Nutrition and food limitation of deposit-feeders. I. The role of microbes in the growth of mud snails (Hydrobiidae)

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ABSTRACT

A series of laboratory microcosm experiments demonstrate that somatic growth of the deposit-feeding gastropod, *Hydrobia totteni*, is related strongly to microalgal standing stock. Microalgal standing stock is, in turn, determined by the relative rates of grazing and recovery. Field estimates of *Hydrobia* biomass and steady-state microalgal standing stock closely approximate laboratory results; laboratory studies of the effect of density on somatic growth exhibit a pattern similar to variation within field populations of varying density.

In contrast to algae, bacteria show no diminution of steady-state abundance with increased *Hydrobia* grazing pressure. Apparently, bacteria recover too rapidly to be cropped down. As *Hydrobia* growth does not differ significantly from zero under low algal steady-state standing stock, bacteria probably do not contribute substantially to snail growth.

Measurements of field densities, combined with the field-microcosm data, suggest that *Hydrobia* populations exist under conditions of resource limitation.

1. Introduction

The nutrition of deposit feeders has attracted considerable attention in recent years. Before the work of Newell (1965) and Fenchel (1970), most workers felt that deposit-feeders derived their nutrition from the particulate organic fraction of the sediments (e.g., Sanders, 1958). However, Newell judged correctly that deposit-feeders efficiently digest and assimilate microbial organisms, but digest non-living organic matter poorly. Several subsequent studies have confirmed this result (Hargrave, 1970; Fenchel, 1970; Calow, 1975; Yingst, 1976; Lopez *et al.*, 1977).

Although there seems little doubt that microbial organisms are important quantitatively in the nutrition of deposit-feeders (e.g., Fenchel and Kofoed, 1976), two considerations suggest further study. First, it is not clear that microbial organisms, such as bacteria, necessarily constitute the bulk of the diet. Estimates from ATP analysis of sediments suggest that microbial carbon constitutes only a few per

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cent of the total carbon (e.g., Cammen *et al.,* 1978). Therefore, a deposit-feeder might be relatively inefficient at digesting and assimilating carbon from non-living particulates, yet derive most of its carbon from that source simply because of its abundance (Cammen *et al.,* 1978; Levinton, 1979). Secondly, not all detritus is difficult to digest. Nitrogen-rich detritus may be directly important in the diet of deposit-feeders living in sediments with high influxes of decaying seaweed (Tenore, 1977; Tenore *et al.*, 1979). This would not apply to detritus such as aged *Spartina* which is nitrogen-poor, save for the microorganisms attached to the surface (Lopez *et al.*, 1977).

The relative role of different microbial taxonomic groups of organisms in the nutrition of deposit-feeders is also subject to question. Levinton (1979) suggests that the microbial community is a renewable resource whose abundance may be modeled as a balance between consumption by microbial feeders and the growth rate of the microbial population. In some cases, pelletization of the sediment may limit the availability of particles (Grassle and Grassle, 1974; Levinton and Lopez, 1977). However, the heterogeneity of the microbial community calls into question the relative role of the various microbial organisms in deposit-feeder nutrition. Bacteria have been considered as important in deposit-feeder nutrition (e.g., Newell, 1965; Kofoed, 1975). However, others have calculated that bacteria constitute an insufficient proportion of the available food to be very important to deposit-feeding macrofauna (Cammen *et al.,* 1978; Tunnicliffe and Risk, 1977). Fenchel and Kofoed (1976) concluded that diatoms can be related to deposit-feeder somatic growth. However, no counts of bacteria were made and it is not clear that the diatom standing stock in the lab was comparable to those of field localities.

This study examines the role of various microbial organisms in the somatic growth of the small deposit-feeding snail *Hydrobia totteni.* We shall also compare our laboratory microcosm results to field conditions. We shall show that populations of *H. totteni* are food-limited under typical field population densities and probably derive the bulk of their nutrition from diatoms and filamentous blue-green algae.

2. Materials and methods

We employed *Hydrobia totteni,* a dominant deposit-feeding snail in mud flats adjacent to *Spartina* salt marshes on Long Island, New York, U.S.A. Like other species of *Hydrobia,* these snails swallow small sedimentary particles and scrape microorganisms from larger sand grains (Lopez and Levinton, 1978; Levinton and DeWitt, 1981). We sampled snails monthly with 3.5 cm diameter cores, to a depth of 15 cm below the sediment water interface. For grazing experiments, surface sediment was scraped off the tidal flat and snails were collected on a 0.5

mm sieve. This experiment was employed with immature snails that had recruited to the tidal flat in the summer of 1979.

We collected sediment from the upper cm of the tidal flat near the Flax Pond Marine Laboratory (ca. 300 m to the north of the laboratory), sieved it through a 0.7 mm mesh (it was 35% silt-clay), and placed aliquots to a depth of 5 mm in plastic petri dishes of 9 cm diameter. The petri dishes were enclosed with plastic mesh to prevent the escape of the snails. Dishes were arranged in a row in a recirculating seawater system (ca. 800 liters) in a water depth of 25 cm, directly under a pair of standard fluorescent bulbs. Water was placed in the seawater system one month before; the aquarium water (salinity = 24‰, temperature = 17°C) was recirculated through a filter bed approximately once every hour. A small aliquot of surface sediment transported directly from the field site was placed in each dish to provide an innoculum of microorganisms. The dishes were allowed to incubate under the light (ca. 1.0×10^4 ergs cm^{-2} s^{-1}) for two weeks before snails were placed in the dishes.

After the two week incubation period, snails were placed in the trays under similar light at the following densities: 0, 0.25, 0.5, 1, 2, 3, 4, 6 cm^{-2}. The densities were arranged in a random order to eliminate the potential of bias from factors other than density. A random sample of snails were sacrificed at the beginning of the experiment in order to eventually estimate somatic growth after an elapsed period of 72 days.

After the elapsed period, we estimated standing stock of several types of microbial organisms. We assumed that standing microbial stock represents an equilibrium between consumption and microbial growth (Levinton 1979a). At any given time, snails ingest a specified volume of sediment and extract a fraction of the microorganisms (Lopez and Levinton, 1978). Therefore a higher standing stock signifies higher microbial productivity (= recovery) relative to consumption.

We removed cores of sediment with soda straws (0.6 cm diameter, 5 mm deep), diluted the core in 300 ml of sterilized and millepore-filtered (0.22 micrometers) seawater, and blended the sample for one minute. Then, subsamples were taken and filtered on a Nuclepore Corp. membrane filter that had been stained with a dilute solution of Irgalan black. For counts of bacteria, the sample was stained in a 1:20,000 solution of acridine orange for three minutes before filtrations. For counts of microalgae, no staining was employed. For both algae (at 500×) and bacteria (at 1250×), we counted 20 grids on a Zeiss model 18 compound microscope equipped with a 50 watt quartz halogen ultraviolet epifluorescence apparatus (see Hobbie *et al.*, 1977). In the case of bacteria and diatoms, cells per grid were counted. A simple count was not possible for filamentous blue-green algae because strands were broken up into different lengths by the blender. We therefore counted number of cells rather than number of strands. Subsamples of sediment were weighed separately so that cell counts could be normalized (see

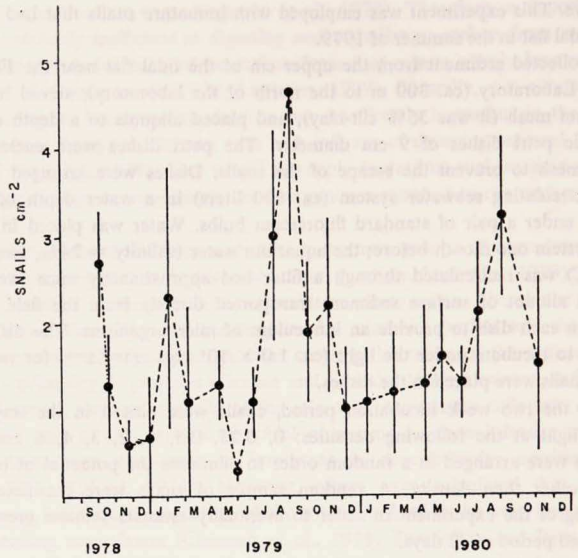

Figure 1. Seasonal variation in densities of *Hydrobia totteni* on a mud flat in the Flax Pond, New York, *Spartina* marsh. Bar indicates 95% confidence limit of mean (N = 10). Recruitment occurs in July-September.

Fig. 3). We estimated differences in microbial abundance on coarse and fine sediment fractions by counting bacteria, diatoms and blue-green algae on sedimentary particles that could pass a 0.0625 mm sieve.

The percent pelletization of the sediment was estimated through a point count technique. Unblended sediment was removed at the end of the experiment, wet-mounted on a slide, and examined at 200×. Intersections of a standard Zeiss grid were used for counts and ca. 2000 points were counted to estimate the percent of the sediment that was pelletized.

The response of the snails to the different density treatments was estimated as follows. Snail somatic growth was estimated by sampling snails from each density, blotting on tissue paper for one minute and wet-weighing individually on a Cahn DTL top loading microbalance; shell length was also measured with the aid of a micrometer eyepiece fixed on a dissecting microscope. We found that blotted wet weight was an excellent estimator of shell dimensions. Counts of live snails at the end of the experiment were used to estimate density-dependent mortality. About half-way through the experiment, the number of snails floating were counted to see

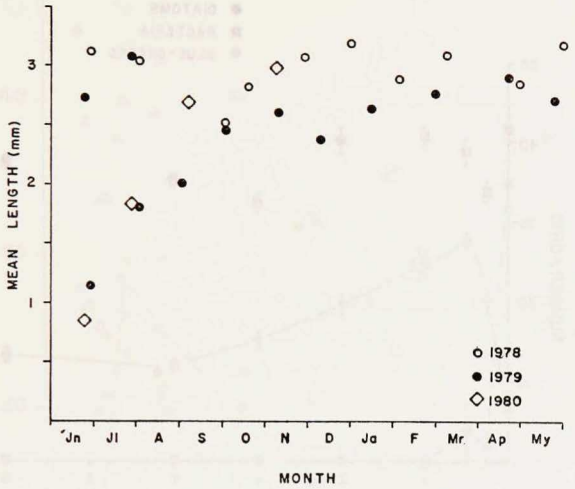

Figure 2. Seasonal variation in mean shell length (in mm) of three successive year classes. Sample size is usually greater than 100.

if density-dependent emigration from the sediment had occurred (as in Levinton, 1979b).

3. Results

We illustrate the seasonal variation in density of *Hydrobia totteni* at the Flax Pond site in Figure 1. Recruitment occurs in summer; density decreases in the early fall and hovers subsequently at about densities of 1-2 snails per square cm. Aside from the early fall, no seasonal decline in population density can be detected. Variation between months probably reflects spatial variation; it is therefore likely that biological or physical disturbance plays little role in reducing population density. The initial decline in density after juvenile recruitment may be due to density-dependent emigration (Levinton, 1979b) or predation.

Figure 2 illustrates seasonal variation in body size of the two year classes, 0^+ and 1^+, that may be present at any given time. In the summer, reproducing adults may be distinguished from recruiting juveniles by size and the eroded shell texture of the older individuals. In two years, 1979 and 1980, we have found that snails do not survive long after reproduction. By fall, the juvenile year class is the only one present. Therefore there is complete turnover of the population between years;

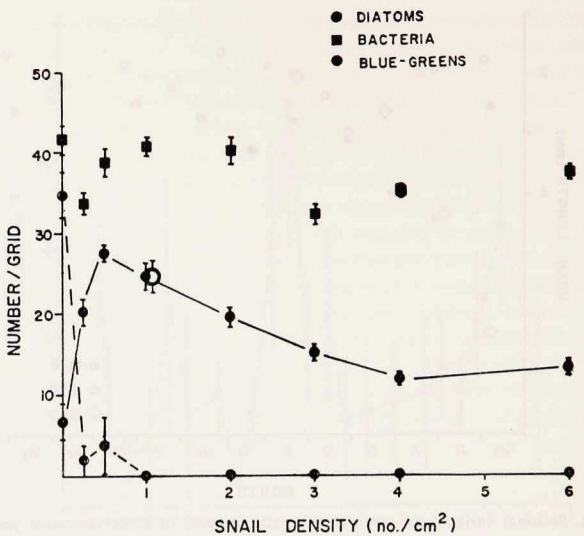

Figure 3. Steady-state abundance of bacteria, diatoms, and cells of filamentous blue greens, as a function of snail density in the laboratory. For bacteria, grid count divided by 9.00×10^{-6} yields number per mg sediment. For algae, the appropriate factor is 5.39×10^{-6}. Open circle indicates diatom abundance in field situation, based on 20 sediment cores, 20 grids/core (see text). Error bars denote 95% confidence limit.

this makes the similarity in population density between years in winter more meaningful.

Figure 3 shows the laboratory results of our estimate of standing stock of bacteria, diatoms and filamentous blue-green algae (*Oscillatoria* sp.). All three components are known to be efficiently digested and assimilated by *Hydrobia* (Kofoed, 1975). We therefore assume that our results reflect an interaction between grazing and renewal. Despite the efficient digestion of bacteria by *Hydrobia* (Lopez and Levinton, 1978), there is no effect of increasing snail density upon bacterial standing stock (Fig. 3). However, there is an apparent effect on the filamentous blue greens and diatoms. Filamentous blue greens are abundant in the absence of snails; however, standing stock declines to zero at a density of 1 snail per square cm. For all practical purposes, the blue greens are absent even at snail densities of 0.25 cm^{-2}. At low snail densities, diatom standing stock varies reciprocally with filamentous blue-green algae. Apparently, *Oscillatoria* is competitively superior

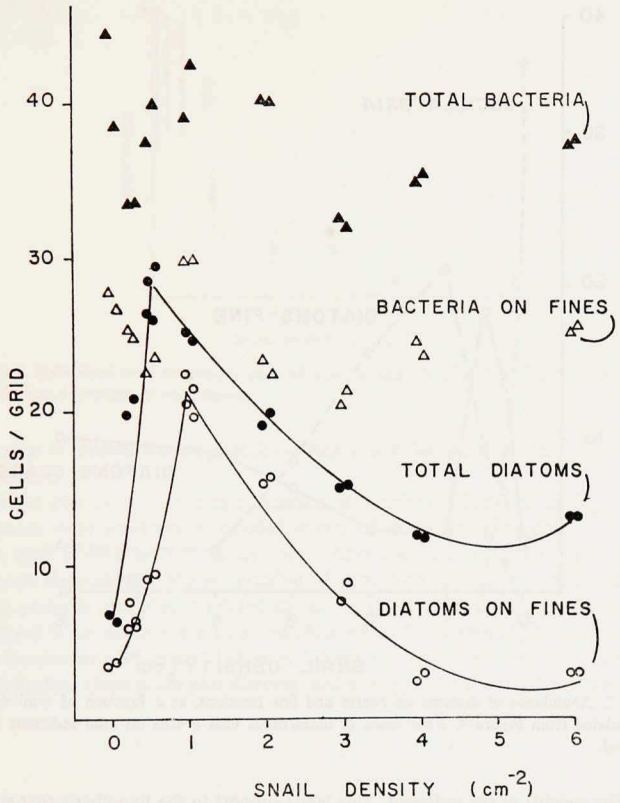

Figure 4. Bacteria and diatom standing stock for whole sediment, and for fraction with particles less than 62 microns particle diameter. Each point represents the mean number of cells per grid (N = 20) counted from a single sediment core. Error bars are small and comparable to Figure 4.

under conditions of minimal grazing (Fenchel and Kofoed, 1976). Above densities of 0.5 snails cm^{-2}, diatom standing stock declines to minimal values.

Figure 4 illustrates microbial standing stock of diatoms and bacteria on the whole sediment sample, and on particles less than 62 microns in diameter. Approximately 60 percent of the bacterial standing stock is associated with the less than 62 micron fraction, even though this particle size range is only about

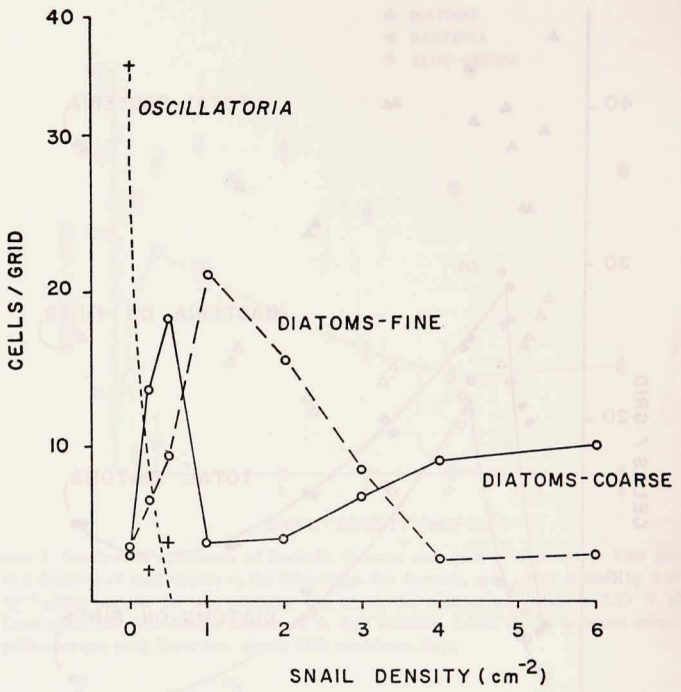

Figure 5. Abundance of diatoms on coarse and fine fractions, as a function of snail density. Calculated from Figure 4. Abundance of filamentous blue greens on total sediment is also plotted.

35% (by weight) of the sediment. This lends support to the hypothesis that surface area is a strong component in the control of bacterial standing stock; the average surface area of the larger particles is approximately half that of the less than 62 micron size fraction.

Diatoms show a particle size-dependent difference in the snail density at which diatom standing stock reaches a maximum (Fig. 4). In the total sediment, diatom density reaches a peak at 0.5 snails cm^{-2}; in the less than 62 micron fraction, diatoms reach a maximum at 1 snail per cm^{-2}. Repeat sampling was done at and around the peaks to ensure that this result was not fortuitous. By implication, at a snail density of 0.5, most of the diatoms are on larger particles; at a density of 1.0 most diatoms are on the fine particles. Figure 5 summarizes the calculated

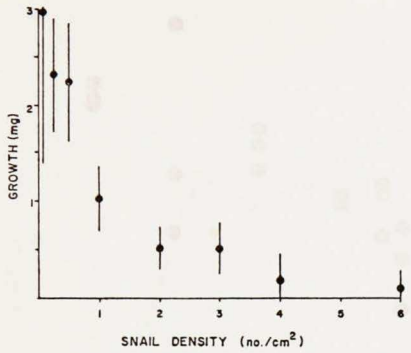

Figure 6. Individual total dry weight gain of snails in mg (± 95% confidence interval) after 72 days as a function of snail density.

difference in diatom standing stock on larger and fine particles, as a function of snail density.

Weight gain of the snails as a function of density is illustrated in Figure 6. A few snails were accidentally included in one of the controls, so data is available for a snail density of 0.08 snails cm^{-2}. Above a density of 0.5 cm^{-2}, growth decreases dramatically; the relationship of growth to density is clearly not linear and is probably not simply related to density itself. Snail growth is similarly not depressed when diatoms are rare and filamentous blue-green algae are abundant, as at the density of 0.08 cm^{-2}. Figure 7 shows the relationship between total algal standing stock (blue-green plus diatoms) and snail growth; the relationship is strong

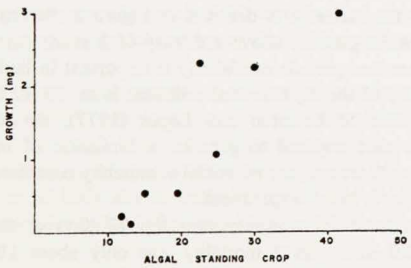

Figure 7. Relationship between snail growth and algal standing stock (number of cells per grid, filamentous blue greens plus diatoms) measured at the end of the experiment: $r = 0.90$, $p < .01$.

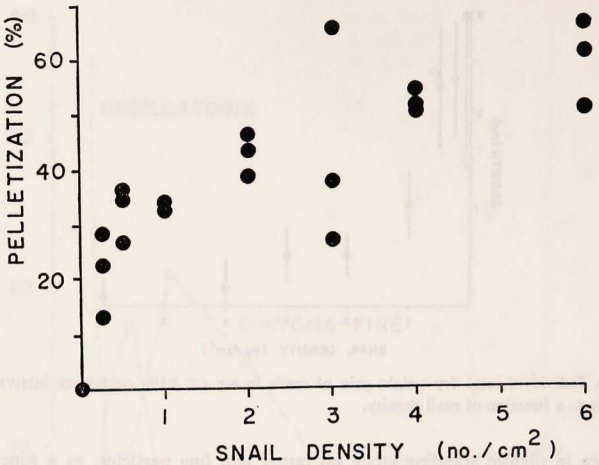

Figure 8. Steady-state percent pelletization of the experimental sediment, as a function of snail density.

($r = 0.90$, $p < .01$). This suggests that snail growth is strongly dependent upon steady state algal abundance, which is a balance between grazing and recovery. Very clearly, bacteria have little to do with snail growth variation, as bacteria do not vary monotonically over the range of snail densities investigated. Therefore, bacteria are not likely to be important in the total nutrition of the snails. At low algal standing stock (i.e., at 4 or 6 snails cm^{-2}) snail growth did not differ significantly from zero (95% confidence). At high snail density, feeding rate was probably depressed greatly (Levinton, 1979b).

Pelletization of the sediment is depicted in Figure 8. Percent pelletization increases to an apparent plateau, above a density of 2 snails cm^{-2}. However, it is unlikely in this case that particle availability is important in limiting snail growth. The percent silt-clay of the experimental sediment is ca. 35%. Using the assumptions and calculations of Levinton and Lopez (1977), the abundance of fine particles surpasses that required to generate a limitation of ingestable particles due to pelletization. Therefore, the microbial community constitutes the only important renewable resource in this experiment.

Figure 9 shows the total mortality over the 72 days of the experiment. At densities of 0.5-2.0 snails cm^{-2} mortality was only about 10%. Above these densities, mortality was approximately three times greater.

Although snail growth is directly attributable to the abundance of diatoms and blue-greens, it is not clear how this relates to field conditions. We collected soda

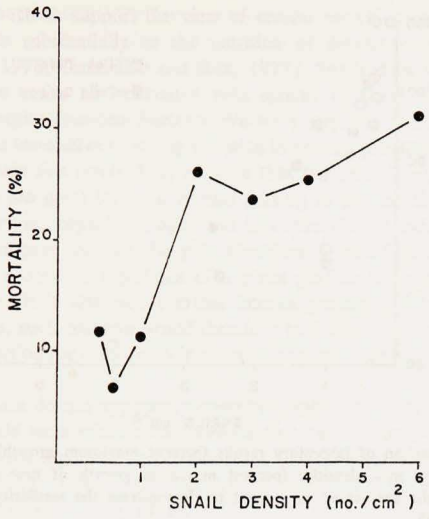

Figure 9. Percent mortality, as a function of snail density.

straw cores at the Flax Pond site on 10 August 1979 and estimated *Hydrobia* density with core sampling. We used a previously established weight-shell length regression to calibrate the August snail abundance in terms of a density equivalent to that used in the experiment. The results are plotted in Figure 3; as can be seen, the snail population collected in August was equivalent to an experimental snail density of ca. 1 snail cm^{-2}. The data demonstrate that algal standing stock in the laboratory approximates adequately field conditions of grazing, to the extent that a gulp of sediment in the laboratory or the field provides the same amount of food.

One last piece of evidence permits a calibration of somatic growth in the laboratory with field conditions. In October, 1980 we collected samples from a variety of sites in Flax Pond. Figure 10 shows the variation of body size of the 0+ year class as a function of density, compared with our laboratory results. The similarity of decline of body size in both laboratory and field conditions argues for the role of resource limitation in field populations of *Hydrobia.*

4. Discussion

Our results suggest that diatoms and blue-green algae are the principal food of the deposit-feeding snail *Hydrobia totteni.* For the silty sediments of Flax Pond,

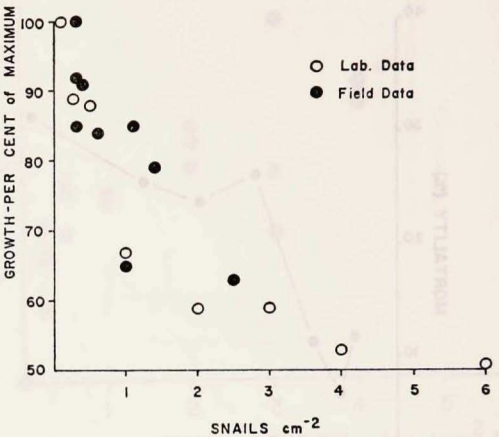

Figure 10. Comparison of laboratory results (percent maximum growth) with field samples over a range of snail densities (percent maximum growth of new recruits). Field and laboratory results are scaled as percent to demonstrate the similarity in relationship of density to growth.

sediment pelletization does not have a major effect on feeding limitation. Furthermore, bacterial standing stock is not affected by *Hydrobia* grazing, despite the fact that *Hydrobia* is known to digest efficiently bacteria in sediments (Lopez and Levinton, 1978). Despite standing stocks of ca. 10^9 cells per gram of sediment, it is unlikely that bacteria contributed meaningfully to somatic growth of the snails. Snail growth declines to zero despite high bacterial abundance.

Snail growth is affected strongly at densities above 0.5 cm^{-2}. Because (a) field diatom densities are close to those measured in our microcosms (Fig. 3), and (b) laboratory and field individuals show a similar decline in somatic growth with increasing density (Fig. 10), we feel justified in concluding that *Hydrobia* populations in Flax Pond are food-limited with respect to somatic growth. The similar population density maintained despite complete population turnover (after recruitment in the summer) suggests that population size is regulated by limiting resources as well. Food limitation may affect the reserves available for allocation to reproductive activities.

In these experiments, we have used standing stock of microbes as an estimate of available food for deposit-feeders. This is valid as long as standing stock represents a steady state between consumption and microbial production. The decline of algal standing stock with increasing snail density implies that equilibrium standing stocks are being reduced due to grazing.

Our data for bacteria support the view of several recent authors that bacteria do not contribute substantially to the nutrition of deposit-feeding macrofauna (Cammen *et al.*, 1978, Tunnicliffe and Risk, 1977). Snails show strong variations in growth over a series of treatments with similar bacterial abundance. Snail growth is zero, despite abundant bacteria. We were surprised to find that bacterial standing stock was insensitive to strong variation in grazing pressure. Several factors may help to explain this result. It is possible that the rate of population growth of the bacteria is too great for even intense grazing to prevent the bacteria from reaching their carrying capacity. Lopez and Levinton (1978) estimated ca. 50% digestion with one pass through the gut. Therefore it would take only one cell division between successive ingestions of a given particle for complete bacterial recovery to occur. It is also possible that intense grazing selects eventually for indigestable forms; such bacteria would therefore be impervious to digestion. This might involve selection for forms with increased attachment strength to sedimentary particle surfaces.

Although bacteria do not apparently contribute substantially to the nutrition of *H. totteni,* it would be a mistake to conclude that other deposit-feeders gain no benefit from bacterial digestion and assimilation. In particular, smaller forms such as meiofauna probably depend upon bacteria for nutrition (e.g., Alongi and Tietjen, 1980; Stewart and Levinton, 1981).

Our results seem to suggest that *H. totteni* can subsist entirely upon microalgae. Furthermore, populations in the field appear to be living under conditions of food limitation. It is possible that non-living detritus also contributes to *Hydrobia* nutrition under field conditions (e.g., Tenore, 1977). From November to March, the tidal flat at Flax Pond is usually completely covered by the sea lettuce *Ulva rotundata.* Decomposition of this seaweed probably contributes nitrogen-rich detritus directly to the sediment. In the late spring and summer the sediment is bare of seaweed and inputs are probably slight.

The change in domination of the sediment from blue greens to diatoms with increased grazing pressure was first observed by Fenchel and Kofoed (1976). They ascribed the success of diatoms to disturbance of the sediment which created an unfavorable microenvironment for the filamentous blue greens. Their data furthermore suggested that *Hydrobia* did poorly on a sediment dominated by *Oscillatoria,* perhaps because of the indigestability of this algae. Our results differ; *H. totteni* seems to grow well on sediments poor in diatoms and rich in *Oscillatoria.* This is consistent with Kofoed's (1975) finding that *Hydrobia* efficiently assimilates *Oscillatoria.* We therefore suggest that diatoms become competitively dominant under modest grazing because of the low recovery rate of *Oscillatoria* under even modest grazing pressure. This implies that microbial availability is strongly dependent upon grazing pressure, which is likely to vary on a small spatial scale. Differential digestion of given microbial organisms by different species (e.g., Bianchi and

Levinton, 1981) will create further heterogeneity. Therefore consumer spatial heterogeneity is of great importance in microbial dynamics.

Our data on diatom standing stock as a function of particle size are enigmatic. Diatoms on particles greater than 62 microns reach a peak in standing stock at a lower grazing pressure than for diatoms on particles finer than 62 microns. We have no ready explanation for this difference. However, it is of interest that snails grew well when diatoms were mainly on particles larger than 62 microns (Fig. 6). Other evidence suggests that *Hydrobia* mainly scrapes the surface of such particles (Lopez and Levinton, 1978; Levinton and DeWitt, 1981). Therefore, *Hydrobia* feeding may vary from scraping to swallowing of particles with equally vigorous somatic growth.

The role of microalgae in the nutrition of *Hydrobia* confirms Levinton's (1979) model of resource limitation of deposit-feeders by renewable resources. Our experimental results demonstrate that algal recover rate is too slow to permit food to be superabundant for deposit-feeding populations under typical field population densities of *Hydrobia*. Thus, interspecific competition for resources may be a driving force in the evolution of morphological change in deposit-feeding species (Fenchel, 1975). We suggest, however, that population density and particle size alone are probably insufficient to predict the success of a given deposit-feeding species. Deposit-feeder-microbial interactions may vary strongly from species to species and may change with grazing intensity and sediment reworking. Differences in detrital input (Tenore *et al.*, 1979) may also generate strong heterogeneity. These factors suggest that interspecific interactions may be complex and variable, depending upon local environmental conditions.

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REFERENCES

Alongi, D. M., and J. H. Tietjen. 1980. Population growth and trophic interactions among free-living nematodes, pp. 151-166, *in* Marine Benthic Dynamics, K. R. Tenore and B. C. Coull, eds., Univ. of South Carolina, Columbia, 451 pp.

Bianchi, T. S. and J. S. Levinton. 1981. Nutrition and food limitations of deposit-feeders. II. Differential effects of *Hydrobia totteni* and *Ilyanassa obsoleta* on the microbial community. J. Mar. Res., *39*, 547–556.

Calow, P. 1975. The feeding strategies of two fresh water gastropods, *Ancylus fluviatilis Mull.* and *Planorbis contortus* Linn. (Pulmonata) in terms of ingestion rates and absorption efficiencies. Oecologia, *19*, 33–49.

Cammen, L., P. Rublee, and J. Hobbie. 1978. The significance of microbial carbon in the nutrition of the polychaete *Nereis succinea* and other aquatic deposit-feeders. Univ. of North Carolina Sea Grant Publ., UNC-SG-78-12, 1–84.

Fenchel, T. 1975. Character displacement and coexistence in mud snails (Hydrobiidae). Oecologia, *20*, 19–32.

—— 1970. Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr., *15*, 14–20.

Fenchel, T., and L. H. Kofoed. 1976. Evidence for exploitative interspecific competition in mud snails. Oikos, *27*, 367–376.

Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaets. J. Mar. Res., *32*, 253–284.

Hargrave, B. 1970. The utilization of benthic microflora by *Hyalella azteca* (Amphipoda). J. Anim. Ecol., *39*, 427–437.

Hobbie, J. E., R. J. Daley, and S. Jasper. 1977. Use of Nucleopore filters for counting bacteria by fluorescence microscopy. Appl. Environ. Microbiol., *33*, 1225–1228.

Kofoed, L. H. 1975. The feeding biology of *Hydrobia ventrosa* (Montagu). I. The assimilation of differing components of the food. J. Exp. Mar. Biol. Ecol., *19*, 233–241.

Levinton, J. S. 1979a. Deposit-feeders, their resources and the study of resource limitation, pp. 117-141, *in* Ecological Processes in Coastal and Marine Systems, R. J. Livingston, ed., Plenum Publ. Co., New York, 548 pp.

—— 1979b. The effect of density upon deposit-feeding populations: movement, feeding and floating of *Hydrobia ventrosa* Montagu (Gastropoda Prosobranchia). Oecologia, *43*, 27–29.

Levinton, J. S., and T. H. DeWitt. 1981. Relation of resource spectrum variation and body size to particle selectivity in mud snails (Hydrobiidae). Submitted to Ecology.

Levinton, J. S., and G. R. Lopez, 1977. A model of renewable resources and limitation of deposit-feeding benthic populations. Oecologia (Berl.) *31*, 177–190.

Lopez, G. R., and L. H. Kofoed. 1980. Epipsammic browsing and deposit-feeding in mud snails (Hydrobiidae). J. Mar. Res., *38*, 585–599.

Lopez, G. R., and J. S. Levinton. 1978. The availability of microorganisms attached to sediment particles as food for *Hydrobia ventrosa* Montagu (Gastropod:Prosobranchia). Oecologia (Berl.), *32*, 263–275.

Lopez, G. R., J. S. Levinton, and L. B. Slobodkin. 1977. The effect of grazing by the detritivore *Orchestia grillus* on *Spartina* litter and its associated microbial community. Oecologia (Berl.), *20*, 111–127.

Newell, R. C. 1965. The role of detritus in the nutrition of two marine deposit-feeders, the probobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc. Zool. Soc. Lond., *144*, 25–45.

Stewart, S., and J. S. Levinton. 1981. The relation of sediment volume and surface area of the sediment-water interface to population growth of the mud flat oligochaete, *Paranais litoralis*. Submitted to J. Exp. Mar. Biol. Ecol.

Tenore, K. R. 1977. Growth of the polychaete *Capitella capitata*, cultured on different levels of detritus derived from various sources. Limnol. Oceanogr., *22*, 936–941.

Tenore, K. R., R. B. Hanson, B. E. Dornseif, and C. N. Weiderhold. 1979. The effect of organic nitrogen supplement on the utilization of different sources of detritus. Limnol. Oceanogr., *24*, 350–355.

Tunnicliffe, V., and M. J. Risk. 1977. Relationships between the bivalve *Macoma balthica* and bacteria in intertidal sediments: Minas Basin, Bay of Fundy. J. Mar. Res., *35*, 499–507.

Yingst, J. Y. 1976. The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. J. Exp. Mar. Bio. Ecol., *23*, 55–69.

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