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A new look into the small-scale dispersal of free-living marine nematodes

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ABSTRACT. We tested experimentally the hypothesis that prevailing locomotion/feeding strategies and body morphology may lead to more active dispersal of free-living marine nematodes, besides passive transport. Neutral Red was applied to the sediment inside cores and the red plume formed during the flood tide was divided into near, middle, and distant zones. At 0.5 m and 1 m from the stained cores, sampling nets were suspended 5 and 10 cm above the sediment-water interface. Dispersion behaviors were defined as a function of a) the numbers of stained recaptured nematodes in comparison to their mean densities in the sediment, b) movement in the sediment or swimming in the water column, and c) body morphology. Tidal currents with average velocities of 9 cm/s resuspended the numerically dominant nematode taxa *Sabatieria* sp., *Terschellingia longicaudata* de Man, 1907, *Metachromadora* sp. and *Viscosia* sp. The recapture of stained nematodes as far as 2 m from the original stained cores showed that, despite their small body size, they can disperse through relatively large distances, either passively or actively, via the water column during a single tidal event. Recapture patterns in the sediment and in the water column indicate that nematode dispersal is directly influenced by their body morphology and swimming ability, and indirectly by their feeding strategies, which ultimately define their position in the sediment column. Besides stressing the role played by passive transport in the water column, our experiment additionally showed that mobility and feeding strategies also need to be considered as determinant of short-scale nematode dispersal.

KEY WORDS. Dispersion behavior; intertidal flats; nematode; Paranaguá Bay.

Dispersal processes ultimately determine the present and potential distribution range of a species. Dispersal can also affect the rates of genetic changes and the processes of adaptation, speciation and evolution of organisms (Gibbs *et al.* 2010). Since free-living marine nematodes lack planktonic larvae and are considered poor swimmers, passive and/or "rafting" strategies are currently favored in the literature to explain juvenile and adult dispersal. The rapid dispersal of meiofauna has been ascribed primarily to water column processes, including passive erosion and active emergence, which exert a major influence on recruitment and colonisation in larger spatial scales (Chandler & Fleeger 1993, Commito & Tita 2002). Passive large-scale dispersal modes may include transportation through the water column, erosion/suspension, emersion/suspension and rafting on algal mats and floating debris (Boeckner *et al.* 2009, Derycke *et al.* 2008).

Although the literature on meiofaunal organisms is extensive, little is known about ranges and mechanisms actually involved in different dispersal modes at small spatial scales. The difficulty in studying such small organisms alive in field conditions explains why there are so few studies on the relationships between dispersal abilities and their morphological and behavioural features. As a result, predictions on the relationship between dispersal modes and the resulting distribution patterns remain problematic. Chandler & Fleeger (1993) first suggested that any behavioral features which increase the probability of nematodes to become suspended may account for their presence in the water column. More recently, active small-scale migration of nematodes was associated to their mobility and feeding strategies, mainly in the case of larger species, able to move actively through the sediment (Schratzberger *et al.* 2004, Gallucci *et al.* 2008). The organisms most commonly found in the water column dwell in the upper layers of sediment and so are more susceptible to passive suspension (Palmer & Gust 1985, Commito & Tita 2002). This is especially true in high-energy areas, in which meiofaunal taxa are resuspended by waves and tidal currents (Boeckner *et al.* 2009). The nematode species that are most susceptible to passive dispersal are probably the epigrowth feeders, such as *Ptycholaimellus ponticus* (Filipjev, 1922), which depend primarily on seaweed or bacteria found on the sediment surface (Commito & Tita 2002). Species from deeper sediment layers are rarely resuspended (Eskin & Palmer 1985). Jensen (1981) showed that the phytal, epistrate-feeding nematode, *Chromadorita tenuis* (G. Schneider, 1906), can rapidly swim (5 cm.s^{-1}) from the sediment to submerged vegetation. A writhing or serpentine swimming behavior insures that it remains in suspension long enough to be dispersed.

Though a number of passive dispersal modes have been proposed for larger spatial scales, the relative importance of nematode transport over the sediment or in the water column in the scale of centimeters or meters remains poorly understood. We tested herein the hypothesis that, besides passive erosion from the sediment, prevailing locomotion/feeding strategies and body morphology may lead to a more active dispersal of free-living marine nematodes. By using a vital stain and recapturing nematodes *in situ* in a subtropical unvegetated tidal flat at Paranaguá Bay (S Brazil), this study aims 1) to assess the relative importance of nematode dispersal in the water column and over the sediment during a single tidal event in small spatial scales; and 2) to determine whether small-scale dispersal depends on nematode behavior such as movement (swimmer vs. non-swimmer; active vs. lethargic) and body morphology.

MATERIAL AND METHODS

Study site

The study was carried out on an unvegetated tidal flat in the estuarine complex of Paranaguá Bay, in the state of Paraná, Brazil (25°ð32'48"S, 48°ð26'12"W, Fig. 1). Local tides are diurnal or semidiurnal during the peaks, and maximal tidal amplitude is about 2 m. Mean salinity is 12-29 in the summer and 20-34 in the winter.

Field experiment

The experiment was carried out in two replicate 3 x 3 m experimental areas that were 50 m apart. The surface of the study site was above tide line at low tide. A PVC corer, 30 cm in diameter and 30 cm in length, was inserted in the center of each area, in order to isolate the sediment to be stained. At low tide, 120 ml of 0.1% Neutral Red, a vital stain, were injected 1-2 cm into the sediment in the center of each corer. At this concentration, at least three hours were necessary to effectively stain the nematodes, as previously established in lab tests (Thomas & Lana 2008). To avoid experimental artifacts, no sampling was carried out inside the corers before or just after the experiment. Sediment properties, taxa composition, behavioral characteristics and dominant trophic groups were determined from four random samples, 2.5 cm in diameter and 3.0 cm in length, taken at each experimental area one week after the experiment. Previous field surveys had showed that taxa composition and overall nematode abundance are rather stable from day-to-day or week-to-week at the studied area.

Shortly before the arrival of the first tidal wave, corers were removed, so that water would flow freely over the stained portion of the sediment. The red stained plume that formed over the sediment was delineated and divided into zones as follows (Fig. 2): near zone (≤0.5 m from the original corer position); middle zone (0.5-1 m from the original corer position); and distant zone (1-2 m from the original corer position). Five sediment core samples, 2.5 cm in diameter and 3 cm in length, were taken from each of these zones just after the flood tide to check for stained animals. The samples were kept in water collected at the study site for subsequent lab analysis of nematode behavior. Four hand-made similar to phytoplankton nets, 30 cm in length and 10 cm in width, with a 42-¼m mesh, were used to capture the stained nematodes in the water column (Fig. 2). They were also installed before the arrival of the tidal wave and held in position by stakes in the sediment as follows: a low-near net, 5 cm above the sediment-water interface and a

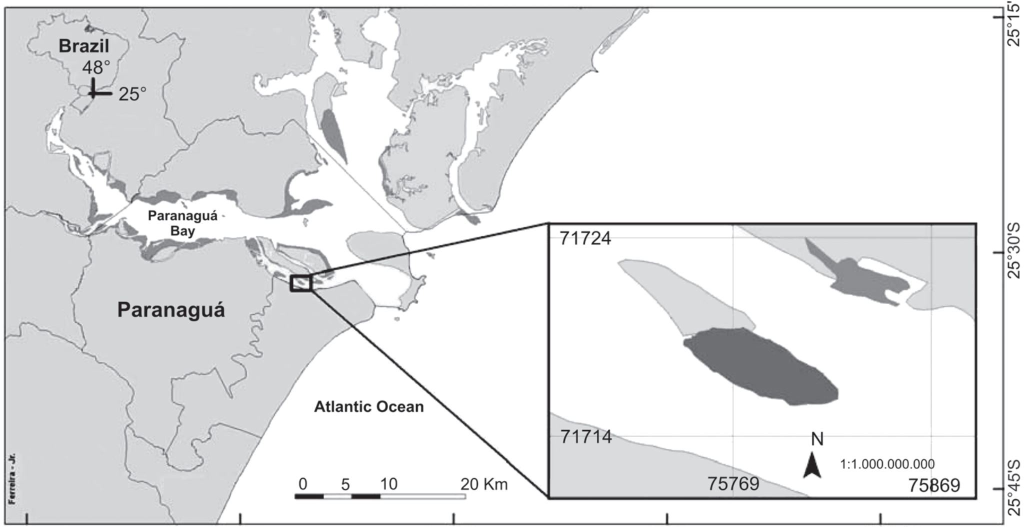

Figure 1. Paranaguá estuarine complex and sub-estuarine sector of Cotinga, where the study site the Papagaios tidal flat is located (dark gray area).

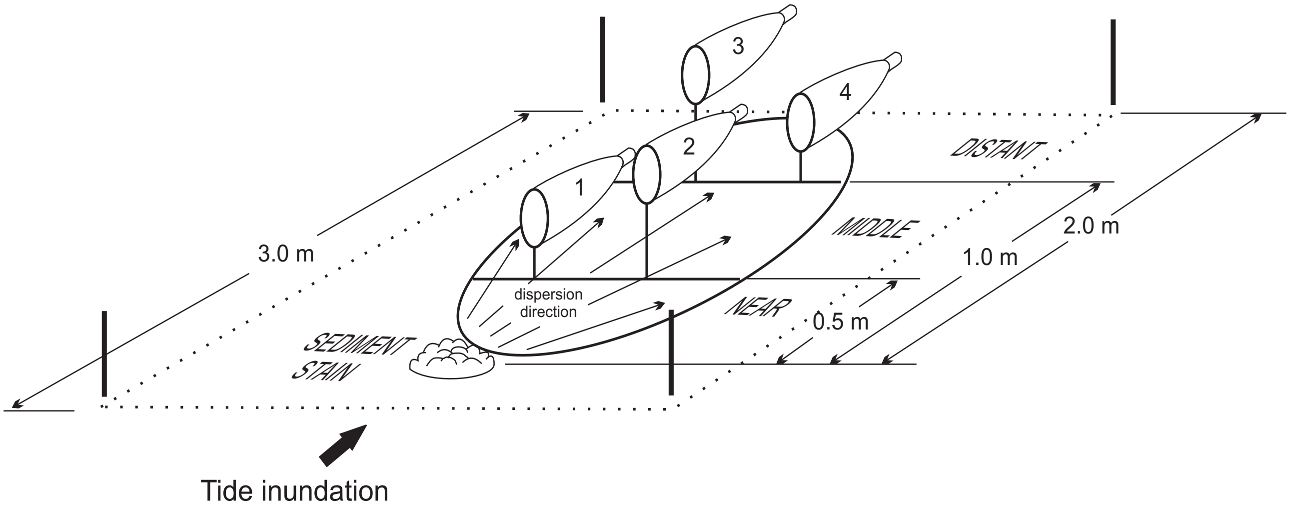

Figure 2. Schematic illustration of the dispersal experiment: (1) low-near net, (2) high-near net, (3) low-distant net, (4) high-distant net.

high-near net, 10 cm above the sediment-water interface, at 0.5 m from the stained point (between the near and middle zones) and at 1 m from the stained point (between the middle and distant zones). A collecting cup in the end of each net served as a floater, keeping them elevated in the water column and parallel to the bottom. After the tidal flat had been covered by a water column of approximately 0.5 m, the nets were sequentially removed (from distant to near zones) so as to guarantee they were exposed for similar times. After removal, nets were rinsed with local water to extract the captured organisms.

Tidal velocity and direction were measured using a flowmeter (model 2030R6, General Oceanics Inc., Miami, FL, USA) with a large helix in order to maximize flow measurement in low-energy areas. The flowmeter was mounted on a tripod, at 30 cm above the sediment. At 5-min intervals, the rotations of the helix were quantified using the flowmeter counter. The water column was measured using a topographic level rod, and the direction of the current was determined using a GPS. The data were entered into a spreadsheet, and the velocity was calculated as a function of the velocity in the graphs provided by the manufacturer.

Analysis of dispersal in the sediment and water column

The sediment and water column samples were screened under a stereoscopic microscope (SZH-ILLD; Olympus Optical Co., Japan) with an ocular grid. Nematodes were kept alive in filtered water from the experiment area, for observations of their movement in the sediment or swimming in the water column. Samples were kept at a constant temperature (22-23°ðC) and a photoperiod of approximately 12 hours. Recaptured stained nematodes were categorized as active/swimmer (active in the sediment and with swimming capacity), active/non swimmer (active in the sediment, without swimming capacity) and lethargic (without active movements in the sediment or in the water column).The stained nematodes were collected using a micropipette and set aside to be mounted on permanent slides. A modified technique from DeGrisse (1969) was used to clear the animals. The samples for biological characterization of the stained source association were processed according to the procedures proposed by Somerfield & Warwick (1996). Samples fixed in 10% formalin were rinsed in a 63-¼m mesh sieve. The contents on the sieve underwent three flotation extractions (40 min each) with colloidal silica (Ludox TM-50, diluted at a specific gravity of 1.15; Sigma-Aldrich, St. Louis, MO, USA). The supernatant was slowly evaporated in glycerol, and then mounted on permanent slides. Genus identification was performed under optical microscopy (BA300; Motic Instruments, Richmond, B.C., Canada), using the pictorial key devised by Platt & Warwick (1983, 1988) and modified by Warwick *et al.* (1998). Trophic groups were treated, as proposed by Moens & Vincx (1997), as microvores, ciliate-feeders, deposit-feeders, epigrowth-feeders, facultative predators or predators.

Data processing

Our experiment was not designed to estimate dispersal rates or assess the statistical significance of temporal or spatial variation in dispersion, considering the small size of the animals and the difficulty to recapture them in the sediment and in the water column. However, our data were sufficient and suitable to answer our working questions regarding the nature of nematode dispersal. We related the traveling distances by recaptured stained nematodes to the different categories (active/swimmer, active/non swimmer, and lethargic). We also related nematode dispersal abilities, as empirically shown by field work, to the morphology and to the life history traits of the involved species.

RESULTS

Sediment characteristics

Sediment of the first experimental area was composed of 83.3% of very fine sand and 12.6% clay, and the second of 90.8% of very fine sand and 6.5% clay. Levels of organic matter and calcium carbonate were slightly lower in the first experimental area than in the second (4.7% $CaCO_3$ and 2.7% OM vs. 7% $CaCO_3$ and 3.7% OM).

Both experimental areas were regularly and progressively covered by the flood tide, with water levels increasing by approximately 20 cm in one hour. Currents were from the west throughout the experiment, with a mean velocity of 9 cm/s.

Stained source association

A single taxon, *Terschellingia longicaudata* de Man, 1907, was formally identified to species level. All the remaining organisms were referred to twenty-two nematode genera. Six genera were numerically dominant and present in all the samples (Tab. I). The dominant taxon was *Comesa* sp., which accounted for 19% of the total nematode fauna, followed by *T. longicaudata*, which accounted for 16%. *Microlaimus* sp., *Metachromadora* sp., *Sabatieria* sp. and *Viscosia* sp. were co-dominants, accounting together for 30% of the observed animals (Tab. I).

In the first experimental area, *T. longicaudata* was the most abundant species with mean densities of 323.3 individuals per 10 cm^2, followed by *Comesa* sp. with 316, *Microlaimus* sp. with 209.3, *Metachromadora* sp. with 196.6, *Viscosia* sp. with 174 and *Sabatieria* sp. with 156.6 individuals per 10 cm^2. In the second experimental area, *Comesa* sp. was the most abundant genus with mean densities of 294 individuals per 10 cm^2, followed by *T. longicaudata* with 170.6, *Sabatieria* sp. with 72.6, *Metachromadora* sp. with 66.6 and *Microlaimus* sp. with 54 individuals per 10 cm^2 (Tab. I).

The most abundant trophic groups were epigrowth-feeders (accounting for 48% of the organisms), followed by microvores (16%), deposit-feeders (14%), facultative-predators and ciliate-feeders (11%) of the local nematode community and predators accounted for only 0.3% of the organisms.

Captured nematodes

The technique used for capturing the stained individuals showed an expected reduction of stained nematode num-

Table I. Families, genera and trophic groups (Moens & Vincx 1997) of nematodes found in the two experimental areas, expressed as mean densities per 10 cm^2 and standard deviations.

Family	Genus or species	Trophic group	Area I		Area II	
			Mean	SD	Mean	SD
Anoplostomatidae	*Anoplostoma*	Ciliate-feeders	4.0	2.6	8.6	2.3
Axonolaimidae	*Axonolaimus*	Ciliate-feeders	62.0	2.0	23.3	6.5
	Parodontophora	Deposit-feeders	4.6	1.6	0	0
	Bathylaimus	Ciliate-feeders	4.0	1.7	0.6	0.6
Chromadoridae	*Prochromadora*	Epigrowth-feeders	10.0	7.8	2.6	2.3
	Chromadorita	Epigrowth-feeders	38.0	12.5	19.3	6.6
Chromadoroidea	*Dichromadora*	Epigrowth-feeders	99.3	18.6	48.6	6.6
Comesomatidae	*Sabatieria* sp.	Deposit-feeders	156.6	48.0	72.6	10.0
Cyatholaimidae	*Cyatholaimus*	Epigrowth-feeders	7.3	2.3	6.6	2.1
Desmodoridae	*Chromaspirina*	Facultative-predators	16.6	2.9	16.6	3.1
	Desmodora	Epigrowth-feeders	88.0	20.6	31.3	1.5
	Metachromadora sp.	Epigrowth-feeders	196.6	27.7	66.6	4.5
Ethmolaimidae	*Comesa*	Epigrowth-feeders	316.0	46.5	294.0	33.0
Linhomoeidae	*Terschellingia longicaudata*	Microvores	323.3	28.9	170.6	8.1
	Terschellingia sp.	Microvores	8.6	6.6	3.3	2.9
Microlaimidae	*Microlaimus*	Epigrowth-feeders	209.3	5.8	54.0	4.6
Neotonchidae	*Gomphionema*	Facultative-predators	32.6	8.1	24.6	0.5
Oncholaimidae	*Oncholaimus*	Facultative-predators	9.3	4.5	5.3	3.1
	Viscosia sp.	Facultative-predators	174.0	56.3	43.3	5.1
Oxystominidae	*Halalaimus*	Microvores	0	0	0.6	0.6
Selachinematidae	*Halichoanolaimus*	Predators	7.3	3.5	2.6	1.2
Xyalidae	*Daptonema*	Deposit-feeders	115.3	23.2	49.3	4.1
	Theristus	Deposit-feeders	31.3	9.1	26.0	3.7

bers in the sediment as a function of the distance from the stained corer. Eighteen individuals were captured in the near zone sediment, whereas only seven were captured in the distant zone sediment (Tab. II). In the water column, eight stained nematodes were captured in the near net and 12 in the distant net, (Tab. III).

Table II. Number of stained nematodes captured in the sediment of the three zones (near = 0-0.5 m, middle = 0.5-1.0 m and distant = 1.0-2.0 m) after a flood tide.

Species	Near	Middle	Distant
Viscosia sp.	2	0	1
Metachromadora sp.	6	4	1
Terschellingia longicaudata	8	5	4
Sabatieria sp.	2	1	1
Total	18	10	7

Table III. Number of stained nematodes found in the nets placed in the water column after a flood tide.

Species	Net			
	Low		High	
	Near	Distant	Near	Distant
Viscosia sp.	2	1	1	2
Metachromadora sp.	3	2	0	1
Terschellingia longicaudata	2	2	0	4
Total	7	5	1	7

The identity of recaptured stained nematode taxa in the water column and sediment clearly differed from that observed for the stained source association. Stained organisms of only four of the twenty-two identified genera were found in the sediment. However, these four genera included *T. longicaudata*, *Metachromadora* sp., *Sabatieria* sp. and *Viscosia* sp., all of which were highly abundant in the stained source association. Stained organisms of three of these taxa (*T. longicaudata*, *Metachromadora* sp. and *Viscosia* sp.) were also recaptured in the nets.

The microvore *T. longicaudata* presented the most evident dispersal behaviour, with four stained individuals recaptured in the distant zone, five in the middle zone, and eight in the near zone (Tab. II). In the water column, four stained individuals were recaptured in the high-distant net, two in the low-near and two in the low-distant net. Under lab conditions *T. longicaudata* presents a very active behavior, characterized by wave-like motions of the body and tail, both in the sediment and in the water column (Tab. IV).

Only one individual of the epigrowth-feeder *Metachromadora* sp. was recaptured in the distant sediment zone, four in the middle zone and six in the near zone (Tab. II). Three individuals were recaptured in the low-near and two in the low-distant nets (Tab. III). When we simulated resuspension of sediment particles under lab conditions, *Metachromadora* sp. did not remain active in the water column and rapidly settled on the bottom (Tab. IV).

Numbers of captured individuals of the facultative-predator *Viscosia* sp. and the deposit-feeder *Sabatieria* sp., were low in all sediment zones, only one of each in the distant and two in the near zone (Tab. II). However, the presence in the distant and high nets showed that *Viscosia* sp. can disperse over distances > 1 m through water column. Alive *Viscosia* sp. specimens can move fast in the sediment and alternate active swimming with inactive periods, when they curl and float at the water surface (Tab. IV). Contrary, under lab conditions, alive *Sabatieria* sp. specimens move fast in the sediment, but no active movements were observed in the water column (Tab. IV).

DISCUSSION

The capture of stained nematodes as far as 2 m from the original stained cores showed that, despite their small body size, they can disperse through relatively large distances via the water column during a single tidal event. Such distances would not be reached by horizontal migration in the sediment. COMMITO & TITA (2002) reported similar patterns in an unvegetated intertidal flat, with dispersal ranging from 0.75 m to 2 m after a flood tide.

Our experimental design was not aimed at distinguishing passive dispersal (by resuspension) from active dispersal (by active displacement from the sediment to the water column). However, local hydrodynamics and dispersal trends, together with the fact that most of the animals found in the water column also belonged to the most abundant genera in the stained source association, suggest that passive resuspension is

Table IV. Movement categories and their relationship with body morphology and behavior observed in the stained nematodes captured.

Movement categories	Body morphology	Behavior observed	Species
Active/Swimmer	Slim body, long tail	Active in the sediment and with swimming capacity	*Viscosia* sp. *T. longicaudata*
Active/Non swimmer	Slim body, long tail	Active in the sediment, without swimming capacity	*Sabatieria* sp.
Lethargic	Robust, truncated body, tail short and conical	Without active movements in the sediment or in the water column	*Metachromadora* sp.

indeed the main transport vector. Stained individuals of four among the six most abundant stained source taxa (*T. longicaudata*, *Metachromadora* sp., *Sabatieria* sp., and *Viscosia* sp.) were recaptured in the sediment, and three of them (*T. longicaudata*, *Metachromadora* sp., and *Viscosia* sp.) were recaptured in the water column. This may be attributed to the tidal current of 9 cm/s, able to resuspend and transport the most abundant genera which dwell in the uppermost sediment layers in muddy areas (Commito & Tita 2002).

Although nematodes are considered poor swimmers (Palmer 1984, Fegley 1985), they are commonly found in plankton samples (Boeckner *et al.* 2009) and at the sediment-water interface. However, their abundance in the water column is always much lower than in the sediment (Palmer 1984). The low numbers of nematodes recorded in our experiment can be explained by the difficulty in recapturing such small organisms and by the fact that the experiment addressed a single tidal cycle. Despite the low recorded densities, the observed patterns strongly indicate that the step by step distances reached by nematodes after a series of tidal events can explain their known large-scale dispersal.

The differential capture of stained organisms in nets placed at different heights indicates that most individuals only reached greater heights in the water column when distant from the stained source point, either by active swimming (*T. longicaudata*), passive transport (*Metachromadora* sp.*)* or a combination of both (*Viscosia* sp.). Many nematodes are able to counteract the force of gravity (Ullberg & Ólafsson 2003b) by means of dorsoventral contractions, with the aid of longitudinal muscles and wave-like motions (Jensen 1981, Palmer 1988). They can actively change their vertical position in the water column after resuspension by controlling, even if only partially, horizontal displacement and transport velocity during dispersal. For example, *T. longicaudata*, which presents a small, thin and uniform body, also showed the ability to remain in the water column and reach distances of >1 m by active swimming, aided by tail motions.

Besides stressing the importance of passive transport, our experiment showed that mobility and feeding strategies also influence nematode dispersal. The reduced number of replicate models, especially in the nets placed in the water column, made it impossible for us to perform more rigorous statistical analyzes. However, patterns of recapture in the sediment and in the water column strongly indicate that nematode dispersal after a flood tide is directly influenced by body morphology and swimming ability, and indirectly by feeding strategies, which ultimately define their position in the sediment column. Species that live in the superficial sediment layers are normally exposed to bioturbation, such as that caused by macrofauna, or wave and tidal effects. It is likely that they will exhibit more active patterns of horizontal or vertical movement than do species that live in deeper sediment layers.

Microvores, represented solely by the very active *T. longicaudata*, were recaptured in all three dispersal zones and presented the highest dispersal rates. *Terschellingia longicaudata* is dominant in sandy and muddy areas, where the main food source is dissolved organic matter (Moens & Vincx 1997). This species, which presents a small, thin and uniform body, was able to remain in the water column and reach distances of >1 m by active swimming, aided by tail motions. This agrees with the model developed by Crofton (1966), which correlates the body size of nematode parasites (free-swimming phase) with their swimming ability, and predicts that only small individuals can freely swim with undulating motions, since water viscosity can hinder the movements of larger organisms.

Viscosia sp. also live in the uppermost sediment layers under normal environmental conditions (Heip 1985). However, species of this genus can migrate to deeper sediment layers in the presence of bioturbation (Pinto *et al.* 2006). They show even greater agility in remaining in the water column and reaching, possibly by means of active body movements, distances >1 m during a tidal cycle. Fonseca-Genevois *et al.* (2006) reported that the colonization of an aluminum plate by *Viscosia* probably occurred due to the combination of passive dispersal (resuspension) and active swimming for short distances. The limited swimming ability of *Viscosia* sp. individuals, resulting from their body size, might have been overcome by the high frequency of wave-like motions of their bodies, as well as their floating ability, observed under lab conditions. Therefore, the morphological and behavioral characteristics exhibited by these individuals suggest that they are very active when dispersing via the water column by water currents.

Stained individuals of the deposit-feeder *Sabatieria* sp., which live in the deepest layers of sediment (Schatzberger *et al.* 2000), were recaptured in the distant zone but not in the nets placed in the water column. They did not display swimming movements in the water column. According to Schatzberger *et al.* (2000), *Sabatieria* sp. individuals are not very agile, which rules out the possibility that they will disperse actively via the sediment, at least on the scale considered (⩾1 m), during a single tidal cycle. Most probably individuals were passively transported by the water flow just above the water-sediment interface.

Genera that dwell in the upper sediment layers, such as the epigrowth-feeders *Ptycholaimellus* Cobb, 1920, *Metachromadora* Filipjev, 1918 and *Chromadora* Bastian, 1865, are commonly captured in the water column or resuspended sediment (Commito & Tita 2002). As such, they are more liable to erosion and transport than are those that dwell in deeper sediment layers (Eskin & Palmer 1985). Bell & Sherman (1980) showed that *Metachromadora* specimens were the most abundant in the water column approximately 500 m from the original point and were able to recolonize a defaunated area after a single tidal cycle. In our case, stained individuals of *Metachromadora* sp., which have a non linear body with a short and conical tail, were recaptured >1 m from the stained point. This could not be explained by their body morphology or by their ability to swim or remain in the water column. It seems that these individuals were simply resuspended because of their presence on the upper sediment layers and transported via tidal action, without showing any active swimming behavior. Other studies also suggest that the superficial or subsuperficial distribution of *Metachromadora* species, together with their body morphology and lethargic behavior, increase their susceptibility to passive resuspension (BELL & SHERMAN 1980, ESKIN & PALMER 1985). Conversely, stained individuals of the epigrowth-feeders *Comesa* sp. and *Microlaimus* sp., which are among the most abundant taxa in the stained source association, were not recaptured in the sediment or the water column. The ability for active vertical migration in the sediment and avoidance of tidal effects (RIEGER & OTT 1971) could explain such unexpected patterns at least in the case of *Microlaimus* sp.

Although local hydrodynamics certainly plays a major role in promoting large-scale dispersal of nematodes, species-specific feeding and mobility behaviors may modulate their absolute and relative recolonization rates in the scale of centimeters or meters. Once resuspended in the water column, nematodes may swim actively or be passively transported depending on their body morphology or behavior. As such, alternate models for nematode dispersal at small spatial scales still need to be developed, taking into account body morphology, swimming ability and feeding strategies, which may be equally or more important for ultimate dispersal than their liability to become suspended as a function of their relative position in the sediment column.

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