J. Exp. Mar. Biol. Ecol., 1984, Vol. 76, pp. 177–190
Elsevier

JEM 240

COMPETITION FOR DISSOLVED GLUCOSE BETWEEN MEIOBENTHOS AND SEDIMENT MICROBES[1]

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Abstract: Meiobenthos, small invertebrates inhabiting the surface layers of marine sediments, can absorb dissolved organic matter (DOM). Experiments were performed to test if meiobenthos can compete with sediment microbes for uptake of small amounts of [^{14}C]glucose. Meiofaunal glucose uptake rates were measured by themselves and in the presence of sediment microbes. Glucose uptake by meiofauna was not inhibited by the presence of bacteria, nor did it appear that bacterial uptake was inhibited by meiofauna. Thus, there was no direct or interference competition. Uptake rates by 1 cm^3 of sediment (bacteria) were four orders of magnitude greater than those of individual meiofauna, but on a biomass specific basis, meiofaunal uptake was in the same range if not higher than that of sediment bacteria. Thus, the potential for indirect or resource competition exists. Since bacterial biomass dominated the system studied, uptake of glucose was dominated by bacteria. The results support the hypothesis that in natural sediments, where the biomass of bacteria is higher than that of meiofauna, heterotrophic uptake is primarily a microbial process. However, resource competition between meiofauna and bacteria for DOM in sediments probably exists where bacterial biomass is low relative to meiofaunal biomass.

INTRODUCTION

The uptake of dissolved organic matter (DOM) by marine organisms is an important process at many trophic levels (Sepers, 1977). Glucose concentrations range from 10^{-9} to 10^{-6} in the water column and 10^{-7} to 10^{-5} in sediments (Southward & Southward, 1972; Hanson & Snyder, 1980; Gocke *et al.*, 1981). Bacteria possess a low transport constant (the substrate concentration at which uptake of DOM proceeds at half the maximal rate), in the range of 10^{-8} to 10^{-7} M, compared to invertebrates which range from 10^{-6} to 10^{-5} M, or algae ranging from 10^{-5} to 10^{-4} M (Sepers, 1977). Glucose concentrations are so low in the water column that it is probably only available to bacteria. But it is in the range available to invertebrates in sediments. The smallest metazoans associated with marine sediment bacteria are meiobenthos. Many marine macrobenthos are known to absorb DOM (Stephens, 1972, 1982; Stewart, 1979). But meiofauna, with a larger surface to volume ratio, should benefit most from DOM. Of the meiofaunal taxa, oligochaetes, turbellarians, nematodes and polychaetes can absorb glucose (Chia & Warwick, 1969; Ahearn & Gomme, 1975; Lopez *et al.*, 1979; Meyer-

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Reil & Faubel, 1980). Although crustaceans are not thought to absorb glucose (Stewart, 1979), calanoid copepods, a taxon closely related to the harpacticoids among the meiofauna, are reported to absorb glucose (Chapman, 1981). Although there is debate as to the role of DOM in invertebrate nutrition, many reviewers agree that epidermal carrier-transport mechanisms exist and that there is sufficient DOM in the sediments to account for a majority of the energy requirements of benthic invertebrates (Stephens, 1972; Jørgensen, 1976; Stewart, 1979; Southward & Southward, 1982).

When more than one group of organisms utilize a resource in the same habitat, such as DOM, competition takes place. Some studies show that microbial uptake of DOM in the water column (Wright & Hobbie, 1966; Crawford *et al.*, 1974) and in sediments (Munro & Brock, 1968) is predominantly by bacteria and can effectively inhibit heterotrophy by algae. These results suggest that at low in situ levels utilization of DOM by invertebrates is also inhibited by bacteria (Sepers, 1977), i.e., animals cannot compete with bacteria for the low levels of available DOM (Siebers, 1982). However, *Mytilus edulis* larvae can compete with bacteria for DOM (Manahan & Crisp, 1982), and microalgae can also compete with bacteria (Wheeler *et al.*, 1977; Saks & Kahan, 1979). Thus, competition between trophic levels for DOM does exist. Two types of microbial competition occur (Fredrickson & Stephanopoulos, 1981). Indirect, exploitation or resource competition occur when a common resource is reduced and consequently, net growth rates of populations are reduced. Direct or interference competition occurs when toxic or inhibitory substances are released which affect microbial populations. It is not likely that microbes and meiofauna secrete substances toxic to one another; so, resource competition is most likely since DOM is available to both in the benthos.

The object of this study was to determine if competition occurs for dissolved glucose between meiofauna and sediment microbes. Glucose uptake was measured for the total benthic community and for meiofauna separately. Uptake by the sediment microbes (heterotrophic bacteria and microalgae) was estimated by the difference between total uptake and meiofaunal uptake. Direct and indirect competition was distinguished by measuring uptake in two incubations; one with meiofauna alone, and one with meiofauna and sediment (microbes) present.

Materials and Methods

The meiobenthos used in this study were extracted from muddy salt marsh sediments at the Belle W. Baruch Institute's field laboratory near Georgetown, South Carolina, U.S.A. (33°20.0′N;79°10.0′W). Meiofauna of muddy sediments live in the top centimeter, where oxygen is plentiful (Coull & Bell, 1979). Meiofauna can be infected with microbial ectocommensals (Herman *et al.*, 1971; Tietjen, 1971). Animals with obvious microbial contamination were not used. All animals used in the experiments were hand sorted from the sediment and rinsed three times in filter-sterilized (0.2 μm) artificial sea water (Instant Ocean). Some bacteria may be associated with meiofaunal guts or

epidermis. Uptake by these associated bacteria are included as meiofaunal mediated uptake.

Uptake by the aerobic benthic community was measured as the uptake of 1 cm^3 of sediment, collected to a depth of 0.7 cm. The uptake due to microbes alone was estimated by subtracting appropriate values for meiofauna (as defined above) and sediment adsorption (uptake by formalin-poisoned samples).

Glucose uptake was measured for meiofauna and sediment microbes in two treatments (Fig. 1). One treatment had sediment and meiofauna separately. I refer to this

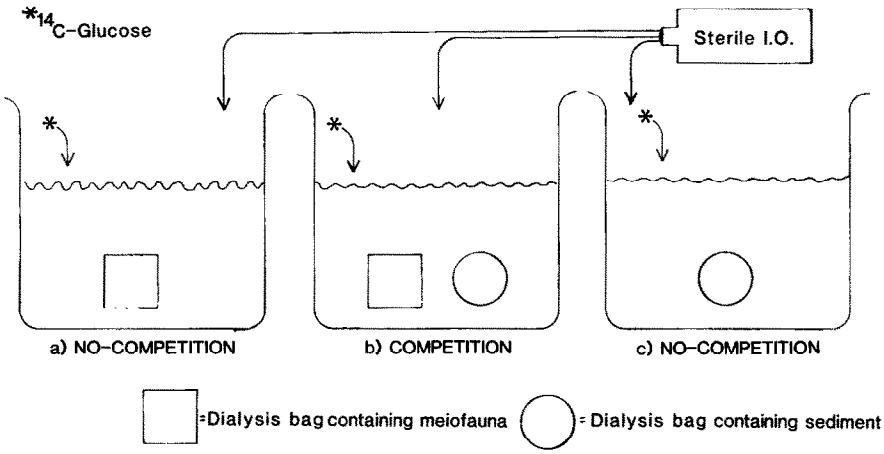

Fig. 1. Schematic of experimental design used in determining the ability of meiobenthos to compete with bacteria for glucose: two treatments were present: meiofauna and bacteria alone (a and c) i.e., no competition, and meiofauna and bacteria together (b) i.e., competition; two dialysis bags each of meiobenthos and bacteria were used in each run of the experiment; the experiment was run at three concentrations; label was added to the external media and allowed to diffuse into the dialysis bags.

as the no-competition treatment; i.e., no direct or interference competition. The second treatment put sediment and meiofauna in the same incubation. I refer to this as the competition treatment. If glucose uptake by meiofauna or sediment microbes is the same in the two treatments, no direct competition occurs. A comparison of the uptake velocities between the microbial community and meiofauna represents a measure of indirect competition.

To measure meiofaunal glucose accumulation, an easy method for separating meiofauna and bacteria was required. This was accomplished by sieving and sorting meiobenthos and placing them in dialysis bags. They could easily be incubated with and without sediment (microbes). Three incubations (in three beakers) were used in an experiment (Fig. 1): (a) meiofauna alone, no competition with bacteria for glucose; (b) meiofauna and sediment together, competition for glucose; and (c) sediment alone, no microbial competition with meiofauna. Since some meiofauna were included in the sediment plugs, the competition incubation (b) really represents a double ration of

meiofauna (compared to the sediment incubation (c)). The dialysis bags were permeable to glucose which could diffuse into any bag for use by either meiobenthos or sediment microbes. In all cases, the sediment microbes were in separate bags from meiobenthos; thus, when the dialysis bags, each containing sediment microbes or extracted meiofauna, were incubated together, competition for the substrate existed (Fig. 1).

Each replicate dialysis bag of meiobenthos contained the following assemblage (mean ± SE): copepods (59 ± 5), nematodes (105 ± 19), ostracods (19 ± 5) and polychaetes (15 ± 5). These numbers roughly correspond to that found in 1 cm^3 of saltmarsh sediment. One-cm^3 plugs of saltmarsh sediment were also placed in separate dialysis bags. These plugs of sediment were unprocessed, i.e., they were not sieved or otherwise dispersed. When appropriate values are subtracted for meiofauna and sediment adsorption, uptake by microbes remains. Two dialysis bags of either meiofauna or sediment were used in each beaker.

Glucose, D-[^{14}C(U)] (spec. act. = 329 mCi · $mmol^{-1}$) was obtained from New England Nuclear and diluted in filter sterilized Instant Ocean (SIO) for use as the limiting resource in the experiments. Labeled glucose was added to the beakers containing the dialysis bags and the volume brought up to 100 ml with SIO (Fig. 1). Experiments were performed at three different final concentrations of labeled glucose; 2.0, 4.0, and 15.0 $\mu g \cdot l^{-1}$ (corresponding to 1.1, 2.2, and 8.3 10^{-8} M). All experiments were incubated 4 h at 20 °C. The beakers were not stirred or agitated to promote diffusion of the label into the dialysis bags, because this disturbance would have adversely affected meiofaunal metabolism and behavior (Vernberg *et al.*, 1977) and dispersed sediment would have had higher uptake rates (Hall *et al.*, 1972).

Diffusion of glucose into the dialysis bags was checked during the first experiment (2.0 $\mu g \cdot l^{-1}$). Parallel, formalin-poisoned, competition experiments (where meiofauna and sediment were incubated together) were carried out as controls. In both the live and dead competition experiments, 20-μl subsamples were taken from the beakers and from inside the dialysis bags to check if diffusion of labeled glucose was the same in all beakers and all bags.

After an incubation period, the sediment samples were immediately filtered and washed to remove unincorporated label. Meiofaunal uptake was stopped by adding full strength formalin to the beakers. The meiofauna were rinsed, sieved, and sorted by taxa into separate scintillation vials. Both sediment microbes and fauna were solubilized with 1 ml of Packard Soluene 100. Radioactivity was counted in a Packard Liquid Scintillation Counter, using Packard Insta-gel as a cocktail, for 60 min or until 10^6 counts were reached. For the sediment samples a quench curve was constructed by adding [^{14}C]toluene to a dilution series of estuarine sediments. For meiofauna, a second quench curve was constructed using water. Counting efficiency for each sample was determined from external standard channel ratios.

Random samples were taken to assess the abundance of bacteria and meiofauna in the sediments at the time of the experiments. After the uptake of glucose by individual meiofauna was measured, the uptake attributed to meiofauna in 1 cm^3 of sediment could

be calculated. This number was used to estimate glucose accumulation in sediment due to meiofauna.

Meiofaunal biomass was determined from parallel background samples. The meiofauna was dried for 24 h at 55 °C, then carbon and nitrogen concentrations were determined using a Hewlett-Packard 185 CHN analyzer. Bacterial biomass, from background samples, was calculated by determining the cell biovolume and abundance using acridine epifluorescence microscopy (Daley & Hobbie, 1975; modified as described in Montagna, 1982) and then converting biovolume to biomass using the factors in Luria (1960).

Since it was necessary to conduct the experiments with different concentrations on different days, days and concentration were confounded. The data were analyzed using analysis of covariance (ANCOVA) procedures. The covariable is substrate concentration (S), and the treatment effect of interest is glucose uptake with and without direct competition. The analysis was performed in two steps; first, the treatment regressions were tested for parallel slopes; second, if the treatment slopes were parallel, the regression lines were tested for differences in elevation; i.e., which line had the higher or greater least square mean (LSM). Least square means are reported, because they are the sample means adjusted for the slope of the uptake line. All statistical analysis was performed using SAS software (Helwig & Council, 1979).

RESULTS

The benthic community did not change appreciably throughout the course of the study (Table I). Although nematodes increased during the third experiment, nematode biomass did not (unpubl. data).

An assumption in this study was that diffusion of the labeled glucose was similar in all three beakers (Fig. 1). It appears as if more label was sequestered in the live-sediment bag than in either live meiofauna or both dead bags (Table IIa). But the diffusion process was the same in all three beakers ($P = 0.4658$), and in all bags ($P = 0.1204$) (Table IIb). Approximately 10–15% of the initial label concentration disappeared during the course of the experiment.

TABLE I

Description of the benthic community at the study site during the three experimental periods.

Date	Concentration tested ($\mu g \cdot l^{-1}$)	$\bar{X}$ cm^{-3} ($\pm$ SE)				
		Nematodes	Copepods	Ostracods	Polychaetes	Bacteria ($\times 10^{11}$ cells)
23 July 1981	2	30.5 (5.0)	6.2 (1.0)	2.3 (0.3	1.1 (0.1)	1.1 (0.4)
8 Oct. 1981	15	47.3 (8.9)	3.9 (0.7)	1.9 (0.3)	6.3 (1.0)	2.7 (0.9)
19 Febr. 1982	4	112.1 (3.8)	2.7 (0.2)	2.6 (0.4)	5.3 (0.5)	1.5 (0.6)

Meiofaunal community uptake velocities of glucose are illustrated in Fig. 2. The data were examined by a two-way ANCOVA: the covariable was substrate concentration, and the two main effects were taxa (copepods, ostracods, nematodes and polychaetes) and treatment (competition for substrate and alone). The slopes were parallel ($P = 0.5203$) and there were differences in the adjusted means among the taxa

TABLE II

Label concentrations (DPM · ml^{-1}) inside dialysis bags from one competition experiment where parallel formaldehyde killed controls were also incubated: each of the treatments were contained in one beaker (Fig. 1); A, raw data; B, ANOVA table; parentheses indicate bags are nested within beakers.

A	Treatment beakers	
Dialysis bags	Live (12,110)[a]	Dead (14,172)[a]
Meiofauna	5,993 7,075	6,585 5,921
Sediment	8,626 12,968	7,543 6,816

[a] Label concentration in treatment beakers (outside bags) at end of experiment.

B Source	d.f.	MS	F	P
Beakers	1	7,599,151	0.80	0.4658
Bags (beakers)	2	9,512,786	3.63	0.1264
Error	4	2,624,139		

TABLE III

Two-way ANOVA for meiofaunal uptake of glucose: the covariable is S (the substrate concentration) and the independent effects were taxa and treatment; prior analysis demonstrated that slopes for all lines (eight taxa and treatment combinations) were parallel ($P = 0.5203$); the least-square means ($\pm$ SE of the LSM) for the level effects were: no competition = 21.49 (5.29), competition = 10.08 (4.64); and copepods = 12.13 (7.46) and polychaetes = 41.27 (7.02) 10^{-6} μg glucose · l^{-1} · individual^{-1} · h^{-1}.

Source	d.f.	MS	F	P
Taxa	3	2789	6.31	0.0018
Treatment	1	1147	2.60	0.1171
S	1	6	0.01	0.9073
Error	3	442		

($P = 0.0018$) (Table III). Although uptake for the no-competition treatment (21.5 $\pm$ 5.3 μg glucose · l^{-1} · cm^3 sediment^{-1} · h^{-1}) was greater than that for the competition treatment (10.1 $\pm$ 4.6), the difference was not significant ($P = 0.1171$).

Glucose accumulation by sediment microbes was calculated by correcting total sediment uptake for meiofauna accumulation and sediment adsorption (Table IV).

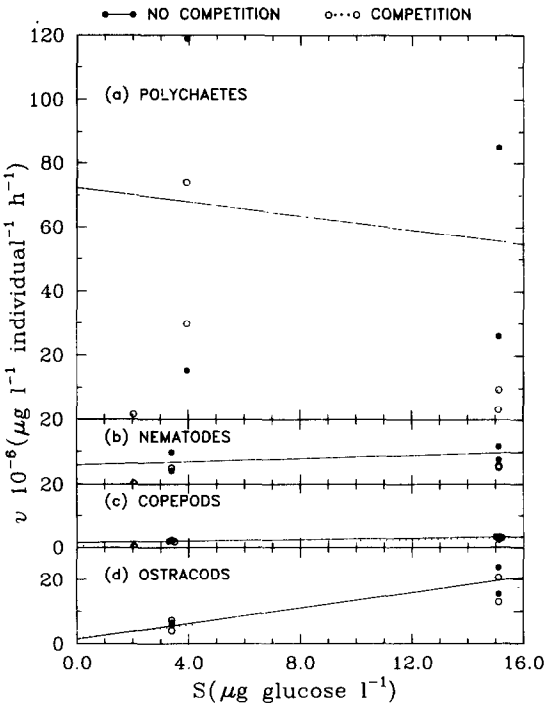

Fig. 2. Uptake velocity of meiobenthos taxa vs. glucose concentration: the velocity (v) axis is on the same scale in subfigures a–d; the two treatments are meiobenthos alone and in competition with bacteria for glucose.

TABLE IV

Estimation of microbial community accumulation of labeled glucose.

		DPM · ml^{-1} sediment			
		A	B	C	D[a]
S (μg · l^{-1})	Treatment	Live sediment	Poisoned sediment	Meiofauna predicted	Microbial community
2	Competition	1471	612	27	832
		2058	612	27	1419
	No competition	–	–	–	–
4	Competition	6432	1003	1599	3830
		8930	1003	1599	6329
	No competition	20730	1003	1889	17838
		12113	1003	1889	9221
15	Competition	44457	3315	685	40457
		69834	3315	685	65834
	No competition	66599	3315	1521	64805
		55699	3315	1521	53905

[a] D = A – B – C.

Uptake velocity (v) of glucose by sediment bacteria (Fig. 3) was calculated as described by Wright & Hobbie (1966). Bacterial glucose uptake was not affected by presence of meiobenthos (P = 0.2366, Table V). Since the incubation period was long (4 h) and respiration correction was not made, recycling of label undoubtedly occurred and the uptake measured was not total uptake, but a measure more close to assimilation (Hobbie & Crawford, 1969). The uptake velocity of individual meiofauna was four orders of magnitude slower than that of 1 cm^3 of sediment (compare Fig. 2 and 3).

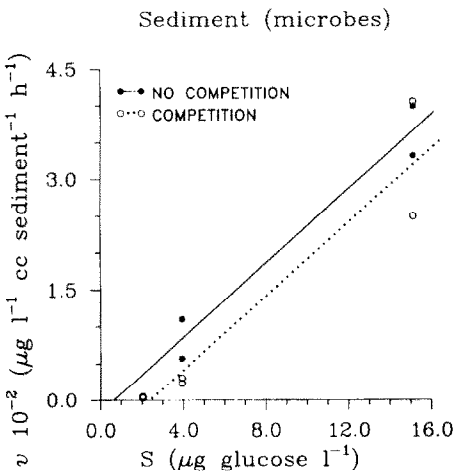

Fig. 3. Uptake velocity of sediment bacteria vs. glucose concentration: the two treatments are bacteria alone and bacteria in competition with meiobenthos for glucose.

TABLE V

ANCOVA for bacterial glucose uptake: covariable is S, the substrate concentration, and treatment is bacterial uptake in competition and no-competition with meiofauna for glucose; prior analysis demonstrated the two treatments had parallel slopes (P = 0.9712); the least-square means (± SE of the LSM) for the competition and no-competition treatments were 1.45 (0.20) and 1.87 (0.25) 10^{-2} μg glucose · l^{-1} · ml sediment^{-1} · h^{-1}, respectively.

Source	d.f.	MS	F	P
Treatment	1	0.37	1.68	0.2366
S	1	20.89	88.34	0.0001
Error	7			

The mean biomass (μg C · individual^{-1}) (± SD) of the meiofaunal taxa used in the experiments was: nematodes 0.128 (± 0.03), copepods 0.170 (± 0.29), ostracods 0.721 (± 0.471), and polychaetes 5.81 (± 1.54). Biomass in the experiments was estimated by multiplying the mean biomass per individual by the number of meiofaunal organisms placed in the dialysis bag. The biomass present in a typical dialysis bag was (in μg C):

copepods = 10.0, nematodes = 13.5, ostracods = 13.7, polychaetes = 87.0, and bacteria = 3184. This roughly corresponds to the biomass present in 1 cm^3 of sediment. When biomass specific uptake (μg glucose $\cdot l^{-1} \cdot \mu g\, C^{-1} \cdot h^{-1}$) was plotted for the competition treatments only (Fig. 4), uptake rates by meiofaunal groups were in the

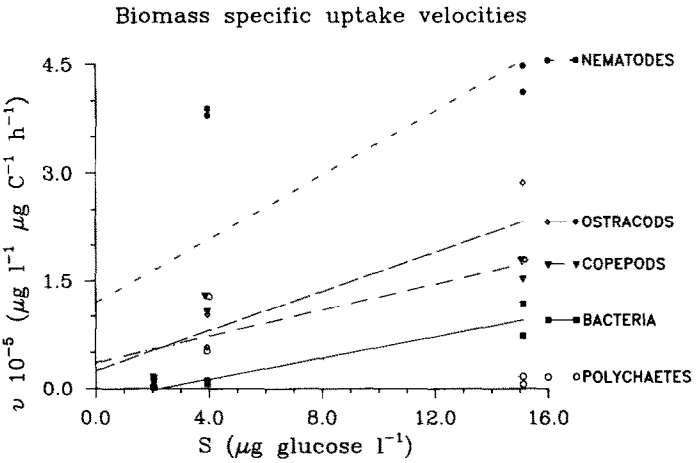

Fig. 4. Uptake velocity adjusted by biomass present (μg carbon) in experiments.

TABLE VI

Biomass specific glucose uptake by the benthic community in the competition experiments (Fig. 1b): A, ANCOVA table for data in Fig. 4; prior analysis demonstrated that the uptake lines for the different benthic groups were parallel (P = 0.1398); B, Tukey–Kramer multiple comparison test on least-square means (Kirk, 1982; p. 119), units are 10^{-5} μg glucose $\cdot l^{-1} \cdot \mu g\, C^{-1} \cdot h^{-1}$; groups connected by a line are not significantly different at the 0.05 level.

A

Source	d.f.	MS	F	P
Groups	4	5.75	6.04	0.0021
S	1	8.76	9.20	0.0063
Error	21	0.95		

B

Nematodes	Ostracods	Copepods	Bacteria	Polychaetes
(2.82)	(1.37)	(1.05)	(0.41)	(0.36)

range of that of bacteria (Table VI). A unit weight of meiofaunal biomass takes up glucose as fast as a unit weight of bacteria. When these weight specific uptake rates are adjusted for the average biomass found m^{-2} of saltmarsh soil, it is demonstrated that microbes are responsible for most of the benthic glucose uptake (Fig. 5).

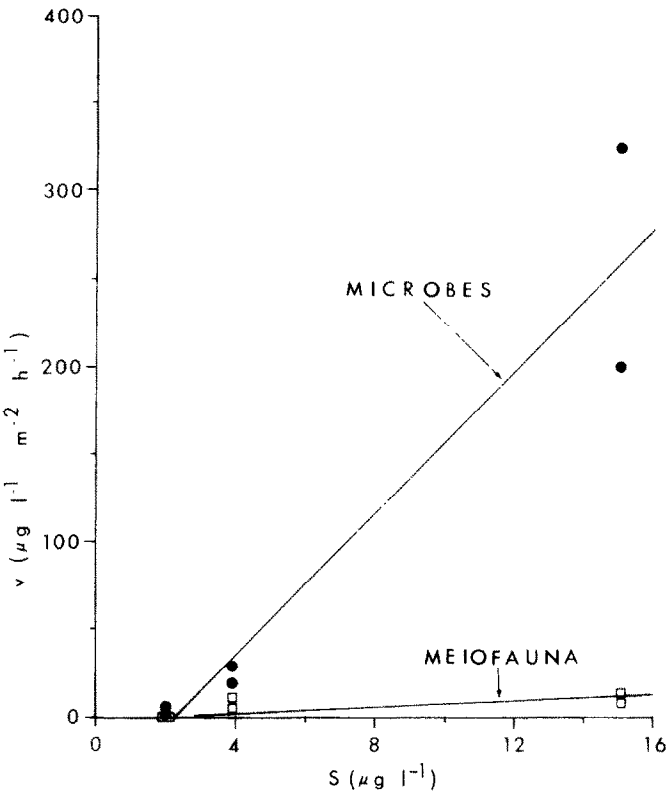

Fig. 5. Predicted uptake velocity of glucose by a m^2 of the benthic community in South Carolina saltmarsh sediments.

Discussion

As expected, direct or interference competition did not occur. Microbial uptake of glucose was not affected by the presence of meiofauna (Fig. 3 and Table V), nor was meiofaunal uptake of glucose influenced by the presence of sediment microbes (Fig. 2 and Table III). Interference competition is known to be important in the interactions of many microbial communities (Brock, 1966; Atlas & Bartha, 1981). But interference competition does not appear to exert an influence in microbial–meiofaunal interactions.

The substrate concentrations used in this study were low (submicromolar). It was possible that bacteria could have utilized glucose so fast that the meiofauna would not have been able to take it up. In this case, resource competition between meiofauna and bacteria would not exist. At first examination this appears to be the case; uptake by 1 cm^3 sediment was four orders greater than that of individual meiofauna (compare Figs. 2 and 3).

Utilization of glucose by microalgae is negligible compared to bacterial uptake in the

benthos (Munro & Brock, 1968). However, in an aufwuchs community, microalgal and bacterial glucose uptake are similar on a weight-specific basis (Saks & Kahan, 1979). Glucose uptake by the benthic microbial community in the present study was probably primarily by bacteria, because bacterial biomass was five to six times greater than microalgae biomass (Montagna, unpubl.). There were high numbers, and consequently high biomass, of bacteria in the saltmarsh sediments tested. The biomass estimates for bacteria were slightly higher, but in the same range, of those found in similar sediments (Rublee, 1982).

On a biomass specific basis, meiofaunal uptake of glucose at submicromolar concentrations is in the same range of that of bacterial uptake (Fig. 4 and Table VI). Thus, meiofaunal taxa (particularly nematodes) are capable of resource competition with bacteria even at low concentrations of glucose, if their biomass is equally as abundant as bacterial biomass. Manahan & Crisp (1982) report that bivalve larvae may also be able to compete with bacteria for DOM.

The conclusion, that meiofauna can compete with bacteria, must be viewed with caution. Bacteria are associated with the guts and epidermis of meiofauna. However, the biomass of these bacteria are proportionately insignificant, when compared to the biomass of the invertebrate. Unless these meiofaunal-associated bacteria are metabolizing at much greater rates than sediment-associated bacteria, these bacteria could not represent a significant proportion of meiofaunal uptake based on a weight-specific basis. This would not seem likely.

If meiofauna can compete with bacteria and DOM is limiting, then it might be expected that they could exclude one another. In the Kiel Bight, meiofauna and bacterial biomass are negatively correlated (Meyer-Reil & Faubel, 1980). But, in South Carolina, meiofaunal and bacterial abundances were not correlated at either a muddy or sandy subtidal site throughout one year (Montagna *et al.*, 1983). In contrast nematodes, a dominant meiofaunal taxon, were positively correlated with ATP in sediments off the Georgia Bight (Hanson *et al.*, 1981). These studies suggest that the relationship between meiofauna and bacteria is not controlled by a single factor and is probably very complex.

Although meiofauna possess the ability to compete with bacteria, the dominance of bacterial biomass in South Carolina saltmarsh sediments suggest heterotrophic uptake of DOM is dominated by microbes (probably bacteria) (Fig. 5). In the sediments studied, meiobenthos most likely resort to bactivory or herbivory to meet their energy requirements.

There is considerable controversy about whether or not marine invertebrates utilize DOM as an energy source (Stewart, 1979). Soft-bodied marine invertebrates, but not freshwater animals, have the capacity to absorb DOM primarily via epidermal carrier transport systems (Stephens, 1972; Stewart, 1979) and there are sufficient quantities of DOM in sediments to be an important energy source for benthic animals (Stephens, 1968; Southward & Southward, 1972; Stewart, 1979). Interstitial water of sediments contains approximately 100 × more carbon as DOM than the open oceans (Sepers, 1977); therefore, DOM should be primarily important to benthic invertebrates (Jørgen-

sen, 1976; Stewart, 1979). Because of their small size, meiobenthos have a higher surface to volume ratio than macrofauna; thus, meiobenthos should be the chief beneficiary of DOM. Using [^{14}C]glucose, Lopez *et al.* (1979) demonstrated that DOM could be more important than bacteria as food for a brackish-water nematode, and that the juvenile nematodes feed primarily on DOM. In contrast, Tietjen & Lee (1975) reported that another marine nematode did not take up DOM. Siebers (1982) has argued that the higher concentrations of DOM in interstitial water are not available to either macrofauna (because shells, tubes, and burrows block it) or meiofauna (because they are restricted to the surface films and are influenced by overlying waters). Fenchel & Jørgensen (1977) point out that most studies use unnaturally high substrate concentrations and neglect measuring net flux, and they argue that free-living protozoans and metazoans do not depend on DOM for their metabolic needs.

Regardless, the present study demonstrates that the meiobenthos do possess the potential to compete with bacteria on a weight specific basis (Fig. 4). Although interference competition does not take place, this potential for DOM uptake might lead to resource competition where meiofaunal biomass is more abundant than bacterial biomass. However, in South Carolina, bacteria are probably the main users of dissolved glucose (and perhaps DOM in general) because bacterial biomass dominates meiofaunal biomass (Fig. 5).

ACKNOWLEDGEMENTS

This paper was extracted from a dissertation submitted as partial fulfillment for the Ph.D. at the University of South Carolina. Financial support was provided by the Belle W. Baruch Institute for Marine Biology and Coastal Research, the Department of Biology, University of South Carolina, and the Biological Oceanography Program of the National Science Foundation (grant OCE-8007968: B. C. Coull, principal investigator). I thank B. C. Coull, R. J. Feller, H. N. McKeller, D. L. Wethey, and D. C. Yoch for their helpful comments on earlier drafts of this manuscript.

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