Particle-size selection by *Pseudopolydora paucibranchiata* (Polychaeta: Spionidae) in suspension feeding and in deposit feeding: influences of ontogeny and flow speed

Abstract *Pseudopolydora paucibranchiata* Okuda suspension feeds and deposit feeds at the sediment–water interface, where it is exposed to a variety of particles differing in physical characteristics and nutritional value. In flume experiments (conducted in August 1994 and May 1995) with two sizes of either suspended or deposited beads, I measured particle-size selection separately in each feeding mode. The same influences of palp width and of ambient flow speed were observed in each mode. At velocities ≤ 0.74 cm s\(^{-1}\) there were no relationships between palp width and the proportion of gut contents composed of large beads. At velocities > 1.8 cm s\(^{-1}\) worms with narrower palps ingested relatively fewer large beads (and more small beads) than did worms with wider palps. Palp width and body length were linearly related, and results were similar when analyzed with body length as the independent variable. As flow speed increased, selectivity changed in a worm-size-specific manner: worms with a palp width < ca. 150 μm (or body length < ca. 12 mm) ingested relatively fewer large beads (and more small beads) as velocity rose, while the proportion of large beads ingested by larger worms remained generally constant. These results are most likely explained by mechanics of particle capture. Furthermore, when deposit feeding, worms of all sizes were biased toward ingesting small beads. In contrast, when suspension feeding, worms were biased toward ingesting large beads, with the exception that worms with a palp width < 125 μm (or body length < 8 mm) were biased for small beads in flows ≥ 4.0 cm s\(^{-1}\). Assuming that in the field (1) particle size is the principle criterion for selection, and (2) the amount of digestible food component in deposited and suspended particles, respectively, is related to particle surface area and volume, I hypothesize that changes in selectivity as velocity rises can cause juveniles to experience a decreasing profitability of suspension feeding and a simultaneously increasing profitability of deposit feeding. Juveniles could maintain a diet of high food value despite flow variations by adjusting the proportion of time they spend suspension feeding relative to deposit feeding.

Introduction

Many infaunal and epifaunal invertebrates feed at the sediment–water interface, where they are capable of both suspension feeding and deposit feeding. These “interface feeders,” including polychaetes, bivalves, crustaceans, and echinoderms (e.g. Dauer et al. 1981; Okamura 1990a), have access to a wide range of potential food particles among deposits, temporarily resuspended material, seston, and plankton that vary in physical characteristics and nutritional value. Spionid polychaetes, e.g. *Pseudopolydora paucibranchiata*, are interface feeders that deposit feed at low flow speeds by collecting particles from the sediment surface with their paired palps. In stronger flow, depending on the flux of suspended particles, many species also lift the palps into the water column to capture suspended particles (Taghon et al. 1980; Dauer et al. 1981). Feeding and growth rates of spionids when they are primarily deposit feeding can differ from those obtained when they are primarily suspension feeding (Taghon and Greene 1992). This discrepancy may be due to differing food resources in suspension or in deposits, and/or differences in the worms’ abilities to obtain and utilize food resources in the two feeding modes.

For tentaculate feeders, particle-selective feeding and its implications for foraging have been more thoroughly
studied in deposit feeding than in suspension feeding. Numerous theoretical and experimental investigations of deposit feeding have addressed selection criteria such as particle size, specific gravity, surface texture, and food value (reviewed by Jumars 1993), and have related selection to extrinsic variables such as appendage or body size, flow speed, and frequency of sediment transport events (e.g. Jumars et al. 1982; Taghon 1982; Whitlatch and Weinberg 1982; Luckenbach et al. 1988; Hentschel 1996). Particle size has emerged in foraging theory for deposit feeders as a critical selection criterion because of its relationship to food value (Jumars 1993). In contrast, most studies of tentaculate suspension feeding have addressed particle selection based primarily on taxonomic identity of prey or categorization of organic vs mineral constituency (e.g. Ronan 1978; Sebens and Koehl 1984; Muschenheim 1987). A few have investigated the role of particle size, either theoretically (Rubenstein and Koehl 1977; Shimeta 1993) or experimentally (e.g. Nicol 1930; LaBarbera 1984; Sebens and Koehl 1984; Okamura 1990b).

Ambient flow speed and animal size are two variables that may greatly influence the diet of interface feeders. Evidence for the importance of these variables has come from models of feeding mechanics and from experimentation. Theory of particle contact by deposit feeders emphasizes geometry and appendage sizes (Jumars et al. 1982; Whitlatch 1989; Hentschel 1996), and models of suspension-feeding mechanics predict strong influences of morphology and flow (Shimeta and Jumars 1991; Shimeta 1993). Among sponions, influences of flow speed (Taghon 1982) and of body size (Taghon 1982; Hentschel 1996) on selective deposit feeding according to particle size have been demonstrated separately. For tentaculate suspension feeding, effects of velocity on particle-size selection have been investigated only for bryozoans (Okamura 1990b), while body-size effects have been previously unstudied. No studies have addressed the interaction of flow speed and animal size.

Effects of flow speed and morphology on selective feeding may have important ecological implications. Variations in velocity affect the partitioning of food resources between suspension and deposits (Jumars and Nowell 1984) as well as the behavior of sponions switching between the two feeding modes (Taghon et al. 1980; Dauer et al. 1981). Any direct influences of flow speed on particle selection may affect the animals' abilities to access the various types of food particles available either in suspension or in deposits. Influences of appendage or body size on selection may also imply ontogenetic variation in feeding or foraging strategies (e.g. Hentschel 1996).

Here I report the first investigation of the interactive influences of velocity and worm size on particle-size selection in both suspension feeding and deposit feeding by a single species. Pseudopolydora paucibranchiata is an abundant spionid polychaete on intertidal mud and sand flats in southern California (Weinberg 1979; Levin 1981, 1982). In these experiments, worms of a wide size range were forced to feed in one mode by offering either only suspended or only deposited particles. Ambient flow speed was varied between treatments.

**Materials and methods**

**Worm collection and maintenance**

I collected Pseudopolydora paucibranchiata Okuda on a 500-μm mesh sieve at an intertidal sand flat in Bodega Bay, California (August 1994 for suspension-feeding experiments and May 1995 for deposit-feeding experiments), and kept them in aerated seawater at 13°C at the University of California, Berkeley. Worms were removed from their tubes, anesthetized in 4% MgCl₂, and measured for body length (tip of prostomium to end of pygidium), palp length, and palp width at the proximal end, using a dissecting microscope with an ocular micrometer. Worms with damaged bodies or palps, or regenerating palps, were not used in experiments. After recovery from the anesthetic, worms were returned to sediment and allowed to burrow and build a new tube. Each worm was placed on the surface of a separate container of sediment, made of a vertical, plastic, 1-ml pipettor tip (0.75 cm widest i.d.) that was sealed at the narrow end (i.e., the bottom) and filled with Bodega Bay sediment that had passed through a 250-μm mesh sieve. Only worms that established a tube by the next day were used for experiments. Worms in these containers were kept submerged in trays filled with seawater from the Bodega Bay Marine Laboratory and fed liberally with a ground paste of Gerber mixed cereal for 1 to 4 d before experiments were conducted.

**Flume experiments**

Experiments were run in a recirculating flume at 13°C. The channel is 15.5 cm wide and 90 cm long, and water is recirculated by a motor-driven propeller. A 10-cm long section of 0.5-cm diameter collimators was placed 11 cm downstream of the entrance, preceded by baffles that aided the flow in diverging from its initial jet. A 2-cm wide strip of 2-mm sand grains was cemented across the flume floor 7.5 cm downstream of the collimators to ensure formation of a turbulent boundary layer when the flume was run at low velocities. The working section of the flume floor (36 cm downstream of the collimators) included a removable Plexiglas plate with a rectangular array of 24 holes, each of which snugly fit a pipettor tip with an individual worm and held it flush with the floor. The array held four columns of worms along the axis of the flow, with centers separated by 2.25 cm, and six rows across the channel, with centers separated by 3.75 cm. These separation distances (ca. 22 worm-tube diameters cross-stream and 37 worm-tube diameters streamwise) ensured that at all experimental velocities there would be no interference of tube wakes with the flow around neighbors (Nowell and Jumars 1984). The flume was filled to 4.3 cm depth with seawater (15 liters) poured through a 5-μm mesh filter bag.

In each experiment I measured selection between two size classes of beads. For suspension-feeding experiments, polystyrene beads (specific gravity 1.02, SoloHill Labs, Inc.) were purchased in nominal size ranges of 25 to 38 and 75 to 90 μm. For deposit-feeding experiments, glass beads (specific gravity 2.45, Cataphote, Inc., engineering grade) were purchased in nominal size ranges of 13 to 44 and 74 to 105 μm. Prior to experiments, beads were washed with distilled water and wet-sieved between 15- and 45-μm Nitex screens (small-bead size class) or between 75- and 100-μm Nitex screens.