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Feeding behavior of *Dipolydora commensalis* (Polychaeta: Spionidae): particle capture, transport, and selection

Jason D. Williams[1,a] and John J. McDermott[2]

[1]Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881, USA
[2]Department of Biology, Franklin and Marshall College, Lancaster, Pennsylvania 17604, USA

Abstract. Particle capture, transport, ingestion, and selection mechanisms used by *Dipolydora commensalis,* a symbiotic worm that inhabits burrows it produces in hermit crab shells, were studied in the laboratory. Worms removed from shells inhabited by *Pagurus longicarpus* were placed in capillary tubes for observation and video-microscopy of feeding. Particles were captured by the palps and transported to the mouth by ciliary and muscular action. Mean transport rates for cysts of *Artemia* from the distal ends of the palps to the mouth ranged from 0.7 to 1.3 mm/sec; those for glass beads, from 0.2 to 0.8 mm/sec. Upon reaching the mouth, particles were engulfed by the lateral lips and ingested. Worms feeding on large particles (>0.2 mm) repeatedly arched the anterior end of the body. Nauplii of *Artemia* were used to determine the ability of the worms to feed on small motile organisms over a 24-h period in the dark. In six trials the percentage of nauplii ingested ranged from 58% to 76%. In particle selection experiments, worms were offered uncoated glass beads and beads coated with fluid from the ribbed mussel, *Geukensia demissa.* In two experiments 91% and 89% of coated glass beads were ingested as compared to 15% and 4% of uncoated beads, respectively. Video-analyses of feeding sequences showed that cysts were often partially ingested and then ejected from the mouth. Uncoated beads transported along the palps often never reached the mouth. These results indicate that *D. commensalis* can actively select particles at the mouth and possibly during transport along the palps.

Additional key words: suspension feeding, deposit feeding, feeding biodynamics, video-analysis, Annelida

Polychaetous annelids of the family Spionidae occupy a variety of marine and estuarine habitats, ranging from soft-bottom sediments to hard calcareous substrates (Fauchald & Jumars 1979). The biology of shell-boring spionids has been studied in considerable detail, in part due to their effects on commercially important species of bivalves (e.g., Haigler 1969; Blake & Evans 1973; Zottoli & Carriker 1974; Sato-Okoshi & Okoshi 1993). Blake (1996) referred those species in the genus *Polydora* bearing notosetae on setiger 1 to the genus *Dipolydora* VERRILL 1879, making the current combination for the species under study *Dipolydora commensalis* (ANDREWS 1891). Although many spionids are non-specific borers, *D. commensalis* burrows exclusively into gastropod shells inhabited by hermit crabs. The burrows of the worm often begin on the columellar side of the shell aperture and extend to the internal apex of the shell via a thin secreted calcareous tube (Andrews 1891; Hatfield 1965; Radashevsky 1989). *D. commensalis* is usually classified as a commensal, but recent research suggests that the nature of this association with hermit crabs may require some re-evaluation. Buckley & Ebersole (1994) showed that the strength of shells inhabited by spionids is reduced, decreasing the resistance of shells to crushing forces applied by predators.

The feeding biology of polychaetes has been summarized by Fauchald & Jumars (1979) and several spionids have been investigated in detail (Dorsett 1961; Dauer et al. 1981; Levin 1981; Jumars et al. 1982; Dauer 1983, 1984, 1985; Yokoyama 1988; Miller et al. 1992; Bock & Miller 1996; Shimeta & Koehl 1997). In most spionids, a pair of peristomial palps are used to capture and transport food particles for ingestion. Particles are usually transported, by a combination of muscular movement and ciliary action, in a median ciliated groove (Dorsett 1961), although in at

[a] Author for correspondence.
E-mail: jwil4024@uriacc.uri.edu

least two species the palps lack a ciliated groove (Dauer & Ewing 1991).

Spionid polychaetes have been classified as either suspension-feeders or deposit-feeders, or as suspension-deposit feeders (Dauer et al. 1981). Suspension-deposit feeding spionids have a mixed mode of feeding, depending on environmental conditions, and change their feeding behavior in the presence of particle fluxes or deposited material (Taghon et al. 1980; Miller et al. 1992; Bock & Miller 1996). Particle capture in spionids occurs primarily through direct interception of food by the palps, although inertial impaction and gravitational deposition may have slight effects (Taghon et al. 1980; Shimeta & Koehl 1997).

Several physical limits may affect the ability of a worm to feed on particles. Mucus secreted at the distal end of the palps and along the ciliary oral groove has a limited strength of adhesion to intercepted particles (Jumars et al. 1982). There are also limits to the size of particles that can be transported along the palps, via ciliary and/or muscular action. The size of the mouth and/or pharynx acts as the final determinant of the size of particles that can be ingested.

Most studies on the feeding biology of spionids have involved species inhabiting soft-bottom substrates. The use of soft-bottom spionids has allowed investigators to study the feeding biology in a variety of contexts (e.g., Dauer et al. 1981; Jumars et al. 1982; Taghon 1982; Taghon & Jumars 1984; Shimeta 1996), in particular, active and passive particle selection. Active particle selection in spionids occurs at the mouth, pharynx, or along the ciliated oral groove of the palps (Dauer et al. 1981; Levin 1981; Shimeta & Koehl 1997).

Passive selection results from particle loss due to limited adhesive strength of mucus on the palps (Self & Jumars 1978; Taghon 1982; Shimeta & Koehl 1997). Such particle loss can occur at the point of initial contact between palp and particle or during particle transport along the palp (Taghon 1982). Size, specific gravity, and texture of food particles can affect the passive selection mechanisms in spionids (Self & Jumars 1978; Jumars et al. 1982; Taghon 1982; Shimeta & Koehl 1997). Passive selection mechanisms, therefore, can cause preferential ingestion of particles that are smaller, rougher, and have lower specific gravities. Passive loss could also determine the ability of a polychaete to engage in a macrophagous, predatory mode of feeding documented in certain spionids (Dorsett 1961; Jumars et al. 1982).

One might expect differences between the feeding behavior of soft-bottom species and *D. commensalis* due to the distinct habitat of this species. The burrow in which *D. commensalis* lives may prevent it from feeding at the sediment-water interface. Additionally, interactions with the hermit crab host may influence the feeding behavior of the worm, which has been reported to feed on fine particles suspended in the branchial currents of the crab (Dauer 1991; Radashevsky 1993), on particles attached to the legs of the crab (Dauer 1991), and on nauplii of *Artemia* being fed to the longwrist hermit crab *Pagurus longicarpus* SAY 1817 (J.J. McDermott, unpubl.). Since the original description of *D. commensalis,* only nonquantitative observations on the feeding behavior of this polychaete have been reported (Radashevsky 1993); however, palp morphology and its relation to feeding mechanisms on small particles was studied by Dauer (1991).

The objective of our study was to investigate the feeding biology of *D. commensalis,* focusing on mechanisms of particle capture, transport, ingestion, and selection, by combining observations of behavior with quantitative measurements of deposit and suspension feeding. The observation of feeding behavior and measurements of feeding rates were made possible by removing the worms from the shells. Worms placed in glass tubes were compared with those in shells inhabited by *P. longicarpus,* as they manipulated cysts and swimming nauplii of *Artemia* and glass beads. Videomicroscopy, a valuable aid in studying the feeding behavior of small invertebrates and their larvae (e.g., Strathmann 1982; Gilmour 1985; Holland et al. 1986; Gallager 1988; Emlet 1990; Hansen & Ockelmann 1991; Nielsen et al. 1993; Mayer 1994; Chen et al. 1996; Hart 1996; Shimeta & Koehl 1997), was used to record the feeding rates of the worms and mechanisms involved in feeding.

Methods

Collections and measurements

We collected by hand 90 hermit crabs (*Pagurus longicarpus)* from southern New Jersey inside of Hereford Inlet on 21 October 1994, in order to isolate *Dipolydora commensalis* for feeding behavior studies. The hermit crabs were maintained in aerated seawater (salinity 32‰) in large plastic containers at 14° C.

Shells were cracked with a hammer and the hermit crabs removed. Presence and burrow morphology of *D. commensalis* were recorded. Although cracking exposed the burrows of *D. commensalis,* worms had to be manipulated out of the burrow. The best method of removal was to snip off the apex of the cracked shell with wire cutters, exposing the lumen of the uppermost whorl. The worm could then be forced out of its burrow by pipetting a stream of seawater through the hole in the apex.

Length of *D. commensalis* was determined by mea-

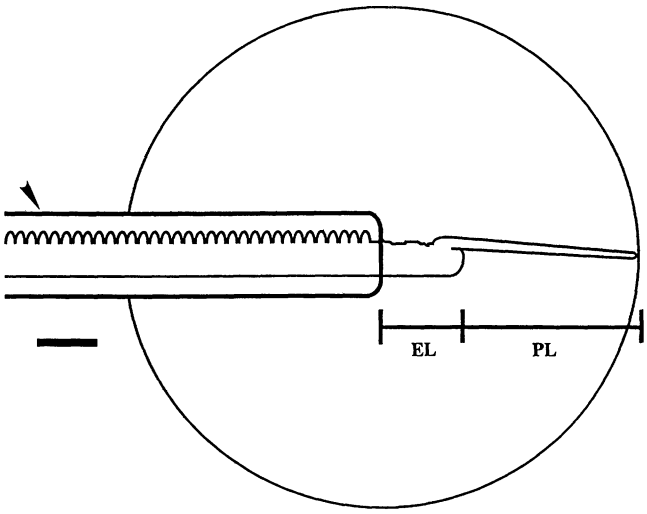

Fig. 1. Diagram of a lateral view of the anterior end of *Dipolydora commensalis* within a capillary tube, indicated by arrowhead. The exposure length (EL) and palp length (PL) are indicated by the horizontal lines. The approximate deposit feeding area of the worm is shown by the circle. The feeding volume of the worm is the half-sphere defined by this circle. Scale bar, 1 mm.

suring each worm as it moved across a glass slide covered with a film of seawater. Worms were isolated in fingerbowls (55 mm diameter) and manipulated into glass capillary tubes (25 mm long, open at both ends, with inside diameter 0.9–1.1 mm). After initial experiments, worms less then 12 mm long were placed in 20-mm tubes while longer worms were placed in 30-mm tubes, in order to minimize differences in worm-to-tube length ratios. All of the above measurements were made with dial calipers (worms to 1 mm). All means are reported with standard deviations.

The palp length and exposure length (Fig. 1) for worms used in the feeding experiments were measured to 0.1 mm using an ocular micrometer (Wild dissecting microscope). In order to measure exposure length—the length of the worm protruded outside the tube (from the end of the mouth to the tube opening)—crushed cysts of *Artemia* were positioned at the tube opening using forceps. Once a worm had moved to the opening and contacted the cysts with its palps, the cysts were moved slowly away from the burrow and exposure length was recorded. This procedure was repeated five times and the maximum exposure length of these trials was recorded for each worm. The maximum exposure length and palp length were then used to calculate the deposit feeding area and feeding volume, the half-sphere defined by the deposit feeding area of the worms (Fig. 1).

Video-microscopy of feeding behavior

Feeding behavior was observed with a dissecting microscope. Worms were fed nauplii of *Artemia* sp. (San Francisco Bay Brand, Newark, CA) with a mean length of 0.56 ± 0.05 mm and width of 0.10 ± 0.01 mm (n=10). Video-microscopy (Panasonic camera and recorder or RCA camera and Panasonic time-lapse recorder) was used to record 14 feeding sequences by 6 worms. The time for naupliar transport from the distal end of a palp to the mouth was determined five times with an electronic stopwatch for each feeding sequence; mean times and standard deviations were then calculated. Mean rate of naupliar transport was estimated by using the mean palp length of worms measured for cyst and glass bead transport. Videotape frames from feeding sequences were digitized with Apple video player card and software (Apple Computer, Inc.) and Adobe Photoshop 3.0 (Adobe Systems, Inc.) to produce Fig. 2.

Unhatched brine shrimp cysts, both capsulated (chorion present) and decapsulated (chorion absent), were also used in feeding experiments. Decapsulated and capsulated cysts were removed from a hatching culture and separated from one another. Capsulated cysts had diameters of 0.24 ± 0.02 mm (n=24), while decapsulated cysts were oblong and measured 0.33 ± 0.03 mm (n=24) long. The time for cyst transport from the distal end of a palp to the mouth was recorded, as described above. Four worms were used to measure 23 feeding sequences. The speed of ingestion of the cysts was too fast to be accurately recorded by stopwatch and was therefore only estimated. Two of the worms used to measure cyst transport time were also used to measure transport time of glass beads (Sigma Co., No. G-1509, 0.25–0.30 mm in diameter). A total of 8 feeding sequences with glass beads were recorded. A two-sample t-test was used to determine if the difference in the mean transport times between cysts and beads was significant ($p<0.01$). Fine particles (<0.1 mm) from crushed cysts or macerated tissue of ribbed mussels, *Geukensia demissa* (DILLWYN 1817), were offered to the worms in order to observe feeding behavior with smaller particles.

Finally, time-lapse analysis (36× real time) was used to observe feeding selection by worms offered coated and uncoated beads. The bead selection protocol (see below) was replicated for these time-lapse recordings.

Feeding on nauplii of *Artemia*

In the first two quantitative suspension feeding trials, ten worms within capillary tubes were isolated in 55-mm fingerbowls containing 25 ml of artificial sea-

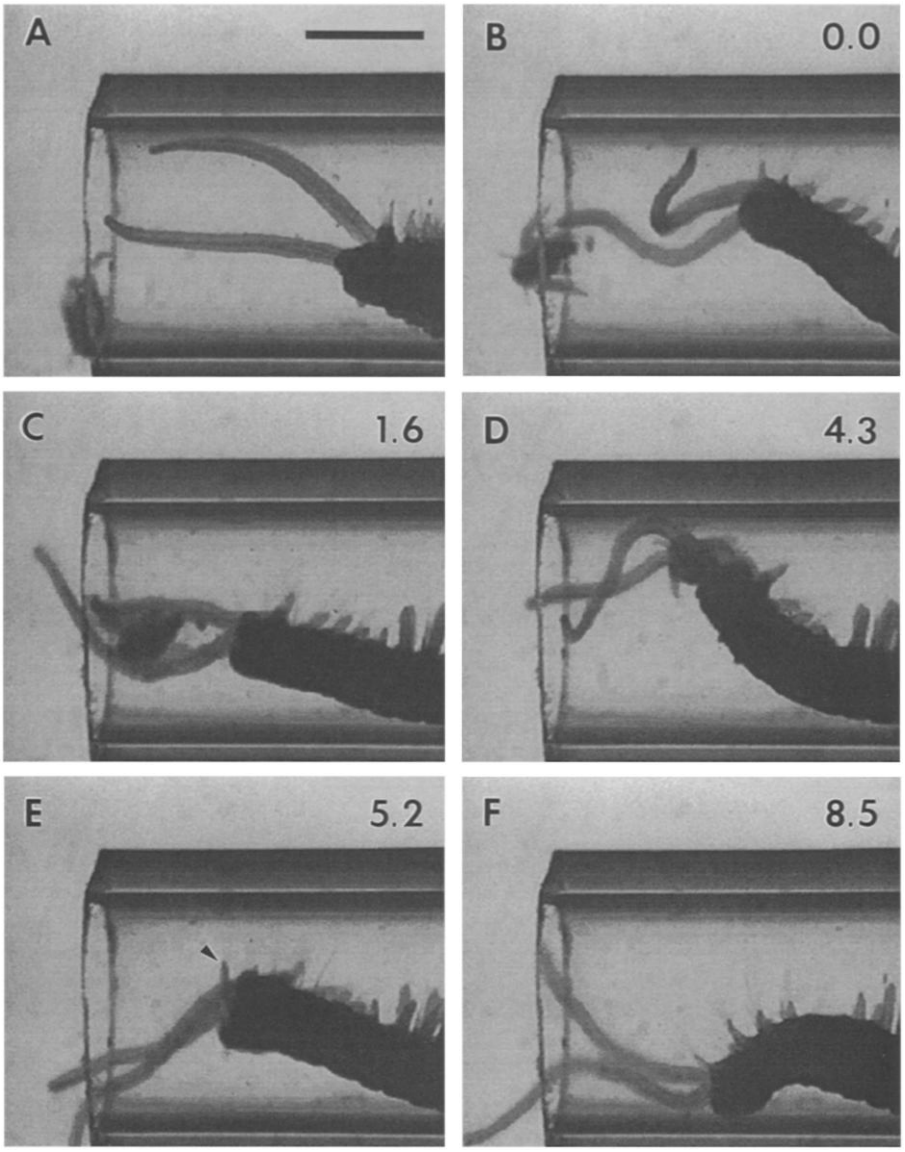

Fig. 2. Feeding behavior of *Dipolydora commensalis* (lateral views). (A) Extended palps; **(B)** naupliar contact; **(C)** naupliar transport; **(D,E)** engulfment, arrowhead indicates trunk appendage of *Artemia;* **(F)** body arching. Elapsed time from the point of initial contact (B) is indicated in seconds in upper right of each frame. Scale bar, 0.5 mm.

water (Instant Ocean; 32‰). Ten motile nauplii were added to each of these bowls, which were maintained in the dark in an incubator at ~12° C for 24 h. The bowls were then removed and remaining nauplii were counted. Controls consisted of 10 nauplii in 25 ml of artificial seawater in each of 10 fingerbowls, similarly treated. Four more feeding trials were conducted using this same protocol, except that 20 nauplii were added.

Bead selection experiments

Feeding selection was studied using glass beads (Sigma Co., No. G-1509). Uncoated beads (n=40) were added to 10 fingerbowls containing 25 ml of Instant Ocean. Ten isolated worms within capillary tubes were then placed in the fingerbowls in such a way that the glass beads were positioned within the deposit feeding area of the worms. The bowls were maintained in the dark at ~12° C for 3 h, after which the number of uningested beads was recorded. Any accumulation of beads at the glass tube opening was noted.

Glass beads were also coated with fluid from macerated ribbed mussels. Excess fluid was drained off after coating and the beads were allowed to air dry overnight. The dry mass of coated beads was mixed with a small volume of Instant Ocean, then added to the fingerbowls. After all uncoated beads were defecated by the 10 worms from the first part of the study (72 h), 40 coated glass beads were added to clean 55-mm fingerbowls in 25 ml of Instant Ocean. Conditions were as described above and the number of uningested beads was recorded after 3 h. A paired t-test was used to determine if the difference in the

means of the two types of ingested beads was significant ($p<0.01$).

Results

Measurements

The range of worm lengths was 5–22 mm (mean = 13 ± 6 mm, n=16); palp lengths, 1.6–5.3 mm (mean = 3.5 ± 1.3, n=13); exposure lengths, 0.7–6.8 mm (mean = 3.3 ± 1.8, n=11); feeding areas, 16.6–307.9 mm^2 (mean = 158.9 ± 106.0, n=11); feeding volumes, 25.5–2032.2 mm^3 (mean = 872.0 ± 750.1, n=11). No correlation was found between worm length and palp length or exposure length.

Feeding behavior

In the absence of food, the worms were usually found with the anterior end and palps several millimeters within the opening of the glass capillary tube. However, in the presence of nauplii or coated glass beads, the worms were often found with their palps extended out of the tube, actively lashing through the water, or with anterior end also extended.

The series of events involved in feeding by the worm are shown in Fig. 2. Worms were presumably able to detect the presence of nauplii, cysts, and coated beads before physical contact, as evidenced by an increase in the rate of palp movement. Both palps were irregularly lashed through the water (Fig. 2A), occasionally touching the bottom of the fingerbowl. This type of palp movement occurred in the presence of either deposited food particles (i.e., cysts and coated beads) or suspended nauplii. Deposited particles were contacted during lashing movements, although palps did not appear to regularly search the bottom of the dish for food. When the palps encountered particles, the worm either backed away or immediately began feeding. If the worm backed away, it would eventually move forward and contact the particles again, at which time the feeding process was usually initiated (Fig. 2B). The orientation of the palps exposed the oral groove to the particles. The ciliary action of the oral groove then transported the particles to the mouth of the worm for ingestion (Fig. 2C). Particles were engulfed by the lateral lips of the mouth and ingested into the pharynx (Fig. 2D,E).

Although ciliary action was sufficient to transport cysts and smaller particles (<0.1 mm) to the mouth, muscular manipulation of the larger nauplii and glass beads was also observed. The distal end of the palps wound around the larger particles before transporting them to the mouth. In certain cases, the palps were crossed 1 mm in front of the mouth to trap nauplii and facilitate ingestion. Most often the palps undulated in a wave-like fashion, carrying the particles to the mouth, where the lateral lips immediately engulfed them. After engulfing larger particles (nauplii and beads), the lateral lips opened and closed while the worm repeatedly arched the first five segments of its body dorsally (Fig. 2F). Worms often withdrew into their tubes after feeding, but advanced if offered more food.

Worms were often observed to reject cysts and beads at the mouth. Particles would be transported to the mouth, partially ingested, and subsequently ejected. Rejected particles were dropped next to the head of the worm. In most cases the rejected particles remained untouched by the palps, although particles were sometimes transported back to the mouth.

The feeding events involved in the ingestion of fine particles (<0.1 mm) differed from those seen with larger particles. Fine particles were drawn to the capillary tube by the branchial current of the worm. Ciliary action of the palps transported these fine particles to the mouth for ingestion. No opening and closing of lateral lips, arching, or particle rejection were observed when the worms fed on fine particles.

Video-microscopy allowed us to measure particle transport time along the palps. Measurements of naupliar transport along the palps of six worms ranged from 1.5 to 7.9 sec (mean = 3.3 ± 1.8 sec., n=14). Estimated mean rate of naupliar transport was 1.0 ± 0.5 mm/sec (n=14). Cyst and bead transport rates were measured for four and two worms, respectively. The mean rate of cyst transport among the worms was 1.0 ± 0.2 mm/sec (n=23), while the mean rate of glass bead transport was 0.5 ± 0.2 mm/sec (n=10). Mean cyst transport rates and glass bead transport rates differed significantly ($p<0.001$). Time for ingestion of both cysts and beads was less then 1 sec in most feeding sequences.

Worms were able to reverse direction in the glass tube in the following manner. Palps were extended posteriorly and positioned against the dorsal side of the animal while the anterior end was flexed over the ventral side. The worm then moved its anterior end forward and over the pygidium. Fecal pellets, composed of partly digested nauplii and cysts, or glass beads, were deposited at both ends of the tube. Worms were never observed to move fecal pellets with their palps.

Feeding on nauplii of *Artemia*

The results of six feeding trials using nauplii are shown in Table 1. Four worms offered 20 nauplii ingested all present, showing that worms can consume

Table 1. Results of six laboratory feeding trials using swimming nauplii of *Artemia*; carried out from 14 November 1994 to 27 February 1995. Mean ± standard deviation (SD), range, and mean percentage of nauplii ingested by *Dipolydora commensalis* (n = 10) in the dark over a 24-h period.

Initial no. of nauplii	Numbers of nauplii ingested		
	Mean ± SD	Range	Percentage
10	7.2 ± 2.7	2–10	72
10	5.8 ± 4.2	0–10	58
20	13.9 ± 7.1	0–20	70
20	15.2 ± 6.6	1–20	76
20	15.1 ± 5.0	2–19	76
20	11.5 ± 5.6	2–17	59

Three worms were replaced after the third trial; length of worms, 5–22 mm.

at least 20 nauplii within a 24-h period. No nauplii were missing from the controls after 24 h. No apparent relationship was observed between the number of nauplii eaten and worm size. Worms were found at the end of the tubes with palps exposed and irregularly lashing when observed at the end of the 24-h period.

Bead selection experiments

Mean, range, and percentage of uncoated and coated glass beads ingested by *D. commensalis* in 3 h is reported for 10 worms each fed 40 beads (Table 2). The mean number of coated vs. uncoated beads ingested significantly differed ($p<0.001$) in both experiments. While 9 worms ingested 30–40 coated beads in both experiments, no worm ingested more than 16 uncoated beads. At the end of the 3-h period, an accumulation of uncoated beads was observed around the tube ends of worms in both experiments, whereas no accumulation of coated beads occurred. Time-lapse video-microscopy and observations with the dissecting microscope showed that feeding activity, i.e. extension and lashing of palps, is reduced in worms subjected to uncoated beads as compared to coated beads or nauplii. Time-lapse video-microscopy also showed that uncoated beads accumulated because the palps failed to transport the beads to the mouth. Partial transport, followed by bead loss, resulted in the accumulation of uncoated beads at the tube ends. Worms placed with coated beads were found with palps extended and lashing, immediately after bead addition and at the end of the experiment. In time-lapse video-microscopy, coated beads were ingested as seen in Fig. 2 for nauplii.

Table 2. Results of two selection experiments (24 March 1995 to 4 April 1995) using uncoated glass beads and glass beads coated with fluid from macerated ribbed mussels (*Geukensia demissa*). Mean ± standard deviation (SD), range, and mean percentage of beads ingested by *Dipolydora commensalis* (n = 10) within a 3-h period.

Bead type	Numbers of beads ingested		
	Mean ± SD	Range	Percentage
Uncoated	6.0 ± 6.5	0–16	15.0
Coated	36.3 ± 6.7	18–40	90.8
	$P < 0.001$		
Uncoated	1.7 ± 3.4	0–11	4.3
Coated	35.7 ± 3.7	28–40	89.3
	$P < 0.001$		

Same worms used in both experiments; length of worms, 5–22 mm.

Discussion

Although feeding behavior in the presence of fine particles has been studied in *Dipolydora commensalis* (Dauer 1991), here we have described particle capture, ingestion, and selection mechanisms of the worm on larger particles and motile nauplii. We found that *D. commensalis* is capable of active particle selection at the mouth, as observed in the spionid *Streblospio benedicti* (Levin 1981). That *D. commensalis* can reject particles at the mouth was shown by the ejection of the cysts following partial ingestion. The mechanism of rejection was not determined; particles may have been ejected by contraction of the muscles of the pharynx, by a reversal in the ciliary flow of the pharynx, or by a combination of ciliary and muscular action. Particle selection observed in the laboratory may be an artifact resulting from the use of particles not encountered in the natural environment of the worm.

Time-lapse analysis showed that particle selection also occurred during transport along the palps in *D. commensalis* (i.e., coated glass beads were readily ingested by the worms, uncoated glass beads were seldom ingested). Worms were less active when fed uncoated beads but did contact and transport some beads along the palps. However, transport along the palps was usually suspended before the uncoated beads reached the mouth. Particle selection in this case could result from cessation of ciliary activity. We think that this selection is produced by an active mechanism for three reasons: (1) there was no significant water flow or shearing force in the experiments; (2) the deposited uncoated beads had approximately the same specific gravity as the coated beads (which were readily transported to the mouth); and (3) some uncoated beads were ingested (indicating that they could be fully transported). An alternative explanation for the pref-

erential selection of coated beads is that the smooth surface of uncoated beads adheres only weakly to mucus.

Particle rejection along the palps has been found in other spionids (Levin 1981; Shimeta & Koehl 1997), as well as preferential selection of etched glass beads over smooth glass beads (Self & Jumars 1978). Further studies directed specifically at mucous adhesion and the ciliary action of the palps and pharynx are needed to determine the selection mechanisms of *D. commensalis*.

The naupliar feeding experiments indicate that *D. commensalis* can engage in a predatory, macrophagous mode of suspension feeding, as do other spionids (Taghon et al. 1980; Jumars et al. 1982). The percentage of nauplii captured in 24 h (58–76%) shows that the worm can feed on relatively large, motile zooplankton in the dark. Observations suggest that prey are captured through a combination of mucus adhesion, ciliary action, and mechanical manipulation. Compared to the volume of water in the dishes, the total feeding volume of the worms (Fig. 1) is low (mean = 3.5 ± 3.0%, n=11), suggesting that over the 24-h feeding period the worms must detect the presence of the nauplii and actively capture them. The nauplii must be directly contacted, because their swimming motion is stronger than both the ciliary action of the palps and the branchial current (J. Williams, pers. obs.).

While direct interception is necessary for the capture of larger particles and motile organisms, fine particles with low specific gravities can be carried toward the worm by its branchial currents and drawn into the ciliated oral groove of the palps, to be transported to the mouth. The selection observed during feeding on cysts and glass beads was absent in the case of fine particles. Body movements (arching, opening and closing of lateral lips) were never observed when worms fed on fine particles.

Dauer (1991) hypothesized that the papillae covering the palps of *D. commensalis* are primarily sensory organs. The present experiments with coated glass beads indicate that the worm has chemosensory ability, as suggested for other species of polychaetes (Bock & Miller 1996). When offered uncoated beads, the feeding activity of the worms is low and most worms are found with palps unextended from the capillary tubes. Yet in the presence of coated beads, the worms begin active feeding responses (extended palps and irregular lashing). A conditioned response, such as that documented in certain gastropods (Wood 1968), could have resulted in preferential ingestion of coated beads since uncoated beads were added before coated beads in the selection experiments. However, the above analysis of the feeding behavior of the worms and the fact that uncoated beads were often untouched by the palps suggests that sensory perception, rather then a conditioned response, resulted in preferential ingestion of coated beads. The present experiments do not provide evidence that the papillae are in fact sensory organs, but the results indicate that organic matter on the coated beads induces a feeding response. The experiments also support the conclusion that *D. commensalis* is primarily a suspension feeder (Dauer 1991) as shown by the ability of the worm to feed on swimming nauplii. Capture and subsequent ingestion of deposited materials occur when the palps brush the bottom of the fingerbowl during their irregular lashing.

Worms in their natural burrows displayed feeding responses essentially the same as those in capillary tubes, although the exposure length of the worms was less in the former. A lesser exposure length is expected in the natural burrows, where the presence of *P. longicarpus* would inhibit the worm from extending anterior portions of its body. Short exposure length has been found in spionids that are susceptible to browsing organisms (Woodin 1982, 1984). Mechanical abrasion by the chelipeds of hermit crabs has been shown to inhibit epibiont growth (Walker 1988) and may also remove the palps, as do predators on soft-bottom spionids. Dauer (1991) reported that average palp lengths for the largest females of *D. commensalis* ranged from 0.5 to 0.8 mm (it is unknown whether preserved or live specimens were measured). Although palp growth was not tracked, the palp length of worms isolated in the present study for 138 days increased noticeably; mean length was 4.2 ± 1.2 mm (n=7). This suggests that the short palp length of *D. commensalis* under field conditions is a result of factors such as abrasion, rather than reflecting a genetic limit. Worms that initiate active feeding responses only in the presence of food may reduce palp loss.

Dipolydora commensalis appears to benefit from its association with host hermit crabs in a variety of ways. Food particles suspended in the branchial currents of the crab, deposited material resuspended by the feeding activity of the crab, and food particles dropped during feeding may all be used by the worm. Further investigations into the feeding of *D. commensalis,* directed specifically at the natural diet of the worm, would better define the symbiotic association between *D. commensalis* and hermit crabs.

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