are characteristic of the surface waters near Coal Oil Point. The sediments associated with the seep contain large amounts of fresh oil. Natural gas also emanates from these active intrusion areas, forming a cauldron of bubbles on the sea surface and making areas of active seepage very easy to identify. Sediment cores taken in the center of active seepage contain about 25% oil and practically no living meiofauna (Montagana and Spies, 1985), so at station A we sampled on the margin of active seepage as did Spies *et al.* (1980).

Station B, within the oil seep area, is distinctly different from station A. There is much less fresh oil in the sediments and little gas or oil seepage. The sediments contain a preponderance of weathered tar, but small droplets of fresh oil occur in many samples. Beneath the surface sediments there is a layer of asphalt-like tar that occurs at depths of 4–12 cm. Only a small fraction of the sea floor within the seep can be characterized as being "A" type sediments. "B" type sediments are much more common. It has been estimated, based on our experience diving at the seep, that "B" type sediments comprise as much as 98% of the sea floor area within the seep.

Station C is about 1.4 km east of the oil seep, and the dominant current is westerly (about 85% of the time, Toby Goddard, personal communication); thus, most of the benthic seep product will usually be transported away from station C. However, there

are hydrocarbons present in all southern California coastal sediments (Reed *et al.*, 1977). At station C, sediment hydrocarbons exhibit a highly weathered character (Stuermer *et al.*, 1982). There is no seep at station C and fresh oil has never been observed there.

Given the locations of the stations relative to active seepage and the amount of fresh oil and tar that are visible when sorting sediments from the three stations, it was surprising to find that the total amount of extractable hydrocarbons was greatest at station B (4.8 mg · g^{-1}), but was the same at stations A (2.1 mg · g^{-1}) and C (1.1 mg · g^{-1}). The differences in total amounts of hydrocarbons may represent differences in the relative amount of weathered tar present, because it is a dominant component of the total extractable hydrocarbons. The amount of extractable material present at stations B and C did not change during the four sampling periods in 1985 of this study, and these values were about one-half of those which were reported for the same stations in 1977 by Stuermer *et al.* (1982). There is a very heterogeneous distribution of hydrocarbons in the sediment, porewater, and dissolved and particulate fractions of the water column at the Isla Vista seep, indicating that the life-style and feeding habits of the organisms at this site will have a dramatic effect on their hydrocarbon exposure (Stuermer *et al.*, 1982). Clearly, hydrocarbon exposure is a very complex process which has not been investigated here in terms of heterogeneity of distribution or the individual components of seeping petroleum.

Previous studies found higher abundances of macroinfauna at station B than at station C (Spies and Davis, 1979; Davis and Spies, 1980). Total abundances of benthic meiofauna taxa were not significantly different at stations B and C during the course of the present study (Table 7). However, abundances of total meiofauna and nematodes were greater in areas at the margin of active petroleum seepage (station A) than at either stations B or C (Table 7). Station A had the greatest numbers of total meiofauna as well as nematodes.

Meiofaunal responses to petroleum have been studied by either monitoring post-spill recovery or experimentally oiling sediments. Monitoring of South African and French beaches after oil spills demonstrated that harpacticoid densities were depressed, while nematode densities were not, and that recovery occurred within 6 months (Fricke *et al.*, 1981; Bodin and Boucher, 1983). In contrast, after experimental oiling of a Louisiana salt marsh, meiofauna densities either remained the same (Smith *et al.*, 1984) or increased (Fleeger and Chandler, 1983). When oil was added to mesocosms, meiofaunal densities decreased (Frithsen *et al.*, 1985). Harpacticoids and ostracods were the most sensitive taxa to oiling; by contrast, foraminiferans and ciliates increased in abundance (Frithsen *et al.*, 1985). Recolonization of oiled sediment trays by harpacticoids, ostracods, and polychaetes occurred within 1 week, whereas nematodes took up to 90 days (Alongi *et al.*, 1983). It is evident that the presence of oil is not the only factor affecting meiofaunal population density in either recovery from spills or in adapting to the presence of chronic exposure. Differences in spatial, successional and

recruitment processes among taxa all play important roles in meiofaunal population density. In general, it appears that while copepods are more sensitive to oil than nematodes, the increased dispersal ability of copepods allows their populations to recover more quickly.

The ratio of nematodes to copepods has been suggested as a good indicator of organic (sewage) pollution (Raffaelli and Mason, 1981; Raffaelli, 1982; Amjad and Gray, 1983). However, factors such as seasonal variability and contagion can mitigate the usefulness of N/C as a predictive tool (Coull *et al.*, 1981; Shiells and Anderson, 1985). Because trophic enrichment via microbial hydrocarbon degradation has been hypothesized to explain the high macroinfaunal densities at the seep (Spies *et al.*, 1980; Spies and DesMarais, 1983; Montagna *et al.*, 1986), the N/C ratio should increase going from stations C to B to A along a gradient of increasing organic (petroleum) enrichment. The N/C ratio was greater at station A than at stations B or C, which is consistent with this hypothesis. On South African sandy beaches, oil decreased the number of harpacticoids, while nematode densities remained the same; organic enrichment increased the number of nematodes, while harpacticoid densities remained the same (Hennig *et al.*, 1983). Thus, both oil and sewage can have the same net effect on the N/C ratio but for different reasons. In the Coal Oil Point region the high N/C ratio at station A is a function of both higher nematode densities at station A and lower copepod densities at A compared to B and C.

There was also a trend of increasing bacterial abundance in going from station C to B to A. This was consistent with the hypothesis that direct counts of bacteria increase with increasing organic carbon content of sediments (Dale, 1974; Rublee, 1981).

Population abundances in most ecosystems are controlled mostly either through predation and/or disturbance (i.e. storms and biopertubation) or through food limitation. At the oil seep there are three other unique disturbance mechanisms due to the presence of oil that can control population densities: (1) toxicity of seeping oil, (2) modification of sedimentary characteristics (e.g., mechanical disturbance of sediments by effusing gas and increased sediment cohesiveness due to sand grains sticking together), and (3) modification of interstitial space (e.g., oil filling the interstitial space displacing pore water). While the impact of these forms of physical and chemical disturbance on meiofaunal populations was not evaluated here, their potential contribution to modifying sedimentary (and hence, meiofaunal habitat) characteristics, either alone or in conjunction with those factors examined in the present study, cannot be ignored.

Predation by juvenile fishes does not appear to be an important factor influencing population abundances at the seep when compared to nonseep sites (Table 5). This finding is consistent with the general hypothesis that fish predation is not an important controlling factor of meiofaunal populations in sandy sediments (Coull and Bell, 1979). The theory that fish predation is unimportant in sandy sediments is based on the fact that meiofauna are closer to the surface (because the RPD is shallower) in muddy

sediments than in sandy sediments and are thus more available to predators that use either visual cues or are tactile epibenthic feeders. One might hypothesize that within the study area there is a gradient of predation potential based on the distinct Eh profiles, where the aerobic zone at station A is shallower than B, which in turn is shallower than C (Fig. 3). Meiofaunal samples were taken only to the depth of the visual RPD, and densities (number per volume of sediment) of meiofauna were much greater at A than B than C. Shallow RPD layers and lower Eh are distinct properties of oiled sediments (Kalke *et al.*, 1982). Dungeness crabs consumed more littleneck clams in oiled sediments, presumably, because the clams were shallower and burrowed more slowly in oiled sediment (Pearson *et al.*, 1981). The increased densities of macrofauna and nematodes at the oil seep cannot reasonably be explained by less fish predation pressure at the seep site relative to nonseep sites. Intrameiofaunal predation or predation by macrofauna are possible alternative explanations but have not been studied here.

The base of benthic food webs rests upon food sources that are either photoautotrophically derived via primary production by microphytobenthos, chemoautotrophically derived via CO_2 fixation by bacteria or heterotrophically derived via degradation of organic matter by heterotrophic bacteria. Harpacticoids seem to be dependent on microalgal productivity (Table 6; Montagna *et al.*, 1983), and they were not more abundant at the seep relative to the nonseep sites. Although no dependent relationship between bacteria and nematodes was demonstrated over time, bacterial abundances increased with proximity to active seepage as do the occurrence of *Beggiatoa* mats. There are extensive kelp forests between the shore and the seep and comparison sites during much of the year. However, there was no evidence that allochthonous organic matter was being carried at disproportionately greater rates into the seep area (Fig. 4). In fact, it appears there may be more accumulations of allochthonous organic matter at the comparison site during the stormy season. Bacterial productivity (based on cell abundances, biovolumes, and FDC) at station A was 340% greater than station C, and station B was 44% greater than station C. There were also greater rates of hydrocarbon degradation and sulfate reduction at the seep than the non-seep station (Montagna *et al.*, 1986). Therefore, bacterial secondary production appears to be much greater at the oil seep and could be a result of the utilization of organic carbon and energy derived from the decomposition of seeping petroleum.

5. Conclusions

Although all meiofauna taxa did not uniformly correlate with the presence of seeping oil with increased densities like macrofauna, total meiofauna and the dominant taxa, nematodes (an average of 82% of all meiofauna for all samples), had higher abundances near active seepage. Increased infaunal densities at the seep (stations A and B) compared to the nonseep site (station C) cannot be explained by decreased predation pressure by fish or by other external sources of carbon. Bacterial productiv-

ity appears to be greater at the seep than at the non-seep site. We suggest that the increased meiofaunal and macrofaunal densities associated with the seep are a function of the seep microbial community adapting to utilize petroleum as a source of carbon and energy and that this increased microbial carbon is being consumed by benthic invertebrates in general and nematodes in particular.

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