

Biodiversity and community structure of free-living marine nematodes from the Larsemann Ice Shelf, East Antarctica

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Subtidal (500–700 m) meiofaunal assemblage of the Larsemann Ice Shelf, East Antarctica, is described with special emphasis on the free-living marine nematodes. The sampling was conducted with a 25 × 25 × 40 cm VSNL Spade Box corer and sub-sampling was performed with an acrylic core (4.5 cm dia.). The meiofauna comprised of eight taxa dominated by nematodes. A total of 75 nematode genera and 4 species were identified. They were randomly distributed and showed a significant difference ($P < 0.05$) between the sampling stations. The total density varied from 239 to 639/20 cm² and maximum density was recorded at a water depth of 722 m. Nematodes constituted >82% of the total meiofauna. A total of 1053 nematodes were isolated from the three cores. Vertically, ~90% nematodes were in the surface (0–2 cm) sediment, and their abundance decreased with sediment depth. Among the nematodes, selective feeder and non-selective deposit feeder were most abundant at the surface sediment, whereas omnivores and predators were higher at depth. *Sabatieria* and *Paralinhomoeus* were the most common genera. The higher nematode abundance at the surface was possibly due to their preferences to the freshly arriving food particles in the sediment–water interface. Availability of predatory omnivores in the deeper layers was perhaps due to their adaptation to the sedimentary conditions and could be their part of survival strategy in the harsh Antarctic environment.

Keywords: East Antarctica, Larsemann Ice Shelf, nematodes, *Paralinhomoeus* sp., *Sabatieria* sp., subtidal meiofauna.

Introduction

STUDIES on Antarctic benthos have largely described the macrobenthic community that too from the peninsular region, the Weddell and Lazarav Seas^{1–5}. Antarctic benthic macrofauna is very old, usually found in good numbers with high species endemism³, whereas very little is known about the Antarctic meiofauna. This is due to the finer size and structure of nematodes, which requires a

higher level of expertise for taxonomic identification. The Larsemann Ice shelf is characterized by low microbial diversity⁶ but no earlier study is devoted to meiofauna, especially the nematodes.

Meiofaunal assemblage from maritime Antarctica has been described earlier^{7,8}. According to Gray *et al.*⁹, the challenge for researchers is to find the variation of species diversity as a function of depth.

Nematodes are numerically the dominant animal group in most marine meiobenthic habitats with ubiquitous distribution as well as high abundance and diversity¹⁰. The free-living forms inhabit the world's entire seabed habitat¹¹. Due to their higher density and diversity as well as wider distribution, nematodes are considered as one of the most important faunal groups in Antarctica⁸.

Although the Antarctic nematodes have been reviewed recently⁵, the study of free-living nematodes from the Larsemann Ice shelf is far from adequate. The purpose of the current study was to determine the composition and abundance of benthic meiofauna with special reference to the nematodes from three muddy offshore sites along the Larsemann Ice Shelf of East Antarctica. Additionally, we examined the main factors governing the distribution of meiobenthos and especially the free-living nematodes at three muddy offshore sites.

Materials and methods

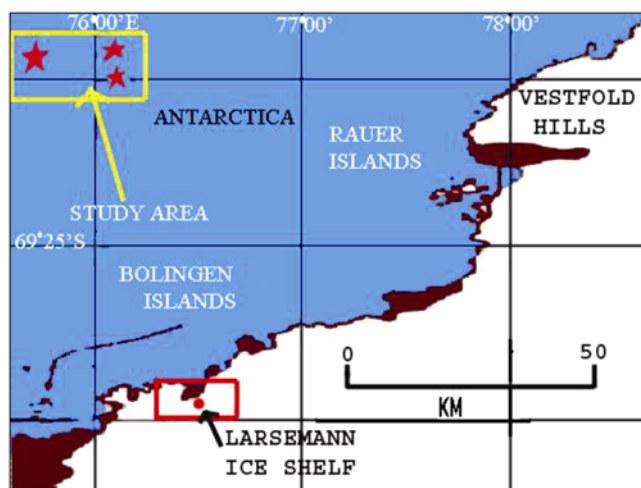
The Larsemann Hills (lat. 69°23'S, long. 76°53'E) in the Prydz Bay, an ice-free polar oasis on the Ingrid Christensen Coast, Princess Elizabeth Land, East Antarctica, is located approximately midway between the eastern extremity of the Amery Ice Shelf and the southern boundary of the Vestfold Hills (Figure 1). The region consists of two main peninsulas, i.e. Stornes and Broknes, together with a number of scattered offshore islands. At 50 km², the Larsemann Hills is the second largest of only four major ice-free oases found along East Antarctica's 5000 km coastline.

During austral summer (February–March) 2006, a detailed seabed sampling was conducted at three near shore Antarctic locations in the Larsemann Ice shelf (Figure 1 and Table 1). Sampling was done onboard *R.V. Akademik Boris Petrov* with a 25 × 25 × 40 cm VSNL

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Table 1. Details of the sampling locations in the Larsmann Ice Shelf area, East Antarctica

Station nos.	Water depth (m)	Core length (cm)	Core section studied for meiobenthos (cm)	Latitude (°S)	Longitude (°E)
1	721.7	18	14	69°09'958"	75°53'123"
2	551.8	32	14	69°19'467"	76°05'009"
3	525.0	23	10	69°21'951"	76°06'296"

**Figure 1.** Map of the study area (yellow).

spade box corer. Sub-sampling was performed with an acrylic core (4.5 cm dia.). All the cores were stored frozen and transported to the onshore laboratory at Goa, where sub-samples were taken using an acrylic corer (5 cm dia.) down to a sediment depth of 14 cm. Three cores were taken at three different stations. The sediment sample of two cores was sectioned into seven depth layers 0–2, 2–4, 4–6, 6–8, 8–10, 10–12, 12–14 cm whereas the third core was sectioned only up to 10 cm depth. All samples were fixed with neutralized 5% formaldehyde solution. The meiofauna was extracted from the sediment by decantation over a 45 µm mesh sieve. The material retained on the sieve was stained with Rose Bengal and identified to a possible taxon level, under a stereo zoom microscope. All nematodes were extracted subsequently, counted, sorted by hand picking and mounted on permanent glycerin slides. On the basis of morphological characters, each specimen was identified to the generic level and a few of them up to the species using pictorial keys¹².

Meiofaunal group diversity was measured with PRIMER software¹³ by using Shannon–Wiener diversity (H') function, evenness (J') and group level richness (d). Nematode generic diversity was calculated by Shannon's index of diversity (H). All nematodes were classified according to their feeding type¹⁴. The abundance in each sub-section and at each sampling station was subjected to analysis of variance (ANOVA) to determine whether significant ($P < 0.05$) differences occurred between different stations, located at different water depths.

Results

Composition of meiofauna

Meiofaunal density ranged from 239 to 639 individuals/20 cm² with nine major groups. Nematoda and Harpacticoida were the most dominant groups. The samples also contained Turbellaria and Foraminifera, Ostracoda, Amphipoda and Polychaeta in minor abundances. The depth-wise distribution of meiofauna is presented in Figure 2. The density of total meiofauna generally showed a decrease with sediment depth and at a particular station, subsurface maxima was observed. At most stations, the highest densities occurred above the 2 cm horizon, and densities below 2 cm dropped to low values, these values being similar at all stations except stn 2 where increase in density was observed at depths. Nematodes, strongly dominated the taxa with an overall contribution of 82%. Their contributions at individual stations were 76% (stn 1); 82% (stn 2) and 91% (stn 3). Among other taxa, harpacticoides and foraminiferans were dominant at stn 1 with a contribution of 9% followed by eggs, 7% and amphipods, 4%. At stn 2, invertebrate eggs comprised of 10%, followed by harpacticoid copepods (7%) and turbellarians (5%). Foraminifera contributed only 3%. At stn 3, turbellarians and harpacticoids contributed 6% and 5% respectively, followed by ostracods (4%) and foraminiferans (3%).

Nematode abundance

A total of 1053 nematodes belonging to 75 genera and 4 species were isolated from the three sediment cores. The highest nematode diversity (59 genera) was observed at stn 1, whereas only 20 genera were common for three stations (Table 2). The highest nematode density (490/20 cm²) was at stn 1 and lowest (218/20 cm²) at stn 2. Station 3 was represented with moderate value (345/20 cm²). Maximum nematodes were found in the surface (0–2 cm) sediment layers. Despite their low occurrence, the nematode density increased at the deeper sediment layers. This trend was particularly pronounced for some genera (Figure 3). Although nematodes were present in the entire core, results from the one-way ANOVA revealed significant differences in the number of genera recorded at different stations ($P < 0.05$) and at different sediment depths ($P < 0.001$).

INDIAN CONTRIBUTION IN SOUTHERN OCEAN

Table 2. Nematode genera collected from three different stations

	Station 1	Station 2	Station 3		Station 1	Station 2	Station 3
<i>Sphaerolaimus</i> sp.	+	+	+	<i>Diplopeltis</i> sp.	+	-	-
<i>Sabatieria</i> sp.	+	+	+	<i>Cervonema</i> sp.	+	-	-
<i>Chromadorella</i> sp.	+	-	+	<i>Southerniella</i> sp.	+	-	-
<i>Metalinhomoeus</i> sp.	+	+	+	<i>Tricoma</i> sp.	+	-	-
Unidentified sp.	+	+	+	<i>Synonchium</i> sp.	+	+	-
<i>Terschellingia</i> sp.	+	+	+	<i>Megadesmolaimus</i> sp.	+	-	-
<i>Halalaimus</i> sp.	+	+	+	<i>Gammanema</i> sp.	+	-	-
<i>Acantholaimus</i> sp.	+	+	+	<i>Amphimonhystera</i> sp.	+	-	-
<i>Actarjania</i> sp.	+	+	+	<i>Laimella</i> sp.	+	-	-
<i>Theristus</i> sp.	+	+	+	<i>Dorylaimopsis</i> sp.	+	-	-
<i>Halanonchus</i> sp.	+	+	-	<i>Quadricoma</i> sp.	+	-	-
<i>Vasostoma</i> sp.	+	+	-	<i>Epacanthion</i> sp.	+	-	-
<i>Meylia</i> sp.	+	+	-	<i>Mesacanthion</i> sp.	+	-	-
<i>Dolicholaimus</i> sp.	+	-	-	<i>Metacyatholaimus</i> sp.	+	-	-
<i>Pierrickia</i> sp.	+	+	+	<i>Filitonchus</i> sp.	+	-	-
<i>Hopperia</i> sp.	+	+	+	<i>Hopperia</i> sp.	+	-	-
<i>Meyersia</i> sp.	+	+	+	<i>Desmolorenzenia</i> sp.	+	-	-
<i>Daptonema</i> sp.	+	+	+	<i>Oxystomina</i> sp.	+	-	-
<i>Subsphaerolaimus</i> sp.	+	+	+	<i>Terschellingia longicaudata</i>		+	+
<i>Viscosia</i> sp.	+	+	+	<i>Metalinhomoeus longiseta</i>	+	-	-
<i>Araeolaimus</i> sp.	+	+	+	<i>Leptolaimus</i> sp.	+	-	-
<i>Axonolaimus</i> sp.	+	+	+	<i>Astomonema</i> sp.	+	-	-
<i>Gomphonema</i> sp.	+	+	-	<i>Oxyonchus</i> sp.	-	-	+
<i>Oncholaimus</i> sp.	+	+	-	<i>Siphonolaimus</i> sp.	-	-	+
<i>Cheironchus</i> sp.	+	+	+	<i>Richtersia</i> sp.	-	+	+
<i>Paralinhomoeus</i> sp.	+	+	-	<i>Dichromadora</i> sp.	-	-	+
<i>Chromadorella</i> sp. 1	+	-	-	<i>Siphonolaimus niger</i>	-	-	+
<i>Spilophorella</i> sp.	+	-	+	<i>Filitonchus ewensis</i>	-	-	+
<i>Oxystomina</i> sp. 1	+	+	-	<i>Campylaimus</i> sp.	-	-	+
<i>Metasphaerolaimus</i> sp.	+	+	-	<i>Steineria</i> sp.	-	+	+
<i>Odontophora</i> sp.	+	+	+	<i>Metadesmolaimus</i> sp.	-	+	+
<i>Phanodermopsis</i> sp.	+	-	-	<i>Actinonema</i> sp.	-	-	+
<i>Halichoanolaimus</i> sp.	+	+	+	<i>Anoplostoma</i> sp.	-	-	+
<i>Micoletzkyia</i> sp.	+	-	+	<i>Stylotheristus</i> sp.	-	-	+
<i>Crenopharynx</i> sp.	+	-	-	<i>Siphonolaimus</i> sp. 1	-	-	+
<i>Anoplostoma</i> sp. 1	+	-	+	<i>Marylynnia</i> sp.	-	+	+
<i>Paracomesoma</i> sp.	+	-	-	<i>Linhystera</i> sp.	-	+	+
<i>Eumorpholaimus</i> sp.	+	-	-	Total no. of genera	59	35	40

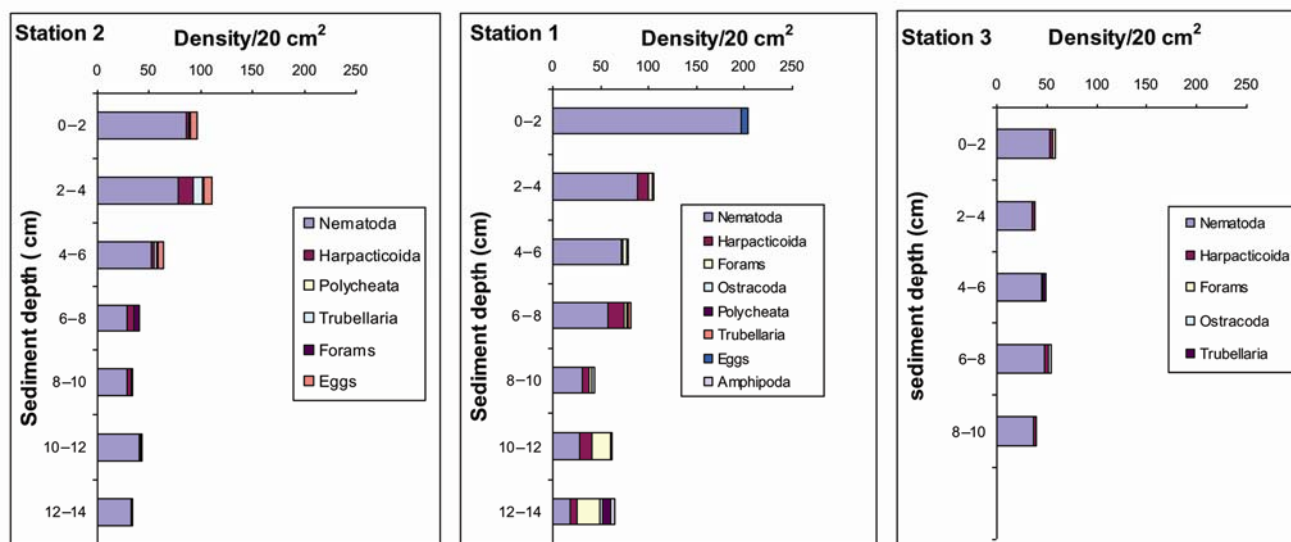


Figure 2. Vertical distribution and abundance of meiofauna.

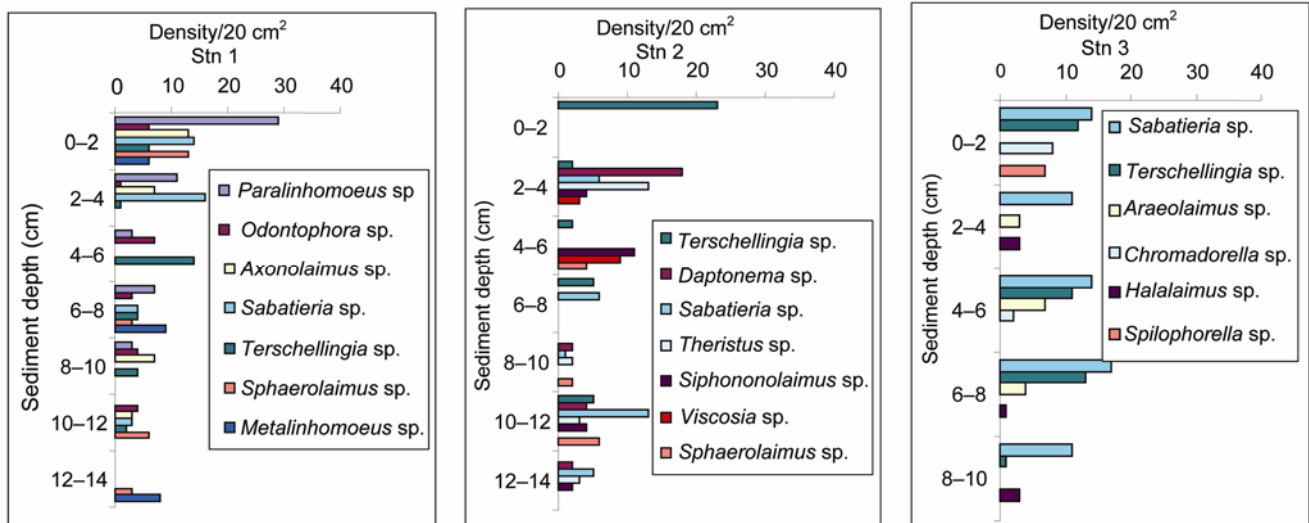


Figure 3. Distribution of dominant nematode genera at three stations.

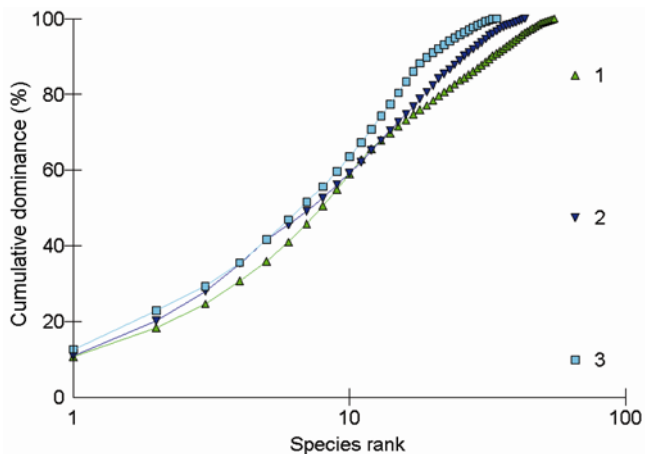


Figure 4. k -Dominance curve for different stations.

A density of 490/20 cm² nematodes was found at stn 1, of which 40% were in the top 0–2 cm sediment section and was the highest among all the three stations. *Paralinhomoeus* was the most dominant genera, followed by *Sabatieria* and *Axonolaimus* (Figure 3). At mid depth, 72 nematodes were observed and *Terschellingia* and *Paralinhomoeus* were dominant. A total of 57 nematodes were observed in the next (6–8 cm) section where *Paralinhomoeus* and *Sabatieria* were again dominant. The decrease in density of nematodes was steady with the sediment depth. Only 31 nematodes were recovered at the sediment depth of 8–10 cm, whereas 28 nematodes were found in the 0–12 cm section. The lowest recovery (18/20 cm²) was from the 12 to 14 cm section where *Sphaerolaimus* was dominant. A total of 345/20 cm² nematodes were recorded at stn 2. The highest abundance of 86/20 cm² was in the surface layer. The dominant genera were *Terschellingia* and *Sabatieria*. A decreasing trend continued

thereafter with a density of 78/20 cm² in the 2–4 cm section. *Daptonema*, *Theristus* and *Linhystra* were the dominant genera. A density of 78/20 cm² was recorded from the 2 to 4 cm section with the dominance of *Daptonema* and *Theristus* genera. The density of 52/20 cm² was found in the 4–6 cm section and *Pandolaimus* sp. was the dominant nematode. As shown in Figure 3, the nematodes were abruptly distributed below 6 cm with a density of 28 in 6–8 cm. The values increased considerably in 10–12 cm (40/20 cm²) and again decreased to 32/20 cm² at deeper sections. At the sediment depth of 4–6 cm, 52/20 cm² nematodes were found among them, *Siphonolaimus* and *Meyersia* were dominant. Density of nematode was very low in the rest of the sections where *Sabatieria* was dominant.

At stn 3, *Araeolaimus*, *Sabatieria* and *Terschellingia* were the dominant genera. The upper 0–2 cm sediment layer contributed to the highest nematode density (53 nos) followed by at 2–4 cm (36 nos) and at 4–6 cm (45 nos). At 6–8 cm section, 47 nematodes were observed. *Sabatieria* and *Terschellingia* were dominant. At the depth of 8–10 cm, the density of 37 nos was recorded. Again, *Sabatieria* was dominant, contributing 13% of total nematode community, with *Terschellingia* being the second dominant genera. The density dropped sharply below 8 cm and only 11 nematodes were recovered from 8 to 10 cm section. Multiple k -dominance curve facilitated the discrimination of benthos according to species-relative contribution to standard stock. Dominance curve was plotted using all the nematode data for different stations. As shown in Figure 4, stn 1 is placed low, indicating high nematode diversity, whereas stns 2 and 3 are placed above respectively. The diversity indices presented in Table 3 also confirm higher Shannon–Wiener index at stn 1.

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Table 3. Indices of group diversity for nematofauna at three different stations

Diversity indices	Stations			Mean \pm SD
	1	2	3	
Species richness (<i>s</i>)	14.85	12.42	12.40	13.22 \pm 1.41
Margelf's index (<i>d</i>)	3.24	3.01	3.04	3.10 \pm 0.12
Evenness (<i>J</i>)	0.91	0.91	0.82	0.88 \pm 0.05
Shannon–Wiener index (<i>H'</i>)	2.32	2.26	2.07	2.21 \pm 0.12
Total no. of genera	59	35	40	44.6 \pm 12.6
Dominant nematode genera	<i>Paralinhomoeus</i> , <i>Sabatieria</i> , <i>Terschellingia</i> , <i>Axonolaimus</i> , <i>Sphaerolaimus</i>	<i>Terschellingia</i> , <i>Sabatieria</i> , <i>Daptonema</i> , <i>Siphonolaimus</i> , <i>Theristus</i>	<i>Sabatieria</i> , <i>Terschellingia</i> , <i>Araeolaimus</i> , <i>Chromadorella</i> , <i>Halalaimus</i>	

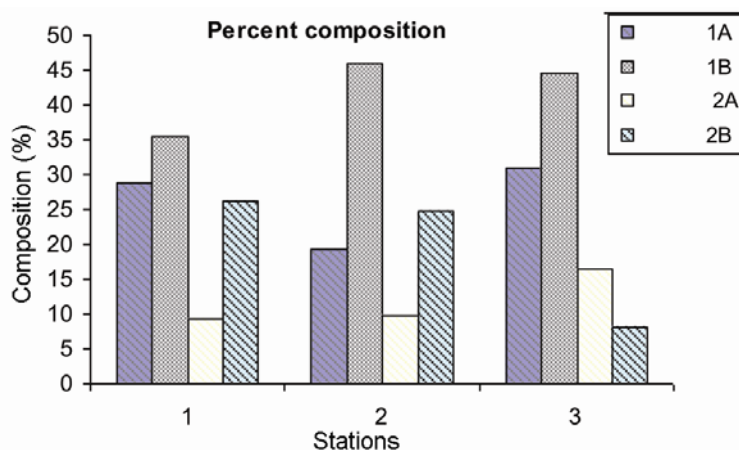


Figure 5. Nematode feeding types (%) at three different stations.

Feeding type of nematodes

The data on the nematode feeding types showed a significant dominance ($P < 0.001$) of deposit feeder. At stn 1, 39% of the nematodes were non-selective and 35%, selective feeders in the surface layer (Figure 5). The epistrate and omnivore were abundant in the mid- and deeper depths. At stn 2, selective feeders were most abundant at top layer and their density decreased downwards. Non-selective and predators were higher at deeper sediment depth. At the third station, selective and non-selective feeders were most dominant in all the sub-sections. However, predator and non-selective feeders were higher in deeper sections. Nematode feeding types showed different abundance patterns among the stations and between the sediment sections (Figure 3). A distinct pattern was seen in their vertical distribution and feeding habit, selective feeders being dominant in the top sediment layers. Overall, *Paralinhomoeus* and *Sabatieria* were most dominant at stn 1. However, the maximum density of selective feeding *Paralinhomoeus* occurred in the surface layers. Non-selective feeding *Sabatieria* appears to burrow deeper into the sediment as their density was higher in deeper sections. *Terschellingia*, *Sabatieria*, *Dap-*

tonema, *Siphonolaimus* and *Theristus* were most abundant at stn 2. Among these, the selective feeding *Terschellingia* was dominant in the top layer, whereas their density was very low at 12–14 cm. The non-selective deposit feeding *Sabatieria* showed higher abundances in lower sediment depths. *Sabatieria*, *Terschellingia*, *Araeolaimus* and *Halalaimus* were most abundant at stn 3. Among these, *Terschellingia* and *Sabatieria* were mostly found in the top 0–2 cm layer. After that, a sharp decreasing pattern was observed till 12 cm where another increasing peak occurred at deeper depths.

Discussion

The values for total meiofauna densities were comparable to those reported from similar depths in the Indian Ocean¹⁵. However, some caution is warranted because different sampling strategies have been used together with different collection and extraction techniques. Nevertheless, the meiofaunal density in the present study was marginally higher perhaps due to the higher amount of food input from the surface water and biogeochemistry of sediments¹⁶. Although data on organic carbon and sedimentary chlorophyll *a* was not available for compari-

son, the evidence that nematodes are influenced directly or indirectly by the quality and quantity of food supply is diverse^{17,18}. Due to the high abundance of deposit feeder at surface and deeper depths (Table 3), the Index of equality (J') was high in the respective sections. Such trend possibly could result from the partitioning of available resources (food, oxygen, texture, etc.). While discussing the vertical distribution of deep-sea meiofauna, Ingole *et al.*^{15,19} suggested that, food availability is the key factor for downward movement of meiofauna in the sediment. Further, as shown in Figure 2, although a general decrease in nematode abundance was seen in sediment depths, the unexpected increase in their abundance at some section suggests the availability of buried organic matter in the deeper sections. An important feature of nematode populations is that there are a large number of species present in a single habitat²⁰. Predatory *Sphaerolaimus* was usually found at deeper depth. *Sphaerolaimus* sp. usually avoids areas of higher organic input²¹ and was therefore restricted to the deeper sediment sections. On other hand, the non-selective feeding *Sabatieria* and selective feeding *Terschellingia* are efficient explorers of organic material^{22,23}. Consequently, they were mostly recorded in the sediment surface. The higher abundance of both these species in the top layer could be vital in marine decomposition processes through the direct consumption of detritus and more importantly, through grazing of heterotrophic bacteria. Hence, the specific feeding strategies and availability of organic material ultimately restrict the nematode species at particular location of sediment depth.

The smaller individuals, with their lower mobility, were preferentially found in the upper sediment layers. This is attributed to the inability of these organisms to penetrate into the deeper layers of the sediment. While describing the vertical distribution of benthic foraminifera and other meiofauna, Gooday²⁴ and Soetaert and Heip²⁵ reported that, species richness usually decreases with increasing sediment depth. Moreover, the meiofaunal diversity depends on the habitat and a geographical location of the study area. Nevertheless, the muddy sediment contains high diversity than the sandy habitat²⁶. The finer particles are known to contain high organic carbon and may be the striking sedimentary feature for observed higher nematode density in upper sections.

Vertical distribution of nematodes

As shown in Figures 2–4, the nematode diversity was remarkably high in the top 0–2 cm sections compared to other layers which may be due to more favourable conditions at superficial layers (less compact, more food), enabling more species to coexist. Soetaert and Heip²⁵ showed that smaller individuals, with their lower mobility, were preferentially found in the upper sediment layers, and

attributed this to the inability of these organisms to penetrate into the deeper layers of the sediment. The vertical distribution of nematodes showed 70% of the individual actually inhabited in upper 4 cm of the sediment (Figure 3), which agrees with the earlier studies²⁷. In deeper waters, penetration of nematodes into the sediment diminishes, mainly due to the resource limitation. However, sometime the deep burrowing macrofauna such as polychaete and burrowing holothurians and anemones may facilitate the immigration of finer organisms in deeper sections through the bioturbation, which may help nematode to inhabit in deeper sedimentary layers¹⁹. Consequently, we believe that, the feeding habit is important in regulation of the meiobenthic populations. It is in agreement with Soetaert *et al.*¹⁶ who suggested that, community structure of deep water nematodes is controlled by the biogeochemical condition of the sediment because food availability will decide the type of species that can survive in the preferred habitat. Although some other factors may affect the distribution of deep sea nematodes, in general the large sized organisms are more prominent at the eutrophic sites, whereas smaller organisms became more dominant in oligotrophic environments²⁸. This is most clearly expressed as a shift towards smaller sized taxa with increasing water depth²⁹. Our study also corroborates this finding as one of the most abundant *Paralinhomoeus* spp. was dominant at the surface layer. The reported average size of this genera is 3.8–4.4 mm, which is relatively larger compared to *Sphaerolaimus* sp. (length 1.6–1.8 mm) that was recorded in higher numbers at deeper sediment depth. Production in the pelagic water and delivery of food material in the form of particle flux to the seabed has been considered as main factors influencing the benthic structure³⁰.

The principle factor appeared to be the feeding pattern, which help to exploit the abundant food resource available in the surface sediment. Accordingly, the rich fauna, especially the nematodes not only utilize the abundant food material, but also help in rapid processing of food particles and make it available to other smaller and larger fauna. As a result, the role of nematodes as 'conveyor belt organism' in benthic habitat is explained in the food-rich environment, such as a continental Antarctica.

The community was dominated by deposit-feeding genera. Approximately, one-third of all nematode species however belong to the genus *Sabatieria* and *Terschellingia*, in agreement with earlier studies³¹. However, the k -dominance curves for nematode species clearly suggest the necessity of additional sampling to understand the nematode biodiversity of the area. Many nematodes have special food requirements and choose food according to their feeding habit³², hence selective recruitment of nematodes probably occurs at particular patches in the sediment concomitant to the quality and quantity of available food material. However, there are many sluggish nematodes in silty sediments which apparently do

not move over larger distances, so they are confined to a particular sediment depth, e.g. *Sphaerolaimus*, mostly found only at deeper sections.

Conclusion

Although comparing meiofaunal diversity on ocean-wide scales is difficult, primarily due to limited data sets and lack of species identification, the trends in the generic diversity and distribution were similar to those of Atlantic or Mediterranean and a distinct contrast was obvious between the North and South Polar regions. Surface productivity could be one of the drivers contributing to the striking difference in the nematode diversity.

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