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ACTIVE AND PASSIVE SETTLING BY MARINE BENTHIC NEMATODES

by

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ABSTRACT

ACTIVE AND PASSIVE SETTLING BY MARINE BENTHIC NEMATODES

Rodney Duane Bertelsen
Old Dominion University, 1997
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This study investigates whether active processes participate in the settlement of marine benthic nematodes. The settling rates of three estuarine benthic nematode taxa were examined in a linear flume using two treatments defined by the type of sediment bed placed in the flume. One treatment bed contained sediments rendered "unattractive" by boiling. The other treatment bed contained unaltered "attractive" sediment. Preliminary still water choice experiments confirmed the attractive and unattractive properties of these sediment treatments with each taxon. Recolonization trays placed in the field confirmed that each taxon did disperse in the water column. One taxon (*Theristus* sp?) exhibited significantly higher settling velocities over the attractive sediment bed than the unattractive sediment bed. Although like most other benthic nematode taxa, *Theristus* sp? does not swim, its active behavior, coiling ability, a body length over 1 mm, and weak adhesive glands may be factors that enable or enhance its settling rate over attractive sediments or retard settling

rates over unattractive sediments.

For my parents.

"I should have done this a long time ago. ... So, five card stud, nothing wild, and the sky is the limit." J.-luc Piccard

ACKNOWLEDGMENTS

Many thank you's are in order here. I'll start with two corporate contributors, Patco Pumps for contributing an impeller pump and Acrylite for contributing the acrylic plastic used to construct the flume main walls.

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INTRODUCTION

Benthic meiofauna are infaunal organisms whose size ranges between approximately 50 µm and 500 µm. Meiofaunal species that remain within this size range throughout their lives are sometimes called permanent meiofauna. The two most common permanent meiofauna taxa are nematodes and copepods (Coull 1988).

Permanent benthic meiofauna are typically found in clumped distributions (e.g. Nixon 1976; McLachlan et al. 1977; Thistle 1978; Findlay 1981; Hogue 1982; and Pinckney and Sandulli 1990) with patch sizes typically on the order of several centimeters (e.g. Findlay 1981(2 - 5 cm); Hogue 1982(1 - 3 cm); Pinckney and Sandulli 1990 (6-8 cm); and Nixon 1976(2 - 5 cm)). Hypotheses concerning clustered distributions may be assembled into four main categories: (1) attraction to clumps of food (Gray 1968; Gerlach 1977; Lee et al. 1977; Findlay 1981; Hogue and Miller 1981); (2) predation or predator avoidance (Coull 1986; Chandler 1989; Johnson and Strathmann 1989); (3) settling by passive hydrodynamic processes (Hulings and Gray 1976; Grant 1980; Eckman 1983; Hannan 1984; and Butman 1989); and (4) a combination of physical and biotic factors (Hicks 1984; Austin and Warwick 1989).

Although benthic meiofauna are considered sedentary

(Sterrer 1973; Coull 1988) their distribution patterns can change remarkably over just a few hours thus implying good dispersal characteristics (e.g. Thistle 1980; Reidenauer and Thistle 1981; and Chandler and Fleeger 1983). Notably Sherman and Coull (1980) found meiofaunal abundances on an intertidal mudbar could recover from a disturbance within half a tidal cycle. Permanent benthic meiofauna typically do not produce dispersal larvae and so dispersal is apparently accomplished by adults. Possible means of dispersal by meiofauna include moving within sediment, crawling on top of sediment, or resuspension in the water column. Crawling through or on top of sediment is relatively slow and is probably effective only at a scale of a few centimeters (see Chandler and Fleeger 1983). Resuspension, however, moves meiofauna at rates up to nearly that of the water flow and thus may be effective at a scale of meters to kilometers. Resuspension commonly occurs with many types of meiofauna and may involve passive processes (i.e. erosion) and/or behavior (see Palmer 1988). Resuspension may include the attachment of an individual to some other material (e.g. rafting; Coull 1988). The abundance and composition of meiofauna in suspension appears to vary widely from study to study. Palmer (1988) reported that in general copepods are the most common taxon in the water column while nematodes are relatively rare. Bell and Sherman (1980) calculated the proportions of meiofauna in the water column and sediment by quickly taking and freezing cores that included both sediment and water. They reported that 2% of all nematodes and 25% of harpacticoid copepods were suspended in the overlying water or bedload sediments. They suspected that they underestimated nematode numbers citing that perhaps nematodes were more common in the water column during other parts of the tidal cycle (all their samples were taken 1 hr prior to low tide) and because Sherman and Coull (1980) reported that nematodes could recolonize defaunated sediment after one half tidal cycle. Hagerman and Rieger (1981) sampled the water column at various depths in a tidal creek and found about 500 nematodes m^{-3} at all depths. Of all the meiofauna they collected, they estimated that between 10 and 30% were from surrounding sandy sediment sources. The remainder came from mud and phytal sources. Palmer and Gust (1985) also sampled a tidal creek at three depths (17 cm; 37 cm; 57 cm) and found nematodes to be the most common taxon found in the water column, numbering up to 1200 m^{-3} (with total meiofaunal abundances reaching 14000 m^{-3}). Meiofaunal diversity in the water column can be high. Fleeger et al. (1984) caught all but one of the meiofaunal taxa found in surrounding sediments in emergence traps.

One question concerning water-borne dispersal is whether an organism's settling is merely a matter of currents and gravity (passive) or a matter of choice (active)(see Eckman 1979). While there exists evidence for passive settling, such studies are biased against the alternative of choice because they either do not provide alternative sediments types, use strong flume flow rates, place structures within the flow, and/or collect samples high in a flow where meiofauna are not likely to exhibit potential choices(i.e. Eckman 1979 and Hannan 1984). It is closer to the sediment bed, perhaps around the last few centimeters, where the interactions of flow, chemical cues, and meiofaunal settling capabilities give these organisms a reasonable chance for altering their settling fate (see Crisp 1974, Butman 1987, and Moore *et al.* 1994).

Although benthic meiofaunal organisms in suspension typically experience flow velocities beyond their swimming capabilities (Butman 1987), they may nonetheless, be able to alter their settling location by adjusting their sinking rates. At least one benthic nematode species has two settling behaviors (Hopper and Meyers 1966). One behavior is a thrashing (side to side) motion which helps to keep the nematode suspended and the other is a still coiled position with the head end projecting downward. Hopper and Meyers also determined that this nematode was chemically attracted to cellulose mats and fungi. Jensen (1981) found a benthic nematode that actively swam toward a macroalga. In the laboratory, the attraction was circumstantially determined to be chemical. These observations were all made in still water. On the other hand, Palmer (1984) did not note any particular movements in the nematodes she observed in suspension.

Crisp (1974) believes that larval remote sensing of chemical cues is unlikely in flow. He states that any soluble attractant would be diluted to "virtually zero" at the outer boundary of the viscous sub-layer and points out that experiments showing a soluble substance influencing settling of larvae were performed in still water containers. However, all his examples involve hard bottom taxa were flow velocities are generally higher and surfaces are more irregular than soft bottoms. Although Raimondi (1988) later supported this view, by using a crushed barnacle extract as a cue to investigate the role of chemical cues in barnacles (*Chthamalus*), he was able to induce settling of barnacle larvae 2 m higher in the intertidal zone than it normally occurs. He hypothesized that this could indicate "long range" (long range was not defined) detection of a persistent powerful chemical cue but discounted his hypothesis after examining treated and untreated panel arrays placed high in the intertidal zone. However, he left the panels in place for 24 hours and close enough together to possibly compromise the results. Recent empirical investigations of chemical cues in flows near the sediment water interface suggest that cues can be persistent and rise at least several centimeters into a turbulent flow. Moore *et al.* (1994) simulated the excurrent siphon of the clam *Mercenaria mercinaria* in a flume with a sand bed and found an odor plume rising over 3 centimeters less than 5 centimeters downstream of the siphon.

Meiofauna descending in a moving body of water, travel through a gradient of flow velocities that range from the loosely defined "free stream" velocity (what you and I might experience in the middle of a large river) to virtually zero at the sediment water interface. Within this gradient of velocities or "boundary layer" are three dynamically defined regions: (1) the turbulence dominated layer, (2) the turbulence generating layer, and (3) the bed layer made up primarily with the viscous sub-layer (see Vogel 1983, Middleton and Southard 1984, and Moore *et al.* 1994). These layers are not delineated by any mass properties, but by dynamic properties. The outer two layers, turbulence dominated and turbulence generating contain eddies (smaller and more energetic in the turbulence generating layer) which effectively mix and homogenize water and small particles. In estuarine waters with significant tidal and/or wind driven flow, these layers extend from the bottom to the surface (Wright, 1989). Hauspie and Polk (1973) and Hagerman and Rieger (1981) found no differences in meiofaunal concentrations sampled at different depths within the turbulence-dominated layer. Hannan (1984) captured meiofaunal sized larvae in a manner consistent with passive particles because the collection traps were placed over a meter off the bottom of Buzzards Bay, well inside this turbulent layer. Within these layers, flow velocity is roughly a function of the logarithmic distance to the bed, hence the terms "log layer" or "log-normal layer" are used to describe this region. This velocity profile is significance because the greatest changes in velocity occur near the bed. As a consequence a relatively small alteration in settling velocity can have a disproportionate change in distance traveled downstream. If the flow is not highly turbulent, next to the sediment-water interface is the bed layer comprised two sub-layers, the viscous and diffusion sub-layers. The diffusion sub-layer lies next to the bed (only several microns thick) and is characterized by the near absence of flow. The viscous sub-layer is on the order of one or two millimeters thick depending in part on the flow velocity and roughness of the bed (i.e. Moore *et al.* 1994 calculated a 2.07 mm thick viscous sub-layer at a 3.8 cm/sec free stream flow rate and 350 μm mean sand grain diameter) and is characterized by slow and near laminar flow. Because the flow is laminar, molecular diffusion, not turbulent diffusion, dominates the process by which chemicals leave the sediment.

Investigations that link the elements of weakly swimming meiofaunal sized organisms, presence and absence of attractive chemical cues from the sediment water interface, and natural flow conditions are relatively new. Butman and Grassle(1992) and Grassle *et al.* (1992) investigated the settling of a larval polychaete, *Capitella* sp.I, over attractive (organic-rich) and unattractive sediments in still water and various flume flow velocities. The focus of their experiments was to determine if larvae that show selectivity of sediments in still water would render the same choice under flow conditions. They found that larvae preferentially settled on squares of organic-rich sediments both in still water and slow or fast flows. From their data they inferred that sediment contact was required by the larvae as part of the selection process. They, however, acknowledged the need for direct observation of the settling process. Observations of the initial release of larvae in the flume revealed that the larvae swam quickly downward. This behavior suggests a strong geotaxis thus rendering this organism unsuitable to test a remote sensing hypothesis. More recently, Turner *et al.* (1994) studied the effect of flow and chemical cues on oyster (*Crassostrea virginica*) larvae settling and concluded that remote sensing of chemical cues in turbulent boundary layers does occur and furthermore that chemical gradients (see Crisp 1974) were unnecessary as a settlement inducer. The potential recolonization of disturbed habitat (sensu Sherman and Coull 1980) by nematodes through means of water-borne suspension in properly scaled flow environments, with remote recognition of benthic chemical cues and active settling is examined in this investigation.

MATERIALS AND METHODS

Field Collection Site Description

Field observations and collections were made along an intertidal sandy beach on the Elizabeth River, Norfolk, Virginia (Figure 1). The beach contained relatively clean and well sorted sand with a mean ϕ of 1.3. The redox potential discontinuity (RPD) was typically about one cm.

The water at the site is estuarine and is part of the tidally affected portion of the Elizabeth River, a tributary of the lower Chesapeake Bay. Tidal amplitude is roughly 0.6 meters(neap tides) to 1.3 meters(spring tides) (NOAA 1992). However, wind can dominate the scheduled tides by pushing water into or out of this river (pers. obv.). Salinity ranged between 12.2 ‰ and 19.4 ‰ and temperature ranged between 5 °C and 27 °C (Mike Lane, Applied Marine Research Laboratory, pers. comm.).

Flume dimensions

All experiments were conducted with a 0.4 m by 2.5 m linear flume. The flume and water pumping system delivered a unidirectional turbulent flow at depths up to 5 cm and

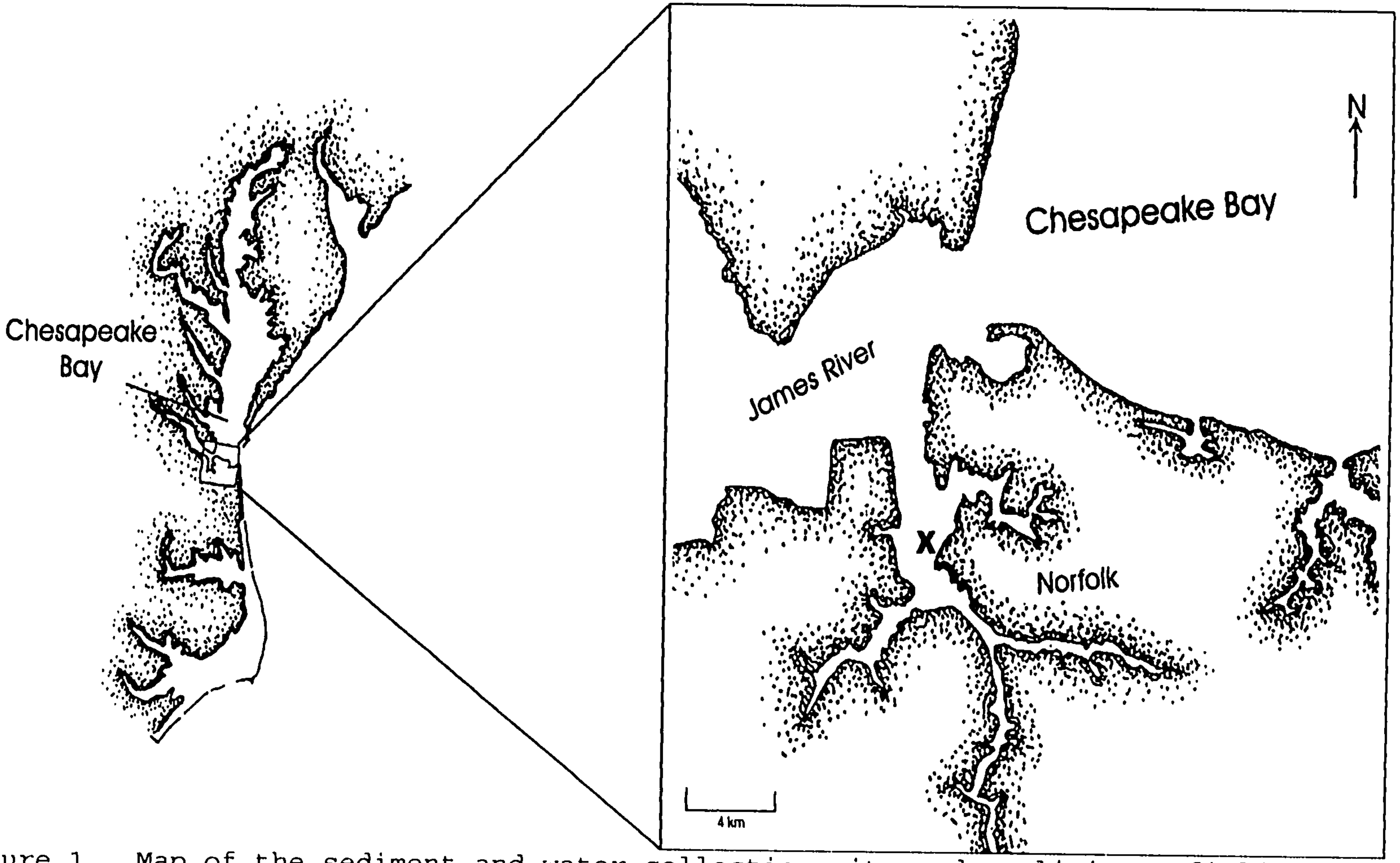

Figure 1. Map of the sediment and water collection site and preliminary field studies. The site is marked with an "X".

current velocities to 5 cm sec^{-1} (with shallower flow depths much higher velocities are possible). Water entering the flume passed through a collimator made of drinking straws arranged with the bottom straws longer than the upper straws. This collimator thus not only "strains" out large eddies (> 1 cm) but also "preformed" the boundary layers by slowing the water flow next to the bed (Figure 2). The system supporting the flume recirculated about 5000 liters of water. A series of stand pipes and storage tanks promoted the settling of particles and non-swimming animals from the water. Storage tanks located underground served to stabilize the water temperature. The water was delivered to the flume through a constant pressure head tank located above the laboratory. The water velocity and depth in the flume were regulated through the interaction of three devices. One was a ball valve that regulated the amount of water entering the flume. The second was a scissors jack that raised and lowered the head end of the flume bed. The third was a vertically louvered exit gate that regulated the flow of water leaving the flume.

Selection of live taxa

Ultimately, three nematode taxa were used for the flume

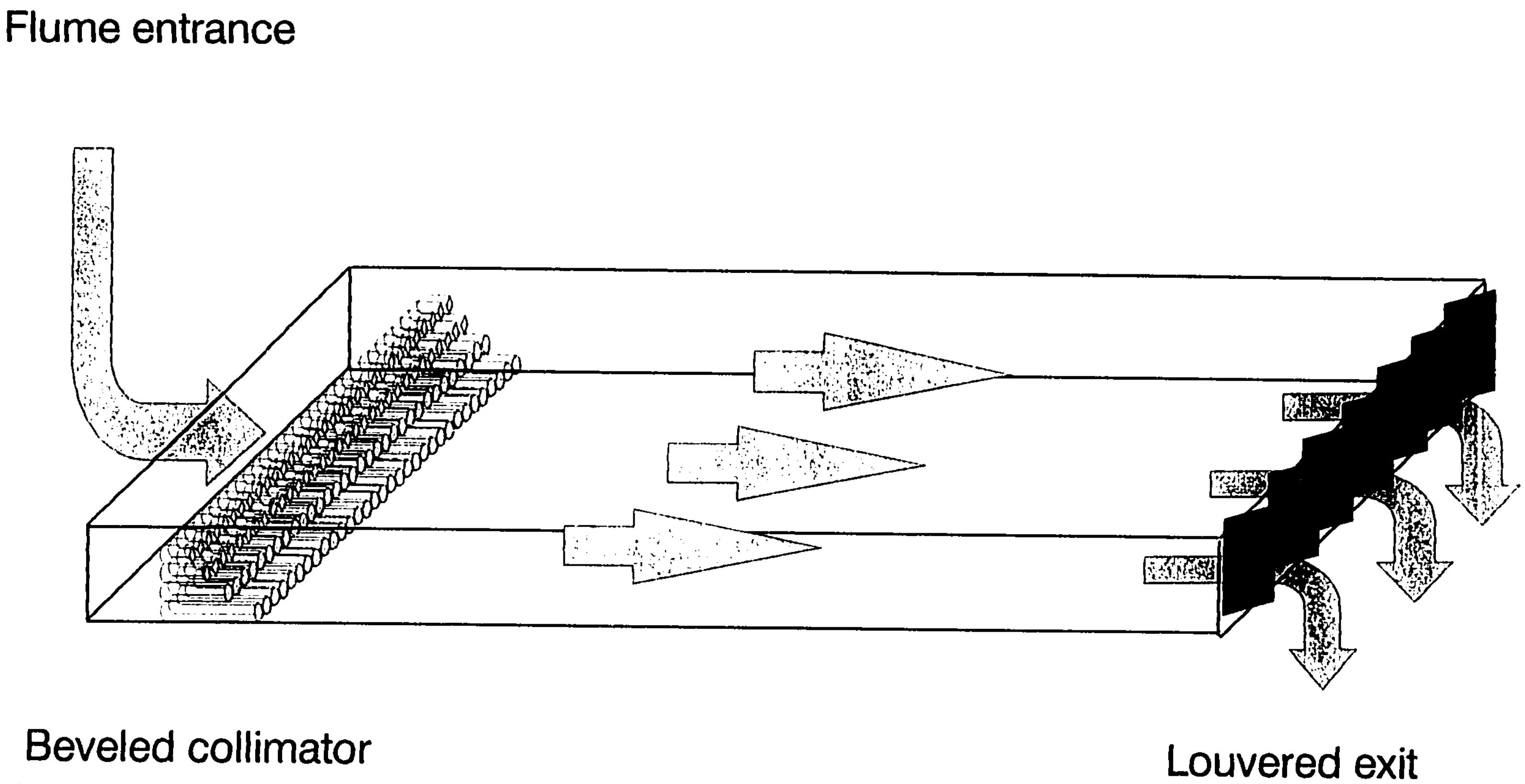

Figure 2. Diagram (not to scale) showing the main features of the linear flume used in the study.

experiments. The three taxa used were *Theristus* sp?, *Halalaimus* sp., and *Paranticoma* sp. Each taxon met the following four criteria: (1) it was abundant enough such that finding specimens was not difficult, (2) it was hardy in the laboratory, (3) it could disperse in the water column, and (4) it showed a preference for natural sediment over boiled sediment in a still water choice experiment (see Gray 1966a).

The first two criteria, abundance and hardiness, were determined by collecting, holding and inspecting specimens. Abundance was evaluated subjectively. To be rated hardy, individuals of a given taxon must exhibit zero mortality after three days. The taxa chosen for these experiments could be kept in a clean watch glass for more than a week; however, many would become less responsive after four or five days.

The third criterion was resolved using recolonization dishes in the field. To determine which taxa enter the water column during ebb and flood tides, dishes containing defaunated sediment were placed on the intertidal zone at low tide. Six 10 cm diameter by 5 cm height glass culture dishes were filled with sediment from the study site. The sediment was defaunated by mixing it in a blender at high speed for one minute (Dr. Peter Jumars, Univ. of Washington, pers. comm.). Visual inspection of test aliquots of sediment confirmed defaunation. Culture dishes were placed at the study site such that the upper rim of each dish projected one cm above the surrounding sediment. The dishes were arranged in the intertidal zone parallel to the water's edge at low tide. Two trays were recovered 2 h after placement, and then two more were recovered every hour after that time. The last two were recovered 6 h after placement. The taxa found in the sediment trays were presumed to have reached the tray through the water column.

The fourth criterion requires that individuals of a given taxon exhibit an attraction for sediment from its habitat over the same sediment altered by exposure to boiling fresh water. The "attractive factors" (sensu Gray 1966a) in untreated sediment are now accepted as bacteria and their exudates, and/or microflora and their exudates (i.e. Gray 1966b; Gerlach 1977; and Montagna 1984). A still water choice experiment (see Meadows 1964) was used to confirm whether a sediment had retained any attractiveness. In these experiments, a known number of worms was introduced along an intersection consisting of a narrow trough between two adjacent mounds of sediment placed in a small watch glass (Figure 3). One mound contained untreated natural sediment, the other was boiled in fresh water for over 10

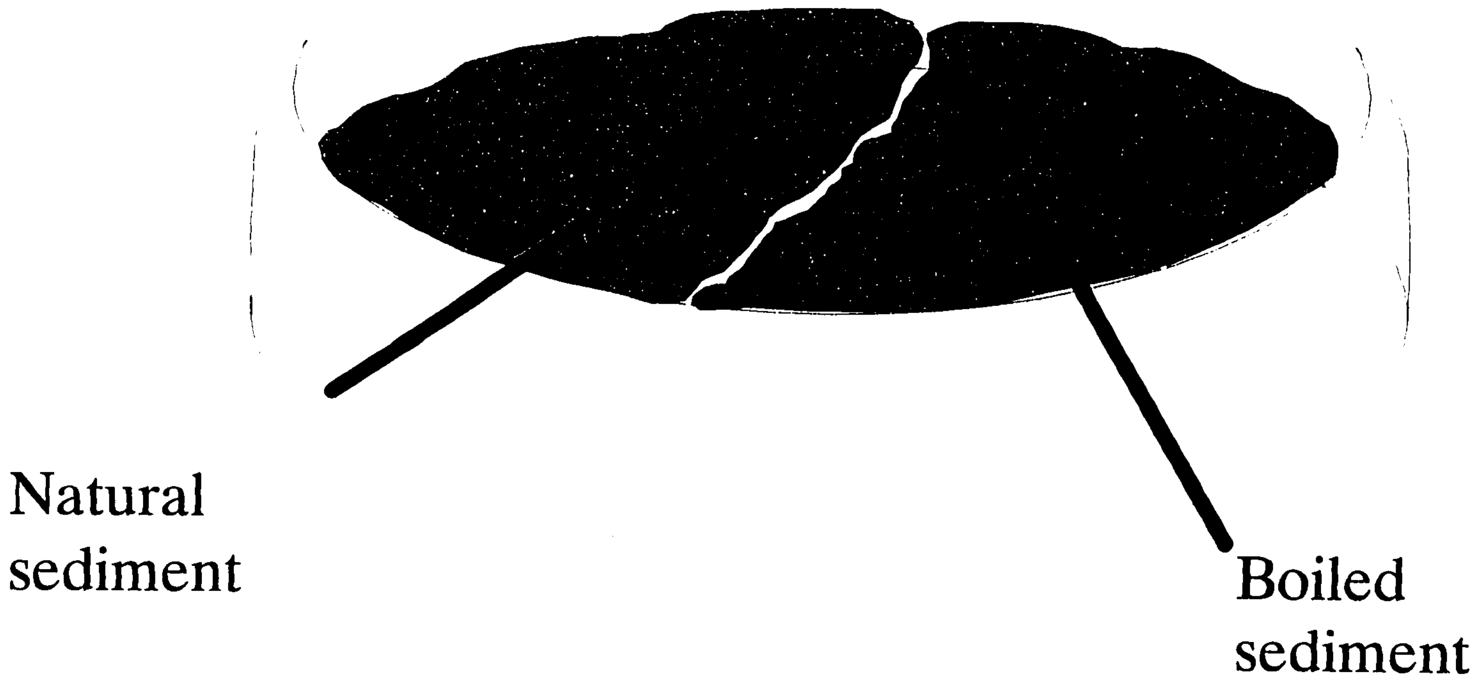

Figure 3. Diagram of the choice experiment in still water. Nematodes were offered two types of sediment and placed atop the intersection of the sediment types.

minutes. Boiling denatures bacterial and microflora exudates in the sediment and kills most of the bacteria and algae (Gray 1971). After six hours, the mounds were separated and examined for worms. If the worms showed no preference for either sediment the expected ratio of worms between the two sediments was 1:1. A chi-squared analysis was used to determine if there were significant departures from a 1:1 ratio.

Collection and separation of nematodes from sediment

"Clean" (free from any adhering sediment) worms of all taxa were required for all laboratory experiments. Adhering sediment particles may alter settling rates. Modifications of a method described by Couch (1988) proved to be a reliable means of obtaining large numbers of clean nematodes. Several liters of surface sediments (top 1-2 cm) were collected at low tide with a shovel and bucket. These were taken back to the laboratory and elutriated. Typically, a 0.5 l aliquot of sediment would be elutriated for 15 minutes. The time and amount varied considerably due primarily to variations in the amounts of fine flocculent detritus within different collections. An elutriator was constructed of PVC pipe and 1 mm screen (Figure 4). The flow into the elutriator was adjusted so it was strong

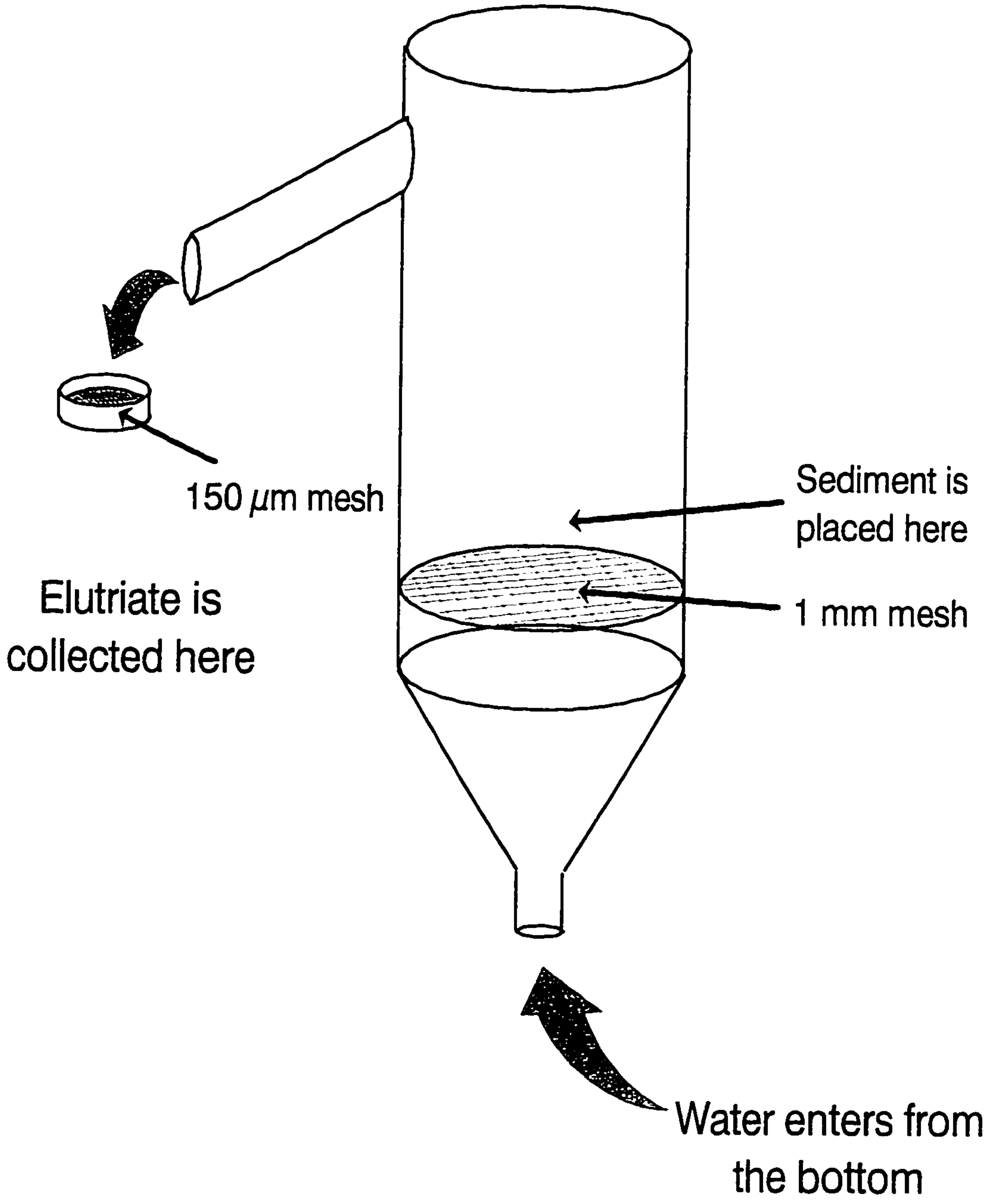

Figure 4. Diagram of the elutriation setup used to separate nematode and lighter particles from the sandy fraction of the sediment.

enough to mix the sand particles but not so strong as to suspend and carry sand out of the elutriator. The outflow containing detritus, other fine particles, and meiofauna were collected over a 150 µm mesh screen. Although the mesh opening was greater than the 50 µm minimum size defined for meiofauna, smaller screen sizes, such as 63 µm, always clogged and overflowed within seconds and thus were unsatisfactory. Selection of the 150 µm mesh was determined by trial and error to be optimal. The elutriate collected by this screen entrained animals far smaller than 150 µm, including ciliates. The detritus and animals were rinsed into a collection bottle. Typically, the elutriation process was repeated with additional aliquots of sediment until I had collected between 10 and 30 ml of elutriate. The elutriation process generally required 30 minutes to 1 h per sediment sample.

The final piece of equipment used to produce clean nematodes was made up of funnels, screens and sand. A 1-3 mm layer of clean oven dried beach sand was placed upon a 150 µm nylon screen. The grain size of the sand was between 250 µm and 500 µm. By trial and error, this grain size range was determined to produce the greatest number of nematodes. The screen was glued with rubberized silicone cement about 1 cm below the top of a funnel (Figure 5).

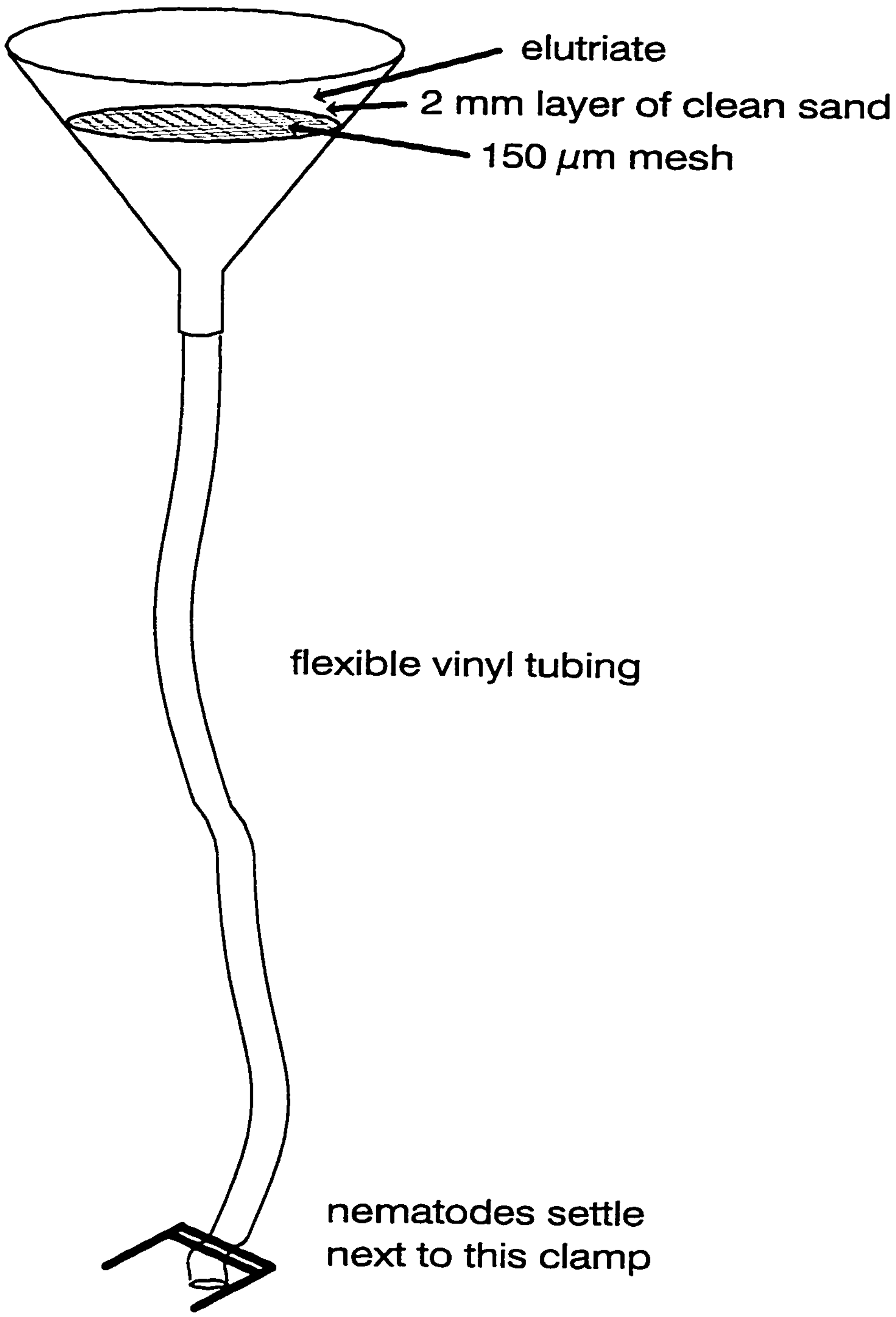

Figure 5. Diagram of the funnel apparatus used to produce "clean" (free from adhering sediment) nematodes.

Material collected from the elutriator (about 5 to 10 ml) was layered on top of the clean beach sand after the entire apparatus was filled with estuarine water. The movements of the nematodes through the sand effectively cleaned adhering particles from their cuticles. Subsequent movements through the screen caused them to settle through the funnel and into a short section of vinyl tubing. Nematodes were periodically collected through a valve at the bottom of the tube. Times between collections, determined by the rate at which nematodes accumulated in the tube, ranged between 30 minutes and six hours. Scheduling the removal of nematodes was determined by visual inspection of the funnels. Typically, I would run 2-4 funnels to collect several thousand nematodes over a 2-6 h period. Upon removal from the funnels, nematodes were placed into large glass trays that were floated inside a running sea water table in the laboratory. The nematodes were floated in the table to keep them at the same water temperature used in the flume and settling chambers. Worms not used within 36 h were discarded. Gluing the screen about 1 cm below the top of the funnel was my primary change in the Couch (1988) method. Her screen was placed close to the narrow part of the funnel. Placing the screen up higher provided a much larger surface area to spread the elutriate and so helped to increase the number and rate of nematodes collected. However, because of the larger screen, nematodes dropping vertically were less likely to fall near the hole in the bottom of the funnel and would instead make contact farther up the sides of the funnel. After continuously using a funnel for several weeks a bacterial and/or algal film developed along the walls of the funnel. Nematodes contacting such a film tended to stay put and did not settle into the vinyl tube. Occasionally running hot fresh water through the funnel then wiping out the funnel with pipe cleaners restored the funnel's collection efficiency. This method also was effective in concentrating the gastrotrichs present in the sediment.

The effect of shape on settling rate

Nematodes can alter their settling velocity by changing shape. For example, a worm in a coiled configuration will settle at a faster rate than one uncoiled (e.g. Hopper and Meyers 1966). To confirm that the nematodes used in this study settled at different rates in different configurations, nematodes were preserved in 10% formalin then soaked in estuarine water to remove the formalin. The preservation process left the nematodes in various degrees of coiling. Nematodes were categorized into one of four different degrees of coiling: (1) straight, uncoiled; (2) arc, preserved in an open semicircle; (3) circle, preserved in a circle; and (4) coiled, preserved in a tight coil consisting of two or more turns. Nematodes in various degrees of coiling were placed into a 20 cm (width) by 20 cm (height) by 2 cm (depth) settling chamber to determine their still water settling velocity. Worms were timed over a 5 cm distance in the middle of the chamber. The still water settling velocity for each worm of each taxon was determined over four separate trials.

Selection and length measurement of individual live nematodes

Selecting worms for the flume experiments began by haphazardly pipetting a small portion of the nematode mass from the large glass trays to a small watch glass. From here, all worms in the watch glass were used if they belonged to one of the three taxa I was investigating unless they had a broken cuticle or body wall, suctorians or fungi on the cuticle, any coloration not normally seen for a given taxon, or a lack of movements typical for a given taxon when the individual was handled.

The length of each worm was measured using a dissecting microscope fitted with a calibrated reticle. Determining the length of a live squirming nematode proved very difficult. Although the length of any given worm could not be measured very precisely, the overall average length given for each taxon represents a good and accurate estimate.

Still water settling rates

Herein, still water settling rate refers to the rate that live nematodes settled in the absence of water currents and in the absence of any cues that might come from sediment on the bottom or fouling on the side walls. A related term, passive settling refers to the settling rate at which animals settle as "inert" objects. To render an animal inert, an animal might be preserved or more commonly, narcotized with magnesium chloride or tricaine methanesulfonate. Narcotizing animals is primarily done to immobilize cilia which could alter settling. Because nematodes are not covered with cilia and the effect of this treatment on nematode behavior is apparently not known, I chose not to narcotized them. Tricaine methanesulfonate does alter polychaete larval behavior (Butman et al. 1988). To determine still water settling rates, each worm was placed into a clean settling chamber and timed to the nearest 0.01 second over a 5.0 cm descent. This procedure was repeated four times. The settling rate for any given worm was defined as the average of the four trials.

Flume preparation

The flume held a 3 cm thick bed of sediment. The sediment bed consisted either of natural (and thus "attractive") sediment or boiled (and thus "unattractive") sediment. For both sediment treatments, the sediment was screened through a 1 mm sieve to remove any large gravel, pieces of brick, glass, and shells. Removing the large fragments permitted me to use a rubber squeegee to smooth the surface of the sediment. Large fragments would invariably become trapped against the squeegee and thus destroy a level surface. A level surface was confirmed by closing the flume's exit and flooding the flume with just enough water rise to the level of the sediment. Low areas would puddle water and would be subsequently filled with surrounding sediment until the bed was completely level. The sediment used in the bed was collected from the same area and at the same time as the nematodes. For each taxon, roughly half the trials were run over natural and half over boiled sediments.

Flume trials

During these experiments the flume bed angle was always maintained at 0° (parallel with the floor) and the louvered exit was always set to the maximum closed position. The ball valve entrance was then adjusted to deliver a 5 cm water depth. Once the desired water depth was achieved, I would allow the flume system to run without adjustment and check the depth of the water every 15 minutes. If the flume conditions held steady for 1 hour, I would begin experiments. These conditions produced a flow velocity of about 1.4 cm/sec at 2 cm above the sediment bed. The "local" Reynolds number (see Vogel, 1983; chap 8) for the flume was on the order of 10,000 indicating a smooth turbulent flow.

Once the still water (passive) settling trials were completed, the worm was transferred via a disposable glass pipette to the flume and placed into a small glass tube whose axis was parallel to the water flow. The tube was suspended 2 cm above the sediment bed. The combination of the worm's movements and the current within the tube would cause the worm to meander toward the downstream opening in the tube. The time from when the worm left the tube until it contacted the bed was measured with a stop watch. The distance downstream from the suspended tube was measured and recorded. Some trials were rejected when an occasional large eddy, formed or perhaps did not completely break up in the collumnator, and the worm moved quickly up or down after leaving the suspended tube. These rejections were very obvious and relatively rare (less than 5% of trials). More common were lost trials. These occurred when I lost direct visual contact with the worm prior to settling. A good trial required a steady even release of the worm from the tube.

Other flume measurements

Salinity was measured at the start of each day's observations. Water temperature was recorded every 30 minutes. In practice, temperature varied little during a day. Prior to the start of a set of trials, I recorded the flume's current on videotape. Backlighting with high intensity lamps caused the particles in the water to show up on videotape. A ruler was briefly placed at the front of the flume to use as a length calibration. The camera contained a stop watch and date stamp which I used to mark time. The videotape was run for three to five minutes prior to the release of worms.

Data analysis

Chi-squared analysis was used for the determination of unattractive sediment (choice experiments) where the expected ratio of worms in attractive and unattractive sediment if no choice occurred was 1:1. ANOVA and the Mann-Whitney U test were used with the flume data. Because there were two treatments and the taxa were analyzed separately, the ANOVA model conformed to a t-test (Sokal and Rohlf 1981). Analysis of nematode behavior was conducted using Fisher's exact probability test (Siegel 1956).

The analysis of settling rates for each taxon involved three separate tests. The first test was to compare the still water settling rates for individuals of a given taxon *destined* for the two different flume bed treatments. This test serves to check the process of selecting the worms over the course of many months. If worms *destined* for the two treatments represent randomly selected samples of the population, there should be no difference in the mean still water settling. Where significant differences were found, subsequent analyses were limited to those worms with still water settling rates between the 25th and 75th percentiles (interquartile range) of all observations for that taxon. This insured that further comparisons included only those nematodes having similar (i.e. not significantly different) still water settling velocities. The second test compared settling rates in the flume. If the worms of a given taxon were attracted to the natural sediment and not to the unattractive sediment, the mean settling rate would be higher over the natural sediment than the unattractive sediment. The third test compared the difference between the still water and flume settling rates. The rational was to control any non-significant bias in the still water settling rates for worms destined for different treatments. This paired the still water rate of a given worm with the settling rate in the flume. By subtracting the still water rate from the flume settling rate, a negative number would indicate that worm settled faster in the flume than in the still water chamber. Positive numbers would indicate slower settling in the flume than in the still water chamber. In practice, however, worms tended to settle slower in the flume than in the still water settling chamber. Thus the differences, regardless of the taxon or bed treatment, tended to be positive numbers. Given this empirical observation I would therefore expect the difference values to have larger positive numbers for the unattractive treatment and smaller (although positive) numbers for the natural sediment. While I did not investigate why the same worm tended to settle slower in the flume than in the still water settling chamber (I did not discover this until after I had finished collecting data), I believe that two factors contribute to this phenomenon. One was that in the flume the stopwatch starts the moment the worm leaves the tube. Acceleration from rest to terminal velocity requires a certain amount of time. A downward motion of the worms (settling) normally was not apparent until the worms had moved 1-2 cm away from the tube. In the still water settling chamber, the worms were already descending at terminal velocity when they reached the first mark where the stopwatch was started. The second factor was that when the worms in the flume reached the final few millimeters, it often appeared that settling slowed perceptively just prior to contact with the bed. I cannot, however, offer any definitive proof that this is what occurred, only that these were my impressions developed largely in hindsight.

Behavioral observations of individuals in the flume were grouped according to whether a given behavior accelerated or slowed settling. Because there were two experimental treatments (attractive and unattractive sediment beds) these behavioral scores fit into a 2 X 2 contingency table. The Fisher exact probability test applied to this table is very useful with my small sample size (Siegel 1956).

RESULTS

The recolonization trays produced 10 identifiable nematode taxa comprising 166 individuals as well as other meiofaunal taxa (Table 1). All three taxa ultimately used in the flume experiments were found in the recolonization trays. Choice experiments showed that these three taxa had a highly statistically significant ($p < 0.001$) attraction for natural sediment over boiled (Table 2).

The Elizabeth River sampling area contained a well sorted sand with a mean phi of about 1.3. Boiling the sediment did not markedly alter it's physical properties (Table 3a). Water temperature ranged between 12 and 26°C and salinity between 10 and 16‰ (Table 3b). Underground storage tanks near the flume maintained the temperature of the water close to the water temperature of the Elizabeth River (Figure 6).

Settling rates of worms preserved in various configurations were determined to see how shape affected settling velocities. Coiled worms settled at roughly twice the rate of worms configured in open arcs or straight lines (Figure 7). Variances across these groups were not all homogeneous (Levene $p=.033$) therefore an ANOVA with the more conservative Scheffe multiple range test and α set at .01

Table 1. Results of the recolonization experiments. A total of ten recolonization trays were deployed at low tide (9:00 am; 10-30-87). Two trays were removed each hour starting after 2 hours after low tide. Given is the sum of the taxa found for both trays removed at each sampling period.

Taxon	Immersion time (hrs)					
	2	3	4	5	6	totals
NEMATODA						
Theristus sp?	3	9	22	21	20	75
Halalaimus sp	0	0	4	9	1	14
Paranticoma sp	1	4	0	0	2	7
Other nematodes	4	9	31	18	8	70
CRUSTACEA						
Ostrocoda	1	11	9	11	6	38
Amphipoda	0	0	1	9	1	11
POLYCHAETA						
Polydora ligni	0	0	0	0	1	1
Streblospio benedicti	0	0	1	0	1	2
Polychaeta larvae	0	0	0	0	1	1
OTHER						
Gastrotricha	0	0	1	0	0	1
Turbellaria	0	0	1	0	0	1
Unidentified	0	1	13	8	1	23

Table 2. Results of the still water attractive (natural) vs unattractive (boiled) choice experiments. Animals were introduced at the intersection of a patch of boiled sediment and natural sediment. Sampling of the sediments occurred 20 hours after introduction. In sampling the sediments a small residual amount of sediment was left between the two sediment types in the dish ("Middle"). Nematodes found in the "Middle" were considered indeterminate ("missing") for statistical analysis.

Taxon	Unattractive (Boiled)	Middle	Attractive (Natural)
Theristus sp?	1	3	25
Halalaimus sp	33	10	58
Paranticoma sp	11	0	40

Table 3. Physical parameters of sediments used in the flume and the temperatures and salinities measured while using the flume. (A.) A comparison of sediment analyses for sediment taken from the collection sites. One portion was analyzed as collected (i.e. - Natural = "attractive sediment treatment "), the other portion was boiled (i.e. "unattractive sediment treatment). See methods for details concerning the sediment treatments. (B.) Temperatures and salinities in the flume by month (1989-1990).

A.

	%Sand	%Silt	%Clay	Mean Φ	Sorting	%volatiles
Natural	99.28	0.02	0.70	1.25	0.64	0.502
Boiled	98.89	0.16	0.95	1.30	0.62	0.509

B.

Month	Temperature °C	Salinity ‰
August	23.6	14
September	23.4	14
October	17.7	11
November	12.1	10
March	13.2	14
May	15.5	12
July	26.0	15
August	25.4	15
September	24.6	15
October	21.7	15
November	16.3	16
December	12.9	16

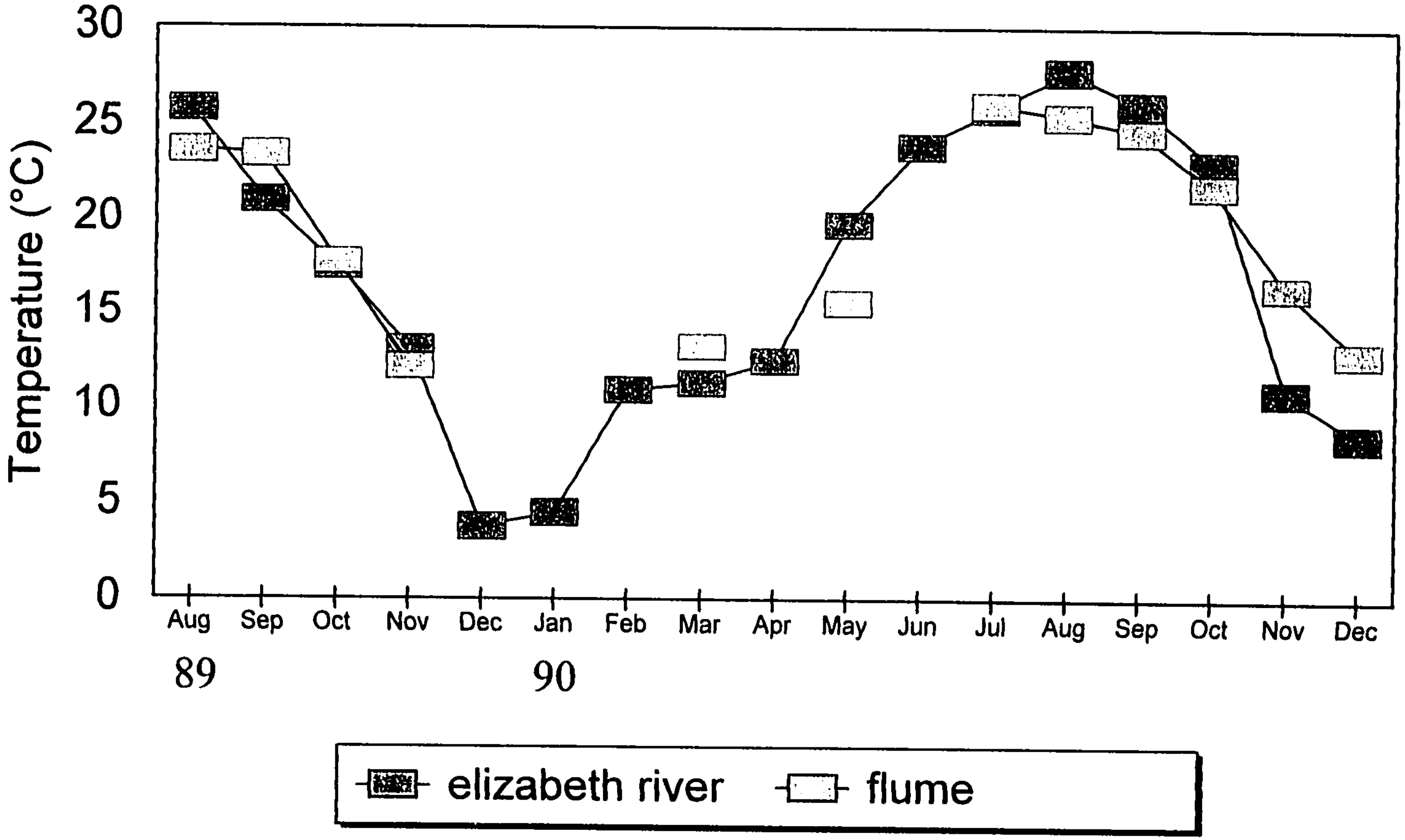

Figure 6. A comparison of the Elizabeth River surface water temperatures with the water temperature of the flume. This comparison represents an approximation because the Elizabeth River temperature is taken on a single day during the month whereas the flume temperature represents an average temperature for all observations taken during a given month.

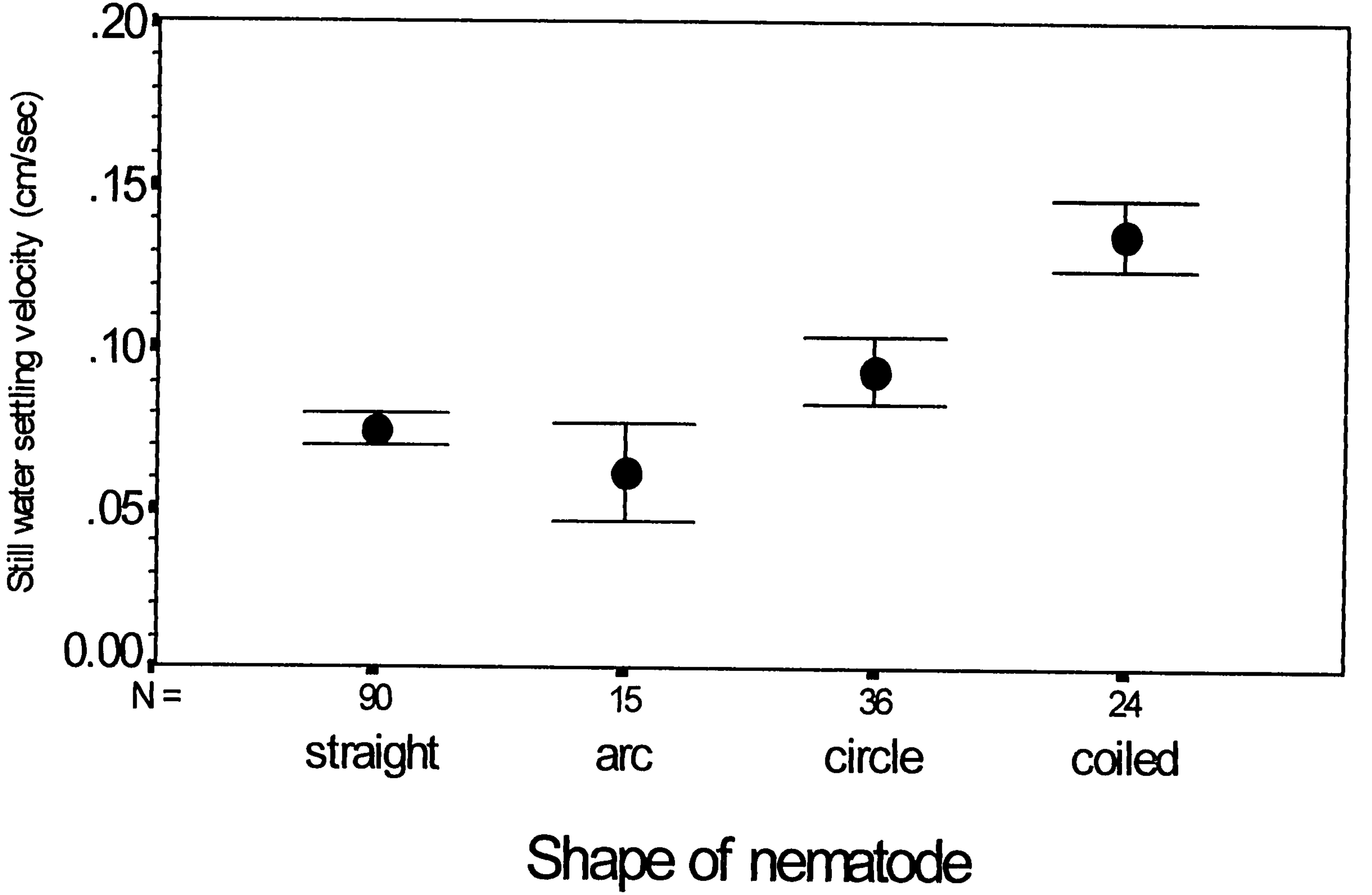

Figure 7. A comparison of still water settling velocities of nematodes preserved in various body configurations. Error bars represent the standard deviation about the mean settling velocity for configuration.

(Norušis 1993) was used to test for differences in the settling rates between groups. Coiled worms settled at a statistically significant faster rate than all other worm configurations. Worms preserved in circular shapes settled significantly faster than those in arcs or straight shapes, whereas there was no significant difference in settling rates for worms in arcs or straight shapes (Table 4). Of the three nematode taxa used, *Theristus* sp? was the smallest (mean size 1.4 mm ± 0.020 SE) and by far the most active. When drawn into a tube or transferred into a dish, it often alternately coiled from one side to the other. A coil might be held for several seconds before unwinding then coiling back the other way. At other times it would thrash back and forth. In this motion the worm whipped its body into a u-shape to one side, then to a u-shape to the other side. One cycle of this motion required less than one second. This thrashing motion did not impart any directional motion (swimming) to the worm. The *Theristus* sp? I worked with may have comprised a complex of up to three extremely similar taxonomic species. Setal counts both around the mouth and along the body varied in preserved specimens. Setal counts around the mouth varied between six to eight. Body setae varied between absent to approximately four. These worms did not vary in any other generally accepted taxonomic

Table 4. The settling rates of nematodes (all taxa combined from the collection site) preserved in four different degrees of coiling; (1) straight; (2) arc; (3) circular; and (4) coiled. ANOVA test results show highly significant ($p<<0.001$) different settling rates. Homogenous groups (Scheffe multiple range test with significance level set a .01) are indicated by the same letter.

Shape	N	Settling velocity (cm/sec)	Std error	Homogenous groups
Straight	90	0.076	0.003	A
Arc	15	0.062	0.007	A
Circle	36	0.094	0.005	B
Coiled	24	0.136	0.005	C

character such as amphid shape, buccal cavity, pharynx position, ovary shape in females, and tail shape. Although setal counts can constitute specific and/or generic characters, I found no consistent authority concerning the disposition of these taxonomic characters below the family level (see Chitwood 1951; Hope 1971; and Platt and Warwick 1983). Although there was inconclusive taxonomic evidence the *Theristus* sp? that I worked with constituted more than one taxonomic species, I never perceived even the slightest behavioral difference between individuals. Their live appearance, size, color, and actions appeared to be identical. Because identifying these nematodes with a setal count would have required killing them, I had no choice but to consider them one taxon. Nonetheless, from all behavioral aspects that I observed, and all features that were readily visible under a dissecting microscope, *Theristus* sp? constituted one taxon. *Theristus* sp? has a clear anterior region extending to the beginning of the intestine. The intestine was always packed with ingested material that had a light brown to gold color. The cuticle was clear. *Theristus* sp? was never difficult to collect as it comprised the most abundant taxon encountered on this beach.

Halalaimus sp. was the longest worm I worked with, averaging 2.1 mm (±0.025 SE) in length. Individuals were easy to locate in a dish of worms because of their large size and the midgut area normally had a reddish-brown to pink hue. Females would often have one to three white eggs just behind this body region. Their activity level was intermediate in relation to the three nematode taxa of my study. It was capable of coiling into a tight mass although this did not occur as often or as quickly as with *Theristus* sp?. Also, *Halalaimus* sp. never exhibited quick thrashing movements. A tightly coiled *Halalaimus* sp. contained roughly three to five turns whereas a coiled *Theristus* sp? would contain only about 1.5 to two turns.

Paranticoma sp. was slightly shorter (1.9 mm ±0.025 SE) than *Halalaimus* sp. and appeared to be slightly thinner on average. *Paranticoma* sp. was relatively easy to find due to its size and a whitish longitudinal muscle layer that gave the body wall an overall frosted white color. Over the frosted white coloration was a distinct thin clear cuticle. It was the most sluggish and the most adhesive (i.e. it was the most difficult to transfer between glassware) of the three. *Paranticoma* sp. never thrashed but was capable of coiling as tightly as *Halalaimus* sp. although coiling motions were slower.

For each taxon, over 100 observations of still water and flume settling velocities were completed (Table 5). These observations are blocked by flume treatment bed. In both the still water settling chamber and in the flume, the larger taxa, *Halalaimus* sp. and *Paranticoma* sp., settled faster than *Theristus* sp?. In comparing these velocities across bed treatment, a t-test was performed where assumptions of normality were met, otherwise the Mann-Whitney U test was performed (Table 6). The first test was a check of the still water settling velocities to determine if there were any biases in worms selected for the flume with unattractive sediment versus those selected for the attractive sediment. For *Halalaimus* sp., there was a significant difference ($p<0.001$) in the still water settling velocities. Those individuals destined for the flume with attractive sediment had significantly higher still water settling velocities (0.145 cm sec^{-1}) than those individuals destined for the flume with unattractive sediment (0.114 cm sec^{-1}). Therefore, tests on observations in the flume for this taxon cannot be performed using all observations. For *Theristus* sp?, although the difference in still water settling velocities was not statistically significant, the relatively low probability value of 0.256 indicates some bias. In this case, *Theristus* sp? destined for the attractive bed settled faster than those destined for the

Table 5. Still water settling rates and vertical settling rates in cm/sec for each taxa. Standard error is given in parentheses. N is the number of observations. Results based on the entire flume data set.

Taxon	Treatment	N	Still water settling velocity	Flume settling velocity	Still water minus Flume settling velocities
Theristus sp?	Unattractive	70	0.0870 (0.0034)	0.0561 (0.0027)	0.0309 (0.0032)
	Attractive	57	0.0926 (0.0033)	0.0654 (0.0029)	0.0272 (0.0024)
	Overall	127	0.0895 (0.0024)	0.0603 (0.0020)	0.0293 (0.0021)
Halalaimus sp	Unattractive	46	0.1138 (0.0057)	0.0781 (0.0038)	0.0357 (0.0046)
	Attractive	55	0.1454 (0.0053)	0.0852 (0.0042)	0.0603 (0.0040)
	Overall	101	0.1310 (0.0042)	0.0819 (0.0029)	0.0491 (0.0032)
Paranticoma sp	Unattractive	54	0.1209 (0.0048)	0.0788 (0.0046)	0.0420 (0.0033)
	Attractive	55	0.1150 (0.0051)	0.0718 (0.0051)	0.0433 (0.0048)
	Overall	109	0.1179 (0.0035)	0.0753 (0.0034)	0.0427 (0.0029)

Note : Because these worms, regardless of species, tended to settle at a slightly higher rate in the still water chamber than in the flume (see results), the last column is interpreted this way ... the larger the positive number - the *slower* the worm tended to settle in the flume - the closer to zero, the *faster* the worm tended to settle. A negative number would have meant that the worm settled faster in the flume than in the still water chamber.

Table 6. A statistical summary comparing the still water settling velocities, flume settling velocities, and settling differences between the unattractive and attractive bed treatments for each taxon used in these experiments. Where assumptions of normality are met the Student's *t* test was used elsewhere the Mann-Whitney U test was substituted(p value for test statistic given in ()).

Taxon	Test results		
	Still water settling velocities	Flume settling velocities	Settling differences
Theristus sp?	1.17 (.244)	2.32 (.022)	0.91 (.362)
Halalaimus sp	676* (.0001)	NA	NA
Paranticoma sp	0.83 (.407)	1.03 (.308)	1444* (.804)

* Mann-Whitney U test substituted for *t* test.

unattractive bed. Because of this I decided to look at the statistical test results of tests two and three for *Theristus* sp? using not only all observations but also for those observations between the interquartile range as described under methods. There was no significant difference nor indication of bias in the still water settling velocities of *Paranticoma* sp.

Column two on Table 6 gives the results for testing differences in the flume settling velocities for each taxon by flume bed treatment. The flume settling velocity for *Theristus* sp? was significantly higher over the attractive sediment bed than the unattractive sediment bed ($p=0.02$). There was no significant difference in the flume settling velocities for *Paranticoma* sp.

Column three tests on Table 6 gives the results for the testing of still water minus flume settling velocities. There were no significant differences in the settling difference for *Theristus* sp? or *Paranticoma* sp. For *Paranticoma* sp., the conclusion to draw from all three tests is that this taxon does not alter settling velocity in response to the different bed treatments. For *Theristus* sp?, the three tests on all observations do not yield a firm conclusion. The flume settling velocity test suggests that this nematode does alter its settling velocity by showing a higher settling rate towards the attractive sediment than the unattractive sediment. In the still water settling velocity test, although not statistically significant, worms chosen for the attractive sediment treatment showed higher settling velocities than those chosen for the unattractive sediment. This bias is apparent in the third test which compares still water settling velocities minus flume settling velocities. This test, because it indicates no significant difference in the change in velocities between still water and the flume, does not support conclusions from the flume settling velocity test. Because of the consequence of this statistically non-significant bias in still water settling velocities, an interquartile range filter was nonetheless applied to observations of *Theristus* sp? as well as *Halalaimus* sp.

After applying the interquartile range filter (Table 7) to the still water settling velocities of *Theristus* sp? and *Halalaimus* sp the same procedures used to compile Table 5 were performed on the remaining data (Table 8). The remaining observations contained no statistically significant differences in still water settling velocities for individual worms destined for either flume treatment (Table 9). For *Halalaimus* sp. the conclusion of the three tests was that this taxon showed no capability to alter its

Table 7. The means and interquartile values for the still water settling velocities for each taxa.

Taxon	Mean	Interquartiles 25th %tile	 75th %tile
Theristus sp?	0.0895	0.068	0.110
Halalaimus sp.	0.1310	0.099	0.158

Table 8. Still water settling velocity, flume settling velocity and velocity differences in cm/sec for Theristus sp? and Halalaimus sp. after applying an interquartile filter on each taxon. Standard error is given in parentheses. N is the number of observations. (Compare with table 5 which is based on the entire data set).

Taxon	Treatment	N	Still water settling velocity	Flume settling velocity	Still water minus Flume settling velocities
Theristus sp?	Unattractive	36	0.087 (0.002)	0.055 (0.004)	0.032 (0.003)
	Attractive	34	0.089 (0.002)	0.065 (0.003)	0.023 (0.003)
	Overall	72	0.088 (0.001)	0.060 (0.003)	0.028 (0.002)
Halalaimus sp	Unattractive	23	0.121 (0.004)	0.075 (0.005)	0.046 (0.006)
	Attractive	28	0.126 (0.003)	0.076 (0.005)	0.050 (0.005)
	Overall	51	0.124 (0.002)	0.077 (0.003)	0.048 (0.004)

Table 9. A statistical summary (using Student's *t*) comparing the still water settling velocities, flume settling velocities, and settling differences between the unattractive and attractive bed treatments for Theristus sp? and Halalaimus sp. after applying an interquartile filter on these data.

Taxon	Test results		
	Still water settling velocities	Flume settling velocities	Settling differences
Theristus sp?	0.50 (.617)	2.03 (.046)	2.00 (.050)
Halalaimus sp	1.07 (.292)	0.15 (.884)	0.55 (.586)

Note: Because still water settling velocities of *Paranticoma* sp destined for the attractive bed treatment and unattractive beds did not significantly differ, an interquartile range filter was unnecessary.

settling rate between sediment bed treatments. For *Theristus* sp? the conclusion of the three tests was that it does alter its settling velocity and shows a greater settling velocity over attractive sediments than unattractive sediments.

The distance traveled down the flume was also recorded but is not presented with statistical tests because I did not have the means to accurately determine flow rates for each observation (unlike the vertical distance which was set at 2 cm). However, these measurements have empirical value to demonstrate what effect alteration in settling velocities have on horizontal distance traveled. More specifically, how does significantly different settling velocities of *Theristus* sp? translate into horizontal distance covered under the general conditions in the flume? For the taxa that did not show significant changes in settling velocities, the distances traveled down the flume were within 2 cm across the two bed types (Table 10). However, Theristus sp? settled 10 cm farther over unattractive beds than attractive beds.

Occasionally behavioral observation notes were taken during the flume trials (roughly 15% of the trials). Observations were made for only a few trials primarily because of the small size of the organisms and typically

Table 10. Median horizontal distance (cm) traveled down the flume by taxon and bed treatment.

Taxon	Horizontal distance (cm) Unattractive bed	Attractive bed
Theristus sp?	29.3	19.0
Halalaimus sp	19.5	18.0
Paranticoma sp	21.3	23.0

Note: To be consistent with statistical tests on settling velocities, distances for *Theristus* sp? and *Halalaimus* sp are based on observations after applying an interquartile filter (see text).

poor water clarity. Thus the following results on behavioral observations must be viewed with caution even though I do not believe I biased these observations in any way.

Thirty-nine flume observations encompass eight behaviors ver four taxa. These behaviors are; (1) worm holds an open configuration then coils toward the end (roughly the last 0.5 cm), (2) worm coiled tightly, (3) worm coiled most of the time, (4) worm holds in an arc shape, (5) worm thrashed most of the time, (6) worm open and thrashed alternatively, (7) worm in open shape, (8) worm coiled then open at the end. Behaviors one to three enhance settling. Behavior four is neutral whereas behaviors five to eight retard settling.

Nine behavioral observations were made of *Theristus* sp? with three observations made over the unattractive beds and six observations made over the attractive beds. All observations over unattractive beds showed behaviors that retard settlement. Over the attractive bed, three observations were behaviors that enhanced settling, two were neutral, and one observation was a behavior that retards settling. The Fisher exact probability test on these behaviors indicates that there is no statistically significant difference in the behavior of *Theristus* sp? over the two bed treatments, however the probability level was low (p = 0.14).

Results summary

Three taxa of nematodes were investigated for the possibility of altering their settling rates by remotely sensing attractive versus non-attractive sediment beds. One taxon, *Theristus* sp?, exhibited a significantly higher settling velocity over attractive sediment beds than over non-attractive sediment beds. Although the results of the Fishers exact test was not statistically significant, the finding was qualitatively supported by behavioral observations; however, caution must be advised because of the low number of observations and the non-rigorous fashion in which they were collected.

DISCUSSION

These experiments indicate that some nematode taxa can alter their settling rates based on sediment attractiveness. There are four factors that I propose play key roles in settling control by nematodes. These factors are body length, flexibility, activity level, and adhesiveness.

Longer worms should have a greater capacity to alter settling rates by changing their shape than shorter worms. The settling rates for nematodes depend in part on the nematode's density and projected area (the area projected onto a plane normal to the flow) (see Vogel 1983, chapter 5). While a nematode cannot do much about its density, it can by coiling, transform itself from a cylinder-like shape into something approaching a sphere or disk. Theoretically, if a nematode shaped as a cylinder with a length fifty times its radius transformed itself into a perfect sphere, the projected area of that nematode would decrease 72% regardless of its length. However, the difference in projected area would be greater for larger worms (e.g. 0.058 mm^2 for a 2 mm length nematode; 0.014 mm^2 for 1 mm length nematode; and only 0.004 mm^2 for a 0.5 mm length nematode).

A second factor is flexibility. Coiling is the wrapping of a worm from an extended body position into a shape ranging from a circle (a loose coil) to a closed spiral (a tight coil). This body configuration enhances settling velocity over the open, straight, or u-shaped configuration. The ability to form a coil is very common in the taxa I examined; however, I found one taxon which was never observed to coil. I attempted to use this taxon in my flume studies but was forced to give it up when it proved too difficult to handle due to its tendency to tightly adhere to glassware.

A third factor is activity level. The activity level between taxa of nematodes varies considerably from sluggish to frenetic. The activity level within a taxon seemed remarkably consistent. A slow sluggish taxon obviously would not make a good candidate for potential settling control. Important types of activities are swimming and thrashing. Swimming is characterized by a rapid side to side whipping of the body that results in directed non-random movement. A similar side to side whipping of the body but without resulting in a directed movement, I have termed "thrashing". Although I have not found any references that discuss what might permit one taxon to swim while others merely thrash, I believe that *Theristus* sp?'s very symmetrical shape with both head and tail coming to nearly identical blunt points preclude it from generating any directed motion. Swimming movement directed vertically (upward or downward) would obviously alter settling rates. Observed swimming capability in the nematodes from my sampling area was rare. I looked at about 20 distinct taxa and found but one that exhibited some swimming capacity. In the still water settling chamber, its swimming direction was always horizontal. (Note: this taxon was not used in the flume because it was rarely seen.) Thrashing slows settling velocity (Palmer 1984); hence, this motion could be used to delay settling and maintain an individual in the water column.

A fourth factor is adhesiveness. Nematode taxa vary greatly in their ability to attach to substrates. A qualitative sense of this property can be seen while transferring individuals in glass pipettes. Individuals of *Theristus* group are easily dislodged from pipettes whereas Halalaimus sp. are tougher to transfer. Some taxa I looked at during these experiments were nearly impossible to remove from pipettes. Taxa with strong adhesive capabilities might not be dislodged from benthic substrates, thus they are rarely, if ever, found settling from the water column. While this factor does not directly reflect upon settling, I am suggesting that a taxon that rarely enters the water column is less likely exhibit control over settling.

Given all these qualities, a medium-large body size, exceptional mobility with coiling and thrashing ability, and relatively poor adhesive glands, *Theristus* sp? was able to alter its landing point by about 10 cm between sediment types when released 2cm above the bed in a 1 ½ cm/sec flow in a flume. What this means outside the laboratory is difficult to assess given the simplicity of my experiment (i.e. boiled vs natural sediment and a consistent linear flow) and the complexity of the field, however, the following inference can be made concerning an appropriate scale for attractive cues in sediment patches. Given the poor swimming ability of nematodes, a single lone small patch (e.g. ~10 cm in diameter) of attractive sediment cannot draw specific nematodes to it. Rather, I predict that attractive cues in sediment would be found either in larger patches (i.e. on the order of meters) or small patches that are aggregated into larger complexes.

This study examines the settlement of benthic nematodes and from that how dispersal, flow, and behavior may interact to explain rapidly changing distribution patterns. I propose that active insertion into the water column, passive erosion into the water column, passive transport, passive settlement, and active settlement are all required components for a general conceptual model explaining dispersal for benthic nematodes. The relative weight of each of these components varies with each taxon; however, I predict that the best candidates to exhibit active settlement would have a large body size, be capable of coiling their body, display rapid movements, and have weak adhesive caudal glands.

Early speculations about the dispersal of benthic meiofauna did not include the possibility of water-borne transport. Sterrer (1973) viewed benthic meiofauna as sediment bound and dispersal a matter of plate tectonics. Scheibel (1974) placed recolonization trays onto submerged buoyant platforms secured several meters above the substrate by ropes (see Sarnthein and Richter 1974) and upon finding harpacticoid copepods and nematodes in the trays within three days (the third day following deployment was his first sampling time), suspected that meiofauna, especially nematodes, had crawled up the ropes securing the trays.

By the early 1980's, not only was the presence of benthic meiofauna, including nematodes, established in the water column (e.g. Bell and Sherman 1980; Hagerman and Rieger 1981; Sharma and Webster 1983) but hypotheses concerning subsequent distribution patterns from water-borne meiofauna were discussed. The conventional view positioned active and passive processes for dispersal and settlement as alternative hypotheses to explain benthic meiofaunal recruitment. Initial studies concluded that passive processes best explained observed patterns (e.g. Eckman 1979; Hogue and Miller 1981; Eckman 1983; and Hannan 1984). However, these and other studies approached the question with active processes positioned as a null hypothesis. The distribution patterns of meiofauna were investigated with respect to structures that physically and substantially altered the flow of water. Such structures were typically ripples, tubes, or arrays of tubes. Higher abundances of meiofauna would be predicted in places where flow models calculated areas of low shear stress (areas where smaller and lighter particles and therefore meiofauna would tend to settle). Biological choices such as using sediments with different attractive properties were not offered. Perhaps because of this, results from these studies generally supported passive settlement although some results were difficult to explain. For example, Eckman (1983) placed straws in arrays of various densities in the field and flume. In one of the field studies, an amphipod (*Corophium salmonis*), a polychaete (*Manayunkia aestuarina*), and nematodes (nematodes were lumped into one taxon) did not fit the passive settlement hypotheses. He speculated that behavioral responses might be responsible for these observations, specifically that these taxa were avoiding the straws which resembled plants (bulrush) in more landward, higher, and therefore harsher environments. However, no experimental data were presented to support this interpretation. More recently, passive settlement alone does not appear to satisfactorily explain harpacticoid copepod distributions (Kern and Taghon 1986; Kern 1990). As in Eckman's research, Kern and Taghon (1986) worked with various densities of straws but also varied food levels in sediments and found that harpacticoid copepods respond positively to enriched sediment. They also implicated behavior in order to explain results; however, few of their results were statistically significant.

Studies in ecology that explore the role of behavior typically exhibit higher variance components than studies of physical factors (pers. comm., Dr. Michael Childress, Florida State University). Behavior is often difficult to quantify, compare, and/or contrast. Sometimes behavior is implicated by circumstantial evidence such as looking at distribution patterns following a treatment because direct observation would be impossible or very difficult. However, given the results of behavioral studies (see introduction) and these results it would be surprising to find nematodes exhibiting a behavior such as suggested by Eckman; that nematodes avoided straws because they physically mimicked a bulrush stand. Literature seems to suggest that most nematode behaviors are chemically based and not physically based (see below). That is, if nematodes do in fact avoid bulrush stands, I suggest that a response cue would more likely be a bulrush exudate and not the physical presence of thin vertical structures placed at some particular density.

While evidence of physically based responses in nematodes are rarely found, a variety of chemically based responses appear in the literature. For example, some nematodes respond to bacteria (Tietjen and Lee 1977), generalized food deposits (Gerlach 1977), diatoms (Romeya et al. 1983), oxygen (Sharma and Webster 1983), and predators (Watzin 1983). Within the water column, specific benthic nematodes respond to fungi on the substrate(Hopper and Meyers 1966) and algae floating at the surface(Jensen 1981). However, one physically based response has been documented in nematodes. Within sediment, some nematodes will descend deeper into sediment in response to currents (Palmer and Molloy 1986; Fegley 1987) while other nematodes actively enter the water column at subcritical flows (Armonies 1988). Behaviors subject to a physical cue such as current flow should be more common in the sediment or at the sediment water interface because by being anchored to a substrate, a nematode would be stationary against a current. Within the water column nearly all benthic nematodes, being non-swimmers, are carried along with the current minus some drag. I have not found evidence in the literature of any physically based responses of benthic nematodes while in the water column.

I have presented evidence that passive processes may not explain the entire picture for nematode settlement. The view that active versus passive settlement are alternative hypotheses that may be tested by examining distribution patterns is outmoded. A broad based conceptual model for benthic meiofauna of vegetated and unvegetated bottoms by Palmer (1988) integrates both active and passive processes. In this model, passive processes were generally believed the dominant process especially in moderate current scenarios. However, a recruitment study (Kern and Taghon 1986) and model (Kern 1990) suggest that active processes for meiobenthic copepods are more important than previously realized.

My conceptual model of nematode dispersal is offered with Figure 8. Starting with nematodes living in the sediments (in a box labeled "Local movements within the sediment"), flow is a cue most strongly realized by those

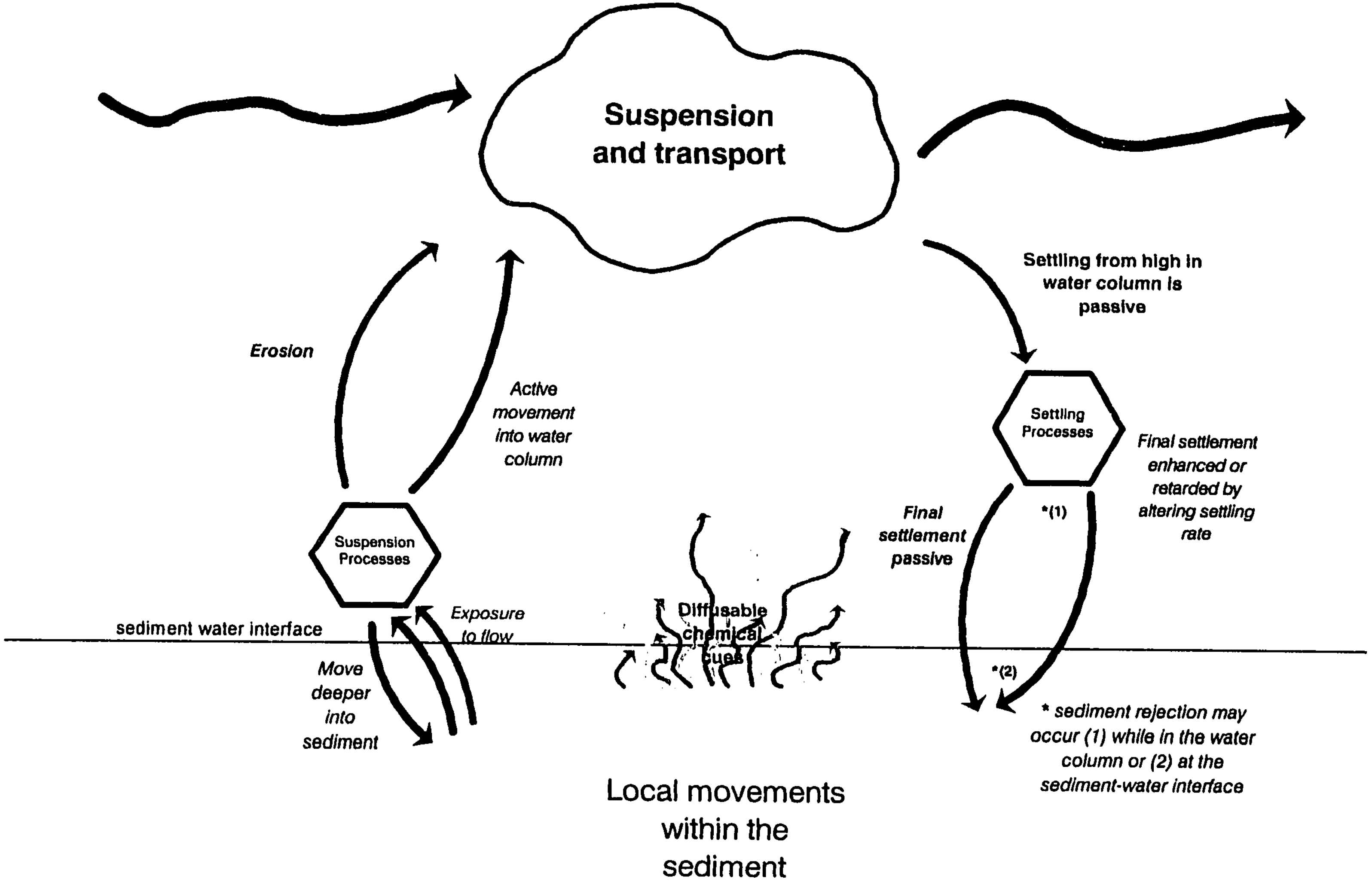

Figure 8. A conceptual model of nematode dispersal. Dark arrows represent active pathways and gray arrows represent passive pathways.

nematodes near the sediment water interface. Reported literature (given above)indicates that some nematodes respond by burrowing deeper, thus avoiding the flow. Entrance into the water column by other nematodes may be active or passive. Active entrance into the water column may be a response to factors such as overcrowding, depletion of food supplies, or the presence of a predator. Passive entrance into the water column may result from a strong velocity shear and/or vertical velocity fluctuations, perhaps coupled with a slow burrowing response for any reason. Regardless of how any nematode enters the water column, all are transported passively due to their poor swimming capabilities. Settlement, however, may be induced or compelled depending on the taxon involved and the physical conditions. The scale at which settlement or rejection cues may operate has not been determined although conventional wisdom has periodically tried to discount the possibility of long range persistent cues (see introduction). If long range cues exist the diffusive properties of turbulent flows should render these cues as generalized "presence" indicators without direction (e.g. a direction might be indicated by a chemical concentration gradient possible in near bed flows). Short range cues operating in the near bed layers of flow would be highly effected by physical conditions such as the roughness of the bed and structures such as ripples or tubes. Whether long range and/or short range cues play a role, some taxa upon sensing favorable landing conditions (i.e. the presence of a particular fungi or algae) or perhaps in some cases, the absence of adverse landing conditions, may coil, stop thrashing, or swim downwards toward the sediment. Adverse conditions for some taxa may induce thrashing, upward swimming, or holding the body in an outstretched manner to retard settling. Other taxa, lacking the means to quickly change body configuration or having a very small body size are obliged to settle purely through physical (passive) processes.

General summary and conclusions

Of three taxa of nematodes investigated for the possibility of altering their settling rates by remotely sensing attractive versus non-attractive sediment beds, one taxon, *Theristus* sp?, exhibited a significantly higher settling velocity over attractive sediment beds than over non-attractive sediment beds. Although Fisher's exact test on the behaviors of *Theristus* sp? did not provide statistically significant support, the probability level of this test was relatively low.

This study provides the first evidence that not all benthic nematodes settle as passive particles to the sediment. Some may remotely sense cues from the sediment bed and actively alter their settling velocity. I predict that those taxa that are able to alter settling rates in response to conditions in the sediment will share the following characteristics: (1) a body length >1 mm, (2) the capability of swimming or coiling the body, (3) the capability of quick movement, (4) weak or absent caudal glands.

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Autobiographical Statement and Publications

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