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## Epipsammic browsing and deposit-feeding in mud snails (Hydrobiidae)

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### ABSTRACT

A study of feeding behavior of *Hydrobia ulvae* Pennant, *H. ventrosa* Montagu, *H. neglecta* Muus, and *Potamopyrgus jenkinsi* Smith (Hydrobiidae, Gastropoda) on a wide size range of sediment fractions showed that these snails are capable of feeding on material adhering to sediment particles by swallowing small particles (deposit-feeding), and by browsing upon particle surfaces, which we call "epipsammic browsing". Epipsammic browsing on small particles is accomplished by taking particles into the buccal cavity, scraping off attached microorganisms, and then spitting out of the particle. This feeding mechanism has not been previously described for molluscs. Epipsammic browsing could allow utilizing food adhering to sand grains that are small enough to be swallowed.

### 1. Introduction

In a pioneering study, Newell (1965) suggested that *Hydrobia ulvae* digested only living microorganisms from ingested sediments. Several more recent studies on various deposit-feeders have shown efficient digestion of microorganisms while organic debris was inefficiently utilized (Hargrave, 1970; Fenchel, 1970; Kofoed, 1975a; Yingst, 1976; Wetzel, 1977; Lopez *et al.*, 1977; Cammen *et al.*, 1978). Nutritional value of organic debris depends upon parent material, age and nutrient

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supply (Tenore *et al.*, 1979; Tenore and Rice, 1980). Where organic debris is more abundant than living microorganisms in sediment, deposit-feeders may obtain much of their nutrition from inefficient digestion of debris rather than efficient use of microorganism (Cammen *et al.*, 1978). Conditioning of the detritus by microorganisms may increase the palatability of the litter itself for detritus-feeding animals (Bärlocher and Kendrick, 1975).

Deposit-feeders may rely more on microorganisms than debris as their main nutritional source. Organic debris in sediments is very heterogeneous, and it becomes more refractory with time. An animal relying on this material would require an extensive set of digestive enzymes to utilize food whose nature varies with season and location. Furthermore, it would require enzymes capable of digesting cellulose, lignin, and other refractory materials. In contrast, animals relying on microorganisms might have a more constant food supply that can be digested with fewer enzymes. Organic debris is usually relatively rich in carbon and poor in nitrogen, vitamins and trace elements. Deposit- and detritus-feeders may be limited more frequently by protein supply than carbon (Newell, 1965; Longbottom, 1970; Fenchel and Jørgensen, 1977; Tenore, 1977). Microorganisms are enriched sources of potentially limiting protein.

Hydrobiid snails are considered to be deposit feeders which ingest sedimentary particles and assimilate the associated microorganisms (Fenchel, 1975b; Fenchel *et al.*, 1975; Kofoed, 1975a; Lopez and Levinton, 1978). The distribution in Danish waters of four species of hydrobiid snails (*Potamopyrgus jenkinsi*, *Hydrobia ulvae*, *H. ventrosa* and *H. neglecta*) may be controlled by habitat selection, local migrations and extinctions, and interspecific competition (Fenchel, 1975a). *H. ulvae* are larger when they are sympatric with *H. ventrosa* than when they occur alone (Fenchel, 1975a). For all species, median particle size ingested is a simple function of body size and sediment composition (Fenchel and Kofoed, 1976). Benthic algae, mostly diatoms, are an important food source, and these authors described particle size selectivity by animals of different sizes in terms of selection of diatoms of different sizes. The small size difference between sympatric *H. ventrosa* and *H. neglecta* cannot be explained simply by resource partitioning through character displacement of body size (Fenchel, 1975b). Nevertheless, this combination of species is common in Denmark. If these species do partition the food resource on the basis of size, it is not reflected in animal size. Quantitative differences in digestive enzymes between *H. ventrosa* and *H. neglecta* may in part explain their sympatric distribution without size displacement (Hylleberg, 1976).

Gut contents of *H. ulvae* can contain more diatoms than the offered sediment (Fenchel *et al.*, 1975). The animals might be able to distinguish between diatoms and similarly-sized sand grains, or they might concentrate diatoms by scraping them from particle surfaces. The reported "negative" digestion of diatoms (pro-

portionally more diatoms in feces than in sediment, on a weight basis) by *H. ventrosa* when fed narrow size fractions of sediment (i.e. 20-45  $\mu\text{m}$ ) also suggests the same possibilities (Lopez and Levinton, 1978).

*Hydrobia* spp. can occur on a wide variety of substrates. We have found abundant populations of *H. ulvae* in well-sorted sand in Kerteminde Fjord, Denmark and in the intertidal mud slicks of the Wadden Sea near Skallingen, Denmark. Subtidal *H. ulvae* populations in the Limfjord, Denmark occur in fine-grained sediment that has been almost completely pelletized by itself and *Abra alba* (Jørgensen, 1977). In the eastern Baltic, *H. ulvae* and *H. ventrosa* are found on exposed sand, rocks and *Fucus* (Koli, 1961, cited in Fenchel, 1975a). Fretter and Graham (1962) stated that the distribution of *H. ulvae* is unrelated to sediment type.

Nevertheless, hydrobiids may prefer certain sediments over others, and population abundance may be controlled by sediment type. *H. ulvae* preferred finer sediment grades when given a choice of different fractions or natural sediments, but greatest abundance occurred in some sandy sediments (Barnes and Greenwood, 1978). However, in other choice experiments *H. ulvae* showed no preference to sediment size fractions (Fenchel *et al.*, 1975). Abundance of *H. ulvae* in samples from the North Kent coast was correlated with sediment grain size; more snails were found in finer sediment (Newell, 1965). Sediment type may also affect individual size. *H. ulvae* from salt marshes attained a larger mean size than those from sand flats and sandy-mud flats (Chatfield, 1972).

The extent to which food controls distribution and abundance of hydrobiids is not known, but it is clear that they are not restricted to deposit-feeding upon sedimentary microflora. *H. ulvae* can feed upon *Enteromorpha* and *Ulva* (references cited in Newell, 1965). *Hydrobia* spp. are able to float at the water surface and feed upon the microbial film (Newell, 1962). Baltic populations of *H. ulvae* and *H. ventrosa* browse on rocks (Koli, 1961, cited in Fenchel, 1975a), and *H. ventrosa* can browse on large sand grains (Lopez and Levinton, 1978).

Given this evidence, we studied the feeding rates of four hydrobiid species upon a wide range of sediment particles to help elucidate the relationship between sediment grade and hydrobiid abundance.

## 2. Materials and methods

We measured feeding rates of snails upon different fractions of sediment.  $^{14}\text{C}$  was used to label the surfaces of the sediment particles. The amount of ingested label was then used to calculate feeding activity in terms of sediment surface area treated by the animals.

*a. Collection.* *H. ulvae* were collected from Munkebo, Kerteminde Fjord. *H. ventrosa* and *H. neglecta* were collected from a pond near Kalø Slotsruin, Aarhus Bay, and *P. jenkinsi* were collected from Seden Strand, Odense Fjord.

Feeding experiments on *Hydrobia* spp. were carried out with sediment and water (24‰) collected at Munkebo. The sediment was a well-sorted quartz sand, 230  $\mu\text{m}$  median diameter. For experiments on *P. jenkinsi*, sediment and water (14‰) collected at Seden stand were used. This sediment was more poorly sorted, and contained a large amount of shell fragments. Sediment fractions (< 40 $\mu\text{m}$ , 40-80 $\mu\text{m}$ , 80-160 $\mu\text{m}$ , 160-315 $\mu\text{m}$ , 315-630 $\mu\text{m}$ , 630-1000 $\mu\text{m}$ ) were prepared by wet sieving and decantation, then stored at 2°C until needed. All experiments were conducted at 20°C. Seawater was filtered (0.2  $\mu\text{m}$ ) before use.

*b. <sup>14</sup>C labeling of sediment fractions.* Approximately 10  $\mu\text{Ci}$  <sup>14</sup>C-glucose (carrier-free, acidified to pH 2) was added to a plastic centrifuge tube containing 6 ml sediment fraction and 30 ml seawater, and incubated in the dark at 20°C for 15 minutes. The tube was shaken several times during incubation. At the end of the labeling period, the sample was centrifuged 5 minutes at 1000 rpm, decanted, and washed twice with 30 ml seawater. Labeled, washed sediment was stored 1 hour in dark before use. Preliminary experiments showed that <sup>14</sup>C associated with sediment after incubation and washing was lost from the sediment at  $\sim 1\text{-}4\% \times \text{hr}^{-1}$ .

*c. Feeding experiments.* One day before beginning a feeding experiment, the experimental animals were placed on unlabeled sediment fractions in glass petri dishes. The animals were transferred to dishes containing only seawater one hour before starting an experiment. One dish was set up for each sediment grade. An experiment was started by placing 4 ml labeled sediment into each dish containing 80 or 100 snails. The remaining sediment was preserved with 3% formalin-seawater, and used to determine specific activity of the sediments ( $\text{dpm} \times \text{mg}^{-1}$  dry sediment).

Animals were allowed to feed on labeled sediment for 20 minutes. Animals that crawled away from the sediment were gently pushed back with forceps. In all experiments practically all animals displayed active movement and feeding activity. At the end of the feeding period, the animals were sieved from the sediment, rinsed in seawater, and cleaned of remaining adhering material with tissue paper.

Because mean gut passage time of food particles in actively feeding snails is approximately 30-40 minutes (Fenchel, 1972), presumably little or no ingested material was lost due to egestion during the 20 minutes feeding period. Very little label was lost as snail metabolic products during this period (Kofoed, 1975b). The animals from each sediment size class were then divided into groups of 10 animals. Each sub-group was immediately dropped into scintillation vials containing 5 ml formalin-seawater (3%). The contents were then blended with an Ultra-Turrax blender (IKA WERK, Breisgau) for 40 sec., and mixed with 5 ml Instagel (Packard). The blender tip was washed in 5 ml seawater in a separate scintillation vial.

Labeled sediment was prepared for scintillation counting by drying (105°C) and weighing, then placing it in a scintillation vial with 5 ml water, allowing it to rehy-

drate for several hours. Samples were then homogenized in an ultrasonic bath for 15 minutes followed by addition of 5 ml Instagel. Before Instagel was added to the  $< 40 \mu\text{m}$  sediment fraction, the sample was also homogenized with an Ultra-Turrax blender. Samples were then counted for a least 40 minutes or 10,000 cpm and corrected to dpm. All counts were well above background.

Detailed observations of feeding behavior on various grades of unlabeled sediment were made with an inverted microscope at low magnification ( $40\times$ ), and recorded on videotape.

### 3. Results

Feeding rates ( $\text{dpm ingested} \times \text{animal}^{-1} \times \text{hr}^{-1}$ , row 1) and sediment labelling ( $\text{dpm} \times \text{mg}^{-1}$ , row 2) were used to calculate feeding rates upon sediment surfaces (row 6) (Tables 1 to 4). Relative surface feeding rates (row 7) were calculated by dividing surface feeding rates of each sediment class (row 6) by the maximum feeding rate of that row. Feeding rates upon sediment surfaces include swallowed particles and  $^{14}\text{C}$ -labelled material scraped from non-ingested particles. Calculating the results on an areal basis rather than by volume or weight avoids giving undue importance to sediments that were browsed.

#### *H. ulvae* 4-4.5 mm (shell length)

*H. ulvae* fed most rapidly upon  $< 40 \mu\text{m}$  and  $40\text{-}80 \mu\text{m}$  sediments (Table 1, row 7). Feeding was approximately 3 times faster on  $40\text{-}80 \mu\text{m}$  than on  $80\text{-}160 \mu\text{m}$  and was lowest on  $315\text{-}630 \mu\text{m}$ . These snails cannot ingest particles larger than  $\sim 200 \mu\text{m}$  (based on fecal pellet measurement), so feeding upon larger particles was due solely to browsing.

#### *H. ventrosa* (2.5-3.0 mm)

*H. ventrosa* fed approximately 3 times faster on  $< 40 \mu\text{m}$  sediment than on  $40\text{-}80 \mu\text{m}$  sediment (Table 2). Feeding rates upon the 4 larger sediments classes averaged approximately 20% maximum feeding rate. These snails cannot swallow particles larger than  $\sim 120 \mu\text{m}$ .

#### *H. neglecta* (2.5-3.0 mm)

In contrast to *H. ventrosa*, *H. neglecta* displayed maximum surface feeding rate on  $40\text{-}80 \mu\text{m}$  sediment, which was approximately 30% faster than on  $< 40 \mu\text{m}$  and twice that of  $80\text{-}160 \mu\text{m}$  (Table 3). There were no differences in the 3 larger sediments, on which the snails fed at approximately 25% maximum rate. Maximum ingestible particle was  $\sim 120 \mu\text{m}$ .

#### *P. jenkinsi* (3.0-3.5 mm)

Maximum feeding rate was on  $80\text{-}160 \mu\text{m}$  sediment, which was approximately twice that for  $40\text{-}80 \mu\text{m}$  and  $160\text{-}315$ , and 20% higher than  $< 40 \mu\text{m}$  (Table 4).

Tables 1 to 4.

row 1:  $\text{dpm} \times \text{animal}^{-1} \times \text{hr}^{-1}$ ,  $\bar{x} \pm \text{S.D.}$  Sample number ( $n$ ) refers to number of groups of 10 animals that fed for 20 minutes.

row 2:  $\text{dpm} \times \text{mg}^{-1}$  sediment,  $\bar{x} \pm \text{S.D.}$ , dry weight.

row 3:  $\mu\text{m}^2 \times \text{mg}^{-1}$  sediment; surface area of each sediment fraction was estimated by assuming particles were spheres having density of  $2.6 \times 10^{-9} \text{mg} \times \mu\text{m}^3$ , and diameter equal to the geometric mean of the upper and lower limits of that fraction, except for the  $< 40 \mu\text{m}$  fraction, where  $1 \mu\text{m}$  and  $40 \mu\text{m}$  were used as limits.

row 4:  $\text{dpm} \times \mu\text{m}^{-2}$  sediment =  $\text{dpm} \times \text{mg}^{-1}$  (row 2)  $\div \mu\text{m}^2 \times \text{mg}$  (row 3).

row 5:  $\text{mg sediment treated} \times \text{animal}^{-1} \times \text{hr}^{-1} = \text{dpm} \times \text{animal}^{-1} \times \text{hr}^{-1}$  (row 1)  $\div \text{dpm} \times \text{mg}^{-1}$  sediment (row 2).

row 6:  $\mu\text{m}^2$  sediment treated  $\times \text{animal}^{-1} \times \text{hr}^{-1} = \text{dpm} \times \text{animal}^{-1} \times \text{hr}^{-1}$  (row 1)  $\div \text{dpm} \times \mu\text{m}^{-2}$  sediment (row 4).

row 7: % maximum feeding rate; values in row 6 divided through by maximum value in row 6.

Values which are not statistically different have a continuous line beneath them.

Note: in rows 5 and 6, variance of the computed quotients were estimated

$$\approx \left( \frac{\mu_x^2}{\mu_y} \right) \left( \frac{\text{var}\{x\}}{\mu_x^2} + \frac{\text{var}\{y\}}{\mu_y^2} \right).$$

Table 1.

<i>H. ulvae</i>	Sediment Size Fraction ( $\mu\text{m}$ )						
	<40	40-80	80-160	160-315	315-630	630-1000	
1) $\text{dpm} \times \text{animal}^{-1} \times \text{hr}^{-1}$	5,543 $\pm 446$	2,937 $\pm 248$	725 $\pm$ 91	492 $\pm$ 75	196 $\pm$ 25	922 $\pm$ 288	$n = 4$
2) $\text{dpm} \times \text{mg}^{-1}$ sediment	8,515 $\pm 694$	610 $\pm 74$	239 $\pm$ 7	206 $\pm$ 3	210 $\pm$ 8	178 $\pm$ 13	$n = 4$
3) $\mu\text{m}^2 \times \text{mg}^{-1}$	3.66 $\pm 10^8$	4.08 $\pm 10^7$	2.05 $\pm 10^7$	1.03 $\pm 10^7$	5.19 $\times 10^6$	2.90 $\times 10^8$	
4) $\text{dpm} \times \mu\text{m}^{-2}$ sediment	2.33 $\times 10^{-5}$ $\pm .19$	1.50 $\times 10^{-5}$ $\pm .18$	1.17 $\times 10^{-5}$ $\pm .03$	2.00 $\times 10^{-5}$ $\pm .03$	4.05 $\times 10^{-5}$ $\pm .15$	6.14 $\times 10^{-5}$ $\pm .45$	
5) mg/sediment treated- $\text{animal}^{-1} \times \text{hr}^{-1}$	.651 $\pm .075$	4.815 $\pm .711$	3.033 $\pm .390$	2.388 $\pm .365$	0.933 $\pm .124$	5.180 $\pm 1.660$	
6) $\mu\text{m}^2 \times 10^9$ treated- $\text{animal}^{-1} \times \text{hr}^{-1}$	238.3 $\pm 27.5$	196.5 $\pm 29.0$	62.2 $\pm 8.0$	24.60 $\pm 3.8$	4.8 $\pm$ 0.6	15.0 $\pm$ 4.8	
7) % maximum surface feeding rate	<u>100%</u>	<u>82.5</u>	<u>26.1</u>	<u>10.3</u>	<u>2.0</u>	<u>6.3</u>	

Table 2.

<i>H. ventrosa</i>	Sediment Size Fraction ( $\mu\text{m}$ )						
	<40	40-80	80-160	160-315	315-630	630-1000	
1) dpm $\times$ animal <sup>-1</sup> $\times$ hr <sup>-1</sup>	1,090 $\pm$ 315	241 $\pm$ 56	178 $\pm$ 75	244 $\pm$ 11	286 $\pm$ 50	593 $\pm$ 216	<i>n</i> = 4
2) dpm $\times$ mg <sup>-1</sup> sediment	12,300 $\pm$ 764	849 $\pm$ 290	462 $\pm$ 70	430 $\pm$ 146	321 $\pm$ 13	337 $\pm$ 123	<i>n</i> = 4
3) $\mu\text{m}^2 \times$ mg <sup>-1</sup>	$3.66 \times 10^8$	$4.08 \times 10^7$	2.05 $\times 10^7$	1.03 $\times 10^7$	5.19 $\times 10^8$	2.90 $\times 10^8$	
4) dpm $\times$ $\mu\text{m}^{-2}$	$3.36 \times 10^{-5} \pm .21$	$2.08 \times 10^{-5} \pm .71$	2.25 $\times 10^{-5} \pm .34$	4.17 $\times 10^{-5} \pm 1.42$	6.18 $\times 10^{-5} \pm .25$	11.62 $\times 10^{-5} \pm 4.24$	
5) mg treated $\times$ animal <sup>-1</sup> $\times$ hr <sup>-1</sup>	0.089 $\pm$ .026	.284 $\pm$ .117	.385 $\pm$ .172	.567 $\pm$ .194	.891 $\pm$ .160	1.760 $\pm$ .906	
6) $\mu\text{m}^2 \times 10^9$ treated- $\times$ animal <sup>-1</sup> $\times$ hr <sup>-1</sup>	32.6 $\pm$ 9.5	11.6 $\pm$ 4.8	7.9 $\pm$ 3.5	5.8 $\pm$ 2.0	4.6 $\pm$ 0.8	5.1 $\pm$ 2.6	
7) % maximum surface feeding rate	100	35.6	24.2	17.8	14.1	15.6	

Table 3.

<i>H. neglecta</i>	Sediment Size Fraction ( $\mu\text{m}$ )						
	<40	40-80	80-100	100-315	315-630	630-1000	
1) dpm $\times$ animal <sup>-1</sup> $\times$ hr <sup>-1</sup>	644 $\pm$ 126	578 $\pm$ 125	294 $\pm$ 69	287 $\pm$ 21	362 $\pm$ 70	873 $\pm$ 105	<i>n</i> = 4
2) dpm $\times$ mg <sup>-1</sup> sediment	12,300 $\pm$ 764	849 $\pm$ 290	462 $\pm$ 70	430 $\pm$ 146	321 $\pm$ 13	337 $\pm$ 123	<i>n</i> = 4
3) $\mu\text{m}^2 \times$ mg <sup>-1</sup>	3.66 $\times 10^8$	$4.08 \times 10^7$	$2.05 \times 10^7$	$1.03 \times 10^7$	$5.19 \times 10^8$	$2.90 \times 10^8$	
4) dpm $\times$ $\mu\text{m}^2$	$3.66 \times 10^{-5} \pm .21$	$2.08 \times 10^{-5} \pm .71$	$2.55 \times 10^{-5} \pm .34$	$4.17 \times 10^{-5} \pm 1.42$	$6.18 \times 10^{-5} \pm .25$	$11.62 \times 10^{-5} \pm 4.24$	
5) mg treated $\times$ animal <sup>-1</sup> $\times$ hr <sup>-1</sup>	.054 $\pm$ .011	.681 $\pm$ .057	.636 $\pm$ .178	.667 $\pm$ .232	1.128 $\pm$ .223	2.591 $\pm$ .994	



Table 3 (continued)

6) $\mu\text{m}^2$	19.8 $\pm$	27.8 $\pm$	13.0 $\pm$	6.9 $\pm$	5.9 $\pm$	7.5 $\pm$	$n = 4$
treated $\times$	4.0	2.3	3.6	2.4	1.2	2.9	
animal <sup>-1</sup> $\times$							
hr <sup>-1</sup> $\times 10^6$							
7) % maximum	71.2	100	46.8	24.8	21.2	27.0	
surface							
feeding rate							

Table 4.

<i>P. jenkinsi</i>	Sediment Size Fraction ( $\mu\text{m}$ )						$n$
	<40	40-80	80-100	100-315	315-630	630-1000	
1) dpm $\times$	1,925	1,660	1,534	1,364	717 $\pm$ 87	1,614	$n = 5$
animal <sup>-1</sup>	$\pm$ 236	$\pm$ 236	$\pm$ 154	$\pm$ 325		$\pm$ 180	
$\times$ hr <sup>-1</sup>							
2) dpm $\times$	11,841	2,674	515 $\pm$ 28	453 $\pm$ 79	256 $\pm$ 51	350 $\pm$ 15	$n = 3$
mg <sup>-1</sup>	$\pm$ 304	$\pm$ 186					
3) $\mu\text{m}^2 \times$	$3.66 \times 10^6$	$4.08 \times 10^7$	$2.05 \times 10^7$	$1.03 \times 10^7$	$5.19 \times 10^6$	$2.90 \times 10^6$	
mg <sup>-1</sup>							
4) dpm $\times$	$3.24 \times 10^{-5}$	$6.55 \times 10^{-5}$	$2.51 \times 10^{-5}$	$4.40 \times 10^{-5}$	$4.93 \times 10^{-5}$	$12.1 \times 10^{-5}$	
$\mu\text{m}^{-2}$	$\pm .08$	$\pm .46$	$\pm .14$	$\pm .77$	$\pm .98$	$\pm .52$	
5) mg	.163 $\pm$ .020	.621 $\pm$ .098	2.979	3.011	2.801	4.611	
treated $\times$			$\pm .340$	$\pm .888$	$\pm .652$	$\pm .550$	
animal <sup>-1</sup>							
$\times$ hr <sup>-1</sup>							
6) $\mu\text{m}^2$	49.8 $\pm$ 7.3	25.3 $\pm$ 4.0	61.1 $\pm$ 7.0	31.0 $\pm$ 9.1	14.5 $\pm$ 3.4	13.4 $\pm$ 1.6	
treated							
animal <sup>-1</sup>							
$\times$ hr <sup>-1</sup>							
$\times 10^6$							
7) % maxi-	81.5	41.4	100	50.7	23.7	21.9	
imum sur-							
face feed-							
ing rate							

Feeding upon the 2 largest sediments were approximately 20% maximum. These snails cannot ingest particles larger than  $\sim 180 \mu\text{m}$ .

We noticed that all species were more mobile when feeding on the larger sediment fraction.

*Direct observation of feeding behavior.* All species were observed with an inverted microscope, but we used larger *H. ulvae* for detailed observations. When *H.*

*ulvae* was presented with  $< 40 \mu\text{m}$  sediment, simple deposit-feeding ensued (i.e. swallowing of sedimentary particles). We could observe no obvious selection or rejection of particles, though the difficulty of following very small particles makes this uncertain. Fine sediment was not ingested as discrete particles, but rather as large clumps of agglutinated material. Small sand grains ( $40\text{-}160 \mu\text{m}$ ) were frequently swallowed, but more often the snail would take a particle (sometimes two at once for small grains) into the buccal cavity for about one second, followed by spitting out of the particles. Some particles were taken in and spit out several times. Radular activity often occurred while the particles were retained within the buccal cavity. When presented with large sand grains, snails browsed on the surface.

#### 4. Discussion and conclusions

*a. Browsing vs deposit-feeding in Hydrobia ulvae.* Because 4-4.5 mm *H. ulvae* cannot ingest particles larger than approximately  $200 \mu\text{m}$ , feeding on the two larger sediment fractions must have been exclusively due to grazing (Table 1). It is interesting, then, to estimate the importance of grazing on the four smaller sediment fractions. Fenchel and Kofoed (1976) measured egestion rates of *Hydrobia* spp. feeding on different sediment size fractions by counting fecal pellets produced by animals feeding on each fraction. Because they counted only pellets composed of ingested particles of each fraction (e.g. pellets produced by animals feeding on  $62\text{-}125 \mu\text{m}$  sediment were counted only if they were composed of  $62\text{-}125 \mu\text{m}$  particles), they measured the rates at which animals fed by swallowing particles (= deposit-feeding). We have converted by interpolation egestion rate vs particle size data for 4-4.5 mm *H. ulvae* from Fenchel and Kofoed (1976) to the size fractions used in our experiments. These results are compared with the results of our experiment on *H. ulvae* in Table 5.

Fenchel and Kofoed (1976) measured maximum deposit-feeding rate on a relative weight basis of 4-4.5 mm *H. ulvae* when the snails fed on  $< 40 \mu\text{m}$  sediment. The animals did not deposit-feed on the three larger size fractions. In our experiment maximum feeding rate, when calculated by sediment weight, occurred upon  $40\text{-}80 \mu\text{m}$  sediment while feeding upon  $< 40 \mu\text{m}$  sediment was only 13.5% as rapid (Table 5). These feeding rates combine the amount of sediment that was swallowed with the amount of sediment scraped but not swallowed. If we assume that *H. ulvae* deposit-fed upon  $40\text{-}80 \mu\text{m}$  sediment 0.92 times as fast as its rate upon  $< 40 \mu\text{m}$ , then the amount of  $40\text{-}80 \mu\text{m}$  sediment swallowed in experiment #1 is  $0.92 \times 0.651 \text{ mg} \times \text{animal}^{-1} \times \text{hr}^{-1} = 0.60 \text{ mg } 40\text{-}80 \mu\text{m}$  sediment swallowed  $\times \text{animal}^{-1} \times \text{hr}^{-1}$ . This is only 12.5% of the measured amount of sediment treated. The same type of calculation indicates that 15.3% of  $80\text{-}160 \mu\text{m}$  sediment treated in experiment #1 was due to deposit-feeding. We cannot make any calculation for  $< 40 \mu\text{m}$  sediment.

Table 5. Deposit feeding and browsing by 4-4.5 mm *H. ulvae*.

	Sediment size fraction ( $\mu\text{m}$ )					
	<40	40-80	80-100	160-315	315-630	630-1000
1) mg sediment treated $\times$ animal <sup>-1</sup> $\times$ hr <sup>-1</sup> , deposit-feeding + browsing (this study)	.651	4.815	3.033	2.388	0.933	5.180
2) % maximum sediment treatment rate, weight (this study)	13.5	100	63.0	—	—	—
3) % maximum ingestion, weight (Fenchel and Kofoed, 1976)	100	92.1	71.0	0	0	0
4) mg sediment ingested $\times$ animal <sup>-1</sup> $\times$ hr <sup>-1</sup> (this study)	?	0.60	0.46			
5) % sediment treatment by deposit-feeding	?	12.5	15.2	0	0	0

row 1: mg sediment treated  $\times$  animal<sup>-1</sup>  $\times$  hr<sup>-1</sup>, deposit-feeding + browsing; from Table 1, row 5.

row 2: % maximum sediment treatment rate, weight = values in row 1 divided through by maximum value in row 1. Because there was no particle ingestion in the three larger size classes (see row 3), relative sediment treatment rates have been calculated only for the 3 smaller size classes.

row 3: % maximum ingestion rate; from Fenchel and Kofoed (1976) converted to particle size fractions used in this study.

row 4: mg sediment ingested  $\times$  animal<sup>-1</sup>  $\times$  hr<sup>-1</sup>; if maximum particle ingestion rate was with < 40  $\mu\text{m}$  sediment, then sediment ingestion rate on 40-80  $\mu\text{m}$  sediment =  $\frac{92.1 \times .651}{100}$  = .60 mg.

row 5: % sediment treatment by ingestion (= deposit-feeding); mg sediment ingested  $\times$  animal<sup>-1</sup>  $\times$  hr<sup>-1</sup> (row 4)  $\div$  mg sediment treated  $\times$  animal<sup>-1</sup>  $\times$  hr<sup>-1</sup> (row 1)  $\times$  100.

The implication of the above exercise is that most of the feeding by *H. ulvae* upon 40-160  $\mu\text{m}$  particles, which are small enough to be ingested, was not due to deposit-feeding but to some sort of browsing activity. We suggest that the feeding behavior we observed of *H. ulvae* upon small sand grains is such an activity. Most feeding upon small sand grains may be due to epipsammic browsing (radular scraping within the buccal cavity followed by particle rejection) instead of particle swallowing. If this is so, the behavior we observed is normal and adaptive; the animals are not simply rejecting particles, but seem well adapted to removing surface-bound material from sediment particles. In contrast, the cumacean *Cumella vulgaris* can

feed by deposit-feeding on mud and "epistrate-browsing" on coarse sand, but cannot effectively feed on small sand grains (Wieser, 1956). Ignorance of this type of feeding behavior may lead to some confusion, for it is quite possible that the bulk of the gut contents of a snail may consist of sand grains, while most of the food may come from sand grains that were scraped and spit out. This process may explain the enrichment of diatoms within *H. ulvae*, with respect to sediment, noted by Fenchel *et al.* (1975). Moreover, data showing "negative" digestion of diatoms, which is clearly impossible, for small *H. ventrosa* feeding on finer sediment fractions (10-20  $\mu\text{m}$ , 20-45  $\mu\text{m}$ ) strongly suggest that these animals browsed attached diatoms from these small particles (Lopez and Levinton, 1978). At present we cannot estimate the importance of browsing upon silt particles, but we suggest that its relative importance increases with increasing sediment particle size.

*b. Relative surface feeding rates: comparisons of species.* *P. jenkinsi* had a strikingly different feeding behavior than the *Hydrobia* spp., with maximum feeding rate upon 80-160  $\mu\text{m}$  particles. This is not surprising because the median diameter of ingested food particles is significantly larger for *P. jenkinsi* than for *Hydrobia* spp. (Fenchel, 1975b). Differences between relative surface feeding rates of 2.5-3.0 mm *H. ventrosa* and *H. neglecta* supports the suggestion that factors other than body size are important in controlling interactions between these two species (Fenchel, 1975b; Hylleberg, 1976). *H. neglecta* fed most readily on 40-80  $\mu\text{m}$ , which may suggest that epipsammic browsing is important. *H. ventrosa* appears to be more specialized than the other species for feeding on fine sediment fractions. Egestion of *H. ventrosa* is most rapid on fine sediment, and there is evidence of epipsammic browsing even on 10-20  $\mu\text{m}$  sediment (Lopez and Levinton, 1978). *H. ulvae* fed readily upon < 40  $\mu\text{m}$  and 40-80  $\mu\text{m}$  sediments. For those two sediment classes, *H. ulvae* appears to be more like *H. neglecta* than *H. ventrosa*. Of all the species, *H. ulvae* was the poorest browser on larger particles (> 160  $\mu\text{m}$ ).

We cannot yet determine whether distribution and abundance of hydrobiids is in part explained by feeding rates upon sediment surfaces, nor can we determine the importance of deposit-feeding and epipsammic browsing, although it will obviously depend upon sediment type. These experiments were conducted to determine the effect of sediment grade on ingestion of  $^{14}\text{C}$ -labelled material associated with particle surfaces, and as such does not necessarily reflect the nutritional value of the sediment. Microbial uptake and surface adsorption of  $^{14}\text{C}$ -glucose were both probably involved in sediment labelling. We do not know whether feeding on a given sediment grade varies with the amount of food available. We also do not know how hydrobiids encounter their food. We have investigated the availability of surface bound food, which may consist mainly of microorganisms, but the nature of associations between microorganisms and sediment particles is diverse. Most bacteria in sediment may be adhering quite firmly to sediment particles

(Wieser and Zech, 1976; Meyer-Reil *et al.*, 1978), although Weise (1975) suggested that approximately 50% of the sediment bacteria were interstitial (Weise, 1975, quoted in Bodungen *et al.*, 1976). In sediments where most bacteria are attached, the encounter rate of a snail with bacteria is a simple function of the surface feeding rate of a snail. Benthic diatoms, however, range from completely immobile species to large, very mobile cells (Round, 1965; Harper, 1969). Large, (< 20  $\mu\text{m}$ ) mobile diatoms are considered to be an important food for *Hydrobia* spp. (Fenchel and Kofoed, 1976), but it remains to be determined how often a snail finds such cells as discrete particles or as a temporary part of the epipsammic layer.

If food for deposit-feeders consists of epipsammic microorganisms, then small particles should be selected (Taghon *et al.*, 1978), but if food items are selected as individual particles (i.e. motile diatoms), particle selectivity may be similar to that predicted for filter-feeders (Lehman, 1976). Because hydrobiid snails utilize both attached and free microorganisms in the sediment, a model of their feeding should take into account the differences in food value of different particles.

Motile diatoms are attached to sediment particles by mucus slime even while moving (Harper and Harper, 1967). Attachment strength of diatoms may control their availability for *Hydrobia ventrosa*; strongly attached forms are less liable to be digested than free cells (Lopez and Levinton, 1978). Epipsammic diatoms have stronger tests than motile species (Harper and Harper, 1967) which may protect them from digestion. The prosobranch *Theodoxus fluviatilis* (Neritidae) digests only those algae that are broken during ingestion (Neumann, 1961). Many factors may affect microbial attachment onto surfaces: turbulence and wave action (Meadows and Anderson, 1968), nutrients (Jannasch and Pritchard, 1972; Paerl, 1975), temperature (Fletcher, 1977) and light (Nagata, 1977) (see Marshall, 1976, for more detailed discussion). We suspect that grazing by epipsammic browsers may have a profound effect on attachment strength of microorganisms to substrates, resulting in selection for strongly attached microorganisms (Fenchel and Kofoed, 1976; Nicotri, 1977; Lopez and Levinton, 1978; Kofoed, unpublished observations).

Another aspect of epipsammic browsing deals with its relationship to coprophagy. Levinton and Lopez (1977) suggested that coprophagy is rare in *Hydrobia* spp. because feces produced by a deposit-feeder would be less nutritious than uningested sediment until there was significant microbial recolonization (e.g. Hargrave and Phillips, 1977). However, if pellets are produced by an animal that is very selective in its food intake, and epipsammic browsing can be considered an efficient form of selection, then feces may be enriched in food relative to sediment, on a volume basis, despite efficient assimilation. Under these conditions coprophagous deposit-feeding might be nutritionally profitable (see, for example, Risbec, 1935). It would be interesting to determine whether coprophagy in hydrobiids is significant when

animals are browsing on sediment particles or when they are deposit-feeding. It may be possible to estimate the extent of epipsammic browsing by examining the amount of wear of radular teeth (Runham, 1969).

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