

## Selective Grazing by the Mud Snail *Ilyanassa obsoleta*

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**Summary.** Mud snails (*Ilyanassa obsoleta*) starved for 48 h were allowed to feed on sediments in laboratory microcosms. Sediment cores sliced at 2 mm intervals were compared to snail stomach contents for per cent carbon and nitrogen, plant pigment contents and species composition of benthic diatoms. Concentrations of carbon, nitrogen, phaeopigments, phycocyanin and chlorophyll were enriched in the top 2 mm of the sediments compared to 7–10 mm depth by a factor of 2–10. In turn, these materials were 20–40 times more concentrated in snail guts than in the surface sediments. Snail feces were enriched for carbon and nitrogen by 5–7 times over the surface sediments. Bacterial chlorophyll peaked at about 3–4 mm in the sediments and was not detectable in the snail stomach contents. The C/N ratio of the snail stomach contents was only 6 compared to a ratio of 8.5 for their feces and 12 for the surface sediments.

The percentage of migratory diatoms (e.g. *Nitzschia* and *Navicula*) decreased with depth where non-migratory species, such as *Fragilaria pinnata*, dominated. These migratory species were more common in the snails than in the sediments on which they were feeding.

A comparison of daily ingestion rates to the animal's energy budget shows that this selective ingestion is sufficient to meet *Ilyanassa's* energy needs.

### Introduction

Do detrital consumers utilize dead organic matter directly or must it first be converted to microbial tissue before assimilation? Since 1938, when ZoBell and Feltham (1938) demonstrated that bacteria could be assimilated by marine organisms, this question has remained unanswered.

Newell (1965) attempted to distinguish between the feeding types "detritivore" and "microbivore" using the molluscs *Hydrobia* and *Macoma*. Both animals use only a small part of the organic carbon contained in their ingested food. This ingested material is identical to the nitrogen-rich component of the food. Newell and later Darnell (1967) suggested that animals feeding on detritus could be feeding on the associated microflora and fauna rather than the detritus itself. Subsequent microscopic work following microbe density through the digestive tracts of a variety of marine invertebrates has shown that bacteria, fungi, ciliates and some algae are very efficiently removed from the sediment matrix on which they feed (Hargrave 1970; Fenchel

1972; Chua and Brinkhurst 1973; Pitts and Cowley 1974; Hylleberg 1975; Lopez and Levinton 1978).

The microbial portion of detritus should be easier to digest and more nutritious than the structural carbohydrates which make up the bulk of plant detritus. Bacterial cells (13–88% protein, 12–28% carbohydrates and 1–41% lipids; Kofoed 1975) represent a valuable source of food for an organism. Microalgae, particularly the diatoms which do not have the vast reserves of structural carbohydrates seen in terrestrial plants, contain a high percentage of protein (17–50%) and low (3–6) C/N ratios (Darley 1977).

Labelled substrate studies of detritivore assimilation show high efficiencies for microbial carbon and very low efficiencies for sterile plant material (Kofoed 1975; Wetzel 1977; Lopez et al. 1977).

Enzymatic data provide no clear answer to this question. Most aquatic molluscs and crustaceans have at least a weak cellulase activity (Yokoe and Yasumasu 1964; Hylleberg 1972; Elyakova 1972; Monk 1976), but there seems to be no correlation between the presence of structural carbohydrases and feeding type. For instance, the enzymatic activity spectrum of a carnivore was similar to that of a detritivore (Hylleberg 1972).

While microorganisms are certainly nutritious food, there is some question whether their density in the sediments is sufficient to allow organisms to use them. Cammen et al. (1978) have compared the ingestion rates of a suite of deposit-feeding invertebrates to their rates of oxygen consumption. Using normal standing stocks of bacteria and algae, they conclude that microbial carbon could account for less than 10% of the metabolic needs of these animals.

It is also possible that these animals are benefitting from symbiotic gut bacteria. Many invertebrates do have a resident gut fauna (Johannes 1964; Johannes and Satomi 1966). Guerinet et al. (1977) have even suggested that such microorganisms can fix nitrogen within sea urchins when the echinoderms are feeding on nitrogen-poor algae.

Such considerations yield the following antipodes: either detritivores are capable of selecting food enriched in living carbon, or they derive most of their nutrition from assimilating dead matter.

For one prominent eastern Atlantic detritivore, *Ilyanassa obsoleta*, both mechanisms have been proposed. Based on labelling experiments, Wetzel (1977) states that *Ilyanassa* ingests and assimilates sediment bacteria and algae, but not *Spartina alterniflora* detritus. However, by calculating the numbers of microorganisms found in the sediments on which *Ilyanassa* feeds, Cammen et al. (pp. 75–76) conclude that *Ilyanassa's* carbon budget can only

be balanced by its feeding on non-living carbon. A high degree of food selectivity could explain both of these results, and we have investigated that possibility in this study.

*Ilyanassa obsoleta* is one of the predominant grazers of intertidal and subtidal sandflats, mudflats, and salt marshes along much of the Atlantic coast of the United States and in isolated Pacific Coast bays. It is a deposit-feeder which subsists mainly on benthic algae although it is also scavenges larger dead animal remains (Scheltema 1964; Wetzel 1977; Brown 1969). It possesses the hydrolytic enzymes necessary for metabolizing some of the principal components of algae as well as the plant polysaccharides contained in salt marsh grasses (Brown 1969).

## Methods

Experiments were conducted in 765 cm<sup>2</sup> laboratory microcosms which had been previously used to determine the effects of snail grazing on benthic diatom community structure and metabolism (Connor 1980). The microcosms contained 5 cm of sediment collected from Great Sippewissett Marsh, Massachusetts, from which the meiofauna and macrofauna had been removed by sieving and repeated freezing and thawing.

These sediments were incubated in the microcosms with filtered seawater under "grow" lights. Standing stocks of pigment biomass and percent carbon and nitrogen in the sediments were assayed by taking cores to a depth of 1 cm with a coring barrel 21 mm in diameter. The cores were carefully extruded and sectioned at 2 mm intervals, about the thinnest section we could slice with a razor blade. After taking these cores from the containers, we added six mud snails, *Ilyanassa obsoleta*, which had been collected 48 h earlier at Great Sippewissett Marsh and held in filtered seawater. The snails were allowed to graze on the sediments for an hour, then immediately frozen. Their stomachs were dissected out and the gut contents extruded. Gut contents from several snails were pooled for each of the analyses. Another group of snails was allowed to feed for 24 h, then held in filtered seawater and their feces collected.

Carbon and nitrogen content were determined for the various samples with a Perkin-Elmer 240 CHN Analyzer after oven-drying (48 h at 65° C) to constant weight and grinding the dried sample. Pigment contents were determined by extracting with 5 ml of 90% methanol overnight at 40° C and determining peak height minus baseline for phaeopigments (440 nm), phycocyanin (615 nm), chlorophyll (666 nm) and bacterial chlorophyll (760 nm). Pigment concentrations were calculated (Connor 1980) and normalized to the wet weight of the sample.

Sample contamination by fragments of stomach tissue would have had a minimal effect on these measures. We measured the percentage carbon and nitrogen of the stomachs of unfed snails and the absorbance of their extracted tissues. The dry weights of the stomachs of unfed snails were only 5–10% those of fed snails. The average percentage carbon and nitrogen from these tissues were slightly below those of the stomach contents.

The stomach pH of *Ilyanassa* ranges from 6.0–6.5, with buffering due to crystalline style material (Brown 1969). Complete digestion in these snails takes about twelve hours (Brown 1969). Our estimates of chlorophyll in the stomach contents may be slightly low, but we saw no additional peaks in the spectra of snail stomach contents which might result from pigment breakdown products. In addition, the ratio of absorbance at 666 nm to that to 550 nm was higher in the stomach contents than in the surrounding sediment, suggesting that chlorophyll breakdown was not far advanced.

The diatoms in the stomachs of the snails and in the sur-

rounding sediments were compared in two stages. Initially, a random sample of 400 to 650 diatom frustules was determined to genus from three sliced sediment cores and the pooled stomach contents of two groups of five snails. Secondly, a more detailed taxonomic comparison based on approximately 300 frustules per sample was made between a sample of the pooled 0–2 mm sections of two sediment cores and samples of the pooled stomach contents of two groups of six snails. The diatoms were prepared for microscopic examination by oxidation of the organic matter in the samples, repeated washing of the cleaned siliceous frustules and final mounting in Hyrax on permanent slides (Hasle and Fryxell 1970). Taxonomic determinations were made with oil-immersion, phase-contrast optics at a magnification of  $\times 1,000$ . The permanent slides have been deposited in the Hellerman Diatom Herbarium: HDSM 1540–1550.

## Results

The per cent carbon and nitrogen declined with increasing depth in the sediment (Fig. 1, top). Per cent carbon and nitrogen content of the surface 2 mm was nearly twice that of sediment between 7 and 10 mm. Phaeopigments (440 nm absorbance), phycocyanin and chlorophyll were enriched by about a factor of five in the top 2 mm (Fig. 2, top). Bacterial chlorophyll, which requires less light energy for the oxidation of H<sub>2</sub>S, peaked below the surface at about 3–4 mm, the approximate depth of the redox discontinuity layer.

While snails could enrich their food slightly by feeding only in the top 2 mm of sediment, there was an even greater enrichment in the snail stomach contents compared to these surface sediments. Their stomachs contained 20–40 times more carbon and nitrogen, and their feces contained 5–7 times more carbon

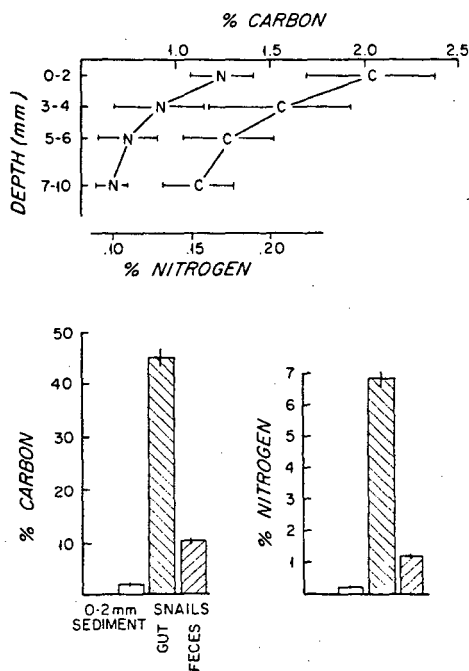


Fig. 1. Carbon and nitrogen content of sediments and the stomach contents and feces of *Ilyanassa obsoleta* feeding on those sediments. Top. Distribution of per cent carbon and nitrogen with core depth in laboratory microcosms. Bars denote two standard errors of triplicate samples. Bottom. Percentages carbon and nitrogen in *Ilyanassa*'s stomach contents and feces compared to the sediment surface layer. Bars denote two standard errors of five samples.

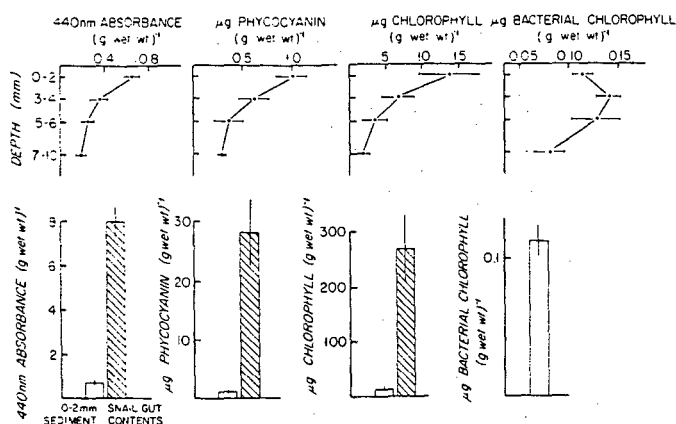


Fig. 2. Plant pigment concentrations of sediments and the stomach contents and feces of *Ilyanassa obsoleta* feeding on those sediments. Top. Distribution of plant pigments with core depth in laboratory microcosms. Bars denote two standard errors of triplicate samples. Bottom. Plant pigment concentrations in *Ilyanassa*'s stomach contents and the sediment surface layer. Bars denote two standard errors of triplicate samples

Table 1. Selective feeding by *Ilyanassa obsoleta* as demonstrated by a comparison of its stomach contents to the sediment surface layer

Sediment Character (g wet wt)-1	0-2 mm sediment	Snail gut content	Snail selectivity (gut conc./ sediment conc.)
440 nm Absorbance	0.656	7.93	12
µg Phycocyanin	1.0	28.0	28
µg Chlorophyll	13.8	265.0	20
µg Bacterial chlorophyll	0.11	0	0
% Carbon	2.04	45.4	22
% Nitrogen	0.17	6.85	40

and nitrogen than the surface sediments by per cent dry weight (Fig. 1, bottom). The snails' stomach contents were enriched for phaeopigment, phycocyanin and chlorophyll concentrations by about the same extent as carbon and nitrogen, but we could not detect any bacterial chlorophyll in their stomach contents (Fig. 2, bottom).

Several of these parameters were enriched differentially by the snails. Chlorophyll and phycocyanin concentrations were increased over surface sediment levels by twice as much as the phaeopigments and nitrogen by twice as much as carbon (Table 1). The C/N ratio of the surface sediments was about 12 while the C/N ratio of the snails' stomach contents was only 6 and that of their feces about 8.5.

We found it useful for ecological interpretation to group the diatom taxa into migratory versus non-migratory species, approximated by the distinction between epipsammic (sand-associated) and epipellic (silt-associated) assemblages and the most frequent association of these diatom taxa with each (Round 1971; McIntire 1977). Such a classification of diatoms with respect to their vertical migratory behavior in sediments is not a stringent one, especially for comprehensive taxa such as families and genera which are likely to be heterogeneous in this respect. We classified problematic taxa based on diatom size and relative migratory ability (Harper 1969). Taxa in the Centrales, Fragilariaceae and Achnantheaceae (generally this last family was characterized by small individuals in our samples) have been considered non-migratory; all other pennate taxa have been

treated as migratory. The most abundant species of non-migratory diatoms in the samples was *Fragilaria pinnata*. Individuals of *Nitzschia* and *Navicula* predominated among the migrating groups.

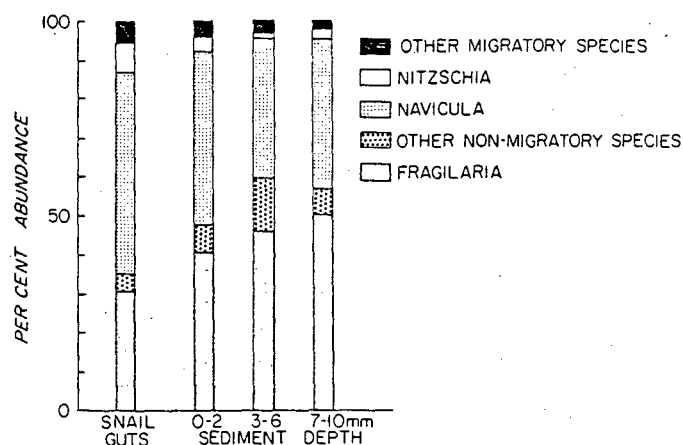


Fig. 3. Percentate abundance of benthic diatom groups found in *Ilyanassa*'s stomach contents and at different sediment depths in laboratory microcosms. Each bar represents counts of 400-650 diatom frustules

Table 2. The percentage abundance of vertically migrating and non-migrating benthic diatoms in the top 2 mm of surface sediment and in the stomach contents of two pooled groups of *Ilyanassa obsoleta* feeding on those sediments. Only diatom species with greater than 2% relative abundance in at least one sample have been listed within families. Two standard errors for the percentages is indicated

Diatom taxa	Sediments	Snails	
		Group A	Group B
Coscinodiscaceae			
Fragilariaceae	64.3	39.5	54.7
<i>Fragilaria pinnata</i> Ehr.	64.3	38.1	54.3
Achnantheaceae	6.8	15.3	4.9
<i>Achnanthes hauckiana</i> Grun.	2.6	4.3	1.7
<i>Achnanthes lemmermanii</i> v. <i>ob-</i> <i>tusa</i> Hust.	0	9.0	0.7
Total non migrating	72.3	55.9	59.6
Naviculaceae	21.9	22.8	26.1
<i>Amphipleura</i> sp.	0.3	2.6	0.7
<i>Navicula cf. diserta</i> Hust.	3.2	5.7	7.0
<i>Navicula pygmaea</i> Kuetz.	6.8	3.2	2.8
<i>Navicula cf. salinarum</i> Grun.	4.8	3.6	6.6
Gomphonemaceae	0	0	0.3
Cymbellaceae	1.3	9.6	2.8
<i>Amphora coffeiformis</i> (Ag.) Kuetz.	1.0	8.5	2.1
Epithemiaceae	0.3	0.3	0.3
Bacillariaceae	4.2	11.4	11.1
<i>Nitzschia frustulum</i> (Kuetz.) Grun.	1.6	2.9	2.8
<i>Nitzschia laevis</i> Hust.	0.6	4.6	0.3
Total migrating	27.7 (±2.5)	44.1 (±3.0)	40.4 (±2.9)

In the initial set of observations confined to examining only the genera of diatoms in the sediment profile and the snails, the relative abundance of non-migratory taxa in the 0–2 mm level was approximately 10% less than that in the subsurface levels (Fig. 3). Snail stomachs contained 10% less of the non-migratory groups than the 0–2 mm section.

In our second set of observations comparing the diatoms in the stomachs with the top 2 mm of sediment, non-migratory taxa were about 15% less frequent in the snails than in the surrounding sediments. Migratory taxa accounted for 40–45% of the snails' stomach contents, but represented only 28% of the total sediment diatom assemblage (Table 2). In particular, *Nitzschia* was almost three times more abundant in the snails than in the surface sediments.

## Discussion

These data show that *Ilyanassa obsoleta* exhibits a high degree of selectivity for the particles it eats. Not only does it select for high organic content and living plant pigments, as demonstrated by its preference for chlorophyll over phaeopigments, but it also takes a specific fraction of the benthic diatom community.

The most selected food are the migratory species of diatoms which are concentrated in the surface sediments by their daily migrations to the sediment-water interface, which allows for easy capture by the snails. Selective feeding on specific types of benthic diatoms has also been demonstrated for grazing gastropods in the rocky intertidal by Nicotri (1977), who found that intertidal limpets and littorines could not effectively graze on diatoms which were tightly attached to rock surfaces. The grazers more efficiently removed those individuals which extended up above the substrate.

Assimilation of these epipelagic species may be easier because the non-motile, epipsammic forms are attached quite strongly to inorganic particles of no nutritional benefit (Harper 1969). *Ilyanassa* may assimilate these species in two ways. Lopez and Kofoed (in press) have shown that hydrobiid snails will take small particles into their buccal cavity, scrape off the attached microorganisms and spit out the particle, a process they call epistrate browsing. It is also possible that the crystalline style, which *Ilyanassa* develops only when deposit-feeding (Brown 1969), aids in the detachment of microorganisms from particles as a preparation step for digestion (Lopez in press).

Is *Ilyanassa's* selectivity for carbon and chlorophyll sufficient to balance the snails' energy budget? Edwards (1979) has done extensive work on the energy budget of *Ilyanassa obsoleta* living in Connecticut salt marshes. For a hypothetical adult 20 mm snail with an shell-free dry weight of 107 mg, daily respiration at 20° C would require 0.7 mg C, production 0.2 mg C and mucus and DOM secretion 3.2 mg C. We have estimated ingestion rates for *Ilyanassa* (Connor 1980). A snail this size ingests at least 47 mg dry wt of sediment daily. If we take the difference in per cent carbon between stomach contents and feces, this snail would assimilate 16 mg C daily, easily sufficient to meet its metabolic needs. Chlorophyll assimilation would be approximately 37 µg daily.

An enrichment of microbial food items on the order of 10–20 times their standing stock in the sediments has been generally the amount calculated as necessary to meet metabolic needs solely through living material (Fenchel 1972; Baker and Bradnam 1976; Cammen et al. 1978). Our calculations for the amount of organic carbon ingested daily by *Ilyanassa* agree well with

Cammen's (1980) model for benthic invertebrate deposit feeders. He predicts our 107 mg snail should eat 12 mg C daily. Without selective feeding his model predicts that this same snail should need to eat 361 mg of sediment, almost nine times the amount the snails actually eat.

The literature is replete with examples of different means of selective feeding by detritivores (Fenchel and Jorgensen 1977). Some choose specific particle types which would contain preferred foods. Coull (1973) reported that meiofauna will select organically-coated over plain sand, and in some cases will select for specific species of bacteria. Particle size selection is common among deposit-feeding detritivores (Fenchel et al. 1975; Hylleberg and Galluci 1975) and filter-feeding ones (Winter 1978). Selection of feeding depth is also common (Whitlatch 1974), especially selection for surface sediment particles which are finer and probably greatly enriched in bacteria.

Another kind of sediment selection which is widespread among benthic fauna is coprophagy, the ingestion of fecal pellets. Several animals can survive on a diet of fecal pellets (Johannes and Satomi 1966; Frankenberg and Smith 1967), which are enriched in bacteria and have a higher oxygen consumption than their surrounding sediment (Hargrave 1976). Levinton and Lopez (1977) have attempted to explain an area's carrying capacity for *Hydrobia* totally in terms of fecal pellet formation and breakdown.

Animals can also sort sediments to enrich their diet in microbial fauna. Pitts and Cowley (1974) have found that the crab *Uca pugilator* selectively removes yeast cells, *Rhodotorula mucilaginosa*, from the surrounding sediment. The mullet *Mugil cephalus* uses pharyngeal filtering to select the fine particles richer in bacteria (Odum 1968). By comparing plant pigment concentrations in the surrounding sediment to the contents of the mullet's stomach, Odum (1970) calculated that a mullet must filter 100 g of sediment to get one gram of stomach material.

We have shown that *Ilyanassa obsoleta* has the capacity to select for plant pigments at about one-quarter of the extent of mullet, but from these data we cannot determine if this selectivity is due to an active sediment sorting or *Ilyanassa's* choosing particularly rich feeding areas. We do know, however, that if *Ilyanassa* is simply choosing rich microhabitats, its capabilities are much better than our selective strategy of sampling the top 2 mm. The absence of bacterial chlorophyll and the increased abundance of migratory diatoms in the snails' stomach contents would suggest that they must be feeding at the very edge of the sediment water interface.

These diatoms represent a high quality food in a specific microhabitat. The same adaptations which allow migratory diatoms optimal light capture at the sediment surface also provide an enriched microhabitat suitable for exploitation by grazers. In an environment which provides a small amount of high quality food diluted by large amounts of low-quality non-living carbon and inorganic mineral grains, these nutritionally-enriched microhabitats must play a large role in a deposit feeder's overall nutrition. While *Ilyanassa* may be capable of assimilating non-living organic matter, its marked selective ingestion for carbon, nitrogen, chlorophyll and specific species of diatoms suggests that living material is more important to the snail's growth and nutrition.

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