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**FEEDING GROUPS AND SIZE ANALYSIS
OF MARINE MEIOBENTHIC NEMATODES
FROM SOUTH CAROLINA, USA ⁽¹⁾**

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RÉSUMÉ

L'étude des groupes trophiques de Nématodes marins dans des substrats sableux et dans des substrats vaseux d'un marais saumâtre — complexe d'estuaire — a montré comme on le supposait, la dominance des consommateurs de particules dans la vase et celle des consommateurs d'épistrates dans le sable. Néanmoins, des changements saisonniers se produisent dans les groupes trophiques de transition qui se retrouvent dans les deux stations. Le diamètre moyen des Nématodes est le même aux deux stations, mais la variabilité de ce diamètre est significativement plus élevée dans la vase que dans le sable. Il semble qu'il y ait peu de différence pour un Nématode fouisseur, qu'il soit élané ou robuste, mais les formes interstitielles doivent avoir des tailles similaires pour s'ajuster dans les interstices. Une forte diversité trophique chez ces Nématodes de sable de taille similaire, implique une bonne utilisation des ressources.

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There is not doubt that the marine free-living Nematoda are the most ubiquitous meiobenthic organisms, yet they do not receive the ecological emphasis they deserve because of their enormously difficult taxonomy. One ecologically significant way to approach complex nematode assemblages is through the medium of buccal structure examination with a goal of at least, elucidating intra-nematode trophic relationships. It was to this end that we initiated a seasonal study of nematode feeding groups at two subtidal stations in the *Spartina* estuarine complex of the North Inlet area of South Carolina, USA.

Based on buccal structure and gut contents many nematodes appear to be ingesting similar foods, suggesting interspecific competition for the same resources. Are there additional mechanisms that allow many nematode species to co-exist or is it all based on food supply? Herewith, we suggest a relationship between nematode body-diameter, and sediment granulometry and speculate on this relationship in maintaining (or an aid in maintaining) nematode trophic diversity in sands and muds.

METHODS AND MATERIALS

This study is a part of the long-term studies (initiated in September 1972 and continuing) on the meiofauna of the North Inlet Estuary, Georgetown, South Carolina, USA (33° 20.0'N, 79° 10.0'W).

Four replicate quantitative samples for faunal analysis are collected monthly at two subtidal stations in the estuary. One area in Bread and Butter Creek (BB) has a muddy substrate; the other area, Debidue (DD), is sandy. Samples are collected monthly by hand coring with 3.5 cm (inner diameter) core tubes within a m² area at the station marker at 1 m depth at low tide. Additional samples are collected and analyzed for sediment organic carbon and granulometric analysis and temperature, salinity, pH and Eh are always measured in the field at the time of sample collection. In the lab each sample is extracted by the shaking-supernatant technique of WIESER (1960) and all meiofauna identified to major taxon immediately. Every third nematode is removed from the sample for further classification.

Each sexually mature nematode was examined and classified to feeding group, and several key characteristics were measured by means of an eyepiece graticule: diameter of the buccal cavity, head, and body (median); morphology of the buccal teeth and cephalic setation; and gut contents. The feeding group designation follows WIESER's (1953) classification, but we have further separated out the forms based on additional data. WIESER (1953) defined four (4) nematode feeding categories i.e. Group 1 A (selective deposit feeders), Group 1 B (non-

selective deposit feeders), Group 2 A (epistrate feeders) and Group 2 B omnivore-predators). Since the nematodes from the two stations were completely different and to retain notice of these differences we used subcategories (modified from BOUCHER, 1973) noting these different types (e.g. 2A1, 2A2, ... 2A5, etc...). A Listing in Table I or Figures 1 and 2 of such categories as 2A3, 2B5, etc. simply indicates that they were « different » (perhaps only in gut contents) than the Group 2A2 from the other station, but all belonged to Group 2 A (epigrowth feeders). Table I gives the characteristics of these nematode subcategories. The gut cavity of all nematodes was examined microscopically. Not all nematodes had identifiable gut contents, some were empty or contained only fluids. Contents of a liquid nature were not identifiable.

RESULTS

The mud station (BB) is located just subtidally to an intertidal *Spartina* derived mud flat. The sediment is a well sorted mud (medium grain size 5-32 μm ; $S_o = 1.09-1.22$) composed of fecal pellets, *Spartina* debris and clay particles. Sediment organic carbon, which ranges between 1.6 and 5.2 % is highest in September-October. The overlying water column and upper 2-5 mm of sediment is oxidizing (Eh + 40 to + 200 mv). Water column salinities range between 29-35 ‰ and water-sediment interface temperatures between 10.5-29.8°.

The sand station (DD), just inside the North Inlet Estuary mouth, lies subtidal to an extensive sand flat. The sediment and granulometry changes seasonally, with median grain sizes of 175-200 μm ($S_o = 1.20-1.34$) in the late Spring and Summer, and 250-350 μm ($S_o = 1.31-1.57$) the remainder of the year. Organic carbon measures 0.1-1.0 % reaching the 1 % mark in the finer summer sediments. In general, the sediment is oxidizing to 8 cm (+ 100 to + 210 mv); below that it is reducing (- 20 to - 170 mv). The reducing layer, however, migrates vertically seasonally and is deepest in the winter. Overlying water column salinities range from 26 ‰ (after Spring runoff) to 35 ‰ and the temperature range is the same as reported for the Bread and Butter Station.

No attempt was made to identify the nematodes to species. Therefore a feeding group does not represent a single species or even a single genus. Stations could, however, be characterized by the relative abundances of each group. Figures 1 and 2 illustrate the seasonal pattern of the nematodes feeding groups at the two stations.

The mud station, Bread and Butter (Fig. 1) was, as expected, dominated overall by deposit feeders (82.4 %). Group 1A2 (selec-

tive) comprised 38.5 %; Group 1A1 (selective) 27.0 % and non-selective deposit feeders (Group 1B1) made up the remaining 16.9 %. Other groups were much less frequent: omnivore-epigrowth feeders, (Group 2B3) comprised 8.5 % of the total and epigrowth carnivores (2A2) and epigrowth feeders (2A1) 4.8 % of the total. Seasonally there is consistency with dominance of the two types of selective deposit feeders and non-selective deposit feeders during late summer — early fall (Sept.-Nov.).

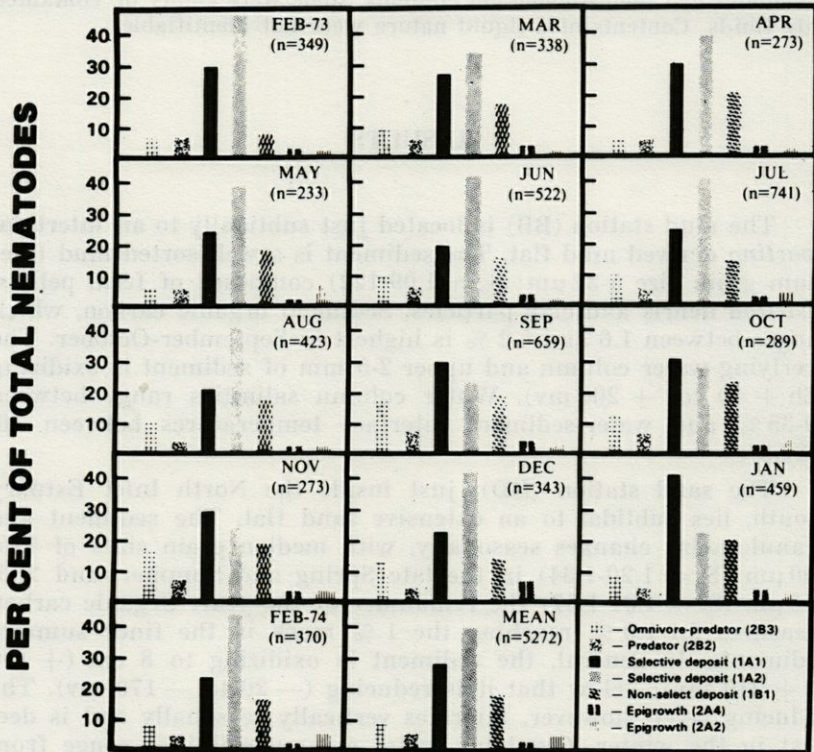


FIG. 1. — Relative abundances of the nematode feeding groups at the mud (Bread and Butter) station monthly during the study period (February 1973 - February 1974) and the mean abundance of each group.

The sand station, Debidue (Fig. 2) was not as clearly dominated by one or two groups. Large epigrowth feeders (Group 2A5) comprised 20.8 %, omnivore-predators (Group 2B4) also made up 20.8 % other predators (Group 2B5) ranked a close third at 19.7 % while small epigrowth feeders (2A4) ranked fourth at 16.6 %. Carnivore-

epigrowth feeders (2A3) and non-selective deposit feeders (1B2) made up the remaining 10.1 %. Monthly each feeding group was relatively consistent with an increase (from 5 % in May and 15 % in September) in the deposit feeders (1B's) during the summer months when the sediment was finer.

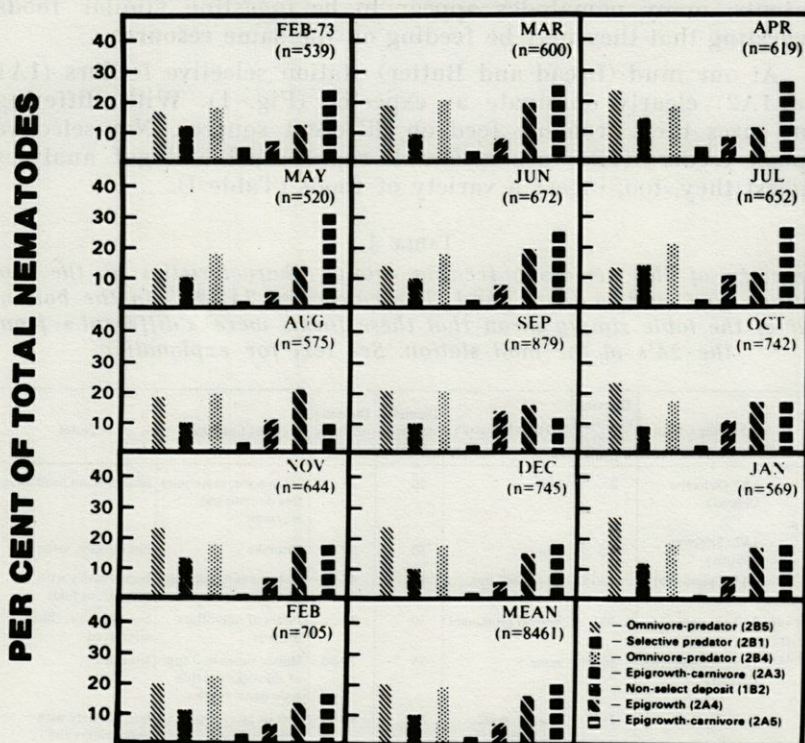


FIG. 2. — Relative abundances of the nematodes feeding groups at the sand (Debidue) station monthly during the study period (February 1973 - February 1974) and the mean abundance of each group.

DISCUSSION

NEMATODE FEEDING GROUPS.

Several authors (e.g. WIESER, 1953, 1959 a, b, c, 1960; KING, 1962; HOPPER and MEYERS, 1967 a, b; TIETJEN, 1969; COULL, 1970; BOUCHER, 1973; WARD, 1973, 1975) have studied the distribution of

feeding types in various habitats, and the general consensus is that morphological differences are due to the available food at particular locations. TIETJEN and LEE (1973, 1977) have shown that certain nematodes are indeed selective when given a choice between food sources and that a relatively large number of different nematodes can coexist at a single site. Based on buccal structure and gut contents, many nematodes appear to be ingesting similar foods suggesting that they may be feeding on the same resource.

At our mud (Bread and Butter) station selective feeders (1A1 and 1A2) clearly dominate as expected (Fig. 1). With differing head sizes they probably feed on different sources. Non-selective deposit feeders (1B1) are also well represented and gut analyses suggest they, too, ingest a variety of foods (Table I).

TABLE I

Summary of the nematode feeding groups characteristics at the two stations, one mud and one sand. The categories 2A3-2A5 in the bottom half of the table simply mean that these forms were « different » from the 2A's at the mud station. See text for explanation.

Feeding Group	Diameter of Buccal Cavity (μm)	Teeth Structure	Diameter of Head (μm)	Diameter of Body (μm)	Gut Contents	Notes
1A1 (Selective Deposit)	2	none	20	35	often none, sometimes fine detritus and inorganic	small lips, no head setae
1A2 (Selective Deposit)	4-5	none	30	50	Pastelike	lips obvious, setae
2A1 (Epigrowth)	10-15	Chitinized lips, resemble setae	15	45-50	Detritus and inorganic crystals	buccal cavity with numerous folds
Bread and Butter (Mud) 2A2 (Epigrowth)	30	Several prominent	30	35	Pieces of microflora, detritus	buccal cavity, chitin reinforced
1B1 (Non-selective Deposit)	30-40	none	35	70-80	Highly variable, 3 spp. of microflora, nematode parts, forams	large lips
1B2 (Predator)	15	one set, meet medially	30	40-50	One or more spp. of microflora and metazoan fragments	buccal cavity with chitin ridges and denticles
2B3 (Omnivore Predator)	40-50	Heavy chitinized lips	40	50-60	Highly variable, whole metazoans, fragments, detritus, microflora	
2A3 (Carnivorous Epigrowth)	30	few visible	40-45	40-50	Whole diatoms, metazoans in pastelike contents	amphid close to anterior ($5\ \mu\text{m}$) pointed chitinous lips, strong pharynx
2A4	10	> 3, Irreg., 45° from wall	25-30	35-40	Pastelike, inorganics and organics	triangular lips, chitin reinforced
2A5	10-15	none	35-40	40-50	Fragments of microflora, inorganic particles	strong musculature in pharynx suggests sucking and scraping
Debidue (Sand) 1B2 (Non-selective Deposit)	30	none	40-45	50-55	All types of contents	
2B1 (Selective Predator)	25-30	Two sets	40-45	50	3 spp. of microflora, pieces metazoans	very heavy lips, chitinized
2B5 (Omnivore Predator)	40	large, sharp (2 rows)	40-45	50	At least 3 spp. of microflora, metazoans, detritus	18 pointed, chitinous lips

Perhaps the most striking feature of the mud fauna was the existence of several transitional feeding groups which were found in much greater abundance at the sand station. For example, epigrowth feeders (Groups 2A1 and 2A2), characteristic of sandy substrates, also occurred in the mud. Although they are relatively similar in buccal morphology to the sand epigrowth feeders (2A4, 2A5, Table I), we doubt they could « scrape » food from the soft, muddy Bread and Butter sediment particles. Rather, they probably break the soft fecal pelleted particles apart and ingest the associated bacteria. Predators (Group 2B2) are the best established of the transitional groups, and they show very little morphological difference from sand predators (except for cephalic setation). Some overlap was anticipated since, by nature, predators are not limited to the interstitial environment. Group 2B3, the omnivore-predators, are probably also a transitional feeding group which feeds on a diet that runs the gamut from whole organisms to detritus covered with bacterial films. This group differs from its sand counterparts (2B5, Table I) in that most sand specimens had cuticular punctuations while the mud specimens did not. The diet of these two feeding groups at the mud and sand stations are considerably alike, and they appear to be occupying similar ecological positions in the two communities.

At our sandy site the nematode taxocene is not dominated by any one feeding group. Instead, two feeding groups exist in almost equal abundance: the epigrowth feeders (Groups 2A4 and 2A5) and the predators (Groups 2B1, 2B4, 2B5). The dominance of the epigrowth feeders was to be expected and is correlated seasonally with changes in microfloral production (R.G. ZINGMARK, pers. comm.), but the predator density was not. Some predators (Groups 2B1) have no visible gut contents, and we suspect that they attack prey, pierce the outer membranes with their large tooth, and suck out the tissues and fluids, although some specimens did have one species of diatom in the gut indicating selective predation. Others (Group 2B4) with heavy buccal armature and at least 3 species of microflora and fragments of metazoans in the gut, are probably somewhat selective.

Non-selective deposit feeders (Group 1B2) represent a small percentage of the feeding groups in the sand and reach their maximum abundance in the summer (June-Sept. see Fig. 2) at the time of increased silts and clays in the sediments. They probably represent a transitional fauna normally associated with high silt-clay contents. They appear to show little selectivity in nutritional sources and apparently scavenge the detritus associated with the finer summer sediments.

WIESER (1960) stated that the main difference in nematode feeding habits appears to be the preponderance of epistrate (epi-growth) feeders in sand and deposit feeders in mud. Our data simply substantiate this hypothesis, but indicate a high number of predators in the sandy environment; an observation not reported previously. Further, our data confirm that mud and sand habitats in North Inlet may be characterized by dominant feeding groups, but are linked to one another by transitional groups present in smaller percentages than those that dominate the station similar to the observations of WARD (1973).

NEMATODE DIAMETER AND SEDIMENT SIZE.

REMANE (1933) suggested that a relationship exists between the substrate composition and the body length of organisms inhabiting it. Smaller meiofaunal organisms were to be found in sandy substrates, and larger specimens in muddy sediments. In sand habitats the organisms would be expected to move interstitially, and thus be smaller. In mud where little interstitial space exists, nematodes should be larger burrowing forms, and WIESER (1959 c) reported that substrates with a median grain diameter of less than 200 μm do not support an interstitial fauna, but are the habitats of burrowing forms. Yet in his Chilean study, WIESER (1959 a) found little correlation between length of nematodes and grain size. However, WARD (1975) found that there was a correlation between the size range of nematodes and the substrate: longer forms were present at coarse, well sorted habitats and nematodes of more uniform length in other sediments, but WILLIAMS (1972) could find no correlation between length or diameter of nematodes with pore space in shell gravels.

Although we could not accurately measure nematode length, we explored the relationship between body diameter and substrate composition. This appeared to be at least as important a limiting factor because if the maximum body diameter is smaller than the interstice, a nematode can probably slither through the space regardless of its body length, although in soil nematodes mobility is maximized when mean particle size is about 1/3 nematode body length (PITCHER, 1975). Based on 13,733 nematodes measured and classified to feeding group (5,272 from mud, 8,641 from sand), we could find no significant differences (Mann-Whitney U-test, $p > 0.05$) in mean body diameter between the nematodes from the two stations (sand, $\bar{X} = 46.4 \mu\text{m}$; mud $\bar{X} = 49.9 \mu\text{m}$). Even though nematodes of muds may be longer (REMANE 1933, WARD 1975), we cannot substantiate that they are, in a statistical sense, "wider".

However, testing the null hypothesis that both populations came from the same normally distributed population and therefore, have the same variances, we find a highly significant difference ($p \leq 0.001$) between the faunas. The sand nematodes had a very small variance ($S^2 = 22.3$) and the mud nematodes a large variance ($S^2 = 179.3$) and this we did not expect. We had presupposed that the mud fauna would be uniformly large (they were not) and the sand fauna uniformly small (as they were), as suggested by REMANE (1933), SWEDMARK (1964) and WIESER (1959 c).

If we calculate pore space (after CRISP and WILLIAMS, 1971, for well sorted sediments) with both of our stations having sorting coefficients ~ 1.00 , we find that the interstices at the sand station would have varied between $61.3 - 122.5 \mu\text{m}$ over the study period and $1.8 - 11.2 \mu\text{m}$ at the mud station. Obviously the sand interstices are of sufficient magnitude to accommodate the nematodes of the diameters encountered, but the mud "interstices" if they exist at all (since the sediment is 95 % silts and clays), obviously cannot accommodate the measured nematodes in between the sediment particles. The sand fauna being all similar sized ($S^2 = 22.3$) is limited within a small range of body diameters which are particularly adapted for movement through the specific amount of available interstitial space. At the mud station, there does not appear to be an optimum diameter, but rather, once the interstitial space gets below the critical diameter it makes no difference if the nematode is « skinny » or « fat ». In fact, the large variance in diameter ($S^2 = 179.3$) suggests that size (diameter) is partially responsible for allowing these nematodes to coexist. At the sand station (with all the nematodes being of similar diameter) diameter and, therefore pore space, cannot be a significant agent in resource partitioning. However, if we attempt a quantification of « trophic diversity », by calculating H' Diversity (using the feeding groups as species), we find that the sand fauna trophic diversity is significantly greater (Mann-Whitney « U » test at 0.001) than the mud fauna trophic diversity (sand, $H' = 1.79 \pm 0.03$ mud $H' = 1.50 \pm 0.80$). The sand fauna then, even though of similar diameter, appears to be able to utilize an array of food gathering mechanisms to partition the available resources. WILLIAMS (1972) also suggests that in sands unknown factors must be responsible for the distribution and our data certainly support this.

Hypothetically, then, one could envision a gradient of nematode diameters, along a sediment gradient from coarse shell gravels to muds. One would predict the mean nematode diameter to linearly decrease to the limit of the interstitial existence (median of $200 \mu\text{m}$? — WIESER, 1959 c). Once sediment median diameters (and considering, of course, sorting etc.), went below the theoretical interstitial

limit, one would predict a random arrangement of diameters, since it would appear to make little difference as to *burrowing* effectiveness whether the nematode is slender or robust. The obvious test of the hypothesis is to collect along such a gradient and measure diameter. Ideally, one would like to identify the nematodes to species but that is beyond the scope of our expertise.

The study was the first, and admittedly preliminary, attempt to assess the ecological significance of the omnipresent nematodes within the framework of ongoing meiofauna studies of the North Inlet Estuary. Subsequently, Bruce E. HOPPER has agreed to assist us in our effort to continue ecological studies with the nematodes and his effort should build substantially upon the base provided here. Clearly the need exists for a detailed study of the microflora, microfauna, and meiofauna that these organisms ingest on a seasonal basis as well as detailed nematode taxonomy in order to more accurately assess the role of the marine meiobenthic nematodes in the North Inlet Estuary.

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ABSTRACT

Feeding group analysis of marine nematodes in a sandy habitat and a muddy habitat in a salt marsh — estuarine complex indicated, as expected, the dominance of deposit feeders in mud and epigrowth feeders in sand. There were, however, seasonal changes in the feeding groups and, both stations were linked by transitional feeding groups more dominant at the other station. Mean nematode diameter was significantly greater in the mud than in the sand. It appears to make little difference to a burrowing nematode whether it is slender or robust, but interstitial forms must be similarly sized to fit into the extant interstices. Resource partitioning of these similarly sized sand nematodes is most likely accomplished by high « trophic diversity ».

ZUSAMMENFASSUNG

Die Analyse von trophischen Gruppen bei marinen Nematoden in sandigem oder schlammigem Untergrund eines Aestuars hat gezeigt, dass — wie zu erwarten — Partikel-Fresser im Schlamm und Aufwuchs-Fresser im Sand dominieren. Allerdings sind jahreszeitliche Schwankungen festzustellen, und beide Stationen waren durch Ueberganggruppen verbunden. Der mittlere Durchmesser der Nematoden unterschied sich nicht von einer Station zur anderen, dagegen war die Schwankungsbreite bei den schlammbewohnenden Nematoden beträchtlich höher als bei den sandbewohnenden. Es scheint für einen grabenden Nematoden von geringer Bedeutung zu sein, ob er schlank oder umfangreich ist, dagegen müssen interstitiell lebende Formen von etwa gleicher Grösse sein, um in die vorhandenen Lücken zu passen. Verteilung des Nahrungsangebots unter diesen Sand-Nematoden mit untereinander ähnlicher Grösse ist wahrscheinlich durch hohe "trophische Diversität" gewährleistet.

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