

Induction of Suspension Feeding in Spionid Polychaetes by High Particulate Fluxes

Gary L. Taghon, Arthur R. M. Nowell, and Peter A. Jumars

Induction of Suspension Feeding in Spionid Polychaetes by High Particulate Fluxes

Abstract. *The feeding behavior of three species of spionid polychaetes varied with water velocity. At moderate flows the worms ceased deposit feeding, formed their feeding tentacles into helices, and lifted them into the water column to capture material in suspension. This behavior was apparently a response to increased flux of suspended matter at high flows rather than to flow velocity alone. Organisms capable of switching their feeding behavior may be common in dynamically variable benthic environments.*

Deposit-feeding polychaete worms are a major group in soft-bottom areas of both the shallow and deep sea (1). These sediment-inhabiting annelids ingest food materials found on the sediment surface or within the sediment. Deposit feeders in general are considered to exploit a different food source than benthic suspension feeders, which obtain their food by removing it from the overlying water. Indeed, differences in factors controlling food supply are one explanation for the alternative development of predominantly deposit- or suspension-feeding benthic communities (2). Higher wa-

ter velocities increase the flux of suspended materials, favoring suspension feeders, while removing fine-grained particulate matter from the sediment or preventing the deposition of this material, to the disfavor of deposit feeders.

A clear-cut distinction between these two feeding modes is probably unrealistic. Because there can be considerable resuspension of bottom materials by water currents in both the shallow (3) and deep sea (4), it could be advantageous for an animal to adjust its feeding behavior to utilize food in suspension or deposited on the bottom, depending on the

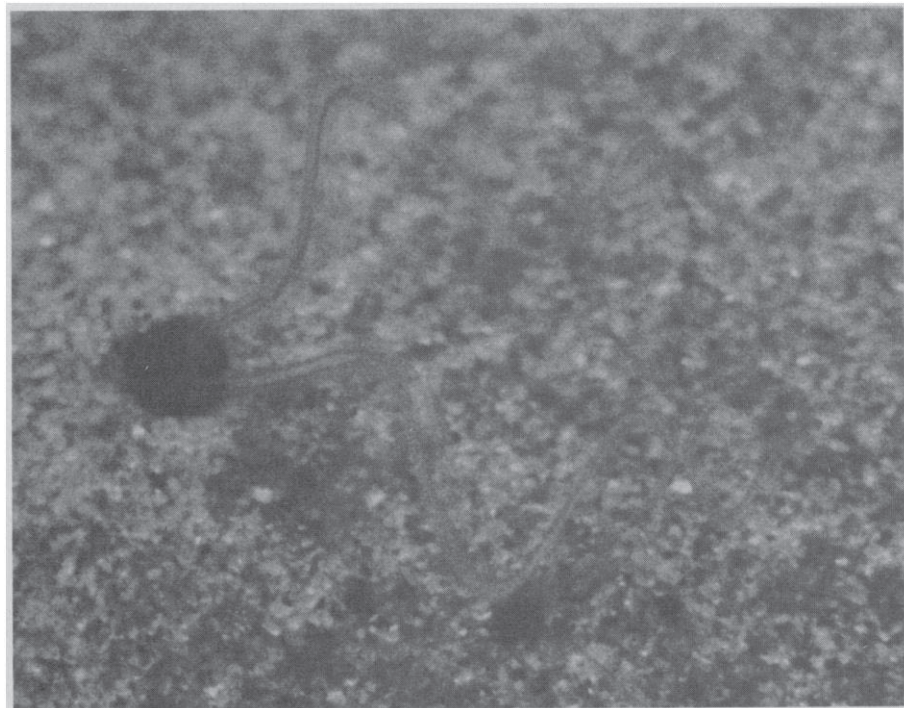


Fig. 1. Tentacles of *Pseudopolydora kempj japonica*, held in characteristic helical arrangement during suspension feeding. The current is moving from left to right at about 13 cm/sec ($\times 4$).

dominant source of food at a particular time.

Spionid polychaetes are a widely distributed benthic group (5). They are usually considered to be deposit feeders, although facultative suspension feeding is known for this family (6, 7). We report a novel suspension feeding mechanism in three species of spionid polychaetes. Apparently the mechanism is employed in response to the increased flux of suspended materials occurring at high water velocities.

A seawater flume at the Friday Harbor Laboratories provided controlled flow velocities (8). The flume operated with continuously supplied Puget Sound seawater or with a pump and filter system that recirculated the water while removing particulate matter (9). A recessed box in the flume bottom contained the sediment and animals; the sediment-water interface was coplanar with the flume bottom. *Pseudopolydora kempii japonica*, *Boccardia proboscidea*, and *Pygospio elegans* were collected from the intertidal zone of False Bay on San Juan Island, Washington, by sieving sediments through a screen with 500- μ m mesh. The sieved sediment, free of macrofauna, was placed in a flume box. Worms, sorted and placed on the sediment surface, usually burrowed and established new tubes within 1 hour. Experiments were performed with one species at a time. Water velocity was measured with a commercial quartz-coated hot film (TSI, Inc., model 1231W) operated at 20°C overheat by a TSI anemometer (8). Vertical position of the probe was determined by a precision vernier. Mean velocities were calculated

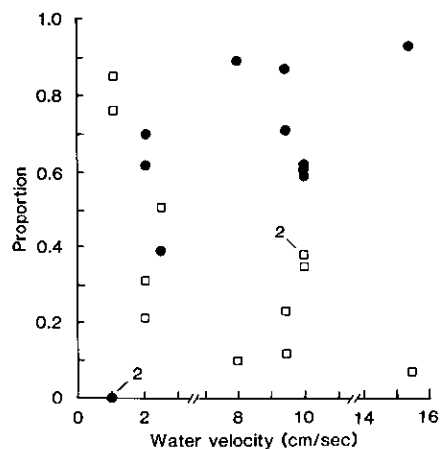


Fig. 2. Proportion of *P. kempii japonica* deposit feeding (\square) or displaying helical tentacles (\bullet) versus water velocity 0.4 cm above the bed. Each pair of data points represents an average for 90 worms. Numbers in the body of the figure are numbers of replicate observations falling at the same point.

from 30-second analog averages of the d-c voltages. Concentrations of suspended particulates were measured by filtering 1.0-liter samples of seawater (collected at the outflow flume end) through tared Millipore HAWP filters (nominal pore size, 0.45 μ m), rinsing with filtered distilled water to remove salts, drying at 60°C, and weighing to the nearest 0.01 mg.

Spionid polychaetes possess two anterior feeding tentacles. During feeding, the tentacles are extended from the tube and, during conditions of low flow (0 to 2 cm/sec) (10), held on or near the sediment surface. Food particles are picked up near the distal ends of the tentacles and transported to the mouth via a ciliated groove. At higher water velocities (~ 5 cm/sec), the worms lift their tentacles into the water column and extend them downstream, with the axes parallel to each other and to the bed. The tentacles are twisted into gradually tapering helices (Fig. 1).

Behavior was observed under low magnification while the water flow through the flume was varied. Results for *P. kempii japonica* are given in Fig. 2. (Results for *B. proboscidea* and *P. elegans* are qualitatively similar; however, the larger size and greater abundance of *P. kempii japonica* make it best suited for quantitative observations.) As water velocity increased, the proportion of *P. kempii japonica* feeding on deposited particles decreased (Spearman's $\rho = -.50$, $P < .05$), while an increasing proportion extended their tentacles in the helical arrangement ($\rho = .39$, $.10 < P < .15$) (11).

Since the helical shape increases the surface area of the tentacle normal to the flow, it seems likely that the worms were suspension feeding. To see whether the worms were capable of this behavior, we introduced newly hatched brine shrimp upstream of the sediment box. The shrimp were captured along the entire length of the tentacles, transported to the mouth by ciliary action, and ingested. Natural flocculent material was also captured. Dimensionless indices for capture modes by a single fiber (as a spionid tentacle may be considered) can be computed according to formulas discussed by Rubenstein and Koehl (12). The values for the brine shrimp experiment are (i) effectiveness of capture due to direct interception, approximately 1.0; (ii) effectiveness of capture due to inertial impaction, approximately 0.009; and (iii) effectiveness of capture due to gravitational deposition, approximately 0.003. These calculations and the visual observations suggest that direct interception by the tentacle is the primary means by

which these annelids feed on larger particles in suspension. However, the importance of inertial impaction may be underestimated if the helical tentacles impart centrifugal forces to the water passing through them.

To determine whether the helical form of the tentacles was controlled by the worms or formed passively during high flow due to some structural characteristic, several animals were narcotized in 7.5 percent $MgCl_2$ and implanted in the sediment with their tentacles exposed to the flow. At water velocities that induced control worms to hold their tentacles helically, the narcotized specimens' tentacles trailed limply downstream. A great deal of control over tentacle shape and positioning is undoubtedly exerted by the worm. For example, as water velocity increased, the number of complete turns made by the tentacles also increased (13), adding to the effective filtering surface at higher particulate fluxes. This level of control may not be typical of other deposit-feeding polychaetes, such as ampharetids and terebellids, which do not show comparable tentacle musculature (14) and which have difficulty feeding at comparable flow velocities (15).

To determine whether the helical arrangement was a response to the increased flux of suspended material that occurs at high water velocities or a re-

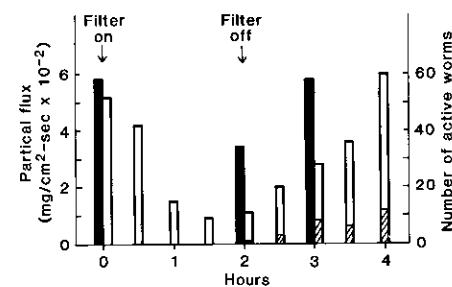


Fig. 3. Feeding behavior as a function of particulate matter flux. Closed bars represent particulate flux; open bars, number of worms displaying helically arranged tentacles; cross-hatched bars, number of worms deposit feeding. The number of worms feeding with extended tentacles was determined every 30 minutes. Particulate flux was calculated by multiplying the water velocity (12 cm/sec) by the suspended particulate matter concentration (determined from the median of three 1.0-liter water samples taken for each calculation). The water samples were obtained at time 0, and then the pump and filter system was engaged. Two hours later, water samples were taken before the pump and filter were disengaged, and the flume was again operated with continuously renewed water from the laboratory seawater system. Samples of this water were taken 1 hour later. Worms responded gradually to engagement or disengagement of the filter because of the large volume of the flume system (~ 270 liters).

sponse to higher water velocity per se, the flume's pump and filter system were used to vary the concentration of suspended particulate matter (Fig. 3). By the time approximately 40 percent of the particulates (by weight) was filtered out, most worms had withdrawn their tentacles into their tubes. When the experiment was repeated with the filter element removed from the recirculation system, the concentration of suspended particulate matter (and hence the particulate flux) remained constant, as did the number of worms actively feeding. Thus it was not the operation of the pump and filter that inhibited feeding behavior, but the reduced particulate flux.

It has been known for some time that certain benthic organisms, including some spionids, nereids, fabricine sabelids, and oweniids among the polychaetes (6), tellinids among the bivalves (16), and amphipods among the crustaceans (17) are capable of both suspension and deposit feeding. The growing understanding of benthic boundary layer dynamics and rapidly improving flow measurement technology now permit an analysis of the factors influencing the preferred feeding mode. We suggest that animals capable of switching their feeding behavior typify environments of rapidly varying flow characteristics. Rather than being a troublesome anomaly in trophic classifications (6), such animals form a distinctive indicator group of their own.

GARY L. TAGHON
ARTHUR R. M. NOWELL
PETER A. JUMARS

Department of Oceanography,
University of Washington, Seattle 98195

References and Notes

1. R. R. Hessler and P. A. Jumars, *Deep-Sea Res.* **21**, 185 (1974); P. A. Jumars and K. Fauchald, in *Ecology of Marine Benthos*, B. C. Coull, Ed. (Univ. of South Carolina Press, Columbia, 1977), p. 1.
2. H. L. Sanders, *Bull. Bingham Oceanogr. Collect.* **15**, 345 (1956); D. J. Wildish, *Helgol. Wiss. Meeresunters.* **30**, 445 (1977).
3. M. R. Roman and K. R. Tenore, *Estuarine Coastal Mar. Sci.* **6**, 37 (1978); D. K. Young, *Vie Milieu Ser. A 22* (Suppl.), 557 (1971).
4. E. T. Baker and R. A. Feely, *Science* **200**, 533 (1978); P. E. Biscaye and S. L. Eittrheim, *Mar. Geol.* **23**, 155 (1977); R. A. Kerr, *Science* **208**, 484 (1980).
5. K. Fauchald, *The Polychaete Worms* (Natural History Museum of Los Angeles County, Los Angeles, 1977), p. 22.
6. _____ and P. A. Jumars, *Oceanogr. Mar. Biol. Annu. Rev.* **17**, 193 (1979).
7. D. M. Dauer, C. A. Maybury, R. M. Ewing, unpublished manuscript.
8. A. R. M. Nowell, P. A. Jumars, R. F. L. Self, in preparation.
9. The filter removes particles $> 10 \mu\text{m}$ in size.
10. All water velocities are for 0.4 cm above the bed, the approximate height at which the helical tentacles are held.
11. Proportions at any given water velocity do not always sum to 1.0 because a few worms usually engaged in other activities (such as tube building).
12. D. I. Rubenstein and M. A. R. Koehl, *Am. Nat.* **111**, 981 (1977).
13. When the water velocity is 5 cm/sec, the median number of turns in a helical tentacle is 1 ($N = 10$); at 12 cm/sec, 1.25 ($N = 8$); at 19 cm/sec, 2.25 ($N = 6$); and at 26 cm/sec, 2 ($N = 9$). The trend of increased coiling of the tentacles as velocity increases is highly significant ($P < .01$, Jonckheere trend test) [A. R. Jonckheere, *Biometrika* **41**, 133 (1954)].
14. R. P. Dales, *J. Mar. Biol. Assoc. U.K.* **34**, 55 (1955).
15. In comparable experiments with *Hobsonia florida* (Ampharetidae) and *Thelepus crispus* (Terebellidae), increased flow velocities simply reduced the proportion of individuals successfully feeding.
16. A. E. Brafield and G. E. Newell, *J. Mar. Biol. Assoc. U.K.* **41**, 81 (1961); R. N. Hughes, *ibid.* **49**, 805 (1969).
17. E. L. Mills, *J. Fish. Res. Board Can.* **24**, 305 (1967).
18. We thank the director of the Friday Harbor Laboratories, University of Washington, for providing laboratory space and equipment. We also thank M. A. R. Koehl and S. Vogel for helpful suggestions and J. A. Taghon for photography. Supported by DOE contract DE-AT06-76-EV-75026 (DE-EV-75026-86) and ONR grant N00014-75-C-0502.

19 May 1980