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## Feeding Responses of Juvenile and Adult *Streblospio Benedicti* Webster (Spionidae) to Organic Chemicals Bound to Glass Microbeads

Heidi Kathryn Mahon  
Old Dominion University

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**FEEDING RESPONSES OF JUVENILE AND ADULT  
*STREBLOSPIO BENEDICTI* WEBSTER (SPIONIDAE) TO  
ORGANIC CHEMICALS BOUND TO GLASS MICROBEADS**

by

Heidi Kathryn Mahon  
B.S. July 1999, Truman State University

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Old Dominion University in Partial Fulfillment of the  
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Approved by:

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Daniel M. Dauer (Director),

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Mark J. Butler, IV (Member)

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William F. Resetarits, Jr (Member)

## **ABSTRACT**

### **FEEDING RESPONSES OF JUVENILE AND ADULT *STREBLOSPIO BENEDICTI* WEBSTER (SPIONIDAE) TO ORGANIC CHEMICALS BOUND TO GLASS MICROBEADS**

Heidi Kathryn Mahon  
Old Dominion University, 2003

Director: Dr. Daniel M. Dauer

Spionid polychaetes feed at the sediment-water interface using a pair of ciliated palps. Polychaetes select food particles based upon characteristics including size, texture, specific gravity and organic coatings. Juvenile and adult spionids have different stable isotopic carbon signals, indicating the potential to differentiate organic cues ontogenetically. In the present study, the feeding responses of juvenile and adult *Streblospio benedicti* Webster to seven organic coatings bound (five amino acids and two carbohydrates) to glass microbeads were tested. Juveniles and adults were highly selective for all seven types of organically coated beads. Juveniles were highly selective for threonine; whereas adults were highly selective for proline. These differences may reflect ontogenetic diet shifts that evolved to maximize net energy gain for each developmental stage. This study also gives indirect support that microphagous feeders may be capable of active selection for organically coated particles.

**This thesis is dedicated to my husband, Andrew,  
and to my parents for all their love and support.**

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## INTRODUCTION

Adequate quantities of usable resources are necessary to sustain animal populations and increase the fitness of the individual animal (Levins 1965, MacArthur & Pianka 1966, Pyke et al. 1977, Pulliam 1981). Food provides animals with energy and other nutrients to function, grow, and reproduce (MacArthur & Pianka 1966). Fitness is measured by the animal's success in converting resources to reproductive products (Levins 1965). In this study I tested the ability of juvenile versus adult organisms to select food particles with different organic coatings. My work integrates aspects of optimal foraging theory, ontogenetic niche shifts and active particle selection by a tentaculate, microphagous feeding spionid polychaete, *Streblospio benedicti* Webster.

### Optimal foraging theory

Optimal foraging theory predicts that foraging behaviors should maximize net energy or nutrient gain over time in order to increase fitness (MacArthur & Levins 1967, Emlen 1966, Taghon 1981). In the development of optimal foraging models, five foraging components have been widely studied: (1) optimal diet, (2) optimal patch selection, (3) optimal time allocation between patches, (4) optimal patterns and speeds of movement, and (5) optimal central place foraging (Pyke et al. 1977, Orians & Pearson 1979). All models except optimal diet models have focused on motile macrophagous feeders. Macrophages handle food items singly and generally feed on larger food items than microphages, which handle food items in bulk (sensu Fauchald & Jumars 1979). For motile macrophages time and energy expended in movements within and between patches are foraging costs balanced against energetic or nutritional gain of optimizing

diet selection (Schoener 1971, Pyke et al. 1977). Some macrophages are non-motile during foraging and are referred to as sit-and-wait feeders that simultaneously monitor for mates and predators, expending no additional energy searching for food (Schoener 1971, Stephens & Charnov 1982). Sit-and-wait feeders encompass many diverse taxa including nemerteans, sea anemone, leeches, insect larvae, spiders, frogs, and fish (Cooper et al. 1985, Zamer & Shick 1987, Marshall 1995, Hauber 2002, Elliott 2002, McBrayer & Reilly 2002). Microphagous feeders include both motile and non-motile species and in the marine environment include suspension and deposit feeders (Fauchald & Jumars 1979, Taghon 1981, Self & Jumars 1988). In optimizing their diet, macrophages and microphages differ greatly in the relative roles of (1) active versus passive selection of food items and (2) post-ingestion mechanisms (Penry & Jumars 1987, Penry & Jumars 1990).

### **Pre-ingestion food selection**

Most optimal diet models are based upon the ability of an animal to actively select among food items (Schoener 1971, Pyke et al. 1977). Active diet selection is more likely for macrophagous herbivores and carnivores that may respond to stimuli of the food during handling (Young 1928, Schmidt-Nielsen 1979, Vernberg 1981). Microphagous feeders handle particles in bulk and have less chance of actively selecting food items on an individual basis (Fauchald & Jumars 1979, Taghon 1981). However, in microphagous feeding, passive selection occurs as a consequence of the mechanics and morphology of the feeding structures (Taghon 1981, Shimeta & Jumars 1991, Shimeta & Koehl 1997).

Microphages use a variety of mechanisms to collect food items (Schmidt-Nielsen 1979). For most suspension feeders, cilia or setae create small-scale currents directing

particles from ambient currents to collection surfaces for retention and capture (Shimeta & Jumars 1991, Shimeta & Koehl 1997). Suspension feeding collection surfaces typically produce mucus that act as filtering mechanisms (Jorgensen 1977, Rubenstein & Koehl 1977, Schmidt-Nielsen 1979, Vernberg 1981, Shimeta & Jumars 1991). Many microphages have elongate projections (e.g. tentacles, palps, siphons) placed into ambient currents to contact and/or transport suspended particles (Jorgensen 1977, Vernberg 1981, Lopez & Levinton 1987, Shimeta & Jumars 1991, Shimeta & Koehl 1997).

Microphagous deposit feeders collect particles at or below the sediment-water interface with tentacular projections or an eversible pharynx (Fauchald & Jumars 1979, Dauer et al. 1981, Dauer 1984, Lopez & Levinton 1987, Peterson & Skilleter 1994). For both tentacular and pharyngeal deposit feeders, mucus is important in particle capture and transport (Fauchald & Jumars 1979, Dauer 1984).

Marine tentaculate feeders have been widely studied and capture food items based upon a variety of characteristics such as size (Whitlatch 1974, Fenchel 1980, Taghon 1982, Dauer 1983, Dauer 1985, Luckenbach et al. 1988, Self & Jumars 1988, Okamura 1990, Dauer 1991, Hentschel 1996, Shimeta 1996, Bock & Miller 1999, Horng & Taghon 1999), surface texture (Self & Jumars 1978), specific gravity (Self & Jumars 1978, Self & Jumars 1988, Mayer et al. 1993), and organic coating of the particle (Taghon 1982, Taghon & Jumars 1984, Bock & Miller 1997, Conova 1999, Riordan & 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 & Jumars 1984, Bock & 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, Conova 1999). However, most studies of microphagous feeding have not disregarded the possibility of active selection (Taghon 1981). 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, Kihlslinger & Woodin 2000). Both passive and active selection can occur when an animal is capturing a food item, and food can be obtained by a diversity of mechanisms and adaptations (Jorgensen 1977, Schmidt-Nielsen 1979, Vernberg 1981, Vernberg & Coull 1981).

Although particle selection among tentaculate microphagous feeders is thought to be passive, sensory abilities may allow suspension feeders and deposit feeders to evaluate their environment and select between food items (Dauer 1984, Storch & Schlötzer-Schrehardt 1988, Dauer 1991, 1997, Qian & Chia 1997,). Ciliated papillae, which are thought to be mechano- or chemoreceptors, occur on the palps, antennae, tentacular cirri, or pharynx of many microphagous feeding polychaetes (Storch & Schlötzer-Schrehardt 1988, Qian & Chia 1997). For example, the spionid polychaetes, *Paraprionospio pinnata* and *Streblospio benedicti* have eversible papillae located on the prostomium, and these papillae are thought to serve as receptors for particle selection because rejection of particles has been observed at the pharynx (Levin 1981, Dauer 1984, 1985).

### **Gut residence time**

Particle selection for microphagous feeders can also take place after ingestion (Penry & Jumars 1990). Ingestion rate is influenced by several components: (1) food abundance, (2) food palatability, (3) feeding time availability, and (4) nutritional content (Cammen 1980, Taghon 1981). Assuming that microphages have limited abilities to

select new patches of food, altering ingestion rates allow the microphage to maximize net energy gain (Taghon 1981). Microphages may alter ingestion rates and gut residence times in response to food quality (Cammen 1980, Taghon 1981, Penry & Jumars 1990). Changes in gut residence time may be determined by whether ingested particles are labile or retractile to enzymatic activity (Taghon 1981, Penry & Jumars 1990). Two conflicting hypotheses have been developed which try to predict a microphage's ingestion rate response to food quality (Taghon 1981). One hypothesis alleges supports that ingestion rates vary inversely with food quality (Cammen 1980, Kihlslinger & Woodin 2000). The other hypothesis suggests that ingestion rates are positively correlated with food quality (Hylleberg 1975). The difference between these two hypotheses suggests that more than one factor influences ingestion rate (Taghon 1981). Digestion of particles is determined by the gut residence time and therefore digestion must increase with increasing gut residence time and gut length, suggesting that juveniles may experience morphological constraints (Penry & Jumars 1987, Penry & Jumars 1990).

### **Ontogenetic niche shifts**

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. Ontogenetic niche shifts in macrophages are well known especially during metamorphosis (Hughes & Sherr 1983, Werner & Gilliam 1984). Some of the best-studied species have been amphibians, insects and fishes (Werner & Gilliam 1984). 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 (Forward et al. 1995, Hardege

et al. 1998, Gosselin 1997). A pelagic stage has certain advantages, such as dispersal (Strathmann 1974, 1986), to benthic invertebrates, especially those that are sessile as adults. Therefore, benthic invertebrates with a pelagic dispersal phase have early life stages that are spatially distinct from adults.

Ontogenetic diet shifts within the same habitat that do not involve extreme changes in diet are not well studied (Werner & Gilliam 1984). In these situations, juveniles of benthic invertebrates are more likely to be limited by food than adults (Penry & Jumars 1990, Hentschel 1996). Adaptive ontogenetic changes in feeding mode, diet, or digestive capabilities may serve to overcome juvenile limitations (Gosselin & Chia 1994, Hentschel 1998a, de Lestang et al. 2000, Viherluoto & Vitasalo 2001).

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 is constant with body size, then the total extent of digestion depends on the time that material resides in an individual's gut (Penry & Jumars 1990). Because gut volume increases as body volume increases, but ingestion rate decreases as body volume increase, gut residence time will increase with increasing body size, and juveniles will have a digestive disadvantage relative to adults of the same species (Cammen 1980, Penry & Jumars 1990, Hentschel 1996, Mayer et al. 1997). 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). Other factors affecting potential juvenile food limitation are insufficient mobility to capture food, inability to handle certain food items, or

inability of digesting large food items (Gosselin & Chia 1994, Hentschel 1996, de Lestang et al. 2000, Branstrator 2000, Viherluoto & Vitasalo 2001).

One means to overcome this digestive constraint associated with small body size is for juveniles to ingest a higher quality diet than conspecific adults (Penry & Jumars 1990). Juveniles 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 in four surface deposit-feeding spionid polychaete species (Hentschel 1998a). The  $\delta^{13}\text{C}$  data show that the juveniles receive much of their carbon from benthic diatoms whereas the adults receive most of their carbon from macroalgal detritus, providing evidence of an ontogenetic diet shift (Hentschel 1998a). Changes in particle selectivity due to water velocity also varies among microphagous polychaetes of different sizes (Shimeta 1996). As water velocity increases, small worms ingested more small particles, but large worms ingested constant numbers of large and small particles (Shimeta 1996). Ontogenetic shifts in both particle size selectivity and  $\delta^{13}\text{C}$  are supported by lipid variations in microphages polychaetes (Hentschel 1998b). Lipid data demonstrates an increase of storage lipids and cell membrane lipids with increasing size of spionids, which means smaller worms may have less energetic reserves and may be more susceptible to food limitations than adults (Hentschel 1998b).

### ***Streblospio benedicti* Webster**

Spionid polychaetes are widely distributed in marine and estuarine sedimentary habitats and are found from intertidal zones to deep canyons (Foster 1971). Spionids use a pair of ciliated tentacular palps to capture particles at or near the sediment-water interface and deposit feed or suspension feed depending upon the water velocity (Taghon

et al. 1980, Dauer et al. 1981, Jumars et al. 1982, Taghon & Jumars 1984, Shimeta & Jumars 1991, Shimeta & Koehl 1997). At low velocities, spionids deposit feed on the sediment surface with their palps, but at higher velocities, spionids tend to suspension feed with their palps in the water column (Dauer et al. 1981, Taghon & Greene 1992, Bock & Miller 1996, Shimeta & Koehl 1997).

*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; it moves when the food supply is depleted (Dauer 1984). It egests distinct fecal pellets that are long rods and are placed, by the worm, in a pile on the sediment surface. *Streblospio benedicti* is commonly found throughout the world in estuaries and wetlands and it can colonize stressed areas (Levin 1984, Levin & Creed 1986, Levin et al. 1987, Bridges 1993).

The goal of this study was to determine if juvenile and adult *Streblospio benedicti* demonstrate differences in selectivity, which could indicate an ontogenetic diet shift. To test this, the selectivity of juveniles and adults for glass microbeads coated with amino acids and carbohydrates that represented different organic cues was measured. Both juveniles and adults were highly selective for organically coated beads compared to beads lacking an organic coating. Juveniles were more selective for the amino acid threonine whereas adults were more selective for the amino acid proline, indicating the potential for an ontogenetic diet shift.



## METHODS

Juveniles and adult *Streblospio benedicti* were collected from the Lafayette River, Norfolk, Virginia, U.S.A. (36°48.931' N, 76°17.435' W) because cultures of *S. benedicti* were not able to be maintained in the laboratory (see Appendix 1). The worms were separated into two life stages, juvenile and adults, using body length as the determining factor in separating the life stages. Worms less than 4 mm in length were considered juveniles and worms greater than 7 mm in length were considered adults. In observing hundreds of *S. benedicti*, I did not observe any worm measuring 4 mm or less having embryos or gametes. Any worm damaged or brooding young was not used in the experiments because these conditions may have affected their feeding.

To test particle selection, organic coatings were attached to glass beads using a binding chemical APTS (3-aminopropyltriethoxysilane). APTS is a chemical that covalently binds organic coatings to glass or quartz. Organic coatings were attached to clear glass beads and glass beads stained red were not given an organic coating. Three types of experiments were run to test selectivity: a bead color experiment, two APTS (3-aminopropyltriethoxysilane) experiments, and seven organic coating trials. The color experiment tested if *S. benedicti* can differentiate between red beads and clear beads. The APTS experiments tested if the chemical APTS affects selectivity of the beads. Thus, these first two experiments were designed to test for potential experimental artifacts associated with bead color or the presence of the APTS binding chemical. The third set of experiments tested the hypothesis that juveniles and adults have different selectivity for organic coatings due to an ontogenetic diet shift.

## **Experimental design**

Twenty feeding chambers were used in each of the three types of experiments. Ten chambers were used only for juveniles and ten were only for adults. The feeding chambers were glass dishes with a diameter of 10 cm and a depth of 8 cm. Each chamber was filled with sterilized sediment and artificial seawater. Sediment was sieved through a 500  $\mu\text{m}$  mesh screen to remove macrofauna and was frozen for 3 days. The sediment was then heated to 80°C for 2 days before it was added to the feeding chambers. Ten worms were placed into each feeding chamber and allowed to acclimate for 24 h. The feeding chambers had a temperature of 25°C and salinity of 21 psu; these conditions remained constant throughout the experiments. The chambers were closed systems with no additional seawater or sediment input, therefore the worms were forced to deposit feed on the glass microbeads provided.

Glass microbeads (Mo-Sci Corporation) were used in the experiment as artificial food particles. The beads ranged from 20 to 45  $\mu\text{m}$  and had a specific gravity of 2.6 (approximately the same specific gravity as natural quartz). I used two different colors of beads, (red, clear) in the experiments, so I could distinguish the worms' choice of bead type in each experiment. Beads designated as red beads were stained with a red glass stain and clear beads were not stained.

For each of the studies described below, I used the same experimental protocol when dispensing and recovering the beads. I introduced the beads into the feeding chambers by a pipette in a 1:1 ratio. The ratio was determined by weight since the beads were the same density and size. I applied the beads around each worm's tube so that the tube opening was completely surrounded by the beads.

The worms were given 3 hours to feed on the beads, and I then collected the fecal pellets using a pipette, making certain that surface sediment, with non-ingested beads, was not removed. Fecal pellets were removed before the beads were added to insure that the fecal pellets collected were defecated during the experiment.

Each feeding chamber was considered a replicate; therefore, all fecal pellets from one chamber were put into the same vial. The fecal pellets were then sonicated to break up the pellets and create a homogenous mixture. An aliquot of the mixture was examined on a compound scope and counted the first 100 beads. The color of each bead was noted and recorded. All data were proportions (p) and square root transformed before using any statistical test.

After each experiment, I removed the surface sediment from the entire feeding chamber and added new sterilized sediment. This was to insure that all beads from one treatment were removed before adding another treatment. Worms were then given 3 hours to acclimate to the new sediment.

### **Bead stain effect**

The effect of the stain was tested on the red beads by adding a 1:1 ratio of red and clear beads with no surface coatings in equal proportions into the 20 feeding chambers. After 3 hours the fecal pellets were removed and analyzed. The data were analyzed using a t-test with each of the feeding chambers considered a replicate.

### **APTS effect**

The organic compounds were covalently bound to the glass microbeads using the chemical APTS. APTS was coated onto the beads using the Brotherton et al. (1976)

method as follows. One hundred grams of beads were water-washed and added to 95 ml of deionized (DI) water. Five ml of APTS was then added and refluxed the solution for 1.5 hours. The beads were then washed five times with 200 ml of DI water, aspirated to a wet cake and stored at room temperature until use.

The effect of APTS was tested by coating only clear beads and then placed equal proportions of clear and red beads into the 20 feeding chambers. After 3 hours, the fecal pellets were removed. The data were analyzed by a t-test considering each feeding chamber as a replicate. In another APTS experiment, the effects of both red and clear beads coated with APTS were tested. The red and clear beads were added to the chambers in equal proportions. After 3 hours the fecal pellets were removed and analyzed.

### **Organic coating experiments**

Seven organic coatings were bound to glass microbeads and tested independently. Five amino acids and two carbohydrates were tested. The five amino acids used in the experiments were: glycine, proline, taurine, threonine, and valine. The two carbohydrates used in the experiments were galactose and glucose.

The amino acids were bound to the clear beads by the Lappi et al. (1976) method as follows. After APTS was bound to the clear beads, 5 g of beads were maintained in 10 ml of DI water at 4°C for 15 min. The beads were washed with DI water and incubated at 4°C in a buffered solution of the amino acid for 1 hour. Then the beads were washed and frozen in buffer until needed in the experiment. Freezing the solution kept the amino acids from denaturing.

The carbohydrates were bound to the clear beads using the following method of Gray (1974). After APTS was bound to the clear beads, 100 mg of carbohydrate and 52 mg of sodium cyanoborohydride were dissolved in 5 ml of potassium phosphate (pH 7.0). This solution was kept at room temperature for two weeks until use in the experiments. The binding of carbohydrates to the APTS takes a minimum 10 days to be completed; therefore, the reaction was allowed to continue for 14 days to insure as much carbohydrate was bound as possible.

To each feeding chamber, organically coated clear beads and APTS coated red beads were added in a 1:1 ratio. The worms were allowed to feed on the beads for 3 hours, subsequently the fecal pellets were removed and analyzed using a two-way ANOVA testing for effects of organic coating and life stage. Another analysis used was the Boneferoni multiple comparison test to indicate differences among each experiment.

## RESULTS

### Bead stain effect

*Streblospio benedicti* ingested the red beads in equal proportion to the clear beads (t-test,  $p = 0.386$ ,  $df = 19$ ), indicating that *S. benedicti* did not differentiate between beads stained red and those that were clear. Therefore the red stain used in later experiments for differentiating the organically coated beads from uncoated beads did not bias the results.

### APTS effect

However, *S. benedicti* was highly selective for clear beads coated with APTS over the red beads that were not coated (t-test,  $p = 0.033$ ,  $df = 19$ ). This extreme selection for APTS shows that this chemical could bias results if the experiment did not control for it. Therefore all red beads and clear beads were coated with APTS and given to the worms. When given the new APTS beads, *S. benedicti* ingested the red beads in equal proportion to the clear beads (t-test,  $p=0.758$ ,  $df=19$ ). This experiment was considered the control experiment to which each of the organic coating experiments were compared. To insure that APTS did not confound the organic treatment results, all beads were coated with APTS. The red beads received no additional coating and are referred to as “APTS coated beads” in the following results. All clear beads were coated with APTS plus an organic coating. The clear beads are referred to as “organically coated beads” in the following results.

### Organic coating experiments

*Streblospio benedicti* selected organically coated beads over uncoated beads but there was no significant life stage effect (Table 1). However the interaction effect was significant. When the juvenile and adult data were combined, over 80% of the beads ingested by *S. benedicti* were organically coated (Fig. 1).

Table 1. Two-way ANOVA testing the effect of organic coating and life stage (juvenile vs adult) on glass selection by *Streblospio benedicti*. Asterisks indicate significance.

| Source          | DF  | Sum of Squares | Mean Square | F value | P value   |
|-----------------|-----|----------------|-------------|---------|-----------|
| Organic Coating | 7   | 3.3012         | 0.472       | 38.88   | <0.0001 * |
| Life Stage      | 1   | 0.0003         | 0.003       | 0.22    | 0.6390    |
| Interaction     | 7   | 0.5210         | 0.074       | 6.14    | <0.0001 * |
| Error           | 144 | 1.7469         | 0.012       |         |           |
| Total           | 159 | 5.5717         |             |         |           |

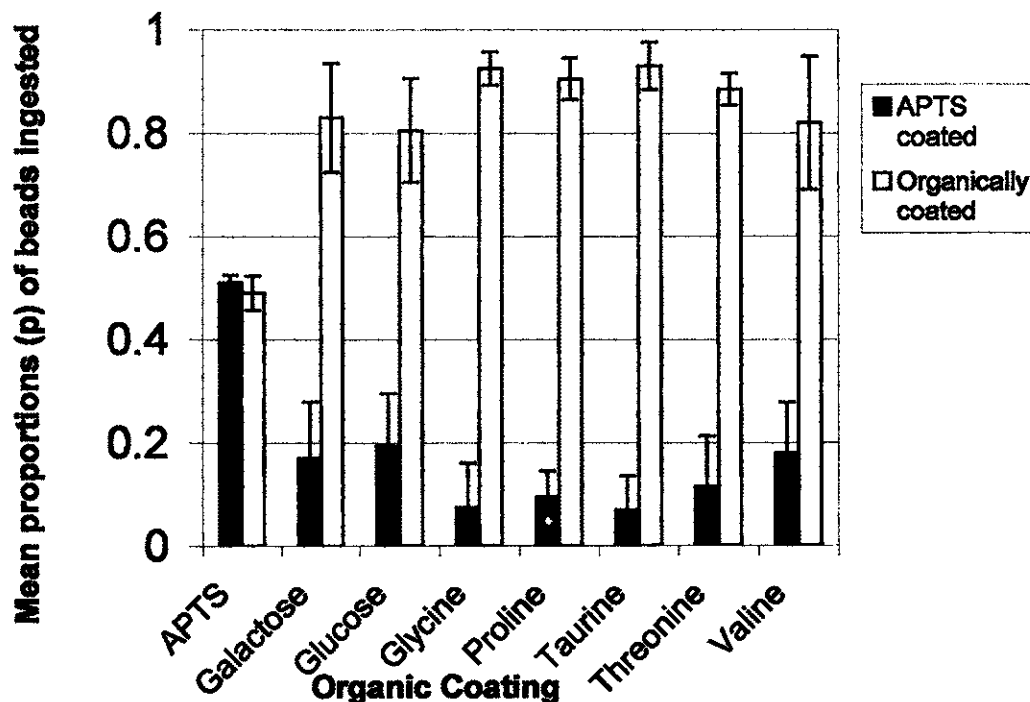


Fig. 1. Organic coating effect. Mean proportions (p) of beads ingested by *Streblospio benedicti* in eight trials where APTS coated beads were compared to organically coated beads. Shown are untransformed proportions. Each treatment indicates the combined data of juveniles and adults. Bars indicate one standard deviation. n=20

The life stage and organic coating effects were not independent, as shown by the significant interaction effect in the two-way ANOVA, indicating juveniles and adults selected for organic coatings differently. The difference between juvenile and adult selection for all organic coatings was tested using a Bonferroni multiple comparison test. Juveniles and adults differentially selected proline and threonine (Fig. 2).



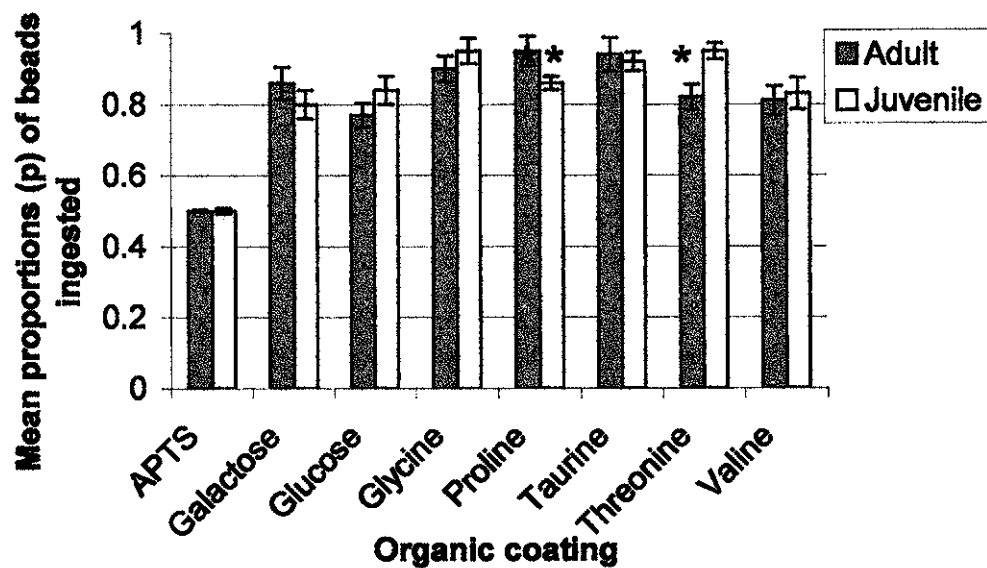


Fig. 2. Life Stage Effect. Mean proportions (p) of coated beads that were ingested by juvenile versus adult *Streblospio benedicti*. Asterisks indicate significant differences of adult and juvenile selectivity. Bars indicate one standard deviation. n=10

## DISCUSSION

All organisms must obtain certain specific, essential compounds in order to grow and reproduce (Levins 1965, MacArthur & Pianka 1966). These essential compounds must be produced by the organism or obtained from the food ingested by the organism (Levins 1965). Animals are unable to synthesize certain amino acids and fatty acids; therefore, they must acquire these compounds from the food they ingest (Lopez & Levinton 1987, Mayer et al. 1995). In comparison to other food sources, sediment has less protein and carbohydrate (Table 3), and therefore, less energy and nutrients available for assimilation (Bowen et al. 1995, Mayer et al. 1995). Since the sediment is a poor food source relative to other food sources for marine benthos, deposit feeders should evolve adaptations that enable selectivity for particles that maximize net nutrient or energy gain (Mayer et al. 1993, Mayer et al. 1995).

Table 2: Average values (percent dry weight) of proteins and carbohydrates from food sources in the marine environment. (References: *a.* Hedges et al. 2002, *b.* Taylor et al. 1999, *c.* Wahbeh 1997, *d.* Lourenco et al. 2002, *e.* Wilson 2002, *f.* Gatenby et al. 2003, *g.* Mian & Percival 1973, *h.* Haake et al. 1993, *i.* Burdige et al. 2000, *j.* Tselepides et al. 2002, *k.* Welker et al. 2002)

| Food Source              | Protein                               | Carbohydrate                      |
|--------------------------|---------------------------------------|-----------------------------------|
| Plankton                 | ~ 53 % <sup><i>a</i></sup>            | ~ 44 % <sup><i>a,b</i></sup>      |
| Macroalgae<br>(detritus) | 13.6-24.5 % <sup><i>c,d,e,f</i></sup> | 40-47 % <sup><i>d,e,f,g</i></sup> |
| Sediment                 | 7.4-28 % <sup><i>h,i,j,k</i></sup>    | 5-9 % <sup><i>h,i,j,k</i></sup>   |

Ontogenetic niche shifts are adaptations that reduce mortality and may allow juveniles to overcome food limitations (Gosselin & Chia 1994, Hentschel 1998*a*, de Lestang et al. 2000, Viherluoto & Vitasalo 2001). Storage lipids and cell membrane

lipids tend to increase with increasing size of spionids, which means smaller worms may have less energetic reserves and may be more susceptible to food limitations than adults (Hentschel 1998b). One means to overcome this digestive constraint associated with small body size is for juveniles to ingest a higher quality diet than conspecific adults (Penry & Jumars 1990). In the present study, juveniles and adults differed in selectivity for two organic compounds, proline and threonine. Although the absolute differences in proportions of these two amino acids were not large, the results indicate the possibility of ontogenetic diet differences based upon organic coating type. Proline is an amino acid that can serve as a direct energy metabolite in environments where nitrogen and/or energy may be limiting and it can be used directly in the production of ATP (Behmer & Joern 1994). The amino acid threonine has been linked to growth. Growth rates of juvenile *Capitella* sp. I (Polychaeta) were correlated with levels of the amino acids histidine, phenylalanine, threonine, and valine (Marsh et al. 1989). Summarizing, adults selected for an amino acid that acts as an energy source and juveniles selected for an amino acid that stimulates growth. Selecting for particles coated in threonine may allow the juveniles to grow at a more rapid rate than selecting other amino acids. The rapid growth would allow the juvenile to overcome digestive constraints.

Another means to overcome digestive constraints is for juveniles to ingest a higher quality diet by changing their food absorption rate (Hentschel 1996). Food absorption can be changed by altering the ingestion rate or gut residence time (Ahrens et al. 2001). Gut residence time and ingestion rate are inversely proportional to one another. By increasing the ingestion rate, the gut residence time is decreased whereas a decrease in ingestion rate increases gut residence time (Penry & Jumars 1987, Karrh &

Miller 1994). There is conflicting evidence for whether an increase in organic matter causes an increase or decrease in ingestion rate (Taghon 1981, Penry & Jumars 1987, Taghon & Greene 1992, Karrh & Miller 1994, Kihlslinger & Woodin 2000, Riordan & Lindsay 2002), suggesting that ingestion rate may be influenced by more than just food quality. In some instances, *Streblospio benedicti* decreases its ingestion rate when feeding upon high organic sediment (Mayer et al. 1993), whereas in others it increases its ingestion rate (Kihlslinger & Woodin 2000). An increase in ingestion rate enables the microphage to process large areas of food. On the other hand, a long gut residence time allows for more absorption of each food particle. Balancing these factors, permit the microphage to increase the quality of diet (Penry & Jumars 1990).

Sensory structures located on the feeding appendages of a microphage allow the animal to evaluate each food item, which may enable the animal to increase the quality of diet by active selection mechanisms. Several spionid polychaetes have sensory structures located on the palps and prostomium (Dauer 1984, 1985, 1991, 1997, Riordan & Lindsay 2002) and rejection of particles at the site of the everted pharynx has been observed in several spionid species (Dauer et al. 1981, Levin 1981, Dauer 1984, 1985). *Streblospio benedicti* has eversible papillae located on the prostomium that may detect chemical compounds as particles are transferred from the palps to the pharynx (Dauer 1984, Dauer et al. 2003). Ferner and Jumars (1999) demonstrate that spionid polychaetes are capable of detecting and responding, by changing their ingestion rate and feeding behavior, to dissolved chemical compounds. Spionids are also capable of responding to chemical compounds bound to particles (Taghon 1982, Taghon & Jumars 1984, Bock & Miller 1997, Riordan & Lindsay 2002).

In the present study, juvenile and adult *Streblospio benedicti* selected organically coated beads over APTS coated beads, which may indicate active selection, when compared to selectivity of APTS coated beads over uncoated beads. The means of the uncoated beads from first APTS experiment were compared to the means of the APTS coated beads (t-test,  $p=0.033$ ,  $df=19$ ). Also the means of the organic coating experiments were averaged and compared to the mean of the APTS coated beads (t-test,  $p<0.001$ ,  $df=69$ ). *Streblospio benedicti* were highly selective for APTS beads when combined with uncoated beads (Fig. 3A). However, *S. benedicti* showed a higher selectivity for coated beads in combination with the APTS coated beads (Fig. 3B).

Without determining behavior of the worms in the organic coating experiments, active selection cannot be confirmed because the differences in selectivity can be a consequence of the “stickiness” of the coated beads (Taghon 1982, Dauer 1984). “Stickiness” can be described as the adherence of particles to the feeding appendages of an organism. It is assumed that “stickiness” increases with increasing size of the compounds, indicating that passive adherence to mucus is thought to be directly related to the complexity of the chemical coating (Riordan & Lindsay 2002). Because only 3% of APTS binding sites on each particle are actually bound to an organic compound (Brotherton et al. 1976, Kurth & Bein 1995, Riordan & Lindsay 2002), the organically coated beads are only slightly more complex than the uncoated and APTS beads. The complexity difference between these beads does not account for the observed differences in Fig. 3 (Kurth & Bein 1995, Riordan & Lindsay 2002). Active particle selection is a likely alternative and is consistent with previous observations of pharyngeal particle rejection in several spionid species (Dauer et al. 1981, Levin 1981, Dauer 1984, 1985).

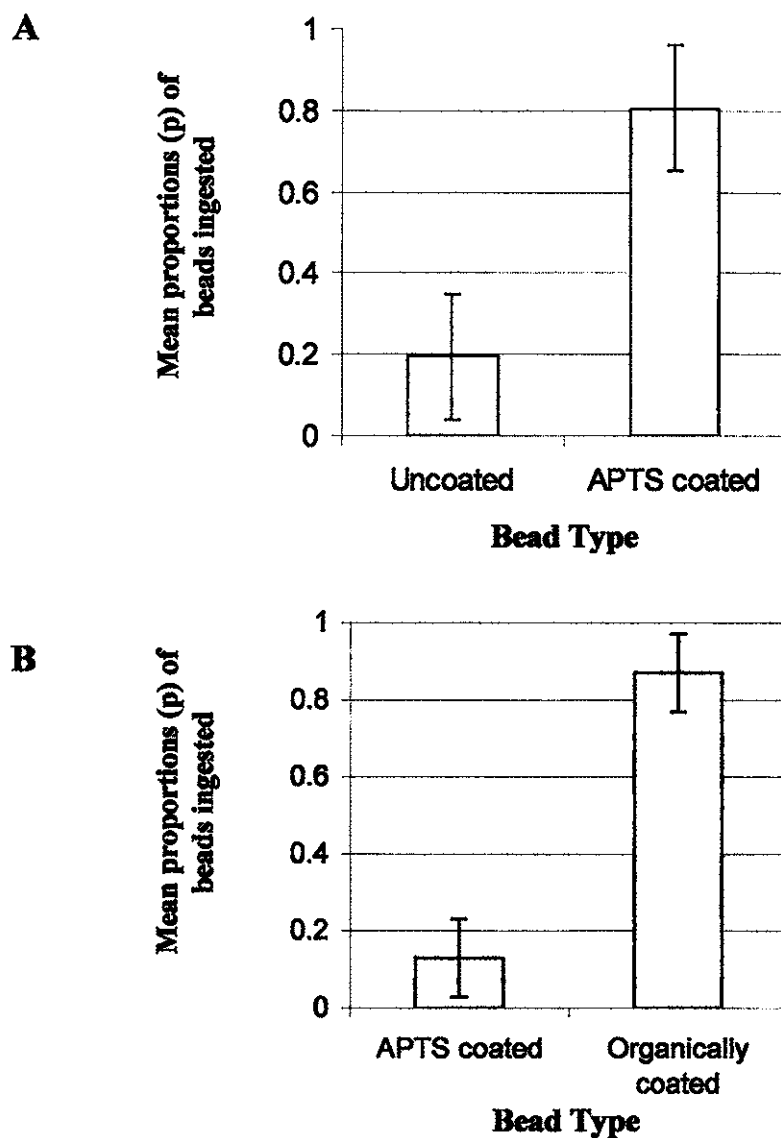


Fig. 3: Effect of practice coating on animal selectivity. Selectivity for APTS beads by *Streblospio benedicti* when uncoated or organically coated beads were present. **A.** First experiment compared ingestion of beads with no coating versus APTS coated beads.  $n=20$ . **B.** Experiment comparing ingestion of APTS coated beads with beads coated with the seven organic coatings (averaged data).  $n=20$ . Bars indicate one standard deviation.

## CONCLUSIONS

All animals need to acquire energy for metabolic processes. The energy they acquire may be used immediately or can be stored until it is needed. The optimal foraging theory states that organisms should feed upon a food source that will maximize their net energy gain while expending the least amount of energy. Nutrients are also a necessity of metabolic processes. Adaptations, such as ontogenetic shifts and sensory structure, have evolved, which aid in selection of food items to maximize energy and nutrients. In the current study, juvenile deposit feeders have shown evidence of an ontogenetic diet shift. This diet shift is not discrete shift, but a shift to selecting more nutritious particles to overcome competition and morphological constraints as well as low food availability. The current study also shows evidence for active selection in a microphage.

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## APPENDIX 1

### **Culturing technique of *Streblospio benedicti* Webster**

*Streblospio benedicti* were attempted to be cultured with the following method.

First, ambient sediment was collected from the Lafayette River, which has an abundant supply of *S. benedicti*. The sediment was put through a 500  $\mu$ m sieve to remove debris and large particles, then it was frozen for 1 week to kill any organisms living in the collected sediment. After freezing the sediment, the sediment was heated it for 2 days to guarantee all organisms were killed and was sterilized. The sterilized sediment and artificial seawater (temperature = 25°C, pH = 7.8, psu = 18) were added to each of three 20 L aquaria. The depth of the sediment in each aquarium was approximately 8 cm and the depth of the water was approximately 20 cm. The water was aerated continuously to ensure proper dissolved oxygen levels considering all the aquaria were closed systems.

One week after the aquaria were assembled, *S. benedicti* were collected from the Lafayette River and added 100 worms that were not damaged to each aquarium. The worms were fed every three days with two different food types. One half of the water was changed in the aquaria every other week to guarantee the health of the worms. The water removed from each aquarium was run through filter paper to collect any larvae that had been removed with the water. The filter paper was rinsed into the aquarium to return the larvae back into the aquarium.

The worms were fed a combination of two food types. The first food was a finely ground mixture of alfalfa cubes and marine fish food. Each aquarium received 3 grams of this mixture every other day. The other food given to the worms every other day was



the phytoplankton *Isochrysis galbana*, which also had to be cultured to provide enough for the worms.

*Isochrysis galbana* is gold-brown alga (5-8  $\mu\text{m}$ ) that contains large lipid storages. The culturing of *I. galbana* was also labor intensive because the cells are sensitive to temperature and salinity changes. The *I. galbana* cultures were maintained under grow lights for 14 h a day. To provide nutrients to the algal cells Guillard's f/2 medium was added to the algal cultures. The temperature, pH, and salinity of the cultures were held constant at 25°C, 8.0, and 3.0 psu. The cultures were maintained under constant aeration.

The first attempt at culturing *S. benedicti* failed when all three populations died. It was concluded that the failure was due to the reproductive mode of the population of *S. benedicti* that was collected. This population produced planktotrophic larvae, which spends a relatively long time in the water column feeding before reaching competency and settling into the sediment. Therefore to overcome this problem, *S. benedicti* were collected from a population in Beaufort, NC, which is known to produce lecithotrophic larvae, assuming it would be easier to maintain a culture with worms that have this mode of reproduction because the larval period is shorter and the larvae do not feed in the water column because they have a yolk sac. Following the same procedure, cultures of the Beaufort population also failed.

Two more attempts with the Beaufort population were tried. The amount of *I. galbana* was increased for all aquaria during the second attempt trying to provide the worms with more live food to mimic the natural environment. During the third attempt the water was changed less often, assuming that the water change might induce stress and

increased the instability of the culture. Both the second and third attempts to culture the Beaufort population failed.

## VITA

**Heidi Kathryn Mahon**

Old Dominion University  
Mills-Godwin Building  
Department of Biological Sciences  
Norfolk, VA 23529

### *Education*

- Bachelor of Science in Biology at Truman State University (July 1999)
- Master of Science in Biology at Old Dominion University (December 2003)

### *Technical Skills*

- Use of Scanning Electron Microscope
- Boat Operator
- Benthic invertebrate taxonomist (specialized in Chesapeake Bay fauna)
- Sediment analyst
- SCUBA certified

### *Publications and Presentations*

- Functional morphology and feeding behavior of *Streblospio benedicti* and *S. shrubsolei* (Polychaeta: Spionidae). Daniel M. Dauer, Heidi K. Mahon, and Rafael Sardá Hydrobiologia (in press)
- Oral presentation entitled, "Responses of *Streblospio benedicti* to chemical cues bound to glass microbeads" given at the 2002 Benthic Ecology Meeting
- Oral presentation entitled, "Responses of *Streblospio benedicti* to chemical cues bound to glass microbeads" given at the Spring 2002 Atlantic Estuarine Research Society Meeting
- Oral presentation entitled, "Responses of *Streblospio benedicti* to chemical cues bound to glass microbeads" given at the Summer 2002 Aquatic Sciences Limnology and Oceanography Meeting

### *Professional Organizations*

- Atlantic Estuarine Research Society

### *Awards*

- Awarded Best Oral Presentation by a Masters Student at Atlantic Estuarine Research Society meeting Spring 2002