Potential impact on bacteria of grazing by a macrofaunal deposit-feeder, and the fate of bacterial production

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ABSTRACT: Bacterial biomass and production were compared to the carbon requirement and sediment processing capability of the deposit-feeding polychaete *Euzonus mucronata* (Treadwell) on a sand beach in Oregon, USA. Mean bacterial abundance ranged between sampling dates from 5.2 to 12.0 × 10^7 cells g^{-1} sediment and mean biomass ranged from 1.5 to 3.4 µg C g^{-1} sediment (0.36 to 0.84 g C m^{-2} to 15 cm depth). Daily bacterial production based on tritiated thymidine incorporation on 7 December 1982 is approximately 55 mg C m^{-2} d^{-1}. The carbon requirement of *E. mucronata*, equal to the sum of annual production and respiratory loss of carbon, was 7.0 to 8.0 g C m^{-2} yr^{-1} (19.3 to 21.9 mg C m^{-2} d^{-1}). Although bacterial production exceeded the carbon requirement of *E. mucronata*, the low bacterial density limits direct utilization of bacterial carbon to <10 % of the average daily carbon requirement of *E. mucronata*, despite its relatively high sediment-processing capability. Conversely, *E. mucronata* ingests <10 % of bacterial production per day. Because of their low density, sediment bacteria are probably not a major carbon source to other sand beach macrofauna. Bacterial turnover times (mean = 10 d) were similar to reported turnover times at much higher cell densities in other sediments, indicating that bacterial production exceeds macrofaunal production by one or more orders of magnitude in many environments. It is likely that macrofauna seldom consume more than a few percent of benthic bacterial production. Future studies of the fate of benthic bacterial production should examine the role of microbial and meiofaunal grazers.

INTRODUCTION

Some macrofauna efficiently remove and assimilate bacteria from sediment and detritus (Newell 1965, Hargrave 1970a, Hylleberg 1975), while at least some types of detritus may be very refractory (Newell 1965, Fenchel 1970, Fenchel & Blackburn 1979). This comparison led to the hypothesis that bacteria are the primary food resource of deposit-feeding macrofauna. The hypothesis has since been challenged by studies which showed that the amount of bacterial biomass actually ingested was not sufficient to supply the carbon requirements of deposit-feeding macrofaunal species (Baker & Bradnam 1976, Wetzel 1977, Cammen 1980a, Jensen & Siegismund 1980, Levinton & Bianchi 1981, Hammond 1983). It is now generally accepted that bacteria are not the principal food source of many,

if not all macrofaunal detritivores, and research on the food resources of deposit-feeders has tended to shift to microalgae, available detritus, and the utilization of relatively refractory detritus (Tenore et al. 1982, Levinton et al. 1984, Carman & Thistle 1985, Smith et al. 1985, Stuart et al. 1985, Kemp 1986).

Recent research on interactions between bacteria and benthic fauna continues to focus on defining the role of bacteria as a potential food resource (e.g. Findlay et al. 1984, Phillips 1984, Carman & Thistle 1985). Relatively little is yet known of the actual or potential effect of macrofaunal grazing on bacteria. Macrofaunal grazing at realistic levels can stimulate bacterial activity (Hargrave 1970b, Morrison & White 1980); bacterial densities may not be reduced by macrofaunal grazing (Levinton & Bianchi 1981) except at macrofaunal densities greatly in excess of natural densities (Hargrave 1970b, Moriarty et al. 1985). In the present study the carbon requirements and ingestion rate of the deposit-feeding polychaete *Euzonus mucronata*

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(Treadwell) are compared to bacterial biomass and production, in order to evaluate the potential impact of macrofaunal grazing on bacteria as well as the potential utilization of bacteria by *E. mucronata*. Methods for measuring bacterial production are relatively new and, with the exception of Moriarty et al. (1985), estimates of benthic bacterial production have not been compared to the potential utilization of bacteria by benthic macrofauna.

The specific goals of the present study were to: (1) determine whether bacterial biomass could be a significant food resource of *Euzonus mucronata*; (2) determine the fraction of bacterial production which could be grazed by *E. mucronata*; and (3) evaluate the role of macrofaunal grazing on bacteria based on this information.

METHODS

Site description. The study species, *Euzonus mucronata*, is very abundant in the upper intertidal of high-energy sand beaches of the northeastern Pacific, dominating macrofaunal biomass and numbers in the elevations at which it occurs. The study site was the upper intertidal of a sand beach 7 km south of Yaquina Bay, Oregon, USA (44° 33.8′ N, 124° 04.4′ W). The *E. mucronata* population at the site is located in a sharply delineated region between the lower and extreme high water levels, herein referred to as the *Euzonus* 'band'. Tides are semi-diurnal with a maximum daily amplitude of about 3 m. Sediment is well-sorted medium-fine sand (0.27 mm median grain size; Bosworth 1976) with 0.5 to 0.7 % organic matter (ash-free dry weight). Nearshore water temperatures are 9 to 15 °C (Gonor et al. 1970) and sand temperatures were generally 9 to 15 °C in the upper 15 cm. Freshwater seepage occurs near the upper elevation limit of *E. mucronata* and at low tide can lower interstitial salinities to 6 to 7 ‰, grading to 32 to 34 ‰ at the lower elevation limit of the *Euzonus* band.

Ingestion, production and respiration of *Euzonus mucronata*. The sediment ingestion rate of *E. mucronata* was measured using direct observations of feeding individuals. An observation aquarium was constructed from two 15 × 15 cm Plexiglas sheets separated by silicone tubing (3.5 mm spacing when compressed), and held together by spring clamps. The silicone tubing was perforated on the inner surface and could be connected to a vacuum aspirator. The aquarium was filled with freshly collected sand from the study site. A 2 to 3 mm layer of sand dyed with methylene blue was embedded 5 to 10 cm below the sediment surface. Groups of 5 adult worms were taken directly from freshly collected sand and placed on the

sediment surface, and usually burrowed directly or diagonally downward and encountered the dyed sand after 5 to 15 min. All individuals observed (>50) first burrowed entirely into the sediment, then began feeding while continuing to burrow. Three min after an individual was observed starting to ingest the blue-dyed sand layer, formalin (final concentration 2 % formaldehyde) was drawn through the sand. Worms were observed to stop feeding within 10 s and none were observed egesting sand in response to the formalin. The preserved worm was then cut into 2 mm sections and the gut contents of each section were examined. The total number of sections and the position along the body of the most posterior section containing blue-dyed sand were used to estimate the rate at which sediment passes through the gut. Feeding experiments were conducted at 12 °C, approximately the annual average temperature at the study site.

Because feeding may have been affected by the confined nature of the observation aquarium, feeding in the observation aquarium was compared to feeding in a larger container. Ten worms were placed in the observation aquarium and allowed to pass blue-dyed sand entirely through the gut, displacing an easily identified plug of dyed sand a few centimeters from the layer of dyed sand. The distance the blue-dyed sand was displaced from the dyed sand layer was measured. The same individuals were then placed in a larger container (10 × 10 × 20 cm) of freshly collected sand with an embedded layer of blue-dyed sand 10 cm below the sand surface. The average linear displacement of ingested dyed sand in the larger container was compared to the average linear displacement in the observation aquarium. This displacement is related to the body length of the worm, its burrowing rate, and the rate at which sand passes through the gut by the equation:

$$D = (B - LC^{-1})C \qquad (1)$$

where D = displacement (cm) of dyed sand (negative displacement is opposite to the direction of burrowing); B = burrowing rate while feeding (cm min⁻¹); L = body length (cm); and C = time (min) to pass sand through the gut. Thus, the displacement of dyed sand serves as an integrative measure of feeding and burrowing rate, and comparisons of sand displacement should be a reasonable means of assessing whether worms were feeding normally in the aquarium. As a second test of normal feeding, worms were placed in the larger container and allowed to burrow up and down for 12 h before carefully dissecting the sand to measure displacement of dyed sand above and below a dyed layer 10 cm below the sand surface.

The amount of sand retained in the gut was measured in 20 freshly collected individuals selected for a

at 11 °C to facilitate mixing. Eight 2 g portions of sand were removed from each core for isotope dilution experiments. In addition, two 5 g portions were removed from each core and fixed in 10 % formalin-seawater for bacterial enumeration and cell size measurements. One ml of 0.22 μm filtered seawater, containing 1 μCi of ^{3}H-Tdr (20 Ci mmole^{-1}) and varying amounts of unlabelled Tdr, was mixed into replicate portions, which were then incubated for 45 min at 11 °C. Uptake of ^{3}H-Tdr was linear at 11 °C for at least 60 min in preliminary experiments.

Incubation was terminated by the addition of 0.57 ml of 1.0 N NaOH, which was added to controls prior to the addition of isotope. Samples were then heated at 100 °C for 2 h. The solution was transferred to a centrifuge tube with two 1 ml rinses of hot 0.3 N NaOH and centrifuged at low rpm to remove fine sediment particles. The supernatant was transferred to a glass vial, acidified with 3.5 ml of concentrated ice-cold HCl, and kept on ice for 45 min. The precipitated DNA was collected on a 0.45 μm Millipore HA filter and rinsed with 5 ml of ice-cold 5 % TCA. Collected DNA was hydrolyzed in a 15 ml glass scintillation vial with 0.5 ml of 0.5 N HCl, which was heated to 100 °C for 15 min. The filter was then dissolved in 1 ml of ethyl acetate and the sample counted in 10 ml of Aquasol-2 scintillant (New England Nuclear). Counting efficiency determined by internal and external standards was 42 % and background in controls averaged 50 cpm (due in part to retention of unincorporated label on the filter).

The efficiency of extraction of DNA from sediment was measured by mixing a solution of DNA (0.5 mg Escherischia coli DNA [Sigma] in 1 ml of saline citrate solution) into 2 g of fresh sand and processing as described above. Samples of 0.3 ml were removed for assay as described by Burton (1956) from the final solution prior to collection of precipitated DNA on the filter, and from the post-collection filtrate. The absorbance at 600 nm was compared to the absorbance of DNA standards.

Bacteria were removed from the sediment by homogenization at 23 000 rpm in a Viltis 45 homogenizer and enumerated by the AODC method (Hobbie et al. 1977). Homogenization speed was similar to that used by Dale (1974), Meyer-Reil et al. (1978), and Montagna (1982). The optimum time of homogenization was determined by homogenizing replicate 5 g portions from a mixed core for 30 s, and 1, 2, 4, 10, and 15 min. The number of cells recovered was greatest after 10 min. At 15 min, fragmented detrital matter was difficult to distinguish from red-fluorescing bacteria. For this reason, 10 min was selected as the optimum time of homogenization, in agreement with Montagna (1982). As a measure of seasonal variation in numbers,

bacterial populations were also sampled and enumerated on 4 August 1982 and 7 April 1983.

Bacterial cells were photographed at 1260× using Kodachrome 400 slide film, which was later examined at 25× with a dissecting microscope. Cells were sorted into size categories and equivalent volumes were calculated as described by Rublee (1982). A conversion factor of 0.22 g C cm^{-3} biovolume was used to estimate bacterial carbon biomass (Bratbak & Dundas 1984).

The density of wet sand (18.5 % water) from the study site was 2.056 g ml^{-1}. This factor was used to convert bacterial biomass and production per gram of sand to the areal equivalents.

RESULTS

Euzonus mucronata ingestion rate

The mean gut clearance time of 19 adult individuals ranging from 2.6 to 7.2 mg AFDW (mean 5.05 mg AFDW) was 3.375 ± 0.342 min (mean ± 95 % confidence limits), and was not significantly correlated with body AFDW (r^2 = 0.05). The mean displacement of dyed sand by 10 individuals was − 2.40 ± 0.41 cm (in the opposite direction to burrowing) in the observation aquarium, and was not correlated to body AFDW. Mean displacement was − 2.91 ± 0.27 cm in the larger container, not significantly different from the displacement in the observation aquarium. In the 12 h trial, mean displacement was − 3.41 ± 0.26 cm (n = 55), significantly greater than in the observation aquarium. Greater negative displacement indicates shorter gut clearance times or slower burrowing rates than in the observation aquarium.

The mean weight of sand in the guts of 16 individuals ranging from 1.1 to 15.7 mg AFDW, as percent of total body weight, was 57.7 % (± 11.0 %) of total dry weight (including sand) and 1.83 (± 0.56) times the AFDW. There was no evident correlation between the dry or ash-free dry weights of individuals and the amount of sand in the gut expressed as a proportion of total body weight (r^2 = 0.06 for dry weight, 0.05 for AFDW). AFDW averaged 90.2 % (± 6.6 %) of the dry tissue weight, excluding sand; the proportion AFDW:dry weight varied slightly but significantly (t = 4.97, p < 0.001) with dry weight:

$$\text{AFDW (dry weight)}^{-1} = -0.0152 \text{ (dry weight, mg)} + 1.0134, \text{ (n = 16, } r^2 = 0.68). \qquad (2)$$

The predicted ingestion rate for a typical adult (ca 10 mg dry weight) is therefore about 2.5 g dry sand d^{-1} or 15 mg organic matter d^{-1}. This ingestion rate is an order of magnitude higher than for other deposit feeders of similar size (cf. Cammen 1980b, Fig. 2) and could

indicate a possible methodological error. For example, ingestion rates may be higher in short-term trials and when individuals are first placed in contact with sediment. However, observations of similar displacements of dyed sand in containers of different size and over short-term and 12 h test periods support the estimated ingestion rate. The ability of *Euzonus mucronata* to continue burrowing in drained sand when other macrofauna are immobilized (e.g. haustoriid amphipods, Kemp pers. obs.) may depend on removing sand from in front of the body by ingesting it and passing it rapidly through the gut.

Euzonus mucronata production and respiration

Expressed as production per m^2, total annual production was 2.21 g C m^{-2} yr^{-1}, and production by cohorts was 1.23 g C m^{-2} yr^{-1} for the 1980 cohort and 0.98 g C m^{-2} yr^{-1} for the pre-1980 cohort (Kemp 1985, unpubl.). Daily production averaged over the year was 6.05 mg C m^{-2} d^{-1}.

Temperature and salinity had a significant but comparatively small effect on weight-specific respiration (ANOVA; Table 1), and therefore were not considered in estimating annual respiration. Varying body weight resulted in an order of magnitude decrease in weight-specific respiration over the size range examined (Fig. 1). The regression equation of respiration (R, μl O_2 mg AFDW^{-1}h^{-1}) versus weight (W, mg AFDW) at 12°C, combining measurements at 3 salinities, was:

$$\log(R) = -0.8131 \log(W) - 0.0221 \ (n = 90, r^2 = 0.75). \quad (3)$$

Annual respiration was calculated using this regression and the number and estimated mean weight of individuals of each cohort in each sample. Total respiration (Table 2) was equivalent to the release of 88.63 g

C m^{-1} yr^{-1} or 4.84 g C m^{-2} yr^{-1} (13.27 mg C m^{-2} d^{-1}). The annual respiration by cohorts was 3.55 g C m^{-2} yr^{-1} for the pre-1980 cohort and 1.30 g C m^{-2} yr^{-1} for the 1980 cohort. The estimated annual carbon requirement of *Euzonus mucronata* in 1980–1981, equal to the sum of respiration and production, was 7.05 g C m^{-2} yr^{-1}. The mean carbon requirement per day over the course of the year was therefore 19.3 mg C m^{-2} d^{-1}.

The regression coefficient of −0.813 is unusually high relative to most other fauna (typical values near −0.25). It is possible that a systematic bias in the response of different sized individuals to test conditions may have resulted in an inaccurately high coefficient. Possible explanations are inadequate equilibra-
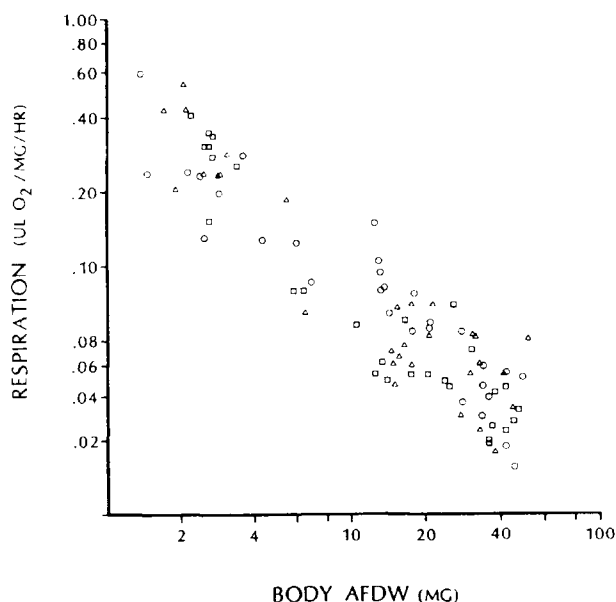

Fig. 1. *Euzonus mucronata*. Respiration (μl O_2 mg^{-1} body AFDW h^{-1}) versus body AFDW at 3 salinities. (□) 6.5‰ salinity; (△) 16‰; (○) 32‰

Table 1. *Euzonus mucronata*. Mean respiration (μl O_2 mg^{-1} AFDW h^{-1}) versus temperature and salinity, and ANOVA of data. Ten replicates per temperature-salinity combination

Salinity (‰)	9 °C	12 °C	15 °C	Mean
6.5	0.080 ± 0.019	0.083 ± 0.014	0.102 ± 0.030	0.088
16.0	0.082 ± 0.012	0.103 ± 0.020	0.081 ± 0.025	0.089
32.0	0.086 ± 0.017	0.165 ± 0.042	0.122 ± 0.028	0.124
Mean	0.083	0.117	0.102	0.101

Analysis of variance				
Factor	df	MS	F	p
Temperature	2	0.0112	8.24	0.001
Salinity	2	0.0115	8.46	0.001
T × S	4	0.0036	2.65	0.05
Error	81	0.00136		

Table 2. *Euzonus mucronata*. Annual respiration estimates. N m^{-1}: mean number of individuals per meter; L: mean length (cm); AFDW: mean ash-free dry weight (mg) per individual; R: respiration (μl mg^{-1} AFDW h^{-1}); R(int): total respiration (μl × 10^6) during interval between sampling; C: carbon respired per interval (g C m^{-1}); C': carbon respired based on respiration regression coefficient of Dangott & Terwilliger (1986)

Date sampled	N m^{-1}	L	AFDW	R	R(int)	C	C'
1980 cohort							
15 Jun–19 Jul 1980	21 863	0.431	0.009	45.54	6.37	3.07	0.48
19 Jul–2 Sep 1980	29 498	0.802	0.054	10.25	17.63	8.50	2.70
2 Sep–17 Sep 1980	24 561	1.081	0.130	5.00	5.74	2.77	1.24
17 Sep–23 Oct 1980	18 489	1.462	0.317	2.42	12.25	5.09	3.24
23 Oct–28 Dec 1980	15 819	1.855	0.639	1.37	21.90	10.56	8.86
28 Dec–5 Mar 1981	18 791	1.851	0.636	1.37	26.36	12.72	10.65
5 Mar–11 May 1981	18 132	1.974	0.769	1.18	27.16	13.09	11.81
11 May–22 Jun 1981	16 651	2.581	1.697	0.62	17.19	8.29	10.20
				Total =	134.6	64.89	49.18
Pre-1980 cohort							
15 Jan–19 Jul 1980	3273	3.837	5.472	0.24	3.18	1.53	2.98
19 Jul–2 Sep 1980	2286	4.009	6.228	0.22	3.38	1.63	3.35
2 Sep–17 Sep 1980	3493	3.832	5.448	0.24	1.64	0.79	1.54
17 Sep–23 Oct 1980	3676	3.856	5.552	0.24	4.16	2.00	3.92
23 Oct–28 Dec 1980	3365	4.662	9.727	0.15	7.75	3.73	9.12
28 Dec 1980–5 Mar 1981	3904	4.790	10.540	0.14	9.27	4.47	11.28
5 Mar–11 May 1981	4928	4.628	9.516	0.15	11.82	5.70	13.82
11 May–22 Jun 1981	5358	5.101	12.690	0.12	8.06	3.88	10.53
				Total =	49.26	23.74	56.54

tion time for larger individuals, or a behavioral response of larger individuals to the small respirometer flasks. Dangott & Terwilliger (1986) report a regression coefficient of −0.42 for an Oregon (USA) population of *Euzonus mucronata*, using starved adults in seawater without sand. Respiration (as equivalent C release) was also calculated using this value (Table 2), yielding annual respiration estimates of 2.69 and 3.09 g C m^{-2} yr^{-1} for the 1980 and pre-1980 cohorts, respectively, totalling 5.78 g C m^{-2} yr^{-1}. The annual carbon requirement using their regression coefficient is increased slightly to 7.99 g C m^{-2} yr^{-1} or 21.9 mg C m^{-2} d^{-1}.

Bacterial biomass and production

On 7 December 1982 mean bacterial cell volume was 0.128 μm^3; no substantial variation in cell size with tidal elevation was observed. A conversion factor of 2.816 × 10^{-4} g C cell^{-1} (cell volume × 0.22 g C cm^{-3}) was used to convert all cell counts to carbon biomass. Including samples taken on 4 August 1982 and 7 April 1983 (Table 3), the average value of mean cell densities was 7.75 × 10^7 cells g^{-1}, and the equivalent mean biomass was 2.18 μg C g^{-1} sand or 0.55 g C m^{-2} to 15 cm depth.

The incorporation of isotope in uptake experiments was corrected for a 39.6 % recovery efficiency estimated from the recovery of added *Escherischia coli* DNA. Of the 60.4 % of DNA not recovered on the filter, 10.5 % of added DNA was not recovered from the sand and 44.3 % of the remaining added DNA passed through the filter.

Production was corrected for isotope dilution in each sample (Fig. 2) by the method of Moriarty & Pollard (1981). At 11 °C, daily carbon production was 7.53 to 16.48 % of the standing bacterial biomass, resulting in estimated turnover times ranging from 6.1 to 13.3 d with a mean turnover time of 10 d (Table 4).

DISCUSSION

Bacterial production

Bacterial turnover time on 7 December 1982 averaged 10 d at ambient temperature (11 °C). This is of the same order of magnitude as turnover times reported for sediment bacteria in varied sediment types at temperatures ranging from 17 to 29 °C (Table 5), despite the much lower densities of bacterial populations measured in this low-organic beach sand. The limited information available indicates that benthic bacterial turnover rates vary seasonally by much less than an order of magnitude (Moriarty & Pollard 1981). Based on

the 7 December turnover time and mean cell volume, and on the mean bacterial abundance on 3 sample dates, daily carbon production on this beach was 0.22 μg C g^{-1} sand d^{-1} or 55 mg C m^{-2} d^{-1}.

Utilization of bacteria by *Euzonus mucronata*

The average daily carbon requirement of *Euzonus mucronata* (19.3 or 21.9 mg C m^{-2} d^{-1}, depending on the method of calculating respiration) was about 35 to 40 % of the estimated bacterial production. The carbon requirement estimate does not include mucus secretion or excretory losses and should be considered a minimum estimate. If assimilation efficiency is about 50 %, the study population of *E. mucronata* could derive its daily carbon requirements from bacteria by ingesting most of the bacterial production.

The amount of bacterial production ingested daily was estimated from measured gut clearance time and sand content. Because clearance rate and gut content (as percent of body weight) were not correlated with body weight, total ingestion may be estimated from the mean biomass of *Euzonus mucronata*. Based on continuous feeding throughout the year and an annual mean biomass of 2.5 g AFDW m^{-2} (Kemp 1985, unpubl.), the average ingestion of sand by the 1980–81 population would be 1.95 kg dry sand m^{-2} d^{-1}, equiva-

Table 3. Mean abundance and equivalent biomass of bacteria on 4 Aug 1982, 7 Dec 1982, and 7 Apr 1983

Sampling date	Cells $g^{-1} \times 10^7$	μg C g^{-1} [*]	g C m^{-2}
4 Aug 1982	12.03	3.39	0.84
7 Dec 1982	6.07	1.71	0.42
7 Apr 1983	5.17	1.46	0.36

[*] Assuming cell volume = 0.128 μm³

Table 4. Bacterial production and biomass data for 7 Dec 1982. Cell abundance and production expressed per g dry sand

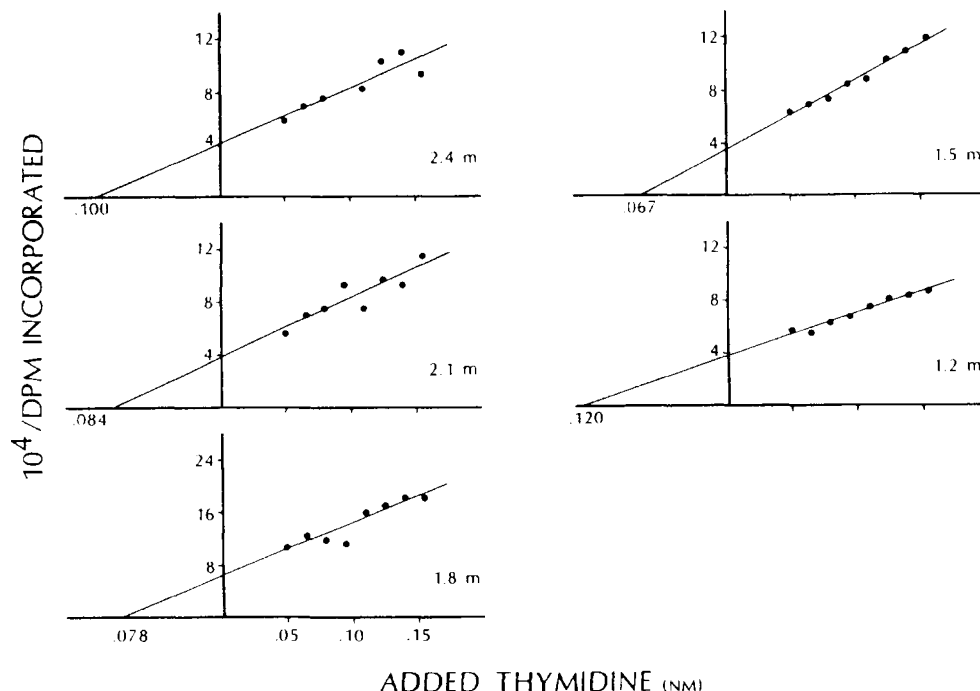| Elevation (m)	Cells $g^{-1} \times 10^7$	μg C g^{-1}	Cells $h^{-1}g^{-1} \times 10^5$	Turnover time (d)
+2.4	4.29	1.21	2.95	6.07
+2.1[*]	6.78	1.91	2.71	10.43
+1.8[*]	4.38	1.23	1.53	11.93
+1.5	7.43	2.09	2.33	13.29
+1.2	7.47	2.10	3.84	8.10
			Mean =	9.96
			SD =	2.91

[*] Upper and lower *Euzonus* band

Fig. 2. Measurement of bacterial production in sediment. Isotope dilution plots of thymidine incorporation versus amount of added thymidine. X-intercept indicates equivalent thymidine diluting added thymidine

nearshore sandy sediments. It is unlikely that macrofaunal deposit-feeders would remove more than a few percent of bacterial production in most sediments, as was shown here for *E. mucronata*, although abundant surface-feeding macrofauna could remove a substantial fraction of bacterial production in a restricted surface layer. For example, Moriarty et al. (1985) calculated that a surface-feeding holothurian could remove as much as 10 to 40 % surface (to 0.5 cm) bacterial production per day in summer on coral reef sand flats. In most sediments, the fate of the majority of benthic bacterial production is unknown.

In pelagic systems bacterial production may be largely consumed by microflagellates (Ducklow 1983) which reproduce rapidly (Sherr & Sherr 1983) and are capable of responding to fluctuations in bacterial numbers. These microflagellate grazers are preyed upon by zooplankton, thus providing an indirect route of transfer of bacterial production to macrozooplankton. An analogous microbial food chain of bacteria, protozoan grazers, and possibly meiofaunal or macrofaunal predators may exist in sediment and account for the remainder of bacterial production. Although very little quantitative data exist on the grazing of benthic Protozoa on bacteria, Fenchel (1975) calculated for a tundra pond that Protozoa grazed approximately 8 % of the standing stock of benthic bacteria each day. Maintaining bacterial numbers would require a bacterial turnover time of 12 d or less, which is comparable to turnover times reported in recent literature. Though these estimates are suggestive of the potential significance of Protozoa as regulators of bacterial production, the importance and trophic position of Protozoa in ɔenthic food chains remains unknown.

Meiofaunal grazing directly on bacteria may remove a substantial part of bacterial production. Montagna (1984) determined that meiofauna of a *Spartina alterniflora* saltmarsh removed 3 % of the sediment bacteria per hour, thus requiring a bacterial turnover time of 30 h to maintain the bacterial population in equiⁱⁱbrium with meiofaunal grazing. Some higher ᵉtimates of bacterial production would suggest that bacterial turnover is rapid enough to outpace this intensity of meiofaunal grazing (Montagna 1984). However, most estimates indicate bacterial turnover times substantially longer than 30 h (Table 5), indicating that meiofaunal grazing may sometimes control bacterial numbers. Alongi (1985), in contrast, found ⁱʰᵃt bacterial numbers and growth rate were little ᵃⁱⁱected by the presence of meiofauna under the conditions of high organic inputs in laboratory microcosms. The role of meiofauna as bacterial grazers is likely to be complex and variable between environments.

In some environments, part of bacterial production would ultimately be available to macrofauna through predation on meiofauna or Protozoa. Although macrofaunal and meiofaunal food chains on intertidal sand beaches may operate independently (McLachlan 1983), predation by epibenthic invertebrate and fish predators on meiofauna (Coull & Palmer 1984) is important and may represent a major trophic link in sand and mud sediments.

Some of these transfer routes have been incorporated in conceptual models (e.g. Tenore & Rice 1980) but remain unquantified. Given that bacterial production greatly exceeds macrofaunal production in most sediments and most of bacterial production is not directly consumed by macrofauna, future studies of the basis of benthic secondary production should place more emphasis on microbial and meiofaunal food chains and their linking to macrofaunal food chains.

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