

SUSPENSION OF MARINE NEMATODES IN A TURBULENT TIDAL CREEK: SPECIES PATTERNS*

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ABSTRACT

Nematodes had a mean abundance of hundreds per m³ in an estuarine creek. They were four orders of magnitude less abundant in the water column than in the sediment. The water column nematode assemblage was dominated by three species of *Metachromadora* which comprised 57% of the suspended nematodes. Other abundant species were *Chromadorita* aff. *minima* and *Ptycholaimellus pandispiculatus*. Numbers of suspended nematodes were highest during the ebb and flood tides when currents were fastest. The two factors that appear to be most important in determining which species are in the water are the vertical distribution and the overall abundance of a species in the sediment. Surficial distributions and high sediment abundance will result in greater representation in the water column. Suspension in the water column and subsequent transport by tidal currents potentially plays a significant role in the local dispersal of certain meiobenthic nematode species. Corollaries to water column dispersal are an improved ability of nematodes in colonizing new habitats, an increased diversity in some habitats as animals are carried between habitats, and an interaction between hydrodynamic factors and benthic topography that affects small-scale spatial distribution.

INTRODUCTION

Until recently, the occurrence of marine free-living nematodes in the water column had not been systematically investigated and data on suspended nematodes were sparse, serendipitous, and anecdotal (Gerlach, 1977). Several recent quantitative studies have demonstrated the consistent occurrence of nematodes in the water column. Nematodes are numerous in sediments but occur in comparatively low abundance in the water column (*e.g.*, Bell and Sherman, 1980; Sibert, 1981; Jacobs, 1984 and references therein; Palmer and Gust, 1985); however, the consistent occurrence of even relatively low numbers in the water column has significant implications for our concepts of nematode dispersal, colonization, diversity, and spatial patchiness.

Palmer and Gust (1985) showed that the water column dispersal of nematodes from tidal mudflats was primarily the result of their passive erosion and suspension. For a few species, active swimming may play a role (Gerlach, 1977; Jensen, 1981) but as hypothesized by Warwick and Gee (1984) for *Ptycholaimellus ponticus*, nematodes with a shallow distribution in the sediment may be transported in the water following erosion. In the Palmer and Gust study, nematodes were the numerically dominant meiofaunal taxon in the sediment (~62%) and in the water (~30%). Over a complete tidal cycle 5% of the total sediment nematodes may be suspended; however, at any

Received 8 May 1985; accepted 23 September 1985.

* Contribution No. 607 from the Belle W. Baruch Institute for Marine Biology and Coastal Research.

one instant in time less than 1% are in suspension (Palmer and Gust, 1985). The percent of sediment fauna suspended was significantly lower for nematodes than for the copepods, foraminiferans, or bivalves (Palmer and Gust, 1985). Nematodes typically have the highest sediment abundance so even a small percentage suspended, results in a large number of nematodes in the water. Palmer and Gust suggested that the low percentage suspended was the result of nematodes behaviorally avoiding the sediment surface and thereby reducing their susceptibility to suspension. In a study of meiofauna behavior, Palmer (1984) found that nematodes rarely emerged from the sediment. When nematodes were artificially suspended (*sensu* Palmer, 1984), 64% were transported downstream at low current velocities (6–8 cm/s) thus, once in suspension, only 36% of the suspended nematodes were able to re-enter the sediment or maintain their position on the sediment surface.

Studies of the vertical distribution of nematodes in marine sediments have demonstrated predictable patterns for certain taxa. Some genera will typically have representatives deep in the sediment while others are only found near the surface (*e.g.*, Fenchel *et al.*, 1967; Boaden and Platt, 1971; Joint *et al.*, 1982; and references in Table I). A simple model of passive suspension predicts that those nematodes abundant in the upper layers of sediment should be the most abundant ones in the water column in proportion to their sediment abundance. Behavioral adaptations however, may certainly reduce passive suspension. For copepods, flow-related behaviors vary among species (Palmer, 1984) and transport in the water column also varies among species (Hagerman and Rieger, 1981; Palmer and Gust, 1985). In the latter study, there was a much higher copepod species diversity in the water than in the sediment with at least 50% of the suspended copepods belonging to species whose centers of distribution were considerable distances away from the study site. Thus, over half of the total copepods in the water were advected from other marsh areas and not locally eroded. Such findings are contingent on careful identification of fauna to species level. Here we report on nematode species patterns from the study of Palmer and Gust (1985).

TABLE I

Relative vertical distribution of species or congeners listed in this study.

| Depth in sediment (cm) Species | 0-1 | 1-2 | >2 | Reference |
|---|------------|-----|----|-----------------------|
| | % at depth | | | |
| <i>Metachromadora obesa</i> ¹ | 95 | 3 | 2 | Ott, 1972 |
| <i>M. vivipara</i> | 80-100 | — | — | Platt, 1977 |
| <i>M. vivipara</i> ² | ~90 | 10 | — | Warwick and Gee, 1984 |
| <i>M. sueica</i> | 93 | 5 | 2 | Platt, 1977 |
| <i>Ptycholaimellus pandispiculatus</i> ¹ | 70 | 20 | 10 | Ott, 1972 |
| <i>P. ponticus</i> ² | 93 | 7 | — | Warwick and Gee, 1984 |
| <i>Anoplostoma viviparum</i> | 80-100 | — | — | Platt, 1977 |
| <i>Terschellingia longicaudata</i> ³ | 40 | 40 | 20 | Ott, 1972 |
| <i>T. longicaudata</i> ² | 41 | 49 | — | Warwick and Gee, 1984 |
| <i>Sabatieria pulchra</i> ² | 32 | 68 | — | Warwick and Gee, 1984 |
| <i>S. cupida</i> | 20-80 | — | — | Platt, 1977 |
| <i>Odontophora setosa</i> | 20-80 | — | — | Platt, 1977 |

¹ Estimated from Figure 6.

² Estimated from Figure 8.

³ Estimated from Figure 7.

Specifically, our goals were to answer the following questions:

- (1) Does the percentage of a nematode species in suspension vary significantly from its proportional representation in the sediment? If so, can this be related to our knowledge of species-specific behaviors or vertical distribution patterns?
- (2) Does the species composition of the suspended nematodes differ from the composition of the mudflat fauna? If so, what fraction of the suspended nematodes are advected?
- (3) Are there differences in the suspension of juveniles *versus* adults or males *versus* females?

MATERIALS AND METHODS

The sample site was an unvegetated mudflat in the North Inlet Estuary, near Georgetown, South Carolina (33°20'N, 79°10'W). Samples were collected during a neap tide in June, 1981, and during the following spring tide. Meiofaunal abundances in the sediment and in the water column were measured simultaneously at 23 times over two, 48-hour periods. Details of the sampling scheme are described in Palmer and Gust (1985). Briefly, replicate water samples were collected at 17, 37, and 57 cm above the bottom using slow-velocity pumps. The number of animals reported here is the product of the proportion of each species in the aliquot of identified individuals and the total number of nematodes counted in that sample. All faunal abundances are corrected for changes in volume of water over the mudflat as described in Palmer and Gust (1985). The final figures reported are the number of animals per cubic meter of water. Samples for spring and neap tides were combined (104 water samples, 23 sediment samples) since Palmer and Gust (1985) found no spring/neap differences for total nematodes. Calculations of total nematode abundance in the water are considered conservative since sediment-water interface data were not included (Palmer and Gust, 1985). Concurrently with pump samples, sediment samples were taken with a 2.5 cm diameter corer to a depth of 1.5 cm (7.36 cm³ of sediment) and adjusted to number per m³. This depth is well below the redox potential discontinuity zone (which was <1 cm in June) and would include most of the nematodes present (Coull and Bell, 1979).

Nematodes were fixed at the time of collection in borax buffered formalin and stained with Rose Bengal. Every second animal was removed from the sample, dehydrated, and mounted in anhydrous glycerine (Seinhorst, 1959) for identification to species and sex or life stage (male, female, juvenile). Palmer and Gust (1985) give a full presentation of the results for all major taxa and the hydrodynamic results of interest in testing the hypothesis of active water-column entry *versus* passive erosion.

RESULTS

Nematodes were approximately four orders of magnitude less abundant in the water column than in the sediment. The three most abundant nematodes in the water column were all species of the genus *Metachromadora* (Desmodoridae). *Metachromadora* (*Metachromadora*) *chandleri* (Chitwood, 1951) and *Metachromadora* (*Neonyx*) *obesa* Chitwood, 1936 were co-dominant in the water column, but only ranked thirty-third and thirty-fifth in abundance among the sediment fauna (Table II). *Metachromadora* (*Metachromadoroides*) *remanei* Gerlach, 1951, was third in abundance in the water but ranked seventh in the sediment. Five and one half percent of the sediment abundance of *M. chandleri* and *M. obesa* were in suspension. Although *M. remanei*,

TABLE II

Composition and abundance of suspended and sediment nematode assemblages

| Taxon | Water column | | | Sediment | | | | |
|---|--------------|------|------|----------|---------|------|------|------|
| | Mean | SE | Dom | Mean | SE | Dom | Rank | % |
| <i>Metachromadora chandleri</i> | 136 | (17) | 24.3 | 2303 | (2303) | 0.2 | 35 | 5.9 |
| <i>Metachromadora obesa</i> | 122 | (16) | 24.6 | 2366 | (2367) | 0.2 | 33 | 5.2 |
| <i>Metachromadora remanei</i> | 42 | (8) | 8.1 | 31215 | (7706) | 4.1 | 7 | 0.1 |
| <i>Chromadorita aff. minima</i> | 42 | (9) | 9.6 | 373 | (373) | 0.2 | 45 | 11.3 |
| <i>Ptycholaimellus</i> | | | | | | | | |
| <i>pandispiculatus</i> | 29 | (5) | 5.7 | 339600 | (46877) | 34.3 | 1 | <0.1 |
| <i>Viscosia papillata</i> | 8 | (3) | 1.3 | 51281 | (11417) | 6.8 | 6 | <0.1 |
| <i>Daptonema erectum</i> | 7 | (3) | 1.9 | 2138 | (1479) | 0.9 | 36 | 0.3 |
| <i>Daptonema</i> sp. 1 | 7 | (2) | 1.6 | 0 | (0) | 0 | — | — |
| <i>Daptonema</i> spp. | 6 | (4) | 0.7 | 11564 | (4474) | 1.2 | 12 | 0.1 |
| <i>Desmodora cepalata</i> | 6 | (2) | 1.2 | 3616 | (2251) | 0.5 | 25 | 0.2 |
| <i>Microlaimus</i> spp. | 5 | (2) | 1.5 | 993 | (993) | 0.1 | 43 | 0.5 |
| Chromadoridae spp. | 5 | (2) | 1.1 | 1019 | (1019) | 0.1 | 40 | 0.5 |
| <i>Spilophorella paradoxa</i> | 4 | (2) | 1.5 | 928 | (928) | 0.1 | 44 | 0.5 |
| <i>Terschellingia</i> | | | | | | | | |
| <i>longicaudata</i> | 4 | (2) | 0.8 | 62728 | (18757) | 6.7 | 5 | 0.4 |
| <i>Sphaerolaimus</i> sp. 1 | 3 | (1) | 1.0 | 8760 | (3554) | 1.1 | 15 | <0.1 |
| Oncholaimidae sp. 1 | 3 | (1) | 0.7 | 0 | (0) | 0 | — | — |
| <i>Anoplostoma</i> cf. <i>viviparum</i> | 3 | (2) | 0.4 | 13573 | (6844) | 1.0 | 9 | <0.1 |
| Linhomoeidae spp. | 3 | (1) | 0.5 | 1019 | (1019) | 0.1 | 41 | 0.3 |
| <i>Sabatieria</i> spp. | 3 | (1) | 1.9 | 7706 | (4647) | 0.7 | 17 | <0.1 |
| Leptolaimidae sp. 1 | 2 | (1) | 0.5 | 4856 | (3453) | 0.3 | 20 | <0.1 |
| Desmodoridae spp. | 2 | (1) | 0.3 | 0 | (0) | 0 | — | — |
| <i>Oncholaimoides striatus</i> | 2 | (2) | 0.6 | 0 | (0) | 0 | — | — |
| <i>Theristus</i> spp. | 2 | (1) | 0.5 | 7290 | (6011) | 0.7 | 18 | <0.1 |
| <i>Graphonema</i> sp. | 2 | (1) | 0.6 | 0 | (0) | 0 | — | — |
| <i>Sabatieria pulchra</i> | 2 | (1) | 0.4 | 97533 | (19218) | 11.9 | 2 | 0.1 |
| <i>Metachromadora</i> spp. | 2 | (1) | 0.6 | 0 | (0) | 0 | — | — |
| <i>Spirinia</i> spp. | 2 | (1) | 1.0 | 1098 | (1098) | 0.1 | 38 | 0.2 |
| <i>Dorylaimopsis metatypica</i> | 2 | (1) | 0.3 | 3764 | (2605) | 0.3 | 24 | 0.1 |
| <i>Eurystomina</i> sp. | 2 | (1) | 0.3 | 0 | (0) | 0 | — | — |
| <i>Antomicron</i> sp. | 1 | (1) | 0.2 | 0 | (0) | 0 | — | — |
| <i>Halalaimus</i> spp. | 1 | (1) | 0.2 | 12410 | (5696) | 0.8 | 10 | <0.1 |
| Cyatholaimidae spp. | 1 | (1) | 0.7 | 3837 | (2904) | 0.3 | 23 | <0.1 |
| Leptolaimidae spp. | 1 | (1) | 0.3 | 2854 | (2070) | 0.2 | 28 | <0.1 |
| <i>Viscosia brachylaimoides</i> | 1 | (1) | 0.2 | 1776 | (1776) | 0.1 | 37 | <0.1 |
| <i>Daptonema</i> sp. 2 | 1 | (1) | 0.2 | 75577 | (13133) | 8.6 | 4 | <0.1 |
| Others | 1 | (1) | 0.4 | 1076 | (1076) | 0.2 | 39 | 0.1 |
| Monhysteridae spp. | 1 | (1) | 0.1 | 2839 | (2063) | 0.3 | 29 | <0.1 |
| <i>Sigmophoranema</i> sp. | 1 | (1) | 0.8 | 0 | (0) | 0 | — | — |
| <i>Marylynia</i> sp. | 1 | (1) | 0.1 | 0 | (0) | 0 | — | — |
| <i>Axonolaimus spinosus</i> | 1 | (1) | 0.3 | 0 | (0) | 0 | — | — |
| <i>Odontophora</i> sp. 1 | 1 | (1) | 0.3 | 0 | (0) | 0 | — | — |
| <i>Tripylloides</i> sp. | 1 | (1) | 0.4 | 10192 | (3215) | 1.3 | 13 | <0.1 |
| Comesomatidae spp. | 1 | (1) | 0.2 | 0 | (0) | 0 | — | — |
| <i>Sabatieria americana</i> | 1 | (1) | <0.1 | 373 | (373) | 0.2 | 46 | 0.3 |
| <i>Theristus</i> sp. 1 | 1 | (<1) | 0.3 | 0 | (0) | 0 | — | — |
| <i>Odontophora</i> sp. 2 | 1 | (<1) | 0.3 | 81246 | (20178) | 7.7 | 3 | <0.1 |
| <i>Parasphaerolaimus</i> sp. | 1 | (1) | 0.1 | 8488 | (3634) | 0.8 | 16 | <0.1 |
| <i>Adoncholaimus</i> cf. | | | | | | | | |
| <i>thalassophygas</i> | 3 | (1) | 1 | 22735 | (8065) | 2.6 | 8 | 0.1 |
| <i>Enoploilaimus</i> sp. 1 | 1 | (1) | 0.1 | 0 | (0) | 0 | — | — |
| <i>Terschellingia</i> sp. 2 | 1 | (1) | <0.1 | 2874 | (2045) | 0.2 | 27 | <0.1 |
| <i>Metachromadora setosus</i> | <1 | (<1) | 0.2 | 0 | (0) | 0 | — | — |

TABLE II (Continued)

| Taxon | Water column | | | Sediment | | | | % |
|---|--------------|------|------|----------|--------|-----|------|------|
| | Mean | SE | Dom | Mean | SE | Dom | Rank | |
| <i>Oxystomina</i> spp. | <1 | (<1) | 0.5 | 4815 | (4815) | 0.3 | 21 | <0.1 |
| <i>Dracograllus</i> sp. | <1 | (<1) | <0.1 | 0 | (0) | 0 | — | — |
| Oncholaimidae spp. | <1 | (<1) | 0.1 | 0 | (0) | 0 | — | — |
| <i>Xyala</i> sp. | <1 | (<1) | 0.1 | 0 | (0) | 0 | — | — |
| Chromadoridae sp. 1 | <1 | (<1) | <0.1 | 2366 | (2367) | 0.2 | 32 | <0.1 |
| <i>Oncholaimus</i> sp. | <1 | (<1) | 0.1 | 0 | (0) | 0 | — | — |
| <i>Nygmatonchus</i> sp. 1 | <1 | (<1) | 0.1 | 0 | (0) | 0 | — | — |
| Enoplolaimidae spp. | <1 | (<1) | 0.1 | 0 | (0) | 0 | — | — |
| Desmodoridae sp. 1 | <1 | (<1) | 0.1 | 0 | (0) | 0 | — | — |
| Cyatholaimidae sp. 2 | <1 | (<1) | <0.1 | 0 | (0) | 0 | — | — |
| <i>Rhynchonema</i> sp. | <1 | (<1) | <0.1 | 0 | (0) | 0 | — | — |
| <i>Cobbia</i> sp. | <1 | (<1) | 0.1 | 0 | (0) | 0 | — | — |
| <i>Calyptronema</i> cf. <i>maxweberi</i> | 0 | (0) | 0 | 3413 | (1705) | 0.9 | 26 | — |
| Ironidae sp. | 0 | (0) | 0 | 3913 | (2280) | 0.5 | 22 | — |
| <i>Laimella filipjevi</i> | 0 | (0) | 0 | 9313 | (4249) | 1.0 | 14 | — |
| <i>Laimella</i> sp. | 0 | (0) | 0 | 993 | (993) | 0.1 | 42 | — |
| <i>Sabatieria celtica</i> | 0 | (0) | 0 | 2718 | (2085) | 0.4 | 30 | — |
| <i>Sphaerolaimus</i> sp. 2 | 0 | (0) | 0 | 2367 | (2367) | 0.1 | 34 | — |
| <i>Terschellingia</i> sp. 1 | 0 | (0) | 0 | 11961 | (9335) | 0.9 | 11 | — |
| <i>Theristus</i> 17s | 0 | (0) | 0 | 5007 | (2933) | 0.4 | 19 | — |

The mean number of animals, the standard error of the mean (SE), and dominance (mean percent species representation in each sample) are shown. Percent is the percent of sediment nematodes in the water column. For the water column, species are listed in descending order of mean number of animals per m³. For sediment species, ranks are according to a species' abundance per m³. Authorities for species are listed in Gerlach and Riemann, 1973, 1974.

was less dominant in the water than the other two *Metachromadora* species, only 0.1% of *M. remanei*'s sediment abundance was suspended as compared to ~5% for *M. chandleri* and *M. obesa*.

Juveniles represented the largest proportion of the *Metachromadora* species in the water column (76–92%) (Table III). Local sediment abundance of *M. chandleri* and

TABLE III

Mean sample percentages of females (F), males (M), and juveniles (J) for those species abundant (>1%) in the water column

| Species | F | M | J | n |
|--|------|------|------|------|
| <i>Metachromadora chandleri</i> | 9.5 | 14.0 | 76.3 | (75) |
| <i>Metachromadora obesa</i> | 3.3 | 4.6 | 92.1 | (79) |
| <i>Metachromadora remanei</i> | 8.3 | 11.2 | 80.4 | (49) |
| <i>Chromadorita</i> aff. <i>minima</i> | 39.2 | 53.2 | 7.6 | (48) |
| <i>Ptycholaimellus pandispiculatus</i> | 39.4 | 22.8 | 37.8 | (41) |
| <i>Viscosia papillata</i> | 41.7 | 16.7 | 41.7 | (12) |
| <i>Daptonema erectum</i> | 72.7 | 27.3 | 0 | (11) |
| <i>Daptonema</i> sp. 1 | 15.4 | 57.7 | 26.9 | (13) |
| <i>Desmodora cephalata</i> | 33.3 | 11.1 | 55.6 | (9) |
| <i>Spilophorella paradoxa</i> | 40.0 | 50.0 | 10 | (10) |

n = number of samples in which the species abundance was not equal to zero.

M. obesa were too low to determine sex ratios or adult:juvenile ratios, but for *M. remanei*, 69% of the animals in the sediment were juveniles in comparison to 80% in the water.

A high proportion (11.3%) of the sediment abundance of *Chromadorita* aff. *minima* (Kreis, 1929) was suspended (Table II). In contrast to the *Metachromadora* species, most suspended *C. minima* were adults (39% females, 53% males, and 8% juveniles) (Table III). Most *C. aff. minima* were suspended on the ebb tide, and fewest at slack tide (Table IV).

The most abundant sediment dweller, *Ptycholaimellus pandispiculatus* (Hopper, 1961) only made up 6% of the nematodes in suspension (Table II).

Five species [*Viscosia papillata* Chitwood, 1951; *Daptonema erectum* (Wieser and Hopper, 1967); *Daptonema* sp. 1; *Desmodora* (*Pseudochromadora*) *cephalata* Cobb, 1920; and *Spilophorella paradoxa* (DeMan, 1888)] each comprised 1–2% of the water column assemblage. *Daptonema erectum*, *Desmodora cephalata*, and *S. paradoxa* were represented by 0.2–0.5% of their sediment abundance. *Daptonema* sp. 1 apparently was transported from another area because it was not present in the sediments at the experimental site. *Viscosia papillata* had a moderate to high sediment abundance, but was not proportionately common in the water column. The remaining species (Table II) were too rare to discuss in detail.

When currents were fastest *i.e.*, mid-ebb and flood tides (Palmer and Gust, 1985), more nematodes were suspended (Table IV). The *Metachromadora* species in particular had a wide disparity between ebb/flood and slack tides.

DISCUSSION

The *Metachromadora* species are thick bodied with numerous stiff setae and conspicuous lateral alae (wing-like extensions of the cuticle along the length of the body). *M. chandleri* (= *parasitifera* Timm, 1952) is a lethargic species described from rich detrital mud (Timm, 1952) but *M. obesa* is common on sand surfaces (Ott, 1972). Other species of *Metachromadora* for which the vertical distribution has been inves-

TABLE IV

Nematode mean abundance in the water column (per m³) during ebb, flood, and slack currents of neap and spring tides. Data given for dominant species (>1% only)

| Species | Neap | | | Spring | | |
|--|--------|-------|-----|--------|-------|-----|
| | Flood | Slack | Ebb | Flood | Slack | Ebb |
| | n = 24 | 12 | 19 | 20 | 10 | 19 |
| <i>Metachromadora chandleri</i> | 150 | 14 | 194 | 192 | 40 | 131 |
| <i>Metachromadora obesa</i> | 130 | 5 | 152 | 170 | 34 | 142 |
| <i>Metachromadora remanei</i> | 40 | 4 | 96 | 37 | 14 | 23 |
| <i>Chromadorita</i> aff. <i>minima</i> | 33 | 16 | 91 | 30 | 16 | 45 |
| <i>Ptycholaimellus pandispiculatus</i> | 10 | 0 | 32 | 24 | 18 | 36 |
| <i>Viscosia papillata</i> | 10 | 0 | 15 | 11 | 1 | 3 |
| <i>Daptonema erectum</i> | 1 | 3 | 20 | 0 | 0 | 18 |
| <i>Daptonema</i> sp. 1 | 5 | 3 | 7 | 9 | 0 | 16 |
| <i>Desmodora cephalata</i> | 1 | 0 | 10 | 3 | 29 | 3 |
| <i>Spilophorella paradoxa</i> | 2 | 1 | 6 | 6 | 7 | 2 |

See Table I for magnitude of variation (SE).

n = number of samples processed.

tigated are also found near or at the surface (Platt, 1977; Blome, 1983). Bell and Sherman (1980) found *M. pulvinata* to be third most abundant in their water column samples taken near (0.5 km) our study site and Sherman and Coull (1980) found that *M. pulvinata* and *M. remanei* were capable of recolonizing a disturbed site (0.5 km from our site) within one tidal cycle. Warwick and Gee (1984) report *M. vivipara* to have a shallow distribution in the sediment and suggest that it is likely to be dispersed by suspension.

In our study, the abundance of *M. chandleri* and *M. obesa* in the water column was disproportionately high in comparison to their sediment abundance. Our results, in conjunction with the earlier studies suggest that the surficial or slightly subsurficial vertical distribution of *Metachromadora* (Table I), their morphology, and their lethargic behavior increased the probability of their suspension. Furthermore, the relatively low abundance of *M. chandleri* and *M. obesa* in the sediments and high abundance in the water, suggests that at least a proportion of the study site water column population may have been derived from other marsh areas. Indeed, a large sand bar, which is a typical habitat for *M. obesa*, is just upstream of the sampling site.

All three species displayed tidal periodicity in water column abundance with lowest numbers during slack water when bottom friction velocity was well below that necessary to erode sediments (Palmer and Gust, 1985; Table IV). This reinforces the conclusion of Palmer and Gust (1985) that nematodes were passively dispersed. Flow dynamics and meiofaunal response in other marsh areas must have followed a pattern similar to that observed above the mudflat because a significant relationship between flow over the mudflat and meiofaunal suspension was found for both locally eroded and advected animals. Current transport is probably a major factor in the dispersal and colonization abilities of *Metachromadora* species.

If nematodes do reach other habitats, these immigrants enhance the diversity of the nematode community in that habitat. For example, the *M. obesa* found in our sediment samples may have been advected from the nearby sandbar. We cannot know whether those specimens are part of a reproducing mudflat population or just immigrants which have managed to survive. Specimens were undamaged and fully stained upon collection. The consistent presence of these nematodes in the water suggests that immigration may occur each tidal cycle. The same processes presumably operate on less abundant species which occur in the surface sediments.

Chromadorita aff. *minima* has only been reported in the original description from the English Channel (Gerlach and Riemann, 1973) and there are minor morphometric and morphological differences between our specimens and the original description. Other species of *Chromadorita* reportedly swim (Jensen, 1981) and occupy both sedimentary and phytal habitats. The ability to survive in the water column would be advantageous to a phytal species which requires a small, patchy, ephemeral (in North Inlet) habitat such as macroalgae.

Ptycholaimellus (= *Hypodontolaimus*) *pandispiculatus* is a characteristic species of the surface layers of subtidal sediment (Ott, 1972). It may not be particularly prone to suspension (<0.1% of sediment abundance was suspended here), but because it is so abundant in the sediment (Table II), even if only a small percentage is suspended there can be significant effects on the dispersal of the species. Bell and Sherman (1980) found *P. pandispiculatus* to be the second most abundant species suspended at the sediment-water interface and in the water column above the sediment, concomitant with a high sediment abundance. We found lower numbers in the water, but our samples were taken 17 cm off the bottom, not at the sediment-water interface. We may not have captured specimens near the bottom. Even so, *P. pandispiculatus* was among the most abundant suspended nematode species in this study and also among

the first and most abundant species to recolonize the disturbed area of Sherman and Coull (1980). The combined evidence from Bell and Sherman (1980), Sherman and Coull (1980), and our study suggests that the dispersal capabilities, and thereby the colonization abilities of this species are enhanced by advective currents.

Spilophorella paradoxa, a cosmopolitan species, is found on many coasts in the North Atlantic (Gerlach and Riemann, 1973). *Daptonema erectum* has been found all along the eastern coast of the United States (Florida and Georgia—Gerlach and Riemann, 1973; South Carolina—Eskin, 1985; New York—Eskin, pers. obs.). *Viscosia papillata* has been found from Texas to Maryland on the Gulf and Atlantic coasts (Gerlach and Riemann, 1974). All of these species have a wide geographic distribution, which may be a result of their tendency to be suspended, and probably transported by currents. Thus, suspension may play an important role in nematode zoogeographic patterns.

Abundant sediment species such as *Sabatieria pulchra* (G. Schneider, 1906), *Ter-schellingia longicaudata* De Man, 1907 and *Odontophora setosa* (Allgen, 1926) consistently have been found in the deeper sediment layers (Table I) and this may explain why they were rarely suspended.

Current transport apparently plays a significant role in the dispersal of certain meiobenthic nematodes. Water column dispersal of nematodes depends on their vertical distribution in the sediment. Other considerations include the sediment abundance of a species (e.g., *Ptycholaimellus pandispiculatus*) and their morphology or behavioral characteristics (swimmers vs. non-swimmers, lethargic vs. active). A corollary to the role of current transport in dispersal is an enhanced ability to reach and thereby colonize new or disturbed habitats (Sherman and Coull, 1980). Diversity may be affected as animals are carried from habitats in which they may be abundant to new habitats where they settle. Even if it is an unsuitable habitat for the colonizers, if they are constantly being deposited, they will be represented in samples. Once meiofauna are in the water column, they are subject to the same hydrodynamic forces and associated interactions with bottom topography as any small planktonic organism (e.g., Eckman, 1979, 1983; Hannan, 1984). Small-scale patchiness, such a conspicuous feature of nematode communities, may also be significantly influenced by current transport (e.g., Hogue and Miller, 1981). These ideas await further testing.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the financial and logistic assistance of the Belle W. Baruch Institute for Marine Biology and Coastal Research, and grants OCE80-07968 and OCE83-08114 from the National Science Foundation to B. C. Coull, and from Sigma Xi, the Slocum-Lunz Foundation, and the Byron K. Trippet Fund to M. A. Palmer. We also wish to thank Laura Foster for mounting hundreds of nematodes on slides. This manuscript has benefited from critical comments by Drs. B. C. Coull and S. A. Woodin.

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