Journal of Marine Research, 42, 957–968, 1984

The role of bacterial exopolymer and suspended bacteria in the nutrition of the deposit-feeding clam, *Macoma balthica*

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ABSTRACT

Potential nutritional contributions of bacterial exopolymer and suspended bacteria to the detritus feeding estuarine clam, *Macoma balthica*, were examined separately in laboratory ^{14}C labelling experiments. Significant removal and assimilation of suspended bacteria by *M. balthica* was observed within two days, although the low clearance rates suggested planktonic bacteria may not be among its major food sources. Sediment-bound and dissolved bacterial exopolymer did not appear to be directly metabolized by *M. balthica*, as evidenced by the 1–2 week lag in ^{14}C uptake into clam tissue.

1. Introduction

Several studies suggest bacteria are a source of nutrition for the deposit-feeding clam, *Macoma balthica* (Fenchel, 1972; Newell, 1965; Newell, 1970; McLusky and Elliot, 1981; Tunnicliffe and Risk, 1977), an abundant and cosmopolitan inhabitant of many temperate estuarine benthic communities (Vassallo, 1969; Wolff and de Wolf, 1977; Chambers and Milne, 1975; Ratcliffe *et al.*, 1981; Nichols and Thompson, 1982). *M. Balthica* removes 95–99% of the bacteria from ingested sediment (Fenchel, 1972) and a strong correlation has been observed between the abundance of *M. balthica* and bacteria in estuarine sediment (Tunnicliffe and Risk, 1977). Assimilation of bacteria by *M. balthica* has not been directly demonstrated, however.

Several aspects of the role of bacteria in the nutrition of *M. Balthica* have not been thoroughly investigated. For instance, it has been calculated that *M. balthica* may have to suspension feed to meet its daily nitrogen requirement (Tunnicliffe and Risk, 1977; McLusky and Elliot, 1981), but it is not clear whether it is able to efficiently utilize populations of planktonic bacteria, since very small particles are believed to be at least partially rejected (Gilbert, 1977). Also, the role of bacterial extracellular polymers (exopolymers) in the nutrition of *M. balthica* and other benthic invertebrates is completely unknown. Exopolymer is an abundant bacterial by-product in sediments (Geesey, 1982) adhering to the surface of particles. *M. balthica* preferentially selects particles with organic coatings (Taghon, 1982). However, many deposit-feeders may

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lack enzymes capable of attacking these polysaccharides, judging from studies with analogous structural polysaccharides of higher plants (Kristensen, 1972).

In this paper we assess the ability of *M. balthica* to filter and assimilate suspended bacteria and to utilize bacterial exopolymer as a secondary source of nutrition. Our studies involve laboratory microcosm experiments, in which ^{14}C uptake in clam tissue from ^{14}C-labelled bacteria and bacterial exopolymers were monitored along with depletion of suspended bacteria. We shall demonstrate that planktonic bacteria can be filtered from solution and rapidly assimilated by suspension-feeding *M. balthica*, whereas particle-bound and dissolved exopolymer may require some microbial conversion before it can be utilized as a nutritional source.

2. Methods

a. Bacteria and bacterial exopolymer. A precipitation and dialysis procedure (Palomares *et al.*, 1979; Corpe, 1975) was modified for harvesting radiolabelled bacterial exopolymer. Sterile, 50-ml volumes of seawater growth media containing 7.5 g/L peptone, 10.0 g/L glucose, and 300 uCi/L of ^{14}C-[u]-D glucose (ICN Pharmaceuticals, Inc., #11050), were dispersed in 250-ml erlenmeyer flasks, inoculated with 2 ml logarithmic phase *Pseudomonas atlantica* T6C, and agitated at 120 rpm on a mechanical shaker for 5 days at 25° ± 2°C. The incubated culture was then transferred to 250 ml polypropylene centrifuge bottles and centrifuged at 10,000 g for 30 min. at 4°C. The bacterial pellet was rinsed with filtered seawater, transferred to 200 ml round-bottom flasks, frozen with dry ice/isopropenol, and lyophilized on a multi-port freeze-dryer. The decanted supernatant, containing the dissolved bacterial exopolymer, was then precipitated with equal volumes of 4°C acetone. The precipitate was centrifuged (2500 g, 4°C, 10 min), supernatant fluid discarded, and the polymer pellet redissolved in Milli-Q purified water. In order to remove residual salts and solvents, dissolved polymer was reprecipitated, centrifuged, dissolved in distilled water, and dialyzed for 48 hrs at 4°C against three changes of distilled water (20 volumes each). Fifty milliliter portions of dialyzed polymer solution were lyophilized as previously described. Polymer yields obtained with this method (133 mg/100 ml of culture) were consistent with values reported by Corpe (1972) for the same strain. Activities (cpm/mg exopolymer or bacteria) were determined by liquid-scintillation counting (Packard Model 3320 Tricarb) using channels-ratio for quench factor correction.

b. Experimental setup. Clams were collected from South San Francisco Bay and acclimated to laboratory conditions for 48h at 12°C before being used in experiments. Six unstirred seawater systems (three experimental systems and three controls) were set up to investigate removal of suspended bacteria and sediment-bound bacterial exopolymer (Fig. 1). To test for removal and assimilation of suspended bacteria by *M. balthica*, thirty 20-21 mm sized clams were placed into each of two experimental aquaria (Systems 1A and 2A). Carbon-14-labelled, lyophilized bacteria were resus-

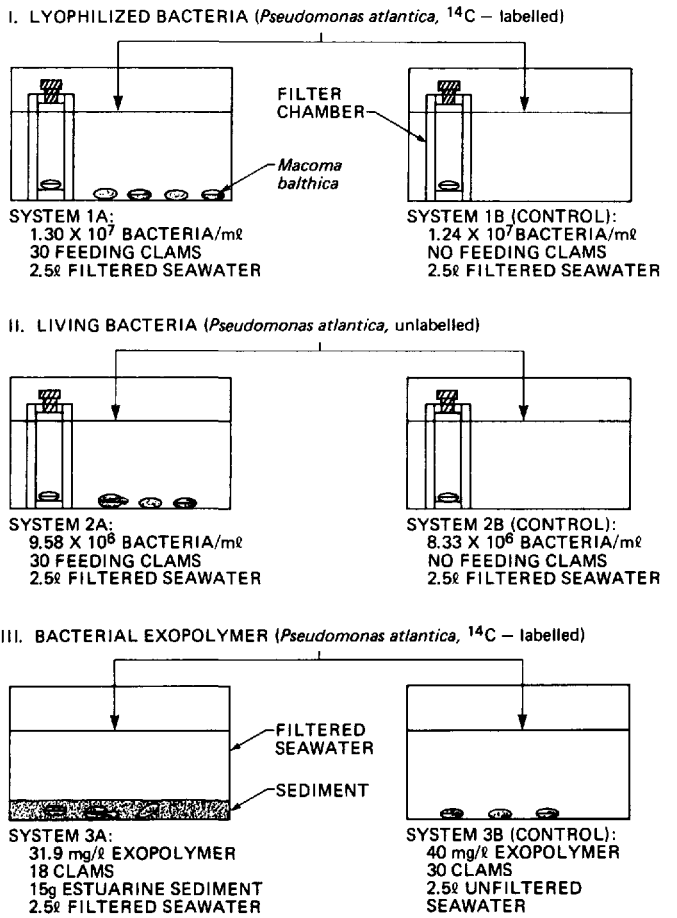

Figure 1. Schematic diagram of the six aquaria used in our study of assimilation of suspended bacteria and sediment-bound bacterial exopolymer by the deposit-feeding clam, *Macoma balthica*. Systems 1A and 2B were used in assessing clearance rates and assimilation of lyophilized and living bacteria, respectively. System 3A was used to examine potential utilization of particle-bound exopolymer as another secondary source of nutrition. Systems 1B and 2B were similar to 1A and 2A respectively, but lacked suspension-feeding clams. System 3B contained bacterial exopolymer but no sediment. The bacteria and exopolymer in Systems 1 and 3 were labelled with ^{14}C. All clams were 20–21 mm in length.

pended and added to filtered seawater in Systems 1A and 1B. Unlabelled living bacteria were added to 2A. Five additional clams were kept within plexiglass filter chambers in systems 1A, 1B, 2A and 2B. These chambers were fitted with 0.4 μm Nuclepore filters to exclude particulate material, but allow water exchange. The five "control" clams were exposed to the same solutions as the 30 "feeding" clams in Systems 1A and 2A, but were excluded from contact with suspended bacteria. Systems

1B and 2B served as control aquaria to assess changes in bacterial density in the absence of feeding clams. The five clams in filter chambers in these systems were to allow diffusion of clam metabolites through the system, although the quantity of metabolites would be less than in aquaria containing feeding clams.

Eighteen clams were added to a third, experimental aquarium (system 3A) to study exopolymer assimilation from estuarine sediments. Carbon-14-labelled, lyophilized bacterial exopolymer was dissolved, filtered through an 0.3 μm glass fiber filter, and mixed with 15 g aerobic, estuarine sediments for 24 hours. Since the exopolymer readily sorbes to estuarine sediment (Harvey, 1981), polymer-enriched sediment was collected by centrifugation and added to the system. Final concentration of exopolymer, most of which was sediment-bound, was 31.9 mg/L. Thirty clams also were added to system 3B which had 40 mg/L dissolved exopolymer but no sediment. System 3B was employed to monitor assimilation of unbound polymer.

Because specific activities differed between 3A and 3B, absolute values of ^{14}C uptake into clam tissues and solution ^{14}C decrease for these systems are not comparable. All aquaria were held at 12° ± 2°C and contained 2.5 L of filtered (0.3 μm) seawater, except for System 3B, which contained unfiltered seawater. The unfiltered seawater was to provide a source of natural marine bacteria that may be capable of converting dissolved exopolymer to a more utilizable substance.

c. Determination of bacterial number, ^{14}C, and clearance rates. The disappearance of added bacteria from solution was determined from changes in absorbance (520 nm) and from measurements of particulate ^{14}C, determined by subtraction of ^{14}C measurements before and after filtration. Metabolites were not separated from $^{14}CO_2$ in the solute phase. However, Birkbeck and McHenry (1982) showed that only 2% of the ^{14}C in solution in such experiments is $^{14}CO_2$. Absorbance measurements were correlated to direct bacterial counts using an acridine orange epifluorescence technique (Hobbie *et al.*, 1977). Six clams (1 nonfeeding from a filter chamber and 5 feeding) in Systems 1A and 2A, three clams in System 3A, and five clams in System 3B were removed at each sampling date, dissected into foot, mantle, gill and digestive gland, dried at 90°C, weighed, and reflux-digested at 80°C in 1N NaOH, KOH until a clear solution was obtained. Mean levels of ^{14}C (DPM/mg tissue) were determined by liquid scintillation counting. Where appropriate, ^{14}C in clams from the filter chamber were subtracted from ^{14}C in feeding clams to determine ^{14}C incorporation from feeding alone.

The rate of bacterial clearance was determined by a modification of the indirect suspension-depletion method (Willemsen, 1952). The experimental design allowed correction for changes in bacterial population due to cell death, adsorption onto solid surfaces, and bacterial growth stimulated by the presence of clam waste products in the absence of feeding clams. The latter could not be completely accounted for, since the total number of clams (feeding and nonfeeding) in our test and control aquaria were different. Hence, the unaccounted growth stimulation of dissolved waste products from

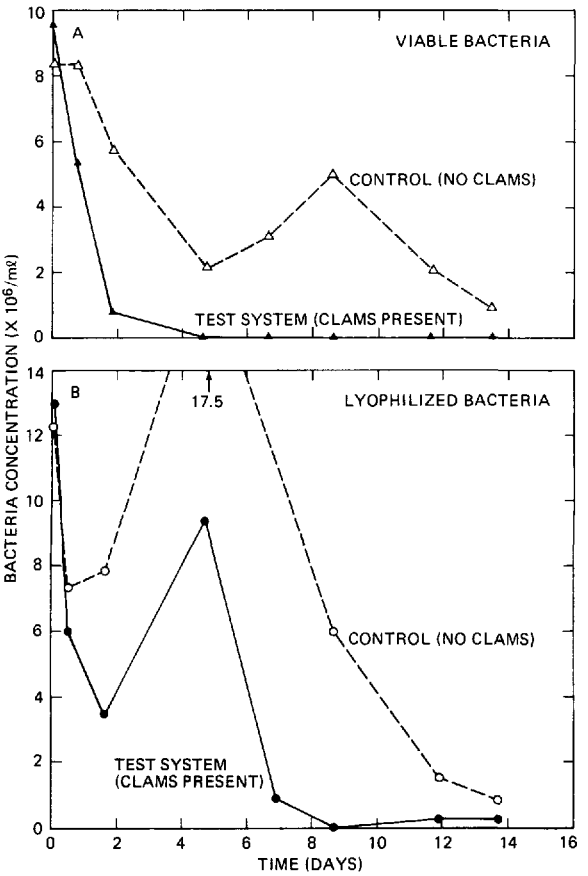

Figure 2. Depletion of suspended bacteria, *Pseudomonas atlantica*, by the clam, *Macoma balthica*, as a function of time. Bacterial counts, determined using acridine orange epifluorescence and correlated with absorbance at 520 nm, were made to within ±9.0% at 90% C.I. Figure 2A illustrates decline in numbers of living bacteria in the presence (solid line) and absence (broken line) of feeding clams. Figure 2B illustrates the decline for suspended lyophilized bacteria.

30 feeding clams in the test system may have resulted in some overestimation of filtration rates. Filtration rates were determined using the modified formula of Hargis (1977), i.e.:

$$F = \frac{V}{n} \frac{\ln c_o - \ln c_t}{t} - A$$

where F is the filtration rate in ml clam^{-1} hr^{-1}; V, the volume in ml; n, the number of clams; and c_o and c_t the cell concentrations at times o and t, respectively, in System 1A. A, the correction for changes in bacterial population in the absence of feeding clams

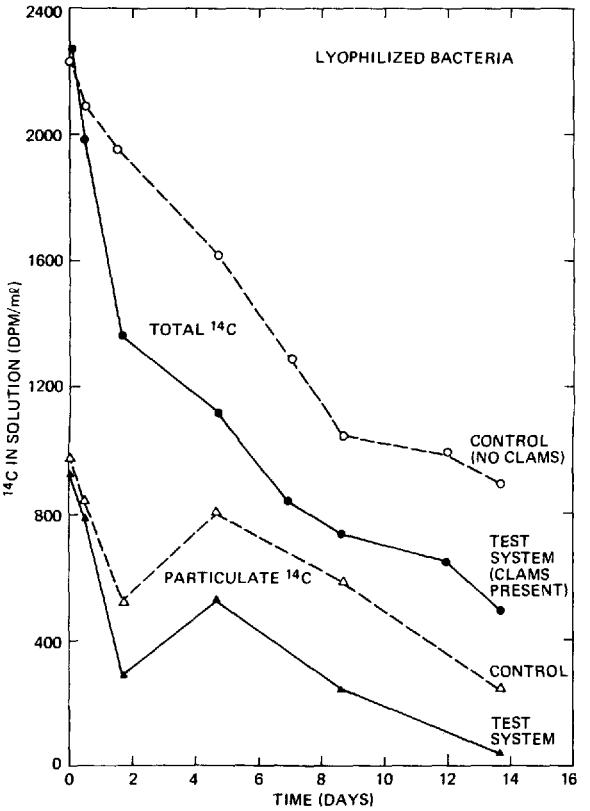

Figure 3. Decrease in total and particulate (>0.4 μm) ^{14}C over time corresponding to the depletion of ^{14}C-labelled lyophilized bacteria illustrated in Figure 2B. Carbon-14 activities are ±1%. Solid lines illustrate total and particulate ^{14}C levels in the presence of feeding clams. Broken lines are for controls in which feeding clams were not present.

may be written:

$$A = [\ln c_o' - \ln c_t']/t$$

where c_o' and c_t' are corresponding cell concentrations in System 1B.

3. Results

a. Suspended bacteria. The rapid decrease in bacterial numbers in Systems 1A and 2A relative to Systems 1B and 2B (Fig. 2) and the three-fold reduction in particulate ^{14}C which occurred in System 1A (Fig. 3) during the first two days of the experiment indicated that *M. balthica* was capable of filtering both lyophilized and living bacteria from suspension. An increase in bacterial number and particulate ^{14}C occurred on day 5 in System 1A, after which both decreased to negligible values. These results suggest a brief establishment of a growing bacterial population after many of the lyophilized

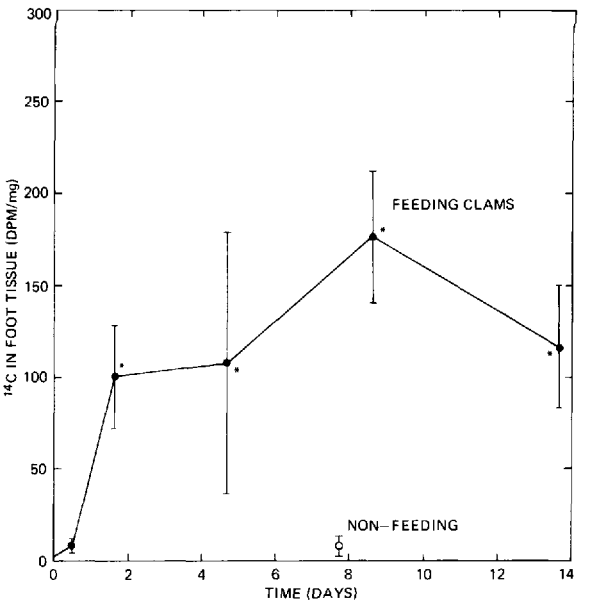

Figure 4. Levels of ^{14}C incorporated into foot tissue of *Macoma balthica* versus time for the lyophilized bacteria (^{14}C-labelled) depletion experiment. The "●" symbols depict the mean level of ^{14}C per mg dry wt for feeding clams; the "○" symbol was for the five nonfeeding clams housed in a filter chamber and exposed to solute ^{14}C only. Error bars are for the standard deviation among 5 individual clams. Asterisks indicate points which are statistically different from the measured values for nonfeeding clams at $p < 0.01$.

cells had been depleted. In the experiment with living bacteria only a continuous depletion of cells was observed. Total ^{14}C declined more rapidly in System 1A than in System 1B, also reflecting the loss of particulate ^{14}C to filtration by *M. balthica* (Fig. 3). Solute ^{14}C made up of bacterial metabolites, metabolic products of *M. balthica* derived from bacteria, and $^{14}CO_2$, declined until day 5 in System 1A, then remained relatively constant until day 14, constituting an increasing proportion of the total pool of ^{14}C in the seawater.

Figure 4 illustrates ^{14}C accumulation in foot tissue of *M. balthica* from System 1A. Uptake into gill, and mantle followed similar trends. Carbon-14 accumulation (46.7 ± 37.1 DPM/mg) in digestive gland was detected in the suspension-feeding animals within 12 hours, but some of this uptake could reflect accumulation of unassimilated bacteria. Uptake in foot muscle should come solely from assimilation of ^{14}C labelled bacteria.

The significant differences between foot-tissue ^{14}C concentrations in feeding animals and concentrations in animals held in filter chambers from day 2 onward ($p < 0.01$ calculated using student-T tests) demonstrated that the assimilated carbon originated from ingestion of bacteria (Fig. 4). The delay in significant accumulation of

^{14}C in foot tissue until day 2, could indicate the time required for detectable carbon transfer from the gut into muscle tissue. The apparent decrease in ^{14}C uptake rate during the second week of the experiment likely reflected the decrease in numbers of suspended bacteria.

Measurements of filtration rates calculated from bacterial clearance differed two- to three-fold between experiments with lyophilized and living bacteria. Rates of 48-72 ml animal^{-1} day^{-1} or 0.05 – 0.07 ml · mg d.w.$^{-1}$ hr^{-1} were observed in System 1A and rates of 168 – 172 ml animal^{-1} d^{-1} or 0.167 – 0.171 ml · mg d.w.$^{-1}$ hr^{-1} were found in System 2A with living cells.

b. Exopolymer. Loss of ^{14}C exopolymer from solution and assimilation by *M. balthica* of ^{14}C-exopolymer (as indicated by uptake into foot tissue) occurred slowly during the initial phases of these experiments (Figs. 5A, B). In the presence of sediment, ^{14}C concentrations in foot tissue were not significantly different from unexposed animals for more than 6 days (in contrast to a significant difference within 2 days when bacteria were the food source). Significant loss of exopolymer from solution also was not observed for more than 6 days. In the absence of sediment, significant ^{14}C incorporation into foot tissue ($p = .01$) and substantial loss of ^{14}C from solution were not observed during the first 14 days of the experiment. The ratio of ^{14}C in clam foot tissue to initial ^{14}C in solution for the two weeks following the initial two week lag in System 3B was 19.7 ± 15.9. The corresponding ratio for the lyophilized bacteria depletion experiment (System 1A) at 14 days was 121.6 ± 37.0. The six-fold difference in this ratio is only partially explained by the difference in solution carbon pool size (21 mg C/L in System 3B vs 83 mg C/L in System 1A).

4. Discussion

Assimilation of ^{14}C from ingestion of bacteria into foot tissue confirms the potential usefulness of bacteria as a nutritional source for *M. balthica*. Microscopic observations indicate that, although some clustering of bacteria did occur, a majority of suspended bacteria in these experiments remained as single, unattached cells. Thus filtration of bacteria from suspension suggests *M. balthica* retains particles as small as 1–2 μm. The range of particle sizes this species can ingest, 1–2 μm to 300 μm (Gilbert, 1977), attests to a remarkable ability to utilize food sources that vary significantly in size.

The rate of filtration by *M. balthica* determined by bacterial clearance (.05 – .167 ml mg^{-1} hr^{-1}) is several orders of magnitude lower than filtration rates calculated from clearance for suspension feeders. Wright *et al.* (1982), for example, observed a filtration rate in *M. edulis* of 460 ml g^{-1} hr^{-1}. It is possible that the inability of *M. balthica* to bury itself in sediment caused a reduction in filtration rate. However, Lee (USEPA Marine Science Center, Newport, OR, personal communication) observed ventilation rates of 0.07 ± 0.03 ml mg^{-1} hr^{-1} in *Macoma nasuta* buried in natural sediments and 0.05 ± 0.02 ml mg^{-1} hr^{-1} in *M. nasuta* in ashed sediments. The similarities of these results to ours suggest a relatively small effect from lack of burial, and reinforces that these species have relatively slow filtration rates.

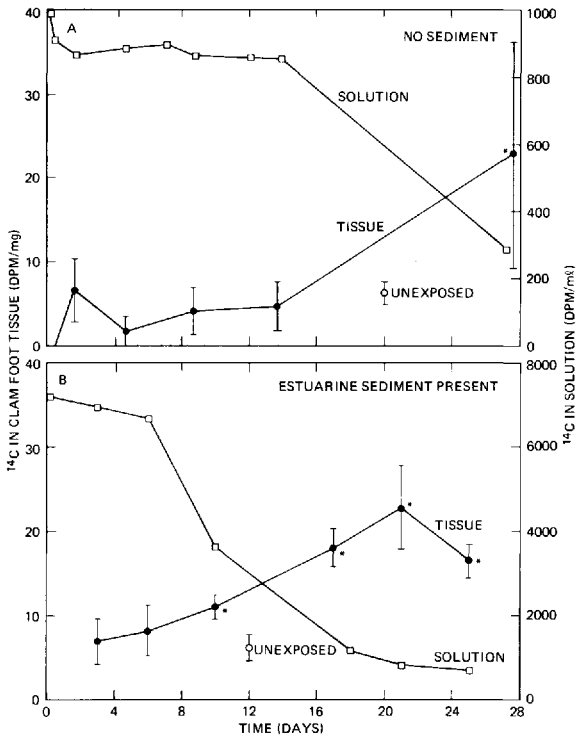

Figure 5. Levels of ^{14}C activity in solution (CPM/ml), squares, and in foot tissue (CPM/mg dry wt), circles, versus time for two static seawater aquaria containing ^{14}C bacterial exopolymer and *Macoma balthica*. Figure 5A and 5B illustrate ^{14}C assimilation in the absence and presence of aerobic estuarine sediment, respectively. The "●"s are the mean ^{14}C values for 5 individuals in Figure 5A and three individuals in Figure 5B. Error bars represent the standard deviation among these individuals. "○"s illustrate the mean ^{14}C concentration for 5 unexposed clams. Asterisks indicate mean values which are statistically different from values measured for unexposed clams at $p < 0.01$.

Dramatic difference in clearance rates between suspension feeders and animals which are mainly deposit feeders are not surprising. The morphological requirements of the two feeding strategies may be quite different in bivalves (Gilbert, 1977). The delicate gill structures and rapid pumping capabilities necessary for efficiently filtering organic-rich particles widely dispersed in a dilute medium are the antithesis of the morphological structures and physiological capabilities necessary for obtaining nutrition by processing massive quantities of relatively nutrient-poor particles. Some species, however, may switch between deposit feeding and suspension feeding in response to changes in environmental conditions (Taghon *et al.*, 1980). Based on its structural adaptations, *M. balthica* is classified as a deposit-feeder (Yonge, 1949), but our results suggest that this species also can feed on suspended bacteria. In the laboratory and in the field we also have observed the influent siphons directed up into the water column. Flexibility in feeding behavior between deposit- and suspension-

feeding has been reported for this species in two earlier investigations (de Wilde, 1975; Rasmussen, 1973).

The potential nutritional contribution of suspended bacteria can be estimated from Bubnova's (1972, 1974) equations for determining daily requirements of organic material and protein:

$$R = pW^m$$

where R is the daily ration (in mg dry wt), p is the coefficient defining the rate of food consumption per mg dry wt of soft tissue, w is the dry weight (mg) of the soft tissues, and m is the coefficient correlating the rate of change in ration with increasing body weight. In a South San Francisco Bay salt marsh, Harvey and Young (1980) found an average (n = 10) of 9.2×10^6 suspended bacteria/mL, a value within the range of abundances reported for other estuaries (Rublee *et al.*, 1983; Wright *et al.*, 1982). Assuming a bacterial density of 9.2×10^6/ml, an average cell diameter (based on differential filtration studies) of 0.4 – 0.6 μm (Wright and Coffin, 1983), and an average bacterial nitrogen content of 14% (Luria, 1960), a 20 mm *M. balthica* would require clearance rates of 1.9 – 6.6 L/day and 1.0 – 3.3 L/day to meet its respective requirements for organic material and nitrogen from suspended bacteria alone. If clearance rates were 0.17 L/day (calculated for System 2) *M. balthica* could only satisfy 3–9% of its required ration for organic material and 5–17% of its required ration for nitrogen from suspended bacteria. At clearance rates of 0.05 (the lowest we observed) or 0.07 L/day (observed for *M. nausta* in experiments employing sediments), the nutritional contribution of suspended bacteria to *M. balthica* would not appear to be too significant.

In contrast to suspended bacteria, bacterial exopolymer does not appear to be efficiently utilized as a direct food source by *M. balthica.* Experiments with both polymer in solution and polymer plus sediment showed lag periods before statistically detectable ^{14}C uptake into foot tissue began. Such lag periods are consistent with an initial bacterial utilization of polymer and subsequent passage of ^{14}C from bacteria to *M. balthica.* Enhancement of direct exopolymer utilization by *M. balthica* by adsorption onto sediment is a possibility. However, the loss of ^{14}C-exopolymer from solution suggests bacterial breakdown and incorporation (judging from the initial 6 day lag in loss) much more closely than adsorption kinetics. The more rapid loss of ^{14}C-exopolymer from solution in the presence of sediment also could reflect a higher initial bacterial biomass in System 3A as compared with System 3B. The inefficient nutritional use of polysaccharide microbial by-products such as exopolymer by *M. balthica* is consistent with the lack of enzymes capable of attacking structural polysaccharides observed in other deposit-feeders (Kristensen, 1972).

5. Conclusion

Field observations, controlled studies, filtration rates, and studies with bacteria directly establish that *M. balthica* is a highly adaptable deposit-feeder, potentially

utilizing bacteria as one source of nutrition. Observations of suspension feeding in this species could reflect the use of suspended bacteria as a secondary food source although this contribution to the overall nutrition of *M. balthica* would appear to be small, based upon measurements of laboratory filtration rates. Bacterial extracellular polymers, which are abundant in estuarine sediments do not appear to be efficiently utilized directly. More studies are needed to investigate the potential utilization of bacterial exopolymer as a source of nutrition for estuarine deposit feeders and the potential role of bacteria in converting this bacterial product into a more useful carbon source. In addition, potential nutritional contributions of seasonally abundant, phytoplankton and benthic microalgae, which were not examined here, may be significant and worthy of investigation.

Acknowledgments. We thank D. Cain and J. Thompson, U.S. Geological Survey, and the two referees for their review and helpful comments on this manuscript.

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Received: *31 October, 1982;* revised: *14 June, 1984*