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ORGANIC ENRICHMENT
OIL SEEP
BACTERIA
MICROALGAE
FOOD WEB

ABSTRACT – The Isla Vista, California, hydrocarbon seep is an organically enriched environment. Microbial biomass and production are enhanced relative to non-seep sediments in the Santa Barbara Channel. This study was performed to determine the rate at which microbial carbon is transferred to higher trophic levels in natural seep sediments. Grazing rates of meiofauna on microbes were studied at three coastal stations representing a gradient of natural hydrocarbon seepage, from very active, to moderate, to none. Sampling was performed in April, July, and December, 1986 to examine possible seasonal differences between the three major oceanographic seasons (upwelling, mixed and Davidson respectively). Samples were limited to the top 1 cm of the sediment, where photosynthesis and most of the meiofauna occur. Meiofaunal community grazing rates were dominated by small polychaetes, and were slightly higher in July. There were no differences in grazing rates between stations, indicating that petroleum exposure had no effect on the feeding behavior of meiofauna. On average, meiofauna grazing rates were $0.0058 \cdot h^{-1}$ on bacteria and $0.0018 \cdot h^{-1}$ on microalgae in the sandy, subtidal environment. The higher rates on bacteria reflect the importance of heterotrophic processes in the seep environment. Since, the biomass of microalgae is much higher than that of bacteria, the consumption of microalgae ($4 \text{ mg C} \cdot m^{-2} \cdot h^{-1}$) is higher than on bacteria ($0.04 \text{ mg C} \cdot m^{-2} \cdot h^{-1}$), indicating the importance of benthic primary production in shallow marine ecosystems. The rates in coastal sediments are comparable to those found in estuarine sediments.

ENRICHISSEMENT ORGANIQUE
SUINTEMENT PÉTROLIER
BACTÉRIES
MICROALGUES
RÉSEAU TROPHIQUE

RÉSUMÉ – La zone de suintements d'hydrocarbure de l'Isla Vista en Californie est un milieu enrichi organiquement. La biomasse et la production des microorganismes sont augmentées par rapport aux sédiments non situés dans la zone d'émanation du détroit de Santa Barbara. Cette étude a été menée pour déterminer à quel taux le carbone des microorganismes est transféré aux niveaux trophiques supérieurs dans les sédiments infiltrés d'hydrocarbure. Le broutage des microorganismes par la méiofaune a été étudié dans trois stations de la côte montrant un gradient d'infiltration d'hydrocarbure naturel, à partir d'un site très actif, vers un site modérément actif, jusqu'à une station inactive. L'échantillonnage a eu lieu en avril, juillet et décembre 1986 en vue d'examiner d'éventuelles différences saisonnières entre les trois saisons océanographiques majeures (upwelling, mixte et Davidson, respectivement). Les prélèvements étaient limités au centimètre supérieur de sédiment où se localisent la photosynthèse et la plus grande partie de la méiofaune. Le taux de broutage par la communauté méiofaunique est dominé par les petites Polychètes et est légèrement plus élevé en juillet. Il n'y a pas de différence de consommation entre les stations, ce qui indique que l'exposition au pétrole n'a aucun effet sur le comportement de nutrition de la méiofaune. En moyenne, le taux de broutage de la méiofaune est de $0{,}0058 \cdot h^{-1}$ sur les bactéries et $0{,}0018 \cdot h^{-1}$ sur les microalgues dans les sables de la zone subtidale. La consommation plus élevée des bactéries reflète l'importance des processus hétérotrophiques dans le milieu d'émanation. La biomasse des microalgues étant beaucoup plus élevée que celle des bactéries, la consommation des microalgues ($4 \text{ mg C} \cdot m^{-2} \cdot h^{-1}$) est plus importante que celle des bactéries ($0{,}04 \text{ mg C} \cdot m^{-2} \cdot h^{-1}$), ce qui montre l'importance de la production primaire benthique dans les écosystèmes marins peu profonds. Les taux des sédiments côtiers sont comparables à ceux des sédiments des estuaires.

INTRODUCTION

The Isla Vista, California hydrocarbon seep is an organically enriched environment (Spies and Davis, 1979; Spies and DesMarais, 1983; Montagna *et al.*, 1986, 1989). The seep lies in 18 m of water, off Coal Oil Point in the Santa Barbara Channel. Seeping hydrocarbons enrich the coastal sediments with carbon (Spies *et al.*, 1980). This carbon is utilized by seep microbes, and there are very high rates of heterotrophic metabolism in these sediments (Montagna *et al.*, 1986; Bauer *et al.*, 1988). The carbon metabolized by microbes is also incorporated into the benthic food web (Spies and DesMarais, 1983). The high carbon content and heterotrophic activity of seep sediments correlate with high abundances of macrofauna (Spies and Davis, 1979) and meiofauna (Montagna *et al.*, 1987; 1989). The high amount of microbial biomass in seep sediments is fueling an active benthic food web.

Organic matter deposited in sediments is decomposed by heterotrophic bacteria. These bacteria form the basis of a detrital food chain with benthic invertebrates and epibenthic fish at the top. The hydrocarbon seep may simply represent an "upside down benthos," where organic matter comes from below to the surface. In addition to heterotrophy there are two forms of autotrophy present in seep sediments. Benthic microalgae are present, as are chemosynthetic bacteria (Spies and DesMarais, 1983; Montagna and Spies, 1985). Chemoautotrophic production by bacteria and primary production by microphytobenthos forms the basis of the grazing food chain. Together, the detrital and grazing food chains can fuel secondary production by benthic invertebrates.

Benthic bacteria (Zobell and Feltham, 1935) and microalgae (Leach, 1970) have long been hypothesized as major food and carbon sources for benthic invertebrates. Diatoms and bacteria are eaten by meiofaunal taxa such as nematodes (Jensen, 1982; Romeyn and Bouwman, 1983) and harpacticoid copepods (Sellner, 1976; Rieper, 1978, 1982, 1984). Previous work in estuaries, has shown that meiofauna grazing rates on bacteria and microalgae are close to the natural growth rates of those populations (Montagna, 1984). Thus, meiofauna can maintain microbial populations in log phase growth by their grazing pressure. Meiofauna should not be limited by food abundance, but by food production. If this hypothesis is true, then there should be concomitantly high rates of meiofaunal grazing when turnover times are high.

The purpose of this study was to examine meiofauna-microbial trophic interactions in a shallow, coastal, hydrocarbon seep. The seep is a good environment to study benthic trophic dynamics, because it is an organically enriched environment. The rate at which microbial carbon was being passed to higher trophic levels was assessed by measuring microbial productivity and meiofaunal grazing rates on microbial populations. These data can be used to test if meiofauna are having an important impact on the growth rates of microbes, by comparing meiofaunal grazing rates and microbial turnover times. The relative importance of the grazing and detrital food chains in seep sediments can also be determined.

The current study was performed at the same time as two other studies. One examining the biogeochemical relationships within vertical profiles of sediments was performed at the same time as this study (Bauer *et al.*, 1988), and the other examining vertical profiles of meiofaunal and microbial biomass (Montagna, *et al.*, 1989). The data on microbial biomass and productivity presented in the present study are derived from these two studies.

MATERIALS AND METHODS

The hydrocarbon seep is in the Santa Barbara Channel between Coal Oil Point and Goleta Point about 800 m offshore of Isla Vista, California, USA (Fig. 1). We sampled three stations with different rates of petroleum seepage. Station A is within the Isla Vista seep and in the center of large quantities of fresh oil and natural gas are seeping from the sediments. In our previous studies, we sampled at the edge 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 $mg \cdot cm^{-3}$ at the surface and increasing to 25 $mg \cdot cm^{-3}$ at 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 $mg \cdot cm^{-3}$ at the surface and increased to 3.5 $mg \cdot cm^{-3}$ (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 $mg \cdot cm^{-3}$ over the entire top 7 cm of sediment (Bauer *et al.*, 1988). Stations B and C have similar granulometry with a median grain size of about 160 µm (Spies & Davis, 1979; Palmer *et al.*, 1988). Stations A and B are within the Isla Vista seep but station C is not (Fig. 1). All stations were at a depth of 18 m in fine-sand sediments.

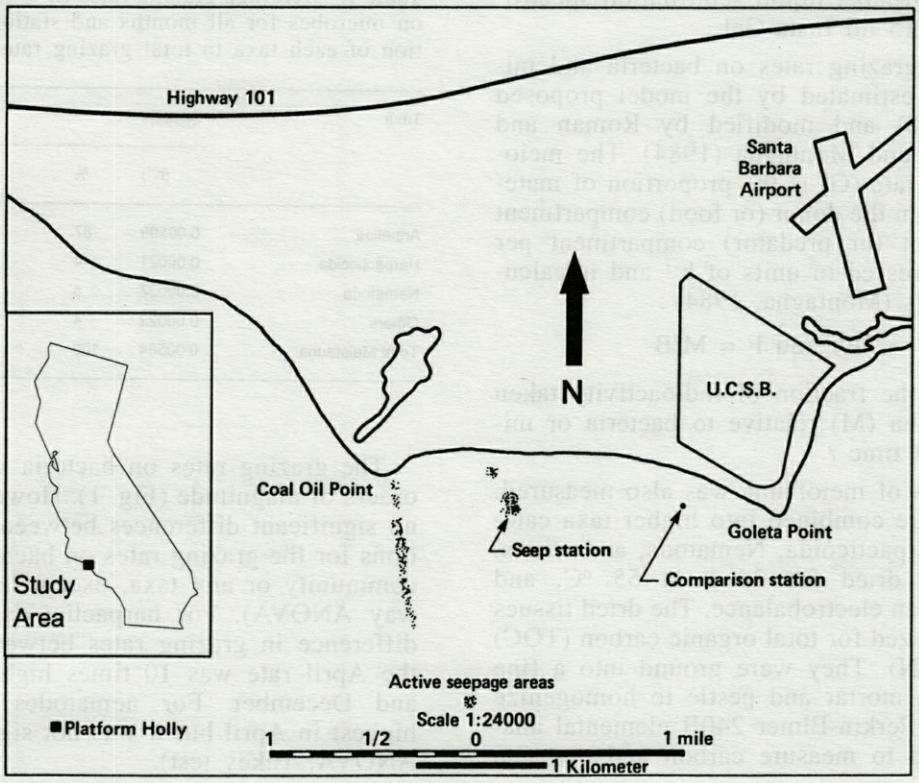

Fig. 1. – Location of sampling sites. The seep stations (A and B) are located east of Coal Oil Point. The comparison station (C) is located south of the University of Santa Barbara (U.C.S.B.) campus. Inset shows location of Santa Barbara in California, USA.

Three sampling periods were chosen to examine different environmental conditions. 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.

In situ meiofaunal grazing rates on bacteria and microalgae were measured by incubating sediment slurries with two radiolabeled substrates, tritiated thymidine (^{3}HTdR) and ^{14}C-bicarbonate ($H^{14}CO$) (Montagna and Bauer, 1988). The top 1 cm (~5.5 cm^3) of 60-cm^3 sediment cores were placed in 60 cm^3 clear centrifuge tubes. Two µCi of ^{3}HTdR and 2 µCi of $H^{14}CO_3^-$ were added to the slurries and samples were incubated for 2 h at *in situ* temperature and light conditions.

Live controls were used to assess label uptake in meiofauna not due to grazing on microbes. A saturated solution of nalidixic acid (200 µg ml^{-1}) plus 5'-deoxythymidine (2 µg ml^{-1}) (hereafter referred to as ND) was used to inhibit prokaryotic uptake of thymidine (Findlay *et al.*, 1984; Montagna and Bauer, 1988). The live controls for this experiment consisted of 3 replicate slurries with $H^{14}CO_3^-$, ^{3}HTdR and ND added. These were incubated in the dark to inhibit photosynthetic fixation of CO_2.

After 2 h, incubations were terminated by adding 2% formalin. A 1-ml subsample was withdrawn from the slurries. The subsample was filtered onto a 0.2 µm Millipore filter and rinsed 3 times with filtered seawater to estimate uptake of $H^{14}CO_3^-$ by microalgae and ^{3}HTdR by bacteria. The subsample was dispersed and suspended in 5 ml distilled water and 15 ml Insta-Gel for dual-label liquid scintillation counting. Meiofauna were separated from sediments by diluting samples with 2% formalin, swirling to suspend the animals, and decanting them and the supernate onto 63 µm Nitex screen filters. Meiofauna were then rinsed into jars and kept in refrigerated 2% formalin until sorting (1 to 2 d).

Sorting was performed using a dissecting microscope. Meiofauna were sorted by major taxa into the following groups : Harpacticoida, Nematoda, Polychaeta, and other meiofauna taxa. The sorted organisms were placed into scintillation vials containing 1 ml distilled water. After sorting, meiofauna were dried at 60 °C to evaporate the water and solubilized by adding 100 µl Soluene tissue solubilizer for 24 h. Samples were

counted by dual-label liquid scintillation spectrophotometry in 15 ml Insta-Gel.

Meiofaunal grazing rates on bacteria and microalgae were estimated by the model proposed by Daro (1978) and modified by Roman and Rublee (1981) and Montagna (1984). The meiofaunal grazing rate (G) is the proportion of material flowing from the donor (or food) compartment to the recipient (or predator) compartment per hour. G is expressed in units of h^{-1} and is calculated as follows (Montagna, 1984) :

$$G = 2F/t \text{ and } F = M/B$$

where F is the fraction of radioactivity taken up by meiofauna (M) relative to bacteria or microalgae (B) at time *t*.

The biomass of meiofauna was also measured. Individuals were combined into higher taxa categories, i.e., Harpacticoida, Nematoda, and others. Samples were dried for 24 h at 55 °C, and weighed using an electrobalance. The dried tissues were also analyzed for total organic carbon (TOC) and nitrogen (N). They were ground into a fine powder with a mortar and pestle to homogenize the sample. A Perkin-Elmer 240B elemental analyzer was used to measure carbon and nitrogen content.

Statistical analyses were performed using 2-way analysis of variance (ANOVA) where stations and seasons were the two main treatment effects. Tukey multiple comparison tests were performed to find post hoc differences among sampling means.

RESULTS

Meiofaunal grazing on both bacteria and microalgae was dominated by small annelid polychaetes (Table I). Juvenile polychaetes were responsible for 87 % of the bacteria, and 55 % of the microalgae consumed by meiofauna. Although juvenile polychaetes are only temporary meiofauna, that is they will grow out of the meiofaunal size class, they apparently have a great energetic impact on microbes. Of the permanent meiofauna, nematodes were the dominant grazers, responsible for 5 % of the bacteria and 27 % of the microalgae consumed by meiofauna.

The overall mean grazing rate for the total meiofaunal community 0.00584 h^{-1} on bacteria and 0.00181 h^{-1} on microalgae (Table I). Therefore, 0.584 % of the bacteria were removed by meiofauna in 1 h, and the turnover time (i.e., the inverse of the grazing rate) that bacteria would require to maintain their population size is 7.1 days. For microalgae, 0.181 % were removed by meiofauna in 1 h, and that the turnover time microalgae would require to maintain their population size is 23 days.

Table I. – Average grazing rates (h^{-1}) of meiofaunal taxa on microbes for all months and stations, and contribution of each taxa to total grazing rate (%).

Taxa	Bacteria		Microalgae	
	(h^{-1})	%	(h^{-1})	%
Annelida	0.00509	87	0.00099	55
Harpacticoida	0.00021	4	0.00015	8
Nematoda	0.00032	5	0.00049	27
Others	0.00022	4	0.00018	10
Total Meiofauna	0.00584	100	0.00181	100

The grazing rates on bacteria varied over two orders of magnitude (Fig. 1). However, there were no significant differences between months or stations for the grazing rates on bacteria by the total community or any taxa, except harpacticoids (2-way ANOVA). For harpacticoids, there was no difference in grazing rates between stations, but the April rate was 10 times higher than in July and December. For nematodes, the rate was highest in April but it was not significant (2-way ANOVA, Tukey test).

The grazing rates on microalgae also varied over two orders of magnitude (Fig. 3A). Again, there were no differences in grazing rates on microalgae for either stations or months for the community as a whole. Harpacticoids and nematodes had different grazing rates in different months. Both had higher grazing rates in July than in April and December. The nematode grazing rate on microalgae at station A was 5 times higher than at B and C. This was the only taxa that had significantly different grazing rates among stations for either bacteria or microalgae.

The total amount of microbial biomass consumed per hour is calculated by the product of the microbial biomass and the meiofaunal grazing rate. These rates varied considerably. Consumption of bacterial biomass varied over 2 orders of magnitude (Fig. 2B), averaging 41.2 µg $C \cdot m^{-2} \cdot h^{-1}$. The total amount of microalgal biomass consumed by meiofauna varied over 3 orders of magnitude (Fig. 3B). The average consumption of microalgal biomass by meiofauna was 3840 µg $C \cdot m^{-2} \cdot h^{-1}$.

Total meiofaunal biomass was always highest at station A (Table II). This was caused by the large amount of nematodes at station A, which dominated community biomass. There was always higher amounts of harpacticoid biomass at station C. There was not a large difference in meiofaunal biomass among the three months (Table II).

The carbon content of the harpacticoid copepods was 57.7 %, nematodes 49.2 % and the other meiofauna 38.6 %.

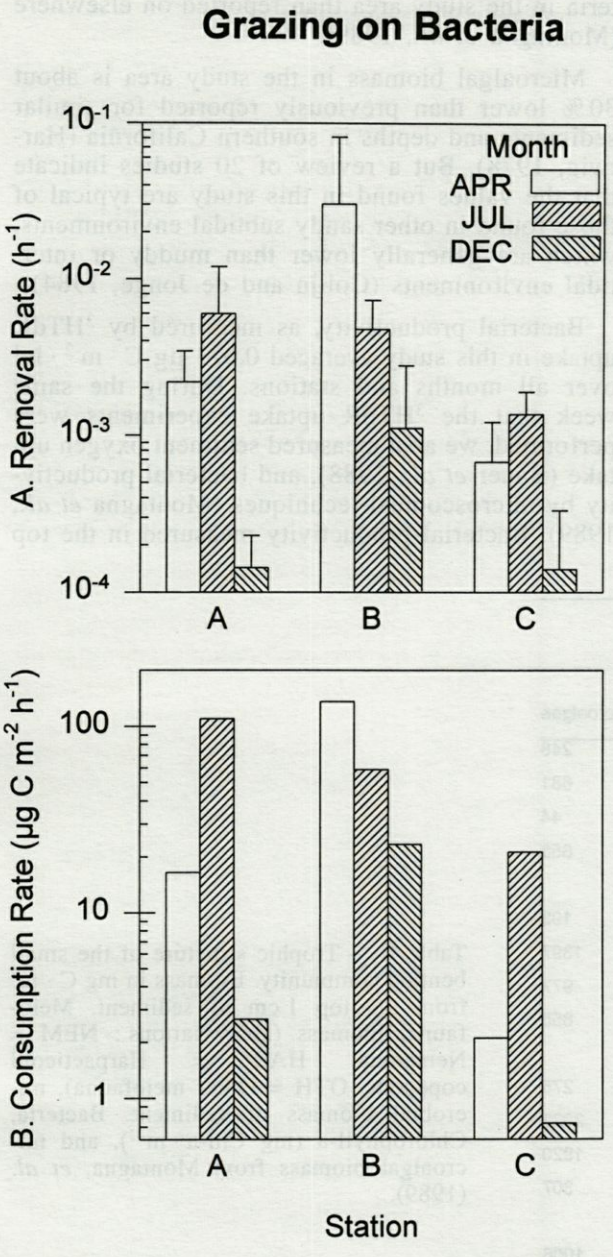

Fig. 2. – Grazing rate of the total meiofauna community on bacteria. A. The clearance rate (% of bacteria removed h^{-1}). The overall mean grazing rate was 0.520 % h^{-1}, and the C.V. was 333 %. B. The amount of bacterial biomass consumed by the total meiofauna community (µg C · m^{-2} · h^{-1}). The overall mean grazing rate was 41.2 µg C · m^{-2} · h^{-1}.

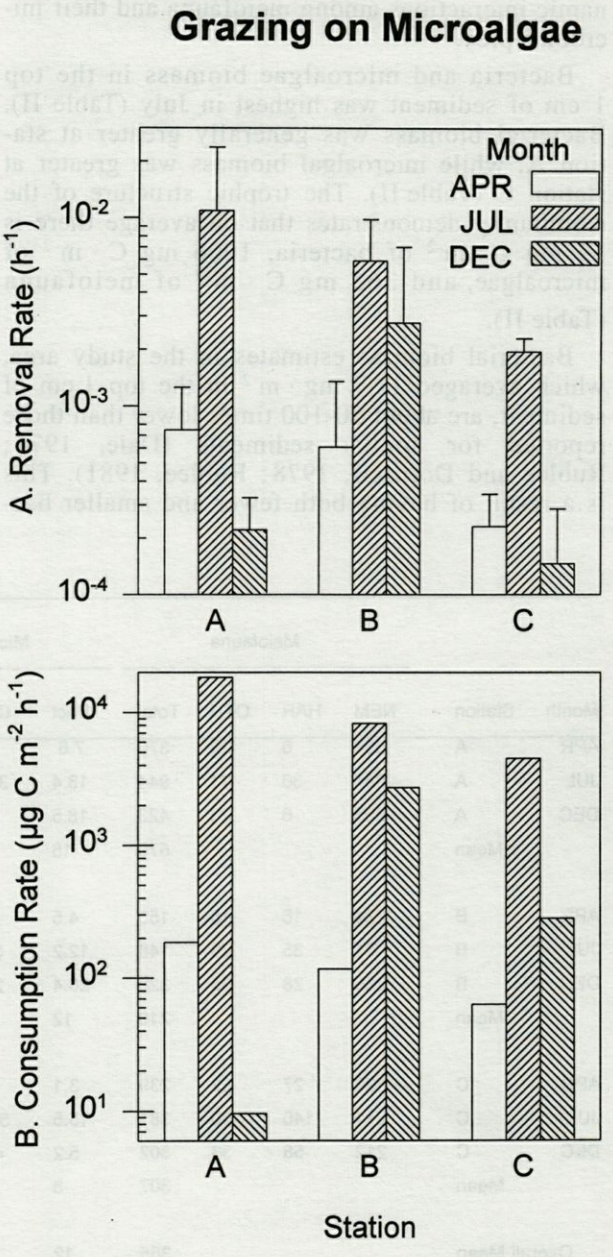

Fig. 3. – Grazing rate of the total meiofauna community on benthic microalgae. A. The clearance rate (% of microalgae removed h^{-1}). The overall mean grazing rate was 0.262 % h^{-1}, and the C.V. was 180 %. B. The amount of microalgal biomass consumed by the total meiofauna community (µg C · m^{-2} · h^{-1}). The overall mean grazing rate was 3840 (µg C · m^{-2} · h^{-1}).

DISCUSSION

Microbial biomass and productivity

Many aspects of microbial biomass and productivity were previously studied. These studies include *Beggiatoa* mats (Montagna and Spies, 1985), benthic metabolism (Montagna *et al.*, 1986), microbial biomass (Montagna *et al.*, 1987; 1989), and microbial production (Montagna *et al.*, 1989; Bauer *et al.*, 1988). A review of these studies and other published studies allows us to compare meiofaunal feeding behavior with microbial dynamics. This is required to assess the dynamics of the "small benthic food web," i.e., trophyc dy-

namic interactions among meiofauna and their microbial prey.

Bacteria and microalgae biomass in the top 1 cm of sediment was highest in July (Table II). Bacterial biomass was generally greater at station A, while microalgal biomass was greater at station C (Table II). The trophic structure of the community demonstrates that on average there is 12 mg C · m^{-2} of bacteria, 1006 mg C · m^{-2} of microalgae, and 365 mg C · m^{-2} of meiofauna (Table II).

Bacterial biomass estimates in the study area, which averaged 11.7 mg · m^{-2} in the top 1 cm of sediment, are about 50-100 times lower than those reported for similar sediments (Dale, 1974; Rublee and Dornseif, 1978; Rublee, 1981). This is a result of having both fewer and smaller bacteria in the study area than reported on elsewhere (Montagna *et al.*, 1989).

Microalgal biomass in the study area is about 30% lower than previously reported for similar sediments and depths in southern California (Hartwig, 1978). But a review of 20 studies indicate that the values found in this study are typical of those found in other sandy subtidal environments, which are generally lower than muddy or intertidal environments (Colijn and de Jonge, 1984).

Bacterial productivity, as measured by ^{3}HTdR uptake in this study averaged 0.073 µg C · m^{-2} · h^{-1} over all months and stations. During the same week that the ^{3}HTdR uptake experiments were performed, we also measured sediment oxygen uptake (Bauer *et al.*, 1988), and bacterial productivity by microscopical techniques (Montagna *et al.*, 1989). Bacterial productivity measured in the top

		Meiofauna				Microbes		
Month	Station	NEM	HAR	OTH	Total	Bact	Chl-a	Microalgae
APR	A	354	6	10	370	7.6	5.6	248
JUL	A	887	36	21	944	18.4	37.6	681
DEC	A	395	6	23	423	18.5	1.0	44
	Mean				579	15		658
APR	B	124	16	15	155	4.5	4.3	192
JUL	B	91	35	23	148	12.2	31.3	1397
DEC	B	265	28	35	328	20.4	21.9	977
	Mean				210	12		855
APR	C	190	27	22	239	3.1	6.2	275
JUL	C	211	140	30	381	15.5	51.9	2322
DEC	C	212	58	33	302	5.2	43.0	1920
	Mean				307	8		307
Overall Mean					365	12		1006

Table II. – Trophic structure of the small benthic community. Biomass in mg C · m^2 from the top 1 cm of sediment. Meiofaunal biomass (abbreviations : NEM = Nematoda, HAR = Harpacticoid copepods, OTH = Other meiofauna), microbial biomass of sediment. Bacteria, Chlorophyll-a (mg Chl-a · m^{-2}), and microalgal biomass from Montagna, *et al.* (1989).

		Heterotrophy		Chemoautotrophy		Photoautotrophy	
Month	Station	Mean	STD	Mean	STD	Mean	STD
APR	A	2085	2275	4.13	3.10	2.93	5.53
APR	B	3847	2914	1.45	0.60	0.85	1.09
APR	C	964	1454	1.73	1.42	0.08	1.70
JUL	A	4718	3879	36.77	2.63	0.07	5.85
JUL	B	1776	2270	2.00	1.01	26.50	2.12
JUL	C	1449	2167	2.54	0.51	2.02	0.98
DEC	A	8620	5109	2.61	3.02	7.76	3.22
DEC	B	32794	9512	5.32	4.05	7.43	7.73
DEC	C	13241	5351	1.63	1.77	8.08	5.78

Table III. – Microbial productivity in the top 1 cm of sediment at the three stations for three months. Bacterial secondary production (µg C · m^{-2} · h^{-1}) measured by the FDC technique (Montagna *et al.*, 1989). Chemoautotrophic production (µg C · m^{-2} · h^{-1}) and microalgal production (µg C · m^{-2} · h^{-1}) was measured by uptake of bicarbonate (Bauer *et al.* 1988).

1 cm of sediment by the microscopical frequency of dividing cells (FDC) technique averaged 7.7 mg $C \cdot m^{-2} \cdot h^{-1}$, 5 orders of magnitude larger than the ^{3}HTdR technique. When oxygen uptake is converted to carbon consumption equivalents, assuming a respiratory quotient of 1.0 (Strickland and Parsons, 1972), calculated total benthic production was on average 42.6 mg $C \cdot m^{-2} \cdot h^{-1}$. Based on oxygen measurements, bacterial production estimates based on FDC seem much more reasonable than the estimates based on ^{3}HTdR uptake and are used for the present study. This is in contrast to Atlantic Ocean estimates, where ^{3}HTdR estimates agreed with oxygen uptake, and FDC was to high (Fallon *et al.*, 1983).

Bacterial production (as measured by the FDC technique) varied over one order of magnitude and increased throughout the study period (Table III). There were differences in bacterial production between months and stations. Production was higher in December (18.2 mg $C \cdot m^{-2} \cdot h^{-1}$) than in July (2.65 mg $C \cdot m^{-2} \cdot h^{-1}$) or April (2.30 mg $C \cdot m^{-2} \cdot h^{-1}$) which were the same (Tukey multiple comparison test).

By dividing the standing stock ($\mu g\ C \cdot m^{-2}$) by the production rate ($\mu g\ C \cdot m^{-2} \cdot h^{-1}$), we can calculate the turnover time (h). The turnover time for the FDC technique is 1.5 h. The FDC rates appear to be high. Other studies indicate that bacterial turnover times range from .75 to 21 days (Moriarty and Pollard, 1982; Riemann *et al.*, 1984).

Autotrophic production was calculated from bicarbonate uptake rates (Bauer *et al.*, 1988). Samples were incubated in the dark and under simulated in situ light conditions ($180\ \mu E \cdot m^{-2} \cdot s^{-1}$). It is assumed that dark uptake is by heterotrophic and chemosynthetic bacteria, and light mediated uptake is by photosynthetic microalgae.

Chemosynthetic production was generally around 3 $\mu g\ C \cdot m^{-2} \cdot h^{-1}$, except for one large value in July at station A (37 $\mu g\ C \cdot m^{-2} \cdot h^{-1}$) (Table III). Station A had the highest production rate. Chemoautotrophic production averaged 6.46 $\mu g\ C \cdot m^{-2} \cdot h^{-1}$ over all months and stations.

Primary production by benthic microalgae varied over three orders of magnitude during the study period (Table III). There were significant interactions between months and stations (2-way ANOVA, $P = 0.0001$). Production was highest at station A in April, but lowest at A in July. In December all three stations were the same. Production averaged 2.01$\mu g\ C \cdot m^{-2} \cdot h^{-1}$ over all months and stations.

Microalgal productivity in the seep, measured by the ^{14}C technique, is yielding rates about 3 orders of magnitude lower than those found in 20 other studies referred to by Colijn and de Jonge (1984). Microalgae can fix CO_2 in the dark, and this process is correlated with nitrogen limitation (Goldman and Dennett, 1986). Since the C:N ratio increases from stations C to B to A (Bauer *et al.*, 1988), the large amount of dark bicarbonate uptake at the seep may actually be due to microalgae and not to chemosynthetic bacteria. In fact, dark productivity averaged 3 times higher than light productivity. In either case, the grazing technique measures grazing on all autotrophs, i.e., anything that will take up CO_2. If the two are combined, then total autotrophic productivity is only about one order of magnitude lower than previous studies in similar sediments (Colijn and de Jonge, 1984).

To examine the impact of meiofauna on autotrophs, we combine autotrophic production as measured in light and dark incubations. The average standing stock of (1.01 g $C \cdot m^{-2}$) divided by the average productivity (8.47 $\mu g\ C \cdot m^{-2} \cdot h^{-1}$) suggests that the microalgal turnover time is 13.6 years. This is slow. At this rate the meiofauna would soon strip the sediment of all algae. Measurement of photosynthesis in the study area based on oxygen production suggest that the correct values are in the range of 36 mg $C \cdot m^{-2} \cdot h^{-1}$ (Montagna *et al.*, 1986). A summary of trophic interactions (Table IV) suggests seep meiofauna could be limited by autotrophic food sources, even though there is an obvious dependence upon heterotrophic food sources.

Component	Process	Station			Average
		A	B	C	
Heterotrophy	Production	5141	12806	5218	7722
	Grazing	51	63	9	41
Chemoautotrophy	Production	15	3	2	6
Photoautotrophy	Production	4	12	3	6
Total autotrophy	Production	19	15	5	12
	Grazing	6195	3707	1620	3841

Table IV. – Trophic interactions of the small benthic community. Meiofaunal grazing rates, heterotrophic production, and autotrophic production ($\mu g\ C \cdot m^{-2} \cdot h^{-1}$). Average at stations for the top 1 cm of sediment from April, July, and December 1986.

Meiofaunal grazing rates

There are two ways to assess the impact of meiofauna grazing on microbial populations, one is to look at the actual amount of carbon being removed, and the other is to compare meiofaunal grazing rates with microbial turnover times. Comparing the microbial biomass consumed to the amount of biomass available is intrinsically interesting. However, biomass consumed is a function of the amount of biomass available. Comparing the grazing rate to production rates may be more valid, since both measures are arrived at independently.

On average, the total meiofaunal grazing rate on bacteria is 0.00584 h^{-1}. This would require bacteria to have turnover times of 7.1 d to maintain their populations in equilibrium under this grazing pressure. If we use the bacterial turnover times suggested by the FDC technique and literature values (reviewed above), then it is certain that meiofauna will not run out of food. Bacterial production and turnover is more than sufficient to satisfy the demands of the meiofaunal population.

Meiofauna are on average removing microalgae at a rate of 0.00181 h^{-1} (i.e., about 0.2 % per h) suggesting that the algae must turnover every 23 days to maintain their populations under the grazing pressure. In contrast, turnover times for benthic algae fall around 16 hours (Colijn and de Jonge, 1984). Microalgal production estimates, based on oxygen production and consumption, indicate that meiofauna are not grazing so fast that they are limited by microalgal food.

Meiofauna consumed bacteria biomass at a rate of about 2 orders of magnitude less than bacterial carbon is being produced by heterotrophy and chemoautotrophy (Table IV). In contrast, Meiofauna consumed microalgal biomass at a rate that was about 2 orders of magnitute larger than the production rate of microalgal carbon (Table IV). Together, these results indicate that in the organically enriched hydrocarbon seep, there is more than enough bacterial production to maintain meiofaunal populations. However, meiofauna appear to have an insatiable appetite for microalgal carbon.

There are large seasonal differences. In previous seep studies it was noted that April, during the upwelling season, has the lowest bottom temperatures, July has the highest chlorophyll and meiofaunal densities, and December has the lowest chlorophyll and meiofaunal densities (Montagna *et al.*, 1987). Harpacticoids and nematodes had highest grazing rates on microalgae in July. This trend suggests that harpacticoids and perhaps nematodes switch food sources seasonally, selecting for microalgae during blooms in July, and preferring bacteria when microalgae are not abundant. In support of this hypothesis, harapacticoids and nematodes had their highest grazing rate on bacteria during April.

The interactions among meiofauna and the microbial community demonstrate the dichotomy of strategies that are used among organisms in the two different food webs. The heterotrophic food web relies on small, rapidly turning over populations of bacteria. These populations are enhanced at the seep. The autotrophic food web is based on large, slowly turning over populations of microalgae. Regardless, of the importance of heterotrophy at the seep, autotrophy is still an important energy source for meiobenthos in shallow benthic ecosystems where light is sufficient. Even though chemoautotrophy is not important in the top 1 cm of sediment (Table IV), it is probably very important in deeper layers of the sediment, where autotrophy is limited by light. The meiofauna community (about 4 mg C · m^{-2}, Table II) is supported by a flow of carbon from microalgae (about 4 mg C · m^{-2}, Table IV) and bacteria (about 0.04 mg C · m^{-2}, Table IV).

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