

## Meiofauna and Chlorophyll Associated with *Beggiatoa* Mats of a Natural Submarine Petroleum Seep

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### ABSTRACT

*Previous studies at the Isla Vista oil seep have suggested that meiofauna, particularly nematodes, might be an important factor in explaining macrofaunal enrichment by making bacterial biomass available to the benthic food web. To explore this possibility, we analyzed meiofaunal abundance and microalgal pigments inside and just outside of bacterial mats at this natural oil seep.*

*The bacterial mats occur where crude oil and natural gas are actively seeping out of the sediment; cores from within the mats contained a great deal of crude oil (up to 50%). Meiofaunal abundances were the same in and out of the bacterial mats (averaging  $1.9 \times 10^6$  individuals  $m^{-2}$ ). However, dramatic changes in community structure were noticed. Harpacticoids made up 19% of the fauna outside the mats but only 1% inside. Pigment concentrations were also the same in both sites with phaeophytin dominating chlorophyll (120 compared to 29.8  $mg m^{-2}$ ). The variance of both microalgal pigments and meiofauna was much greater inside than outside, suggesting that the bacterial mats are a more heterogeneous environment.*

*Although the effect of crude oil toxicity is not clear, the high abundances of microbial and meiofaunal biomass support the hypothesis of benthic enrichment via microbes and meiofauna.*

### INTRODUCTION

Natural petroleum seepage is estimated to contribute 10% of the total hydrocarbons entering the oceans annually (Wilson *et al.*, 1974; National

Academy of Sciences, 1975). The fault-riddled southern California continental borderland has more than 2000 seeps, and seepage from the Coal Oil Point region is the most active known in the world (Allen *et al.*, 1970; Fisher, 1978).

The Isla Vista seep, in the Coal Oil Point region of the Santa Barbara Channel, has recently been the subject of intense study. This seep possesses a heterogeneous distribution of hydrocarbon composition and concentration (Sturmer *et al.*, 1982). The macrofauna of the seep, which is dominated by deposit-feeders, have higher densities than a nearby nonseep site (Spies & Davis, 1979; Davis & Spies, 1980).

Bacterial mats of *Beggiatoa* are associated with active seepage (Spies *et al.*, 1980). Organic-enrichment, via hydrocarbon-degrading and sulfide-oxidizing microbes, has been hypothesized to explain the high faunal densities at the seep site (Spies *et al.*, 1980). Recent evidence suggests meiofauna are central to the enrichment hypothesis. Isotopic ratios of sulfur and carbon are consistent with a trophic pathway of petroleum energy from sulfate reducers to H<sub>2</sub>S to *Beggiatoa* to nematodes and to other infauna (Spies & DesMarais, 1983). Because meiofauna are known to have close trophic links to bacteria in general (Coull, 1973; Gerlach, 1978; Tietjen, 1980; Kuipers *et al.*, 1981), it seems important to initiate studies of meiofauna associated with oil seeps.

This introductory study was designed to investigate links between meiofauna, and microbial mats of oil seeps. Because many studies have demonstrated toxic effects of oil on meiofauna, the first question of interest is: Do meiofauna exist in these areas of actively seeping oil? If meiofauna are present, are they abundant enough to support dynamic trophic processes? Since microphytobenthos are important sources of food to meiofauna (Admiraal *et al.*, 1983; Montagna, 1984), are benthic algae associated with the microbial mats? *Beggiatoa* mats represent the largest concentrations of bacteria at the seeps and are associated with active seepage, so samples were taken inside and outside the mats. We measured the microalgal pigments and meiofaunal abundance and identified the harpacticoid population structure.

## MATERIALS AND METHODS

Sampling was performed by divers at a seep 300 m offshore of Isla Vista, California, USA. The seep is located on a fine-sand bottom at 15 m depth

(Spies & Davis, 1979). *Beggiatoa* mats are not always present, and they depend on relatively quiet waters (R. B. Spies, pers. obs.). Therefore, sampling was carried out in the fall (21 September, 1983) before winter storms. The mats are white and cover areas where oil is actively seeping out of the bottom (see Spies & Davis, 1979, and Spies *et al.*, 1980, for photographs of *Beggiatoa* and mats). Samples were taken both inside and outside of the mats. For meiofauna, cores (50 cm<sup>3</sup> syringes with bottoms cut off and a cross-section 5.5 cm<sup>2</sup>) were taken to a depth of 5 cm. For pigments, cores (5 cm<sup>3</sup> syringes with bottoms cut off, yielding 1.1 cm<sup>2</sup> samples) were taken to a depth of 1 cm.

Meiofauna were extracted by the decantation technique, counted to major taxa, and the harpacticoid copepods identified. The samples from within the mats contained a great deal of oil (up to 10%) and required special processing. Water was added to the sample (5:1), which was then vigorously stirred. The oil phase separated after a few minutes and was removed. No meiofauna are found in the oil fractions of test samples, so this layer was discarded. It was sometimes necessary to repeat this procedure three or four times to remove all of the oil.

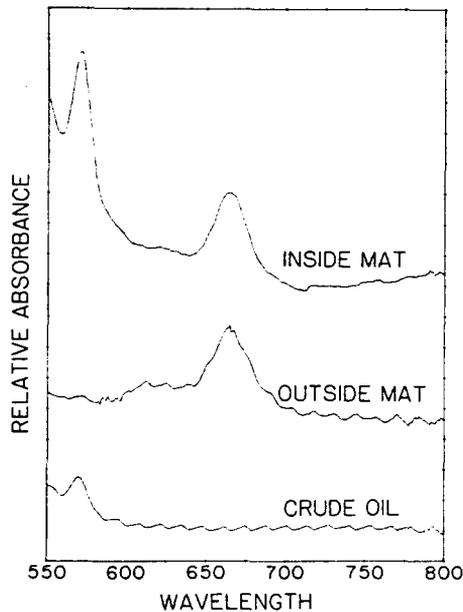


Fig. 1. Relative spectrophotometric absorbance of acetone extracts of samples from inside and outside bacterial mats and of a crude oil sample.

The sediment samples for the pigment analyses were immediately placed on dry ice in the field and stored for four weeks at  $-38^{\circ}\text{C}$ . In addition to preservation, freezing enhances the extraction (American Public Health Association, 1971). The sediment samples were ground for 1 min, then pigments were extracted for 24 h in 90% acetone at  $4^{\circ}\text{C}$  in the dark. Acetone is a more efficient solvent than methanol when extracting chlorophyll from sediment samples for spectrophotometry than methanol (Brown *et al.*, 1981). The concentration of chlorophyll-*a* was determined by spectrophotometry and the phaeophytin-*a* concentration was determined spectrophotometrically after acidification (Lorenzen, 1967). The presence of oil in the mat samples required two special modifications. Oil absorbs strongly between 340 and 500 nm, with an additional peak at 571 nm (Fig. 1). However, past 600 nm the baseline for crude oil was flat. Therefore, centrifugation for 10 min at 500 g (to remove particulate interference) and readings at 750 nm (to subtract sediment oil background) were used to measure pigment absorbance. A second interference by oil was found upon acidification. Addition of acid at high concentration (0.1 M) increased absorbance in the samples containing oil. But this interference subsided when acid at low concentration (0.003 M) was added as suggested by Riemann (1978).

Data were analyzed using BMDP software (Dixon, 1983). The *t*-test was used for meiofauna data (program P3D). Much more complicated analyses were required for the pigment data. The problem is like a two-way analysis of variance (ANOVA): site (in or out of mat) versus pigment

**TABLE 1**  
Concentrations of Microalgal Pigments, Determined by Spectrophotometry, from Inside and Outside *Beggiatoa* Mats

<i>Mat site</i>	<i>Sediment core</i>	<i>Pigment measurements</i> ( $\text{mg m}^{-2}$ )	
		<i>Chlorophyll-a</i>	<i>Phaeophytin-a</i>
Out	1	43.1	117
Out	2	32.9	111
Out	3	32.6	94.0
In	4	25.3	124
In	5	16.6	170
In	6	28.0	107

(chlorophyll or phaeophytin). But phaeophytin is determined after acidification of the same sample from which chlorophyll is measured; thus the pigments are a repeated measure from each core sample and each core comes from only one site. That is, cores are nested even though the pigments are crossed. This is a completely random and partially hierarchical design (Kirk, 1982, p.470). The appropriate statistical model is

$$Y_{ijk} = \alpha_i + \beta_{j(i)} + \gamma_k + \alpha\gamma_{ik} + (\beta\gamma\alpha)_{j(i)k}$$

where the variation of each measurement  $Y_{ijk}$  is a function of  $\alpha_i$  (a site effect), sediment core  $\beta_{j(i)}$  (a nested effect), pigment  $\gamma_k$  (a crossed effect) and interaction terms. Program P2V was used for this analysis.

## RESULTS

The oil seep area is a curious place. Gas bubbles and oil droplets rise to the surface and form oil slicks. *Beggiatoa* mats occur directly over active seepage; thus cores through the mats contain large quantities of oil. One might imagine that nothing could live there at all. This environment does appear to stress microalgae. Phaeophytin concentrations are 4 × greater than chlorophyll (Table 1);  $P = 0.0014$  (Table 2). It is reasonable to hypothesize that chlorophyll would be favored outside the mat and phaeophytin inside the oiled mat, thereby yielding a significant interaction term. Although the data suggest that phaeophytin is more abundant in the mat (the mean,  $\bar{X} = 134 \text{ mg m}^{-2}$ ; standard deviation,

**TABLE 2**  
Analysis of Pigment Data (Table 1) Using a Partially Heirarchical Model  
(Numerator and denominator used in  $F$ -test is shown in brackets)

Source	df	SS	F	P
1 A (site)	1	135	[1/2] 0.55	0.5507
2 B(A) (core)	4	990	[2/5] 0.63	0.7000
3 C (pigment)	1	24707	[3/5] 63.29	0.0014
4 A × C	1	1154	[4/5] 2.96	0.1606
5 B(A) × C	4	1561		

$s = 33$ ) than outside ( $\bar{X} = 107 \text{ mg m}^{-2}$ ,  $s = 12$ ) and chlorophyll is more abundant outside ( $\bar{X} = 36.2 \text{ mg m}^{-2}$ ,  $s = 6.0$ ) than inside ( $\bar{X} = 23.3 \text{ mg m}^{-2}$ ,  $s = 6.0$ ), the interaction term was not statistically significant ( $P = 0.16$ ; Table 2). The lack of significant interaction is probably due to the small numbers of samples and the large variance associated with phaeophytin concentrations, particularly those inside the mat (Table 1).

Meiofaunal populations also exhibited much higher variance inside the mat than outside (Table 3;  $P = 0.0202$ ). The abundances of meiofauna

**TABLE 3**  
Meiofaunal Population Abundances Inside and Outside of the Oil Seep *Beggiatoa* Mats  
( $\times 10^3$  individuals  $\text{m}^{-2}$ )

Site	Sample	Totals	Nematodes	Copepods	Naupli	Oligochetes	Ciliates	Others <sup>a</sup>
Out	1	1880	1200	448	49	62	58	64
Out	2	2960	2360	406	55	20	76	47
Out	3	1880	1340	355	51	0	86	45
Out	4	2500	1860	342	73	11	122	91
Out	5	3040	1800	821	129	33	191	65
In	1	662	632	7	0	16	4	4
In	2	337	326	5	0	4	2	0
In	3	3170	3070	26	0	9	60	5
In	4	511	491	5	0	13	2	0
In	5	2290	2230	0	0	5	53	4

<sup>a</sup>Cumacea, Ostracoda Cipriids, Isopoda, Halacarida, Ophiuroidea larvae, larval Pelecypoda, Gastrotricha, Turbellaria and Foraminifera.

were not significantly greater ( $t$ -test;  $P = 0.1259$ ) outside the mat ( $\bar{X} = 2.45 \times 10^6$  individuals  $\text{m}^{-2}$ ,  $s = 0.56 \times 10^6$ ) than inside ( $\bar{X} = 1.39 \times 10^6$  individuals  $\text{m}^{-2}$ ,  $s = 1.26 \times 10^6$ ). More taxa were found outside than inside. Whereas all of these taxa—Cumacea, Ostracoda Cipriids, Isopoda, Halacarida, Ophiuroidea larvae, larval Pelecypoda, Gastrotrichia, Turbellaria and Foraminifera—were present outside, only a single ostracod or foraminiferan plus several ciprid larvae were found inside the mats. Many larger oligochetes and polychetes were present (Spies & Davis, 1979; Davis & Spies, 1980) but were not of a meiofaunal size.

The harpacticoid copepods were very diverse and abundant at the oil seep site (Table 4). Just outside the mat there were 34 species compared to four inside, with two species occurring in both locations.

**TABLE 4**  
Copepod Species Abundances Inside and Outside of Oil Seep *Beggiatoa* Mats  
(mean number of individuals ( $\pm$  standard deviation) 10 cm<sup>-2</sup>)

Family	Species	Outside	Inside
Longipediidae	<i>Longipedia</i> (cf.) <i>minor</i>	10.9 (6.2)	
Ectinosomatidae	<i>Ectinosoma paranormani</i>	10.6 (7.9)	
	<i>Ectinosoma melaniceps</i>	0.7 (1.0)	
	<i>Halectinosoma kunzi</i>	2.0 (3.2)	
	<i>Microsetella norvegica</i>	0.7 (1.0)	
	<i>Pseudobradya pectinifera</i>	0.4 (0.8)	
	<i>Pseudobradya crassipes</i>	1.1 (1.0)	
Harpacticidae	<i>Zausodes sextus</i>	138.0 (55.9)	
	<i>Zausodes septimus</i>	4.4 (7.9)	
Tisbidae	<i>Tisbe</i> sp.		7.3 (9.4)
Thalestridae	<i>Dactylopodia paratisboides</i>	28.4 (16.1)	
	<i>Diarthrodes dissimilis</i>	37.1 (27.3)	
Diosaccidae	<i>Amphiascoides lancisetiger</i>	29.5 (22.0)	
	<i>Amphiascoides petkovskii</i>	2.9 (6.5)	
	<i>Diosaccus spinatus</i>	0.4 (0.8)	
	<i>Robertgurnea diversa</i>	26.9 (14.8)	
	<i>Robertsonia propinqua</i>	2.5 (2.8)	
	<i>Stenhelia</i> (D.) (cf.) <i>hanstromi</i>	31.3 (11.2)	
	<i>Stenhelia</i> (D.) <i>longipilosa</i>	0.4 (0.8)	
	<i>Stenhelia</i> (S.) <i>peniculata</i>	0.7 (1.0)	
	<i>Stenhelia</i> (S.) <i>proxima</i>	0.4 (0.8)	
	<i>Typhlamphiascus</i> sp.	14.6 (4.6)	
	<i>Pseudoamphiascus</i> sp.		1.4 (2.4)
Ameiridae	<i>Ameira parvuloides</i>	15.7 (9.8)	
	<i>Ameiropsis</i> sp.	0.7 (1.0)	
	<i>Leptomesochra</i> sp.	1.1 (1.6)	
Cletodidae	<i>Acrenhydrosoma karlinga</i>	1.8 (2.2)	0.4 (0.8)
	<i>Cletodes hartmannae</i>	0.7 (1.6)	
	<i>Enhydrosoma hopkinsi</i>	7.3 (6.4)	
	<i>Stylicletodes verisimilis</i>	0.4 (0.8)	
Canthocamptidae	<i>Orthopsyllus illgi</i>	2.5 (3.0)	
Loaphontidae	<i>Normanella bolini</i>	58.2 (31.4)	
	<i>Normanella confluens</i>	14.6 (4.5)	
	<i>Paralaophonte asellopsiformis</i>	16.7 (11.5)	
	<i>Paralaophonte pacifica</i>	2.9 (2.8)	0.4 (0.8)
Anacorabolidae	<i>Laophontodes hedgpethi</i>	0.4 (0.8)	
Total		466	9.5

## DISCUSSION

The pattern we have found is that meiofauna and chlorophyll are predominantly associated with the fringe of the bacterial mats, not in the center. Because the presence of mats is not constant we have not attempted to sample more than once. But the rate of hydrocarbon seepage is relatively constant, so we are confident that the pattern we describe, but not necessarily the magnitude, is representative of bacterial mats at the oil seep. This pattern is also consistent with the finding that ATP is most abundant at the fringes of actively seeping oil (Spies *et al.*, 1980). The *Beggiatoa* mats are found over areas of active seepage. *Beggiatoa* are known to exhibit diel vertical migration in sediments in response to light (Nelson & Castenholz, 1982). The vertical distribution of *Beggiatoa* is also strongly related to the interface of oxic and anoxic sediments (Jorgensen, 1977). We suspect *Beggiatoa* is always present, but unique conditions, such as either low light conditions or lack of oxic sediments, or both, can cause *Beggiatoa* to move to the surface and form the large filamentous mats.

Whereas the bacterial mats are rich in chlorophyll-*a*, the dominance of phaeophytin-*a* indicates microalgal populations are stressed by the presence of crude oil, natural gas or associated sulfide (Table 1). However, the presence of chlorophyll in the mats indicates areas of active seepage are important potential sources of meiofaunal food because microbial biomass is concentrated there. Although the meiofaunal populations were not different inside and adjacent to the bacterial mats (about  $1.4$  and  $2.5 \times 10^6$  individuals  $m^{-2}$ , respectively), community structure did shift (Table 3).

Harpacticoids decreased dramatically from  $0.474 \pm 0.198$  to  $0.009 \pm 0.010 \times 10^6$  individuals  $m^{-2}$  when comparing the fringe to the center of the mat. Therefore, harpacticoids appear to suffer stress from petroleum. Variance for all meiofaunal taxa and pigments increases at the fringe relative to the center of the mats (Table 3). This indicates that the center of the mats, where oil is actively seeping, is a much more heterogeneous environment than the fringes. The fringes, which support a rich and diverse assemblage of meiofauna (Table 4), are probably sites where trophic-dynamic processes are carried on at peak rates. The size of the meiofaunal population at the fringe is certainly large enough to be a significant factor in the coastal food web. In contrast, the bacterial mat

(which is directly over seeping oil) is a heterogeneous environment which appears to have limited stressful effects.

Abundances of macroinfauna at the Isla Vista oil seep are greater than in a similar but nonseep site (Spies & Davis, 1979; Davis & Spies, 1980). Although the details of this apparent benthic enrichment are not known, the presence of petroleum and sulfide suggests an efficient (or supplementary) anaerobic-based food web. This hypothesis is supported by observations of the natural isotopic ratios of carbon and sulfur, which suggest that sulfide is the energy source and petroleum supplies the carbon (Spies & DesMarais, 1983).

Meiofauna appear to be the key intermediate between microbial and infaunal biotransformations (Spies & DesMarais, 1983). Trophic enrichment associated with anaerobiosis and chemoautotrophy in sulfide-rich environments appears to be a common paradigm for salt marshes (Howarth & Teal, 1980), subsurface marine muds (Kepkay *et al.*, 1979), brine seeps (Powell *et al.*, 1983) and hydrothermal vents (Karl *et al.*, 1980). It appears that natural marine oil seeps can be added to this list.

Meiofauna, owing to their small size, share similar spatial and temporal scales to microbes, particularly microalgae (Montagna *et al.*, 1983). As well as grazing on bacteria and benthic diatoms (Admiraal *et al.*, 1983; Montagna, 1984), meiofauna also appear to have roles in biogeochemical cycles (Coull & Bell, 1979; Sikora & Sikora, 1982). So investigating relationships between meiofauna and the sediment microbial community appears to be central to understanding the apparent trophic enrichment in sulfide environments.

The interstitial sulfide at the Isla Vista seep is apparently of biogenic origin (Spies & DesMarais, 1983). Large mats of the sulfide-oxidizer *Beggiatoa* are found at the seep site. Blue-green algae or chlorophyll are often associated with bacterial mats in sulfide-rich environments (Doemel & Brock, 1976; Gallardo, 1977). These microbially-rich environments could be an important food source to meiofauna and the center of radiation for carbon and sulfur incorporation into the food web. Flatfish have been seen feeding at this site by divers.

Pore-water hydrocarbon concentrations are about 1 ppm inside the *Beggiatoa* mats and in the range of 45 to 100 parts per 10<sup>9</sup> outside (Stuermer *et al.*, 1982). Up to 50% of the sediment sample from within the mat can be crude oil. Thus, trophic enrichment by petroleum carbon might be limited by the toxic effect of oil. Meiofaunal abundances,

especially copepods, usually decrease after heavy oiling (Giere, 1979; Bodin & Boucher, 1983). But after an experimental crude oil introduction in Louisiana, densities did not decrease (Fleeger & Chandler, 1983). Chlorophyll pigments also seem not to be affected by spilled oil (Bodin & Boucher, 1983).

Whereas there are indications that natural oil seepage has some stressful effects, the present study suggests that these effects are more than offset by dynamic trophic processes associated with the fringes of spots of active seepage (which are sometimes covered by bacterial mats). Petroleum, via heterotrophic degraders, is the carbon source and sulfide, via oxidizers, is the energy source. Meiofauna feed on both these types of bacteria, as well as the chlorophyllous microbes (either microalgae or cyanobacteria). This petroleum-based carbon eventually gets into the coastal food web by macroinfaunal predation and larval fish predation on meiofauna.

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