

SHORT NOTE

Selective Deposit Feeding by the Deep-Sea Archaeogastropod *Bathybembix aeola*

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ABSTRACT: Analyses of paired sediment and gut samples from specimens of the bathyal trochid gastropod *Bathybembix aeola* (Watson) reveal selective ingestion of fine particles from a mixed mud and sand substrate. The radula is the selecting organ. Results contradict the prevalent notion that sediment-ingesting gastropods are indiscriminant. The standard concept of the unselective deposit feeder as a primitive, generalist vacuum cleaner of the sea floor is difficult to accept from a morphological viewpoint because it requires perfecting a feeding apparatus capable of taking an unbiased sample. Results are compatible with the hypothesis that selective ingestion of fine particles with greater surface area of organic coating is energetically efficient.

Selective feeding is a theoretically appealing adaptive solution to dividing and efficiently using limited resources among the diversity of benthic invertebrates known to coexist in the deep sea (Sanders, 1968; Grassle and Sanders, 1973). In deposit-feeding organisms, however, selectivity may not be so much an ecological problem related to competition and resource partitioning as it is a problem relating the sizes and qualities of particles in the substrate to the sizes of organisms and the biomechanics and morphology of their feeding apparatus. From the point of view of the organism living in an environment in which organic matter is relatively scarce (Filatova, 1969; Sanders and Hessler, 1969), plasticity of feeding behavior may be advantageous (Gage, 1978), and the ingestion of mud may be viewed as a problem in maximizing net energy gain (Taghon et al., 1978).

Instances of selective feeding in the deep sea have been difficult to establish. Inferences in the literature are based on particle-size ranges and types in gut contents (Menzies, 1962; Carey, 1972). However, dramatic differences in gut contents of organisms coexisting in the same environment may reflect microhabitat selection (as in surface vs. subsurface feeding) rather than a morphologically based system of particle selection and rejection. Dredge hauls and grab

samples mix sediments and separate organisms from feeding microhabitats. The difficulty of sampling an organism together with the substrate upon which it is feeding (particularly on and in thinly-stratified sediments) strictly limits inferences of selectivity.

Fortuitous mini substrate samples from the vicinity of the mouth, taken by 2 living specimens of the large (shells > 30 mm high) sediment-ingesting trochid gastropod *Bathybembix aeola* (Watson) at the time of their collection (R/V Soyo Maru sta. T 23, 35°04.6'N, 139°29.0'E, 700 m) provide nearly ideal data for comparison with gut contents. When disturbed, a gastropod crawling on a soft substrate may retract into its shell carrying sediment that is trapped behind the tight-fitting operculum. An individual is thus occasionally capable of providing 2 samples of its feeding substrate: one taken by the retracting foot and the other by the feeding organ or radula.

Paired, snail-collected sediment and gut samples from the two individuals were analyzed separately (4 runs) with a zone-sensing particle-size analyzer, revealing replicate distributions of particle size strongly skewed toward fine sand in the 2 substrate samples, with differential accumulation of the fine fraction in the gut samples. Fig. 1 shows a distinctly bimodal distribution of particles in the gut, with the largest mode in the clay- and silt-size range. The virtual identity of grain-size distributions from the 2 specimens is remarkable.

Inferences of selectivity are strengthened by examination of the radula as a morphological basis of particle selection. *Bathybembix* and an allied group of deep-water deposit-feeding genera (*Calliotropis*, *Cidarina*, *Ginebis*, *Convexia*) have a distinctive radula (Fig. 2a, b, c) with several features that represent good design for ingesting fine particles from a mixed sediment (Hickman, 1980). The radula is of the rhipidoglossate type, with a longitudinal band of robust central

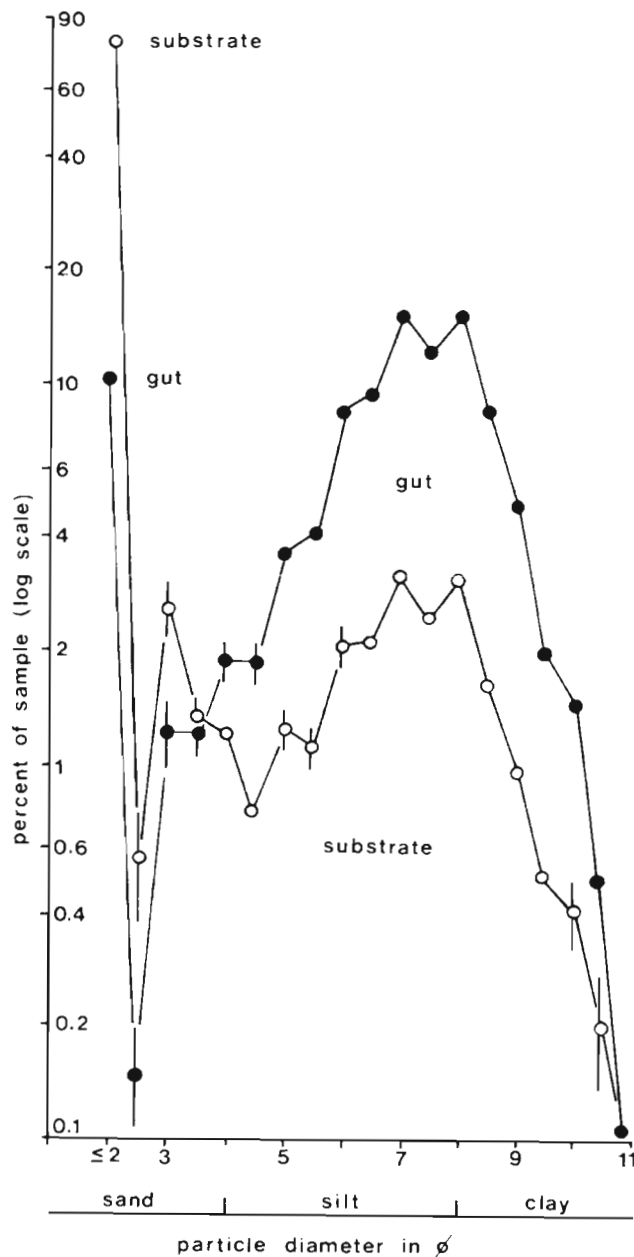


Fig. 1. Grain-size distribution (as particle volume) of material from the gut (solid circles) of *Bathybembix aeola* and from fortuitous substrate samples (open circles) trapped behind the operculum at the time of collection. Data are from 2 specimens; standard errors that exceed dot diameter are shown as vertical lines. The phi scale is logarithmic. Curves cross near coarse silt/fine sand break

(rachidian) and lateral teeth flanked by 2 broad fields of extraordinarily fine and flexible marginal teeth (Fig. 2a). The marginal teeth are rapidly erected and collapsed as the radula is pushed out of the mouth, applied to the substrate, and retracted during each feeding stroke. Although there is no perfect mechanical analogy from the non-biological realm, the margi-

nal sets of teeth can be compared in a general sense to a pair of opposed, highly flexible, rakes or brooms. The size, spacing, and serration of individual teeth define a size range of capturable particles; and their flexibility places an upper limit on the density of particles of otherwise capturable dimensions.

In *Bathybembix* the marginal teeth are unusually fine, thin, and flexible for an archeogastropod. They are 20–50 μm across at the distal end, with fine serrations that have separations on the order of 1–12 μm . Serration separation corresponds with a phi value of 10, just larger than the smallest particles encountered in the substrate (Fig. 1). These teeth are not optimally designed to gather the larger, denser particles in a mixed sediment. It is not surprising that sand grains and tests of microplankton and microbenthos, most of which are greater than 50 μm across, are not incorporated more frequently, although the less dense microplankton has a greater likelihood of retention than dense sedimentary particles of equal size.

The outermost marginal tooth is a unique, broadly spatulate structure that is 125 μm wide in an adult specimen of *Bathybembix aeola* and is inferred to be effective in reducing particle loss during feeding but not capable of particle selection (Fig. 2c).

The rachidian and lateral teeth (Fig. 2b) are not involved in the gathering of particles (Hickman, 1980) although food particles collected by the marginal teeth may be packed and bound together with mucus secretions for removal and transport from this portion of the radula into the esophagus. Fig. 2d illustrates a broad range of particles from the gut for comparison with radular dimensions at the same scale (Fig. 2b, c).

The preference of *Bathybembix aeola* for small particles runs counter to prior assumptions about feeding of sediment-ingesting gastropods. The North American species, *B. bairdii*, has been presumed to obtain its nutrition from the foraminiferans and other shelled microorganisms that are conspicuous in the enlarged hindgut (Dall, 1889; Merriman, 1967; Siebenaller, 1978). I have examined the gut contents of all 4 living species of *Bathybembix* and have found tests of a diversity of calcareous and siliceous marine microorganisms. They are, however, primarily planktonic taxa, not living at the time of ingestion. They are concentrated in the center of the fecal string as part of the undigested residue leaving the stomach.

Bathybembix aeola occurs in dense populations in the bathyal zone off the east coast of Japan as one of the major macroinvertebrate consumers of organic matter in deep-water sediments. Its 3 living congeners also occur in dense populations on the continental slope in the eastern Pacific Ocean. A major source of nutrition in deep-sea sediments of the type that occur on the slope resides in microbial films and epigrowths

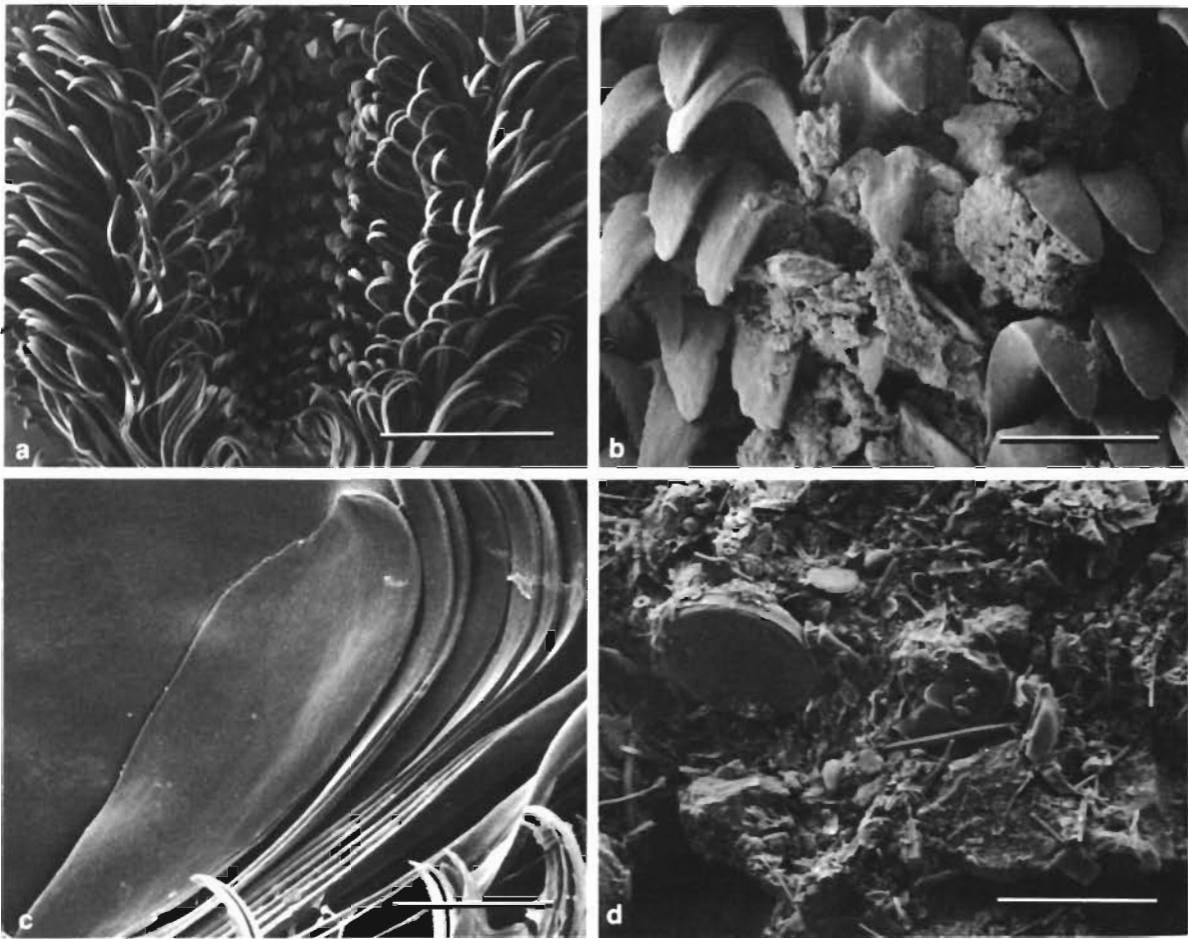


Fig. 2. (a) Radula of *Cidarina cidaris*, a close relative of *Bathybembix*, illustrating typical form of deposit-feeding radula; bar = 400 μm . (b) Central and lateral teeth of radula of *B. aeola* with compacted sediment; bar = 100 μm . (c) Fine marginal teeth and broadly spatulate outermost marginal tooth of *B. aeola*; bar = 100 μm . (d) Sediment with tests of microplankton from central portion of hindgut of *B. aeola*; bar = 100 μm

on sedimentary particles (Fenchel, 1970; Fenchel and Kofoed, 1976; Yingst, 1976; Lopez and Levinton, 1978; Levinton, 1979) or adsorbed organic matter (Emery, 1960; Menzies, 1962; Lenz, 1977). Differential ingestion of the smallest particles, with their greater area of organic coating, follows as an energetically efficient means of maximizing net energy gain (Taghon et al., 1978).

The inference of selectivity in this report is strong for 2 reasons. First, it is based on replicated, within-individual comparison of gut contents with sediment from close proximity to the mouth of the living animal. Second, it is reinforced by morphological data that bear on the mechanical basis of particle selection. Detailed functional morphological data are lacking even in the best experimental studies of shallow-water deposit feeders (e. g. Fenchel et al., 1975; Lopez and Levinton, 1978). We are only beginning to understand

the variety of strategies that organisms employ to obtain nutrition from sedimentary deposits. Full appreciation and documentation will require increasing emphasis both on the fine details of stratification and microhabitats in sediments and on the selective biases that are built into the sampling gear of organisms.

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