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The foraging strategy of a subtidal and deep-sea deposit feeder¹

Abstract—The ampharetid polychaete *Amphicteis scaphobranchiata* is a marine, surface-deposit feeder inhabiting cohesive sediments from continental shelf depths off British Columbia to abyssal habitats off southern California. It uses a previously undescribed method of removing fecal pellets from its feeding area via an elastic (Young's modulus = $7 \text{ MN} \cdot \text{m}^{-2}$), mucous sling fashioned about the modified anterior median branchiae for which the species was named. This sling imparts a force of $4 \times 10^{-1} \text{ Pa}$, sufficient to

yield a maximal pellet velocity of $27 \text{ cm} \cdot \text{s}^{-1}$ and thereby to remove the pellet from the normal radius swept out by the animal's feeding tentacles. These observations indicate that this sedentary animal's food supply depends predominantly on the rate of sedimentation into the pit that is produced via its feeding and defecating activities, rather than on the rate of microbial regeneration or production that goes on within its feeding radius.

Most observations of marine deposit feeders have been made on intertidal animals (e.g. Newell 1979). With few excep-

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tions (e.g. Taghon et al. 1980; Dauer et al. 1981), most of these observations, in turn, have been under the artificial conditions of still water and zero sediment transport. Furthermore, deposit feeders, due to their generally small sizes and cryptic natures, are difficult to observe *in situ*. We therefore seized upon the phenomenon of polar emergence and the facilities of the Friday Harbor Laboratories, San Juan Island, Washington, to study the feeding behavior of *Amphicteis scaphobranchiata* (Moore 1906), a surface-deposit feeding, ampharetid polychaete. The scant published information on ampharetid feeding is summarized by Fauchald and Jumars (1979). We also took advantage of the opportunity to add to the nascent literature on the mechanical and rheological properties of invertebrate mucus (Wainwright et al. 1976; Denny 1980, 1981; Grenon and Walker 1980).

Amphicteis scaphobranchiata first was described in collections taken from soft mud off Vancouver Island, B.C., from a depth of 250 m (Moore 1906). It has been found since in mud from shelf to abyssal depths off southern California (Hartman 1969) and bathyally off Baja California (Fauchald 1972). The specimens we examined were wet-sieved gently from sediments collected at 18-m depth in Massacre Bay, Orcas Island, Washington. They were returned, still in tube fragments at ambient seawater temperature (10°C), to the seawater tables at Friday Harbor and placed in individual freezer containers containing dredged sediments (median diameter 18 µm). We observed about 50 animals 3–5 cm long.

Individuals burrowed quickly from their tube fragments into the sediments and emerged in new locations to construct their tube-pit complexes. When food was provided either by pipetting natural sediments (passed through a 62-µm sieve) into the pit or by placing individuals in a sediment-transporting flume (Nowell et al. 1981), individuals remained in one location indefinitely (through the 6 weeks of our observations), and the natural tube-pit morphology was maintained. When a continuing supply of sediments was not provided, either an aberrantly large and deep pit resulted (as compared with visual observations made by

SCUBA divers *in situ* on 12 and 22 September 1981) or the animal left its tube to reburrow and build a new one. The data come from movies made of two animals which had been kept for 4 weeks during which they were daily fed sieved sediments from West Sound. These data were corroborated by qualitative observations of the remaining specimens.

Photographs were made with a LOCAM, high-speed, 16-mm movie camera fitted with a Nikon macro lens, at speeds of up to 100 frames·s⁻¹ with color-positive film (Kodak Ektachrome II). The feeding pit and surrounding bed were illuminated by two 500-W photoflood lamps. The lights and camera were switched on when the animal appeared at the mouth of its tube, pushing the tapered end of a fecal pellet ahead of its branchiae. The developed film was projected onto a tracing table and examined frame by frame. The diameter of the fecal pellets was used as a scaling length, and the locations of three fixed objects in the plane of view were used to register each frame. From each frame we plotted the locations of the fecal pellet and of the median anterior branchial insertion. From these plots at equal time intervals, we computed distances and velocities.

In subsequent computations there are four sources of error. First, in all calculations, a density of 1.21 was assumed for the fecal pellets. Direct measurement of density (Taghon et al. 1984) yielded a mean value of 1.19 g·cc⁻¹ ($SD = 0.02$, $n = 38$). Second, the velocities of the pellet and the organism were computed from the film speed and a measure of the distances traversed between frames. The LOCAM camera puts a timing mark every 0.01 s on the edge of the film. The number of marks was counted over 20 frames and yielded film speeds of either 0.011 or 0.022 s·frame⁻¹. Third, the scale used in each series of pictures was obtained by assuming the diameter of the fecal pellet to be 1.0 mm. Analysis of fecal pellets previously produced by the photographed animals showed that the mean diameter was 1.0 mm ($SD = 0.03$ mm, $n = 10$). Last, the fecal pellet trajectory was assumed to lie in a plane parallel to the film-transport plane. Measurements of the diameter of the fecal

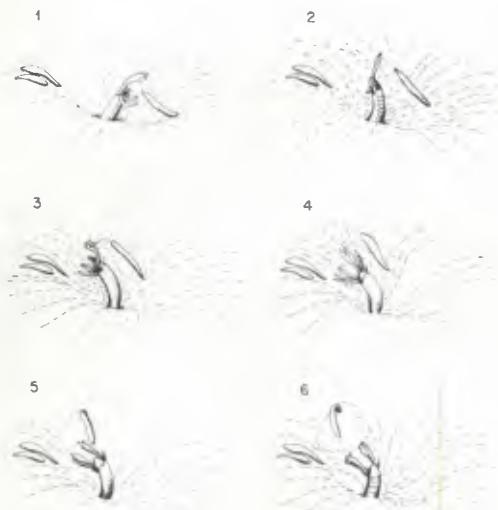


Fig. 1. Sequential sketches of *A. scaphobranchiata* at about 0.02-s intervals. Numbers in frames indicate sequence of action during ejection of fecal pellet. Dotted lines outline mucous sling.

pellet from the start to the end of its travel showed that this assumption would yield an error of no more than 10% in length scale.

While feeding, the animal spreads its tentacles over the sediment surface in front of the tube. The tentacles (up to 30) were initially thrown out about 1 cm from the tube, often to one sector of the feeding "circle" at a time, and then extended along the bed to a distance of about 5 cm. After they were well covered with fine materials, they were withdrawn slowly ($0.5 \text{ cm} \cdot \text{s}^{-1}$) into the tube. If *A. scaphobranchiata* was disturbed while feeding, for example by a pressure wave or a change in fluid velocity, it withdrew rapidly into its tube, pulling its tentacles along.

The cylindrical tube has a diameter of about 8 mm, a wall thickness of 2 mm, and is up to 10 cm long. It is built at a steep angle to the sediment surface with the upper third bent over to parallel the sediment-water interface; usually about the upper 5 mm of the tube opening projects above the plane of the bottom. The tube is constructed from compacted mud and mucus in much the same manner as Dales (1955) describes for terebellid polychaetes. It has, however, a constriction at about a third of its length from the proximal end. If the tube is pulled

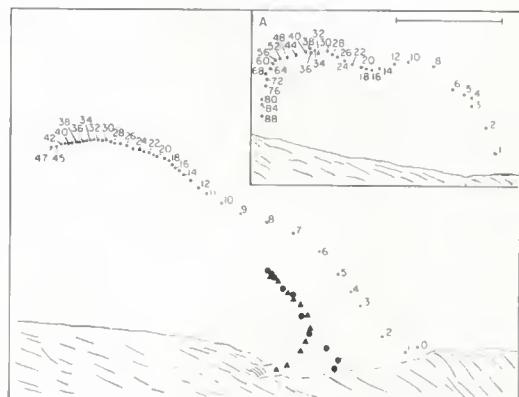


Fig. 2. Locus of points of fecal pellet (numbered) and locus of branchial insertion of *A. scaphobranchiata* (●, during ejection; ▲, during return to tube; interval, 0.01 s). Insert A—full trajectory of fecal pellet. Scale bar is 3 cm. Numbers refer to movie frame sequence, one unit being 0.02 s.

from the surface, it parts at this constriction, leaving the animal in the remaining third, which is just long enough to accommodate the worm. For most of the time that *A. scaphobranchiata* is not feeding, the hooked tips of the anterior median branchiae (see Moore 1906: fig. 56) are curled over the lower lip of the tube, while the other three pairs of branchiae are also curled outward radially around the tube with up to 2 mm of the branchiae extending beyond the tube edge. Aperiodically, these branchiae twitch in a manner reminiscent of porcellanid crab antennae (e.g. Nichol 1932).

Immediately before ejecting a fecal pellet, *A. scaphobranchiata* withdraws from the entrance to its tube. Several seconds later, the narrower tip of the fecal pellet appears, held between the two anterior median branchiae. The pellet is pushed ahead of the animal in a straight line until the animal has about a third of its body length outside its tube. This movement, over a distance of about 12 mm, takes 1.5 s. The other pairs of branchiae are held parallel to the body meanwhile.

The rest of the ejection sequence occurs much more rapidly (Fig. 1). *Amphicteis scaphobranchiata* pivots its body against the tube entrance, bending the two modified branchiae until they reach an angle of 70° to the body. The body keeps on bending

and in 0.09 s after beginning to flex reaches its maximal flexure (Fig. 1, panel 4, and Fig. 2). The pellet does not move from the bed until the extended portion of the body itself attains an angle of 70° to the bed. At full flexure (90° to the bed), the diameter of the portion of the body remaining in the tube is less than half that of the inside of the tube; 12 of the 14 thoracic setigers lie outside. By the time the body is vertical, the pellet is beginning to accelerate.

The pellet is accelerated from the bed not by direct contact with the branchiae, but rather through the stretching of an abundant mucous coating. The maximal acceleration of the pellet (computed for the branchial insertion point) is $91 \text{ cm} \cdot \text{s}^{-2}$ (i.e. 0.1 g, the equivalent of an acceleration of 0 to 88 km·h⁻¹ in 27 s). The attachment of the mucous strand to the narrow end of the pellet produces a very low drag attitude during the period of acceleration. During this time, the pellet rises at an angle of 50°. Its path describes a crude semicircle (Fig. 2, insert A), though detachment of the mucous sling produces a change in the pellet's orientation as it reaches its zenith.

The organism retreats into its tube following a slightly different locus (Fig. 2). By the time the pellet is vertical above the tube, the organism has started to withdraw. The entire sequence, beginning with emergence until final retreat, takes about 1.75 s. In quiescent water, the pellet usually reaches the rearward radius of the feeding cardioid (Nowell et al. 1981: fig. 4c) in 2 s and is effectively out of reach of the tentacles. The pellets are always thrown in this manner and always in the same direction, in still water occupying an arc of about 35° of the feeding "circle." In flowing water, this mechanism of injecting particles directly into the boundary layer has substantial implications for sediment transport (Nowell et al. 1981).

The relative positions of the fecal pellets and the organism (Fig. 2) during acceleration allow the calculation of some properties of the mucus. The stress is computed by knowing the force and the area over which that force operates. The conventional strain may be computed from the change in length of the mucus due to the application of that

force (Wainwright et al. 1976). The ratio of the stress to the strain yields Young's modulus of elasticity. The stress is the mass of the pellet multiplied by its acceleration and is obtained by assuming the pellet to be a cone and using the measured density of 1.21 (Taghon et al. 1984). Acceleration is estimated from sequential frames of the movie. Young's modulus calculated for three separate ejections by the same animal yields values of 6.8, 7.1, and 6.8 MN·m⁻², roughly equivalent to that of rubber (Gordon 1978).

Amphicteis scaphobranchiata thus expends considerable energy and exposes itself to the risks of predation, but toward what end? Continuity demands that, if pellets are hurled out of the feeding area, a feeding pit will result. Under conditions of continuous sediment transport, a steady state pit morphology results from the balance of removal by the feeding process and sedimentation into the feeding pit. A simple but elegant feedback exists in the flume and presumably in nature as well; sedimentation rate is enhanced by reduced shear stresses within the feeding depression. This sediment trap is maintained actively; if the pit is filled (e.g. via an artificial turbidity flow), the animal uses its pair of modified branchiae to plow out the depression before resuming feeding.

Our observations suggest that this species has evolved to make use of sediment transport in its environment and that its rate of food supply depends on the rate of sedimentation into its feeding depression. Neither of the two bodies of extant foraging theory explicitly aimed at deposit feeders considers this feeding strategy. One, designed for mobile deposit feeders that reach high population densities (Levinton and Lopez 1977) scales feeding rate to the breakdown rate and microbial recolonization rate of fecal pellets, while the other assumes an unlimited supply of sediments (Taghon 1981). The elaborate fecal ejection mechanism in *A. scaphobranchiata* and its low population density (fewer than 4·m⁻² in Massacre Bay having been estimated from the SCUBA diving observations cited above, and none having been captured in three 0.06-m² box cores from the site, making unlikely any impact from conspecific neighbors) ar-

gue against the importance of local bacterial regrowth (i.e. within the feeding radius) in supplying the food requirements of this species. How closely natural field sedimentation in the full range of subtidal and deep-sea environments inhabited by *A. scaphobranchiata* approximates an effectively unlimited rate of food supply is not yet clear. Similarly, the relative contributions of vertical sedimentation and horizontal bedload transport in its nutrition remain to be explored. While the importance of microbial growth or regrowth is not precluded, a growing body of evidence (Buhr 1976; Hogue and Miller 1981; Taghon et al. 1980; Dauer et al. 1981; Billett et al. 1983) shows that accurate foraging theories for sedentary deposit feeders will have to take sediment transport into account explicitly.

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