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Nutrition and food limitation of deposit-feeders.
II. Differential effects of *Hydrobia totteni* and *Ilyanassa obsoleta* on the microbial community

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ABSTRACT

We examined the effects of the mud snails *Hydrobia totteni* and *Ilyanassa obsoleta* on microbial communities of sediments in microcosms. Varying density of *Hydrobia*, and the presence of *Ilyanassa*, exerted no effect on steady state bacterial standing stock. This is probably related to the rapid recovery rate of bacteria, despite efficient grazing. In contrast, coccoid blue-green bacteria were abundant when only *Hydrobia* were present but absent when *Ilyanassa* were present. A different suite of digestive enzymes or greater gut residence time in *Ilyanassa* may explain this difference. Filamentous blue greens were efficiently grazed by both snail species. Somatic growth rate of *Hydrobia* was generally depressed by *Ilyanassa*. We conclude that differential digestive (or other) abilities of deposit-feeding species can exert differential effects on the microbial community of sediments.

1. Introduction

Recent work on the biology of deposit-feeders suggests great differences in their abilities to digest and assimilate different fractions of the sediment. Many types of particulate organic matter are refractory to decomposers (e.g., Harrison and Mann, 1975) and are difficult for deposit-feeders to digest and assimilate (Fenchel, 1970; Lopez *et al.*, 1977; Yingst, 1976). However, POM rich in nitrogen may serve as food for deposit-feeders living in bottoms with continual detrital influxes (Tenore *et al.*, 1979). Microbial organisms also vary in the degree of digestion and assimilation. Diatoms and bacteria are efficiently digested and assimilated by many species (Fenchel, 1970; Newell, 1965; Lopez and Levinton, 1978; Kofoid, 1975). However, coccoid blue-green algae are poorly assimilated by *Hydrobia ventrosa* (Kofoid, 1975).

We here report a study of the effects of two different deposit-feeders on the microbial community of an intertidal silty sediment. We have chosen two deposit-feeding snails, *Hydrobia totteni* and *Ilyanassa obsoleta*, to examine whether

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particle-swallowing invertebrates have differential abilities to digest microorganisms and whether this difference results in differences in the microbial composition of sediments. If the latter is true, then deposit-feeders can strongly affect the nutrition of coexisting species; this would have major implications for the study of interspecific competition and resource partitioning. Our approach is simple. We have examined effects on various components of the microbial community by examining laboratory microcosms with varying density of Hydrobia, with and without Ilyanassa.

2. Materials and methods

Hydrobia toteni and Ilyanassa obsoleta maintain persistent and dense populations in soft bottom intertidal flats of the north shore of Long Island, N.Y. Both
Gastropods are deposit-feeders and often co-occur in silty sediments. However, *H. totteni* usually occurs higher in the intertidal zone than *I. obsoleta* (Fig. 1a, Fig. 1b). Furthermore, digestion in *I. obsoleta* is dominantly extracellular (Brown, 1969), while that of *H. totteni* is predominantly intracellular. Because of the broad habitat overlap of these two species, it would be of interest to know the effect of one species upon another.

Both gastropods were collected from a tidal flat at Flax Pond, New York (Levinton and Bianchi, 1981). The *H. totteni* individuals were recruited to the flat in the summer of 1979; we do not know the age of the specimens of *I. obsoleta* that we collected. We used the sediment described by Levinton and Bianchi (1981) to set up petri dishes of 14 cm diameter, filled to a depth of 0.5 cm. We established two replicates each of the following conditions: (1) Control; *H. totteni* density of (2) 0.25; (3) 0.50; and (4) 1.0 snails cm$^{-2}$ without *I. obsoleta*; and *H. totteni* density of (5) 0.25; (6) 0.5, and (7) 1.0 snails cm$^{-2}$, with two individuals of *I. obsoleta* in each dish (0.013 snails cm$^{-2}$). All petri dishes were enclosed with a cylinder of plastic screening to prevent escape of the snails, but to allow water flow.

We maintained the dishes at 19°C, 25%, and at a light intensity of ca. 0.5 × 10$^4$ ergs cm$^{-2}$ under standard fluorescent lights. The experimental light intensity employed here was approximately half of that used by Levinton and Bianchi (1981). At this light intensity, coccoid blue-green algae were relatively more abundant than at higher light levels. After an elapsed time of 106 days, we measured somatic growth of *H. totteni* by weighing individuals blotted dry on tissue paper on a Cahn DTL balance, and by measuring shell length with the aid of a dissecting microscope. We also counted diatoms, filamentous blue-green algae (*Oscillatoria* sp.), bacteria, and coccoid blue greens (a form with a diameter of ca. 25 microns was the only common species present) using the epifluorescent technique described in Levinton and Bianchi (1980). Microbial organisms were counted from paired soda straw samples (0.6 cm diameter) taken to a depth of 0.5 cm in the petri dishes. We counted 20 grids per sample.

3. Results

Figures 2-5 show the counts of filamentous blue-green algae (*Oscillatoria* sp.), diatoms, bacteria, and coccoid blue greens (*Anacystis* ? sp.). In all cases, a one-way ANOVA demonstrates statistically significant heterogeneity among treatments (p < .01). We will emphasize only monotonic trends. As found by Levinton and Bianchi (1981), filamentous blue greens are strongly depressed by modest grazing pressure of *Hydrobia totteni* (Fig. 2). *Ilyanassa obsoleta* similarly depresses *Oscillatoria* standing stock. Filamentous blue-green standing stock in these controls is reduced relative to the controls reported by Levinton and Bianchi (1981), because of the lower light levels used in this experiment.
Figure 2. Relative abundance of filamentous blue green cells (ordinate is number of cells per grid), as a function of *Hydrobia* snail density, with and without *Ilyanassa* (C = control). Error bar is 95% CL. The grid count divided by $5.39 \times 10^{-8}$ yields number per mg sediment.

Figure 3. Relative abundance of diatoms as a function of *Hydrobia* density, with and without *Ilyanassa*. Data reported as in Figure 2.
Diatoms are relatively rare (Fig. 3) when compared to the standing stocks found by Levinton and Bianchi (at twice the light intensity). There is no obvious trend in the data, except a modest difference between the control and the lowest *Hydrobia* density, relative to the other treatments. Bacteria (Fig. 4) show no trend and are similar in abundance across all treatments and controls. Bacteria standing stock is similar to that found by Levinton and Bianchi, despite the two-fold reduction in light levels (however ANOVA shows heterogeneity among treatments, $p <$...
Figure 6. Somatic growth of *Hydrobia totteni* as a function of density: alone, high light (solid line, data from Levinton and Bianchi, 1981); alone, low light (dashed line); low light, with *Ilyanassa* (dotted line). Error bar is 95% CL.

.01). By contrast, coccoid blue-green algae show a dramatic difference under grazing of *H. totteni* without, and with *I. obsoleta*. With no grazing (Fig. 5), coccoid blue greens are very abundant and form a surface layer on the sediment. The presence of *H. totteni* exerts no effect on coccoid blue-green standing stock. We examined feces of *H. totteni* and found that the abundance of live cells, as judged by autofluorescence, is similar to that of the sediment. It therefore seems likely that *H. totteni* is incapable of digesting these coccoid blue greens. However, *I. obsoleta* plus *H. totteni* treatments were nearly devoid of coccoid blue greens. Therefore, *I. obsoleta* probably is capable of efficiently digesting coccoid blue-green algal cells. We cannot exclude the possibility that some interaction between the two snail species causes the decline of the blue green; we do not have data for *I. obsoleta* alone for this experiment. However, subsequent qualitative observations show that *Ilyanassa* can eliminate coccoid blue greens in the absence of *Hydrobia*.

Figure 6 shows somatic growth of *H. totteni* as compared with the growth data reported by Levinton and Bianchi at comparable densities, but under higher light intensity. Growth under all treatments is lower than in the experiment of Levinton and Bianchi. This is consistent with the depressed algal biomass, which we interpret to be an equilibrium between grazing and algal production. In two of the three densities, the growth of *H. totteni* is significantly less when coexisting with *I. obsoleta*. However, at the intermediate density of 0.5 *H. totteni* cm\(^{-2}\), growth is not depressed in the *I. obsoleta* treatment.
4. Discussion

*Ilyanassa obsoleta* and *Hydrobia totteni* maintain persistent populations in silty intertidal sediments of Long Island Sound. Despite broad sympatry in microhabitat, we have demonstrated an overall difference in habitat range. *H. totteni* occurs higher in the intertidal zone than *I. obsoleta* (Fig. 1). Our data represent the distributions of the two species at the time of low tide. It is possible that *I. obsoleta* individuals occur higher on the flat at the time of high tide; however, it is unlikely that *H. totteni* individuals have a significantly different distribution at different stages of the tide (see discussion in Fish and Fish, 1974; Levinton, 1979).

Although these two species may have evolved a slightly different tidal height preference in response to interspecific competition, the degree of overlap is still broad. Furthermore, *I. obsoleta* occurs in medium and coarse sands as well as in other intertidal and shallow subtidal habitats in Long Island Sound. *I. obsoleta* occupies a broader range of habitats than *H. totteni*. However, in all cases, *I. obsoleta* is relatively susceptible to desiccation; this probably is the basis for *H. totteni*’s occurrence in the upper intertidal zone as either: (1) an evolved response; or (2) due to an interference response (Levinton, unpublished data) to interspecific competition with *I. obsoleta* and other deposit-feeders found lower in the intertidal flat. We have maintained *Hydrobia* individuals indefinitely under simulated subtidal conditions with no apparent harmful effects. The genus *Hydrobia* consists of species that are very tolerant of desiccation. The distribution of *H. totteni*, relative to *I. obsoleta*, may be likened to the upper intertidal restriction of the Atlantic barnacle *Chthamalus stellatus* (Connell 1961). This species is excluded from the lower intertidal due to the superior competitor *Balanus balanoides*; however, *B. balanoides* cannot survive the desiccation stress of the upper intertidal zone.

*I. obsoleta* and *H. totteni* exert different effects on the microbial community. Both species are capable of grazing successfully filamentous blue greens faster than algal production, at least under our experimental light conditions. However, *H. totteni* cannot successfully graze the coccoid blue green (*Anacystis* ? sp.) dominant in our cultures. Even with relatively dense populations (e.g., 1 snail cm\(^{-2}\)), coccoid blue greens are abundant. Inspection of fecal pellets suggest that little or no digestion occurs. This result is consistent with Kofoid’s measurement of ca. 5% digestion of *Chroococcus* sp. for *H. ventrosa*. By contrast, *I. obsoleta* effectively reduces coccoid blue-green populations. Fecal material seems less rich than the sediment in living (autofluorescent) cells (qualitative observations).

The difference in grazing effect we have observed may be related to two factors: mode of digestion and gut residence time. Current evidence suggests that extracellular digestion predominates in *I. obsoleta*. Secretion of large amounts of carbohydrates in the gut may be sufficient to break down the cell coating of coccoid blue greens (see Porter, 1973). Although few recent studies are available, intracellular digestion may be the predominant form in *Hydrobia* (Graham, 1939). There-
fore, gut carbohydrases may be less available, and coccoid blue-green cells may pass through the gut undigested.

*I. obsoleta* individuals are also far greater in body size than *H. totteni*. Cammen (1980) reported a logarithmic relation among deposit-feeding taxa between sediment organic particulate ingestion (egestion) rate and body size. The value of the exponent is less than 1, suggesting that an incremental increase in body weight corresponds to a successively smaller incremental increase in egestion rate. The gut residence time can be computed as:

$$ T = \frac{N}{\frac{dN}{dt}} $$

where $T$ is the gut residence time, $N$ is the amount of sediment in the gut (proportional to gut volume if the gut is filled) and $\frac{dN}{dt}$ represents the ingestion ( = egestion) rate. $N$ should increase with linear proportionality to an increase of gut volume and, therefore, body weight, while egestion increases at a rate less than 1. Larger animals should therefore have a longer gut residence time than smaller animals because the ratio $N : \frac{dN}{dt}$ should increase with increasing body weight. Although data do not exist for *I. obsoleta*, Hydrobiids have a value of $T$ of ca. 20 minutes. The predicted longer gut residence time of *I. obsoleta* suggests more opportunity for successful digestion of cells better protected by coatings. Thus the difference in digestion between the two species may not necessarily relate to qualitative differences in mode of digestion.

Our results for bacterial standing stock are similar to those of Levinton and Bianchi (1981); bacterial abundance is not affected monotonically by increasing *Hydrobia* density or by additional grazing pressure by *I. obsoleta*. Therefore, we have found similar bacterial biomass under conditions of varying grazing intensity, different grazing species, and differing light intensities. *Hydrobia* can efficiently digest and assimilate bacteria in sediments (Lopez and Levinton, 1978; Kofoed, 1975). Levinton and Bianchi (1981) suggest that the invariance may be due to rapid bacterial population growth rates, combined with an upper limit (carrying capacity) to bacterial standing stock. Intense grazing may have also selected for relatively indigestible forms, though no direct evidence is available.

As predicted by Levinton and Bianchi, growth of *H. totteni* is greatly reduced with reduced abundance of diatoms and filamentous blue-green algae. However, growth at 1 snail per cm$^2$ suggests that the negative effect of increasing density on feeding rate may be important as well. As seen in Figure 6, the difference in growth rate of *H. totteni* at 1 snail cm$^{-2}$ does not differ significantly between low and high light intensity. This similarity is surprising as total algal abundance (filamentous blue greens and diatoms) found by Levinton and Bianchi at high light intensity is greater than three times the algal abundance at low light intensity.
This suggests that snail interactions (as in Levinton, 1979) contribute to the reduction of growth rate of *H. totteni* between 0.5 and 1 snail cm$^{-2}$. As natural population densities are often greater than 1 snail cm$^{-2}$ (Levinton and Bianchi, 1981), spatial interactions are probably an important component of somatic growth. The apparent negative effect of *I. obsoleta* on the growth of *H. totteni* suggests that the following effects regulate somatic growth of *Hydrobia* in the field: (1) algal abundance, (2) behavioral interactions at high density of *Hydrobia*, and (3) the presence of competitors such as *I. obsoleta*.

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**REFERENCES**


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