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Testing for nematode–granulometry relationships

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Abstract The majority of studies have advocated that diversity of marine nematodes increases with increasing sediment grain size, although the opposite trend has also been suggested. The controversy is partially caused by not taking into account the effect of density on patterns of diversity and by analyzing datasets from different environments. The present study investigated nematode assemblages from sediments varying from very fine sand (mean grain size of 0.12 mm) to very coarse sand (1 mm) in shallow sublittoral marine environments. Contrary to previous studies, species richness was constant along the granulometric spectrum, despite significant changes in composition. The dominant genera were separated into five groups according to their optimum distribution and there was little overlap between these groups. Concepts from

the niche theory explain to some extent the observed patterns. For instance, some of the coexisting genera were from different feeding types.

Keywords Free-living marine nematodes · Sediment · Shallow water · Species richness · Species range

Introduction

The relationship between sediment properties and the fauna has been a central theme in benthic ecology (Gray 1974, Snelgrove and Butman 1994; Anderson 2008). One of the reasons for that is because sediment texture can be easily assessed and largely predicts patterns of the benthos (Ysebaert et al. 2002; Thrush et al. 2005). Abundance and biomass of benthic organisms are generally higher towards fine grains due to a concomitant increase in food availability (Heip et al. 1992), while diversity increases in the opposite direction due to a decrease in dominance (Vanaverbeke et al. 2011). The trend for marine nematode diversity is still controversial. It is accepted that coarser sediments have higher nematode species richness and diversity than finer sediments (Heip and Decraemer 1974; Tietjen 1977; Heip et al. 1985, 1992; Steyaert et al. 1999; Vanaverbeke et al. 2002, 2011). However, the opposite trend has been suggested after analyzing a large dataset and standardizing the samples to a fixed number of individuals (Boucher and Lamshead 1995). This disparity probably arose because the positive trend has been observed in local and regional datasets covering a relatively small part of the granulometric spectrum, while the negative relationship was suggested after comparing different datasets from distinct habitats. Another important issue is that, except for the large-scale study (Boucher and Lamshead 1995), studies did not take into account the potential effect of density on the diversity measures. So far, the relationship between nematode richness across a large

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range of the granulometric spectrum has not been systematically tested (but see Wieser 1959).

In addition to richness and diversity, nematode assemblage composition is also known to change according to the granulometric properties of the sediment (Wieser 1959; Heip et al. 1985; Vincx et al. 1990; Vanaverbeke et al. 2002, 2011). Fine sediments are generally characterized by the families Desmodoridae and Linhomoeidae, while coarse sediments are dominated by the families Enchelidiidae, Xyalidae, Cyatholaimidae, and Chromadoridae (Wieser 1959; Heip et al. 1985; Fonseca and Fehlaue-Ale 2012; Maria et al. 2013; Moens et al. 2013). Although distinct assemblages along the spectrum occur, we still do not know how these changes occur. Is there a gradual change in composition? Or are there distinct communities each with its own optimum distribution? The answers to these questions may also help to understand species ranges and ultimately the richness and diversity pattern along the spectrum. For instance, particularly for intertidal sandy beach nematodes, the mean grain size of 0.2 mm has been suggested to be a critical grain size barrier between sliders and burrowers (Wieser 1959).

The present study aims at testing how nematode assemblages will change in terms of species richness and composition over a sediment grain size spectrum. Particularly, we focus on shallow subtidal marine sediments (1–4 m water depth) to avoid potential confounding effects with depth. If the negative linear pattern suggested for nematodes from different habitats of different water depths is consistent (Boucher and Lamshead 1995), we expect to find that muddier sediments are more diverse than sandier sediments. On the other hand, if the positive linear pattern is valid for free-living nematodes (e.g., Vanaverbeke et al. 2011), we expect to find more diverse communities in coarser sediments than finer ones. Linear trends, positive or negative, are generated by having fewer species tolerating conditions towards one end of the spectrum. In both cases we can expect to find a linear decrease in species composition similarity towards the same end of the spectrum.

Materials and methods

Study site

The study was carried out in São Sebastião, a municipality of the State of São Paulo, Brazil. The area is formed by bays, mangroves, different morphological types of sandy beaches, and coastal islands. Such irregular coastline creates a heterogeneous seascape in terms of granulometry. In an area of approximately 60.8 km², we observed sediments varying from very fine sand to very coarse sand.

Sampling and sample processing

Sediment samples were taken for analysis of nematode assemblages and sediment granulometry from nine sublittoral stations covering a large spectrum of sediment types (Table 1). The survey was done between October 2012 and February 2013. By means of diving, in each station one corer was taken for granulometric analysis (5 cm in depth and 10 cm in diameter) and three corers were taken for the analysis of the nematodes (5 cm in depth and in diameter). Nematode samples were fixed in formalin 4 %. Fauna samples were washed over a 38- μ m sieve, and organisms were extracted by decantation using Ludox[®]-TM-50, at a specific gravity of 1.18 (Heip et al. 1985). From each replicate, a total of 100 nematodes were randomly picked under a dissecting microscope, transferred to a glycerol solution, and later mounted on permanent slides (Somerfield and Warwick 1996). Nematodes were identified to genus level and separated into morphological species. Since samples were identified by different observers, multivariate analyses were performed at genus level. The morphospecies data were only used to estimate the number of species per sample. Grain size analysis was performed by dry-sieving using an automatic shaker. The sediment fractions were defined according to the Wentworth scale (Bale and Kenny 2005).

Table 1 Geographical coordinates and granulometric parameters of the sampling stations

Station	Lat 23° (S)	Long 45° (W)	Mean (mm)	Sorting	Asymmetry	Kurtosis	Classification
#1	49°56.10"	26°34.96"	0.99	1.02	0.51	1.36	Very coarse sand
#2	49°23.03"	28°18.33"	0.75	0.98	−0.04	0.88	Coarse sand
#3	49°22.59"	28°18.81"	0.91	0.84	0.03	0.95	Coarse sand
#4	49°55.02"	30°46.57"	0.31	0.96	−0.18	0.94	Medium sand
#5	50°11.24"	30°41.36"	0.32	1.01	−0.19	1.13	Medium sand
#6	49°11.86"	28°4.47"	0.25	0.69	−0.09	0.77	Fine sand
#7	48°52.75"	24°19.73"	0.17	1.28	−0.28	1.42	Fine sand
#8	49°2.34"	24°10.49"	0.18	1.44	0.15	0.78	Fine sand
#9	49°42.41"	26°9.37"	0.12	0.80	−0.43	1.14	Very fine sand

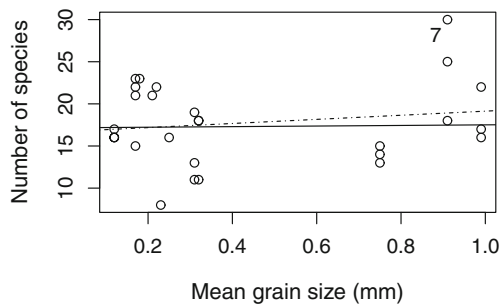


Fig 1 Results of the regression analyses between mean grain size (mm) and nematode number of species. *Solid line* the linear model considering the whole dataset ($y = -2.44x + 16.7$; $r^2 = -0.03$; $p = 0.41$); *dashed line* the linear model after removing the outlier (obs. 7; $y = 0.35x + 17.15$; $r^2 = 0.0$; $p = 0.89$)

Data analysis

To test the relationship between nematode species richness and sediment granulometry, linear regression analysis was conducted using sediment parameters (mean grain size, median grain size, sorting, asymmetry and kurtosis) as explanatory variable. Before running the analysis the assumptions of the analysis were tested [i.e. no serial correlation in the residuals (Durbin-Watson test; -0.21), constant variance of the residuals ($r=0$) and normal distribution of the residuals (Shapiro-Wilk test $p = 0.33$)]. To test for the relationship between sediment properties and the multivariate structure of the fauna, non-parametric forward linear regression analysis was performed (DistLM). In this analysis, highly correlated variables ($r > 0.7$) were excluded and the highest R^2 was used as selection criterion to find the best model. The multivariate structure of the genera composition was further visualized on a non-metric multi-dimensional scaling (MDS). The Bray–Curtis similarity matrix was used to build the similarity matrix of the fauna after square root transformation. Multivariate analyses were conducted on

Primer + Permanova 6 (Anderson et al. 2008). Finally, the visualization of the distribution range of the dominant genera was done on the standardized dataset, i.e. considered the maximum density of each genus in a given sample as 100 %.

Results

Sediment granulometry

Sediments ranged from very coarse sand (#1) to very fine sand (#9) being moderately well sorted at station 6, moderately sorted at stations 2, 3, 4, 6, and 9, and poorly sorted at stations 1, 5, 7, and 8 (Table 1).

Nematodes

The number of nematode species per sample varied from 8 to 30 and was not explained by mean grain size (Fig. 1), sorting, asymmetry, median grain size, or kurtosis ($p > 0.05$). The lack of a relationship was also observed after removing the outlier and considering the sum of species per sampling station.

The nematode community structure along the granulometric spectrum was separated in three main clusters (Fig. 2). One cluster was formed by fine-grained stations (0.12–0.18 mm), the second included fine, medium and coarse sand stations (0.25–0.75 mm), while the third cluster was formed by the coarser stations (0.91–0.99 mm). Mean grain size alone explained significantly 15 % of the variability in community structure (Marginal test; Table 2). All non-correlated variables explained together 36.2 % of the variability (Sequential test; Table 2).

Among the 109 genera identified (Appendix 1), 16 had densities higher than 5 % and occurred in at least three samples. These genera could be separated into five groups according to

Fig 2 Non-metric multi-dimensional scaling (MDS) based on squared root-transformed genus density. *Numbers above symbols* indicate the median grain size in mm. *Color legend* ● very coarse sand; ● coarse sand; ● medium sand; ● fine sand; ○ very fine sand

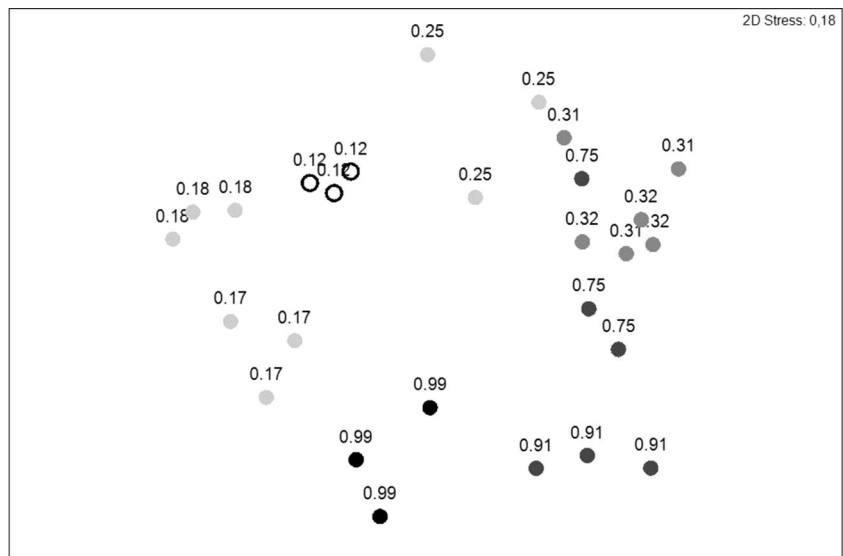


Table 2 Results of the DistLM analysis

	SS	Pseudo- <i>F</i>	<i>p</i>	Prop.	Cumul.
Marginal test					
Mean grain size	12,886	4.29	0.001	0.15	
Sorting	12,048	3.97	0.001	0.14	
Kurtosis	8,224.01	2.72	0.005	0.10	
Sequential test					
Mean grain size	12,886	4.29	0.001	0.15	0.15
Sorting	11,366	4.28	0.001	0.13	0.28
Kurtosis	7,597.5	3.10	0.002	0.09	0.37

Prop proportion of the variability explained; *Cumul* cumulative proportion of the variability explained

their distribution ranges (Fig. 3). *Cobbia*, *Terschellingia*, *Paralongicyatholaimus*, *Microlaimus*, *Sabatieria*, *Daptonema*, and *Odontophora* showed a narrow distribution towards the fine sediments with the abundance peaking around 0.20 mm (fine sand). *Omicronema* and *Rhynconema* peaked at 0.32 mm (medium sand), while *Theristus* and *Mesacanthion* showed a wider range (0.35–0.91 mm) with a peak at 0.75 mm (coarse sand). Distribution ranges of *Epacanthion*, *Enoploides*, and *Chromadorita* were mainly at the coarser sediment (>0.75 mm). *Paracanthonus* and *Draconematidae* showed a narrow distribution at the 1 mm sediment grain size. Within each group of species, more than one feeding type was observed (Fig. 3).

Discussion

The postulated hypothesis that nematode species richness may show a significant relationship, positive or negative, with the sediment grain size was not corroborated with the present dataset: fine sediments were as diverse as coarse sediments. The lack of a pattern in nematode species richness suggests that, for the present dataset, granulometry was not a major driving factor of species richness. This interpretation is in a first moment counterintuitive, especially because nematodes are well known to have a close relationship with the sediment properties (Ward 1975; Heip et al. 1985). However, the lack of a trend could be seen as a result of (1) high variability in species richness among samples of similar granulometry and/or (2) different assemblages with distinct distributions along the spectrum (Fig 3).

High and low species richness at the same mean grain size means that there are other factors rather than grain size structuring the coexistence of nematode species. There are a multitude of other environmental factors that may vary independently of granulometric properties and are known to structure marine nematodes. Examples of important structuring

variables which might be also operating in the present dataset are quantity and quality of the organic matter (Danovaro and Gambi 2002), oxygen availability and the position of the redox layer (Steyaert et al. 2007; Vieira and Fonseca 2013), abundance and composition of macrofauna species (Van Colen et al. 2009, Braeckman et al. 2011), and bacterial biomass and activity (Danovaro 1996), among others. We suggest that, at least for the present dataset, these variables are more important than granulometry in structuring local species richness.

The same rationale presented above can be used to explain high and low abundances of certain nematode genera under an

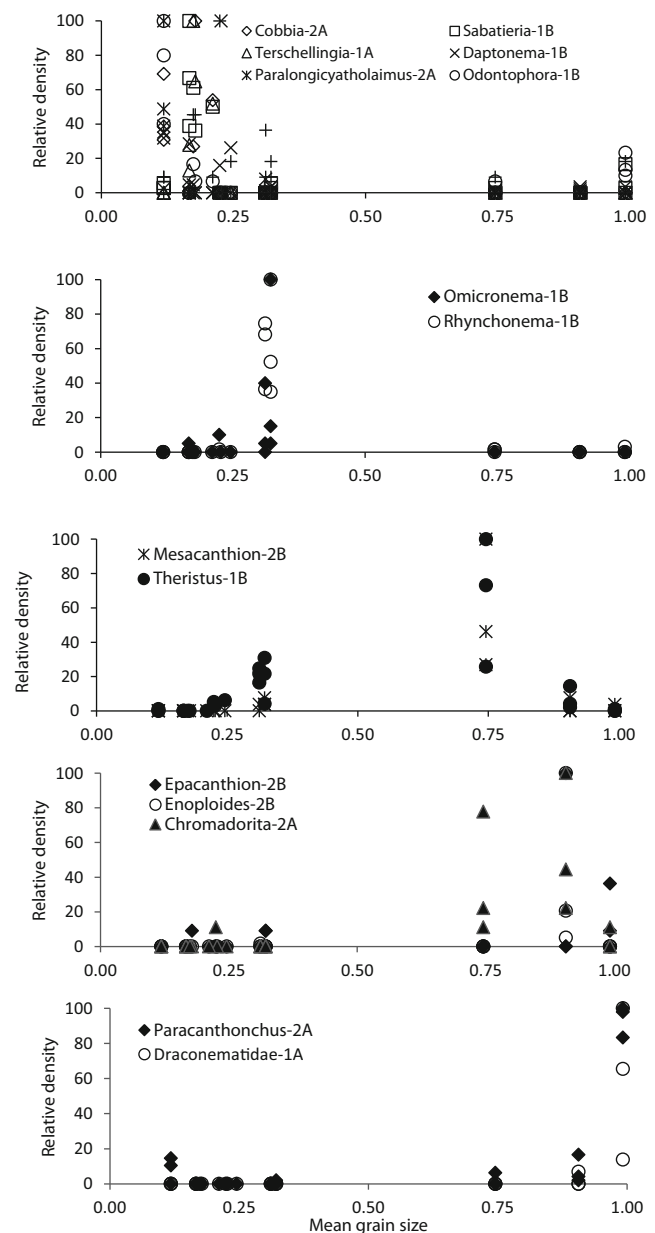


Fig 3 Distribution of the dominant nematode genera among the grain size spectrum with the respective feeding types (sensu Wieser 1953). Data were standardized for each species using the maximum density as 100 %

optimum mean grain size. Although a nematode species might show a preferred mean grain size (i.e. fundamental niche; McGill et al. 2007), other environmental factors can interact with granulometry and affect their fitness limiting their local population growth (i.e. realized niche). Supporting evidence that the realized niche of soft sediments species is the outcome of sediment grain size interacting with other environmental variables has already been suggested for macrofauna (Thrush et al. 2005; Anderson 2008) and meiofauna species (Gray 1966).

As expected from the literature (e.g., Heip et al. 1985; Vanaverbeke et al. 2011), genera composition changed significantly along the granulometric spectrum. Changes in composition were mainly associated with the optimum distribution ranges of the dominant genera. These genera could be separated into five groups, with each group showing a very narrow distributional peak along the spectrum and little overlap with each other. According to the niche theory (reviewed by Chase and Leibold 2003), these group of genera might be occupying distinct environmental niches, i.e. sediment grain sizes (sensu Grinell 1917). In theory, these different groups could be competing or not for resources, depending on their specificity and types of interactions. Given our lack of knowledge on nematode genus/species autecology, we do not know which mechanisms of segregation (if there is one) are operating along the granulometric spectrum. However, at least some of the genera that segregated according to grain size in the present study show distinct body shapes and potential locomotion strategies (e.g., the interstitial long and filiform *Terchellingia* vs. the crawler S-shaped *Draconema*), suggesting that it is unlikely that they compete with each other. Non-overlapping patterns of distinct body shapes have also been suggested for intertidal sandy beach nematodes (Wieser 1959).

The lack of knowledge on nematode autecology is also an impediment to understand the coexistence of genera within these groups. We should expect that the observed coexisting genera are either not competing for the same resource or that they explore differently more than one resource (Chase and Leibold 2003). Although some of the coexisting genera in our dataset were in fact from distinct feeding types (sensu Wieser

1953), there were also coexisting genera within the same feeding type. For instance, *Sabatieria*, *Daptonema*, and *Odontophora* are non-selective deposit feeders (1B) and their abundances peaked at fine sand, while the abundances of the predators (2B) *Enoploides* and *Epacanthion* peaked in coarse sands. There is already evidence of niche segregation on predatory nematodes by showing distinct prey preferences (Moens et al. 2000; Gallucci et al. 2005), and that the feeding classification based on buccal morphology (Wieser 1953) underestimates the functional diversity of marine nematodes (Moens et al. 2005). Additionally, coexisting genera with similar feeding strategies could segregate by inhabiting different sediment layers, as already observed for congeneric species (Fonseca et al. 2007), or any other microhabitat structure not measured in this study.

The present dataset is certainly limited in the number of samples, taxa, and grain size classes, nevertheless it questions the traditional assumption of positive relationship between richness and sediment grain sizes. Our data corroborate the hypotheses (1) that species richness is not primarily dictated by sediment grain size per se (Vanaverbeke et al. 2011), and, as a consequence, the positive and negative results previously reported could be a byproduct of other variables which are co-varying with the sediment granulometry or a consequence of not considering the effect of density diversity patterns; and that (2) along a granulometric spectrum there are several groups of non-overlapping species each exploring a different part of the spectrum (Wieser 1959). The generality of these hypotheses have now to be further tested based on larger datasets and other sets of nematode taxa.

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Appendix

Table 3 Nematode genera identified in each sampling station

Genera and 2 families	Stations								
	#1	#2	#3	#4	#5	#6	#7	#8	#9
Mean grain size (mm)	0.99	0.75	0.91	0.31	0.32	0.25	0.17	0.18	0.12
<i>Acanthonchus</i>			X				X		
<i>Actinonema</i>	X		X	X	X				
<i>Aegialoalaimus</i>								X	

Table 3 (continued)

Genera and 2 families	Stations								
	#1	#2	#3	#4	#5	#6	#7	#8	#9
<i>Anoplostoma</i>							X		
<i>Anticoma</i>			X						
<i>Apodontium</i>						X			
<i>Araeolaimus</i>						X			
<i>Atrochromadora</i>			X						
<i>Axonolaimus</i>				X	X			X	
<i>Bathylaimus</i>	X								
<i>Bolbolaimus</i>					X				
<i>Calomicrolaimus</i>				X					
<i>Camacolaimus</i>	X		X						
<i>Campylaimus</i>								X	
<i>Cephalanticoma</i>							X		
<i>Chromadora</i>		X	X						
<i>Chromadorella</i>	X		X						
<i>Chromadorina</i>	X		X						X
<i>Chromadorita</i>	X	X	X			X			
<i>Cobbia</i>							X	X	X
<i>Comesoma</i>	X	X			X		X	X	X
Comesomatidae								×	
<i>Crenopharynx</i>		X							
<i>Cyartonema</i>								X	
Cyatholaimidae type1						X			X
<i>Daptonema</i>	X	X	X	X	X	×	×	X	X
<i>Desmodora</i>			X				X		
<i>Desmolaimus</i>							X		
<i>Dichromadora</i>		X	X				X		X
<i>Diplopetooides</i>					X	X			
<i>Dorylaimopsis</i>							X		
Draconematidae type 1	X		X						
<i>Endeolophus</i>						X			
<i>Enoploides</i>			X	X					
<i>Enoplolaimus</i>			X	X					
<i>Enoplus</i>			X						
<i>Epacanthion</i>	X		X		X			X	
<i>Euchromadora</i>			X						
<i>Eurystomina</i>			X	X	X	X			
<i>Gammanema</i>	X								
<i>Gomphonema</i>							X	X	
<i>Graphonema</i>			X						
<i>Halalaimus</i>			X		X		X	X	
<i>Halichoanolaimus</i>							X		
<i>Hopperia</i>							X	X	
<i>Hypodontolaimus</i>						X		X	
<i>Ingenia</i>				X	X	X			
<i>Innocuonema</i>						×			
<i>Lauratonema</i>						X			
<i>Linhomoeus</i>		X							

Table 3 (continued)

Genera and 2 families	Stations								
	#1	#2	#3	#4	#5	#6	#7	#8	#9
<i>Longicyatholaimus</i>							X		
<i>Manunema</i>	X								
<i>Marylynnia</i>				X			X		
<i>Mesacanthion</i>	X	X	X	X	X				
<i>Metacyatholaimus</i>								X	
<i>Metadasyneoides</i>	X			X					
<i>Metadesmolaimus</i>			X						
<i>Metalinhomoeus</i>	X		X				X		
<i>Metoncholaimus</i>							X		
<i>Microlaimus</i>	X	X		X	X	X		X	X
<i>Molgolaimus</i>								X	
<i>Monhystrella</i>							X		
<i>Nannolaimus</i>									X
<i>Neochromadora</i>			X						
<i>Neotonchus</i>								X	
<i>Nudora</i>									X
<i>Odontophora</i>	X	X						X	X
<i>Odontophoroides</i>								X	X
<i>Omicronema</i>				X	X	X	X		
<i>Oncholaimellus</i>	X	X				X	X		X
<i>Oncholaimus</i>		X							
<i>Oxystomina</i>	X								
<i>Paracanthonchus</i>	X	X	X		X				X
<i>Paracyatholaimus</i>		X		X		X	X		X
<i>Paralongicyatholaimus</i>									X
<i>Paramonohystera</i>		X							X
<i>Parasphaerolaimus</i>								X	
<i>Phanoderma</i>		X	X				X		
<i>Polygastrophora</i>	X		X	X	X	X	X		
<i>Praeacanthonchus</i>	X								
<i>Prochromadorella</i>	X		X						
<i>Promonhystera</i>								X	
<i>Pselionema</i>								X	
<i>Pseudochromadora</i>		X	X						
<i>Pseudosteieria</i>	X			X		X	X	X	X
<i>Ptycholaimellus</i>	X		X	X		X	X		
<i>Rhynchonema</i>	X	X		X	X	X			
<i>Sabatieria</i>	X	X			X		X	X	X
<i>Scaptrella</i>				X					
<i>Southermiella</i>							X		
<i>Sphaerolaimus</i>			X						
<i>Spilophorella</i>			X		X	X	X		
<i>Spirinia</i>				X			X		X
<i>Steineria</i>		X				X	X		
<i>Stephanolaimus</i>						X			
<i>Subsphaerolaimus</i>							X		
<i>Terschellingia</i>		X		X			X	X	

Table 3 (continued)

Genera and 2 families	Stations								
	#1	#2	#3	#4	#5	#6	#7	#8	#9
<i>Thalassironus</i>						X			
<i>Thalassolaimus</i>							X		
<i>Theristus</i>	X	X	X	X	X	X			X
<i>Trichoeristus</i>						X			
<i>Trileptium</i>					X				
<i>Tripyloides</i>			X					X	
<i>Trochamus</i>			X						
<i>Viscosia</i>	X	X	X	X		X	X		
<i>Wieseria</i>	X								
<i>Xyala</i>	X								
Unidentified genus 1	X								
Unidentified genus 2				X		X	X	X	X

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