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Organic coatings and ontogenetic particle selection in *Streblospio benedicti* Webster (Spionidae: Polychaeta)

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Abstract

Surface deposit feeders select food particles based upon characteristics including size, texture, specific gravity, and organic coatings. Spionid polychaetes feed at the sediment–water interface using a pair of ciliated palps and switch between surface deposit feeding and suspension feeding primarily as a function of water flow. Juveniles and adults of some spionid species have different stable isotopic carbon signals, indicating the ingestion of different food sources and potentially the ability to differentiate organic cues ontogenetically. In the present study, the feeding responses of juvenile and adult *Streblospio benedicti* Webster to seven organic coatings bound to glass microbeads were tested using five amino acids and two carbohydrates. Coated versus uncoated particles were presented in equal proportions based upon surface area. Juveniles and adults were highly selective for all seven types of organically coated beads—87.1% of all beads ingested were organically coated beads. For two of the organic coatings, there were ontogenetic differences; juveniles were more selective of threonine and adults were more selective of proline. These differences may result in ontogenetic diet shifts that allow maximization of energy and/or essential nutrients during critical early life-history stages. Particle selection in tentaculate surface deposit feeders is generally thought to occur primarily during particle contact and transport to the mouth, and is typically characterized as a passive process. Active particle selection at the site of the everted pharynx was observed and quantified for *S. benedicti*. Organically coated particles represented 50% of the ambient experimental treatment, 64.4% of the particles transported along the palp after contact, and 81.8% of the particles ingested after pharyngeal rejection behavior. Of the beads reaching the pharynx, 26.9% were rejected by ciliary sorting on the pharynx before ingestion, and 81.8% of the rejected beads at the site of the pharynx were uncoated. Our study demonstrates that microphagous feeders that generally handle food particles in bulk are capable of significant levels of active selection for organically coated particles.

Keywords: Ontogenetic diet shift; Organic coatings; Particle selection; Spionid polychaetes; *Streblospio benedicti*; Surface deposit feeding

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1. Introduction

Optimal foraging theory predicts that foraging behaviors should maximize net energy or nutrient gain over time in order to increase fitness (MacArthur and Pianka, 1966; Pyke et al., 1977). Marine tentaculate feeders have been widely studied and capture food items based upon a variety of characteristics such as size (Self and Jumars, 1988; Dauer, 1991; Shimeta, 1996), surface texture (Self and Jumars, 1978), specific gravity (Self and Jumars, 1978, 1988; Mayer et al., 1993), and organic coating of the particle (Taghon, 1982; Bock and Miller, 1997; Riordan and Lindsay, 2002). Many of the above particle characteristics may interact passively with properties of the mucus produced by the tentacle, resulting in selection or rejection of a particle (Taghon, 1982; Taghon and Jumars, 1984; Bock and Miller, 1997). For example, mucus stickiness or strength may determine if particles with different specific gravities or organic coatings will be retained during transport to the mouth (Taghon, 1982). However, most studies of microphagous feeding have not disregarded the possibility of active selection (Taghon, 1981; Guieb et al., 2004). Deposit feeders and suspension feeders can select for the highest energetic patch among all of the patches, which indicates that the animals respond to stimuli of the high-energy food (Wilson, 1973; Hylleberg, 1975; Kihslinger and Woodin, 2000).

Ontogenetic niche shifts have evolved in many species and can be interpreted as adaptations that reduce mortality due to such factors as competition (inter- and intraspecific) and predation. For benthic invertebrates, ontogenetic habitat shifts often involve an early life stage that is pelagic or occupies structurally complex habitats (e.g., salt marshes, seagrass beds, and reefs), which provide abundant food or refuges (Gosselin, 1997; Hardege et al., 1998). Ontogenetic diet shifts within the same habitat that do not involve extreme changes in diet are not well studied (Werner and Gilliam, 1984). In these situations, juveniles of benthic invertebrates are more likely to be limited by food than adults (Penry and Jumars, 1990; Hentschel, 1996). Adaptative ontogenetic changes in feeding mode, diet, or digestive capabilities may serve to overcome juvenile limitations (Gosselin and Chia, 1994; Hentschel, 1998a).

For many deposit feeding species, an increase in body size is the only noticeable morphological change that occurs as juveniles develop to adults (Hentschel, 1996). If digestive reaction kinetics are constant with body size, then the total extent of digestion depends on the time that the material resides in an individual's gut (Penry and Jumars, 1990). Because gut volume increases as body volume increases, but ingestion rate decreases as body volume increases, gut residence time will increase with increasing body size; therefore, juveniles will have a digestive disadvantage relative to adults of the same species (Cammen, 1980; Penry and Jumars, 1990; Hentschel, 1996). For example, gut residence time in the polychaete, *Nereis succinea*, is shorter in juveniles than in adults, suggesting that juveniles have significantly diminished absorption efficiencies compared to adults (Ahrens et al., 2001). Size-dependent changes in the ratio of neutral lipids to polar lipids, an indicator of energy storage and nutritional quality, in spionid polychaetes imply that smaller worms have less energetic reserves and may be more susceptible to food limitations than adults (Hentschel, 1998b).

One means to overcome such size-dependent food limitation is for juveniles to ingest a higher quality diet than conspecific adults (Penry and Jumars, 1990). Juvenile surface deposit feeders can ingest a higher quality diet by being more selective microphages or feeding as a macrophage (Hentschel, 1996). Stable isotopic evidence indicates size-dependent differences of food sources in four surface deposit feeding spionid polychaete species (Hentschel, 1998a). The $\delta^{13}C$ data show that the juveniles receive much of their carbon from benthic diatoms, whereas adults receive most of their carbon from macroalgal detritus (Hentschel, 1998a).

Streblospio benedicti Webster is a spionid polychaete that lives infaunally, building tubes within the top few centimeters of sediments (Webster, 1879). In response to water flow, *S. benedicti* switches between suspension feeding and deposit feeding and, when restricted to deposit feeding, it moves to new sediment patches when the local food supply is depleted (Dauer, 1984). The feeding behavior of *S. benedicti* has been well studied (Dauer, 1984). It egests distinct fecal pellets that are long rods and are placed, by the worm, in a pile on the sediment surface. *S. benedicti* is commonly found throughout the world in temperate