

Functional ciliary groups of the feeding palps of Spionid polychaetes

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ABSTRACT

Functional ciliary groups of the feeding palps of spionid polychaetes are reviewed. Six functional ciliary groups have been observed: frontal cilia, latero-frontal cirri, lateral cilia, ciliated papillae, non-motile cilia of the frontal surface and basal transverse cilia. The number of functional ciliary groups present on any species varies from one to four groups. Some ciliary groups, e.g. frontal cilia, are present on the palps of many species while other groups, e.g. basal transverse cilia, are unique to a single species. Additional studies are necessary to clarify the roles of and possible interactions between (1) functional ciliary groups, (2) mucus and (3) hydrodynamics in particle encounter, retention, transport and rejection.

RÉSUMÉ

Groupes ciliaires fonctionnels des palpes "trophiques" des polychètes Spionidae

Une révision des groupes ciliaires fonctionnels des palpes "nutritionnels" des polychètes Spionidae est entreprise. Six groupes ciliaires fonctionnels ont été observés : cils frontaux, cirres latéro-frontaux, cils latéraux, papilles ciliées, cils non mobiles de la surface frontale et cils transverses frontaux. Le nombre de groupes ciliaires fonctionnels présents chez chacune des espèces varie de un à quatre. Quelques groupes ciliaires, comme les cils frontaux, sont présents sur les palpes de beaucoup d'espèces tandis que d'autres groupes, comme les cils transverses basaux, ne sont présents que chez une espèce. Des études complémentaires sont nécessaires pour clarifier les rôles et les interactions possibles entre (1) groupes ciliaires fonctionnels, (2) mucus, (3) hydrodynamique dans la rencontre, la rétention, le transport et le rejet des particules.

INTRODUCTION

Spionid polychaetes are common inhabitants of infaunal and epifaunal communities of marine and estuarine habitats. The ciliated peristomial palps of spionid polychaetes function in (1) feeding behavior (FAUCHALD & JUMARS, 1979), (2) inter- and intraspecific interactions (LEVIN, 1981) and (3) tube construction (MORTENSEN & GALTISOFF, 1944). In feeding behavior the palps may function in particle encounter, retention, transport, and rejection (e.g. TAGHON *et al.*, 1980; DAUER *et al.*, 1981). Spionid polychaetes use their palps to capture particles in suspension, bedload transport and deposited at the sediment surface; direct deposit feeding using the everted

pharynx has also been observed (DARO & POLK, 1973; WILSON, 1983). The potential rapid flux between suspended, bedload, and deposited states caused DAUER *et al.* (1981) to classify spionids as interface feeders. In this paper studies concerning the role of cilia on the palps are reviewed and areas of future research discussed.

DISTRIBUTION OF FUNCTIONAL CILIARY GROUPS WITHIN AND BETWEEN SPECIES

Studies combining feeding behavior and detailed morphological observations have been performed for eight spionid species and Table 1 summarizes the distribution of ciliary groups among these species. Spionid polychaetes with a median ciliated food groove have one or more of the following five functional groups of cilia on their palps: (1) frontal cilia that line the median groove of the palp, (2) latero-frontal cilia organized as compound cilia (cirri), (3) lateral cilia that beat in metachronal waves, (4) non-motile cirri located at the tips of papillae, and (5) basal transverse cilia at the base of the palp. Within a species, the number of functional ciliary groups varies from one to four. For example, *Malacoceros indicus* has only frontal cilia lining the food groove (DAUER & EWING 1991) and *Paraprionospio pinnata* has four ciliary groups - frontal cilia, latero-frontal cirri, lateral cilia and basal transverse cilia (DAUER, 1985). Between species, some ciliary groups, e.g. frontal cilia, are present on the palps of many species while other groups, e.g. basal transverse cilia, are unique to a single species. *Scolelepis squamata* and *S. hutchingsae* lack a median food groove and the cilia of the palps are non-motile and organized into numerous transverse rows (DAUER, 1983, 1987).

TABLE 1. — Distribution of ciliary groups among the Spionidae.

(from 1- DAUER, 1983; 2- DAUER, 1984; 3- DAUER, 1985; 4 - DAUER, 1987; 5 - DAUER, 1991; 6 - DAUER & EWING, 1991).

X: ciliary or cirral group is present. —: ciliary or cirral group is absent.

Species	Frontal Cilia	Latero Frontal Cirri	Papillae	Lateral Cilia	Non-Motile Cilia	Basal Transverse Cilia
<i>Malacoceros indicus</i> ⁶	X	—	—	—	—	—
<i>Polydora commensalis</i> ⁵	X	—	X	—	—	—
<i>Polydora ligni</i> ⁴	X	X	X	—	—	—
<i>Polydora websteri</i> ⁴	X	X	X	—	—	—
<i>Streblospio benedicti</i> ²	X	X	—	X	—	—
<i>Paraprionospio pinnata</i> ³	X	X	—	X	—	X
<i>Scolelepis hutchingsae</i> ⁴	—	—	—	—	X	—
<i>Scolelepis squamata</i> ^{1, 4}	—	—	—	—	X	—

FEEDING BEHAVIOR

The ciliary groups of the palps of spionid polychaetes may function in particle encounter, retention, transport, and rejection. Particle capture implies particle encounter and subsequent retention. Particle transport implies the movement from the site of capture to the pharynx. Particle rejection implies that the particle is not ingested after capture and would include loss during transport as well as transport away from the pharynx.

Particle encounter in the deposit feeding mode occurs as the frontal surface of the palp is placed onto the sediment surface and can be predicted as a function of particle size with larger particles having a higher probability of being encountered (JUMARS *et al.*, 1982). In the suspension feeding mode, particle encounter prediction is a function of encounter mechanism (direct interception, inertial impaction, gravitational deposition, diffusional deposition, electrostatic attraction, SHIMETA & JUMARS, 1991). The frontal surface of the palp is the site of particle encounter, but the ciliary groups of Table 1 probably have no role in particle encounter dynamics of deposit feeding and could only have a role in suspension feeding if currents produced by the cilia of the palps altered ambient flow conditions. DAUER (1984, 1985) hypothesized that both the latero-frontal cirri and lateral cilia of *P. pinnata* and *Streblospio benedicti* created currents that increased particle encounter during suspension feeding. Ciliary currents would be functional only in low ambient flows such as in highly depositional environments or close to the sediment surface in the bottom boundary layer.

Retention of particles in spionid polychaetes is assumed to be due to the adhesive properties of mucus secreted on the frontal surface and the interaction of mucus and surface properties of the particle (roughness, organic coatings) (JUMARS *et al.*, 1982). Hydrodynamic particle retention, produced by cilia of the palps (*sensu* JORGENSEN 1981, 1982), again could only occur under low ambient flow conditions or when the collection surface is sheltered from ambient flow (SHITEMA & JUMARS, 1991). Mucus is particularly important in particle retention of the *Scolecopsis* spp. The non-motile cilia of the *Scolecopsis* spp. were interpreted by DAUER (1983, 1987) as providing a rough textural surface to retain the particle-mucus complex which was transported to the pharynx by complete retraction of the palp frontal surface directly onto the pharyngeal surface. DAUER (1987) hypothesized this mechanism was an adaptation to the highly turbulent habitat occupied by both species and minimized the loss of particles during transport along the food groove of the palp as envisioned by SELF & JUMARS (1978). Particle retention during transport can also be a function of the depth of the food groove. For example, in *P. pinnata* the food groove is deep and wide and particles up to 100 μm in greatest dimension were completely enclosed by the lateral edges of the frontal surface during transport to the pharynx (DAUER, 1985). Particles less than 100 μm make up the vast majority of particles ingested by *P. pinnata* (DAUER, 1980; LUCKENBACH *et al.*, 1988).

Particle transport to the pharynx, as a particle-mucus complex, is primarily accomplished by the beating of the frontal cilia in those spionids with a median food groove. For the *Scolecopsis* spp. the non-motile cilia of the frontal surface serve indirectly in particle transport by holding the particle-mucus complex onto the frontal surface as the palp contracts onto the pharynx (DAUER, 1983).

Frontal cilia may also function in particle rejection from the pharynx by a reversal of the direction of ciliary flow. This mechanism has been observed only in *Polydora ligni* (DAUER *et al.*, 1981). The basal transverse cilia of *P. pinnata* function in particle rejection by the production of a rejection current within the tube. Particles rejected at the site of the pharynx are rejected into the current produced by the beating of the basal transverse cilia and the frontal cilia of the branchiae (DAUER, 1985). DAUER (1988) hypothesized that the particle rejection current of *P. pinnata* enabled the animal to reject particles at the site of the pharynx while allowing the prostomium to remain below the sediment-water interface and thus potentially reducing predation or browsing. In other spionid species the everted pharynx is held at the sediment surface or the edge of the tube and particles are rejected directly onto the sediment-water interface.

The ciliated papillae of spionids do not appear to have any direct function in feeding behavior. DAUER (1991) hypothesized that the papillae of the palp are primarily mechanosensory structures that may be important in interspecific encounters.

The role of the lateral cilia and the latero-frontal cirri is particularly problematic. DAUER (1984, 1985) by analogy to lamellibranch bivalves and lophophores concluded that both ciliary groups functioned in capturing suspended particles by creating currents (lateral cilia) and deflecting the pathway of particles onto the frontal surface (latero-frontal cirri). SHITEMA & JUMARS (1991) consider that cilia that are not protected from ambient flow may be more important in manipulating and transporting captured particles rather than in creating feeding currents. Latero-frontal cirri could aid in retaining the particle-mucus complex onto the frontal surface during transport. However, it is difficult to hypothesize a role for the lateral cilia except for the creation of a feeding current. These cilia are adjacent to the frontal surface (to assist in particle retention) and beat in metachronal waves creating currents directed towards the frontal surface.

CONCLUSION

Spionid polychaetes have been and will continue to be important experimental species in applying optimal foraging theory to marine and estuarine systems (TAGHON, 1982; TAGHON & JUMARS, 1984) and in understanding the role of near-bottom hydrodynamics in feeding behavior (JUMARS, 1993). Spionid polychaetes are excellent experimental subjects for feeding studies because (1) they feed at the sediment-water interface and are easily observed, (2) many spionid species, especially estuarine species, are relatively hardy and survive well under laboratory experimental conditions, and (3) most species place fecal rods at the surface which can be collected and used to estimate feeding rates quantitatively under various experimental conditions. However, interpretation of data and observations concerning feeding of spionids is complicated because (1) they have a mixed feeding mode (deposit feeding, suspension feeding, bedload feeding) and (2) they possess a variety of morphological features that may affect feeding behavior. Additional studies are necessary to clarify the roles of and possible interactions between (1) functional ciliary groups, (2) mucus and (3) hydrodynamics in particle encounter, retention, transport and rejection.

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