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The importance of microalgae, bacteria and particulate organic matter in the somatic growth of *Hydrobia totteni*

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ABSTRACT

Laboratory microcosm experiments reveal that benthic microalgae (filamentous blue-green and diatoms) probably constitute the bulk of nutrition in the somatic growth of the deposit-feeding mud snail *Hydrobia totteni.* Despite an apparent excess of nitrogen in the particulate fraction of the sediment, *H. totteni* grows only about 42% as much in the dark as in the light. Growth in the dark is probably explained by the utilization of filamentous blue greens and, to a lesser extent, bacteria. The additional growth in the light is probably explained by benthic diatoms, as shown in previous studies. Standing-stocks of micro-organisms (bacteria and microalgae) and snail densities (0.5 cm^{-2}, 2.0 cm^{-2}) in laboratory treatments lie within the range of field conditions.

A comparison of snail growth in oxidized and nonoxidized sediments, shows that particulate organic matter typically found in salt marsh sediments does not contribute substantially to somatic growth in *H. totteni.* Added rations of the seaweed *Ulva rotundata* also did not affect snail growth. Much of the available nitrogen may have been mineralized into the water column because *Ulva* is readily decomposed.

1. Introduction

A subject of controversy in recent years has centered around the nutritional importance of particulate organic matter (POM) as food for deposit-feeders and the role of microorganisms in the nutrition of detritivores. Several studies have suggested that many types of decay-resistant particulate organic matter are not easily digested by deposit-feeders and that the microbial community plays a major role in nutrition for deposit-feeders (Newell, 1965; Hargrave, 1970; Calow, 1975; Yingst, 1976; Lopez *et al.,* 1977; Wetzel, 1977; Tsuchiya and Kurihara, 1979; Hanson, 1980). Many detritivores lack the necessary carbohydrases to hydrolyze cellulose and other structural carbohydrates (Hylleberg, 1976). During aging, POM is converted into a usable food source for detritivores by bacteria, fungi and other microbes. Decompositional rates of "aging" POM are largely dependent upon the chemical composition of the source material (Harrison and Mann, 1975; Tenore, 1975; Boiling *et al.,* 1975;

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Cameron and LaPoint, 1978; Haines and Hanson, 1979; Tenore and Hanson, 1980; Tenore and Rice, 1980; Rice and Tenore, 1981; Tenore *et al.*, 1982). Therefore, the assimilation of food depends upon the rate of decomposition in addition to the feeding rate of the detritivore.

The importance of nitrogen content with special reference to microbial "protein enrichment" has been emphasized in recent detritus studies (Tenore, 1977; Haines and Hanson, 1979; Fell *et al.*, 1980). If the microbial community provides an important source of nitrogen to deposit-feeders, and grazing by deposit-feeding increases the turnover rate of microbial biomass (Barsdate *et al.*, 1974; Lopez *et al.*, 1977), then it may be that micro-organisms are a limiting renewable resource to deposit-feeders (Levinton, 1979; 1980). Recent evidence, however, reveals that an increase in nitrogen content with aging may also be due to carbohydrate and phenolic complexes of nitrogenous compounds that yield humic geopolymers, usually not available to detritivores (Tenore and Rice, 1980; Rice, 1982). Nitrogen may also be obtainable directly from the plant substrate depending upon how refractory the detrital source is (Findlay and Tenore, 1982).

If deposit-feeders rely more on the microbial community as a major source of nutrition, it is important to determine what role different microbial organisms have in the nutrition of deposit-feeders. Recent studies have demonstrated that microalgae influence somatic growth in deposit-feeders (Fenchel and Kofoed, 1976; Wetzel, 1977; Jensen and Siegismund, 1980; Levinton and Bianchi, 1981). Moreover, it has been shown that filamentous blue-green algae and diatoms are assimilated efficiently by *Hydrobia* sp. and that coccoid blue-green algae are poorly assimilated (Kofoed, 1975a, b; Bianchi and Levinton, 1981). Other studies report that bacteria are not important quantitatively in deposit-feeder nutrition (Baker and Bradnum, 1976; Tunnicliffe and Risk, 1977; Cammen *et al.*, 1978; Cammen, 1980a; Jensen and Siegismund, 1980).

Using laboratory microcosms, we examine the importance of microalgae and bacteria, relative to POM in the somatic growth of the deposit-feeding snail *Hydrobia totteni* (Experiment I). We will show that POM of salt marsh sediments rich in nitrogen is probably unimportant in the somatic growth of *H. totteni* (Experiment II).

2. Materials and methods

Experiment I. The deposit-feeding gastropod *Hydrobia totteni* was collected from the intertidal mud flats of Flax Pond, New York. Sediment used for this experiment was prepared using methods described by Levinton and Bianchi (1981). Six 1000 ml beakers of 10 cm diameter were filled up to a depth of 1 cm with prepared sediment. Seawater was placed in beakers and maintained in an environmental chamber at 17°C, 25‰ salinity and equiped with air-stones. A snail density of 2.0 cm^{-2} was used in all treatments. Two treatments, each consisting of one control (no snails) and two replicates of 2.0 snails cm^{-2}, were exposed to different light regimes. One treatment

was maintained in constant darkness while the other was placed directly under a pair of standard fluorescent bulbs.

Following a period of 98 days, snails were removed and weighed (Levinton and Bianchi, 1981) to determine somatic growth. The light treatment provided photosynthetic microalgae, bacteria, and the POM provided from the field-collected sediment. In contrast, the dark treatment provided only filamentous blue greens, bacteria, and POM. Sampling and counting of micro-organisms (diatoms, filamentous blue-green algae, coccoid blue-greens and bacteria) were performed using epifluorescence microscopy (Levinton and Bianchi, 1981). Micro-organisms were counted from two soda straw cores (0.6 cm diameter), taken at a depth of 0.5 cm in the glass beakers. For each sample, a total of 20 grids were counted for microalgae and 20 half-grids were counted for bacteria.

Growth differences between light and dark may reflect differences in light-stimulated ingestion rate. To determine if different light regimes affect sediment ingestion rates of *H. totteni,* two treatments, each consisting of ten replicates were used. One treatment was placed directly under a pair of standard fluorescent bulbs and the other was maintained in constant darkness. Sediment was sieved through a 1.0 mm mesh and then distributed in glass culture dishes of 5.0 cm diameter to a depth of 1.0 mm. A snail density of 0.5 cm^{-2} was used in both light and dark treatments. After an elapsed period of 16 hours, pelletized sediment was sieved through an 80 micron mesh for collection of fecal pellets. Pellets were counted directly with the aid of a dissecting microscope. It was assumed that fecal pellet production is proportional to ingestion rate.

Experiment II. The collection of *H. totteni* and sediment was performed using methods described by Levinton and Bianchi (1981). After sieving the sediment through a 0.7 mm mesh, a portion of the sediment was oxidized with hydrogen peroxide and sodium pyrophosphate to remove any particulate organic matter (Sequi and Aringhieri, 1977). Oxidized and nonoxidized sediment was used to set up petri dishes 14.0 cm in diameter, filled to a depth of 0.5 cm. We then added, to the treatments with nonoxidized sediment, dried rations of the green alga *Ulva rotundata* (124.0 mg $dish^{-1}$ once every two weeks) to increase the amount of detrital nitrogen. Live *Ulva* was collected from Flax Pond, rinsed with freshwater, oven dried (at 60°C) and ground to pass through a 123.0 μm mesh sieve. A control (no snails) and three replicates of 0.5 snails cm^{-2} was established using each of the following treatments: (1) oxidized sediment with no detrital nitrogen; and (2) nonoxidized sediment with added detrital nitrogen (*Ulva* rations). A snail density of 0.5 cm^{-2} was used to eliminate interference effects on feeding (Levinton, 1979). Each petri dish was enclosed with plastic screening to maintain water flow but preclude snails from escaping. Petri dishes were maintained in a recirculating seawater (salinity = 25‰) system (ca. 1200 liters) at 20°C, and under a pair of fluorescent bulbs.

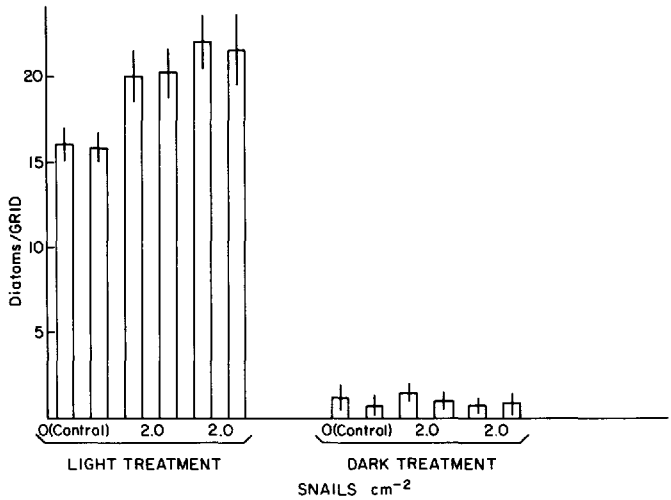

Figure 1. Standing stock of diatoms, in light and dark treatments. The grid count divided by 5.39×10^{-5} yields number per mg sediment. Error bars indicate 95% confidence interval.

After an elapsed period of 98 days, snails were removed and weighed (Levinton and Bianchi, 1981). Micro-organisms were counted from two cores (0.6 cm diameter), taken at a depth of 0.5 cm in the plastic petri dishes. Counting of microalgae and bacteria was performed using methods described by Levinton and Bianchi (1981). A total of 20 grids were counted for microalgae and 20 half-grids for bacteria per sample.

Total percent nitrogen of dried *Ulva* and sediment was determined by replicated analysis with a Perkin-Elmer (Model 240B) elemental analyzer.

3. Results

Experiment I. The experimental estimates of diatoms, filamentous blue-green algae and bacteria are shown in Figures 1–3. In light treatments, the abundance of diatoms and bacteria are consistent with published data (Levinton and Bianchi, 1981). The abundance of bacteria was not significantly different between light and dark treatments. By contrast, the diatom standing stock was substantially greater in the light treatments. Diatoms were significantly more abundant under grazing pressure (control versus 2 snails cm^{-2}–Fig. 1). It is not clear whether this represents the positive effect of grazing, or the increased abundance of *Oscillatoria* sp., which was abundant under no grazing in the light (Fig. 3). Standing stock of filamentous blue-green algae (*Oscillatoria* sp.) is similarly very low under grazing in both light and dark treatments (Fig. 3).

Snail growth showed a significant decline in the absence of diatoms; in the dark treatments, the mean final weight was 2.67 ± 0.501 mg ($N = 50$) as opposed to 4.44 ±

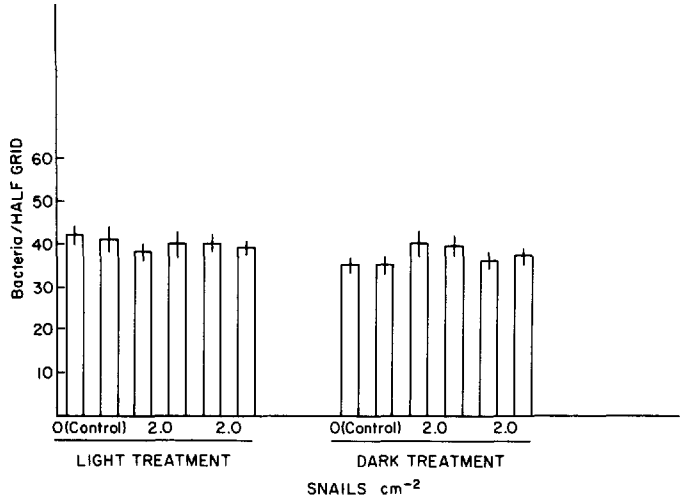

Figure 2. Standing stock of bacteria, in light and dark treatments. The grid count divided by 9.00×10^{-6} yields number per mg sediment. Error bars indicate 95% confidence interval.

1.10 mg ($N = 50$) in the light treatments. The mean weight gain in the dark treatments is ca. 42% of that found in light treatments. These results support the view that diatoms constitute the bulk of nutrition for somatic growth of *H. totteni*.

The feeding rate of *H. totteni* was determined as a function of fecal pellet production over a 16 hour period. In dark treatments, a mean 30.78 ± 9.36 pellets snail^{-1} 16 hrs^{-1} ($N = 10$) was obtained as compared to 30.47 ± 8.24 ($N = 10$) in the lighted treatments.

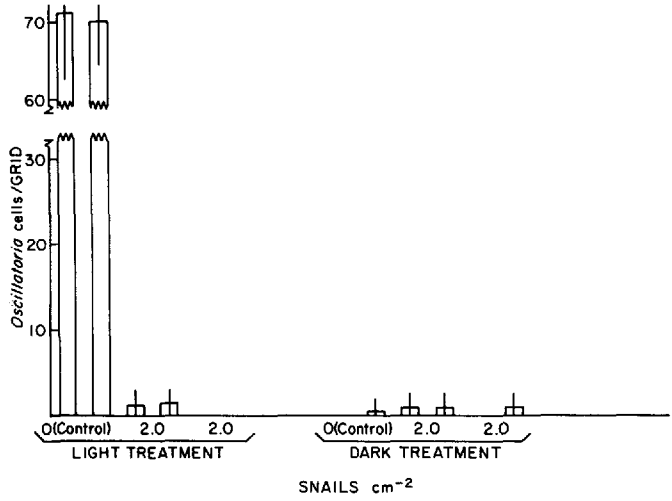

Figure 3. Standing stock of *Oscillatoria* sp., in light and dark treatments. Data reported as in Figure 1.

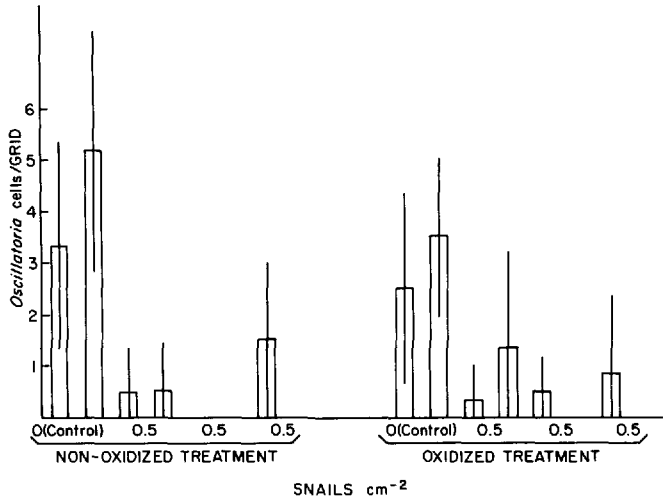

Figure 4. Standing stock of *Oscillatoria,* in oxidized and nonoxidized sediments. Data as reported in Figure 1.

These results suggest that feeding activity of *H. totteni* is not altered with respect to light and dark treatments.

Total mortality over an experimental period of 98 days showed a significant difference, with 10% in light treatments and 40% in dark.

We estimated the weight gain of nitrogen of the snails in the following way. We first measured the nitrogen content of the soft tissues of adult snails (13.06 ± 4.24%, N = 10). We also measured the percent dry weight of the snails accounted for by soft tissues (without the operculum: 4.27%). From these measurements, combined with our measurements of weight gain (mentioned above and converted to dry weight) we calculate that the snails in the dark treatment gained 1.23 mg of nitrogen over the course of the experiment. The sediment nitrogen content was estimated to be 0.255 ± 0.210% (N = 4). The average amount of sediment available in the dish was 108 g. If we assume that all of the sediment nitrogen was available, then 275.4 mg of nitrogen was available to the snails. If we assume that only the top two mm were accessible for feeding, then 22.0 mg N was available per dish.

Experiment II. Figures 4–7 show the experimental estimates of *Oscillatoria* sp., coccoid blue-green algae, diatoms and bacteria. The standing stock of *Oscillatoria* (Fig. 4) is consistent with results obtained by Levinton and Bianchi (1981). There are no significant differences in standing stock of *Oscillatoria* sp. among the oxidized and nonoxidized (*Ulva* ration) treatments. By contrast, the coccoid blue-green algae show a considerable difference among treatments (Fig. 5). The reason for these differences remains unclear at this time.

Counts of diatoms and bacteria are also consistent with earlier estimates (Levinton

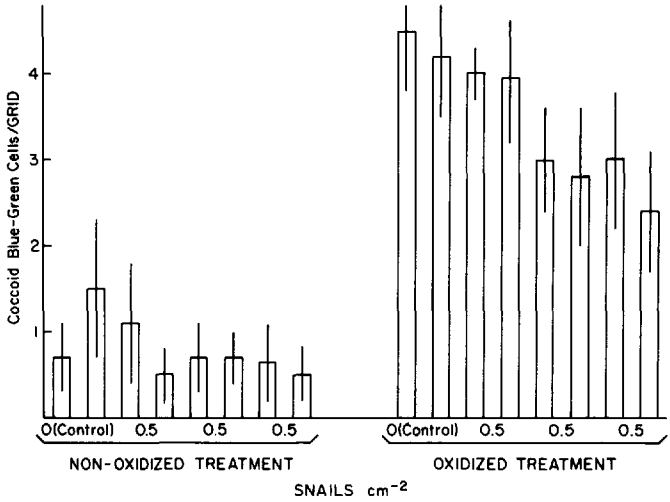

Figure 5. Standing stock of coccoid blue greens, in oxidized and nonoxidized sediments. Data as reported in Figure 1.

and Bianchi, 1981). There are no significant trends in standing stock of bacteria and diatoms with respect to oxidized and nonoxidized (*Ulva* ration) treatments, with the exception that diatoms are significantly more abundant under no grazing in the nonoxidized treatment (Figs. 6–7). This might be due to subsidy by the POM added to the sediment. With the exception of coccoid blue-green algae, standing stocks of micro-organisms are essentially the same in both treatments.

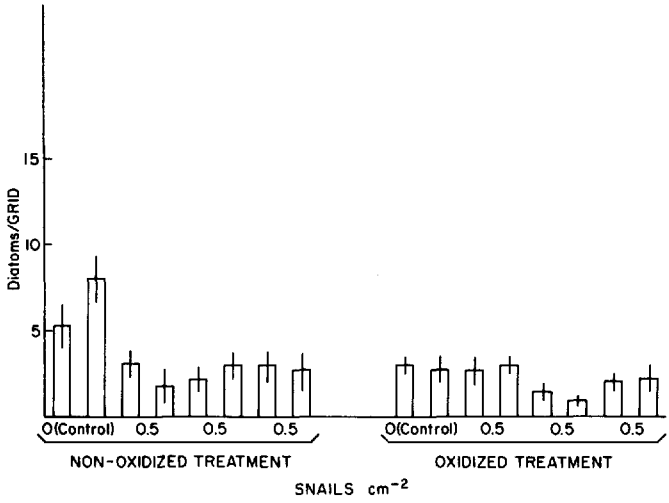

Figure 6. Standing stock of diatoms in oxidized and nonoxidized sediments. Data as reported in Figure 1.

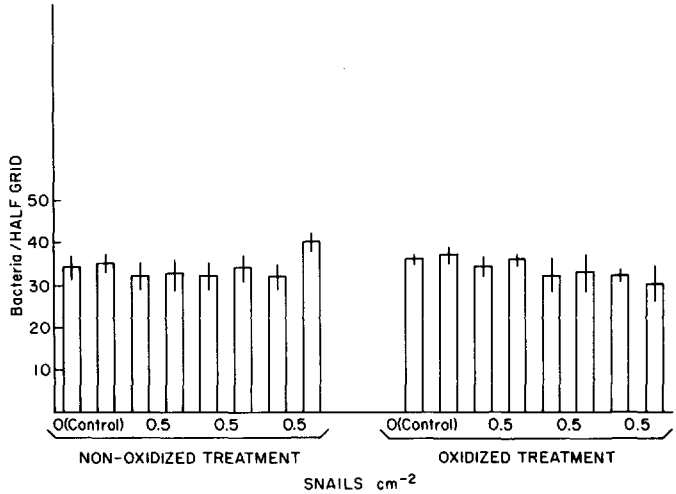

Figure 7. Standing stock of bacteria in oxidized and nonoxidized sediments. Data as reported in Figure 2.

The nitrogen content of dried sediment ranged from 0.01% in the oxidized treatment to 0.21% in the nonoxidized (*Ulva* ration) treatment (Table 1). Despite the high nitrogen content of *Ulva* (1.39%); total percent nitrogen in field sediments was found to be the same as that in the nonoxidized (*Ulva* ration) treatments. It may be that because *Ulva* is easily decomposed, most of the nitrogen was lost by rapid leaching into the water column (personal communication, Donald Rice). The total amount of dried *Ulva* ration added for the duration of the experiment was estimated as having a frond surface area of ca. 150 cm^2 (calculated using known weight and surface area of a frond of *Ulva*), approximately the same as the surface area of the petri dishes used in each treatment. Therefore, one could imagine a frond of *Ulva* decomposing in each dish, similar to that observed at a particular site on an intertidal mud flat.

Somatic growth showed no significant difference in the absence of POM or with the addition of *Ulva* rations (Table 1). As mentioned earlier, the added detrital nitrogen (10.34 mg total N was added over the period of the experiment) may not have been available long enough to affect snail growth, because of rapid efflux of nitrogen into the water column.

Total mortality over a period of 98 days (20%) was the same for both oxidized and nonoxidized (*Ulva* ration) treatments.

4. Discussion

As found by Levinton and Bianchi (1981), our results show that diatoms are the principal food resource for *H. totteni*. In the absence of diatoms, *H. totteni* are able to attain limited growth, presumably through the utilization of bacteria and filamentous

Table 1. Total percent nitrogen (mean ± s.e.) in sediment and snail tissue from Experiments I and II. Snail growth (mean ± s.e.) with respect to light availability and the abundance of particulate organic matter and nitrogen.

Treatment	Snail density cm^{-2}	Snail weight gain (mg)	Percent nitrogen
Experiment I			
Dark	2.0	1.29 ± 0.02*	
Light	2.0	2.17 ± 0.15*	
Sediment			0.25 ± 0.11***
Snail Tissue (Adult)			13.06 ± 1.34**
Experiment II			
Initial field sediment			0.22 ± 0.01***
Initial oxidized sediment			0.01 ± 0.01***
Dried *Ulva*			1.37 ± 0.02***
Control (nonoxidized) with *Ulva* ration			0.21 ± 0.01***
Nonoxidized with *Ulva* ration and snails	0.5	1.54 ± 0.15*	0.21 ± 0.01***
Control (oxidized)			0.0***
Oxidized with snails	0.5	1.80 ± 0.16*	0.01 ± 0.01***

*N = 50
**N = 10
***N = 4

blue greens. Furthermore, it appears that the nonliving POM does not contribute substantially to somatic growth in *H. totteni*.

The observed density of ca. 4.00×10^9 bacterial cells (g^{-1} dry weight) in the whole sediment fraction (<0.7 mm) is in agreement with the range of field densities reported by Dale (1974). Bacterial standing-stock was insensitive to grazing pressure in all treatments (Figs. 2, 7); this was probably due to rapid recovery rate (Levinton and Bianchi, 1981). *H. totteni* is capable of assimilating both bacteria and algae from natural sediment with ca. 40% efficiency (Lopez and Cheng, 1983). Bacterial standing-stock alone, however, is not capable of supporting deposit-feeders with the necessary energetic demands (Cammen, 1980b). More specifically, other studies have suggested that bacteria do not contribute substantially to the nutrition of *Hydrobia* sp. (Jensen and Siegismund, 1980; Levinton and Bianchi, 1981).

Our results show that POM does not contribute to somatic growth in *H. totteni* (Table 1). *H. totteni* is capable of assimilating POM in *Spartina* mud flats with efficiencies that cannot easily be distinguished from nil (G. R. Lopez, personal communication). However, *H. totteni* uses predominantly intracellular digestion to

pick off attached microbes (Lopez and Levinton, 1978), and consequently may not be able to utilize the nitrogen bound in POM. Though we found no correlation with total percent nitrogen in sediment and snail growth (Table 1), recent work has suggested that total percent nitrogen should not be used as an indicator of available nitrogen because of the presence of humic geopolymers (Rice, 1982). By contrast, other studies have shown that POM could be a major food resource in the nutrition of deposit-feeders (Tenore, 1977; Tenore *et al.*, 1979; Tenore, 1984). These results may not be applicable to local *Spartina* mud flats, where most POM comes mainly from decomposing *Spartina alterniflora* (Houghton, 1979). In some years rich growth of *Ulva* in local mudflats may introduce enough usable POM to have a nutritional impact on the snails.

Recent work has shown that microalgae (benthic diatoms) are also high in nitrogen and caloric content (Tenore, 1984). To determine the importance of different species of microalgae in the nutrition of *H. totteni,* assimilation efficiencies would have to be worked out using techniques such as those described by Lopez and Cheng (1983).

The utilization of any resource by deposit-feeders is dependent upon many environmental variables. There may be temporal variation in the abundance of microalgae and the quality of available POM. The different modes of feeding by *Hydrobia* sp. (Lopez and Levinton, 1978; Lopez and Kofoed, 1980; Levinton, 1982) may affect ingestion rate and assimilation efficiency of a particular resource.

The apparent superabundance of nitrogen in salt marsh sediments, relative to the growth needs of the snails, suggests that only a minor portion of standing POM could be a source of nutrition for the snails. Given our light-dark experiment, the most parsimonious accounting for growth is: (a) diatoms plus blue greens in the light; and (b) blue greens in the dark. Bacteria may play a small role as well, but our experimental design can only suggest intuitive judgments. Kofoed (1975a) shows that assimilation of cultured filamentous blue greens is less than for diatoms but still considerable (ca. 50%). Because the mode of growth is in the form of a surface slime, the material is very accessible to the snails; assimilation of filamentous blue greens may be close to the amount measured by Kofoed (1975a).

These results would suggest that POM in *Spartina* sediments of Flax Pond provides little directly to the snails. The inference is only reinforced by our experiment in which POM was completely bleached from the sediment. Growth did not differ in bleached versus unbleached sediment. We suggest, therefore, that in salt marsh mudflats, the microbial paradigm suggested by Fenchel (1970) and Newell (1965) is essentially correct for *H. totteni* and probably for other deposit-feeders using a similar feeding strategy. As the data and arguments of Findlay and Tenore (1982) indicate, this conclusion cannot be universal for all deposit-feeding species in all habitats.

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