University of Ghent
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Academic Year 2002-2003

Biodiversity and Distribution Patterns of Free-living Marine Nematode Communities in the Atlantic Sector of Southern Ocean

Hee Joong Lee

Promotor: Prof. Dr. Magda Vincx

Co-promotor: Dr. Sandra Vanhove

Thesis submitted in partial fulfilment of the requirement for the degree of Doctor of Philosophy (Biology)

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ACKNOWLEDGEMENT

I am finishing a spherical zigsaw puzzle that I did not know where to start. I started anyway from somewhere. From the starting point to today, I have met many people who helped me in one way or another.

Firstly I would like to express my sincere gratitude to Professor E. Gerlaert for providing me the great opportunity to come to Belgium. His dignity and calmness was always impressive. I remember him as one of the very kind persons to me.

Mrs. N. Smol was the person who welcomed and guided me to settle down in Gent. She always has been a great teacher, kind guardian and very open minded friend for me and my family. I am also deeply indebted to her for helping me to overcome my hard time I had some years ago.

Professor A. Coomans was one of the first lecturers during the PINC course. I am very grateful for his lucid explanation for those foreign students who have poor language background. However, I know that he is one of the professors who can see the deepest side of nematology. He made us feel comfortable with lectures, which encouraged us.

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I dedicate this thesis to my mother with love and also sprit of my departed father who could not wait for me to be back.

Hee Joong Lee

July 7, 2003

SUMMARY OF THE CHAPTERS

This study contains 6 chapters that are under the main theme of the free-living marine nematodes biodiversity and distribution pattern in the Atlantic sector of the Southern Ocean. Each chapter investigates biodiversity as the product of ecological and evolutionary processes, except for the first and the last chapter.

Chapter 1 introduces the general purposes of this study and material and methods that each chapter did not show each chapter was prepared as the manuscript for publication, and therefore not proper to include all details in that.

Chapter 2 firstly compares the difference of community patterns at family level and genus level in order to separate the effects of different time scales. For that, nematode communities in two regions, i.e. the east Weddell Sea and the west side of the Antarctic Peninsular that have different tectonic histories, are compared. This approach is based on the fact that the communities of nematodes are old enough to reflect such historical events and still preserve the effects in the form of community structure.

From the pattern obtained from the comparisons of various environmental factors, it is concluded that the different nematode communities found between the two areas are probably due to the different long term history rather than the current ecology.

Additionally, intrinsic causes for diversity are proposed based on the correlation of maturity index and feeding type with diversity.

Chapter 3 tries to project diversity phenomena through the species diversity of *Acantholaimus*, which showed high degree of diversification. The high endemism and coexistence of many species in one sample are attributed to their morphological diversity. There were three different forms of pharyngeal morphology, which might be the result of evolutionary diversion. It seemed that the nematodes in different pharyngeal forms have different biology and diversity, endemism and coexistence are related with that. Intrinsic factors are discussed based on that fact. The nematode with long slender pharynx tend to be rare despite the total species number of species in this forma is not smaller than the one with stronger pharynx and abundant. This implicates that the former probably tend to be *K*-strategists. It seems that such life style is related with diversity and endemism.

In chapter 4 the nematode community recovery processes after iceberg scouring in a shallow coast off Signy Island is explained. Finding that such chronic iceberg scouring causes dramatic changes in abundance, but not other community properties like taxonomic composition, trophic composition, MI and diversity, it conclude that the nematode community in this area has gone through natural selection processes and the current communities are well adapted to such phenomena. A question arose is that whether a local speciation have happened or not due to such sever disturbance that might act as a barrier.

Chapter 5 is parallel to chapter 4 in that the influence of iceberg scouring on nematode community and their recovery is investigated. The material for the study of this chapter comes from the Weddell Sea shelf where the disturbance regime must be different from the shallow coast off Signy Island. Unlike shallow water community that are exposed to chronic disturbances, the community in this area is greatly influenced not only in abundance but also diversity, taxonomic composition, feeding type and MI. The importance of biogenic substrates is proposed. It concludes that the recovery of nematode community in this area must be slow process, not because of nematode resilience but because of the removal of the biogenic 'mats' that are bryozoan and sponge debris.

Chapter 6 is the only taxonomic part and describes *Acantholaimus* species identified for the study of Chapter 3. *Acantholaimus* is currently classified as a member of Chromadoridae. However, this study suggests that Acantholaimus need to be separated from Chromadoridae based on the pharyngeal morphology, cuticular pattern, buccal morphology and round amphids that are internally coiled.

Chapter 1

General Introduction

1.1. General Introduction

Antarctic Ocean is the least known place among other seas about marine free-living nematodes and meiofauna in terms of taxonomy and ecology. The early history of the study of free-living nematode in this area goes up to Linstow (1892) who described some nematode from South Georgia. Since then there were only a few occasions of taxonomic research on the free-living nematodes in the Antarctic regions for more than one century: Cobb (1914), 2 new genera, 25 new species from Ross Sea from the material collected on the Shackleton Expedition; Steiner (1931), The large fauna obtained at Gauss Station by German South Polar expedition; Allgen (1959) ,92 genera, 343 species (13 new genera, 200 new species) from Magellan Region, The Falkland Islands, South Georgia and Antarctic peninsular; Mawson (1956), 36 species from East Antarctica (27 n. sp., 1 n. gen.); Mawson (1958) 24 sp. (10 n. sp.). The remoteness and hostile climate in the Antarctic that hindered people's approach were provably the major reason for the delay of researches in this area.

Owing to improved technology, the researches on the Antarctic meiofauna have been growing during recent decades. Researches on meiobenthos of this area also have been accomplished, marching in step with this growing scientific mood (Herman and Dahms, 1992; Lee *et al.*, 2001a; Lee *et al.*, 2001b; Vanhove, 1997; Vanhove *et al.*, 1999; Vanhove *et al.*, 1998; Vanhove *et al.*, 1995). Due to those studies that focused on the meiofauna and nematode community ecology in Weddell Sea area, our knowledge on meiofauna in this area is accumulating, even though what was found is the part of the iceberg.

Modern ecology tends to view ecology in more global aspects, considering the Earth as a single system (Lawton, 2001). However, there are also important processes that contribute to the global system and without understanding such processes the tries to view the ecology as a simple system might become too superficial. Biodiversity is one of the hottest issues in contemporary ecology and it might be helpful to draw a large picture of the single Earth system. Understanding why diversity in one area differs from others, why a certain taxon has more diverse species than others is a quite complicate matter. Biodiversity is the product of two basic processes that are ecological (competition, migration and biotic and abiotic interactions, for example) and historical (speciation, extinction, for instance) processes which are working on the diversity pattern in different time scales. Although many researches are focused on this subject, there is yet no consensus among scientists (Gray, 2001).

The two different study areas of this study, the east Weddell Sea coast and the Antarctic Peninsula coast, are different in both ecological and historical point of view. Virtually there is no shallow coast in the east Weddell Sea, because it is permanently covered with ice shelf which extends to continental shelf, whilst it is ice free in most areas of AP. This means that the ecological processes of shallow coasts of the two areas might be very different. Since the Antarctic Peninsula is located more to the north and close to South American continent, this area has a closer relationship with other seas than the east Weddell Sea does, which is the matter of the easiness of exchanging community members. Therefore we can consider the Antarctic Peninsula area as intermediate ecological states between the high Antarctic and other temporal seas. Such differences of environmental regime between the east Weddell Sea and the Antarctic Peninsula area might be reflected by faunal communities. Also the two areas have different geological histories (Clarke, 2003) that can go back to several hundred million years ago. Therefore it must be an interesting place to study on how the short term and long term processes influence on the formation of community structures. We do not know whether the current communities are product of ecological processes or historical processes. More specifically speaking, because the current ecological processes will blur out the historical processes with time, we do not know how much track of such historical event is remained in the current community properties.

The expectation that these differences will be mirrored by nematode communities is a part of the background ideas of this study in spite of the fact that marine biotopes have virtually no clear physical barriers and therefore dispersal of community members and other ecological process probably veil the long term historical effects with time. If the communities reflect both contrasting processes, can we differentiate the influences of two different processes? With the aide of fossil records, it would be much easier to compare the influence of the two different processes. However, free-living marine nematodes don't leave any such evidence. Therefore, it is actually impossible to quantify the influence of two different processes. We can only contrast them if possible, and with much speculation involved.

The aim of this study is to visualise the influence of ecological and historical processes on communities and consequent diversity patterns by observing nematode community in different ecological conditions.

1.2. Study area and sampling methods

This study was based on the materials obtained in three different sampling campaigns. The first campaign was accomplished in 1993 by Sandra Vanhove and Miriam Beghyn at the coast of Factory Cove near the British Antarctic Survey base in Signy Island, Antarctica (Fig. 1.1).

The samples were taken in time series from 17th December 1993 until 23rd August 1994. The samples for this study was taken in this area just from after the moment of the retreat of an iceberg that anchored several days and left a scour mark till 250th days after. This iceberg scour mark provided an excellent opportunity to study on a community recovery. More details of situation and sampling methods are described in Chapter 4.

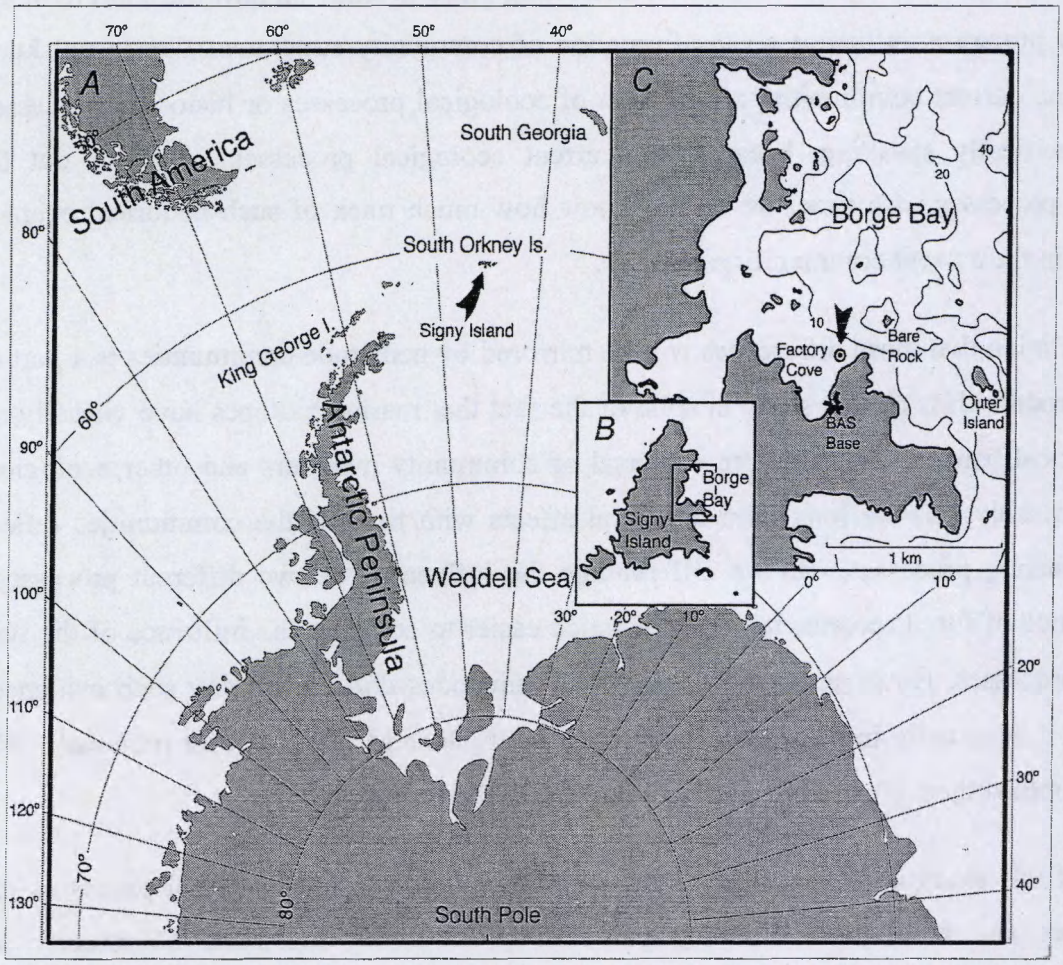

Fig. 1.1 A map showing the sampling station of Signy Island.

The second campaign, the first EASIS (Ecology of Antarctic Sea Ice Zone) cruise, took place from 26th Jamuary till 15th March 1996. The sampling activity during this cruise was focused along the east coast of Weddell Sea. This multi-discipline campaign aimed to 1) investigate the resilience of Antarctic benthic communities in relation with iceberg scouring, 2) define pelago-benthic coupling and the role of suspension feeders, 3) study on population dynamics, reproductive biology and ecophysiology of benthos and fish key species, 4) inventories and measure the biodiversity within high Antarctic benthic community by using ROV sequence and trawl samples, 5) study on the occurrence and characteristics of meiobenthic fauna and 6) provide comprehensive data on food availability and characteristics of pelagic food offer for Weddell seals and Emperor penguins in the Drescher Inlet area (Arntz and Gutt, 1997). Apart from the main objectives of the cruise our own aim was to obtain meiobenthic samples for taxonomic and ecological studies.

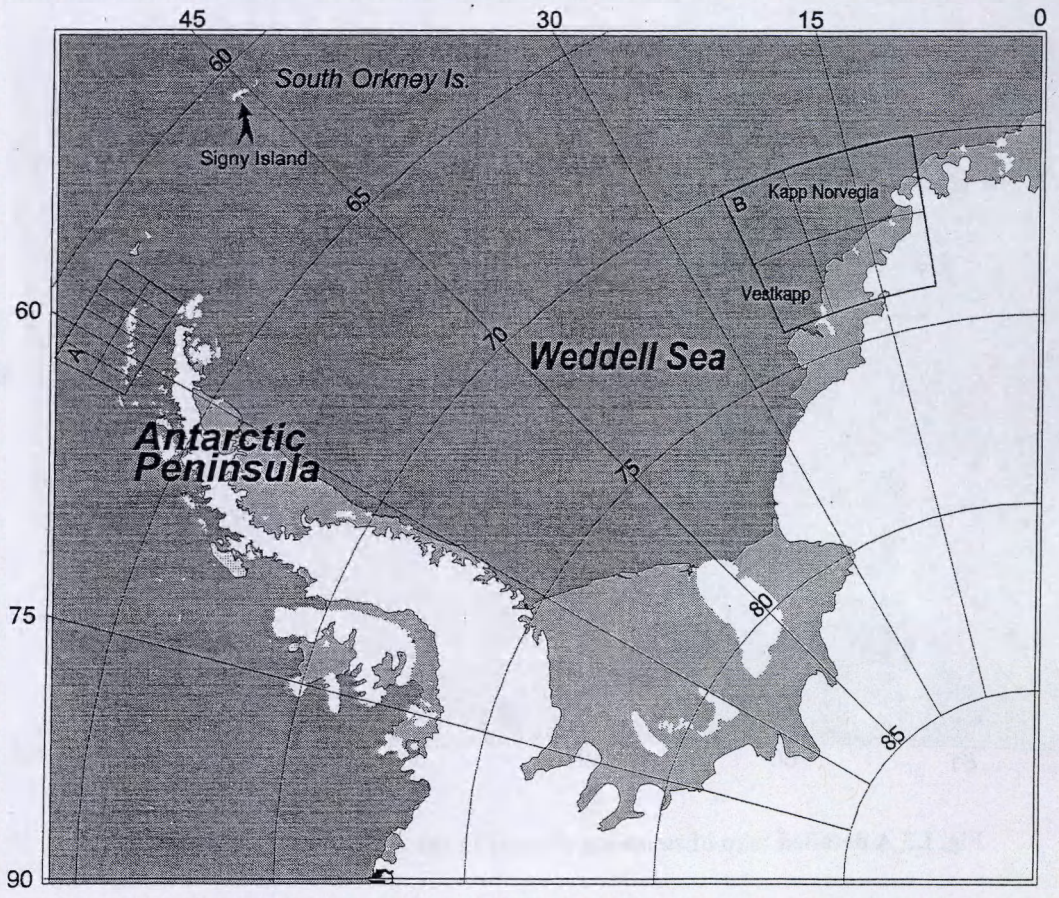

Fig. 1.2 A general map showing the sampling area of the first and second EASIZ expeditions. A, the sampling area of the Antarctic Peninsula. B, the sampling area of the east Weddell Sea coast.

The third campaign, EASIZ II, which began on 13th January from Cape Town in South Africa and finished on 26th at Punta Arenas in Chile, was a kind of continuation of the former campaign (EASIZ I) and basically followed the same objectives of the former one. One objective added to this second EASIZ campaign was to link the biodiversity and evolutionary relationship between high Antarctic and Antarctic Peninsula communities. For this reason, the sampling area was expanded to the Antarctic Peninsula area.

Sampling method from Singy Island was different from the rests. In Signy Island, the sampling station was a shallow spot and therefore samples could be taken by SCUBA divers by using hand corers. The hand corer had a diameter about 5.05 cm that provides a sediment core of 20 cm^2 surface area. The entire sediment was preserved with 4% neutral hot formarin without slice.

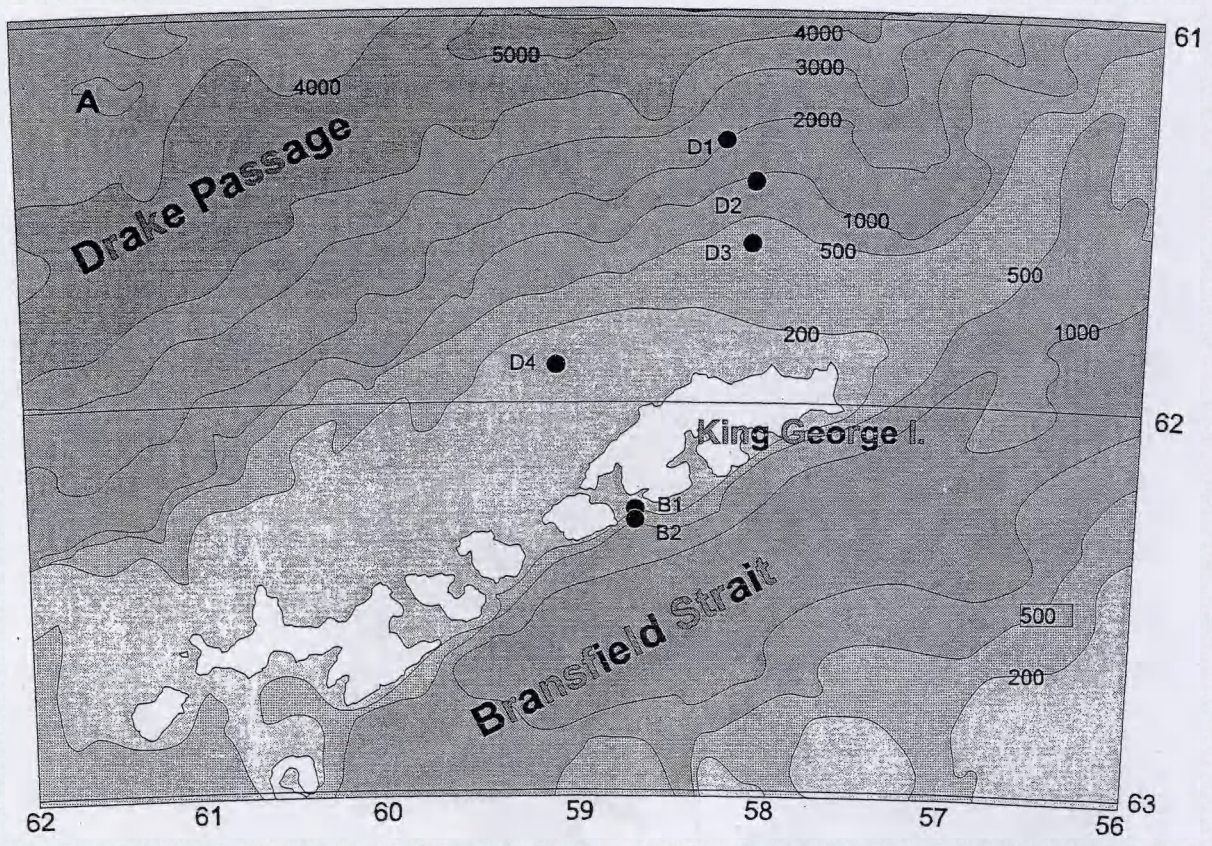

Fig. 1.3 A detailed map of sampling stations in the Antarctic Peninsula

The samples in Weddell Sea were taken mainly by using MG (multi box corer). In some occasions a multi corer was used. However, all sediment samples taken by MG were used for this study. The sediments in box cores were sub-sampled with four hand cores (diameter, about 3.6 cm) for faunal analysis. Three sediment cores cores were sliced 0-1, 1-3, 3-5, 5-10 cm on board and preserved with 4% neutral hot formarin solution. The fourth core was sliced into 1 cm layers up to 3 cm for sediment analysis. Two additional cores with diameter about 5.05 cm was taken for environmental analysis and sliced into 1 cm layer up to 3 cm and divided into 3 fractions using epithermal syringe that provide 1 cm^2 in volume. This series of work provided triplicates of sediment samples in different depth and samples for sediment analysis and measurements of pigments concentration, nutrient composition and bacteria density.

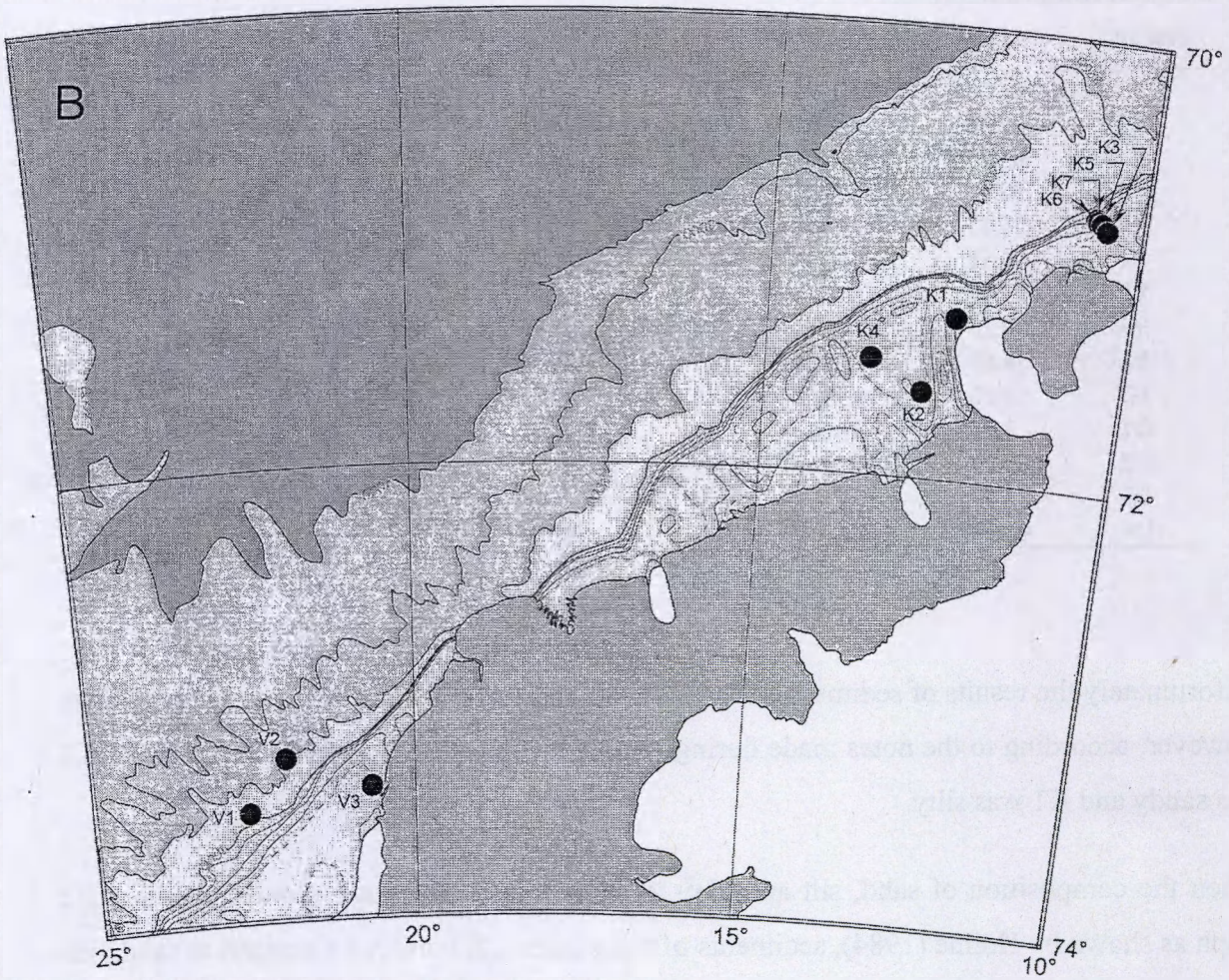

Fig. 1.4 A detailed map showing the sampling stations in the east Weddell Sea.

1.3. Environmental parameters

1.3.1. Sediment texture

The sediment size characteristics of 14 stations are presented in Table 1.1.

The coarsest sediment was found at K3 (144.5 μm and 195.1 μm, mean and median size, respectively) while the finest sediment was found at D1 (7.8 μm and 8.7 μm, mean and median size, respectively). The most part of sediment are sand and silt and clay part were negligible in most stations in this area. In general the granule size decreased with increasing depth. The sediments in Antarctic Peninsula were finer compared with east Weddell Sea sediments.

Table 1.1 Mean and median size of sediment and their size and frequency distribution in 14 stations

Station	mean	median	Frequency %				
			10	25	50	75	90
K3	144.50	195.13	670	424	195	88	19
K4	79.86	100.92	548	261	101	37	10
K5	64.70	107.46	550	281	107	20	3
K6	36.30	49.29	389	157	49	9	2
K7	26.73	32.39	360	129	32	5	2
V1	76.75	101.03	323	169	101	55	11
V2	23.44	38.93	131	81	39	8	2
V3	90.25	112.06	314	171	112	63	19
B1	14.69	14.87	165	92	15	3	1
B2	9.65	10.13	60	29	10	4	1
D1	7.77	8.66	43	22	9	3	1
D2	60.21	147.83	388	269	148	14	3
D3	23.87	35.13	157	99	35	6	2
D4	44.14	83.13	397	203	83	9	2

Unfortunately the results of sediment analysis of two stations – K1 and K2 - are not available. However, according to the notes made during sample treatment on board, the sediment of K2 was sandy and K1 was silty.

When the composition of sand, silt and clay fraction compositions are plotted in a triangle graph as shown by Holme (1984), sediments of two stations, K3 and V3 belonged to sand. Six stations, i.e. V1, K4, K5, K6, D2 and D4 belonged to silty sand. The sediments of two stations, B1 and K3, were sand-silt-clay. Sandy silt sediments were from V3 and D2. The finest sediment, clayey silt, was found at B2 and D1 (Fig. 1.5).

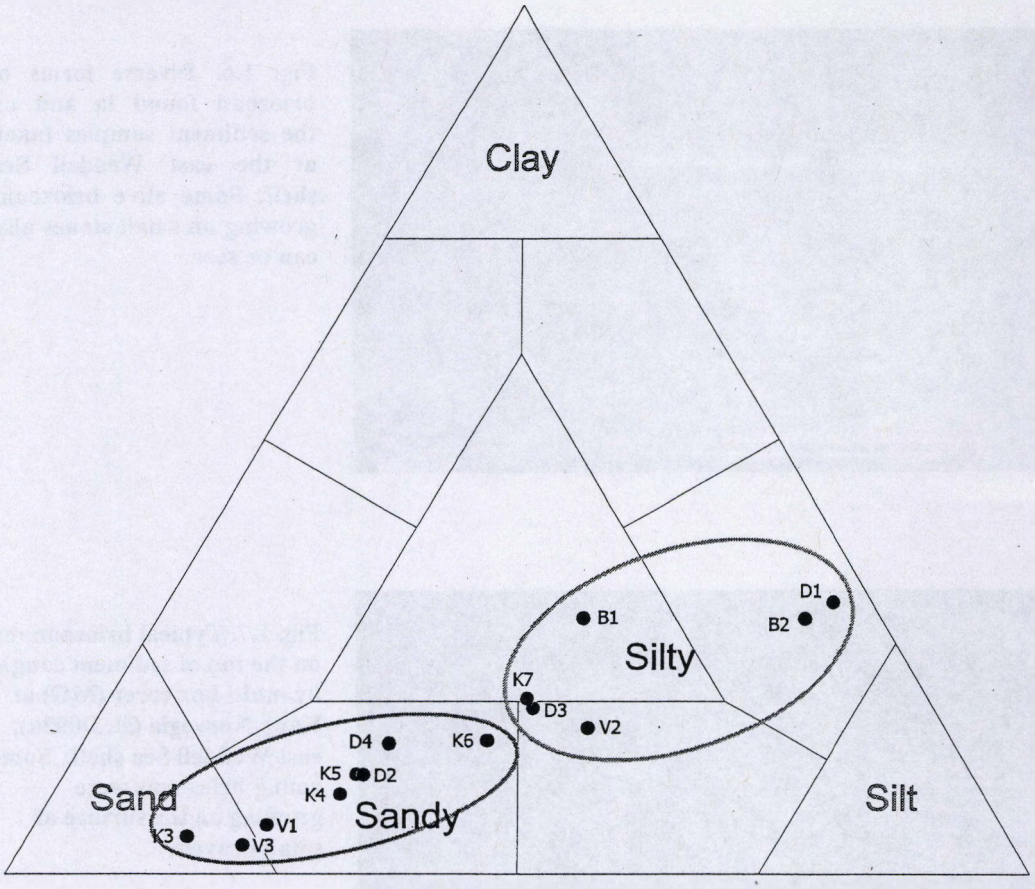

Fig. 1.5. Triangular graph shows the sediment composition of each station. The stations could be roughly separated into two groups, sandy and silty sediment, by sediment composition and size characteristics.

1.3.2. Biogenic substrates

A remarkable feature of east Weddell Sea shelf sediment substrates is that most part of of them are, to a certain degree of thickness, covered by the coverage of sponge or/and briozoan mat. Briozoan and sponge communities are divers and abundant in the coast of east Weddell Sea and they leave hard substrate debris after die (Fig. 1.6). They accumulate on the surface of sediments and formed a mat of various thicknesses. The sediment underneath those mats is ordinary soft sediment and two clearly different micro habitats coexist at the same place (Fig. 1.7). The ecological influence of these mats to associated community must be significant. One of the very obvious phenomena found during sampling is the association of diverse nematode species of family Leptosomatidae, i.e. *Deontostoma* and *Pseudocella*, socially with sponge spicule mat (Fig. 1.8, Fig. 1.9). *Deontostoma* and *Pseudocella* are not found anywhere else in the soft sediment samples of this study.

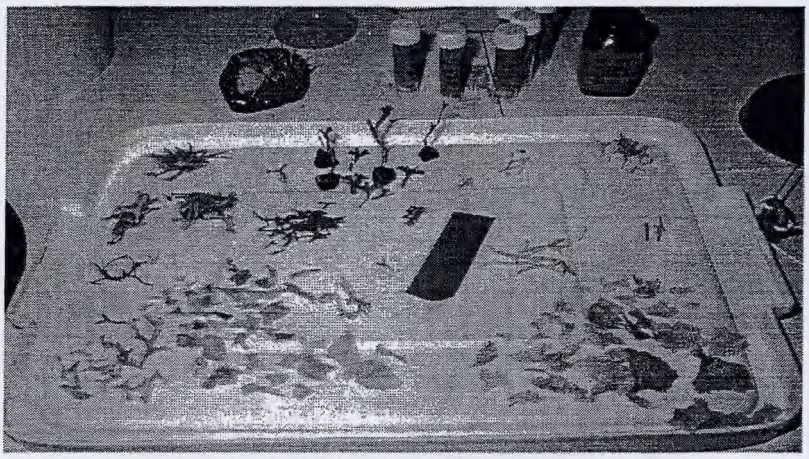

Fig. 1.6. Diverse forms of briozoan found in and on the sediment samples taken at the east Weddell Sea shelf. Some alive briozoans growing on small stones also can be seen.

Fig. 1.7. Typical briozoan mat on the top of sediment caught by multi box corer (MG) at Kapp Norvegia (st. D002a), east Weddell Sea shelf. Some young briozoans were growing on the surface of small gravels.

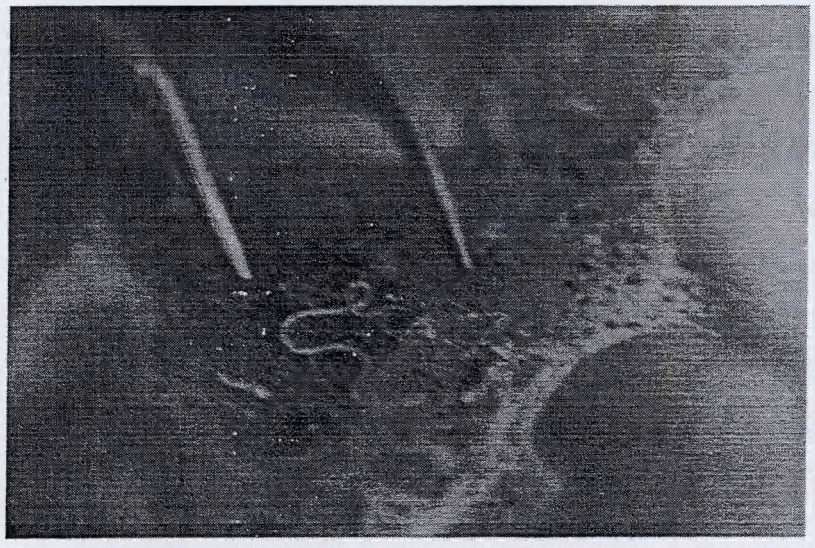

Fig. 1.8. *Deontostoma* sp. living in a sponge spicule mat. They are unusually large for free-living marine nematode. It seemed that they have no problem to move between very sharp glassy sponge spicules.

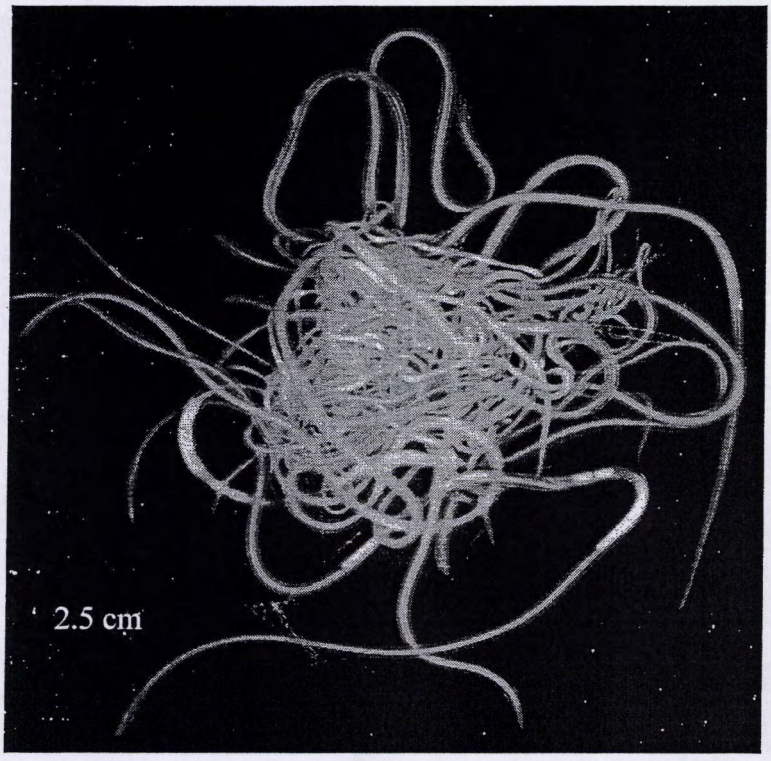

Fig. 1.9. *Deontostoma* and *Pseudocella* species collected from a sponge spicule mat caught by Martin's shopping bag in the shelf of east Weddell Sea during EASIS I sampling cruise.

These nematodes are one of the largest free-living marine nematode species. The photo was taken using a photo camera attached binocular stereo microscope.

1.3.3. Chlorophyll-*a*

The concentration of chlorophyll represented by chlorophyll-*a* (Chl-*a*) varied greatly from station to station and to region to region (Fig. 1.10). There were three stations where the concentration of Chl-*a* was not detected (V1, V2 and K5). All of them are east Weddell Sea stations and either deep sea or disturbed stations. The highest concentration was detected at B2 (average 375 ng/mg dwt) followed by B1 (average 249 ng/mg dwt) and D4 (138 ng/mg dwt), average concentration, which are all from the Antarctic Peninsula. In the case of the east Weddell Sea stations, highest concentration was detected at K4 (average 73 ng/mg dwt) followed by K3 (average 65 ng/mg dwt) and V3 (average 32 ng/mg dwt). In general, the Antarctic Peninsula stations and shallow stations showed higher Chl-*a* concentration compared to the east Weddell Sea stations and deeper stations.

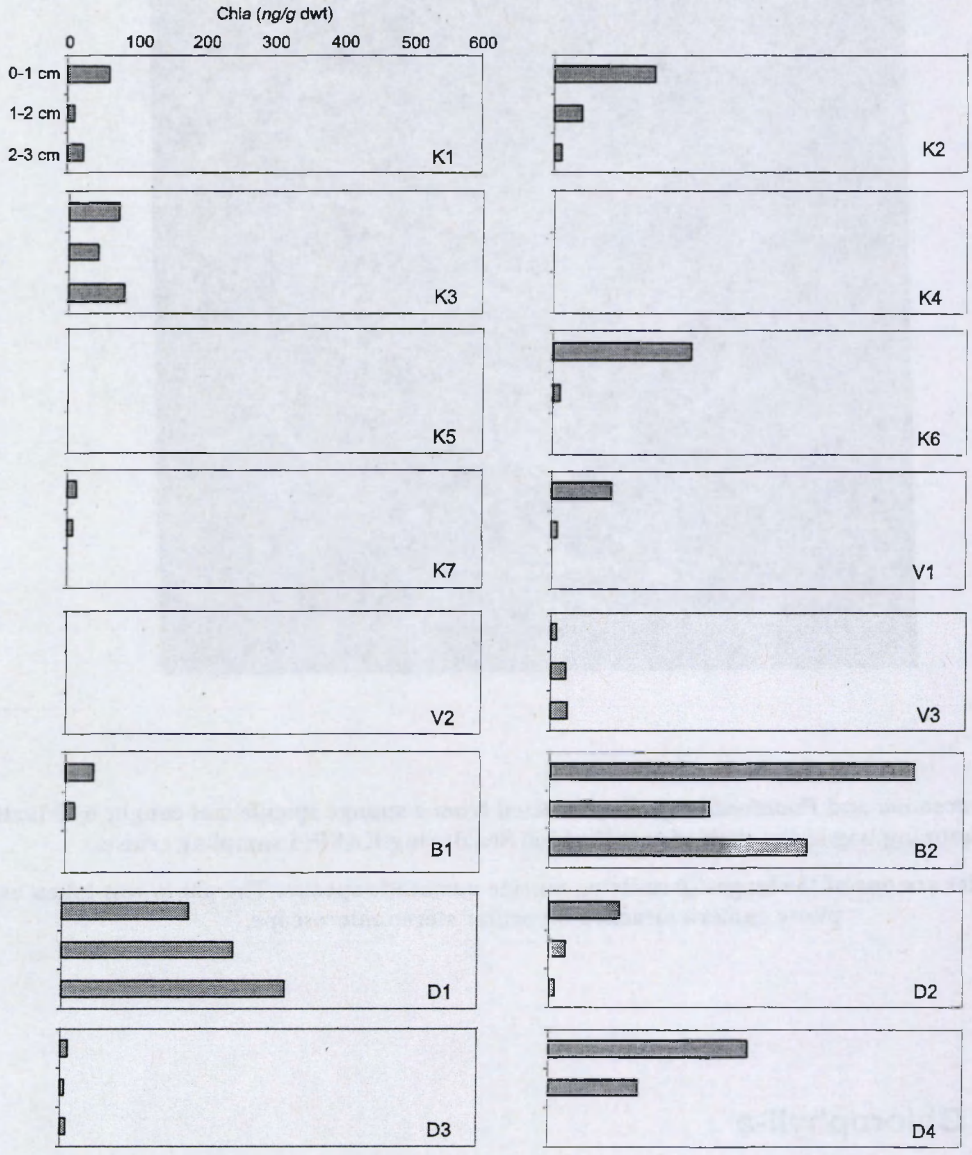

Fig. 1.10. Concentration of Chl-*a* (ng/g, dry weight) in the sediment column from the top to 3 cm deep.

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Chapter 2

Nematode diversity and community structure and the defining factors

2.1. Abstract

Study on nematode communities in the Southern Ocean have a short history and mainly focused on local scale ecology. This study compares nematode communities between two regions of the Atlantic sector of the Southern Ocean – the east Weddell Sea and the coast off the west Antarctic Peninsular - and two areas from each of them - Kapp Norvegia and Vestkapp in the Weddell Sea; Bransfield Strait and Drake Passage in Antarctic Peninsular - in relation to geography, water depth and sediment heterogeneity.

Bransfield Strait communities from the Antarctic Peninsular showed the highest density, which seemed to be related to food availability (higher concentration of Chl-a), but lowest diversity in terms of genus number. Kapp Norvegia and Vestkapp communities showed higher diversity but lower density compared to the Antarctic Peninsular communities. Monhysterids (*Monhystera*) were the most dominant nematode group in the Weddell Sea while Comesomatids (*Sabatieria*) predominated in the Antarctic Peninsular.

The environmental factors influenced differently on the nematode community structure. Depth was the main factor that structures the Antarctic Peninsular communities. The presence of biogenic substrates such as sponge spicules and bryozoan debris was important for characterising the Kapp Norvegia communities. They also seemed to enhance habitat complexity increasing of this area. However, these factors could not overcome the geographical distance between the Antarctic Peninsular and the Weddell Sea, which implies that, for nematode distribution, the historical background is more important rather than local contemporary ecological processes.

Maturity Index (MI) showed a high correlation with alpha-diversity and is recognised as an important intrinsic factor to explain alpha-diversity. This implies that diversity can not be explained solely by local or/and historical ecological processes.

2.2. Introduction

Biodiversity pattern along environmental gradients is in debate, which was triggered by Sanders (Sanders, 1968) who produced hypotheses that marine diversity increases from poles to tropic and from shallow water to deep water.

Although some studies (Rex *et al.*, 1993; Roy *et al.*, 1996; Roy *et al.*, 1998) in northern hemisphere observed latitudinal cline, generalising it is more complicate matter (Clark, 1992; Gage, 1996). Gray (2001) states that high deep-sea alpha diversity can not be directly compared with that in shallow water, because of the differences in habitat diversity between both systems. He doubts if the same pattern exists in the southern hemisphere.

In deed, the Southern Ocean is less studied and answering about the diversity gradient in this marine ecosystem is beyond our data collection and the picture is still unclear, nevertheless it is rather well known that the Antarctic macrobenthic diversity is not lower than other places (Arntz and Gallardo, 1994).

Nematodes are considered as one of the most diverse and wide distributed metazoan organisms. Lambshead *et al.* (2003a; 2003b) proposed the possibility of nematode being a hyperdiverse taxon (> 1 million species) and deep sea as a potential hyperdiverse habitat. This is quite probable when the high number of nematode species that can be obtained from one sample and high species turnover are considered.

Nematodes have many assets as ecological tools: 1) relatively short life-cycles that completes with in the benthic system provide better observation on environment-community linkage 2) being ubiquitous, they are available everywhere 3) relatively small amount of samples of them can be taken with less efforts than for larger animals 4) cosmopolitan distribution of genera make comparison easy while complexity of community structure lead by various taxa provide comprehensive information on local ecology 5) rather easily determinable functional groups such as Wieser's (1953) feeding type and additional MI (maturity index, Bongers *et al.* 1991) provide insights to intrinsic community response to extrinsic changes.

For this reason, they can be considered as ideal objects in many ecological subjects. Research on the Antarctic nematode ecology has a short history and some results are

known to science. Vanhove *et al.* (1997; 1999; 1998; 1995) describe the nematode community response to biochemical profiles and their community structure in relation to various environmental variables in some different regions and bathymetric depths in Antarctic areas. Lee *et al.* (2001a; 2001b) try to contrast physical iceberg scouring effects on two different nematode communities and their resilience. However, our knowledge is still the part of the iceberg.

The aims of this study are 1) to describe the nematode community structure and distribution patterns in the study area, 2) to find out the how geography, depth and sediment heterogeneity influence on the nematode community structure, distribution and their diversity.

2.3. Material and Methods

2.3.1. Sampling area and methods

Samples were collected from 4 different areas of 2 regions in Atlantic sector of Southern Ocean - Kapp Norvegia (KN) and Vestkapp (VK) in the Weddell Sea (WS) region and Bransfield Strait (BS) and Drake Passage (DP) in Antarctic Peninsula (AP) region - during the first and second EASIZ cruise (26th January - 15 March 1996 and 13th January - 26th March 1998, respectively) by means of a multi-box corer (Gerdes, 1990) from stations with different biotopes (Table 2.1).

Table 2.1.Location, depth, gear number, chlorophyll-*a* concentration, sediment type and size of samples for this study

Region	Area	Station	Depth (m)	Gear No.	Location		Chl-*a* (ng/g dwt)	Sediment			Remarks
					Latitude	Longitude		Type	Size (µm) Mean	Size (µm) Median	
WS	KN	K1	182	MG27	71°19.7'	012°24.8'	31.42	Sandy	na	na	sp/br
		K2	216	MG23	71°40.1'	012°47.2'	65.53	Sandy	na	na	-
		K3	243	MG1	70°52.1'	010°29.4'	64.9	Sandy	75.8	111.0	br
		K4	255	MG19	71°32.3'	013°31.7'	73.83	Sandy	51.0	72.4	o. s.
		K5	278	MG24	70°50.1'	010°35.2'	nd	Sandy	28.3	43.4	f. s.
		K6	332	MG25	70°49.4'	010°38.7'	19.19	Sandy	52.1	71.6	br
		K7	298	MG26	70°49.8'	010°38.0'	7.02	Silty	42.5	55.9	sp
	VK	V1	993	MG10	73°34.2'	022°38.0'	nd	Sandy	76.8	101.0	-
		V2	1944	MG14	73°23.7'	022°09.1'	nd	Silty	23.4	38.9	-
		V3	220	MG17	73°28.4'	020°40.8'	31.66	Sandy	94.1	112.1	-
AP	BS	B1	207	MG28	62°15.8'	058°42.7'	249.47	Silty	26.4	38.6	-
		B2	423	MG29	62°16.8'	058°42.1'	375.83	Silty	8.5	9.6	-
	DP	D1	2009	MG32	61°20.6'	058°15.1'	8.09	Silty	7.8	8.7	-
		D2	1028	MG33	61°26.7'	058°06.6'	44.24	Sandy	60.2	147.8	-
		D3	429	MG34	61°34.5'	058°07.0'	78.59	Silty	29.8	36.0	-
		D4	218	MG35	61°53.3'	059°06.9'	138.04	Sandy	25.9	39.2	-

Abbreviations for geographical names: WS, Weddell Sea; **AP,** Antarctic Peninsula; **KN,** Kapp Norvegia; **VK,** Vestkapp; **BS,** Bransfield Strait; **DP,** Drake Passage.

Abbreviations for remarks: sp, sponge spicule mat; **br,** bryozoan debris; **sp/br,** mat mixed with sponge spicules and bryozoan debris; **o.s.,** old scour; **f.s.** fresh scour.

Other abbreviations: na, not available; **nd,** not detected; **-,** inapplicable; **MG,** multi-box corer.

2.3.2. Sample treatment

Three standard meiofauna-hand-cores (10 cm2 surface area) for the meiofauna and a large hand-core (diameter about 6 cm) for sediment analyses were taken from one box-core of each station. The sediment cores were sliced into 5 layers (0-1, 1-3, 3-5, 5-10 cm and the rest) immediately after the samples were recovered on board. Only the three top

layers up to 5cm, where the majority of meiofauna dwells, were used for this study. Meiofauna samples were preserved with 4 % neutral hot (60° C) formaldehyde solution on board before further studies in the home laboratory. Sediments were decanted and sieved over 1,000 and 32 µm mesh sizes. Animals passing the 1,000 µm sieve and retained on the 32 µm sieve were regarded as meiofauna. Final extraction of meiofauna was achieved using the LUDOX centrifugation flotation technique (Heip et al., 1985; McIntyre and Warwick, 1984). The number of all metazoan meiofauna was counted after staining with Rose Bengal. Approximately 100 nematodes (all, in samples with less than 100 individuals) per replicate were randomly picked out and dehydrated in a series of glycerine-alcohol solutions. The dehydrated nematodes were mounted on slides with anhydrous glycerine medium and sealed with paraffin wax.

2.3.3. Data Analysis

Diversity Index. Hill's (1973) diversity indices were calculated for *alpha*-diversity measurement:

Nematode species diversity was measured using Hill's diversity indices (Hill, 1973).

Hill's diversity numbers of a certain order '*a*' is given by:

$$N_a = \left\{ \sum_{i=1}^{s} p_i^a \right\}^{(1-1/a)}.$$

N_0 is the number of species.

$N_1 = \exp(H')$, where $H' = -\sum_{i=1}^{s} p_i \ln(p_i)$.

N_2 is the reciprocal of the Simpson's dominance index, therefore;

$$N_2 = \left\{ \sum_{i=1}^{s} p_i^2 \right\}^{-1}.$$

$N_\infty = p_i^{-1}$, where p_i = the relative abundance of the *i*th most dominant species.

Maturity Index (MI) and Feeding type. One of the indices, which can characterise nematode communities, is Bongers' MI (Maturity Index, Bongers, 1990; Bongers et al., 1991) which is the weighted mean of the *c-p* (colonisers-persisters) values.

The MI can be calculated as:

$$MI = \frac{\sum_{i=1}^{n}(v_i \cdot a_i)}{\sum_{i=1}^{n} a_i},$$

where v_i is the *c-p* value (see Bongers *et al.* 1991) assigned to taxon *i* and a_i is the abundance of taxon *i* in the sample. The MI is more widely used to assess soil pollution levels and the response of soil nematode communities to the pollutant. Bongers *et al.* (1991) suggests that MI may also be useful in assessing disturbance in marine and brackish water sediments.

For feeding type analysis, the traditional feeding classification of Wieser (1953) was used: 1A, selective deposit-feeders; 1B, non-selective deposit-feeders; 2A, epigrowth-feeders; 2B, omnivorous-carnivores.

ANOVA. Analysis of variance (ANOVA) was used to determine significant differences ($p<0.05$) for abundance and diversity. Subsequent post hoc comparison (Turkey HSD) was used on stations or station groups when data are pooled to compare *Acantholaimus* species distribution pattern along different environmental variables.

Multivariate methods. For the analysis of community distribution patterns, following multivariate analysis were performed: TWINSPAN (Two-Way Indicator Species Analysis; (Hill, 1979); Classification - clustering using the Bray-Curtis similarity matrix based; Detrended correspondence analysis (Hill and Gauch, 1980) are based on 4^{th} root transformed species abundance data and Canonical correspondence analysis (CCA; ter Braak, 1986) on 4^{th} transformed and pool abundance data together with environmental data to see if there is any relationship between communities and environmental parameters.

2.4. Results

2.4.1. Diversity and composition of family

Diversity. Total number and average number of families and 10 most important families and their relative abundances of each station are presented in Table 2.2.

A total of 42 families were retrieved from 16 triplicate sample sets. KN and VK showed high family richness containing all families found in this study whilst BS and DP consisted of 26 and 34 families lacking some families. In the case of average species number, VK was significantly higher (24.9) compared with KN (21.7) or BS (20.5). Among 16 stations, K6 in KN showed the highest total family number (34 families), which was equal to the total family number obtained from entire VK or whole area of AP. The least family number (15) was found at K5 which was a fresh iceberg scoured site.

Family composition. Concerning family composition, there were big difference between WS and AP (Table 2.2). In the case of WS, Monhysteridae was most dominant (14.5%) followed by Chromadoridae (13.4%), Comesomatidae (11.8%) and Xyalidae (11.4%). In AP, however, the dominance of Monhysteridae (3.4%) and Chromadoridae (5.0) depressed, and Comesomatidae (20.3%) and Xyalidae (12.9%) took the place over. The high dominance of Neotonchidae (6.5 %) was also remarkable, because this was one of the very rare (0.5%) families in WS.

In KN, dominance was shared by many different families like Epsilonematidae at K1, Comesomatidae at K2, Chromadoridae at K4, Desmoscolecidae at K6 although Monhysteridae was most dominant at 3 stations (K3, K5 and K7). In VK, Monhysteridae dominated the communities except for V1 where Desmodoridae was most dominant. However both areas, KN and VK, showed very similar family composition.

In the case of 2 stations of BS, the most dominant families were Comesomatidae at B1 and Microlaimidae at B2. In spite of difference of the most dominant families, the composition of families was similar between these two stations. In the case of DP, Comesomatidae was uncompromising dominant in all stations. The highest dominance of this family (48.8%) was found at the deepest station (D1). Xyalidae, Chromadoridae,

Leptolaimidae, Monhysteridae, Neotonchidae and Cyatholaimidae were also very dominant in this area.

Table 2.2 Occurrence of families (total family number (TFN) and average family number (MFN)), 10 most dominant families (IMF) and their relative dominance (%) in each station of the study area

Region	WS												
Area	KN							KN	VK			VK	WS
Station	K1	K2	K3	K4	K5	K6	K7		V1	V1	V2		
TFN.	29	25	29	27	15	34	29	42	30	28	28	34	42
MFN	24.7	21.3	24.0	19.7	11.7	27.7	22.7	21.7	24.3	26.0	24.3	24.9	22.6
10 MIF (%)	Epsi (11.6)	Come (22.0)	Monh (15.8)	Chro (25.5)	Monh (27.1)	Desm (20.1)	Monh (16.3)	Chro (14.8)	Monh (14.7)	Desd (17.4)	Monh (26.0)	Monh (15.5)	Monh (14.5)
	Xyal (9.5)	Xyal (21.1)	Desd (12.4)	Come (20.2)	Chro (25.7)	Monh (13.5)	Lept (12.8)	Monh (14.0)	Chro (11.9)	Come (13.3)	Chrom (13.8)	Chro (10.2)	Chro (13.4)
	Micr (9.4)	Chro (19.7)	Desm (10.4)	Mony (18.6)	Xyal (17.4)	Chro (12.5)	Desm (12.3)	Xyal (13.1)	Desm (9.0)	Micr (10.0)	Xyal (10.9)	Desd (10.1)	Come (11.8)
	Chro (8.9)	Monh (10.7)	Chro (10.2)	Xyal (12.2)	Come (7.8)	Xyal (6.8)	Chro (10.4)	Come (13.1)	Xyal (8.5)	Monh (9.9)	Come (9.9)	Come (8.9)	Xyal (11.4)
	Cyat (8.6)	Oxys (7.6)	Xyal (9.9)	Oxys (4.9)	Oxys (5.5)	Desm (6.1)	Xyal (9.4)	Desm (8.4)	Cyat (7.8)	Chro (7.1)	Lept (6.0)	Xyal (7.8)	Desm (7.0)
	Monh (8.6)	Desd (3.1)	Come (9.4)	Lept (3.5)	Spha (5.5)	Oxys (5.7)	Come (8.9)	Oxys (6.1)	Meyl (6.9)	Cyat (6.3)	Oxys (5.7)	Micr (6.7)	Desd (6.8)
	Desm (8.1)	Lept (3.0)	Oxys (5.4)	Desm (3.0)	Pris (2.8)	Micr (4.1)	Oxys (6.3)	Desd (5.3)	Desm (6.4)	Aegi (5.8)	Depl (4.1)	Cyat (5.4)	Oxys (5.4)
	Lept (5.1)	Aegi (2.5)	Micr (4.4)	Anti (2.3)	Aegi (1.4)	Lept (4.1)	Meyl (6.1)	Lept (4.7)	Lept (5.5)	Xyal (5.5)	Micr (3.7)	Lept (4.3)	Lept (4.6)
	Come (4.7)	Anti. (1.4)	Lept (3.3)	Desd (2.2)	Linh (0.9)	Meyl (3.7)	Desd (2.2)	Micr (2.4)	Micr (4.1)	Oxys (3.3)	Desm (3.7)	Desm (4.2)	Micr (3.7)
	Oxys (4.0)	Desm (1.3)	Linh (3.2)	Aegi (1.2)	Onch (0.9)	Cyat (3.3)	Dipl (2.1)	Meyl (2.1)	Aegi (3.4)	Dipl (3.0)	Iron (2.0)	Aegi (4.0)	Cyat (3.0)
	rest (21.6)	rest (9.6)	rest (15.6)	rest (6.4)	rest (5.0)	rest (20.2)	rest (13.3)	rest (16.0)	rest (21.8)	rest (18.3)	rest (14.1)	rest (22.9)	rest (18.4)

Region	AP										
Area	BS		BF	DP				DP	AP	Antarctic (Atlantic Sector)
Station	B1	B2		D1	D2	D3	D4			
TFN	23	25	26	27	31	21	24	33	34	42
MFN	20.0	21.0	20.5	22.0	26.7	19.7	22.3	22.7	21.9	22.4
10 MIF (%)	Come (21.4)	Micr (15.4)	Come (16.8)	Come (48.8)	Come (28.1)	Come (18.4)	Come (20.3)	Come (23.0)	Come (20.3)	Come (15.4)
	Desd (15.1)	Linh (14.6)	Xyal (12.6)	Lept (11.1)	Chro (9.8)	Xyal (17.4)	Xyal (13.1)	Xyal (13.1)	Xyal (12.9)	Monh (11.6)
	Xyal (11.7)	Xyal (14.0)	Desd (12.5)	Xyal (7.3)	Xyal (7.4)	Cyat (10.3)	Neot (9.5)	Chro (6.4)	Desd (6.4)	Xyal (11.4)
	Micr (7.8)	Come (9.9)	Micr (10.8)	Monh (7.0)	Lept (7.3)	Chro (7.6)	Linh (7.0)	Lept (6.3)	Micr (7.0)	Chro (11.0)
	Neot (6.9)	Neot (9.0)	Linh (9.2)	Chro (4.1)	Oxys (5.9)	Monh (6.9)	Desd (7.0)	Monh (5.8)	Neot (6.5)	Desd (6.3)
	Linh (5.6)	Desd (8.6)	Neot (7.7)	Oxys (3.7)	Demd (5.6)	Lept (5.8)	Micr (6.0)	Cyat (5.7)	Linh (5.8)	Desm (5.6)
	Lept (5.2)	Oxys (7.3)	Oxys (5.9)	Sela (2.8)	Desm (4.4)	Neot (5.7)	Monh (5.9)	Neot (5.6)	Lept (5.6)	Lept (5.3)
	Oxys (5.1)	Lept (4.0)	Lept (4.7)	Meyl (2.4)	Tref (4.0)	Desd (4.8)	Lept (5.3)	Desd (5.5)	Chro (5.0)	Oxys (5.0)
	Desm (4.8)	Chrom (3.9)	Cyat (3.4)	Cyat (2.2)	Monh (3.6)	Desm (4.5)	Oxys (3.9)	Oxys (4.1)	Oxys (4.9)	Micr (4.6)
	Cyat (3.6)	Cyat (3.3)	Desm (3.4)	Desm (1.9)	Dipl (3.5)	Micr (3.4)	Chro (3.9)	Micr (4.1)	Cyat (4.7)	Cyat (3.6)
	rest (13.0)	rest (10.0)	rest (8.7)	rest (20.4)	rest (15.2)	rest (12.9)	rest (18.2)	rest (20.3)	rest (18.6)	rest (12.9)

Aegi, Aegialoalaimidae; **Anti**; Anticomidae; **Epsi**, Epsilonematidae; **Neot**, Neotonchidae; **Chro**, Chromadoridae; **Come**, Comesomatidae; **Cyat**, Cyatholaimidae; **Desd**, Desmodoridae; **Desm**, Desmoscolecidae; **Dipl**, Diplopeltidae; **Epsi**, Epsilonematidae; **Iron**, Ironidae; **Lept**, Leptolaimidae; **Linh**, Linhomoeidae; **Meyl**, Meyliidae; **Micr**, Microlaimidae; **Monh**, Monhysteridae; **Onch**, Oncholaimidae; **Oxys**, Oxystominidae; **Pris**, Prismatolaimidae; **Sela**, Selachinematidae; **Spha**, Sphaerolaimidae; **Tref**, Trefusiidae; **Xyal**, Xyalidae;

2.4.2. Environment and community coupling on family level

CCA was carried out in order to test if there is any relationship between environmental factors and nematode communities (Fig. 2.1).

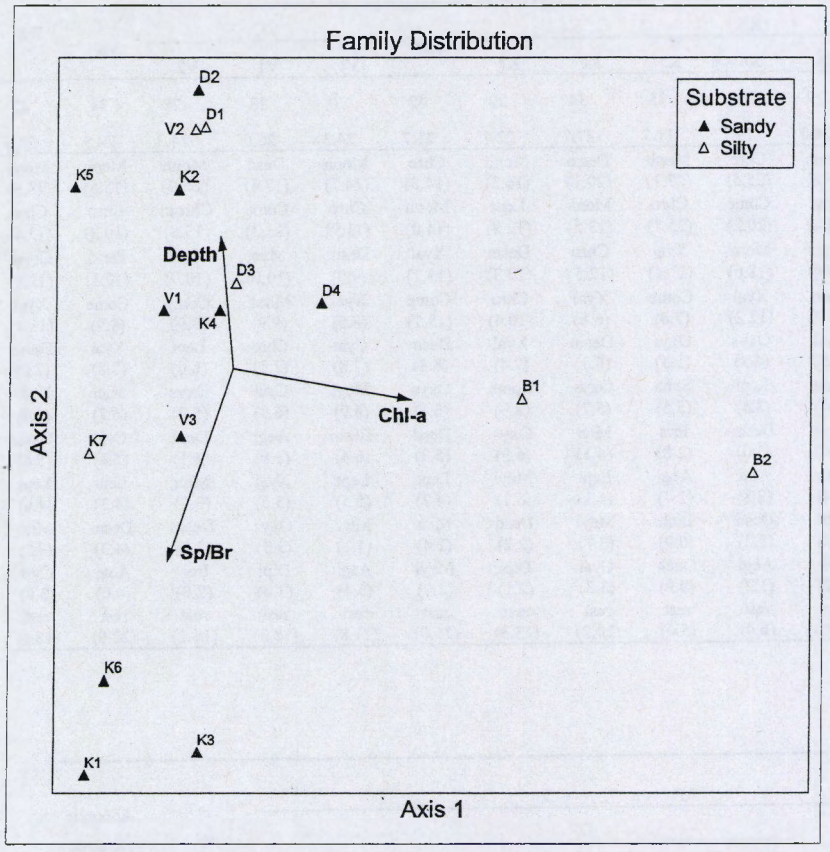

Fig. 2.1. CCA ordination based on 4th root transformed pooled family abundance and environment data.

The results showed that some environmental factors were ruling the communities at some stations: B1 and B2 were influenced by Chl-a concentration, K3, K6 and K1 were related with biogenic mats and V2, D1 and D2 were related with water depth.

2.4.3. Community discrimination based on family composition

Cluster analysis. Cluster analysis based on 4th root transformed family abundance data generated a well defined dendrogram discriminating 4 communities (Fig. 2.2).

One of the replicate of AP deep water station (replicate 3 of D1, 2009 m) seemed to be very different from all others being separated from other clusters.

WS samples formed a large cluster with similarity at about 20% with one exception that a VK slope sample (V1) was clustered together with AP samples in another side.

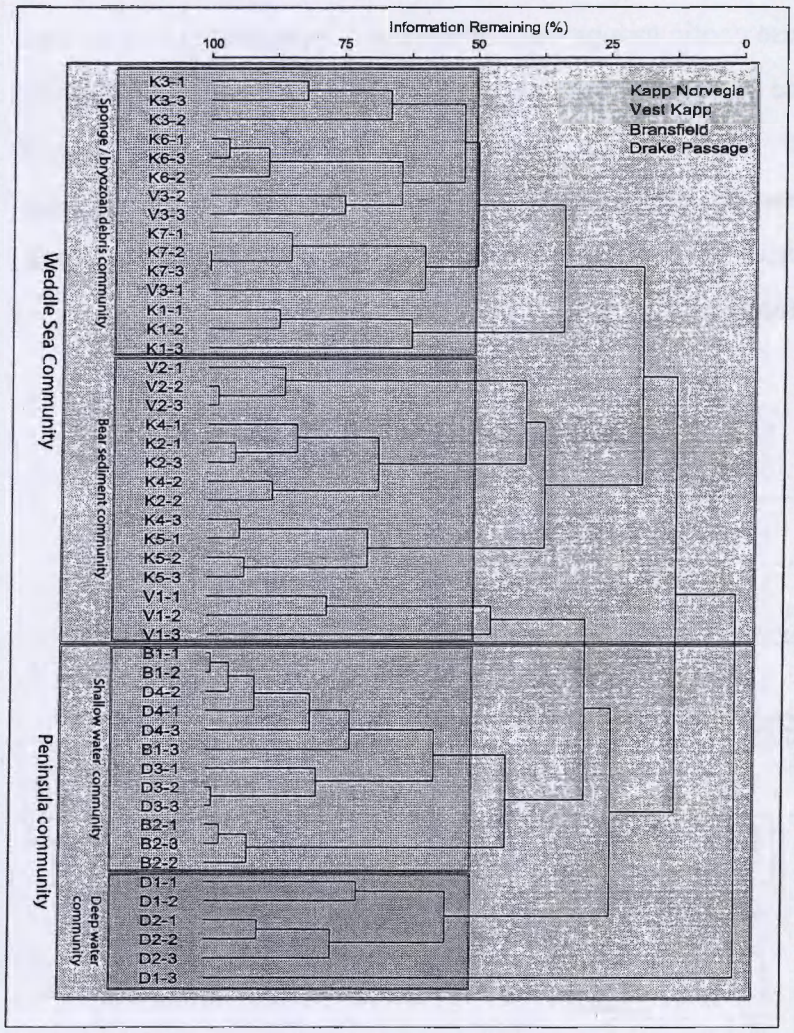

Fig. 2.2. Cluster analysis of 4th root transformed family abundance data using the Bray-Curtis index of similarity and group average linkage clustering.

The AP stations were clearly divided into 2 very meaningful clusters due to depth differences: the deep water (1000 m – 2000 m) and shelf stations. The AP shallow water stations were mixed with an exotic sample (V1). However, V1 was discriminated in the next clustering.

The WS communities were again separated into two meaningful clusters: a biogenic mat covered sediment cluster (K3, BR; K6, BR; K7, SP and K1, SP/BR) and bare sediment cluster. V3 was an exception, which was bare sediment and expected to be in the other cluster. While the mat covered samples were from same area (KN) and similar depth (182-332 m) the bare sediment cluster contained stations from various depths (216-1944 m) and from different areas (KN and VK) and various environmental conditions: V2 (deep water, 1944 m), K4 (old scour, 255 m), K2 (shallow bare sediment, 216 m) and K5 (fresh scour, 278 m).

TWINSPAN. TWINSPAN analysis was carried out based on 4th root transformed abundance data of families for community discrimination and find out responsible families that discriminate communities (Fig. 2.3).

The AP shallow water community was firstly separated from the rest. However, this community was mixed with 2 replicates of V1 (VK slope station, 993 m) and 1 replicate of K2 (KN shallow water, 216 m; bare sediment) because of the existence of Neotonchidae. However these exotic groups were immediately branched out in the next division, due to the presence of Anticomidae, eventually leaving the entire AP shallow water community grouped together. The presence of Desmodoridae and lack of Monhysteridae more or less discriminated BS community from DP shallow water community in the next division. The further division was separation between stations, but some replicates were intermixed.

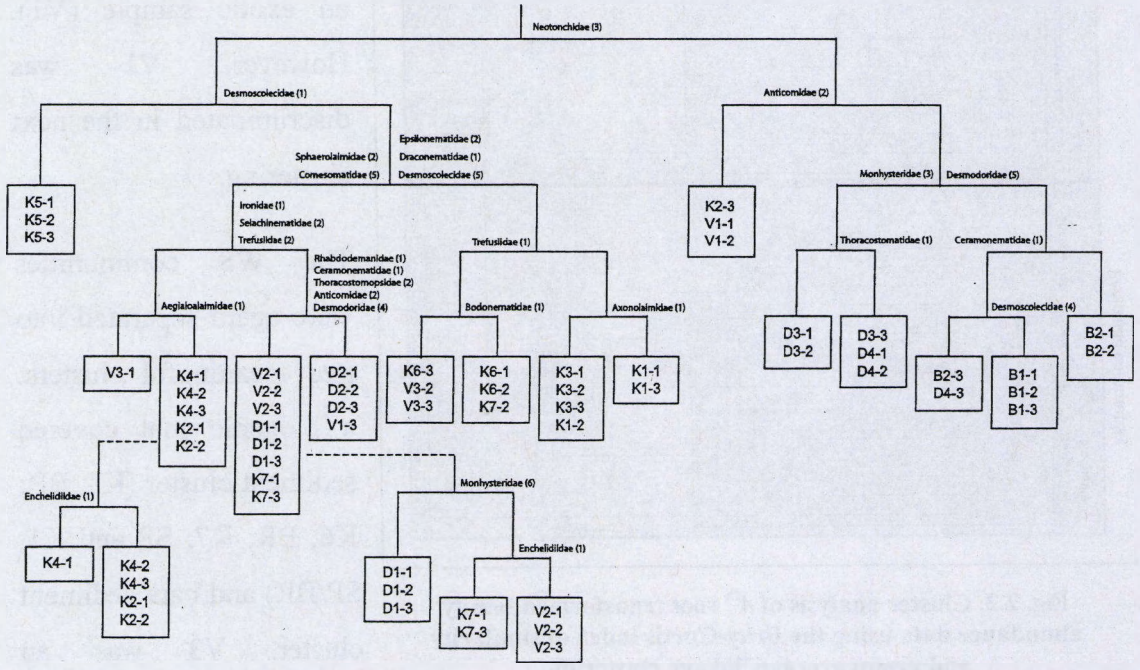

Fig. 2.3. TWINSPAN dendrogram based on 4^{th} root transformed family abundance data.

On the other side, all WS stations which lacked Neotonchidae, except those which clustered with AP shallow communities, were grouped together including AP deep-water communities. Among them, K5 was separated out in the next division due to lack of Desmoscolecidae. The presence of Epsilonematidae, Draconematidae and Desmoscolecidae were responsible for the next division of WS shallow water communities which was mixture of different type of sediment (K6 and K3, BR; 48/K1, SP/BR; V3, bare sediment). This group missed some related stations that were expected to be grouped together, which were K7 (SP) and K2 (bare sediment).

The other group was heterogeneous that came from all different environments. Amongst, deep water community tended to be together because of the presence of Ironidae, Selachinematidae and Trefusiidae, although they failed to exclude a shallow water station (K7, SP) that is expected to be together with the former group. K4 and K2 stayed together.

2.4.4. Abundance, diversity and composition of genera

Density and diversity

Density as a measure of average individual number per sample differed greatly from station to station. The density over 3,000 ind./10 cm^2 were obtained mostly from AP stations whilst one of the lowest density. The WS stations showed in general lower density than in AP, which were all below 2,000 ind./ 10 cm^2. The lowest abundance was found from K5 (73 ind./ 10 cm^2), which was identified as a fresh scour (Fig. 2.4)

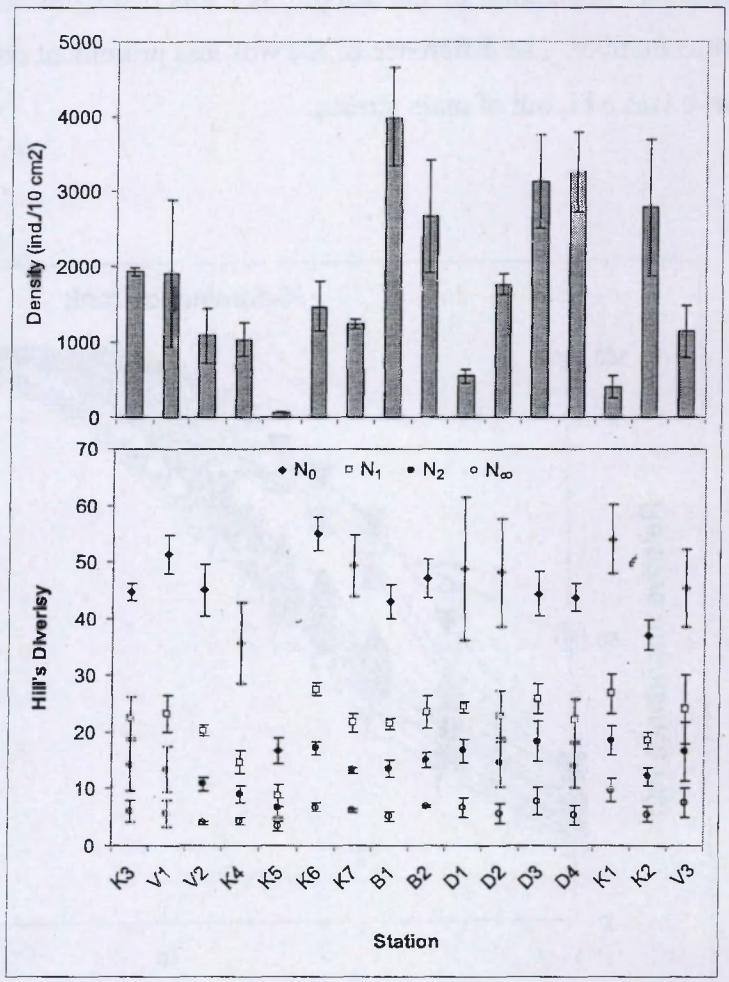

Fig. 2.4. Graphs showing nematode density (A) and Hill's diversity index (B). Error bar shows standard deviation.

Diversity disaccorded with density in that there were no recognisable regional differences. The highest genus number (N_0) was found at K6 (N_0, 54) that followed by K1 (N_0, 53), D2 (N_0, 52) and V1 (N_0, 50). The other Hill's diversity indices showed similar patterns, but with reduced magnificence.

However, it is remarkable that the low value of all Hill's diversity indices found at K5 (N_0, 15.7, for instance) was incomparable with any other results. Another known scour (K4), which is presumably older than K5, also showed relatively lower diversity (N_0, 34.7) with K2 (N_0, 36.0).

K dominance. *K*-dominance plot on the relative abundance of each station showed very similar result in most stations (Fig. 2.5). The apparent differences were, however, found at 3 stations: D1, K5 and K4. St. D3 differed from others in that the proportion of the most dominant genus (*Sabatieria*) was taking almost half (49.8%) of the whole nematode population of the sample. K5 was distinguished from the others due to low genus number. The difference of K4 was less prominent compared with K5 although the curve was a bit out of main stream.

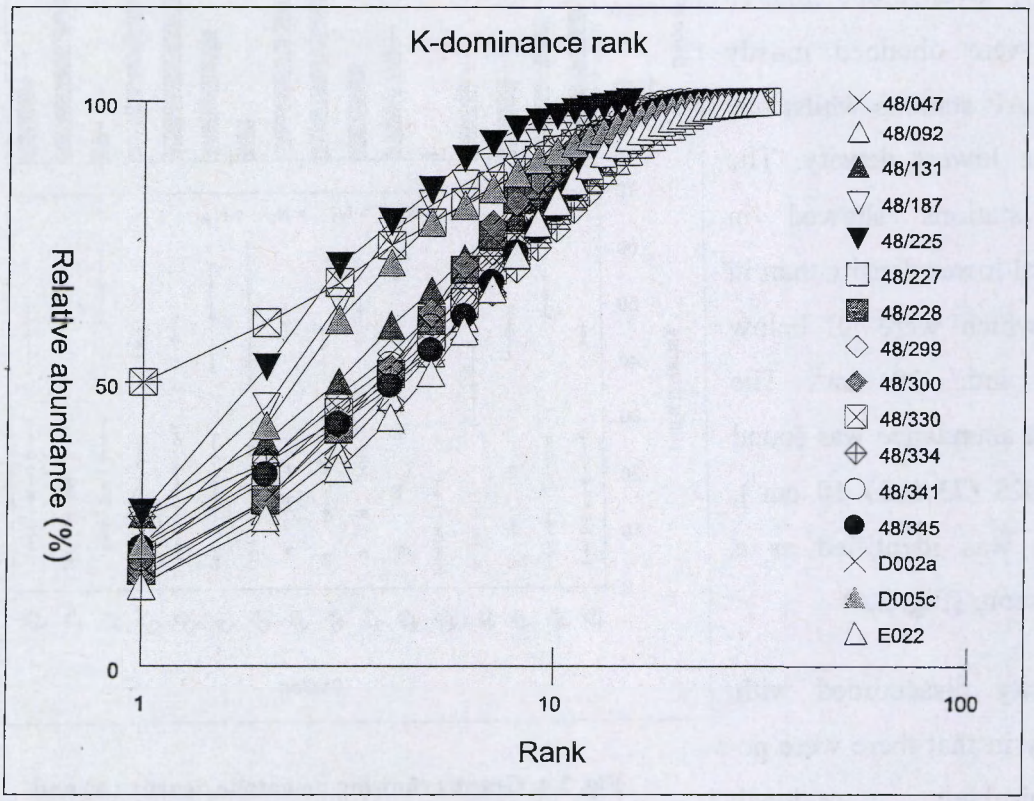

Fig. 2.5. *K*-dominance curves of genus data of each station.

2.4.5. Feeding type and Maturity Index (MI)

Feeding type. Feeding type 1B (non-selective deposit-feeders) was the most dominant feeding group (overall average, 36.9%; range 24.0-47.8%) in majority of stations (Fig. 2.6). It was followed by 2A (epigrowth-feeders; overall average, 31.9%; range, 19.0-43.3%) and 1A (selective-deposit feeders; overall average, 25.1%, range, 7.7-43.8%). The omnivorous-carnivores (2B) were the smallest group (overall average, 5.7%; range, 2.3-19.7%).

Relatively higher proportions (>35%) of 1A was found at WS shelf stations i.e. K6, K7, K1 and E055. This feeding group was extraordinarily reduced in a scour (K5). 1B group tend to be abundant (>40%) at most AP stations (D2, D3 and D4) and soft sediments of WS (V2, K4 and K5). 2A feeding group tended to be more constant than others. Unusually lower proportion was found at K7 and V2. 2B feeding group was the smallest except for K5 where they became remarkably high (19.7%).

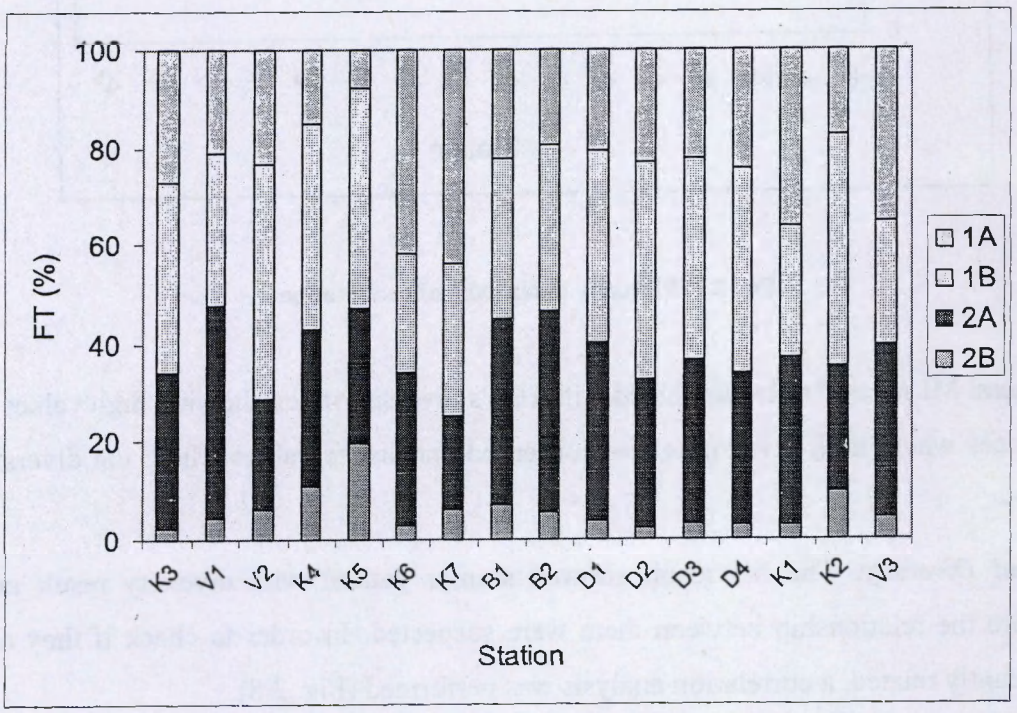

Fig. 2.6. Feeding type composition of each station

Maturity Index (MI). MI showed variation within the range of 1.94 and 2.74 with average of 2.39. When the MI of each station was compared with average, most stations were not significantly different with the average. However, the significantly higher MI scores were found at K6 (MI, 2.74), K7 (MI, 2.60) and D4 (MI, 2.55). On the other hand, the significantly lower values were found at K5 (MI, 1.94) and K4 (MI, 2.12), where both stations are iceberg scoured (Fig. 2.7).

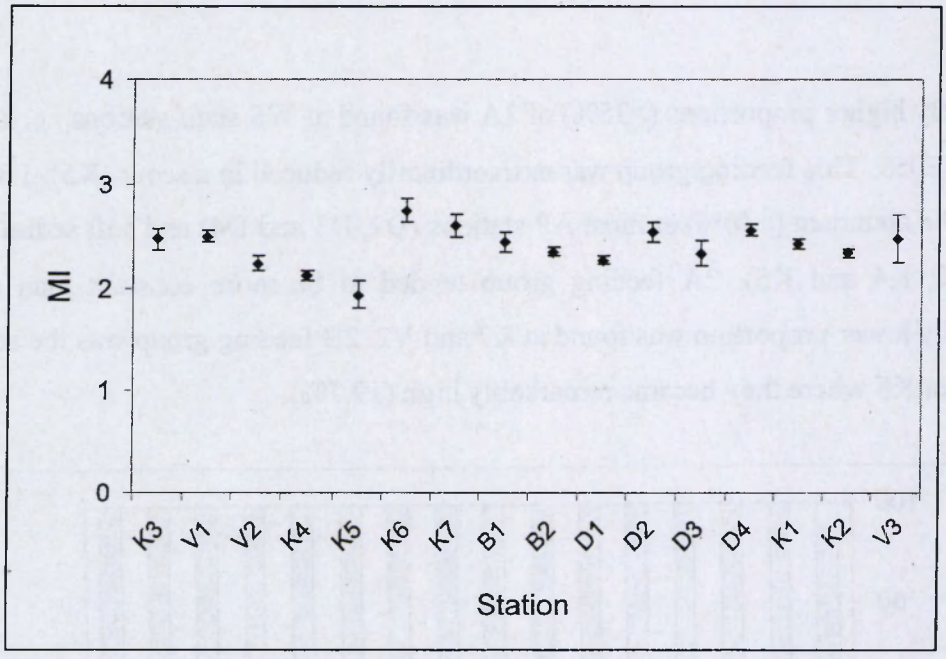

Fig. 2.7. Maturity index (MI) of each station

In general MI seemed to be coincided with Hill's diversity index showing high values in the places where high diversities were observed and lower values where the diversity was low.

MI and Diversity. The MI result showed similar pattern with diversity result and therefore the relationship between them were suspected. In order to check if they are significantly related, a correlation analysis was performed (Fig. 2.8).

The result showed that all Hill's diversity indices were strongly and positively correlated with MI. The strongest correlation was found in N_0 ($r^2 = 0.6219$; $p = 0.0000$). The significance of correlation gradually decreased and consequently the least, but still significantly high correlation was found in N_∞ ($r^2 = 0.2363$; $p = 0.0005$).

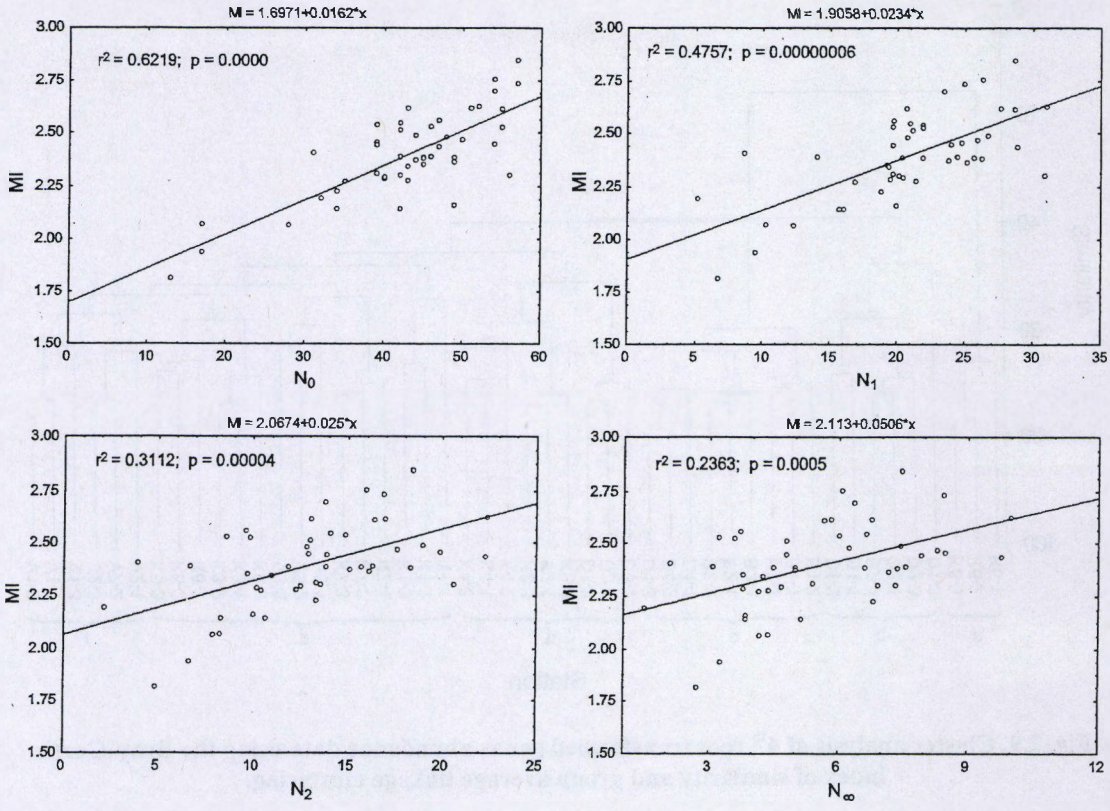

Fig. 2.8. Coordination between MI and Hill's diversity indices

2.4.6. Community discrimination

Cluster Analysis

The result of cluster analysis showed 6 meaningful clusters (Fig. 2.9): a, freshly disturbed station; b, Antarctic Peninsula slope and bathyal stations, c: Antarctic Peninsula shelf stations (excluding D3); d, scours and presumably somewhat disturbed stations; e, WS shelf stations; f, Weddell Sea slope and bathyal stations. Although this result separated different communities well, the dissimilarity between different communities was not very big.

The cluster d was the only one that stations that samples from different areas of different environments were mixed: D3 was from AP shelf break and K2 and K4 were from WS shelf. The close relation between K4 and K2 suggest a possibility that K2 could have been disturbed and on the course of recovery.

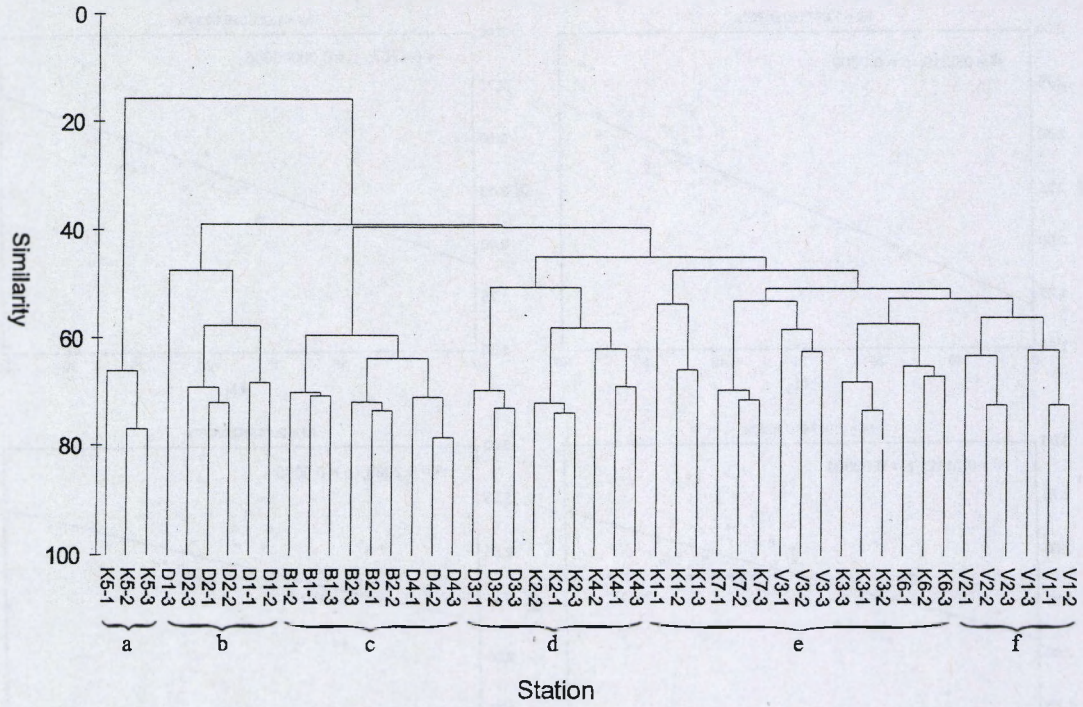

Fig. 2.9. Cluster analysis of 4th root transformed genus abundance data using the Bray-Curtis index of similarity and group average linkage clustering.

Detrended Correspondence Analysis (DCA). DCA result agreed well with cluster analysis (Fig. 2.10).

Firstly the fresh scoured samples (group a, K5) were isolated from others. AP communities were well separated due to water depth (group b and c). The rests were more closely mingled, nevertheless the cluster groups recognised from the cluster analysis stayed more closely.

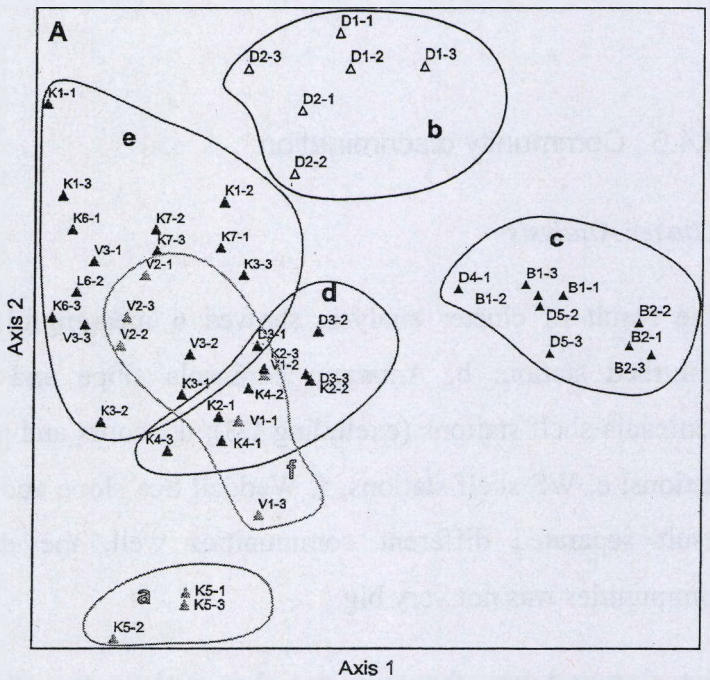

Fig. 2.10. DCA ordination of 4th root transformed genus abundance data.

TWINSPAN. TWINSPAN analysis was carried out in order to see if produces the same result and which genera are responsible for the community discrimination (

Fig. 2.11).

TWINSPAN showed a little different result. First of all, it emphasised the geographical differences by splitting shallow AP stations (TWIN E) from the re The responsible nematode was *Neotonchus*. However, this first division failed to include deeper stations together. The next division separated a mixed group (TWIN D) which was seen in cluster analysis (cluster d). However another WS shelf bare sediment station (V3) joined this group. This separation was due to low abundance of *Desmoscolex* and *Microlaimus*. AP deep water stations were separated in the next division (TWIN A) based on higher abundance of Selachinematidae gen. 1. The remains were deep water stations and biogenic mat stations from WS. This group was divided into two subgroups based on the higher abundance of *Greeffiella* and *Diplopeltoides* in TWIN C and *Southerniella* in TWIN B. TWIN B contained two WS deep water stations and a shelf station while TWIN C consisted of only biogenic mat covered WS shelf stations.

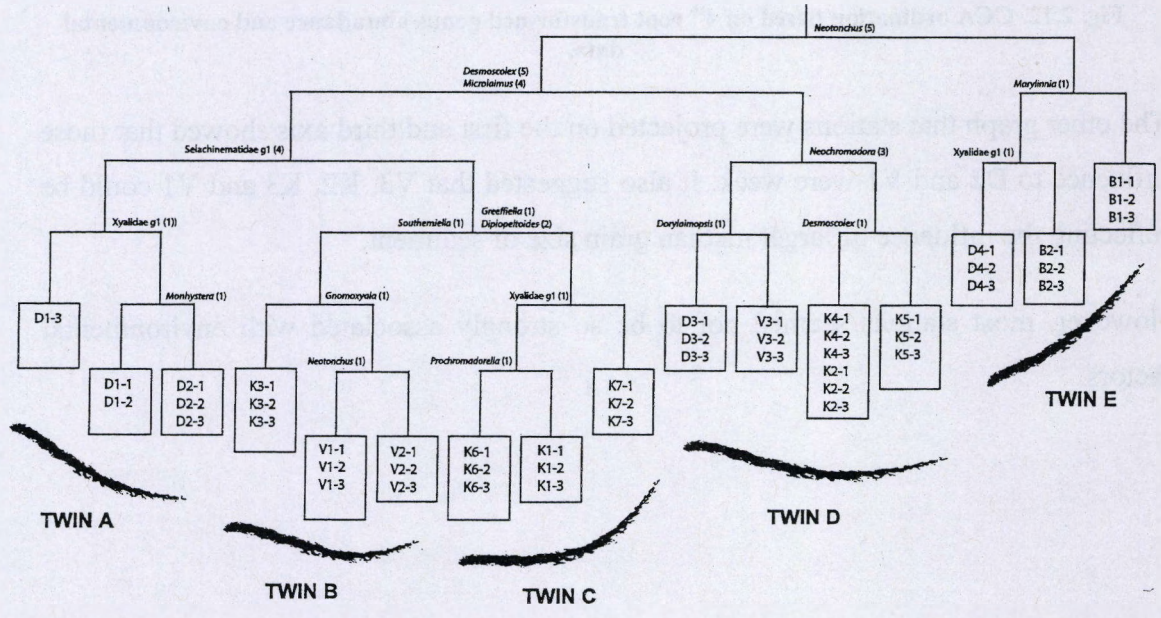

Fig. 2.11. TWINSPAN dendrogram of 4th root transformed genus abundance data.

Canonical correspondence analysis (CCA). CCA was carried out to see if there is any relationship between stations and environmental parameters (Fig. 2.12). The first ordination graph based on the first and second axis suggests that 3 stations (B1, D2 and D1) were under the ruling of chlorophyll-*a* concentration. Water depth also seemed to be important for D1 and V1.

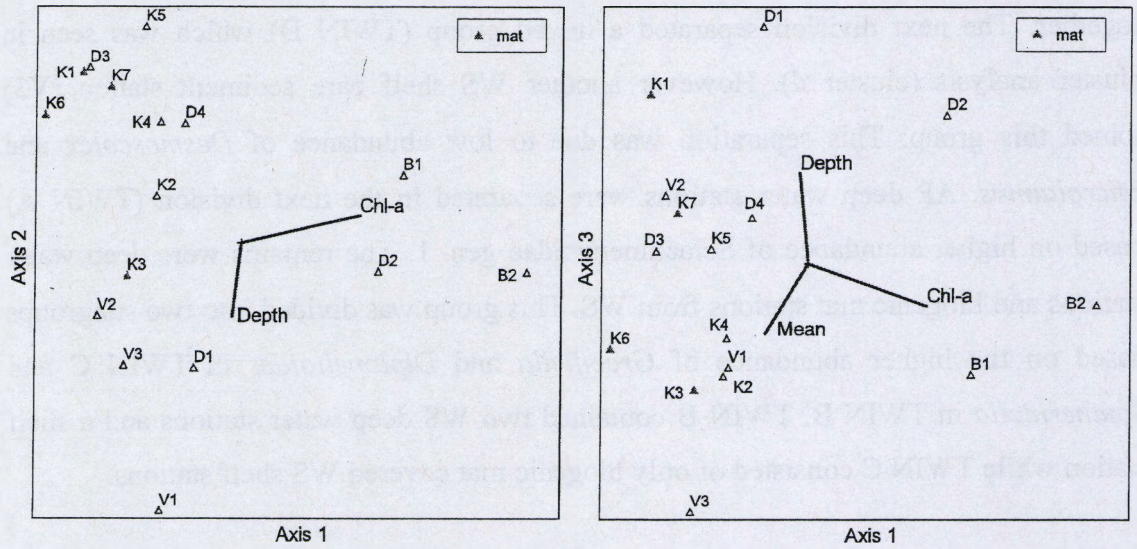

Fig. 2.12. CCA ordination based on 4th root transformed genus abundance and environmental data.

The other graph that stations were projected on the first and third axis showed that those influence to D2 and V1 were week. It also suggested that V3, K2, K3 and V1 could be reflecting the influence of larger median grain size of sediment.

However, most stations seemed not to be so strongly associated with environmental factors.

2.4.7. Environmental influence on nematode community

Geography. In general, AP showed significantly higher density compared with WS (Table 2.3). However, the differences between areas in the same region were not significant.

Table 2.3 Density (ind. /10 cm^2), Hill's diversity index, Maturity Index (MI), feeding type composition (%) and 10 most dominant genera (MDG) of nematode communities from different areas of Atlantic sector of Southern Ocean

	WS				AP			
	KN		VK		BS		DP	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Abundance	1275	924	1379	677	3337	960	2174	1211
N_0	48.0	7.4	48.1	5.8	43.3	4.1	40.9	8.4
N_1	23.3	3.79	20.3	2.2	20.8	2.7	16.7	6.0
N_2	15.06	2.66	16.4	7.8	14.5	1.6	11.6	6.0
N_∞	6.81	1.72	6.45	3.02	6.02	1.07	4.84	2.48
MI	2.51	0.20	2.40	0.17	2.39	0.08	2.42	0.15
1A	26.0	12.8	27.0	7.4	20.9	2.4	26.5	8.6
1B	37.7	9.2	35.1	12.0	33.3	5.0	44.0	16.6
2A	29.3	8.2	33.3	11.4	39.4	5.5	22.7	11.3
2B	7.0	6.4	4.6	1.6	6.4	1.5	6.8	3.3
10 MDG	*Monhystera* (13.6)		*Monhystera* (15.4)		*Sabatieria* (15.4)		*Sabatieria* (20.0)	
	Sabatieria (10.8)		*Molgolaimus* (9.0)		*Microlaimus* (10.4)		*Neotonchus* (5.7)	
	Desmoscolex (7.2)		*Microlaimus* (6.8)		*Neotonchus* (7.9)		Xyalidae g1 (5.6)	
	Neochromadora (7.1)		*Sabatieria* (6.7)		*Metalinhom* (5.7)		*Leptolaimus* (5.2)	
	Halalaimus (4.6)		*Acantholaimus* (5.1)		*Halalaimus* (5.2)		*Monhystera* (4.9)	
	Acantholaimus (4.1)		Xyalidae g1 (3.9)		*Daptonema* (4.5)		*Amphimonhy* (4.1)	
	Xyalidae g1 (4.1)		*Desmoscolex* (3.9)		*Molgolaimus* (4.2)		*Desmoscolex* (3.9)	
	Daptonema (4.0)		*Aegialoa* (3.8)		*Amphimonhy* (4.2)		*Microlaimus* (3.9)	
	Molgolaimus (3.3)		*Neochrom* (3.0)		*Stygodesmo* (3.9)		*Molgolaimus* (3.9)	
	Leptolaimus (2.9)		*Leptolaimus* (2.6)		*Leptolaimus* (3.7)		*Halalaimus* (3.1)	

Aegialoa, *Aegialoalaimus*; ***Amphimonhy***, *Amphimonhystrella*; ***Metalinhom***, *Metalinhomoeus*; ***Neochrom***, *Neochromadora*; ***Stygodesmo***, *Stygodesmodora*.
MDG, most dominant genera.

When diversity between areas were compared, in the case of TGN (total genus number), KN showed the highest value while BS showed the least genus appearance. It was very similar between VK and DP.

Concerning average genus number (N_0), VK and KN showed similarly the highest value while DP showed the lowest value. A consequent ANOVA test showed that the difference of N_0 between neither areas nor regions was statistically significant.

KN showed the highest MI while BS showed the lowest value. The difference only between KN and BS was significant.

In feeding type composition, non-selective deposit-feeders (1B) were most dominant followed by epigrowth-feeders (2A) and selective deposit-feeders (1A) in general. In BS, the most dominant feeding group was 2A. When the proportions of each feeding type of different areas were compared, 2A group in DP was significantly lower than other areas, unless they were not significantly different.

While community properties did not greatly differ between areas and regions, there were differences in genus composition. The differences were bigger between different regions than areas within the same region regardless the similarity of environments. *Monhystera* was the most dominant genus in both area in WS whiles it was *Sabatieria* in both areas in AP. Another remarkable difference of genus composition was the high abundance of *Neotonchus* in AP that was one of the rare genera in WS region. On the other hand, the higher abundance of Chromadorid genera, *Neochromadora* and *Acantholaimus*, were found in WS region.

Water depth. In order to see the influence of water depth to the nematode community samples from different depths of 2 different places (VK and DP) were compared (Table 2.4).

Community properties seemed to change due to depth. In VK, slope showed the highest density while that in shelf and bathyal were similar. Average genus number (N_0), showed the same tendency with density. Evenness, especially N_2, and dominance (N_∞), however, tended to increase with increasing depth, although these differences were not statistically significant. A significantly decreasing tendency from shelf to bathyal was found in MI. Selective deposit-feeders (1A) were significantly higher in shelf compared with other depths. Epigrowth-feeders (2A) were significantly dominant in slope while it was non-selective deposit-feeders (1B) in bathyal. Omnivorous-carnivores (2B) were always the least group, although it was not significant, however, became slightly more abundant in bathyal.

There were discords between VK and DP. In the case of DP, the density significantly decreased with increasing water depth. Diversity did not change with depth. 1B feeding

group were dominant everywhere followed by 2A feeding group. 1A feeding group was relatively depressed and 2B group was negligible. There were no significant differences in feeding group composition between different depths.

Table 2.4 Density (ind. /10 cm^2), Hill's diversity index, Maturity Index (MI), feeding type composition (%) and the 10 most dominant genera (MDG) of nematode communities in different depth regimes of east coast off Vestkapp and Antarctic side of Drake Passage

	VK						DP					
	shelf		slope		bathyal		shelf		slope		bathyal	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Density	1139	344	1908	973	1089	364	3196	531	1766	141	551	91
N_0	45.3	6.8	51.3	3.5	45.0	4.6	44.0	3.0	48.0	9.6	48.7	12.7
N_1	24.0	6.2	23.2	3.2	20.3	1.0	23.9	3.6	22.8	4.5	24.4	0.9
N_2	16.5	5.2	13.4	4.0	10.9	1.3	16.1	4.1	14.5	4.3	16.7	2.0
N_∞	7.6	2.6	5.6	2.4	4.0	0.3	6.6	2.3	5.5	1.8	6.7	1.7
MI	2.5	0.1	2.5	0.1	2.2	0.1	2.4	0.1	2.3	0.0	2.4	0.1
1A	35.4	2.8	21.1	3.0	23.5	2.2	23.2	2.5	23.2	0.8	20.8	3.1
1B	25.1	4.9	31.1	8.8	47.8	5.5	41.6	6.8	44.1	2.7	38.9	8.7
2A	36.2	5.8	44.7	9.5	23.9	6.4	33.9	7.7	31.7	3.4	38.8	11.0
2B	3.3	2.5	3.0	1.4	4.8	0.4	1.4	0.7	1.1	0.1	1.5	0.7
	Monhystera (15.6)		*Molgolaimus* (17.5)		*Monhystera* (25.4)		*Sabatieria* (15.5)		*Sabatieria* (27.1)		*Sabatieria* (48.0)	
	Desmoscolex (8.4)		*Sabatieria* (10.7)		*Acantho* (7.9)		*Neotonchus* (7.8)		*Leptolaimus* (5.9)		*Leptolaimus* (9.9)	
	Acantho (8.4)		*Microlaimus* (10.1)		*Sabatieria* (5.9)		*Monhystera* (6.5)		Xyalidae g1 (5.7)		*Monhystrella* (7.0)	
	Tricoma (7.2)		*Monhystera* (9.6)		Xyalidae g1 (5.2)		Xyalidae g1 (5.6)		*Molgolaimus* (4.6)		Xyalidae g1 (5.3)	
10	Xyalidae g1 (5.0)		*Aegialoa* (5.3)		*Neochrom* (4.6)		*Amphimonhy* (5.4)		*Acanthol* (3.9)		*Acantho* (3.1)	
MDG	*Desmodora* (4.6)		*Paralongi* (4.0)		*Halalaimus* (4.4)		*Leptolaimus* (4.5)		*Desmoscolex* (3.8)		Cyatholaimid (2.2)	
	Cyatholaimid (4.1)		*Neochrom* (2.9)		*Microlaimus* (3.8)		*Microlaimus* (4.5)		*Halalaimus* (3.7)		*Halalaimus* (2.1)	
	Microlaimus (4.1)		Xyalidae g1 (2.6)		*Cervonema* (3.6)		*Desmoscolex* (4.1)		*Syringo* (3.1)		Selachinematid (1.9)	
	Leptolaimus (3.9)		Cyatholaimid (2.1)		*Desmoscolex* (3.5)		*Molgolaimus* (4.0)		*Microlaimus* (2.9)		*Desmoscolex* (1.9)	
	Aegialoa (3.6)		*Halalaimus* (2.0)		*Leptolaimus* (3.5)		*Halalaimus* (3.1)		*Neochrom* (2.8)		Meyliid (1.2)	

Acantho, *Acantholaimus;* ***Aegialoa***, *Aegialoalaimus;* ***Amphimonhy***, *Amphimonhystrella;* **Cyatholaimid**, Cyatholaimidae gen.i 1; **Meyliid**, Meyliidae gen. 1; ***Neochrom***, *Neochromadora;* ***Paralongi***, *Paralongicyatholaimus;* **Selachinematid**, Selachinematidae gen. 1; ***Syringo***, *Syringolaimus.*

It seemed that depth difference within the range from about 200 m to 2,000 m did not influence to the most dominant genus. In VK, *Monhystera* was the most dominant in shelf and bathyal. In slope it was *Molgolaimus* and *Monhystera* was the 4th in rank. *Sabatieria* was always most dominant in all depth. *Sabatieria* became more important at deeper sites (slope and bathyal) in VK, while Desmoscolecina genera (*Desmoscolex* and *Tricoma*) were more important at the shelf station. In DP, the importance of *Neotonchus* decreased with increasing depth while *Leptolaimus* and *Acantholaimus* showed opposite tendency.

Sediment granule size. Nematode community properties between 2 different sediment types, sandy and silty, were compared in each region in order to see how nematode communities are influenced by sediment type (Table 2.5).

Table 2.5 Density (ind. /10 cm^2), Hill's diversity index, Maturity Index (MI), feeding type composition (%) and the 10 most dominant genera (MDG) of nematode communities in different sediment types from Weddell Sea and Antarctic Peninsula

	WS				AP			
	sandy		silty		sandy		silty	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Density	1342	941	1162	248	2512	890	2588	1418
N_0	42.5	12.7	47.2	5.1	45.8	6.7	45.8	6.4
N_1	20.7	6.7	21.0	1.4	22.4	3.7	23.8	2.5
N_2	13.4	4.7	12.1	1.6	14.2	3.7	15.9	2.7
N_∞	6.1	2.4	5.1	1.2	5.5	1.6	6.6	1.6
MI	2.4	0.3	2.4	0.2	2.3	0.1	2.4	0.1
1A	25.3	11.7	33.6	11.5	23.7	0.8	21.1	2.6
1B	34.9	11.1	39.3	10.2	43.0	5.4	36.7	6.9
2A	36.7	8.8	23.5	4.9	32.0	4.9	40.5	8.0
2B	3.1	2.1	3.6	1.5	1.3	0.6	1.6	0.6
10 MDG	Monhystera (12.4)		Monhystera (20.3)		Sabatieria (20.8)		Sabatieria (16.0)	
	Sabatieria (9.8)		Desmoscolex (7.9)		Neotonchus (6.1)		Microlaimus (7.6)	
	Neochromadora (6.4)		Acantholaimus (7.3)		Amphimonhystrella (5.7)		Neotonchus (6.7)	
	Molgolaimus (5.8)		Sabatieria (7.3)		Leptolaimus (5.0)		Halalaimus (4.2)	
	Desmoscolex (5.7)		Leptolaimus (6.9)		Microlaimus (4.6)		Leptolaimus (4.2)	
	Xyalidae g1 (4.3)		Halalaimus (3.8)		Monhystera (4.0)		Molgolaimus (4.1)	
	Halalaimus (3.9)		Tricoma (3.6)		Molgolaimus (3.7)		Desmoscolex (3.6)	
	Acantholaimus (3.7)		Neochromadora (2.8)		Desmoscolex (3.7)		Metalinhomoeus (3.6)	
	Microlaimus (3.6)		Daptonema (2.7)		Halalaimus (3.5)		Daptonema (3.5)	
	Daptonema (3.2)		Amphimonhystrella (2.7)		Xyalidae g1 (3.2)		Xyalidae g1 (3.5)	

The difference of sediment granule size seemed not be important for nematode abundance and diversity. Although there was slight difference in the average of density and N_0 in WS, no statistical significance was found between them. In the case of AP they looked even more similar. There were no difference in other diversity numbers and maturity index (MI) in both places.

When feeding types were considered, 1A group seemed to be lower, while 2A group looked higher in sandy samples in WS. However, only the difference of 2A group was significant. In the case of AP, there were no significant differences of feeding type composition between 2 different types of sediment although 2A group seemed to be higher in silty sediment, which is contrasting result from that of WS.

Finding that the difference of 2A group between 2 different sediment types in AP is not negligible, a different post-hoc analysis method, 'Fisher LSD' that is known to be less conservative than 'Tukey HSD', was applied to see whether that difference was really not significant at all. The result of 'Fisher LSD' analysis showed that the difference was significant ($p=0.034$).

Sediment condition and biogenic mats. For this analysis only samples from KN were selected, where they showed very rich substrate heterogeneity (Table 2.6).

For this analysis only samples from KN were selected, where they showed very rich substrate heterogeneity.

Sediment samples from 4 stations (K3, K6, K7 and K1) were covered with thick biogenic mats that originated from either glass sponges or bryozoans.

A significantly high density was found in bare sediments, which was followed by mat covered sediments. The low density of scoured samples was also very significant compared with bare sediments, but not with mat covered sediments. However, diversity (N_0) was significantly higher in mats than bare sediments while the scoured sediments showed the poorest diversity. Evenness (N_1, N_2) and dominance (N_∞) also showed the same tendency. MI also significantly decreased from mat covered sediments to scoured sediments. Concerning feeding type, 1A group was significantly higher in mat covered sediments while 1B group was significantly lower compared with other sediments. 2A and 2B groups did not show significant differences between different sediment conditions.

Being found important, biogenic mats were looked more closely. They were roughly divided into 3 groups: BR, a mat that bryozoan debris was obviously dominant; SP, mainly composed of sponge spicules; SP/BR; mixture of both bryozoan debris and sponge spicules. One bare sediment station was selected as reference site.

Table 2.6 Density (ind. /10 cm^2), Hill's diversity index, Maturity Index (MI), feeding type composition (%) and the 10 most dominant genera (MDG) of nematode communities in different sediment conditions in KN

	BR		SP		SP/BR		entire mat		bare		scoured	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Density	1702	334	1234	69	403	149	1260	602	2784	910	551	541
N_0	49.8	6.0	49.3	5.5	54.0	3.6	50.8	5.7	37.0	2.6	26.2	11.4
N_1	24.9	3.9	21.7	1.6	26.7	3.6	24.6	3.6	18.4	1.5	11.7	3.7
N_2	15.7	3.4	13.2	0.5	18.5	2.6	15.8	3.2	12.2	1.6	7.8	1.9
N_∞	6.35	1.37	6.13	0.28	9.76	2.02	7.15	2.02	5.44	1.33	3.90	0.86
MI	2.60	0.18	2.60	0.11	2.48	0.23	2.57	0.17	2.27	0.04	2.03	0.13
1A	34.5	8.4	43.8	4.2	36.4	2.1	37.3	7.2	17.6	2.6	11.4	5.4
1B	31.3	9.5	30.9	3.6	26.4	9.5	30.0	8.0	46.9	9.4	43.7	7.8
2A	31.5	7.0	19.0	3.9	34.1	8.6	29.0	8.7	25.5	8.4	29.5	9.1
2B	2.7	1.3	6.3	2.0	3.1	0.2	3.7	2.0	10.0	3.7	15.5	5.7
	Monhystera (14.1)		Monhystera (16.9)		Monhystera (9.2)		Monhystera (14.4)		Sabatieria (17.0)		Neochrom (17.7)	
	Desmoscolex (11.7)		Desmoscolex (12.2)		Desmoscolex (8.5)		Desmoscolex (11.6)		Neochrom (11.1)		Monhystera (16.6)	
	Molgolaimus (7.5)		Leptolaimus (10.3)		Cyatholaimid (8.2)		Sabatieria (6.2)		Monhystera (10.9)		Sabatieria (16.4)	
	Xyalidae gl (5.9)		Sabatieria (8.8)		Glochinema (6.9)		Molgolaimus (5.6)		Daptonema (6.4)		Daptonema (9.5)	
10	Sabatieria (5.3)		Acantho (7.2)		Microlaimus (5.9)		Acantho (4.5)		Halalaimus (6.2)		Halalaimus (4.5)	
MDG	Halalaimus (3.9)		Tricoma (6.3)		Sabatieria (5.0)		Xyalidae gl (4.2)		Theristus (5.9)		Acantholaimus (3.3)	
	Microlaimus (3.6)		Daptonema (4.0)		Acantho (4.9)		Halalaimus (3.8)		Xyalidae gl (5.6)		Cervonema (2.8)	
	Acantho (3.4)		Halalaimus (3.5)		Camaco (4.1)		Microlaimus (3.2)		Cervonema (4.7)		Desmoscolex (2.8)	
	Greeffiella (3.3)		Amphimonhy (2.5)		Amphimonhy (4.0)		Leptolaimus (3.1)		Acantho (3.7)		Leptolaimus (2.7)	
	Neochromadora (3.3)		Molgolaimus (1.9)		Halalaimus (3.7)		Tricoma (2.8)		Desmodora (2.9)		Diplolaimella (2.6)	

BR, bryozoan debris mat; **SP**, sponge spicule mat; **SP/BR**, mixture of sponge spicules and bryozoan debris
Acantholaimus, Acantholaimus; Amphimonhystrella, Amphimonhystrella; Cyatholaimidae, Cyatholaimidae gen. 1;

Among 3 different substrates conditions BR showed significantly higher abundance although it was lower than that of bare sediment in average. SP showed the second in terms of diversity. SP/BR showed significantly lower density among them. On the other hand, when diversity was concerned, SP/BR was the richest in all aspects while the other two substrates showed similar genus diversity. However, MI was lower in SP/BR compared with other substrates.

Those biogenic mats seemed to be favourable for 1A feeding group that was the highest proportion in all mat covered stations. It was relatively lower in bare sediment.

2.5. Discussion

Community structure. The major part of Antarctic continent (east Antarctica) and Antarctic Peninsular part (west Antarctica) have different tectonic histories. While east Antarctica was separated from Gondwanaland and have a long history of glaciation (Clarke, 2003), west Antarctica was connected with Patagonian land (Crame, 1994) and terrestrial faunal and floral similarity remained until late Eocene (Reguero *et al.*, 2002).

Could such historical differences be reflected in nematode community? Our first assumption is that the composition of different taxonomic level might reflect historical and ecological processes differently. The second assumption is that nematode communities in similar biotopes will tend to resemble each other regardless geographical distance. This assumption was hinted by the studies of Conlan *et al.* (1998) and Lee *et al.* (2001a; 2001b) where they found that iceberg scouring in deeper water resulted in similar taxonomic composition with shallow coastal community that are under chronic ice disturbances. Combining these two assumptions, we can expect that the current nematode communities are compromised product between two different processes and therefore family composition between two different areas will retain more historical backgrounds than generic composition.

The cluster analysis based on the family composition suggested 4 different communities: 1) shallow water AP community, 2) deeper water AP community, bare sediment WS community and biogenic mat community Fig. 2.2). It is noticeable that the two largest clusters are representing the different regions. The AP communities are divided into two smaller sub-clusters based on water depth while the WS sub-communities are distinguished by different sediment conditions, i.e. the presence and absence of biogenic mats on the sediments. The implication of these results is that the communities of two different regions are under different ecological regimes: sediment condition is the stronger factor ruling WS communities whereas water depth is more important in AP.

However, TWINSPAN suggests that such regional differences are stronger in shallower systems and deeper communities resemble each other (Fig. 2.3). The results of the same analyses on genus composition (Fig. 2.9,

Fig. 2.11) show basically the same tendency with the result of family composition although it reflected the details of ecological differences in WP.

If we look at the members of each community, AP communities are represented by high abundances of Comesomatidae, Neotonchidae, Linhomoeidae and Desmodoridae. However, these groups become relatively minor in WS.

Table 2.7 Dominance comparisons of four major families between Antarctic areas and Magellan that showed higher dominance in AP

Location	Comesomatidae	Desmodoridae	Linhomoeidae	Neotonchidae
HB (Vanhove et al., 1999)	11.98	10.66	1.69	0.2
WS	10.04	4.75	0.95	0.35
AP	25.00	6.75	4.78	5.31
Magellan (Chen, 1999)	29.40	4.47	15.80	4.12

A study of Chen (1999) describes nematode community in Magellan area. According to him, Comesomatidae, Linhomoeidae Neotonchidae (Ethomolaimidae in his classification), Desmodoridae and Linhomoeidae are important in Magellan area. When his data are compared with our two regions and Halley Bay (Vanhove et al. (1999), there is an increasing tendency of dominance from WS to Magellan and AP shows intermediated values (Table 2.).

When the data are rearranged in the way that the samples from similar biotopes were grouped together in order to see how ecological processes influence to the community structure, unexpectedly the differences of major taxa between different biotopes within the same region were much smaller than that of similar biotopes in different regions (Table 2.4, Table 2.5).

These results suggest that nematode community structures in these regions are under stronger ruling of historical and/or global scale of processes than local ecology. Similarly Lambshead et al. (2003b) found that the nematode families in Clarion-Clipperton Fracture Zone showed biogeographical association rather than with ecological factors and also attributed this to the result of historical processes rather than of current ecology.

Extrinsic factors: geography, water depth and sediments. Local nematode densities are related to environmental factors such as food supply (Boucher, 1980; Fleeger *et al.*, 1989; Lambshead *et al.*, 2002; Vanreusel *et al.*, 1995), sediment texture (Gerlach, 1977;

Heip *et al.*, 1985; Wieser, 1960) and its heterogeneity (Rice and Lambshead, 1992), water depth.(Dinet and Vivier, 1979; Tietjen *et al.*, 1989; Vincx *et al.*, 1994) However, the factors that ruling nematode diversity is relatively less known. There is a consensus on that sandy sediments harbour more diverse community than muddy sediments (Hopper and Meyers, 1967; Tietjen, 1980; Wieser, 1960). When only soft sediments were considered, the results of this study, however, failed to show such tendency in both WS and AP regions.

The sediments of WS, however, show some peculiar features. The soft parts of sediment in the study area were mostly composed of sandy (47%) and silty (37%) fractions and a small amount of clay, which is not special. However, these sediments contain various sizes of stones (from pebbles to boulders) which delivered by icebergs from the continent. These stone particles seem to be very important for sessile suspension feeders as substrate in early developmental stage, since it was often observed from sediment samples that young bryozoans and sponges are attached to even a small stones. Therefore, the presence of those stones provably explains why there are so many sessile animals in this area. Considering the importance of sponge community in this area as structuring organism, it might be considered as a key element for the ecology of this area.

High population of sponge and bryozoan community in Antarctic shelf must have considerable influences on nematode community in two ways. Firstly the dense distribution of them might provide jungle effects: they change local micro-hydrodynamics and consequently increase the sedimentation of organic flux in the water column; they also become habitats by it self and they provide three-dimensional habitat complexity as shelter and substrates. Secondly, after they die, they leave hard substrates that are considered in our study.

These substrates forms mat on the top of soft sediment and the textures depend on the composition of the major material. Bryozoan debris form a very loosely interwoven substrates that can provably protect the sediment from erosion by water current and consequently trap fluxes in the water column, which will enrich the nutritional condition in the sediments. On the other hand, sponge spicules form more compactly interwoven mats that look like glass fiver cotton that is used for insulation. This kind of mats provably has less effects in changing local water current, because they are present more

compressed form on the sediments. The very sharp structure of glass spicules must be also hazardous to soft-bodied macrofauna. However, this does not seem to be problem for nematodes, since macrofauna sized free-living nematodes such as *Pseudocella* and *Deontostoma* are often associated with this type of mats. This type of substrates are widely spread in east WS areas and considered to be important for nematode communities in this area.

These substrates showed significantly higher diversity. However, unlike our expectation that the sediment covered with those mats may provide better nutritional condition for meiofauna, the nematode abundances of these mats were not significantly higher compared with other stations. When it is compared with the only bare sediment from the same depth of the same area (K2) it the nematode abundance was even significantly lower. However, since the abundance in K2 was extraordinarily high among other WS samples, the lower abundances of those mats do not necessarily meat that they have negative effects on nematode abundance.

One more ting to be mentioned is that when the sediments are covered with such mats, the MG did not penetrate deep into sediment and sometimes the upper water was drained during the sampler is retrieved. Although we are always provided with samples that have best conditions, we expect that abundance of nematode in such conditions might be underestimated (K1 is the typical such an example). However, such incidence will influence less on diversity, because nematodes being lost might be more or less in random.

The presence of such mats also positively effected on MI and 1A feeding type. The increase of MI and 1A feeding type was mainly due to increased dominance of *Desmoscolex*. The related group of genera, such as *Tricoma*, *Greeffiella* also became subdominant in such substrates.

There are some studies in which latitudinal gradients are taken into account (Lambshead and Boucher, 2003a; Lambshead *et al.*, 2003b; Lambshead *et al.*, 2002; Lambshead *et al.*, 2000; Rex *et al.*, 2000). For terrestrial system, increasing diversity tendency from pole to low latitude is generally agreed. However, whether or not marine system shows such tendency is not clear (Gray, 2001). When nematode abundances are considered, two regions of the study area show different trends in relation to depth gradients. VK

data show no gradual patterns. However, DP shows a steeply decreasing trend with increasing depth. When diversity is concerned, however, there is no such tendency in both areas.

Concerning with water depth, the more interesting fact is that the nematode communities from different regions become similar in deeper areas although the predominant genera, *Sabatieria* in AP and *Monhystera* in WS, remained the same. Therefore if we generate a large picture on nematode distribution based on multivariate methods, the shallow communities in WS and AP are separated reflecting geological history, while the two areas are connected through deep sea.

Intrinsic factors: MI and feeding type. There are controversial opinions on individual species functions in ecosystems: rivet hypothesis (Ehrlich and Ehrlich, 1981) and redundant species hypothesis (Lawton and Brown, 1993) It is likely that they emphasised two extremes of *r*- and *K*- strategy More *r*- strategists tend to be rivets in the ecosystem compared with *K*- strategists. Their composition is very dependent on the existence of others and always a few of r-strategists dominates over the community and therefore one might feel that their functions are important and their existence is essential for the community. *K*-strategists tend to sustain rather than dominating and often found be negligible. Therefore removing some of them may not influence greatly to the community function. However, it is more likely that the high diversity is achieved by *K*-strategists rather than *r*-strategists.

Bongers (1990) and Bongers *et al.* (1991) established nematode maturity index (MI) which based on *r*- and *K*-selection theory. This index is widely used for habitat assessment in terrestrial system while its use for marine system is not yet so popular. However, some studies have shown that MI gives insights to habitat stability and community function (Lee *et al.*, 2001a; Lee *et al.*, 2001b; Neilson *et al.*, 1996). MI decreases in the events of iceberg scouring in WS continental shelf (Lee *et al.* 2001a). Contrary, iceberg scouring does not change it in shallow coast off Signy Island. This controversy suggests that these two systems have different ecological functions that have been obtained in the course of natural selection due to the frequency of such disturbances (Lee et al., 2001b).

When the MI was compared with Hill's indices the results showed that they were strongly and positively correlated with MI (Fig. 2.8). This strong correlation between MI and diversity suggests that when there is a reason that causes a decline of diversity (like scouring in this study area and consequent increase of competitive stress in the community) the first members to disappear are mostly persisters which have not adapted for *r*-selection. Therefore we confirm that intrinsic factors especially different life strategies are as important as extrinsic factors and suggest to consider in other diversity studies.

MI and feeding type

The correlation between MI and feeding types are tested by Bongers *et al.* (1991). As a result they found that MI has a close relationship with feeding type: 1A group tend to have higher MI (3.7), 2A and 2B have intermediate (about 3.0) and 1B have the least (2.1) c-p value. Therefore, it can be expected in general situation that the nematode community in the course of recolonisation consists of more 1B and less 1A whereas a stable community have an opposite tendency.

Two studies of Lee *et al.* (2001a; 2001b) show that it is true for the community that is not subjected in chronic disturbance. However, when the nematode community is exposed to chronic disturbances, the whole community adapts to such condition and disturbances do not influence either MI or feeding type composition. The adaptation of such a community to disturbance is rather ecological process than evolutionary process: adaptation is achieved rather by restructuring of community members than the adaptation of each member. Of course, in long term we can also expect evolutionary process developing uniquely in such conditions.

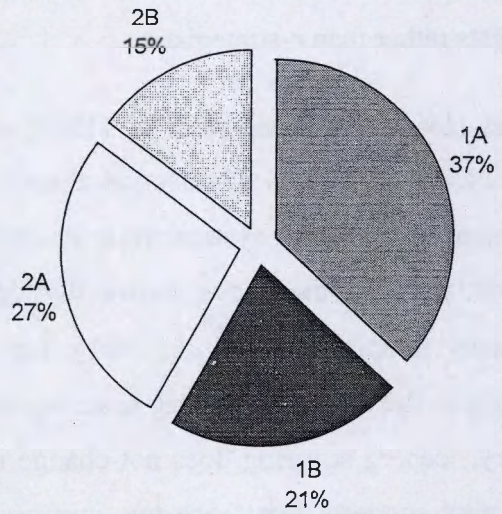

Fig. 2.13 Number of genera that contributed to different feeding type

The 1A feeding type nematodes are supposed to feed on small particles or dissolved organic matter. Therefore the variation of food items for 1A feeding nematodes must be more limited than other nematodes. When the competitive exclusion (Armstrong and McGehee, 1980; Hardin, 1960; Phillips, 1973) is considered, therefore it is more natural to expect that 1A feeding group is the least diverse group. However, the reality is just opposite. In our studies 1A feeding type was the largest group consisting of 80 genera (37%) (Fig. 2.13).

Therefore we propose that resource partitioning is not depending on the diversity of food items, but the nature of animals that are sharing the food items. As explained before 1A feeding group tends more to be K-strategists and this is the main reason why there are more genera 1A feeding groups than in other feeding groups.

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Chapter 3

Acantholaimus species diversity and distribution

3.1. Abstract

Acantholaimus is known as a typical deep sea nematode. However, they were also abundant and highly diverse in relatively shallow coast in the study area. In order to know the species distribution pattern and how different environments influence on their ecology, *Acantholaimus* communities between various biotopes in the east coast of Weddell Sea and the west Antarctic Peninsular were compared. Although *Acantholaimus* was widely dispersed and often subdominant in the Atlantic sector of the Southern Ocean, they never became predominant in all biotopes. The species richness tended to increase with increasing water depth, even though the abundance remained the same in difference depths. There was also a geographical cline in diversity that increased polewards.

Finding 65 species from 16 standard nematode samples was extraordinary. In the extreme cases, 23 species coexisted in one sample, which conflicts to competitive exclusion theory. The extrinsic factors that contributed to high species diversity were water depth and the presence of biogenic substrates on the top of sediments, such as sponge spicule mat and bryozoan debris. Such various substrates might enhance the microhabitat complexity, which provably leads niche diversity and consequent species diversity. However, the high species richness in deep station where sediments are more monotonous seems to imply that the diversity pattern of them is the product of more historical process rather than current ecology.

Acantholaimus had diverse morphological variations, and the difference of pharyngeal shape seemed to be potentially related with life strategy. Comparing the species that have long slender pharynx and elongated terminal bulb with the species that have stronger pharynx with round bulb, the former were much lower in abundance, but as high as the latter. Such linkage between morphology and diversity implies that, in addition to the extrinsic causes, intrinsic factors might be also important for biodiversity.

3.2. Introduction

Since Allgén first described an *Acantholaimus* species from Norway in 1933, there were only 4 species described until Gerlach and Riemann produced 'The Bremerhaven checklist of Aquatic Nematode' in 1973 and 1974 (Gerlach and Riemann, 1973; 1974). Their names start to appear more frequently in taxonomic papers since late 70th of last century. In ecological papers it was even later that their name started to emerge, yet as a part of community members. The scarceness of researches on them is because they appear in deep-sea.

More recent but occasional works, however, start to pay more attention to this genus from various deep-seas since they were important in their samples. Jensen (1988) discussed on them more specifically in the aspect of diversity in relation to the variation of their buccal morphology. Soetart and Heip (1995) found that their abundance distribution is correlated with water depth and therefore defined them as typical deep sea nematode.

The nematodes in the Antarctic are even less known to us than deep-sea ones. Ecological study on Antarctic nematode started from about a decade ago (Dahms *et al.*, 1990; Herman and Dahms, 1992; Lee *et al.*, 2001a; Lee *et al.*, 2001b; Vanhove, 1997; Vanhove *et al.*, 1999; Vanhove *et al.*, 1998; Vanhove *et al.*, 1995). The purposes of these studies are collectively focused on meiofauna or nematode communities rather than specifically to a certain lower taxon.

Vanhove *et al.* (1999) have reported that *Acantholaimus* were common in the southeastern Weddell Sea, from shelf to lower slope (from about 200 m to 2000 m) and did not show a correlation with depth. Lee *et al.* (2001a) found that physical disturbance of iceberg scouring is one of the process that influence of diversity of nematode in the Antarctic region. *Acantholaimus* was one of the genera that were significantly reduced by scoring.

Acantholaimus is very interesting genus in terms of biodiversity. As many as 18 species coexisting in a small area (10 cm^2) were observed in Indian Ocean (Muthumbi and Vincx, 1997). We also found 65 species from our study materials, implicating that the coexistence of many *Acantholaimus* species is not a local phenomenon. These findings

are obviously contradicting with competitive exclusion theory that many ecologists have claimed (Armstrong and McGehee, 1980; Hardin, 1960; Phillips, 1973).

This aims of study are therefore 1) to describe the geographical distribution pattern of *Acantholaimus* species 2) to view how environmental factors, i.e. geography, water depth, and sediment heterogeneity, influence their diversity and abundance.

3.3. Material and Methods

3.3.1. Sampling area and methods

The material for this study comes from four different areas of two regions of Atlantic sector of Southern Ocean: Kapp Norvegia (KN) and Vestkapp (VK) in the Weddell Sea (WS) and Bransfield Strait (BS) and Drake Passage (DP) in Antarctic Peninsula (AP).

Samples were taken during the first and second EASIZ cruise (26th January – 15 March 1996 and 13th January - 26th March 1998, respectively) by means of a multi-box corer (Gerdes, 1990) from stations with different biotopes (Table 3.1).

Table 3.1. Location, depth, gear number, chlorophyll-*a* concentration, sediment type and size of samples for this study

Region	Area	Station	Depth (m)	Gear No.	Location		Chl-*a* (ng/g dwt)	Sediment			Remarks
					Latitude	Longitude		Type	Size (µm) Mean	Size (µm) Median	
WS	KN	K1	182	MG27	71°19.7'	012°24.8'	31.42	Sandy	na	na	sp/br
		K2	216	MG23	71°40.1'	012°47.2'	65.53	Sandy	na	na	-
		K3	243	MG1	70°52.1'	010°29.4'	64.9	Sandy	75.8	111.0	br
		K4	255	MG19	71°32.3'	013°31.7'	73.83	Sandy	51.0	72.4	o. s.
		K5	278	MG24	70°50.1'	010°35.2'	nd	Sandy	28.3	43.4	f. s.
		K6	332	MG25	70°49.4'	010°38.7'	19.19	Sandy	52.1	71.6	br
		K7	298	MG26	70°49.8'	010°38.0'	7.02	Silty	42.5	55.9	sp
	VK	V1	993	MG10	73°34.2'	022°38.0'	nd	Sandy	76.8	101.0	-
		V2	1944	MG14	73°23.7'	022°09.1'	nd	Silty	23.4	38.9	-
		V3	220	MG17	73°28.4'	020°40.8'	31.66	Sandy	94.1	112.1	-
AP	BS	B1	207	MG28	62°15.8'	058°42.7'	249.47	Silty	26.4	38.6	-
		B2	423	MG29	62°16.8'	058°42.1'	375.83	Silty	8.5	9.6	-
	DP	D1	2009	MG32	61°20.6'	058°15.1'	8.09	Silty	7.8	8.7	-
		D2	1028	MG33	61°26.7'	058°06.6'	44.24	Sandy	60.2	147.8	-
		D3	429	MG34	61°34.5'	058°07.0'	78.59	Silty	29.8	36.0	-
		D4	218	MG35	61°53.3'	059°06.9'	138.04	Sandy	25.9	39.2	-

Abbreviations for geographical names: WS, Weddell Sea; **AP,** Antarctic Peninsula; **KN,** Kapp Norvegia; **VK,** Vestkapp; **BS,** Bransfield Strait; **DP,** Drake Passage.

Abbreviations for remarks: sp, sponge spicule mat; **br,** bryozoan debris; **sp/br,** mat mixed with sponge spicules and bryozoan debris; **o.s.,** old scour; **f.s.** fresh scour.

Other abbreviations: na, not available; **nd,** not detected; **-,** inapplicable; **MG,** multi-box corer.

3.3.2. Sample treatment

Three standard meiofauna-hand-cores (10 cm^2 surface area) for the meiofauna and a large hand-core (diameter about 6 cm) for sediment analyses were taken from one box-core of each station. The sediment cores were sliced into 5 layers (0-1, 1-3, 3-5, 5-10 cm

and the rest) immediately after the samples were recovered on board. Only the three top layers up to 5cm, where the majority of meiofauna dwells, were used for this study. Meiofauna samples were preserved with 4 % neutral hot (60° C) formaldehyde solution on board before further studies in the home laboratory. Sediments were decanted and sieved over 1,000 and 32 µm mesh sizes. Animals passing the 1,000 µm sieve and retained on the 32 µm sieve were regarded as meiofauna. Final extraction of meiofauna was achieved using the LUDOX centrifugation flotation technique (Heip *et al.*, 1985; McIntyre and Warwick, 1984). The number of all metazoan meiofauna was counted after staining with Rose Bengal. Approximately 100 nematodes (all, in samples with less than 100 individuals) per replicate were randomly picked out and dehydrated in a series of glycerine-alcohol solutions. The dehydrated nematodes were mounted on slides with anhydrous glycerine medium and sealed with paraffin wax.

All *Acantholaimus* specimens were subjected to species identification based on morphological characteristics. A consequent biometrics of the morphology was used to determine species (appendix 1). Observation was carried out under a Wild M20 light microscope.

3.3.3. Data analysis

Univariate methods. Diversity Index. Hill's (1973) diversity indices were calculated for *alpha*-diversity measurement:

Nematode species diversity was measured using Hill's diversity indices (Hill, 1973).

Hill's diversity numbers of a certain order 'a' is given by:

$$N_a = \left\{ \sum_{i=1}^{s} p_i^a \right\}^{(1-1/a)}.$$

N_0 is the number of species.

$N_1 = \exp(H')$, where $H' = -\sum_{i=1}^{s} p_i \ln(p_i)$.

N_2 is the reciprocal of the Simpson's dominance index, therefore;

$$N_2 = \left\{ \sum_{i=1}^{s} p_i^2 \right\}^{-1}.$$

$N_\infty = p_i^{-1}$, where p_i = the relative abundance of the ith most dominant species.

Analysis of variance (ANOVA) was used to determine significant differences ($p<0.05$) for abundance and diversity between samples or sample sets. Subsequent post hoc comparison (Turkey HSD) was used on stations or station groups when data are pooled to compare *Acantholaimus* species distribution pattern along different environmental variables.

Multivariate methods. For the analysis of community distribution patterns, multivariate analysis were performed: TWINSPAN (Two-Way Indicator Species Analysis; Hill, 1979) based on 4th root transformed species abundance data; Classification - clustering using the Bray-Curtis similarity matrix based on 4th root transformed and pooled abundance data; Canonical correspondence analysis (CCA; ter Braak, 1986) on 4th transformed and pool abundance data together with environmental data to see if there is any relationship between communities and environmental parameters.

3.4. Results

3.4.1. Abundance

Acantholaimus appeared in all stations. They occurred also in all replicates of 13 stations. The exceptions were K5, B1 and B2, where some replicates lacked *Acantholaimus*.

The density of Acantholaimus varied greatly from station to station (Fig. 3.1). The highest average density was found at station K2 (average 100 ind./10 cm^2) whilst the minimum value was found at station K5 (average 0 ind./10 cm^2). The density showed a bimodal pattern separating the stations into two groups showing a gap between 36 and 66 ind./10 cm^2. The stations showed density that is equal to or higher than 66 ind./10 cm^2 were V2, K6, K7, K2, V3 from WS and D2, D3 from AP. The others were equal to or less than 36 ind./10 cm2 were K3, V1, K4, K5, K1 from WS and B1, B2, D1 D4 from AP.

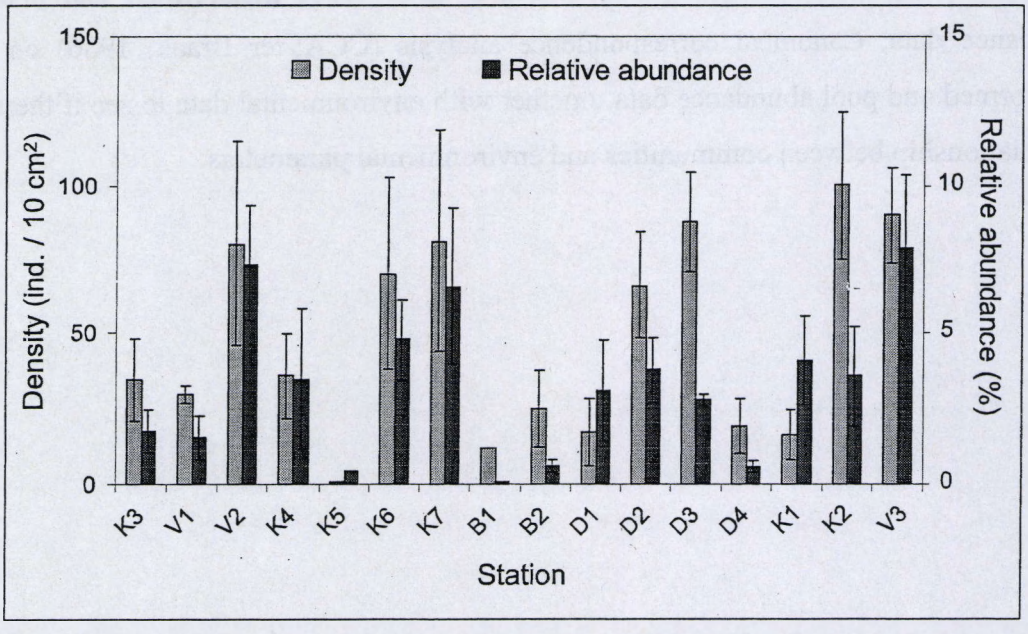

Fig. 3.1 Individual abundance (ind./10 cm^2) of Acantholaimus and their proportion (relative abundance) in the nematode community of each station.

Concerning relative abundance, the patterns were basically in accordance with density. Some remarkable differences of pattern between were, however, found at K1 and D1 where density was low while relative abundance was comparatively high. The opposite cases were B2, D3, D4 and K2.

3.4.2. Diversity

Information concerning species diversity is summarised in Table 3.2.

In total, 65 Acantholaimus species were retrieved from the whole samples. Total species number (TSN) of Acantholaimus differed greatly from station to station. Station V2 showed the highest TSN (23) followed by V3 (TSN=16), K6 (TSN=15), K1 (TSN=13), K7 (TSN=11) and D2 (TSN=11). On the other hand, K5 and B1 marked the least TSN (1) followed by K4, 48300, D4 (TSN = 2) and K2 (TSN=3).

Average Species number (N_0) and other Hill's indices (N_1, N_2 and N_∞) showing almost the same pattern with TSN. A remarkable difference between N_0 and other Hill's indices were that K7 showed high N_0 and became relatively lower in other indices, which implicates low evenness.

Table 3.2. Total species number (TSN) and Hill's diversity numbers of each station (3 replicates)

Station	Area	TSN	N_0		N_1		N_2		N_∞	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
K1	KN	13	6.67	3.21	5.70	2.92	7.34	4.50	3.17	1.46
K2	KN	3	2.67	1.15	2.09	0.87	1.86	0.82	1.59	0.69
K3	KN	4	2.33	1.53	2.02	1.09	1.85	0.84	1.42	0.38
K4	KN	2	1.67	0.58	1.43	0.47	1.33	0.41	1.18	0.23
K5	KN	1	0.33	-	0.33	-	0.33	-	0.33	-
K6	KN	15	6.33	1.53	4.75	1.23	4.02	1.44	2.32	0.67
K7	KN	11	5.33	0.58	3.17	0.87	2.49	1.11	1.67	0.50
V1	VK	7	4.00	1.00	3.79	0.71	4.07	0.82	3.11	0.84
V2	VK	23	12.33	1.53	10.81	0.78	10.87	0.60	5.64	0.60
V3	VK	16	7.67	1.15	5.16	1.42	4.00	1.31	2.37	0.49
B1	BF	1	0.33	-	0.33	-	0.33	-	0.33	-
B2	BF	2	1.00	1	0.96	0.95	0.93	0.88	0.83	0.86
D1	DP	7	3.67	2.31	3.43	2.11	3.79	2.42	2.50	1.32
D2	DP	11	5.67	1.53	4.56	1.15	3.91	0.87	2.31	0.30
D3	DP	4	3.00	0.00	2.48	0.16	2.22	0.26	1.70	0.26
D4	DP	2	1.33	0.58	1.33	0.58	1.36	0.62	1.33	0.58

TSN, total species number; SD, standard deviation.
-, inapplicable.

3.4.3. *Acantholaimus* species distribution pattern and habitat preference

Occurrence and relative abundance. Table 3.3 shows the *Acantholaimus* species list arranged in the importance order of dominance within the *Acantholaimus* population at

each station. Species 14a overwhelmed the *Acantholaimus* community in almost everywhere occurring at 14 stations and being most dominant at 9 stations. The stations where they did not occur were K3 and V1 in WS. It was then often replaced by *A.* 06a which occurred at 7 stations. Station K3 was the only station that these two species did not occur. Station K1 was the station where the importance of these two species was relatively low. Next to them, *A.* 02, *A.* 15 and *A.* 07a were also important, that were once the most dominant species and occurred at 3 or 4 stations. The rests were minor in abundance and occurred locally.

Table 3.3. ***Acantholaimus*** **species list showing up to 10 most important species and their proportion (%) within the** ***Acantholaimus*** **population in the parentheses**

K1	K2	K3	K4	K5	K6	K7	V1
A. 07*a* (22.7)	*A.* 14*a* (77.1)	*A.* 02 (73.3)	*A.* 14*a* (82.1)	*A.* 14*a* (100)	*A.* 29*b* (30.0)	*A.* 14*a* (60.7)	*A.* 06*a* (25.0)
A. 15 (15.9)	*A.* 02 (14.3)	*A.* 04 (13.3)	*A.* 02 (14.3)		*A.* 14*a* (25.0)	*A.* 01*m* (7.1)	*A.* 07*a* (18.8)
A. 11 (6.8)	*A.* 14*d* (5.7)	*A.* 01*a* (6.7)	u.i. (3.6)		*A.* 06*a* (7.5)	*A.* 29*a* (7.1)	*A.* 07*b* (18.8)
A. 11*c* (6.8)	u.i. (2.9)	*A.* 03 (6.7)			*A.* 01*b* (7.5)	*A.* 06*d* (3.6)	*A.* 06*e* (6.3)
A. 43 (6.8)					*A.* 01*c* (5.0)	*A.* 01*e* (3.6)	*A.* 08*a* (6.3)
A. 14*a* (4.5)					*A.* 13 (2.5)	*A.* 01*j* (3.6)	*A.* 10 (6.3)
A. 06*c* (4.5)					*A.* 01*d* (2.5)	*A.* 13 (1.8)	*A.* 14*c* (6.3)
A. 01*i* (4.5)					*A.* 01*f* (2.5)	*A.* 11*c* (1.8)	u.i. (12.5)
A. 37 (4.5)					*A.* 01*k* (2.5)	*A.* 21 (1.8)	
A. 33 (2.3)					*A.* 07*c* (2.5)	*A.* 41 (1.8)	
rest (20.5)					rest (12.5)	rest (7.1)	

V2	V3	B1	B2	D1	D2	D3	D4
A. 15 (15.3)	*A.* 06*a* (39.4)	*A.* 14*a* (100)	*A.* 14*a* (60.0)	*A.* 14*a* (31.6)	*A.* 06*a* (34.3)	*A.* 14*a* (48.0)	*A.* 14*a* (80.0)
A. 06*a* (13.6)	*A.* 14*a* (15.2)		*A.* 02 (40.0)	*A.* 06*a* (21.1)	*A.* 14*a* (20.0)	*A.* 06*a* (36.0)	*A.* 07*a* (20.0)
A. 11 (11.9)	*A.* 15 (7.6)			*A.* 15 (15.8)	*A.* 07*c* (11.4)	*A.* 06*c* (12.0)	
A. 16*a* (6.8)	*A.* 00 (4.5)			*A.* 07*c* (10.5)	*A.* 11 (11.4)	*A.* 01*j* (4.0)	
A. 13 (5.1)	*A.* 14*d* (3.0)			*A.* 16*b* (5.3)	*A.* 33 (5.7)		
A. 08*a* (3.4)	*A.* 01*b* (3.0)			*A.* 14*f* (5.3)	*A.* 14*f* (2.9)		
A. 01*b* (3.4)	*A.* 15*b* (3.0)			*A.* 32 (5.3)	*A.* 29*a* (2.9)		
A. 01*g* (3.4)	*A.* 14*e* (3.0)			u.i. (5.3)	*A.* 29*b* (2.9)		
A. 06*d* (3.4)	*A.* 40 (3.0)				*A.* 07*d* (2.9)		
A. 14*a* (3.4)	*A.* 11 (1.5)				*A.* 14*g* (2.9)		
rest (30.5)	rest (16.7)				rest (2.9)		

u.i., unidentified.

Frequency distribution. Two histograms are produced from *Acantholaimus* species frequency of individuals and samples (Fig. 3.2).

The histogram for individual frequency (Fig. 3.2A) showed that *Acantholaimus* community consisted of a few dominant and many rare species. Among 65 species, 28 species were represented by only 1 individual. There were 13 and 7 species which were represented respectively by 2 and 3 individuals. These 3 groups accounted for about 3/4 (73.8 %) of whole *Acantholaimus* population. The species with greatest individual occurrence was *A.* sp 14a which accounted for 142 individuals. The second most abundant species, *A.* sp 06a, was represented by 66 individuals.

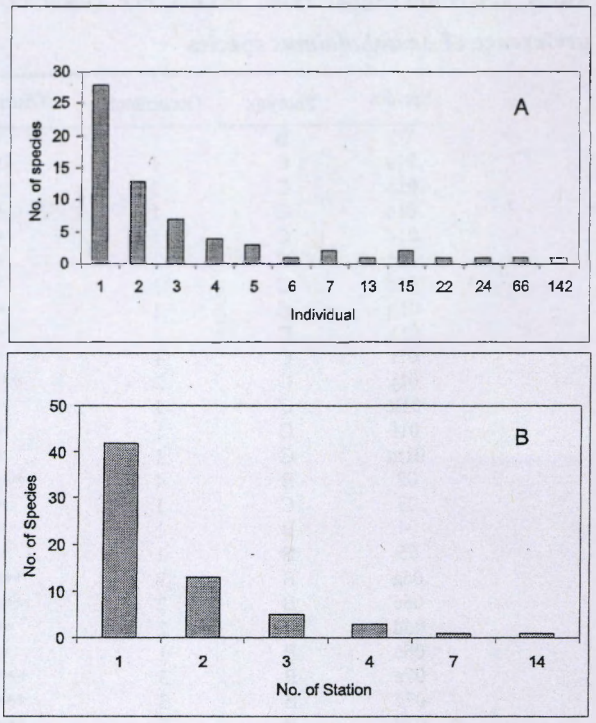

Fig. 3.2. Frequency distribution of Acantholaimus species for individual number (A) and for sample number (B) from study area.

When station numbers were concerned, about 1/3 (42 species, 64.6%) of *Acantholaimus* species occurred only at 1 station. Thirteen species occurred at 2 stations. The species occurred at more than 2 stations were less than 1/6 (10 species) of all samples. Only 1 species, which was *A.* 14a, occurred at more than half the stations (14 stations) being most common. *Acantholaimus* 06a was also very common occurring at 7 stations (Fig. 3.2B).

Habitat preference of* Acantholaimus *species. Table 3.4 summarises the distribution mode of *Acantholaimus* species and their preference. The distribution modes are classified into four categories: very endemic (*, species found in only one station), inter-area (**, species found in some stations of only one area), inter-regional (***, species found in some stations of only one region) and inter-Antarctic (****, species found in different regions).

Table 3.4. Pharyngeal type, occurrence (number of stations), distribution mode and habitat preference of *Acantholaimus* species

Species	Pharynx	Occurrence	Distribution	Preference		
				Locality	Depth	Sediment
00	B	1	*	VK	-	-
01a	C	1	*	KN	-	BR
01b	C	3	***	WD	-	-
01c	C	1	*	KN	-	BR
01d	C	1	*	KN	-	BR
01e	C	1	*	KN	-	SP
01f	C	1	*	KN	-	BR
01g	C	1	*	VK	D	-
01h	C	1	*	KN	-	SP/BR
01i	C	1	*	KN	-	SP/BR
01j	C	2	****	-	-	-
01k	C	1	*	KN	-	BR
01l	C	1	*	VK	D	-
01m	C	1	*	KN	-	SP
02	B	4	****	-	-	-
03	C	1	*	KN	-	BR
04	B	1	*	KN	-	BR
05	B	1	*	VK	D	-
06a	B	7	****	-	-	-
06c	B	2	****	-	-	-
06d	B	2	**	WD	-	-
06e	B	1	*	VK	D	-
07a	B	3	****	WD	-	-
07c	B	3	****	-	-	-
07d	B	2	****	-	-	-
08a	B	2	**	VK	D'	-
10	B	3	***	WD	-	-
11	C	4	****	-	-	-
11b	C	1	*	VK	D	-
12	B	1	*	VK	D	-
13	A	3	***	WD	-	-
14a	B	14	****	-	-	-
14c	B	2	**	VK	D'	-
14d	B	2	***	WD	-	-
14e	B	1	*	VK	D	-
14f	B	2	**	DP	-	-
14g	B	1	*	DP	-	-
15	C	4	****	-	-	-
15b	C	1	**	VK	-	-
15c	C	1	*	KN	-	BR
15d	C	1	*	VK	-	-
16a	B	1	*	VK	D	-
16b	B	2	****	-	D'	-
16c	B	1	*	VK	D	-
17	C	1	*	VK	D	-
18	C	1	*	VK	D	-
21	C	1	*	KN	-	SP
27	C	1	*	VK	-	-
28	B	1	*	KN	-	BR
29a	B	2	****	-	-	-
29b	A	3	****	-	-	-
29c	B	1	*	KN	-	BR
32	C	1	*	DP	-	-
33	B	2	****	-	-	-
36	B	1	*	KN	-	SP/BR
37	C	1	*	KN	-	SP/BR
39	B	1	*	VK	-	-
40	C	1	*	VK	-	-
41	C	1	*	KN	-	SP
42	C	1	*	VK	D	-
43	B	1	*	KN	-	SP/BR
44	C	1	*	VK	-	-
45	C	1	*	VK	-	-
46	B	1	*	KN	-	SP
47	B	1	*	DP	-	-

Among 65 species identified, 61 species occurred in WS and subsequently AP added only 4 more species, presumably typical AP species (*A.* 14f, *A.* 14g, *A.* 32 and *A.* 47). There were 14 inter-Antarctic, 4 inter-regional and 5 inter-area species. There were also 47 typical WS species. Forty two species were supposedly very endemic occurring only at one station. Among these endemic nematodes 19 species were originated from KN, 20 species were from VK and 3 species were from DP (no species were typical for BS).

A total of 15 species appeared only at deep-sea stations (range about 1,000 – 2000 m) those which were all from VK. Three of them were found more than 1 deep-sea stations and the rest found only at 1 deep-sea stations. There was no typical deep-sea species in DP.

Since the samples with biogenic mat samples were restricted in KN sediment preference were analysed only for the KN species to see whether *Acantholaimus* species distribution pattern is related with the particular substrates (sponge spicule mat and/or bryozoan debris). All KN endemic species showed a preference for a specific sediment type, meaning that no single species from soft sediment in this area were endemic. Ten species were found only in the sediment covered with bryozoan debris. Five species were found only in the sediment covered with sponge spicule mat. Another 5 species were found in the sediment where the sponge spicules and bryozoan debris were mixed. No species found in more than 2 different types of sediment.

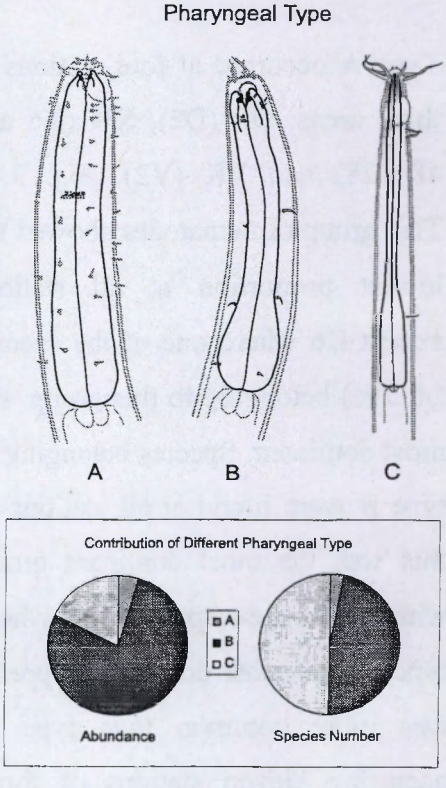

Fig. 3.3. Three different pharyngeal morph types of *Acantholaimus* and their contribution to abundance and species number of their

Morphological diversity and distribution. Acantholaimus species in this study area showed 3 different pharyngeal morphotypes that are supposed to have different ecological strategies (Fig. 3.3). These differences are likely the result of different evolutional states. Type A is more or less simple cylindrical shape with stronger muscles and supposed to be most primitive,

because they share more common features with related families, like Selachinematidae and Cyatholaimidae. Type B and C are provably delivered from type A and in the course of divergence. Type B can be distinguished from type A by more narrowed anterior cylindrical part and posterial round bulb. Type C even has more slender cylindrical part and elongated posterial bulb. In order to see what these differences are signifying in ecological terms, their distribution pattern and contribution to diversity were compared.

The most abundant pharyngeal type was B that accounted for 79.1%, that followed by type C (16.2%) and type A (4.7%). However, the order of type B and C was reversed when the contribution of them to species number was considered. Type C accounted for 49.3% (32 species) while type B accounted 47.7% (31 species). Type A was only 3.0% (2 species) (Table 3.4, Fig. 3.3).

Type A occurred at four stations of three areas: DP (D2), KN (K6 and 48//228) and VK (V2) (Fig. 3.4). This group of nematodes showed the lowest proportion at all stations except K6 where one of the species (*A.* 29a) belonging to this group was most dominant. Species belonging to type B were found at all stations as this was the most dominant group with only one exception at V2 where type C was most dominant. Type C was more common than type A occurring eleven stations of three areas. However none of either type A or type C was found in BS.

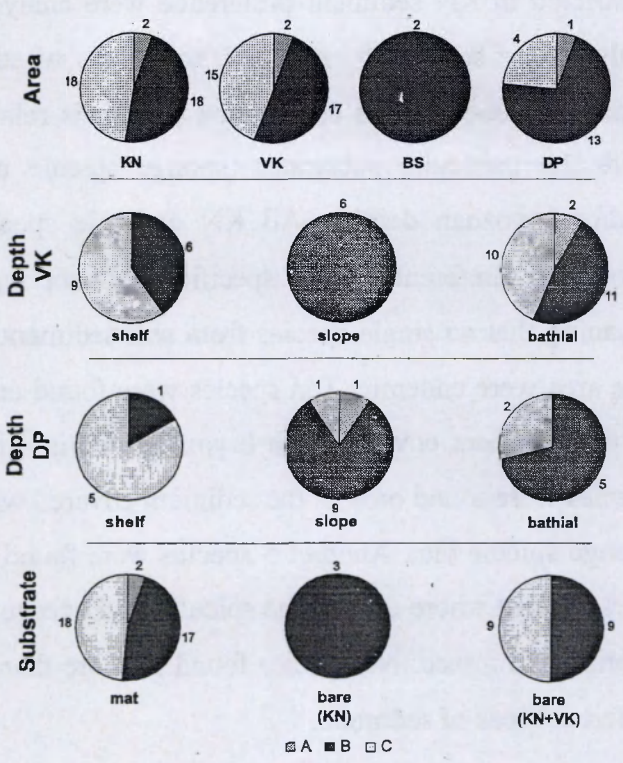

Fig. 3.4. Acantholaimus species composition of different pharyngeal types in different biotopes. Numbers indicate the species contributed. Numbers represent the species occurred.

When distribution mode of different pharyngeal types was compared, 1 species of type A was inter-regional and the other one was inter-Antarctic. In type B, 16 species were endemic, 5 species were inter-areal, 2 species were inter-regional and 10

species were inter-Antarctic. In the case of type C, 26 species were endemic, 1 species was inter-regional and 3 species were inter-Antarctic. There was no inter-areal species in type C (Table 3.4).

Concerning bathymetric distribution of these pharyngeal types, type C was more abundant in the shelf than deeper stations both in VK and DP. Type B was absolutely dominant in the slope of both areas. In biogenic mats, type B and C were comparable while type A was negligible. In the bare sediment of KN, only type B was present. However all bare sediments from the shallow stations (< 400 m) of WS were considered, the proportion of type B and C were equal. No type A occurred in bare sediments.

3.4.4. Environment and community

Geographical difference. In order to see if *Acantholaimus* community properties could be influenced by geographical differences, data was pooled to produce two different spatial scales, i.e. regional and areal (Fig. 3.5).

The regional comparison showed that *Acantholaimus* was more abundant in WS (58 ind./10 cm^2) in general compared with them in AP (42 ind./10 cm^2) in terms of density. However, the difference was not significant. In the case of relative abundance and species number between two regions, the pattern remained the same, but the difference became significant.

In area level, VK showed the highest density (67 ind./10 cm^2). The following KN (54 ind./10 cm^2) and DP (48 ind./10 cm^2) showed similar density while BS showed

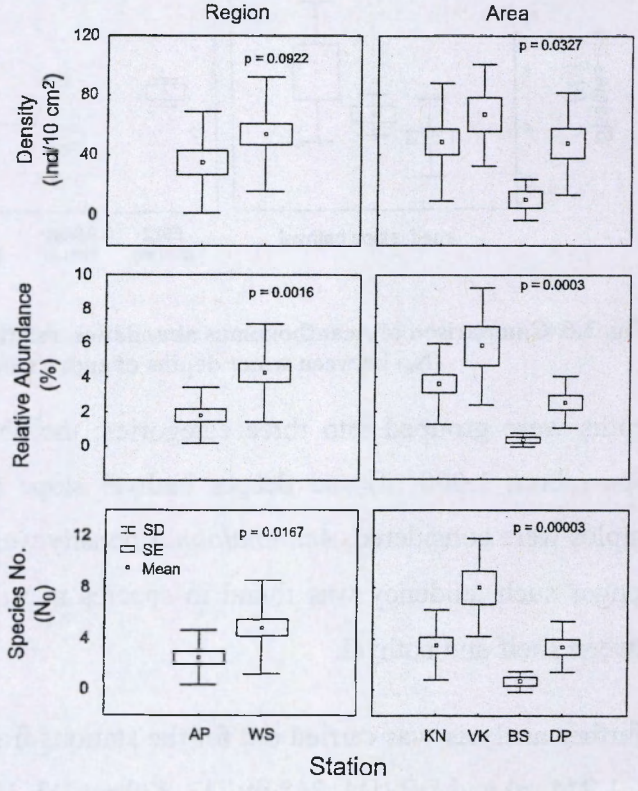

Fig. 3.5. Combined graph of *Acantholaimus* densities, relative abundances and Hill's diversity (N_0) numbers in two different regional and areal scales.

the lowest density (10 ind./10 cm^2). The difference between VK and BS was significant. Relative abundance and diversity showed the same pattern.

Water depth. Fig. 3.6 summarises *Acantholaimus* density, relative abundance (proportion in nematode community) and species number (N_0) between different water depths. Two areas, KN and BS, where the samples were taken only from shallow stations, were not considered.

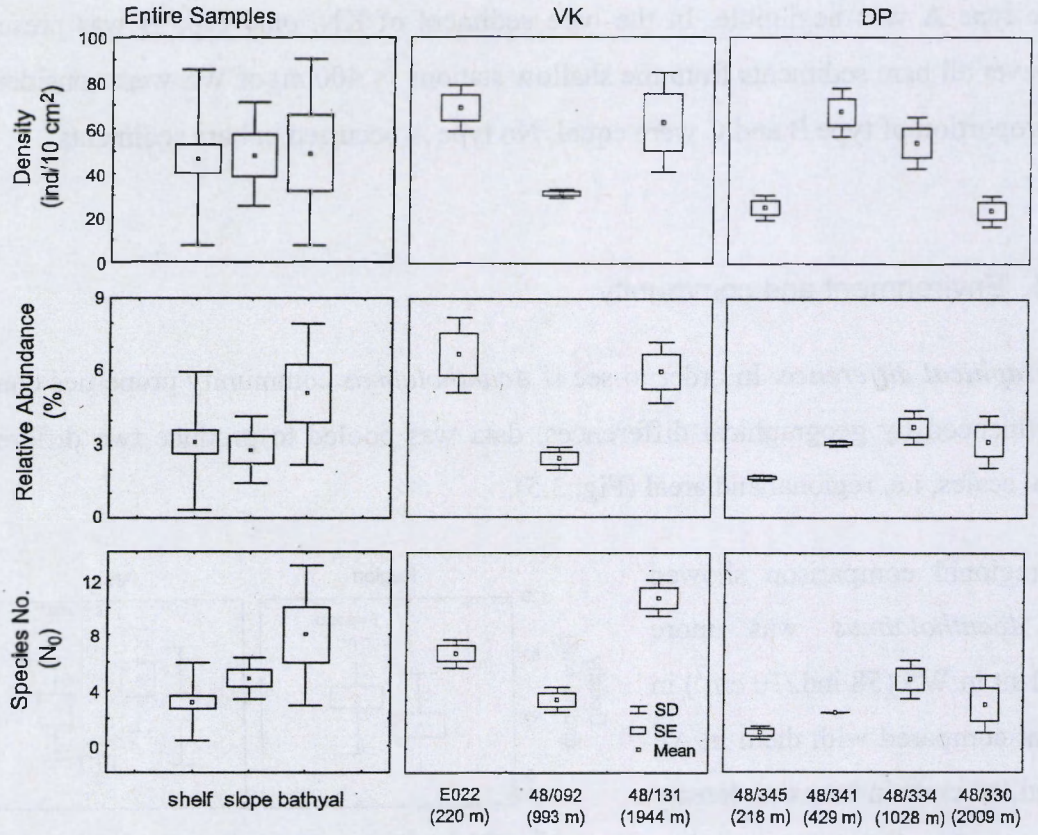

Fig. 3.6. Comparison of Acantholaimus abundance, relative abundance (%) and species number (N_0) between water depths of entire study area, VK and DP.

Depths were grouped into three categories: the shelf (shallower than 450 m), upper slope (about 1,000 m) and deeper bathyal slope (about 2,000 m). When the entire samples were considered, *Acantholaimus* density was not correlated with water depth. A stronger such tendency was found in species number (N_0) with significant difference between shelf and bathyal.

A further analysis was carried out for the stations from VK (V3, 220 m; V1, 993 m and V2, 1,944 m) and DP (D4, 218 m; D3, 429 m; D2, 1028 m and D1, 2,009 m) separately

in order to remove geographical influences and also to see whether the water depth effects differently in two regions.

In VK, both shelf (V3) and bathyal (V2) showed significantly high density compared with slope (V1). The species number, however, showed somewhat different pattern in that the bathyal showed the highest value followed by shelf.

DK showed different patterns than VK. The density tended to decrease significantly with increasing water depth, except for the shallowest station (D4) where it showed very low density. On the contrary, relative abundance and species number seemed to increase with increasing water depth. However, the significant difference was found only between D4 (218 m) and D2 (1,028 m).

Sediment conditions. The sediments of the study area could be basically classified into two groups: sandy and silty. However, some sediments from KN were covered with biogenic mats that increased the heterogeneity of sediment. These biogenic mats were mainly consisted of sponge spicules (SP) or bryozoan debris (BR). These materials present mixed (SP/BR) in general (e.g., K1), but in some areas SP (e.g., K7) or BR (e.g., K3 and K6) were more dominant. In order to test the influence of these different sediment conditions to *Acantholaimus* communities, sandy vs. silty, mat vs. bare sediment and between different mats and bare sediment were compared (Fig. 3.7).

The difference between sandy and silty sediment did not make any difference in *Acantholaimus* community in all aspects.

Concerning mats vs. bare sediment, there were no differences in densities. In the case of relative abundance and species number (N_0), it seemed to be higher in mats covered sediment than in bare sediment, which was not, however, significant in difference.

When those mats were separated based on their origin and bare sediment was restricted only to K2 that was not influenced by scouring, the comparison between them and with bare sediment showed that the different sediment conditions influenced differently to the *Acantholaimus* communities. The bare sediment showed the highest density whilst the SP/BR showed the lowest density. The difference between these two extremes was significant. The density in SP was also higher compared with BR, but not significantly. In relative abundance, the two extremes become very comparable while BR and SP kept

the same proportion. There were no significant differences between different sediment conditions. In the case of species number, the bare sediment becomes lowest while SP/BR becomes highest.

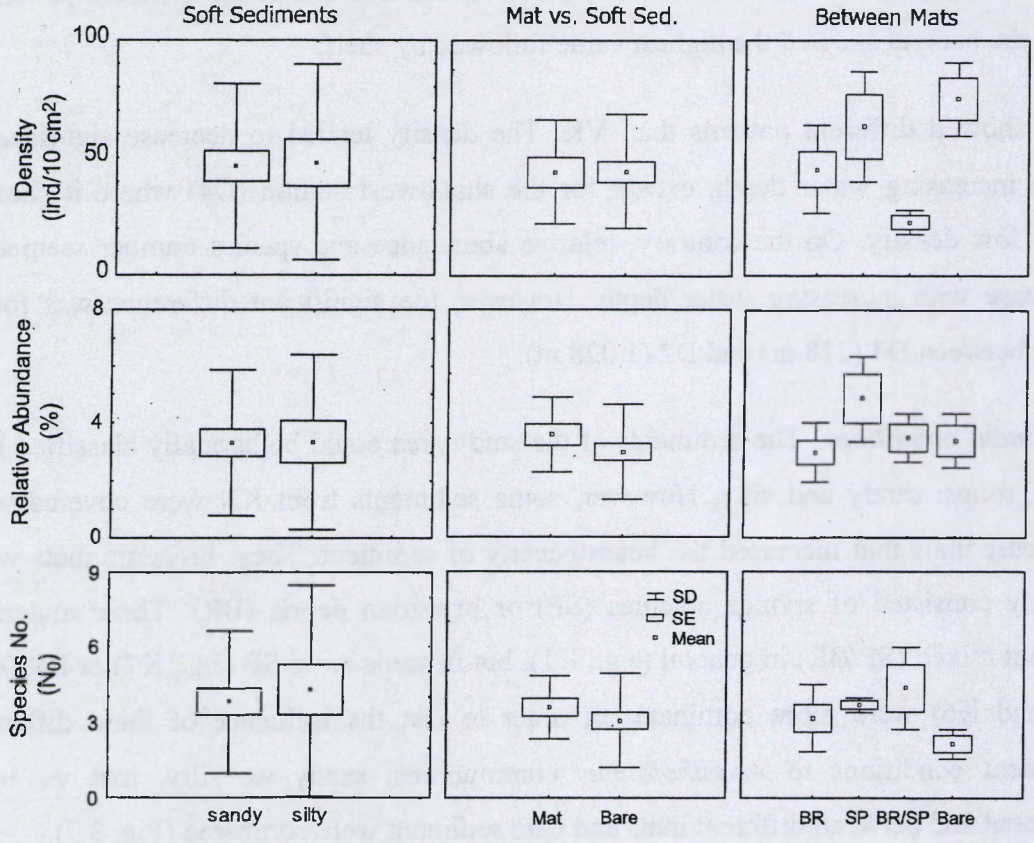

Fig. 3.7. Comparison of Acantholaimus abundance, relative abundance (%) and species number (N_0) between different sediment conditions.

3.4.5. Community discrimination

CCA (Canonical correspondence analysis). The CCA ordination result (Fig. 3.8) showed that none of the environmental factors explain the distribution pattern of *Acantholaimus* species. The biogenic mats were spread over the graph together with bare sediments. The deeper stations (V1, V2, D1 and D3: about 1,000 m or deeper) stayed closer forming a loose group, but without showing a correlation with depth. Geographically separated stations K5 and B1 were plotted at the same point.

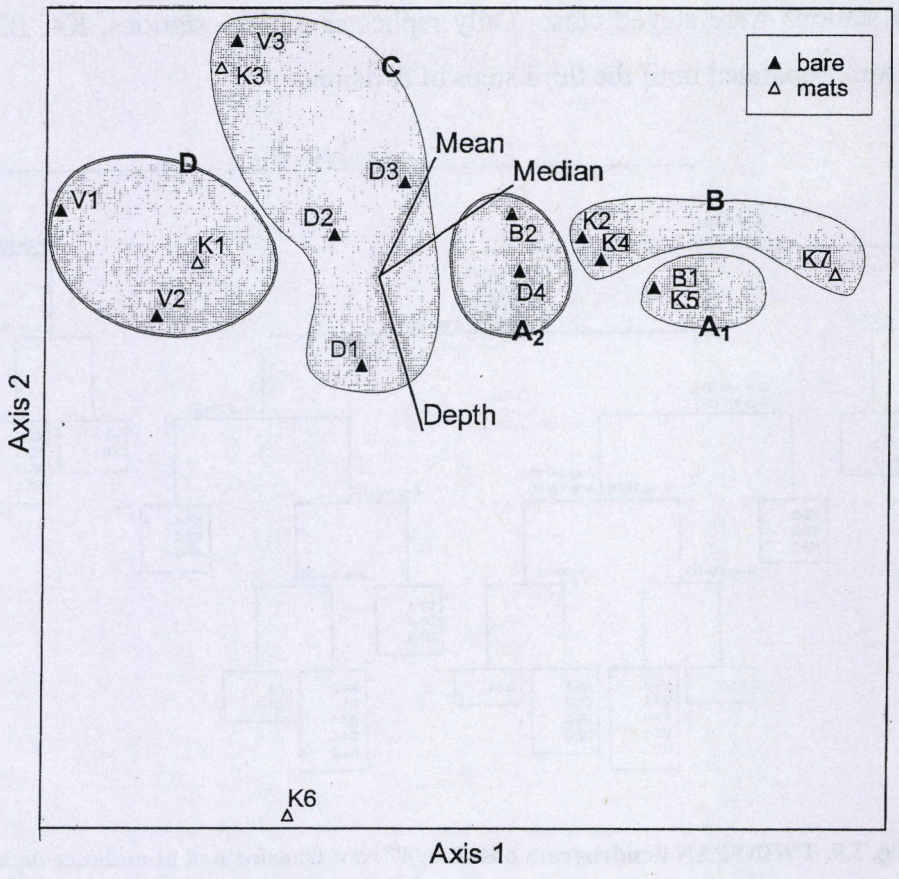

Fig. 3.8. Canonical correspondence analysis (CCA) plot from pooled and 4th root transformed abundance data of *Acantholaimus* species together with environ parameter data.

TWINSPAN (Two-Way Indicator Species Analysis). TWINSPAN analysis resulted in four major branches (

Fig. 3.9). The first division discriminated a group containing all replicates of K2 and K3, two replicates of K4 and one replicate of B2, which was represented by the existence of *A*. 02. The second division branched out a small group that consisted of two replicates of K1 and all replicates of V1 in which *A*. 07a and *A*. 07b were existed. The third division divided the rests into two larger heterogeneous groups. One group represented by *A*. 14a consisted of whole replicates of D3 and K7. This group also included some replicates of stations from KN, BS and DP. The other group was represented by co-existence of *A*. 01b, *A*. 15, *A*. 06a and *A*. 11 was also a mixture of samples from various biotopes. The further divisions broke down the third and fourth groups into several smaller groups with no remarkable pattern. Even though the samples from different geographical locations, water depth and sediment types were intermixed, the replicates

of many stations were stayed close. Only replicates of four stations, K4, B2, K1 and 48/342, were separated until the third steps of division.

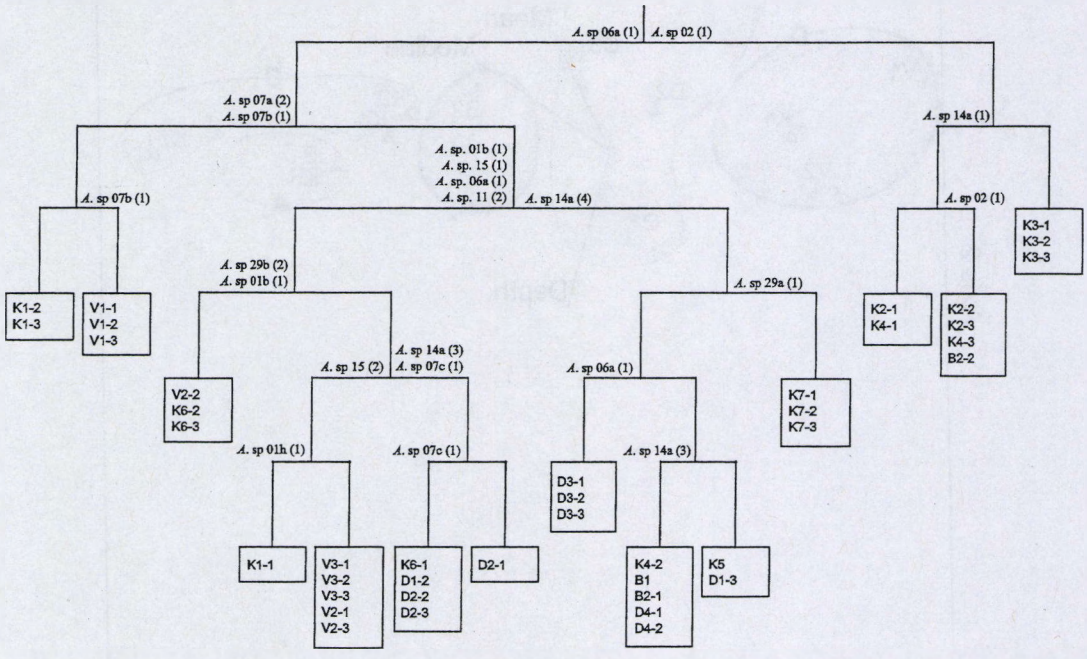

Fig. 3.9. TWINSPAN dendrogram based on 4th root transformed abundance data.

Cluster analysis. Cluster analysis

This analysis showed some differences result from that of TWINSPAN (

Fig. 3.10).

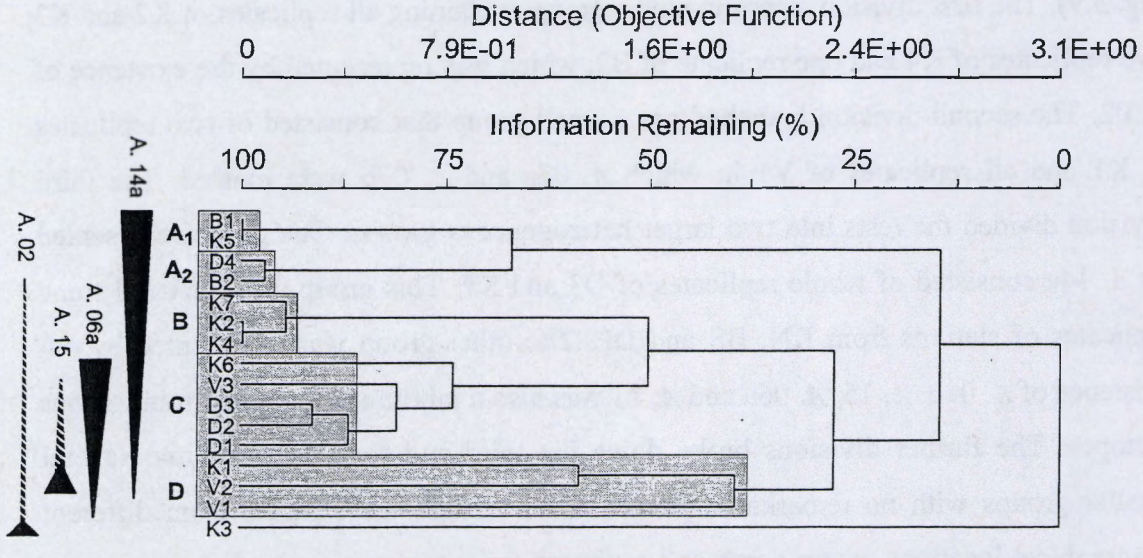

Fig. 3.10. Dendrogram for group average clustering of Bray-Curtis similarities based on pooled and 4th root transformed *Acantholaimus* species abundance data.

Like TWINSPAN, the first separation seemed to be made based on the existence of *A.* 02, but the stations under influence of *A.* 14a or *A.* 06a were excluded eventually leaving K3 alone. Further separations seemed to be influenced by the proportional combinations of *A.* 14a and *A.* 06a which were the first and second abundant and dominant species in the study area. Other species that contributed to form a group of cluster was *A.* 15 which was responsible for the K1 and V2 cluster. However, this kind of clusters was heterogeneous and could not stand for a community.

3.5. Discussion

3.5.1. *Acantholaimus* abundance and diversity

The abundance, dominance and species richness data on *Acantholaimus* from various places are summarised in Table 3.5.

Table 3.5. Individual abundance, relative abundance, species numbers and dominance rank within the community of Acantholaimus in different Oceans

Author (Year)	Depth (m)	Location	Abundance (average)		sp. no. (average)	rank (average)
			Density	%		
Vopel & Thiel (2001)	4037-4158	Pacific	44.0-67.6/71 cm^3	19.1-20.5	-	1
Lambshead *et al.* 2003	4301-4994	Pacific	-	5.9-9.6	7	2-4 (2.6)
Muthumbi & Vincx (1997)	500-2179	Indian	-	-	37 (9.1)	-
Soetaert & Heip* (1995)	123-8380	**	-	5.9-14.3	-	2-3 (2.5)
Tietjen (1989)	5411-8189	Atlantic	-	-	4-11 (?)	1-19 (4.6)
Jensen (1988)	970-3294	Norwegian	-	-	< 4	-
Vanreusel *et al.* (1997)	1915-2033	Pacific	-	1.1(?).7-10.7	-	2 (2)
Gambi et al. (2003)	1050-7800	Pacific	-	>1 – 11.3	-	2-9(?)
Present study	182-2009	Antarctic	1-100.1 (48.1)	0.5-7.9 (3.3)	65 (8.1)	2-47 (10.2)

***results compiled from various sources**
**** North Atlantic and Mediterranean**
(?) lower limit unknown

The density data on *Acantholaimus* is only available from equatorial Pacific (Vopel and Thiel, 2001) while data on relative importance of them are more available in the literature. Although the direct comparison of density from Vopel and Thiel (2001) with that of the present study is not possible because of the difference sediment depth analysed (they used only the top most 1 cm), it is obvious that the abundance of the present study (48 ind. / 10 cm^2) is lower. *Acantholaimus* is recognised as a representative deep-sea nematode since their abundance is positively correlated with increasing water depth (Soetaert and Heip, 1995). Therefore it is unclear whether the low density from this study area is geographical pattern or depth effect.

In spite of the low abundance of *Acantholaimus*, our study shows the highest species number. The highest species number reported before was 39 species from 18 stations in Indian Ocean deep-see transect (Muthumbi and Vincx, 1997). The record breaking species number (65 species) of the current study is from the same numbers of stations (18 stations) and same volume (50 cm^3) of sediment with that of Muthumbi and Vincx.

When the range of species number and their average are compared, the result of the current study showed (average: 8.1 species per station) is a bit lower average but wider range (range: 1-24) than in Indian Ocean deep-sea transect (average: 9.1 species per station, rage: 3-18). This is probably because of that the stations of the current study is from more various biotopes: from shelf to bathyal in depth range, high heterogeneity of sediment due to the presence of biogenic mats and wider spatial area.

However, since *Acantholaimus* is not common in shallow water in general, the occurrence of so many species in the Antarctic shallow continental shelf is remarkable. This suggests two possibilities that *Acantholaimus* is either a cold water nematode and distributed along a certain isothermal area or originated from the Antarctic and dispersed to deep sea.

3.5.2. Environment and community coupling

Abundance of *Acantholaimus* in this study is not correlated with water depth, unlike our common knowledge. This is because of both relatively low abundance in deeper stations and also unusually high abundance in shallow stations. The same results were also found in the Halley Bay (Vanhove *et al.*, 1999) where Acantholaimus showed correlation with sediment size rather than water depth. In the case of DP, it even seemed to be negatively correlated with depth. However, relative abundance and especially diversity increases with depth. This increasing tendency is stronger in DP than VK. For this reason, the ecological process in AP is considered more close to other seas, as it is more to the north, while that of WS is more distinctive.

Unlike the results of Vanhove *et al.* (1999) sediment particle size seemingly does not influence to *Acantholaimus* community structure in all aspects. However, the presence

of biogenic mats in the sediment seemed to have positive effects on Acantholaimus species richness.

While water depth and sediment heterogeneity has minor influence only to relative abundance and diversity, geographical influence is more obvious and vast. *Acantholaimus* community in KN is more abundant and diverse compared with BS. VK also shows the same tendency when it is compared with DP. Eventually the regional comparison between WS and AP shows clear difference in all aspects.

3.5.3. Species composition and habitat preference

Species composition of *Acantholaimus* is very complicate. This complication comes from minor species rather than dominant species. The dominant species are few but widely spread. Minor ones are much more diverse but strongly endemic. Therefore neither dominant nor minor species represent the community larger than sample level.

There were big gab in species number between WS and AP (WS, 61 species; AP, 18 species). This gab is provably not only due to ecological process but also evolutionary process: more speciation happened in WS than in AP.

The distribution pattern of morphological characteristics of pharynx might be suitable to view the insight of evolutionary background, since different morphologies must be the product of evolution. Type A is supposed to be plesiomorphy of other two types, because the species in type shares more common characteristics with related group, Cyatholaimidae and Selachinematidae. This type of pharynx is common in many genera of Cyatholaimidae and Selachinematidae. Type B can be found in some Cyatholaimidae, but not so common. Chromadoridae also have a pharynx with postal bulb. However the pharyngeal lumen of Chromadoridae is stronger compared with that of Acantholaimus. Type C is rather unique in that it has an elongated pharyngeal bulb which type is not so common in the related nematodes. Type B and C are considered developed independently from type A, because there are both intermediate forms between type A and B and type A and C.

Species with type A pharynx are widely spread although they are rare. The proportion of type B in terms of species number is higher in AP and lower slope while type C is

higher in WS shelf. Such a distribution pattern seems to suggest that type C species are diffused from shallow WS to deeper places.

3.5.4. Coexistence of Acantholaimus species

The genus reportedly showing highest species number in a certain restricted area was *Theristus* that comprised of 43 species observed in Gulf of Gascony (Dinet and Vivier, 1979). Tietjen *et al.* (1989) also found from the Puerto Rico Trench and Hatteras Abyssal Plain that most dominant genera are multi-specific: *Theristus* (35 species), *Halalaimus* (16 species), *Acantholaimus* (12 species), and *Desmoscolex* (6 species). 38 species of *Acantholaimus* were retrieved in Indian Ocean deep sea transects (Muthumbi and Vincx, 1997). The 65 *Acantholaimus* species recovered from this study is a new record though these numbers can not be directly compared without consideration the size of area in concern.

Some studies argue that at equilibrium the number of coexisting species can not be more than the number of resources in a habitat due to competitive exclusion (Armstrong and McGehee, 1980; Hardin, 1960; Phillips, 1973). If this principle is true, there must be a couple of hundreds of resources in this study area to satisfy some hundreds species of an average of about genera presumably occurred in each stations of the study area and some tens of them should be assigned to *Acantholaimus* species. Is the coexistence of closely related species unnatural? Intuitionally we know that the answer should be "no", otherwise speciation would not occur. These studies to explain 'competitive exclusion' were accomplished based on extremely simplified experiments or through modelling works in which condition the competition is straight forward and one might has privilege on others, which gives not much chance of resource partitioning.

A habitat is spatial and temporal space that both can be heterogeneous. It fluctuates regularly or irregularly in wide range of time scales. Also the differences between places occur. Every change of chemical, physical and biological varieties in temporal and spatial space will influence differently to the members of the community. Thus, resource partitioning in hyper-dimensional habitats will provably reduce interspecific competition by narrowing the niche overlap and roll shifting between different species. A modelling work of Huisman and Weissing (1999) showed that how a number of

species can coexist sharing limited resources. Using well-known resource competition models (Grover, 1997; Hsu *et al.*, 1981; Huisman and Weissing, 1999; Leon and Tumpson, 1975; Tilman, 1977), they showed that these models could generate oscillations and chaos. They concluded that these oscillations and chaotic fluctuations in species abundance would allow the coexistence of many species on a handful of resources.

Is coexistence then extrinsic matter? Jensen (1988) attributed the coexistence of *Acantholaimus* species to different types of their mouth openings and buccal cavities and a consequent food resource partitioning. It is true that *Acantholaimus* species have different sizes of teeth and buccal cavities and various degrees of muscularisation. An additional explanation for this is also can be found from their various body sizes and shapes that indicate different life styles. Some species have slender and longer body while some have more stout body. For this way they can provably find more specific niches avoiding competition. These varieties can be one of the intrinsic factors that explain the coexistence and resource partitioning of *Acantholaimus* species, which are the answers that can be obtained from direct observation.

However that does not seem to be adequate to explain the coexistence of *Acantholaimus*, because there were also many coexisting species in this area which have very similar type of buccal morphology and body shape.

Bongers, (1990) and Bongers *et al.* (1991) assigned c-p values that called Maturity Index (MI) to different nematode groups according to their life style: higher c-p values (maximum: 5) to the nematodes tend to be persisters (those that are *K*-strategists) and lower c-p values (minimum: 1) to colonisers (those that are *r*-strategists). The nematodes with different c-p values are supposed to behave differently to environmental changes (Table 3.6).

The MI shows insight of nematode autecology to a certain extension with some speculations. Lee *et al.* (2001a; 2001b) found that MI decreased due to iceberg scouring in deeper sites while it remained constantly low in shallow costal area even after scouring. *Acantholaimus* was typically in accordance with MI tendency: higher in individual abundance where MI was high. It might be proper, therefore, to assume that *Acantholaimus* species more tend to be *K*-strategist rather than *r*-strategist, although it is

considered as intermediate state (c-p: 3) by Bongers *et al.* (1991). The extraordinarily large spermatozoa of these species can be evidence supporting this assumption.

Table 3.6. General differences in behavioural tendency between *r*- and *K*-strategists

r-selected	*K*-selected
Capable of rapid increase	Slower growing
Semelparity	Iteroparity
Many offspring	Few offspring
Little or no parental care	Parental care
Matures early	Matures late
Effective dispersal	Limited dispersal
Weak competitor	Strong competitor
Dominates after disturbance	Dominates in static environment

K-strategists take the advantage of stable environments and react slow to excessive food availability. This means that they are provably less greedy in food consumption and less competitive for resources, which can allow more coexisting species regardless their morphological and functional similarity. Therefore, it could be arguably stated that the stronger intrinsic cause of coexistence of many *Acantholaimus* in one place is their *K*-strategic life style than their diverse morphology.

It seems that species groups of type B and C have different ecological strategies. From the morphology, the species with type B pharynx might be stroller since their muscles are well developed, whilst type C are hemi-sessile as their weakly developed and narrow body tells it. Type B has a larger buccal cavity and strong pharyngeal muscle whereas type C has weaker pharynx in general. Such morphological differences suggest that type B species might be *r*-strategists and type C is *K*-strategist. The difference in strategy of them provably leaded their different distribution modes. This provably explains why type B is more endemic and lacking in some circumstances like in the scours.

3.5.5. Endemism or rarity?

According to Tietjen et al. (1989), about 67 and 77% of the species identified from the Hatteras Plain and Puerto Rico Trench area, respectively, are endemic. Among 38

Acantholaimus species from Indian Ocean deep sea transects, 14 identified species appeared to be endemic and 9 species of them occurred only in one station (Muthumbi and Vincx, 1997). About 72% of *Acantholaimus* species from the current study occur only in one station or at least within a local area. In such case, these species appear to be endemic and we treat them as endemic species tentatively without excluding possibility of simple rarity. However, this consideration is subject to future validation.

Endemism is result of isolation of gene pool, therefore occurs more often where the habitat is isolated (Darwin's pinch). However, the marine environment is open system and there are no clear physical barriers. Previously the dispersal of nematodes was thought be slow because they lack plankton stage through out their life cycle (Heip, 1980; Platt and Warwick, 1980; Vincx and Heip, 1991), which could be a part of the explanation for their endemism. Gerlach (1977) have, however, argued that nematodes can be dispersed passively attached to floating sea weed. Palmer (1988) also reported the existence of nematodes in the water column that suspended due to water movement, yet they tend to avoid being washed away by downward vertical migration as proved by Palmer's another experiment (1986). Palmer's two experiments eventually imply that nematodes avoid being drifted, but some of them are inevitably subjected to resuspension. For those resuspended nematodes can passively drift relatively longer distance in shorter time.

Concerning endemism, I feel that we must start from answering some questions that are still doubtful. First, are those supposedly endemic species are really autochthonous? Second, is the water current in this area as strong as the velocity of the place where Palmer's experiment accomplished? Three, are those endemic species especially deeply concerned about resuspension and have special avoidance behaviour? Four, are the speciation rate of this genus faster than dispersion? Five, are those endemic species extreme specialists that can not survive in other area?

We have no concrete answer for these questions. To answer the first question, our knowledge on the nematode inventories of this area is far from complete while it is quite provable that an extremely rare species can appear to be endemic. On the second question, if the velocities of water currents in this area are too slow to resuspend nematodes, we still can accept the low dispersal rate of nematodes as previously considered. However, unfortunately we can not provide water current data of the study

area. Concerning the third question, we lack knowledge about the behaviour of Acantholaimus species. Only thing we can hypothesise is that the role of their relatively longer tail is to prevent from resuspension. We may not need to consider the fourth question, because it is not seemingly. Synchronised speciation of such many species is not conceivable, especially considering that evolutionary process is incomparably longer than ecological process. The answer to the fifth question is also negative, because we can not conceive any exclusively peculiar environmental characteristics and physical barriers in the sampling stations although they are quite heterogeneous in certain points. However, Chase et al. (1998) attributed the high diversity of the deep-sea macrofauna to strong population structure over small scales (134 Km). If it is true for macrofauna, it must be possible for meiofauna population with even over smaller scales. In such case the factor that defines the population size and the limit of distribution might be more intrinsic rather than extrinsic.

Endemism may not need to be suspected. However, the high number of endemic species of one genus in this region is an interesting ecological phenomenon that may need to be explained. My subsequent assumption on the presence of such high number of endemic species is either they (or many of them) are simply rare or they are adapted in certain way, like having a long tail, to avoid passive dispersal and actively aggregate to keep their population within their favourite habitats.

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Chapter 4

Iceberg scouring and the response of shallow coastal community: Case study in Signy Island

Result published:
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4.1. Abstract

A series of ten samples from sediment in and adjacent to a shallow coastal iceberg scour at Signy Island, Antarctica, were taken by hand coring from 17 December 1993 until 23 August 1994. Scouring by the iceberg led to more than a 95% decrease in meiofaunal abundance and to a certain degree of reduction in diversity. Nematodes were always the most dominant group of meiofauna. The return of major meiofauna groups to control levels was accomplished in 30 days, although a decrease in abundance on the 50th day made interpretation difficult. The pioneering meiofaunal colonisers were copepods and ostracods, followed by nematodes. *Microlaimus* sp.1 was dominant among the nematodes throughout the whole period. Epistratum feeders and non-selective deposit-feeders were highly dominant over selective deposit-feeders and predators or omnivores. The Maturity Index, a measure for stress within nematode communities, was relatively low at all times and in controls, which indicates that *r*-strategists are prevailing in this community. In spite of the catastrophic destruction, nematode community structure was not affected by the iceberg impact, and there was no evidence of succession during recovery. This suggests that the nematode community in the shallow subtidal coast at Signy Island is well adapted to ice disturbance

4.2. Introduction

Benthic organisms in shallow Antarctic coasts are exposed to ice scouring. This includes potential scouring by floes in summer and also anchor ice disturbance in winter (Dayton, 1990; Picken, 1984), together with scouring by icebergs. Iceberg scour marks can be found from shallow sites to depths beyond 400 m in polar regions, although some of the deeper ones may date from previous glacial maxima (Picken, 1984). Frequency of iceberg scouring at Signy Island was estimated at once every 50-75 years (Gutt *et al.*, 1996). Global warming may increase the breaking up of ice shelves in Antarctica (Doake and Vaughan, 1991; Gammie, 1995), which would result in a more frequent abrasion of the Antarctic sea floor habitats. A number of studies have focused on the structure of benthic communities under ice disturbances ((Dayton *et al.*, 1970; Dayton *et al.*, 1969) in Cape Armitage and Hut Bay at McMurdo, Antarctic; (Lenihan and Oliver, 1995) at Signy Island, Antarctic; Gutt *et al.* 1996 in the Weddell Sea, Antarctic; (Conlan *et al.*, 1998) in Cornwallis Island, Arctic; (Peck *et al.*, 1999).

All of the above studies were concerned primarily with macrobenthos and none of them treat meiofauna in detail. Meiofauna are, however, useful in assessing environmental disturbance. They have short life cycles, which make their response to environmental change rapid. Due to the lack of planktonic stages in their life cycle the population changes depend more on reproduction than recruitment (Heip, 1980; Platt and Warwick, 1980; Vincx and Heip, 1991). Reflecting this, a number of experimental studies have focused on the effects of various disturbances (see Schratzberger and Warwick 1999). Many studies on marine pollution and disturbance also deal with response and recovery of meiofauna (Boucher, 1980; Giere, 1979; Green *et al.*, 1974; Wormald, 1976); Alongi 1983; (Brylinsky and Gibson, 1994); (Gee and Warwick, 1985). The general conclusions of those studies are that the resilience of meiofauna is strong; nevertheless the response depends on the intrinsic resilience of the particular community and the intensity of disturbance.

Antarctic benthic organisms have been exposed to ice disturbance since the major continental glaciation, which probably started from the late Oligocene (~37–24 Ma) or the beginning of the Miocene (~29–5 Ma) (Arntz *et al.*, 1994). Its long geological history suggests that ice disturbance is possibly the major structuring element in the adaptation

and evolution of benthic communities around Antarctic coasts. The evaluation of responses of meiofaunal communities to iceberg scouring should, therefore, give an insight into community adaptation and evolution, and hence, their resilience. An enhanced understanding of the ecology of Antarctic meiofauna should also help the prediction of community reaction to potential future environmental changes.

The aims of this study were (1) to assess the intensity of scouring by an iceberg and its short-term effect to a meiofauna community, (2) to investigate the recolonisation process or succession of a meiofauna community, (3) to estimate the resilience of a meiofauna community and (4) to study the long-term influence of iceberg scouring on a meiofauna community, with special emphasis on nematodes, in a shallow coast in Antarctica.

4.3. Material and Methods

4.3.1. Sampling area

In mid December 1993, an iceberg was observed grounded in Factory Cove near the British Antarctic Survey base at Signy Island, Antarctica (Fig. 4.1). The site affected was at about 8-9 m depth on a soft sediment bottom graded into solid rock at the landward side. A few days later, on 17 December 1993, the iceberg drifted off leaving a crater of approximately 10 m wide and 50 cm to 1 m deep with furrows showing the direction of its arrival and departure. The sediment in the scour was relatively well-sorted fine sand (median size: about 150 μm).

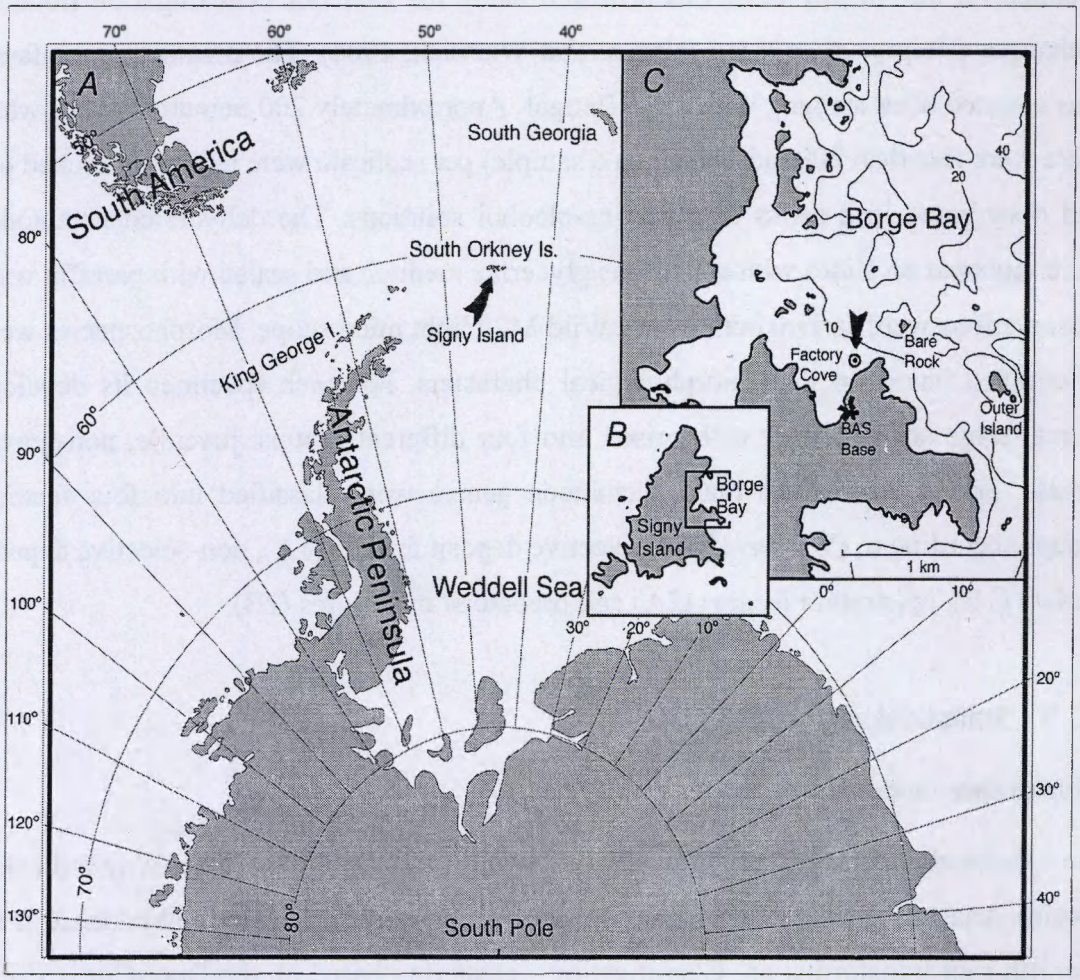

Fig. 4.1 Maps showing the location of Signy Island in the Antarctic (A), Borge Bay in Signy Island (B) and Factory Cove and British Antarctic Survey (BAS) station south of Borge Bay and the location of sampling station (filled circle) with details of surrounding (C).

4.3.2. Sampling and preparation

Duplicate samples from the sediment in and adjacent to the iceberg scour were taken with a hand corer (ø 5.5 cm) by SCUBA divers between 17 December 1993 until 23 August 1994. In total 10 duplicate samples were taken from the inside of the scour mark; on 0 (hereafter D0), 10 (D10), 20 (D20), 30 (D30), 50 (D50), 80 (D80), 110 (D110), 150 (D150), 200 (D200) and 250 (D250) days after impact. Two samples were taken from adjacent sediments as controls; one on day 0 (hereafter C0) and the other on day 170 (C170). The sediment in the core was preserved in 4% warm neutral formaldehyde solution. Sediments were decanted, and sieved using two different mesh sizes (# 1,000 µm and # 38 µm) before centrifugation. The animals passed through the 1,000 µm sieve and retained on the 38 µm sieve were regarded as meiofauna. Final extraction of meiofauna retained on the 38 µm sieve was achieved using the LUDOX centrifugation flotation technique (Heip *et al.*, 1985; McIntyre and Warwick, 1984). The metazoan meiofauna was counted after staining with Rose Bengal. Approximately 200 nematodes (all, when there were less than 200 individuals in a sample) per replicate were randomly picked out and dehydrated in a series of glycerine-alcohol solutions. The dehydrated nematodes were mounted on slides with anhydrous glycerine medium and sealed with paraffin wax. Observations were carried out under a Wild M20 light microscope. Morphospecies were determined based on their morphological characters. For each specimen its developmental stage and sex were categorised into four different groups: juvenile, non-gravid female, gravid female and male. Nematode genera were classified into four feeding groups according to (Wieser, 1953): selective deposit feeders (1A), non-selective deposit feeders (1B), epistratum feeders (2A) and predators/ omnivores (2B).

4.3.3. Statistical analysis

Multivariate methods

The species abundance matrix was analysed by using TWINSPAN (Two-Way Indicator Species Analysis; (Hill, 1979) from pooled and non-pooled nematode abundance data after 4th root transformation. Classification - clustering based on the Bray-Curtis similarity index was carried out using the same data.

Univariate methods

Nematode species diversity was measured using Hill's diversity indices: N_0 (the number of species), N_1 (the exponential of Shannon's index), N_2 (the reciprocal of Simpson's index) and N_∞ (the reciprocal of the relative abundance of the most dominant species) (Hill 1973). The maturity index (MI: Bongers, 1990; Bongers *et al.*, 1991; 1997) was used to characterise the life style of nematode communities. Although the MI is generally used for terrestrial nematode communities, it has been proposed as a useful measure for the study of disturbance effects on marine communities (Bongers *et al.* 1991).

4.4. Results

4.4.1. Meiofaunal abundance

In total 14 meiofaunal groups (for pragmatic reasons, all nauplii were considered as a single group) were recovered and their abundance varied throughout the study (Table 4.1). The least number of meiofaunal groups was found on D0 and D10, whilst the maximum was found at D50, D110, D150 and C0. The iceberg scouring removed about 93.5% of total metazoan density. In general the early samples contained lower numbers of meiofaunal groups. Nematodes were the most abundant group (overall mean 1,180 ind./10 cm^2). An exception was on D50 when nematode abundance was low and numbers of nauplii exceeded those of nematodes. Meiofaunal crustaceans (copepods, ostracods and nauplii) were the second most abundant group (overall mean 92, 31 and 202 ind./10 cm^2, respectively).

The earliest recolonisation of meiofauna was achieved by copepods, which recovered to control levels on D20. On D30, all meiofaunal major taxa exceeded control levels except for ostracods whose initial number at the control site was extraordinarily high. Overall meiofauna abundance decreased after D30, mainly due to the abrupt fall in nematode numbers, which only reached stable levels in 80 days.

4.4.2. Changes in nematode community

Abundance

The most obvious change caused by iceberg scouring was an abrupt decrease of nematode abundance (Table 4.1). The average density of nematodes at the scour mark on the initial day (D0) was about 54.0±2.4 ind./10 cm^2, which was only 4.5% of that of the control site (C0, 1,209±555.8 ind./10 cm^2). The number stayed low until D20 (29±6.3 ind./10 cm^2). A conspicuous increase was found on D30 with a density of 2,352±93.4 ind./10 cm^2, which is almost double the density of the control site on the initial day. This, however, decreased on D50 to 191±119.0 ind./10 cm^2. A larger fluctuation was found on D150 when the density reached the highest value (4,125±1,319.3 ind./10 cm^2) during the study. Except for this case, it seemed that the nematode community was fairly stable from D80 on, with an overall density between 588±39.7 ind./10 cm^2 and 1,216±36.9 ind./10 cm^2.

Table 4.1 Changes of meiofaunal mean abundance of two replicates (ind./10 cm2)

Days	D0		D10		D20		D30		D50		D80		D110		D150		D200		D250		C0		C170	
Date	17/12/1993		28/12/1993		06/01/1994		17/01/1994		05/02/1994		08/03/1994		09/04/1994		16/05/1994		05/07/1994		23/08/1994		17/12/1993		05/06/1994	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Nematoda	54	23.9	19	6.6	29.3	6.3	2352	93.4	183	130	1002	868	976	440	4125	1319	588	39.7	1216	36.7	1209	556	2415	299
Copepoda	10.8	13.4	2.7	2.7	38.6	42.7	70.3	77.3	72.6	36.4	472	23.3	10.1	1.8	76.4	55.5	101	81.5	156	10.7	38	17.9	51.9	22.7
Ostracoda	8.2	2.7	11	1.8	3.8	4.8	89.9	29.8	20.5	2.1	43.9	43.6	28.1	2.1	13.3	0.3	11.2	0.9	11.4	4.2	108	77	20.9	1.5
Nauplii	12.7	13.7	0.2	0.3	1.9	2.1	85	34.9	435	514	401	65	0.6	0.9	122	20.9	201	34.9	1056	58.5	50	24.8	63.5	42.1
Bivalvia	0	-	1.3	0	1.7	0	22.4	11.9	3.4	0	3.2	1.5	3.8	5.4	0	-	0	-	0.4	0.6	13.9	2.4	0	-
Amphipoda	1.3	0.6	0	-	3.6	3.3	1.5	2.1	1.3	1.2	1.3	0.6	0	-	0.2	0.3	1.3	1.8	3.6	3.9	8.9	4.8	2.7	0.9
Polychaeta	0.2	0.3	0	-	0.2	0.3	0.6	0.9	0.2	0.3	0	-	0	-	0.6	0.3	0.2	0.3	8.4	11.9	0.4	0.6	0	-
Oligochaeta	0	-	0	-	0	-	0	-	0	-	0	-	0	-	1.3	0.6	0	-	0.6	0.3	0.2	0.3	0	-
Rotifera	0	-	0	-	0	-	0	-	0	-	0	-	0.2	0.3	0.2	0.3	0	-	0	-	3	1.2	0.6	0.9
Halacaroidea	0	-	0.2	0.3	1.1	1.5	0	-	0.2	0.3	0.4	0.6	0.4	0.6	0.2	0.3	0.2	0.3	0	-	0	-	0	-
Gastropoda	0	-	0	-	0	-	0	-	0.2	0.3	0.4	0.6	0.6	0.3	0	-	0	-	0	-	0.2	0.3	0	-
Tanaidacea	0	-	0	-	0	-	0	-	0	-	0	-	0.8	1.2	0	-	0	-	0	-	0	-	0	-
Kinorhyncha	0	-	0	-	0	-	0	-	0.4	0.6	0	-	0.2	0.3	0.2	0.3	0.6	0.9	0.4	0.6	0	-	0.4	0.6
Priapulida	0	-	0	-	0	-	0.6	0.9	0	-	0	-	0	-	0	-	0.2	0.3	12.2	0.6	0	-	0.8	1.2
TOTAL	87.1	48.6	34.4	5.7	80.2	40.6	2622	90.1	717	680	1924	955	1021	443	4340	1242	903	5.4	2465	124	1432	674	2556	365

SD, standard deviation, - , not applicable

Diversity

Hill's diversity indices calculated at the nematode species level decreased initially after the impact (Fig. 4.2). In general the lowest values occurred 30 days after the scouring and recovery to initial levels occurred on day 50. Among Hill's indices the average species number (N_0) showed a slightly different trend from N_1, N_2 and N_∞ which showed remarkably similar patterns. All indices were initially similar to the control site of the initial day (C0). N_1, N_2 and N_∞ all showed, after the decline to minimum values on D30, a sharp rise to high maximum levels on D50, which then gradually declined again to low levels on D110. This second set of low values was followed by a plateau of moderate to high values until the end of the study.

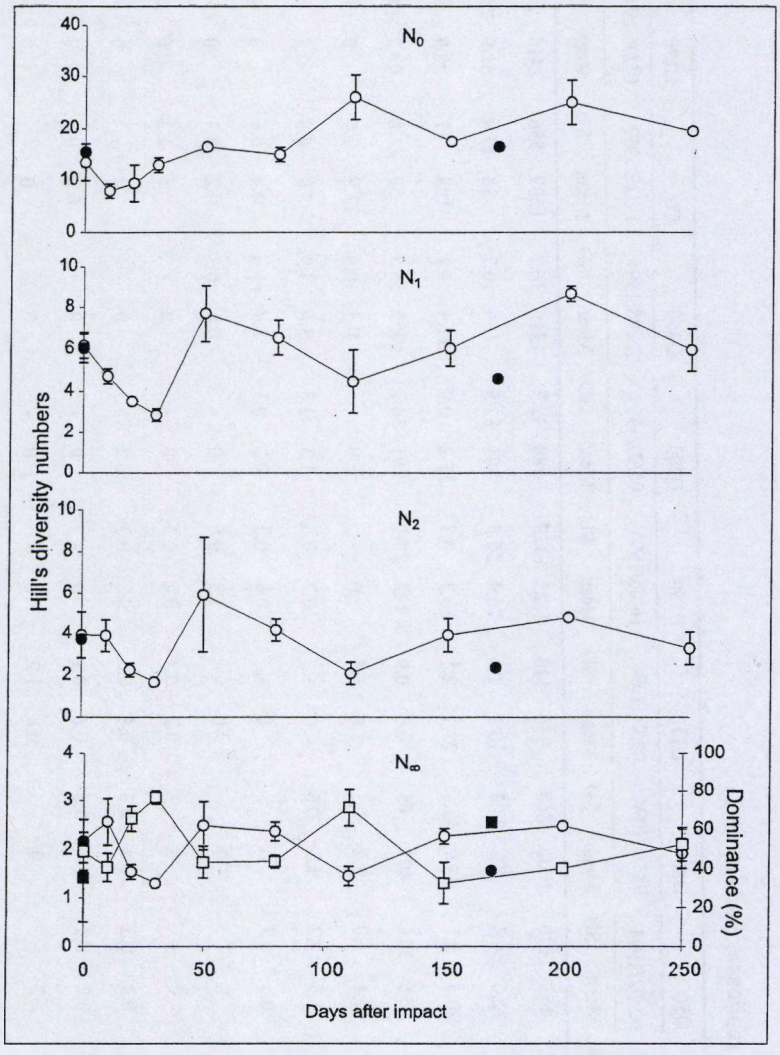

Fig. 4.2 Dynamics of Hill's diversity numbers of nematode communities (error bar, standard deviation; hollow circle, diversity on corresponding days at the scoured site; solid circle, diversity on corresponding days at the control sites; hollow square, dominance of Microlaimus. sp. 1 on corresponding days at the scoured site; solid square, dominance of M. sp. 1 on corresponding days at the control site). The dominance (%) of M. sp. 1 is plotted together with N∞ for comparison. High dominance of M. sp.1 was responsible for the low diversity of day 30 and day 110.

The complex *k*-dominance curves from all samples (Fig. 4.3A) made it difficult to discriminate any particular day from the others. Since more dramatic changes were expected

in earlier days, all curves after D50 were eliminated (Fig. 4.3B), and the result showed better resolution. There were two clearly different tendencies. The *k*-dominance curves of earlier days moved upwards from D0 to D30 (highest position). On D50 the original position of D0 was restored. The curve for C0 was closer to the curves for D0 and D50 than to the curves for other earlier days but somewhat higher.

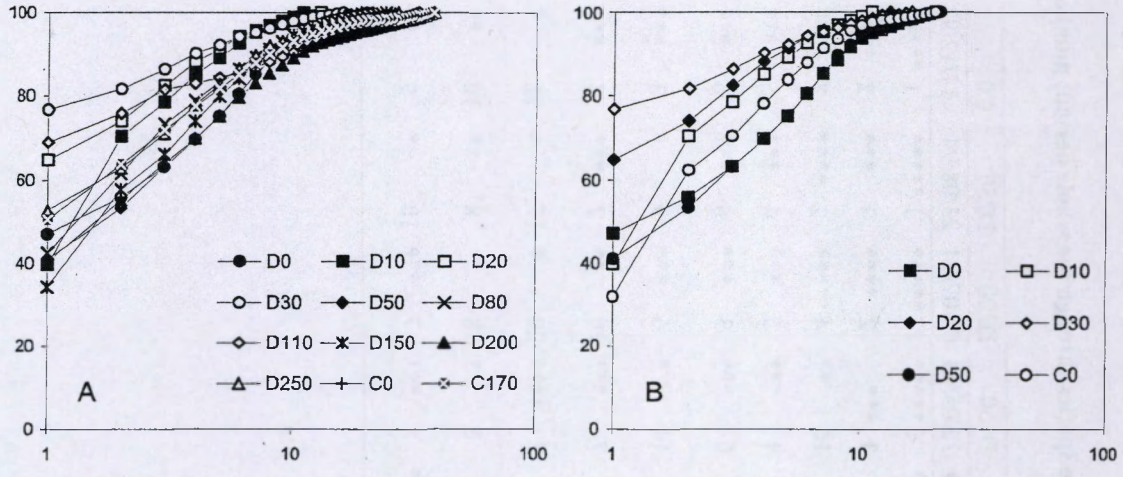

Fig. 4.3 *k*-dominance curves for nematode species from the mean of replicates at each sample day (A) and from the data for early days and the corresponding control day (C0) (B).

Taxonomic composition

In total 65 nematode species of 49 genera in 19 families were found. Only 14 species made up the majority of the community (more than 93% on average, with each species occurring in at least half the samples). Dominance and abundance rankings were calculated for the 10 most abundant species (Table 4.2). *Microlaimus* sp.1 was the most dominant through the whole period. *Sabatieria* sp. was the second most dominant species followed by *Daptonema* sp.1, *Pomponema* sp. and *Odontophora* sp.1. This rank was fairly consistent through the whole study period including controls. In total 4 orders were present. The largest order, in species number, was Monhysterida comprising 33 species followed by Chromadorida with 27 species. Only 3 species of Enoplida were found and 2 species of Tylenchida were also present. In terms of individual abundance, however, Chromadorida accounted for the majority (72.4%) while Monhysterida were represented by 27.3%. Enoplida (0.3%) and Tylenchida (0.1%) were negligible.

Table 4.2 Dominance rank and relative dominance of the most abundant 10 nematode species through the whole period; numbers on the left side of the vertical bars indicate the dominance rank and asterisks indicate relative dominance

Sample	D0	D10	D20	D30	D50	D80	D110	D150	D200	D250	C0	C170	Total
Date	17/12/93	28/12/93	06/01/94	17/01/94	05/02/94	08/03/94	09/04/94	16/05/94	05/07/94	23/08/94	17/12/93	05/06/94	
Microlaimus sp.1	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****	1 *****
Sabatieria sp.	3 ***	2 *****	4 ***	3 ***	2 ****	3 ****	3 ***	3 ***	2 ****	3 ***	2 ****	3 ***	2 ****
Daptonema sp.1	2 ***	5 ***	3 ***	2 ***	3 ****	2 ****	14 *	10 **	4 ***	2 ****	7 **	6 ***	3 ***
Pomponema sp.	4 ***	4 ***	2 ***	4 ***	4 ***	4 ***	6 **	4 ***	5 ***	4 ***	5 ***	2 ***	4 ***
Odontophora sp.1	9 **	6 **	7 **	6 **	5 ***	5 ***	2 ***	6 ***	3 ***	6 ***	6 ***	8 **	5 ***
Neochromadora sp.	5 ***	8 **	5 ***	13 *	7 ***	6 **	7 **	14 *	6 ***	9 *	3 ***	5 ***	6 ***
Eleutherolaimus sp.	6 ***	9 **	10 *	8 **	8 ***	10 **	11 *	7 ***	10 **	7 ***	4 ***	7 **	7 **
Microlaimus sp. 2	- -	- -	- -	--	- -	- -	21 *	2 ****	20 *	17 *	12 *	17 *	8 **
Prochromadorella sp.	11 **	- -	6 ***	10 *	6 ***	9 **	5 **	8 **	8 **	8 **	10 **	4 ***	9 **
Odontophora sp. 2	- -	3 ***	8 *	9 *	10 **	7 **	10 *	5 ***	7 ***	10 *	9 **	13 *	10 **

*: <1%, **: 1-3%, ***: 3-10%, ****: 10-30%, *****: >30%.
-: absent, hence not applicable.

Table 4.3 Integrated table showing the composition of the nematode community as life history stage (%), fecundity, nematode feeding type (%) and maturity index (MI)

Samples	D0		D10		D20		D30		D50		D80		D110		D250		D200		D250		C0		C170	
Date	17/12/1993		28/12/1993		06/01/1994		17/01/1994		05/02/1994		08/03/1994		09/04/1994		16/05/1994		05/07/1994		23/08/1994		17/12/1993		05/06/1994	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Generation																								
Juvenile	49.1	7.9	50	11.4	38	11	28.7	3.9	49.6	4.4	53.4	5.2	52.2	5.8	52.8	9.9	67.3	1.4	45	1.8	49.3	3.6	54.9	3.3
Female -	17.9	5.4	18.3	6.1	15.5	0.4	22.2	0.8	18.4	3.8	15.3	2.1	18	2.7	15.2	0.3	8.2	1.5	13.5	3.4	13.9	4.5	16.1	2.4
Female +	12.4	0.9	13.5	0.8	19.1	6.5	11.3	2.3	7.4	2.6	9	5.3	1.7	0.4	7.9	5.4	3.1	0.7	11.4	1.5	9.8	0.3	3.8	1.8
Male	20.6	1.6	18.3	6.1	27.4	17.1	37.8	5.4	24.6	1.9	22.3	2.1	28.1	3.5	24.2	4.8	21.4	0.6	30.1	6.7	27	1.3	25.1	0.9
Fecundity	41.5	5.6	43.2	9.6	54.3	9.2	33.5	5.4	28.2	3	35.3	11	9	3	32.4	16.2	27.5	8.2	45.9	2.9	42.3	7.4	18.7	5
Feeding type																								
1A	3.5	5	0	-	2.2	0.7	0	-	0.3	0.4	0	-	1.5	0	0	-	0.4	0.6	0.8	0.3	0	-	0.8	0.4
1B	30.2	1.9	45.6	3.9	18.3	2	14.6	1.9	36.9	0.9	43.3	0.6	21.8	7.2	29.7	14.5	23.4	5.6	36.3	6.6	44.2	36.3	22.6	11.5
2A	60.2	3.3	49.7	1.9	69.9	5.4	80.5	1.6	55.6	0.7	51.7	1	75.7	6.6	62.2	20.2	70.1	9	57.1	8	48.5	37.3	70.6	11
2B	6.1	3.6	4.7	2	9.6	8	4.9	0.3	7.3	0.2	5	0.4	1	0.7	8.1	5.8	6.1	2.8	5.8	1	7.4	1	6	0.9
MI	2.12	0.04	2.18	0.01	2.2	0.15	2.1	0.01	2.18	0.05	2.12	0.03	2.02	0.01	2.19	0.16	2.12	0.1	2.09	0.09	2.15	0.03	2.17	0

Female-: non-gravid female; Female+: gravid female.
Fecundity: relative proportion (%) of gravid females to total females.
SD: standard deviation (n=2).
-: not applicable.

Age and sex composition

Juveniles dominated the age structure of the nematode community throughout the whole period (average 49.5%, Table 4.3). The relative proportion of juveniles dipped to minimum values on D20 and D30 (36.8% and 28.7%, respectively). The highest proportion (67.4%) of juveniles was observed on D200. On all other days the values were between 45% and 55.7%. The fluctuation of non-gravid female numbers was less than of other groups. They ranged from 8.8% to 25.9% and averaged 15.9% of the population. Gravid females were a smaller group (average 8.9%). Their proportion was high at first and became extremely low on D110, D200 and C170. A high proportion (37.7%) of males was observed on D30. On other days, however, the values varied between 20% to 30%, except on D10 (17.2%). The fecundity expressed as the proportion of gravid females over total females was relatively higher (>40%) on earlier days (D0-D20).

Trophic composition

The epistratum feeders (2A) dominated the nematode community at this site, accounting for 48.5% to 80.5% of the nematodes (Table 4.3). Together with the non-selective deposit feeders (1B) the two groups comprised more than 90% of the community in most samples. The maximum percentage of these two groups was on D110 showing 97.4%. The smallest feeding group was the selective deposit feeders (1A) which was not detected in some samples. The maximum representation of this group was on D0 when it was 3.5%. The proportion of the selective deposit feeders (1A) and the predators/ omnivores (2B) fluctuated without a clear pattern during the period of investigation. The non-selective deposit feeders (1B) decreased conspicuously in early days after scouring, especially on D20 and D30. In contrast the epistratum feeders (2A) increased in those days. However, the maximum proportion of 1B was found on D10 while the minimum proportion of the 2A feeding group was found at the same day.

Maturity index (MI)

The mean MI (Table 4.3) of the nematode communities through the study period was 2.14 (total range=2.02-2.20). Unexpectedly there was no significant change in MI between sampling periods.

The result of TWINSPAN (Fig. 4.4) suggested that the nematode populations in samples taken on D0, D10, D20 and D50 were different from the rest. The separation of these days was based on the disappearance of *Monhystera* sp. 2. The other samples were split into four different groups: in the second division D110 and D200 were grouped together due to the presence of *Desmolaimus* sp.; in the third division D150 was separated due to the presence of *Daptonema* sp. 3; in the fourth and final division D80 and C0 were differentiated, based on the presence of *Perepsilonema* sp., from D30, D250 and C170. The D30 was a borderline negative in the fourth division.

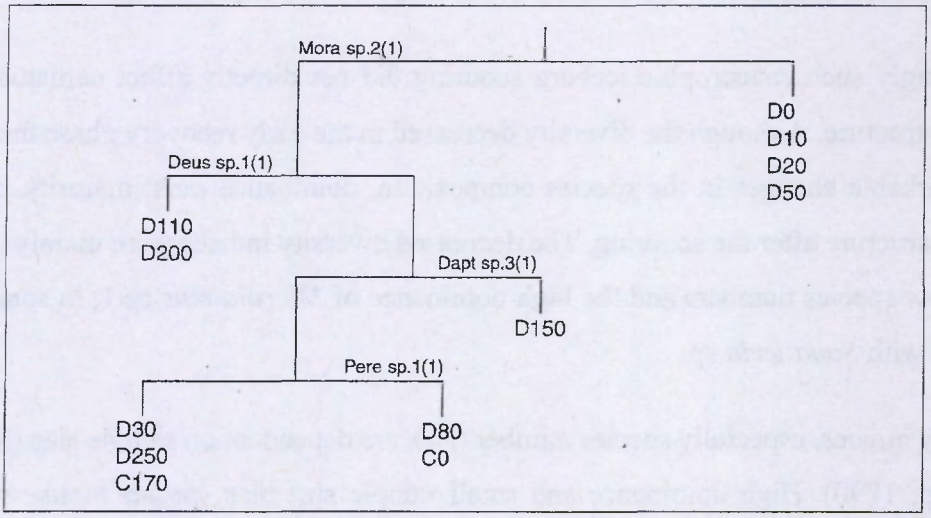

Fig. 4.4 TWINSPAN dendrogram based on 4th root transformed nematode mean abundance data (Mora, *Monhystera*; Deus, *Desmolaimus*; Dapt, *Daptonema*; Pere, *Perepsilonema*).

4.5. Discussion

4.5.1. Initial reduction

Disturbance generally results in a reduction in meiofaunal densities (Danovaro *et al.*, 1995; Giere, 1979; Green *et al.*, 1974; Lambshead, 1986; Schratzberger and Warwick, 1999; Wormald, 1976), although there are some exceptions (Boucher, 1980). The iceberg scouring in the present study produced a dramatic decrease of meiofaunal abundance. The abrupt decrease of meiofaunal abundance in the initial days after scouring compared to the control site emphasises the severity of the effect of iceberg scouring.

Surprisingly such catastrophic iceberg scouring did not directly affect nematode community structure. Although the diversity decreased in the early recovery phase there were no remarkable changes in the species composition, dominance rank, maturity index or trophic structure after the scouring. The decreased diversity indices were mainly because of the low species numbers and the high dominance of *Microlaimus* sp.1, in some cases together with *Sabatieria* sp.

Diversity indices, especially species number (N_0), are dependent on sample size (Soetaert and Heip, 1990). High dominance and small sample size bias species numbers by reducing the chance of encountering rare species. For this reason in early days, when the total nematode density in the sample was less than 200 and dominated by one or two species, species numbers were probably underestimated.

The results of the TWINSPAN analysis discriminated the early days from the later ones because of the absence of *Monhystera* sp.2. However, this analysis failed to group D30 with earlier days when the nematode abundance was high, because *Monhystera* sp. 2 appeared on this day. In fact *Monhystera* sp. 2 was a rare species throughout the whole study period. The presence or absence of this nematode was probably related to the nematode abundance in samples rather than to the scouring effect.

4.5.2. Recovery

Densities

In order to investigate the recovery of nematode communities after scouring it is necessary to have an idea of natural temporal variations for comparisons. A study of Vanhove *et al.* (2000) provides data on temporal variations in a subtidal nematode community for two winter seasons and the summer in between (from April 1991 till November 1992) at a station adjacent to our study site at Signy Island. This study shows that the temporal fluctuation of nematode density in this area seems to be closely related with food availability in the water column and the annual pattern can differ greatly from year to year. Meiofauna appear to bloom during summer and just after the time of pack ice formation. The exceptionally low densities of nematodes in earlier days after iceberg scouring in our study were outside the range of the seasonal fluctuations, even considering the highly patchy distribution of nematodes.

The recovery potential of meiofauna is known to be high. In most cases of disturbance at temperate sites meiofauna recover in a few weeks (Alongi *et al.*, 1983; Brylinsky and Gibson, 1994; Danovaro *et al.*, 1995) or in days or even hours in some cases (Sherman and Coull, 1980; Sun and Fleeger, 1994). The recovery of the major meiofauna groups occurred in 30 days after the impact, although there was an abrupt decrease of their abundance on day 50. (Peck *et al.*, 1999), who studied macrofaunal recovery from the same scoured site, attributed the high abundance occurring on D30 to a storm on the 23rd day after the scouring. A storm event influences the recovery of meiofaunal communities by redistributing organisms, but also indirectly by improving sediment condition.

It would be expected that the abundance of deeper living nematodes such as *Sabatieria* sp. would remain low after the storm. The comparison of the actual density of *Sabatieria* sp. between D20 and D30 (2 and 110 ind./10 cm^2, respectively) revealed an increase of >×50 during 10 days. The increase of total nematode abundance on D30 therefore cannot be explained solely by the storm. Most nematodes observed in this area are primary colonisers, and the rapid reproduction of nematodes in the community must have contributed to the high abundance on D30. The decrease of the nematode abundance on D50, however, is not easily explained. Possible causes include a patchy distribution, depletion of food resources caused by the overpopulation on D30 or sampling error.

Nematode community structure

Species dominance rank stayed fairly stable, showing no evidence of succession during the whole study period. *Microlaimus* sp.1 was the most dominant all the time. *Sabatieria,* sp., the 2nd most dominant species in overall abundance, kept 2nd and 3rd rank except on D20 when it became the 4th important species. *Daptonema* sp.1, the 3rd most dominant species in overall abundance, was more important in earlier than in later days probably because of a response to seasonal food item changes (Vanhove *et al.* 1998). The increase in the number of gravid females in the early days shows that reproduction was stimulated by the low community density after the scouring.

The trophic composition of the nematode population in this study was similar to that found by Vanhove *et al.* (2000). The dominance of the 2A group in our study reflects the very high numbers of *Microlaimus* sp.1. Nematodes belonging to feeding type 1A are probably not successful in a frequently disturbed habitat. The frequent sediment agitation may limit microbial growth, and thereby limit the population of feeding group 1A.

The Maturity Index, MI, of Bongers (1990) is basically an extension of *r*- and *K*-selection theory. (Neilson *et al.*, 1996) found this maturity index to be robust in marine ecological contexts, although it is not yet as popular in marine as in terrestrial nematode studies. For this reason, the direct comparison of MI for environmental stress assessment between different marine habitats or ecosystems must be interpreted with caution.

There are yet no MI data from polar marine systems available to compare with our MI values; it is therefore necessary to compare with studies from other seas. The MI in the present study was comparable with that in an intertidal station near to a sewage outfall in the Tay Estuary, Scotland (Neilson *et al.* 1996) and also with the polluted Ems estuary (Essink and Romeyn, 1994). However, the MI values of the nearest stations from the pollutant source were lower in both studies than the average MI in our study. These comparisons indicate that the MI in the present study is higher than in seriously polluted areas, but lower than in normal marine habitats around Europe. The relatively low and constant values during our study periods further imply that the MI *per se* is not directly affected by iceberg scouring on the short term.

The colonisation capacity of nematodes is defined by their life style rather than their mobility. Colonisers (*r*-strategists) must have more advantage than persisters

(*K*-strategists) in such circumstances. This may imply that natural selection pressure has acted during the long history of Antarctic glaciation in this area and lead to the relatively low but constant MI in our study area. Iceberg scouring in a deeper coastal shelf in the Weddell Sea also resulted in a low MI and a low proportion of the 1A feeding group causing resemblance of the community properties with that of this study (Lee *et al.*, 2001a). Nematode community in the shallow coast at Signy Island seemed to be forced towards 1B and 2A feeding types and *r*-strategists. The regularly disturbed sediments may contain very little old detritus and dissolved organic matter, which microbes can easily utilise, compared with undisturbed stable sediment, and thus the new fresh detritus and benthic diatoms are more common food items in this area. This may explain the extremely low representation of the 1A group.

4.6. Acknowledgement

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Chapter 5

Iceberg scouring and the response of continental shelf community: Case study in the east Weddell Sea

Result published:

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5.1. Abstract

The impact of iceberg scouring on meiofauna communities, especially nematodes, was studied on the Kapp Norvegia shelf in the Weddell Sea, Antarctica. Three stations with different stage of recolonisation following scour were selected on the basis of seafloor video images, sediment characteristics and faunal occurrences. These stations comprised a fresh scour, an older scour and an undisturbed control site where a sponge spicule mat covered sediment with dense epifauna. Meiofaunal abundance and taxonomic diversity were significantly reduced in the fresh scour. The highest abundance and diversity were found in the older scour as compared with the undisturbed site. The abundance and the diversity of nematodes also decreased due to scouring. The abundance in the older scour recovered to the level of the undisturbed site whereas the diversity remained low. Scouring also changed the nematode community composition, with the suborders Desmoscolecina and Leptolaimina being the most sensitive groups. In addition scouring resulted in the decrease of selective deposit feeders and the Maturity Index (MI). The low diversity and the change in nematode generic composition in the older scour compared with the undisturbed site, despite the complete recovery in terms of abundance, suggest that the deep continental shelf nematode community in this area is sensitive to iceberg disturbance.

5.2. Introduction

Iceberg scouring is a catastrophic event that physically disturbs benthic ecosystems in polar regions. Scouring affects wide areas in both polar systems, in depths down to about 70 m in the Arctic and 500 m in the Antarctic (Gutt *et al.* 1996). Iceberg scouring is thus an ecologically important structuring factor in polar benthic ecosystems (Arntz and Gallardo, 1994), and although its long history must have controlled the ecology and evolutionary adaptation of polar benthic organisms, few studies on this topic have been published (Conlan *et al.*, 1998; Dayton *et al.*, 1970; Dayton *et al.*, 1969; Gutt *et al.*, 1996; Lenihan and Oliver, 1995; Peck *et al.*, 1999; Peck and Bullough, 1993). Most of these studies focus on the shallow coastal communities.

There have been few ecological studies of Antarctic meiofauna (Dahms *et al.*, 1990; Fabiano and Danovaro, 1999; Herman and Dahms, 1992; Lee *et al.*, 2001b; Vanhove *et al.*, 1999; Vanhove *et al.*, 1998; Vanhove *et al.*, 1995). Although ice scour has been identified as an important structuring force in deep-water nematode distribution (Vanhove *et al.*, 1999), the present study is the first to consider the effect of iceberg scour on deep-water meiofauna.

5.3. Material and Methods

5.3.1. Sampling area and methods

The continental shelf off Kapp Norvegia in the eastern Weddell Sea is one of the areas where intensive biological studies have been conducted during the EPOS (European 'Polarstern' Study) and the first and second EASIZ (Ecology of Antarctic Sea Ice Zone) cruises. Our knowledge about the benthic fauna in this area is substantial, and this area is one of the places where iceberg-scouring activity is very high. Therefore, this area was selected for our study (Fig. 5.1).

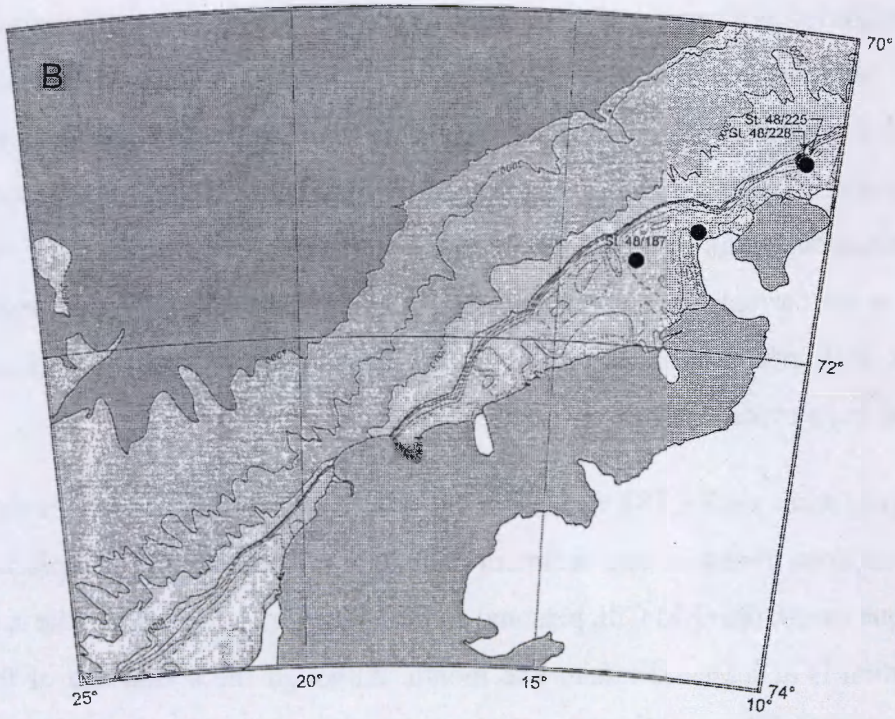

Fig. 5.1 Map showing the sampling sites (stations, solid circle) for this study during the EASIZ II (ANT XV/III). Station 225 was a fresh scour, station 187 was an older scour and station 228 was an undisturbed site.

During the second EASIZ cruise from 13th January to 26th March 1998, samples were taken by means of a multi-box corer (Gerdes, 1990) in order to study the impact of iceberg scouring on meiobenthic communities. Three contrasting stations were selected for this study: Station 225 (water depth, 278 m), station 187 (water depth, 255 m) and station 228 (water depth, 298 m). These stations were regarded as representing a very fresh scour, a relatively older scour and an undisturbed site, respectively. This discrimination was based on the combination of *in situ* observations of the bottom scenery produced by a video

camera attached to the multibox corer, the sediment textural conditions and the macro- and epifauna occurrence (Table 5.1).

Table 5.1Coordinates and description of the sampling stations in the Weddell Sea, Antarctica

Scour condition	Station No.	Depth (m)	Latitude	Longitude	Sediment Median size (μm)	Sediment condition	Epifauna on the sediment samples
Fresh	225	278 m	70°50.1S	10°35.2W	43.4	Very fluid	No
Older	187	255 m	71°32.3S	13°31.7W	32.4	Normal	One hydrozoa
Undisturbed	228	298 m	70°49.8S	10°38.0W	101.0	Sponge spicule mat	Diverse

The station 225, 187 and 228 correspond to K5, K4 and K7, respectively, of other chapters.

The video images at both stations 225 and 187 looked like fresh scours. However, station 225 was regarded as a very fresh scour based on the lack of epifauna and especially on the very fluid sediment condition. The ploughing and pumping activities of the iceberg must resuspend the sediment (Lien *et al.*, 1989), and this resuspended sediment will settle down, especially in the depression of the scour marks. This sediment will be more fluid, because it contains more interstitial water than under normal conditions. After some time, however, water currents will redistribute the fluid fine sediment and underlying compact sediments will remain in scour marks. The fluid sediment at station 225 can thus be considered as an evidence of a very fresh scour mark.

The sediment from station 187 was not as fluid as at station 225, and the presence of a sessile hydrozoan found in one sediment sample from this station, *Symplectoscyphus plectilis*, one month old (J-M Gili, personal communication), suggests that the scour mark at this station is at least older than one month. Although the actual age of this scour remains uncertain, it is considered that it may not be older than one year. The undisturbed reference station, station 228, showed a typical dense cover of epifauna on the seabed, in contrast to the barren surface at the scoured sites. The sediment samples from this station were also different from the sediments of the other stations, in that they were covered with a sponge spicule mat of about 1 cm thick.

Three standard meiofauna hand-cores (10 cm^2 surface area) for the meiofauna and a large hand-core (diameter about 6 cm) for sediment analyses were taken from one box-core of each station.

5.3.2. Sample treatment

The sediment cores were sliced into 5 layers (0-1, 1-3, 3-5, 5-10 cm and the rest) immediately after the samples were recovered on board. Only the three top layers down to 5cm, where the majority of meiofauna dwells, were used for this study. Meiofauna samples were preserved with 4 % neutral hot (60° C) formaldehyde solution on board before further studies in the home laboratory. Sediments were decanted and sieved over 1,000 and 32 µm mesh sizes. Animals passing the 1,000 µm sieve and retained on the 32 µm sieve were regarded as meiofauna. Final extraction of meiofauna was achieved using the LUDOX centrifugation flotation technique (Heip *et al.*, 1985; McIntyre and Warwick, 1984). The number of all metazoan meiofauna was counted after staining with Rose Bengal. Approximately 100 nematodes (all, in samples with less than 100 individuals) per replicate were randomly picked out and dehydrated in a series of glycerine-alcohol solutions. The dehydrated nematodes were mounted on slides with anhydrous glycerine medium and sealed with paraffin wax. Observations were carried out under a Wild M20 light microscope. Identification to genus level was based on morphological characters (Platt and Warwick, 1980). Developmental stages and sex of specimens were categorised into four different groups: juvenile, non-gravid female, gravid female and male. The feeding types were classified according to (Wieser, 1953) into four categories; selective deposit-feeders (1A), non-selective deposit-feeders (1B), epigrowth-feeders (2A) and omnivorous-carnivores (2B).

Sediment analysis was performed with a Coulter-Counter (the sponge spicule mats on the top of sediments from station 228 were removed prior to analysis).

5.3.3. Statistical analysis

Analysis of variance (ANOVA) was used to determine significant differences ($p<0.05$) for the following variables: diversity, feeding type, age guild, maturity index and dominance of nematode genera between stations. Subsequent post hoc comparison (Tukey HSD) was used on stations.

Nematode diversity on genus level was measured using the suite of diversity indices proposed by (Hill, 1973), where N_0 is the number of genera, N_1 is the exponential of the

Shannon's index, N_2 is the reciprocal of the Simpson's index and N_∞ is the reciprocal of the relative abundance of the most dominant genus. The maturity index (MI; (Bongers, 1990; Bongers *et al.*, 1991) is used to characterise the life style of nematode communities.

5.4. Results

5.4.1. Sediment composition

The sediments from the fresh scour and the undisturbed site consisted of silt (median grain size 43.4 μm and 32.4 μm, respectively), while that of the older scour was very fine sand (median grain size 101 μm) (Table 5.1). Although the grain size distributions of the fresh scour and the undisturbed site were similar to each other, there were clear differences in sediment condition. The sediment from the fresh scour was very fluid with more interstitial water than that of the older scour or the undisturbed site. The sediment from the undisturbed site differed from the other stations in having a surface sponge-spicule mat forming the top 1 cm of the sample.

5.4.2. Meiofauna

A total of 20 different meiofauna groups were recovered from the three stations (Table 5.2). There were significant differences in density between the fresh scour and the other stations (fresh scour, 120±15.4 ind./10 cm^2; older scour, 1,326±287.5 ind./10 cm^2; undisturbed site, 1,342±70.8 ind./10 cm^2). The number of meiofauna groups was also significantly low in the fresh scour (7 groups) compared with the older scour (16 groups) and the undisturbed site (13 groups).

Table 5.2 Mean density (ind./10 cm^2) of the meiofauna with standard deviation in the parenthesis (n=3)

Station	Fresh	Older	Undisturbed
Nematoda	72.7 (9.3)	1028.7 (217.5)	1234.3 (69.3)
Copepoda	21.0 (11.3)	89.7 (23.1)	30.7 (10.6)
Ostracoda	1.3 (1.5)	12.0 (10.1)	5.7 (4.7)
Nauplii	22.7 (8.0)	162.0 (25.2)	49.7 (17.1)
Priapulida	0	2.0 (1.0)	0
Kinorhyncha	0	0.7 (1.2)	4.3 (4.9)
Tardigrada	0	0.7 (0.6)	4.7 (0.6)
Turbellaria	0	2.7 (3.1)	0.3 (0.6)
Tanaidacea	0.3 (0.6)	0	0
Rotifera	1.3 (1.5)	0.7 (0.6)	3.0 (1.0)
Isopoda	0	0.3 (0.6)	0
Amphipoda	0	0.7 (1.2)	0
Polychaeta	0.7 (0.6)	22.0 (10.8)	5.3 (5.9)
Oligochaeta	0	1.0 (1.0)	0
Bivalvia	0	1.0 (1.0)	0
Sipuncula	0	0.3 (0.6)	0
Hydrozoa	0	0	1.0 (1.0)
Acarina	0	1.7 (2.9)	2.0 (1.0)
Aplacophora	0	0	0.3 (0.6)
Bryozoa	0	0	1.0 (1.0)
Total	120 (15.4)	1326.0 (287.5)	1342.3 (70.8)

Nematodes were the most dominant meiofaunal group at all stations, and their relative abundance increased from the fresh scour (60.6%) to the older scour (77.6%) and the undisturbed site (92.0%). Crustaceans (copepods, ostracods and nauplii) were the second most dominant group. These two groups made up more than 97% of communities at all stations.

5.4.3. Nematode communities

The abundance of nematodes was significantly lower (73±9.3 ind./10 cm^2) in the fresh scour compared with the older scour (1,029±217.5 ind./10 cm^2) and the undisturbed site (1,234±69.3 ind/10 cm^2), which were comparable (Table 5.2, Table 5.3).

Table 5.3 Mean density (ind./10 cm^2, n=3) of the important nematode genera (> 1% at any station)

Genus	Fresh	Older	Undisturbed
Monhystera	19.7	192.4	206.1
Neochromadora	17.0	181.9	13.2
Daptonema	9.0	119.4	52.6
Sabatieria	1.3	90.4	85.4
Leptolaimus	-	25.1	121.6
Acantholaimus	0.3	45.7	88.0
Halalaimus	3.0	67.5	42.4
Tricoma	-	7.6	78.4
Desmoscolex	-	39.9	145.8
Cervonema	4.3	35.0	1.9
Amphimonhystrella	2.5	3.3	33.1
Molgolaimus	-	9.4	24.9
Aegialoalaimus	1.0	14.6	15.9
Prochromadorella	0.5	19.3	6.4
Sphaerolaimus	4.0	7.0	11.7
Odontanticoma	-	18.5	1.8
Anticoma	0.3	17.0	2.5
Actinonema	-	7.3	12.6
Diplolaimella	-	18.5	-
Tylenchidae genus	1.3	6.1	10.9
Spilophorella	-	11.2	6.7
Camacolaimus	-	5.6	12.0
Microlaimus	-	0.3	15.0
Oxystomina	1.0	2.3	3.0
Pseudosteineria	1.3	3.3	-
Chromadoridae genus	1.5	-	1.9
Prismatolaimus	2.0	0.3	-
Other (No. of other genera)	2.7 (11)	78.8 (39)	240.4 (67)
Total	72.7	1028.7	1234.3

Chapter 5

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5.2. Introduction

Iceberg scouring is a catastrophic event that physically disturbs benthic ecosystems in polar regions. Scouring affects wide areas in both polar systems, in depths down to about 70 m in the Arctic and 500 m in the Antarctic (Gutt *et al.* 1996). Iceberg scouring is thus an ecologically important structuring factor in polar benthic ecosystems (Arntz and Gallardo, 1994), and although its long history must have controlled the ecology and evolutionary adaptation of polar benthic organisms, few studies on this topic have been published (Conlan *et al.*, 1998; Dayton *et al.*, 1970; Dayton *et al.*, 1969; Gutt *et al.*, 1996; Lenihan and Oliver, 1995; Peck *et al.*, 1999; Peck and Bullough, 1993). Most of these studies focus on the shallow coastal communities.

There have been few ecological studies of Antarctic meiofauna (Dahms *et al.*, 1990; Fabiano and Danovaro, 1999; Herman and Dahms, 1992; Lee *et al.*, 2001b; Vanhove *et al.*, 1999; Vanhove *et al.*, 1998; Vanhove *et al.*, 1995). Although ice scour has been identified as an important structuring force in deep-water nematode distribution (Vanhove *et al.*, 1999), the present study is the first to consider the effect of iceberg scour on deep-water meiofauna.

Chapter 5

Iceberg scouring and the response of continental shelf community: Case study in the east Weddell Sea

Result published:
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5.1. Abstract

The impact of iceberg scouring on meiofauna communities, especially nematodes, was studied on the Kapp Norvegia shelf in the Weddell Sea, Antarctica. Three stations with different stage of recolonisation following scour were selected on the basis of seafloor video images, sediment characteristics and faunal occurrences. These stations comprised a fresh scour, an older scour and an undisturbed control site where a sponge spicule mat covered sediment with dense epifauna. Meiofaunal abundance and taxonomic diversity were significantly reduced in the fresh scour. The highest abundance and diversity were found in the older scour as compared with the undisturbed site. The abundance and the diversity of nematodes also decreased due to scouring. The abundance in the older scour recovered to the level of the undisturbed site whereas the diversity remained low. Scouring also changed the nematode community composition, with the suborders Desmoscolecina and Leptolaimina being the most sensitive groups. In addition scouring resulted in the decrease of selective deposit feeders and the Maturity Index (MI). The low diversity and the change in nematode generic composition in the older scour compared with the undisturbed site, despite the complete recovery in terms of abundance, suggest that the deep continental shelf nematode community in this area is sensitive to iceberg disturbance.

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5.3. Material and Methods

5.3.1. Sampling area and methods

The continental shelf off Kapp Norvegia in the eastern Weddell Sea is one of the areas where intensive biological studies have been conducted during the EPOS (European 'Polarstern' Study) and the first and second EASIZ (Ecology of Antarctic Sea Ice Zone) cruises. Our knowledge about the benthic fauna in this area is substantial, and this area is one of the places where iceberg-scouring activity is very high. Therefore, this area was selected for our study (Fig. 5.1).

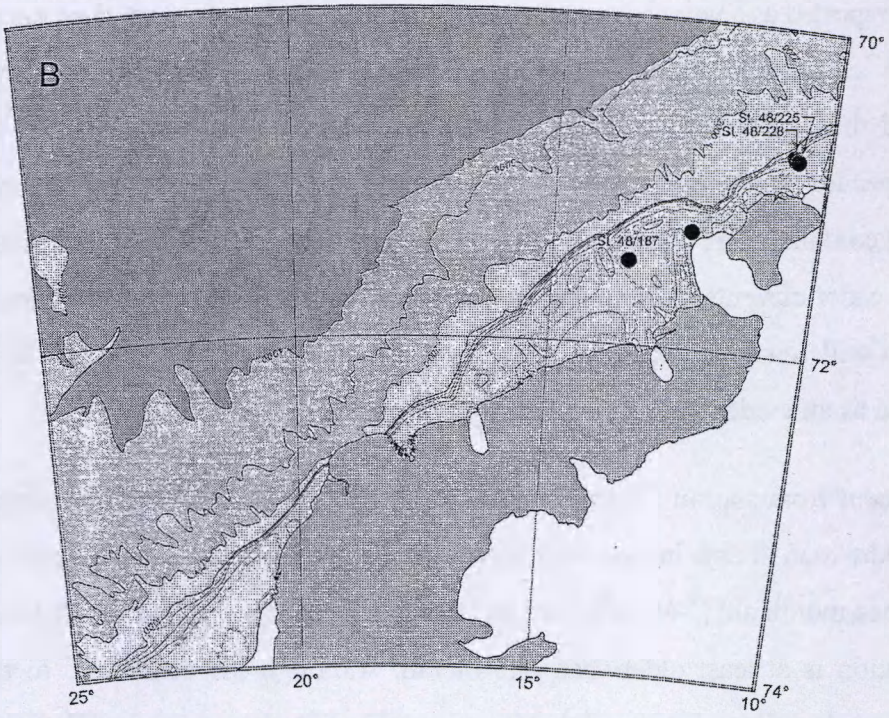

Fig. 5.1 Map showing the sampling sites (stations, solid circle) for this study during the EASIZ II (ANT XV/III). Station 225 was a fresh scour, station 187 was an older scour and station 228 was an undisturbed site.

During the second EASIZ cruise from 13th January to 26th March 1998, samples were taken by means of a multi-box corer (Gerdes, 1990) in order to study the impact of iceberg scouring on meiobenthic communities. Three contrasting stations were selected for this study: Station 225 (water depth, 278 m), station 187 (water depth, 255 m) and station 228 (water depth, 298 m). These stations were regarded as representing a very fresh scour, a relatively older scour and an undisturbed site, respectively. This discrimination was based on the combination of *in situ* observations of the bottom scenery produced by a video

camera attached to the multibox corer, the sediment textural conditions and the macro- and epifauna occurrence (Table 5.1).

Table 5.1Coordinates and description of the sampling stations in the Weddell Sea, Antarctica

Scour condition	Station No.	Depth (m)	Latitude	Longitude	Sediment Median size (μm)	Sediment condition	Epifauna on the sediment samples
Fresh	225	278 m	70°50.1S	10°35.2W	43.4	Very fluid	No
Older	187	255 m	71°32.3S	13°31.7W	32.4	Normal	One hydrozoa
Undisturbed	228	298 m	70°49.8S	10°38.0W	101.0	Sponge spicule mat	Diverse

The station 225, 187 and 228 correspond to K5, K4 and K7, respectively, of other chapters.

The video images at both stations 225 and 187 looked like fresh scours. However, station 225 was regarded as a very fresh scour based on the lack of epifauna and especially on the very fluid sediment condition. The ploughing and pumping activities of the iceberg must resuspend the sediment (Lien *et al.*, 1989), and this resuspended sediment will settle down, especially in the depression of the scour marks. This sediment will be more fluid, because it contains more interstitial water than under normal conditions. After some time, however, water currents will redistribute the fluid fine sediment and underlying compact sediments will remain in scour marks. The fluid sediment at station 225 can thus be considered as an evidence of a very fresh scour mark.

The sediment from station 187 was not as fluid as at station 225, and the presence of a sessile hydrozoan found in one sediment sample from this station, *Symplectoscyphus plectilis*, one month old (J-M Gili, personal communication), suggests that the scour mark at this station is at least older than one month. Although the actual age of this scour remains uncertain, it is considered that it may not be older than one year. The undisturbed reference station, station 228, showed a typical dense cover of epifauna on the seabed, in contrast to the barren surface at the scoured sites. The sediment samples from this station were also different from the sediments of the other stations, in that they were covered with a sponge spicule mat of about 1 cm thick.

Three standard meiofauna hand-cores (10 cm^2 surface area) for the meiofauna and a large hand-core (diameter about 6 cm) for sediment analyses were taken from one box-core of each station.

5.3.2. Sample treatment

The sediment cores were sliced into 5 layers (0-1, 1-3, 3-5, 5-10 cm and the rest) immediately after the samples were recovered on board. Only the three top layers down to 5cm, where the majority of meiofauna dwells, were used for this study. Meiofauna samples were preserved with 4 % neutral hot (60° C) formaldehyde solution on board before further studies in the home laboratory. Sediments were decanted and sieved over 1,000 and 32 μm mesh sizes. Animals passing the 1,000 μm sieve and retained on the 32 μm sieve were regarded as meiofauna. Final extraction of meiofauna was achieved using the LUDOX centrifugation flotation technique (Heip *et al.*, 1985; McIntyre and Warwick, 1984). The number of all metazoan meiofauna was counted after staining with Rose Bengal. Approximately 100 nematodes (all, in samples with less than 100 individuals) per replicate were randomly picked out and dehydrated in a series of glycerine-alcohol solutions. The dehydrated nematodes were mounted on slides with anhydrous glycerine medium and sealed with paraffin wax. Observations were carried out under a Wild M20 light microscope. Identification to genus level was based on morphological characters (Platt and Warwick, 1980). Developmental stages and sex of specimens were categorised into four different groups: juvenile, non-gravid female, gravid female and male. The feeding types were classified according to (Wieser, 1953) into four categories; selective deposit-feeders (1A), non-selective deposit-feeders (1B), epigrowth-feeders (2A) and omnivorous-carnivores (2B).

Sediment analysis was performed with a Coulter-Counter (the sponge spicule mats on the top of sediments from station 228 were removed prior to analysis).

5.3.3. Statistical analysis

Analysis of variance (ANOVA) was used to determine significant differences ($p<0.05$) for the following variables: diversity, feeding type, age guild, maturity index and dominance of nematode genera between stations. Subsequent post hoc comparison (Tukey HSD) was used on stations.

Nematode diversity on genus level was measured using the suite of diversity indices proposed by (Hill, 1973), where N_0 is the number of genera, N_1 is the exponential of the

Shannon's index, N_2 is the reciprocal of the Simpson's index and N_∞ is the reciprocal of the relative abundance of the most dominant genus. The maturity index (MI; (Bongers, 1990; Bongers *et al.*, 1991) is used to characterise the life style of nematode communities.

5.4. Results

5.4.1. Sediment composition

The sediments from the fresh scour and the undisturbed site consisted of silt (median grain size 43.4 μm and 32.4 μm, respectively), while that of the older scour was very fine sand (median grain size 101 μm) (Table 5.1). Although the grain size distributions of the fresh scour and the undisturbed site were similar to each other, there were clear differences in sediment condition. The sediment from the fresh scour was very fluid with more interstitial water than that of the older scour or the undisturbed site. The sediment from the undisturbed site differed from the other stations in having a surface sponge-spicule mat forming the top 1 cm of the sample.

5.4.2. Meiofauna

A total of 20 different meiofauna groups were recovered from the three stations (Table 5.2). There were significant differences in density between the fresh scour and the other stations (fresh scour, 120±15.4 ind./10 cm^2; older scour, 1,326±287.5 ind./10 cm^2; undisturbed site, 1,342±70.8 ind./10 cm^2). The number of meiofauna groups was also significantly low in the fresh scour (7 groups) compared with the older scour (16 groups) and the undisturbed site (13 groups).

Table 5.2 Mean density (ind./10 cm^2) of the meiofauna with standard deviation in the parenthesis (n=3)

Station	Fresh	Older	Undisturbed
Nematoda	72.7 (9.3)	1028.7 (217.5)	1234.3 (69.3)
Copepoda	21.0 (11.3)	89.7 (23.1)	30.7 (10.6)
Ostracoda	1.3 (1.5)	12.0 (10.1)	5.7 (4.7)
Nauplii	22.7 (8.0)	162.0 (25.2)	49.7 (17.1)
Priapulida	0	2.0 (1.0)	0
Kinorhyncha	0	0.7 (1.2)	4.3 (4.9)
Tardigrada	0	0.7 (0.6)	4.7 (0.6)
Turbellaria	0	2.7 (3.1)	0.3 (0.6)
Tanaidacea	0.3 (0.6)	0	0
Rotifera	1.3 (1.5)	0.7 (0.6)	3.0 (1.0)
Isopoda	0	0.3 (0.6)	0
Amphipoda	0	0.7 (1.2)	0
Polychaeta	0.7 (0.6)	22.0 (10.8)	5.3 (5.9)
Oligochaeta	0	1.0 (1.0)	0
Bivalvia	0	1.0 (1.0)	0
Sipuncula	0	0.3 (0.6)	0
Hydrozoa	0	0	1.0 (1.0)
Acarina	0	1.7 (2.9)	2.0 (1.0)
Aplacophora	0	0	0.3 (0.6)
Bryozoa	0	0	1.0 (1.0)
Total	120 (15.4)	1326.0 (287.5)	1342.3 (70.8)

Nematodes were the most dominant meiofaunal group at all stations, and their relative abundance increased from the fresh scour (60.6%) to the older scour (77.6%) and the undisturbed site (92.0%). Crustaceans (copepods, ostracods and nauplii) were the second most dominant group. These two groups made up more than 97% of communities at all stations.

5.4.3. Nematode communities

The abundance of nematodes was significantly lower (73±9.3 ind./10 cm^2) in the fresh scour compared with the older scour (1,029±217.5 ind./10 cm^2) and the undisturbed site (1,234±69.3 ind/10 cm^2), which were comparable (Table 5.2, Table 5.3).

Table 5.3 Mean density (ind./10 cm^2, n=3) of the important nematode genera (> 1% at any station)

Genus	Fresh	Older	Undisturbed
Monhystera	19.7	192.4	206.1
Neochromadora	17.0	181.9	13.2
Daptonema	9.0	119.4	52.6
Sabatieria	1.3	90.4	85.4
Leptolaimus	-	25.1	121.6
Acantholaimus	0.3	45.7	88.0
Halalaimus	3.0	67.5	42.4
Tricoma	-	7.6	78.4
Desmoscolex	-	39.9	145.8
Cervonema	4.3	35.0	1.9
Amphimonhystrella	2.5	3.3	33.1
Molgolaimus	-	9.4	24.9
Aegialoalaimus	1.0	14.6	15.9
Prochromadorella	0.5	19.3	6.4
Sphaerolaimus	4.0	7.0	11.7
Odontanticoma	-	18.5	1.8
Anticoma	0.3	17.0	2.5
Actinonema	-	7.3	12.6
Diplolaimella	-	18.5	-
Tylenchidae genus	1.3	6.1	10.9
Spilophorella	-	11.2	6.7
Camacolaimus	-	5.6	12.0
Microlaimus	-	0.3	15.0
Oxystomina	1.0	2.3	3.0
Pseudosteineria	1.3	3.3	-
Chromadoridae genus	1.5	-	1.9
Prismatolaimus	2.0	0.3	-
Other (No. of other genera)	2.7 (11)	78.8 (39)	240.4 (67)
Total	72.7	1028.7	1234.3

The average genus number expressed as N_0 of Hill's diversity numbers increased significantly with the stage of recolonisation (fresh scour, N_0=16.7±2.0; older scour, N_0=35.3±7.5; undisturbed site N_0=54.7±4.0) (Fig. 5.2). All other Hill's diversity numbers showed the same tendency, although the differences of other indices between the fresh scour and the older scour were not significant. In the case of N_∞, only the difference between the fresh scour and the undisturbed site was significant.

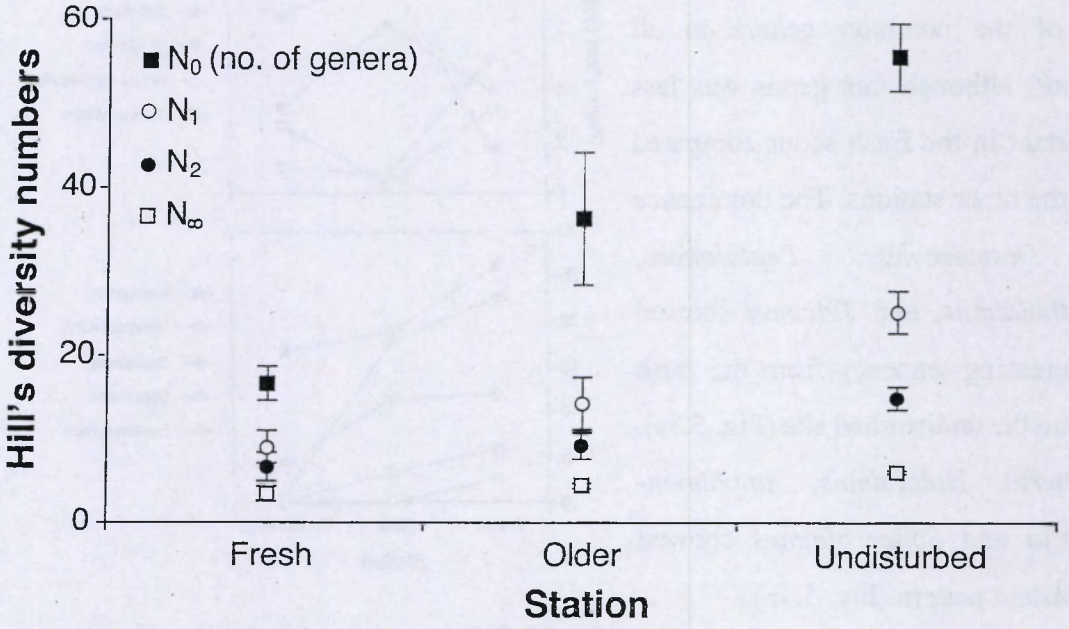

Fig. 5.2 Hill's diversity numbers of the nematode communities (error bar, standard deviation).

There were clear differences in genus composition between all three stations (Fig. 5.3, Table 5.3). The genus *Monhystera* was the most dominant in all stations, but the dominance of this genus decreased towards the undisturbed site (26.1% in the fresh scour, 18.8% in the older scour and 16.7% in the undisturbed site). Next to *Monhystera*, *Neochromadora* and *Daptonema* were the subdominant genera in the fresh and the older scour, but of less importance in the undisturbed site. *Desmoscolex* and *Leptolaimus* were the second and third dominant genera in the undisturbed site, although they were less important in the older scour and absent or very rare in the fresh scour. The most unexpected observation was the rarity of the suborders Desmoscolecina and Leptolaimina in the fresh scour. Leptolaimina were represented only by *Aegialoalaimus* (1.3%), *Prismatolaimus* (2.7%) and *Teratocephalus* (0.7%), and the suborder Desmoscolecina was even entirely absent from the samples.

The genus number and abundance of these suborders increased with the age of the scour (the older scour: 9.3%, 6 genera; the undisturbed site: 34.2%, 14 genera) despite the absence of *Prismatolaimus* and *Teratocephalus* in the undisturbed site. *Sabatieria* was one of the common genera in all stations, although this genus was less important in the fresh scour compared with the other stations. The dominance of *Desmoscolex*, *Leptolaimus*, *Acantholaimus*, and *Tricoma* showed an increasing tendency from the fresh scour to the undisturbed site (Fig. 5.3a). *Sabatieria*, *Halalaimus*, *Amphimonhystrella* and *Sphaerolaimus* showed no constant pattern (Fig. 5.3b).

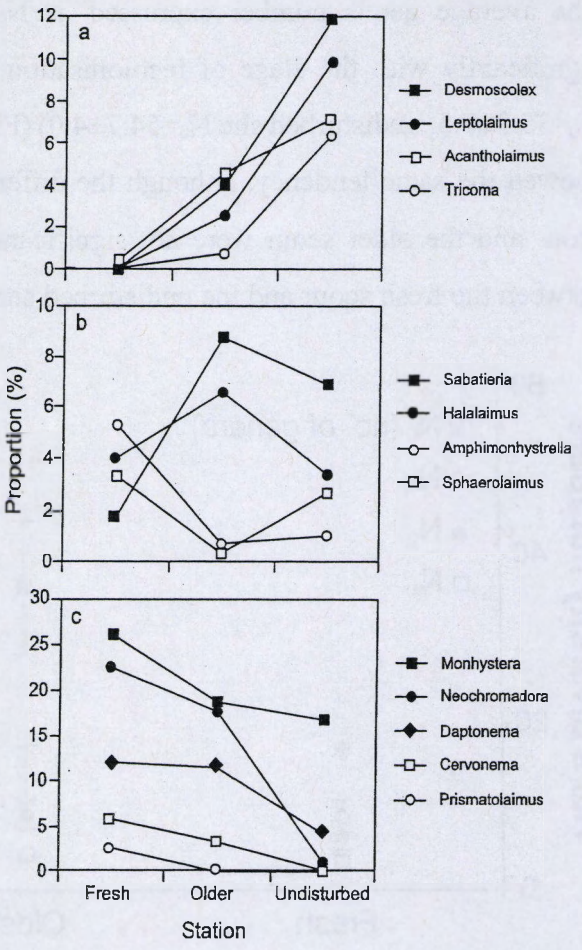

Fig. 5.3 Different tendencies of major nematode genera expressed as the relative proportion according to different degrees of freshness of scours. The nematodes proportionally decreased due to scouring were regarded as persisters (a) and those which increased after scouring were regarded as colonisers (c). The intermediate group (b) did not show a clear trend.

The proportion of *Monhystera*, *Neochromadora*, *Daptonema*, *Cervonema* and *Prismatolaimus* tend to increase at the more recently scoured site (Fig. 5.3c). A similar trend was found at a coarser taxonomic level (mostly family level), except for the family Comesomatidae. Table 5.4 shows the dominance rank of families with a density higher than 0.5%. The families Monhysteridae, Chromadoridae and Xyalidae were dominant in all stations. The families Comesomatidae and Oxystominidae were also common and subdominant in all three stations.

Juvenile stages were predominant in all stations (average: 64.0-69.3%) followed by males (average: 13.7-17.7%), but the differences between stations were not significant (Fig. 5.4). The non-gravid females, the third dominant group (average: 7.9-19.7%), were

significantly lower in the fresh scour compared with the undisturbed site, but differences between the fresh scour and older scour and between the older scour and the undisturbed site were not significant. The gravid females were least abundant (average: 1.3-6.0%) and their proportion was significantly lower in the undisturbed site compared with the other stations

Table 5.4 Relative importance, feeding type (FT) and c-p (coloniser-persister) value of the nematodes (Bongers *et al.* 1991) grouped into families, except for Comesomatidae of which the different genera showed different tendencies

Nematode group	Fresh	Older	Undisturbed	FT	c-p value
Monhysteridae	*****	*****	****	1B	1
Chromadoridae	*****	*****	****	2A	3
Xyalidae	****	****	****	1B	2
Oxystominidae	***	***	***	1A	4
Comesomatidae *Cervonema*	***	**	*	1A	2
Sphaerolaimidae	***	*	*	2B	3
Prismatolaimidae	**			1B	?
Rhabditidae	*	*		1A	1
Teratocephalidae	*	*		1A	3
Comesomatidae *Sabatieria*	*	***	***	1B	2
Trefusiidae			*	1A	4
Epsilonematidae			*	1A	4
Microlaimidae			*	2A	3
Ceramonematidae		*	*	1A	3
Diplopeltidae		*	*	1A	3
Cyatholaimidae		*	*	2A	3
Desmodoridae		*	*	2B	3
Meyliidae		*	***	1A	4
Leptolaimidae		**	****	1A	3
Desmoscolecidae		**	****	1A	4

*: >0.5%, **: 2.5-5%, ***: 5-10%, ****: 10-20%, *****: >20%.

?: unknown.

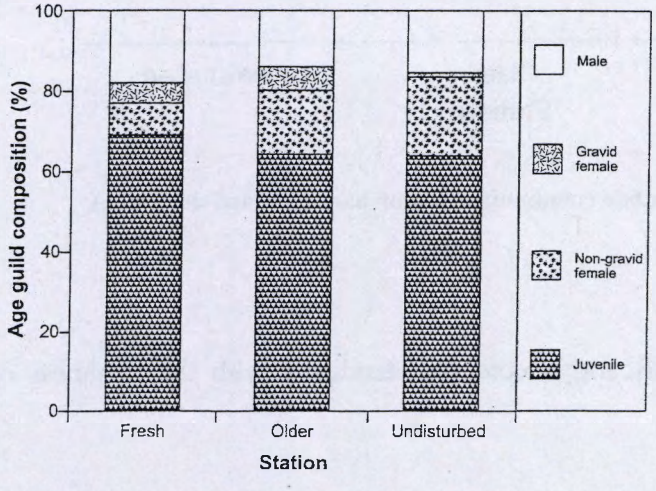

Fig. 5.4 Age and sex composition of the nematode community in three stations with different stages of recovery.

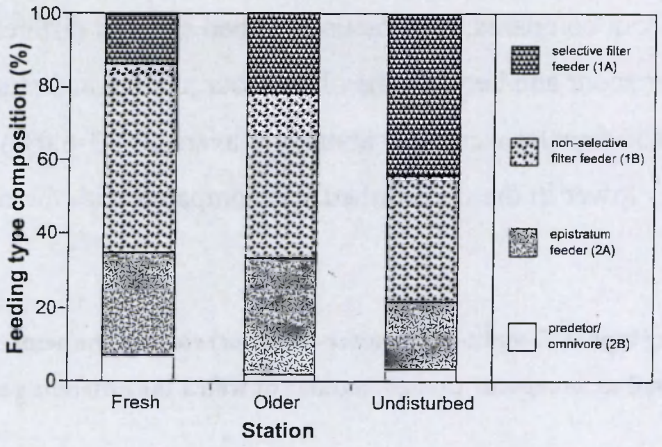

Fig. 5.5 Trophic guild composition of the nematode community in three stations with different stages of recovery.

Among four feeding guilds, the 1A group showed increased in importance from the fresh scour to the undisturbed site (Fig. 5.5). The proportion of this group was significantly higher in the undisturbed site compared with the other stations. The feeding group 1B showed an opposite tendency with the 1A group. The proportion of the 1B group was significantly lower only in the undisturbed site compared with the fresh scour. No significant differences between the stations were observed for the 2A group. Amongst the feeding guilds, the 2B group was the smallest. The proportion of this group was significantly higher in the fresh scour compared with the other stations.

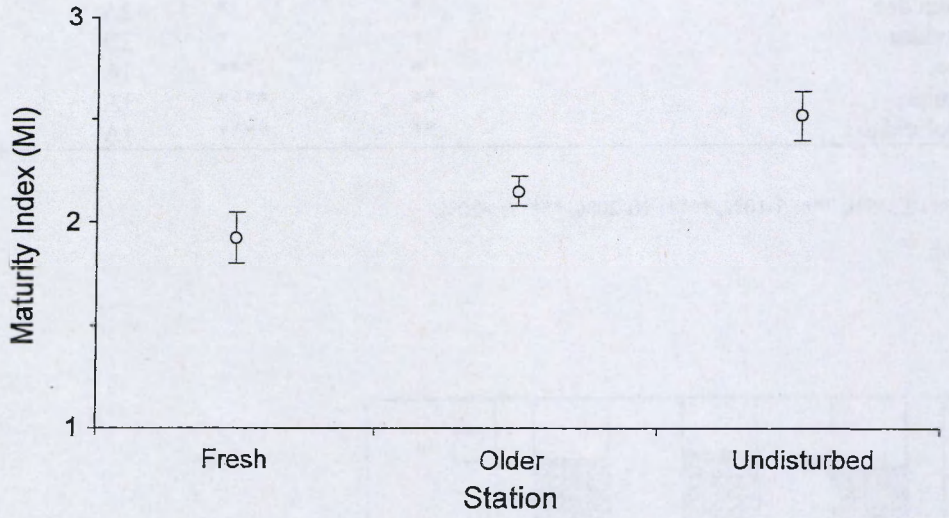

Fig. 5.6 Maturity Index (MI) of the nematode communities (error bar, standard deviation).

The maturity index showed a significantly decreasing tendency with the freshness of disturbance (Fig. 5.6).

5.5. Discussion

5.5.1. Influence of Iceberg scouring on meiofauna

The very low meiofaunal abundance in the fresh scour (<10% than in the older scour and the undisturbed site) is similar to the 93% reduction of meiofauna abundance after iceberg scouring in the shallow coastal sediments of Signy Island (Lee *et al.*, 2001b). Iceberg scouring also decreased the range of meiofauna taxa. Initially it removed most sessile and some motile animals, e.g. hydrozoans, bryozoans, kinorhynchs, tardigrades, turbellarians and acarines. The first immigrants into the scour were motile organisms such as amphipods and isopods, which can be considered as early colonisers. The absence of some lesser motile burrowers, e.g. priapulids, bivalves, sipunculids and oligochaetes, in the undisturbed site in spite of their presence in the older scour may be related to the presence of sponge spicule mats covering the sediment in the undisturbed site.

Previous studies of disturbance have shown time scales of meiofaunal recovery ranging from days to years (e.g. Coull, 1969; Danovaro *et al.*, 1995; Sherman and Coull, 1980). A general conclusion is that the recovery of meiofauna is relatively fast although it may depend on the type, frequency and scale of disturbance. In our study the meiofaunal abundance in the older scour had already recovered to the level of the undisturbed site and the taxon number in the older scour even exceeded that of the undisturbed site (Table 5.2). Unfortunately we cannot provide a good estimate of the recovery time for the meiofauna community in the current deep-water study. Recolonisation of a shallow coast meiofauna community at Signy Island occurred between 30 and 80 days (Lee *et al.*, 2001b), but in view of major differences in the ecological conditions between shallow coastal and deep-water habitats, one might expect that recolonisation of meiofauna in deep-water will occur at a slower rate. Complete recovery of the nematode community in this area may take at least some years.

5.5.2. Influence of Iceberg scouring on the nematode community

Abundance. The pattern of nematode abundance between samples was similar to that of total meiofauna abundance. The extremely low density in the fresh scour shows the severity of iceberg scouring impact in the initial stage. Although the nematode density in the older scour recovered to the level of the undisturbed site, their proportions among meiofauna were still low in the scours implying that nematodes recolonise more slowly than other major meiofauna, e.g. copepods and ostracods. This is probably because of the slower dispersal of nematodes.

Diversity. Nematode diversity was greatly influenced by scouring. The relatively high diversity of nematodes in terms of genus number in the undisturbed site (N_0=54.7±4.0) was in accordance with the results of Vanhove *et al.* (1999) from Kapp Norvegia and Halley Bay (N_0=56±5.0 and 52±10.8, respectively) in the Weddell Sea. However, it was very low in the fresh scour of this study (N_0=16±2.0). The nematode genus number in the older scour site was, unlike the abundance, still low (N_0=36.0±7.5) compared with the undisturbed site, which means that the restoration of nematode community structure is slower than the recovery in abundance.

Iceberg scouring also resulted in the increase of the dominance of a few nematode genera. Each of the three most abundant genera in the fresh and the older scour, *Monhystera*, *Neochromadora* and *Daptonema*, comprised more than 10% of the population while only *Monhystera* exceeded 10% in the undisturbed site. Those three dominant genera made up 60.6% in the fresh scour and 48.1% in the older scour. The three most dominant genera in the undisturbed site, *Monhystera*, *Desmoscolex* and *Leptolaimus*, comprised only 38.4% of the community.

Composition. The nematode genus composition of the fresh scour was more similar to the community in the older scour than the undisturbed community, despite the fresh scour being located much closer to the undisturbed site than to the older scour. Three different trends of nematode response to scouring effects were found (Fig. 5.3). The first group

(Fig. 5.3a), which showed a higher relative abundance in the undisturbed site, was mostly represented by selective deposit feeders (1A). *Acantholaimus* (2A), an exceptional genus in this group, seems to be a typical deep-sea nematode (Soetaert and Heip, 1995; Vanaverbeke *et al.*, 1997) and prefers physically more stable environments. It is not clear which factors influence the sensitivity of *Acantholaimus* to iceberg scouring. The second group (Fig. 5.3c), which was composed of nematodes with various feeding types and different reproductive strategies, showed intermediate properties. The last group of nematodes showed a higher relative abundance in the fresh scour reflecting their recolonisation ability (Fig. 5.3b). The common feature of this nematode group was that most of them were non-selective deposit feeders (1B). Among these three groups the second group seemed to be most sensitive to iceberg scouring. The sensitivity of nematodes in this group is probably caused by their restricted food preference and/or due to their reproductive strategy, because most of them were either selective deposit feeders (1A) and/or persisters.

In general, the feeding guilds in the Antarctic deeper water are more or less evenly shared between 1A, 1B and 2A groups with a slight dominance of the 2A group while the 2B group appears to be the least abundant group (Vanhove *et al.*, 1999). The results of the present study broadly confirmed this tendency although it was biased towards the 1A group in the undisturbed site and towards the 1B group in the other stations.

Sex and age. Reproductive activity at the scoured sites was higher than in the undisturbed site. One of the reasons for the high proportion of the gravid females in the scour samples was the change of nematode generic composition in the communities. The dominant genera in the undisturbed site, *Leptolaimus*, *Desmoscolex* and *Tricoma*, showed a relatively lower fecundity. Therefore the low proportion of *Leptolaimus* and the Desmoscolecina genera in the scours must have influenced the proportion of gravid females. On the other hand, the lower density of the population and therefore the lower competition in the scours may have stimulated the reproduction of nematodes.

5.5.3. Shallow water community vs. continental shelf community in the Antarctic

The influence of iceberg scouring has also been investigated at a shallow coast site at Signy Island (Lee *et al.*, 2001b). The comparison of the results from Signy Island and the Weddell Sea, from this study, provides further insight into the impact of iceberg scouring on the meiofauna and nematode communities. Both areas are under the influence of catastrophic physical disturbances of iceberg scouring; however, the frequency of disturbance is different. The study site on the shelf off Kapp Norvegia is deeper and an occasional iceberg scouring happens at each square meter once every 340 years on the average (Gutt, 2001), whereas scouring can happen much more frequently in the case of the coast at Signy Island (50-75 years, Peck and Bullough 1993). Between scouring events, the seabed of Kapp Norvegia remains more or less constant, whereas the seabed close to Signy Island is under the continuous disturbance of wave action and frequent ice induced disturbances. Therefore a combination of several physical disturbances is structuring the nematode community at shallow Antarctic coasts, whereas only occasional iceberg scour disturbs the nematode community at Kapp Norvegia. The nematode communities of undisturbed habitats in the two areas are also very different. The nematode community at Signy Island is characterised by a low diversity, a high dominance, a low MI and a low proportion of the 1A feeding group. The undisturbed nematode community at Kapp Norvegia shows opposite characteristics. However, iceberg scouring leads to a higher similarity between the characteristics of both nematode communities of Kapp Norvegia and Signy Island. Similarly Conlan *et al.* (1998) found that the scour communities of macrofauna closely resembled inshore shallow water benthos despite remoteness of several hundred meters.

5.6. Conclusion

It is likely that a significant threat for the Antarctic deep-water communities comes from increased iceberg scouring as a result of global warming (Doake and Vaughan, 1991; Gammie, 1995). (Gutt *et al.*, 1996) concluded that a slight increase in iceberg scour could be accommodated by the macrobenthic system because of its adaptation to such disturbance. Meiofaunal communities have a strong natural capacity for recovery from all kinds of disturbance including disturbance by iceberg scouring, but a big contrast is observed between shallow and deep-water communities. Shallow meiofauna seems to be strongly adapted to iceberg scouring as they are frequently faced with different kinds of physical constraints characteristic of shallow water environments. However, the structural recovery of the meiofauna, and more specifically the nematodes, from the deeper continental shelf is a slower process that can take some years, in contrast to the rapid recovery of abundance. This indicates that the communities are much more fragile and that they do not show a similar adaptation as shallow water communities. Probably this is mainly because of the relative constancy of the Antarctic deep-water environment. Hence, the increasing frequency of iceberg scouring due to global warming might have much greater effects on a deep-water meiofauna community, as compared with a shallow community.

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Chapter 6

Acantholaimus species descriptions

6.1. Abstracts

This study analyses morphological characteristics of *Acantholaimus* and describes, as primary results, 17 species of *Acantholaimus* from the Southern Ocean, of which 16 species are new.

In order to investigate the taxonomic position of *Acantholaimus*, the characteristics of amphid and buccal morphology of this genus was compared with related families. The large round amphids are thought to be apomorphous and the multispiral to be plesiomorphous. The amphids of *Acantholaimus* seemed to have no direct relation with the slit form amphids that are common in the family Chromadoridae. *Acantholaimus* has also tooth apophysis that is common in Selachinematidae. No such feature is known in Chromadoridae. This also implicates that *Acantholaimus* is phylogenetically more close to Selachinematidae rather than Chromadoridae.

For this reason, it is suggested to separate this genus together with other related genera from family Chromadoridae.

6.2. Introduction

Since Linstow (1982) described a few free-living marine nematodes from South Georgia, there was not much progress in taxonomic research on nematode in the Southern Ocean for a century. So far, the taxonomic studies accomplished by Allgén (1959) with the material collected by the Swedish Antarctic Expedition 1901-1903 is the major contribution to marine nematode taxonomy in this area. It is also Allgén who first described an *Acantholaimus* species obtained from Norwegian coast. There is, however, no *Acantholaimus* species described from the Antarctic so far.

Acantholaimus is currently considered as one of the most typical deep-sea genera among free-living marine nematodes (Platt and Warwick, 1988). However, it is very common in the Antarctic shelf although their abundance is less than in other deep-seas (Lee, unpublished data). This genus has very important ecological features i.e. high endemism and high degree of coexistence. With increasing interests on biodiversity, such characteristic of this genus might be valuable for ecological studies.

Acantholaimus is problematic in its taxonomic position. On the one hand, Gerlach and Riemann (1973; 1974) put this nematode under family Comesomatidae establishing a new subfamily 'Acantholaiminae'. On the other hand, Lorenzen considered it as a member of Chromadoridae and placed it under the subfamily Spilipherinae.

Considering all those circumstances, taxonomic revision of this genus is needed. The purpose of this study is therefore 1) to describe *Acantholaimus* species from the Antarctic Ocean and 2) to revise their taxonomic position based on morphological characteristics.

6.3. Material and Methods

6.3.1. Sampling area and methods

The material for this study comes from four different areas of two regions of Atlantic sector of Southern Ocean: Kapp Norvegia (KN) and Vestkapp (VK) in the Weddell Sea (WS) and Bransfield Strait (BF) and Drake Passage (DP) in Antarctic Peninsula (AP).

Samples were taken during the first and second EASIZ cruise (26th January – 15 March 1996 and 13th January - 26th March 1998, respectively) by means of a multi-box corer (Table 6.1).

Table 6.1. The location, water depth and sampling gear number of the stations for this study

Region	Area	Station	Depth (m)	Gear No.	Location	
					Latitude	Longitude
East Weddell Sea	KN	K1	182	MG27	71°19.7'	012°24.8'
		K2	216	MG23	71°40.1'	012°47.2'
		K3	243	MG1	70°52.1'	010°29.4'
		K4	255	MG19	71°32.3'	013°31.7'
		K5	278	MG24	70°50.1'	010°35.2'
		K6	332	MG25	70°49.4'	010°38.7'
		K7	298	MG26	70°49.8'	010°38.0'
	VK	V1	993	MG10	73°34.2'	022°38.0'
		V2	1944	MG14	73°23.7'	022°09.1'
		V3	220	MG17	73°28.4'	020°40.8'
Antarctic Peninsula	BS	B1	207	MG28	62°15.8'	058°42.7'
		B2	423	MG29	62°16.8'	058°42.1'
	DP	D1	2009	MG32	61°20.6'	058°15.1'
		D2	1028	MG33	61°26.7'	058°06.6'
		D3	429	MG34	61°34.5'	058°07.0'
		D4	218	MG35	61°53.3'	059°06.9'

Abbreviations for geographical names: KN, Kapp Norvegia; **VK,** Vestkapp; **BS,** Bransfield Strait; **DP,** Drake Passage.

6.3.2. Sample treatment

For sampling and treatment on board cf. Lee *et al.* (2001a). Once the nematodes were extracted they were dehydrated using a series of De Grisse solution. When the nematodes were fully dehydrated, they were mounted on Cobb slide slides with anhydrous glycerine medium and sealed with paraffin wax. Observation was carried out under a Wild M20 light microscope. Drawings were made with the aid of camera lucida attached to the microscope.

Numerical characters of type specimens were measured based on the drawings.

Morphological characters used for the species are mainly the shape of pharynx, size and position of amphids, length of outer labial and cephalic setae and their ratio, position and arrangement of cervical setae and cuticular ornamentation (cf. Fig. 6.1).

6.3.3. Diagnostic morphological characteristics

Acantholaimus species showed variations in many features that can be used for species diagnosis. The characteristics used to species identification of this study are presented in Fig. 6.1 and the consequent morpho-matrix is shown in the appendix (Table 6.2).

The size of adult *Acantholaimus* found in this study ranges from 364 (*A.* sp 43) to >1689 µm (*A.* sp. 11a) including tail (L) or from 265 (*A.* sp. 00) to 951 µm (*A.* sp. 29a) to the anus (L'). The De Man ratios are commonly used for numerical expression of nematode body shape. However, the long filiform tails that are common in Acantholaimus can influence on the ratios which will eventually give biased impressions on their body shape. I, therefore, use L' for the ratios and refer them to a', b': a'=L'/maximum body diameter, b'=L'/pharynx length. This is also useful when the tail is broken, which can often happen to the long tailed nematodes. The body shapes are categorised into three groups: stout (A, a'<15), moderate (B, 30>a'>15) and slender (C, a'>30).

The head shape of *Acantholaimus* showed about four different forms (Fig. 6.1a). Head type A' is more or less truncated. Nematodes belonging to this category were generally stout with minimum difference between head and maximum body diameter. Head type A was most general shape shared by most nematodes. Type B was seen from the nematodes relatively wide body diameter but narrowly tapered head. Nematodes with type C head had elongated body and head.

The relative amphid sizes compared with corresponding head diameter were also vary from >.05 to near to 1 (Fig. 6.1b). Four different categories are: L'=near to 1, L=smaller than 1 but larger than 0.5, M=approximately 0.5 and S=smaller than 0.5.

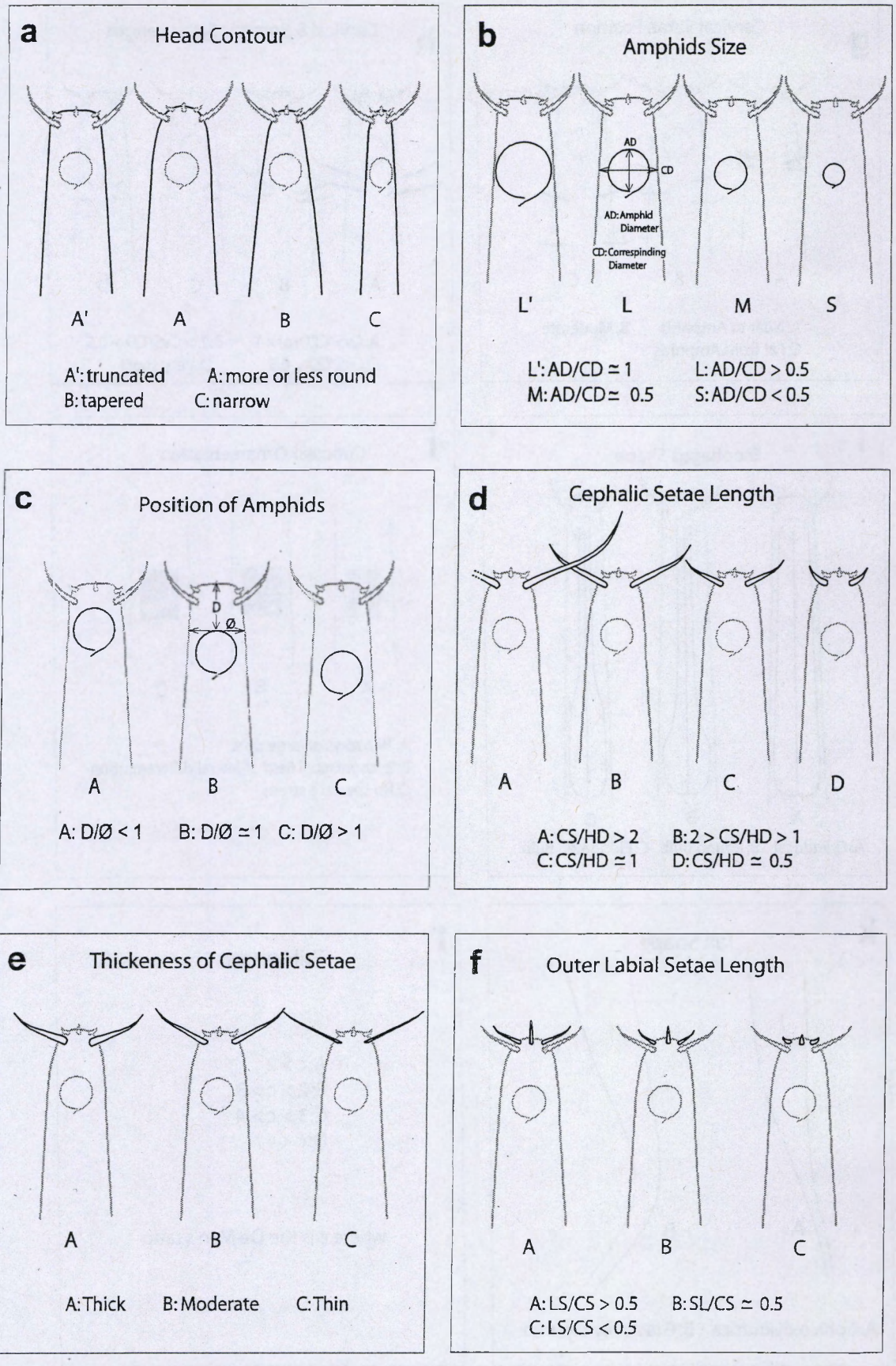


Fig. 6.1 Morphological characteristics used for the identification of Acantholaimus.

CS, cephalic setae length; HD, head diameter; LS, outer labial setae length

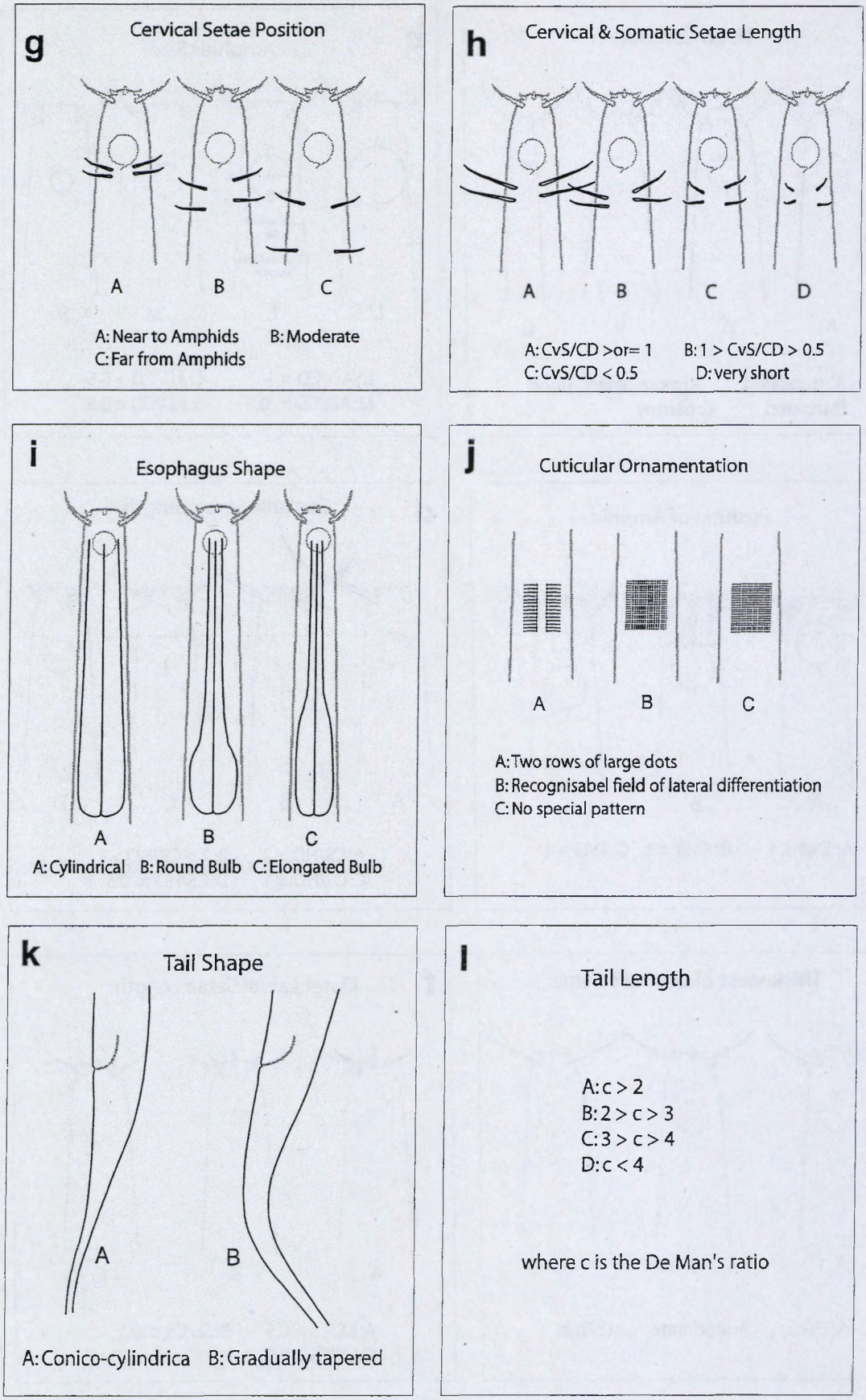


Fig 6.1 continued.

CvS, cervical setae length, CD, corresponding body diameter.

The amphid position was relativised in relation with head diameter (Ø. Three categories were defined as A (D/Ø < 1), B (D/Ø ≈ 1) A (D/Ø > 1) as shown in Fig. 6.1c.

Cephalic setae length was vary from *** to *** µm Relative length of Cephalic setae (CS/HD) was categorised into four groups (Fig. 6.1d): A (CS/HD > 2), B (2 > CS/H > 1), C (CS/HD ≈ 1) and D (CS/HD ≈ 0.5).

Some variations in cephalic setae thickness was observed and categorised into three groups: thick (A), moderate (B) and thin (C) as shown in Fig. 6.1e.

Inner labial setae are mostly papilliform and sometimes difficult to observe. For this reason, it was not considered as diagnostic feature. However, outer labial setae showed more variations and taken account into diagnostic characteristics. Some species has outer labial setae longer than half a cephalic setae length and categorised as type A. When the cephalic setae are setae form but shorter than half a cephalic setae length, it was categorised as type B. Most species have papilliform outer labial setae and categorised as type C (Fig. 6.1f).

Relative distance of the first pair of cervical setae from amphids was also considered as diagnostic characteristics: A=near to amphids, B=moderate and C= far from amphids (Fig. 6.1g).

Cervical setae length (CS) to the corresponding body diameter (CD) was relativised: A (CS/CD > or = 1A), B (1 > CS/CD > 0.5), C (CS/CD < 0.5) and D (near to papilliform) (Fig. 6.1h).

Pharynx showed three different forms: Cylindrical without distinct terminal bulb (A), narrow anterior cylindrical with posterior round bulb (B) and narrow anterior cylindrical with posterior elongated bulb (C) (Fig. 6.1i)

Only one species of *Acantholaimus* in this study distinctively has lateral differentiation of two rows of parallel dots (cuticle type A). Most species have simple punctations with larger dots on the lateral side (cuticle type B) or without lateral differentiation (cuticle type C) (Fig. 6.1j)

Tail shape of *Acantholaimus* is generally conico-cylindrical. When only conical part is considered, there are two different types: a steeply tapered and shorter conical part (tail type A) and a long gradually tapered (tail type B). The length of the former one normally did not exceed 5 times of anal diameter while the later one could easily exceed 5 times (Fig. 6.1k).

De Man ratio c expressed as total body length to tail length was grouped into three categories: $c < 2$ (A), $3 > c > 2$ (B), $3 > c > 4$ (C) and $c > 4$ (Fig. 6.1l).

An additional features for species identification could be the sperm morphology since they show diverse forms and seems species specific. However, one must be careful that the spermatozoa can have metamorphoses during the course of development. They also tend to become narrower while they approach to the vas difference or pass thorough it. Therefore I used it only when it was necessary and otherwise it was supplementary.

As the result, 450 Acantholaimus specimens were retrieved from 16 stations and 65 species were distinguished (Table 6.2). Among those 65 species, the 17 species that both male and female are available are described here as the preliminary results. Descriptions are mostly based on one specimen that was used as type specimen for the species discrimination. The drawings also often omit some characteristics such as punctations, intestine, and vas difference that are not used for species identification or otherwise stated in the text.

Measurements are given as a formula as below:

$$\frac{\text{positonof cephalicsetae,posterialendof pharynx,mid-body(or vulva),anus}}{\text{correspondng bodydiameter}} \quad \text{tatalbodylengh.}$$

Table 6.2 Morphomatrix of Acantholaimus species found in the whole study area.

Species	TS	HC	AS	AP	CSL	CT	OLSL	CSP	C/SSL	E	CO	TS	TL
00	F	A	M	C	B	B	C	A	B	B	C	B	A
01a	M	B	L	B	C	B	A	A	B	C	C	B	D
01b	M	B	L'	C	A	B	B	A	C	C	B	B	B
01c	M	B	L	B	C	B	B	C	D	C	B	B	B
01d	M	B	L	C	C	B	A	C	D	C		B	C/D
01e	J	B	L	B	B	B	B	B	C	C		B	B
01f	J	C	L	C	C	B/C	B			C		B	C/D
01g	F	B	L	B/C	C	B	B	D	D	C		B	
01h	M	B	L'	B	A	B	C	A	D	C	C	B	A/B
01i	F	B	L'	A	B	B/C	B			C		B	A
01j	M	B	L	B	A	B	C	A/B	B	C		B	A
01k	F				B	B	C	C	C	C		B	
01l	J	B/C	L	C	A/B	B/C	A	C	B	C		B	C
01m	M	B	L	A	B	B/C	B	A	B	C		B	C (B)
02	M	A	M	A	C	A	C	B	C	B	A	A	D
03	J	A'	L	B	A	A	C	B	B	C		A	C
04	J	A	S	B	D	A	C			B		B	A/B
05	J	A	M	C	D	C	C	C	D	C (B)		A	D
06a	M	A	S	B/C	D	B		B	C	B		A	C
06c	M	A	S	C	C	B	C	B	C	B		A	D
06d	M	A	S	C	C	B	C	A	B/C	B		A	D
06e	F	A	M/S	C	D	B/C	C	A	B/C	B			
07a	M	A'	S	A/B	C	B	C	B	B	B		B	C
07c	F	A	S	B	C	B	C	B	B	B		B	B
07d	M	A	M	B	C	A	C	B	B	B		-	-
08a	M	A	S	C	C	B	C	A	C	B	B	A	D
10	J	A*	L	A	C	A/B	B	B	C	C		B	A
11	M	A	L	C	A	A	C	B	B	C	B	B	A
11b	M	C	L	C	A	B	B	B	B	C		B	A
11c	M	A	L	B/C	A	B	C	B	B	C		B	A
12	F	A	M	C	D	B	A	A	D	C	B		
13	F	A	M	A	D	B	C	A	D	A	C	A	D
14a	M	A	S	B	C	B	C	A	C	B		A	C/D
14c	M	A	M/S	A	C	B	C	B	D	B	B	A	C/D
14d	M									B			
14e	J									B			
14f	F									B			
14g	M									B			
15c	M	C	L'	C	D	B	B	A	C	C		A	C
15b	J	A	L	C	C	B	B	C	C	C	B	B	C
15d	J									C			
16a	M	A	S	C	A	B	C	A	C	B	B	A	C
16b	F	A	S	C	B	B	A	A	C	B		A	C
16c	M	A	S	C	A	B	C	A	C	B	B	A	D
17	F	C	L	C	C	B	C	A	C	C		A	-
18	F	A	M	C	C	C	B	A	C	C		B	C
21	M	A	L'	A	B	B	C	A	C	C		B	B
27	J	A	L'	A	B	A	C	A	C	C		B	A
28	J	A	S	C	C	A	C	A	C	C*		B	A/B
29a	M	A'	S	A	C	B	B	A	C	B	B	A	B
29b	M	A	S	B	C	A	C	B	C	A		A	C
29c	J	A	S	A	D	B	C	B	C	B	B	A	C
32	F	B	L	B	D	A	B	B	D	C	C	B	C
33	J	B	M	A	B	C	C		C	C	B	B	C
36	M	B	L	C	D	A	C		D	C		B	D
37	M	B	L	B	B	B	C	A	D	C	C	B	B
39	M									B			
40	M	A	L	B	C	B	B	C	D	C		B	
41	J									C			
42	J	A	L'	B	B	C	C	C	D	C		B	C
43	M	A	M	C	C	A	C			B		A	D
44	M									C			
45	M									C			
46	J									B			
47	J	A	M	B	C	B	A	B	C	B		A	C

TS, sex of type specimen; E, esophagus; AS, amphid size; HC, head contour; OLSL, outer labial setae length; TS, tail shape; AP, amphid position; CO, cuticular ornamentation; CSL, cephalic setae length; CSP, cervical setae position; C/SSL, cervical and somatic setae length; CT, thickness of cephalic setae; TL, tail length.

6.4. Results

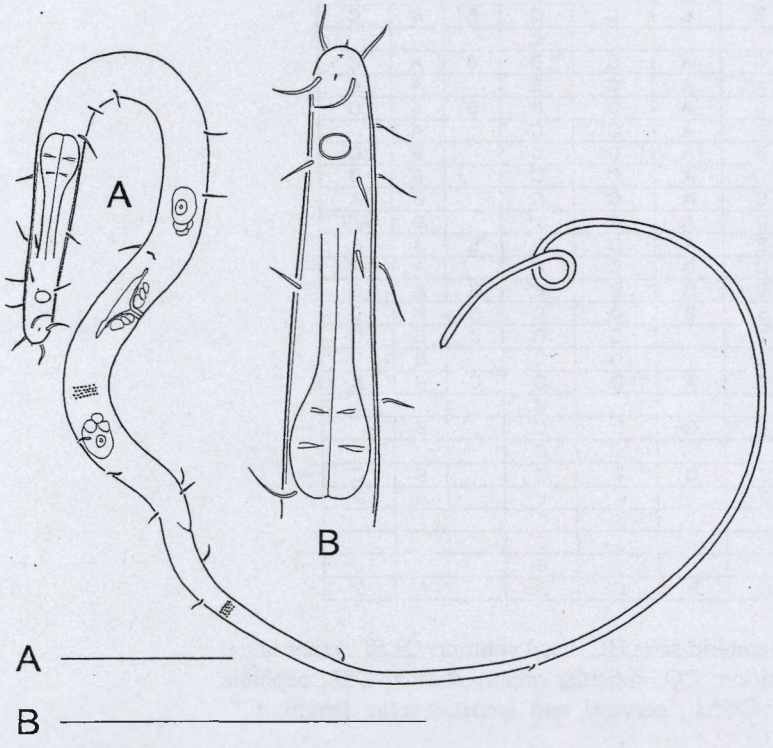
6.4.1. Species descriptions

***Acantholaimus* sp. 01 (n. sp.)** Fig. 6.2

Holotype: A-0942-7 (φ_1), from st. V3

$$\varphi_1 = \frac{-\ 75\ \ 186\ \ 265}{8\ \ 13\ \ 14\ \ 8}\ 650\ \mu m;\ a = 48.1;\ b = 8.6;\ c = 1.4;\ V = 28.6\%$$

Description; Small (651 µm long) and common body shaped nematode. **Cuticle** is annulated with very fine punctations, which becomes larger in tail region. **Lateral differentiations** are not conspicuous. **Amphids** are round, located at 16.5 µm from the anterior end. They are 4.7 µm in diameter (50% corresponding body diameter). **Inner labial sensilla** are not visible. **Outer labial sensilla** are very tiny papillae form. **Cephalic setae** are 8.2 µm long. **Amphidal setae** and **somatic setae** are as long as the cephalic setae (8.2 µm long) and arranged along four longitudinal rows. **Stoma** is small and weekly musculated with tiny teeth. **Pharynx** (75.3 µm long) is cylindrical with posterior round terminal bulb. **Ovaries** are short and antidromously reflected, laying anterior one right and posterior on left to the intestine. **Tail** is very long (465 µm) filiform, representing 71.4% of body length.



Scale bars: 50 µm.

Diagnosis; *Acantholaimus* sp. 01 is characterised by small body size (650 µm), relatively long filiform tail that takes more than 70 % of the whole body, unusually short outer labial sensilla, weakly developed teeth in the stoma and round pharyngeal bulb. This character set is unique among known species. When the distance to the anus is considered, this is the smallest *Acantholaimus* species ever found.

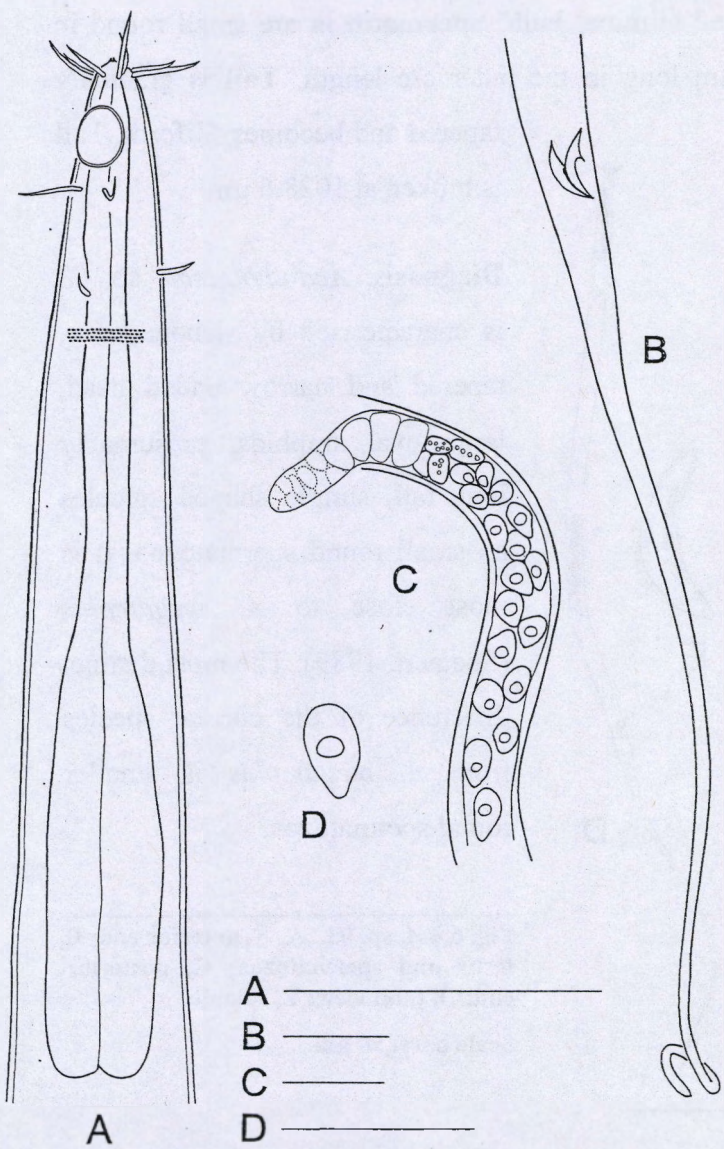
Fig. 6.2 *A.* sp. 01. A, φ_1 total view; B, anterior end.

***Acantholaimus* sp. 02 (n. sp.)** Fig. 6.3

Holotype: A-1344-2 (δ_1), from st. K3

$$\delta_1 = \frac{-}{7}\ \frac{157}{29}\ \frac{M}{38}\ \frac{1035}{24}\ 1493\,\mu m;\ a = 39.7;\ b = 9.5;\ c = 3.3$$

Description; Long slender nematode (1493 µm long). **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are large and longitudinally elongated oval, located at 7.1 µm from the anterior end. They are 8.6 µm in width and 9.3 µm in length (72% corresponding body diameter). **Inner labial sensilla** are small papillae. **Outer labial sensilla** are long (7.9 µm) setae form. **Cephalic setae** are 11.4 µm long. **Amphidal setae** are one pare (10.7µm long). **Somatic setae** are (5.7 µm long) in four longitudinal rows. Stoma is small, weekly armamented. **Pharynx** is cylindrical (157.1 µm), posteriorly expanded to form an elongated terminal bulb. **Spermatozoa** are small (*l*, 24.7 µm; *w*, 13.5 µm) oval in shape. **Spicules** are typical shape, 30.2 µm long in the outer arc length. **Tail** is gradually tapered and becomes filiform, representing 30.7% of body length.



Diagnosis; *Acantholaimus* sp. 02 is characterised by narrow anterior end, relatively long outer labial setae, relatively smaller spermatozoa. This species is similar to *A. microdontus* (Gourbault and Vincx, 1985). However, *A. microdontus* has shorter tail (c=4.4) wider body (a=28.6) and different numbers of amphidal setae (2 pairs).

Fig. 6.3 *A.* sp. 02. A, δ_1 anterior end; B, posterial end; C, testis; D, spermatozoa. Scale bars: 50 µm.

***Acantholaimus* sp. 03 (n. sp.)** Fig. 6.4

Holotype: A-1494-7 (δ_1), from st. K3

$$\delta_1 = \frac{-\quad 138 \quad M \quad 629}{7 \quad 18 \quad 16 \quad 15}$$ tail tip broken

Description; Slender nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are large and longitudinally elongated oval, located at 11.8 µm from the anterior end. They are 9.4 µm in width and 14.1 µm in length (100% corresponding body diameter). **Inner labial sensilla** are small papillae. **Outer labial sensilla** are long (10.6 µm) setae form. **Cephalic setae** are 18.8 µm long. **Amphidal setae** are one pare (8.2 µm long). **Somatic setae** are (7.1 µm long) in four longitudinal rows. Stoma is small, weekly armamented. **Pharynx** is cylindrical (137.6 µm), posteriorly expanded to form an elongated terminal bulb. **Spermatozoa** are small round in shape. **Spicules** are not inflated, 24.7 µm long in the outer arc length. **Tail** is gradually tapered and becomes filiform. Tail is broken at 1028.6 µm.

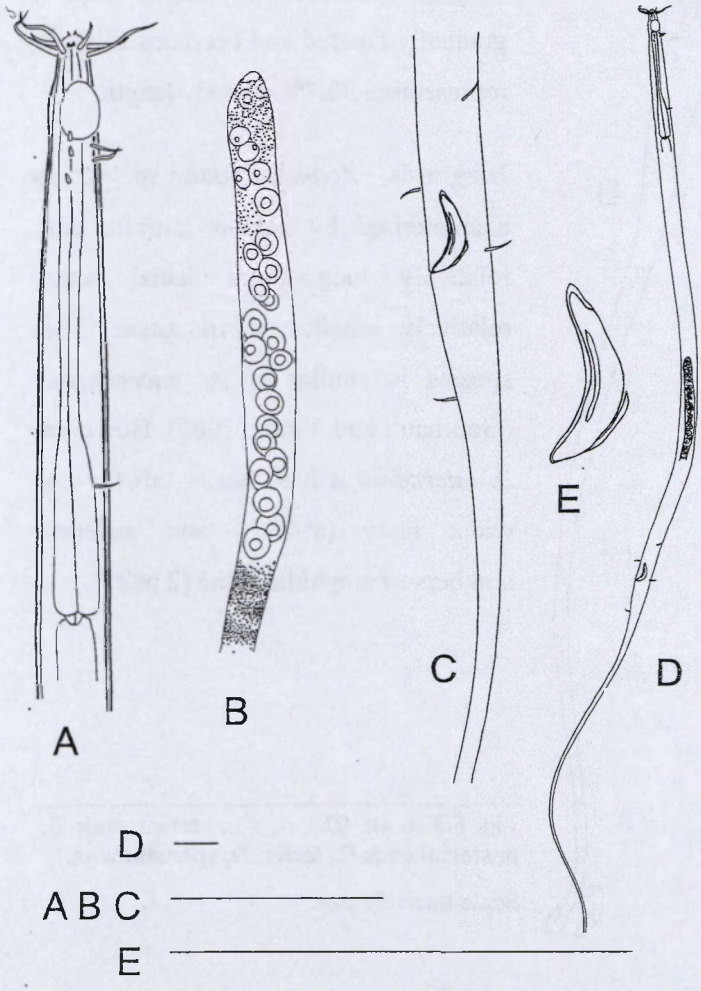


Fig. 6.4 *A.* sp. 03. A, δ_1 anterior end; B, testis and spermatozoa; C, posterior end; D, total view; E, spicule.

Scale bars: 50 µm.

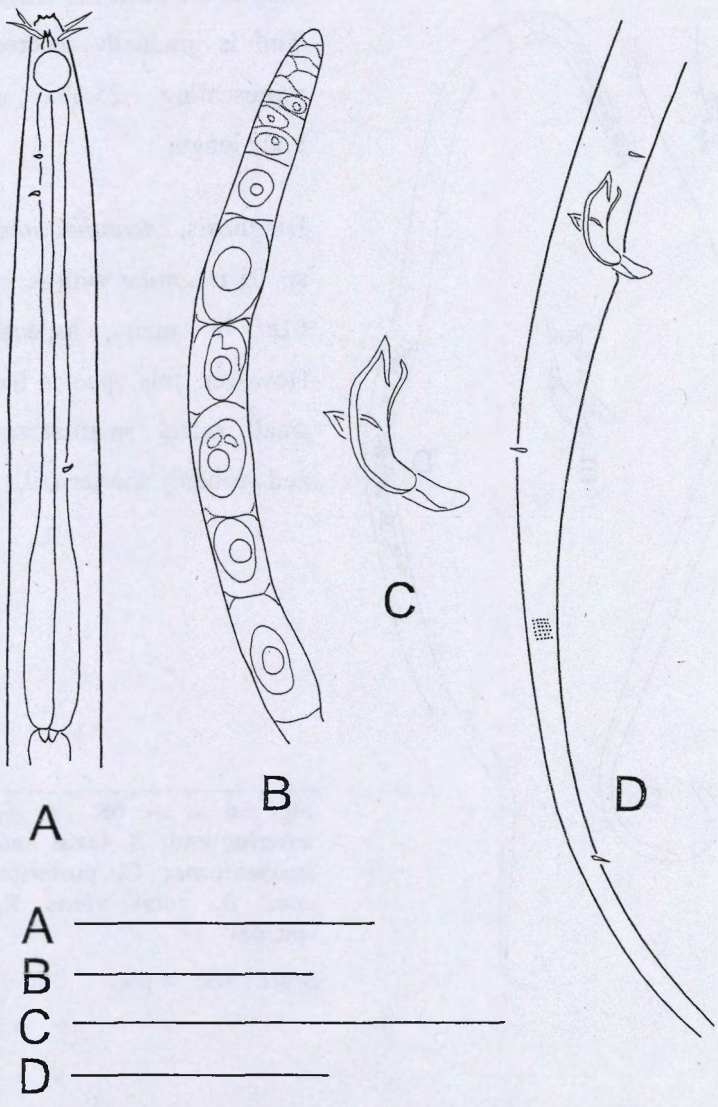
Diagnosis; *Acantholaimus* sp. 03 is characterised by slender body, tapered and narrow ended head, large oval amphids, presumably long tail, simple shaped spicules an small round spermatozoa. It is most close to *A. megamphis* (Soetaert, 1989). The most distinct difference of the current species from *A. megamphis* is smaller round spermatozoa.

***Acantholaimus* sp. 04 (n. sp.)** Fig. 6.5

Holotype: A-1504-10 (♂1), from st.K6

$$♂_1 = \frac{-\quad 120 \quad M \quad 514}{6 \quad 15 \quad 18 \quad 14}$$ Tail tip broken

Description; Slender nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are longitudinally elongated oval, located at 5.9 µm from the anterior end. They are 7.1 µm in length and 5.9 µm in width (80% of corresponding body diameter). **Inner labial sensilla** are small papillae. **Outer labial sensilla** are short (2.4 µm) setae form. **Cephalic setae** are 7.1 µm long. **Amphidal setae** are two in one longitudinal subdorsal row (1.8µm long). **Somatic setae** are scarce and short (2-3 µm long). Stoma is small, weekly armamented. **Pharynx** is cylindrical (120.0 µm), posteriorly expanded to form an elongated terminal bulb. **Spermatozoa** are large (*l*, 14.1 µm; *w*, 7.1 µm) oval in shape. **Spicules** are typical shape, 30.2 µm long in the outer arc length. **Tail** is gradually tapered.



Diagnosis; *Acantholaimus* sp. 04 is characterised by small body, short cervical and somatic setae, large spermatozoa. The most similar species is *A. filicaudatus* (Soetaert, 1989).

However, the current species has smaller amphids, longer body in relation to amphid length (b'=4.3) compared to *A filicaudatus* (b'=2.9).

Fig. 6.5 *A.* **sp. 04. A, ♂1 anterior end; B, testis and spermatozoa; C, spicules; D, posterior end.**

Scale bars: 50 µm.

***Acantholaimus* sp. 05 (n. sp.)** Fig. 6.6

Holotype: A-1473-7 (δ_1), from st. K6

$$\delta_1 = \frac{-\ 119\ \ M\ \ 674}{6\ \ 17\ \ 18\ \ 15}\ 909\,\mu m;\ a = 49.8;\ b = 7.6;\ c = 3.9$$

Description; Long slender nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are large (7.6 µm in diameter, 60% corresponding body diameter) and round, located at 7.6 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are setae form (5.3 µm long). **Cephalic setae** are 7.1 µm long. **Amphidal setae** are two in one longitudinal subdorsal row (2.3 µm long). **Somatic setae** are not observed. Stoma is small, weekly armamented. **Pharynx** is cylindrical (118.8 µm), posteriorly it is expanded to form an elongated terminal bulb. **Spermatozoa** are small round in shape. **Spicules** are typical shape, 18.9 µm long in the outer arc length. **Tail** is gradually tapered, representing 25.8% of body length.

Diagnosis; *Acantholaimus* sp. 05 is similar with A. sp 01c in many aspects. However, this species has small round spermatozoa and probably shorter tail.

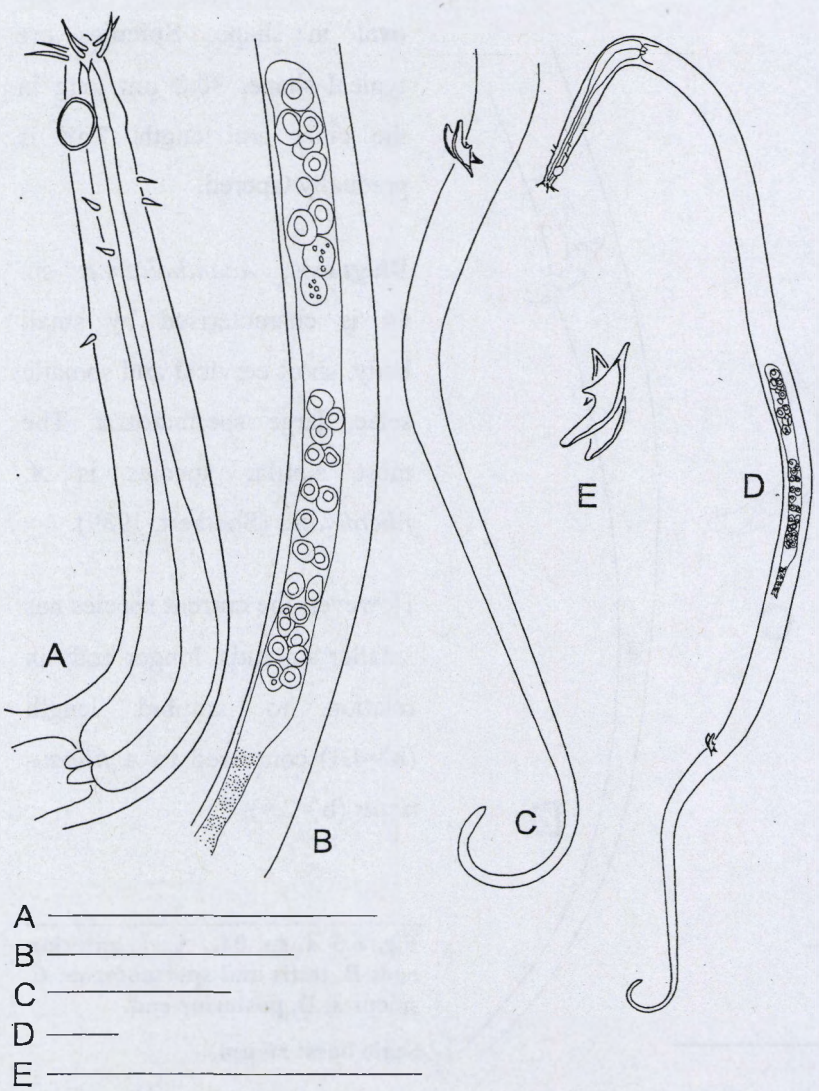


Fig. 6.6 *A.* sp. 05. A, δ_1 anterior end; B, testis and spermatozoa; C, posterior end; D, total view; E, spicules.

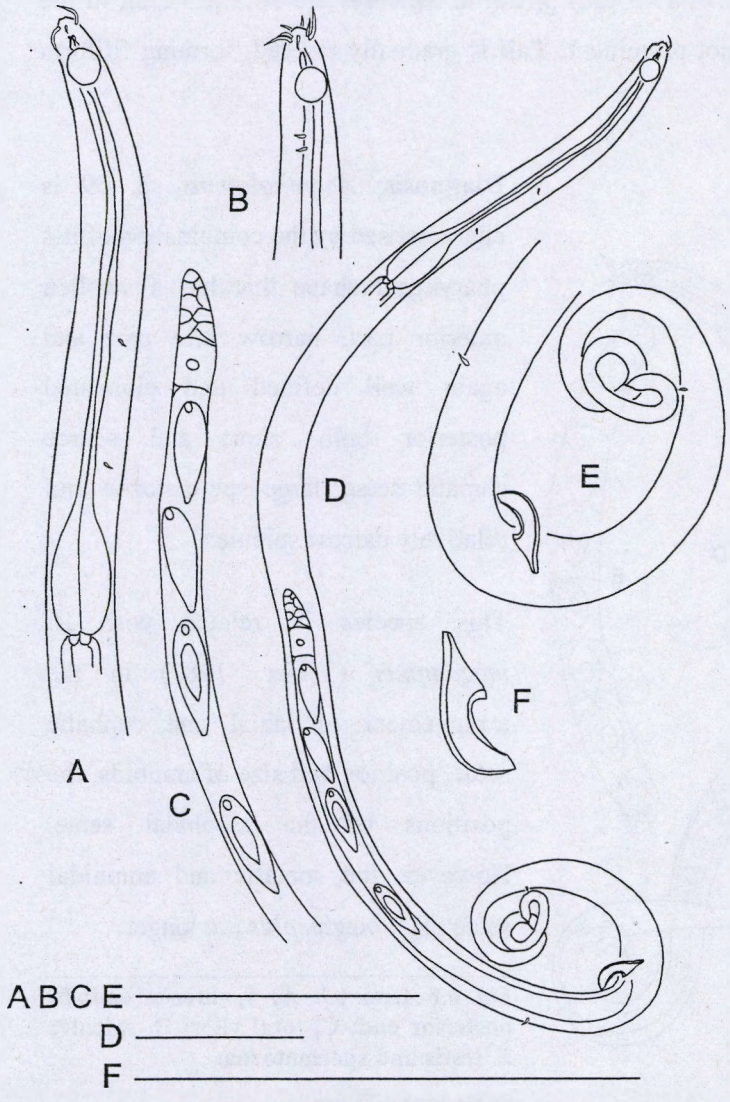
Scale bars: 50 µm.

***Acantholaimus* sp. 08 (n. sp.)** Fig. 6.7

Holotype: A-1237-9 (δ_1), Paratype: A-1204-8 (δ_2) from st. V2

$$\delta_1 = \frac{-}{5}\ \frac{109}{12}\ \frac{M}{13}\ \frac{408}{12}\ 568.2\,\mu m;\ a = 43.9;\ b = 5.2;\ c = 3.6$$

Description; Small slender nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are rather small and longitudinally elongated oval shape (*l*, 6.5 µm; *w*, 5.9 µm; 66.7% corresponding body diameter), located at 5.9 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are setae form (4.1 µm long). **Cephalic setae** are 5.9 µm long. **Amphidal setae** are two in one longitudinal subdorsal row (2.4 µm long). **Somatic setae** are scarce and short (2.4 µm long). Stoma is small, weekly armamented. **Pharynx** is cylindrical (109.4 µm), posteriorly it is expanded to form an elongated oval terminal bulb. **Spermatozoa** are elongated oval in shape. **Spicules** are typical shape, 17.6 µm long in the outer arc length. **Tail** is gradually tapered, representing 28.2% of body length.



Diagnosis; *Acantholaimus* sp. 08 is characterised by small body, remarkably narrowed anterior part of pharynx with elongated oval posterior bulb. Tail is rather short that it has almost no filiform part. The general body shape of this species is similar to *A. vermeuleni* (Muthumbi and Vincx, 1997). However, A. 08 has different pharyngeal shape, shorter tail and more elongated spermatozoa.

Fig. 6.7 *A.* sp. 08. A, δ_1 anterior end; B, δ_2 anterior end; C, testis and spermatozoa; D, total view; E, posterior end; F, spicue.

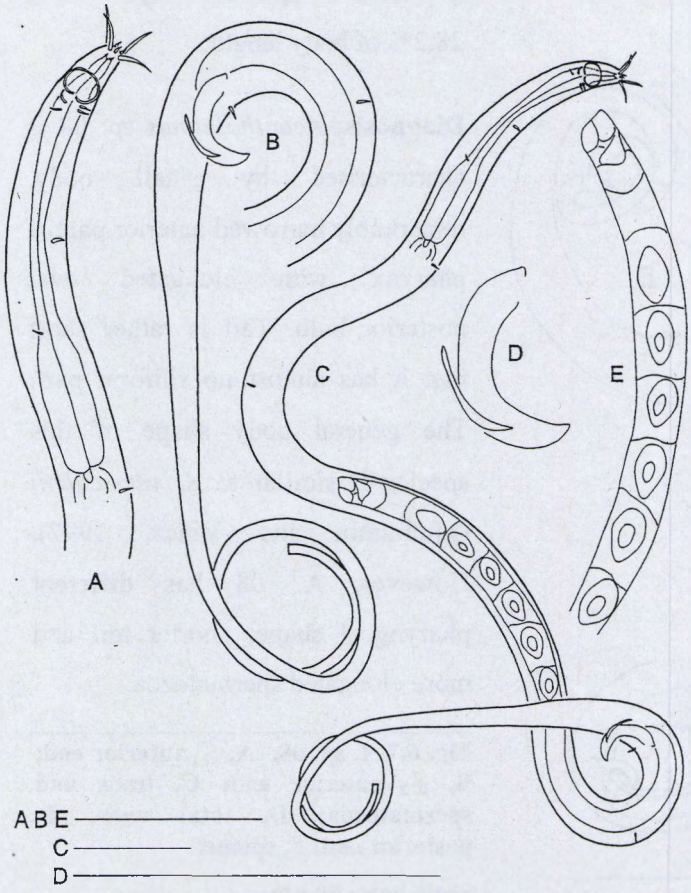
Scale bars: 50 µm.

***Acantholaimus* sp. 09 (n. sp.)** Fig. 6.8

Holotype: A-0805 (δ_1), from st. K1

$$\frac{-}{5}\ \frac{114}{18}\ \frac{M}{19}\ \frac{528}{15}\quad 857.6\ \mu m;\ a = 45.6;\ b = 7.5;\ c = 2.6$$

Description; Slender nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are large and rather wide (*l*, 7.6 µm; *w*, 9.4 µm; 84.2% corresponding body diameter), located at 8.8 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are setae form (2.9 µm long). **Cephalic setae** are 9.4 µm long. **Amphidal setae** are two pairs in two longitudinal rows (3.5 µm long). **Somatic setae** are scarce and short (3.5 µm long). Stoma is small, weekly armamented. **Pharynx** is cylindrical (114.1 µm), anterior part is swollen and mid part is narrow and posteriorly expanded to form an elongated oval terminal bulb. **Spermatozoa** are large (*l*, 24.7 µm; *w*, 13.5 µm) piriform. **Spicules** are 30.2 µm long in the outer arc length and proximal inflation is not prominent. **Tail** is gradually tapered, forming filiform end, but the tip is broken.



Diagnosis; *Acantholaimus* sp. 09 is characterised by the combination of it's pharyngeal shape that has a swollen anterior part, narrow mid part and again well defined and elongated posterior bulb, short and scarce somatic setae, large spermatozoa and relatively narrow spicules.

This species is related with *A. megamphis* (Vivier, 1985) in the arrangement of labial and cephalic setae, position and size of amphids, the positions of the amphidal setae. However, the somatic and amphidal setae of *A. megamphis* are longer.

Fig. 6.8 *A.* sp. 09. A, δ_1 anterior end; B, posterior end; C, total view; D, spicule; E, testis and spermatozoa.

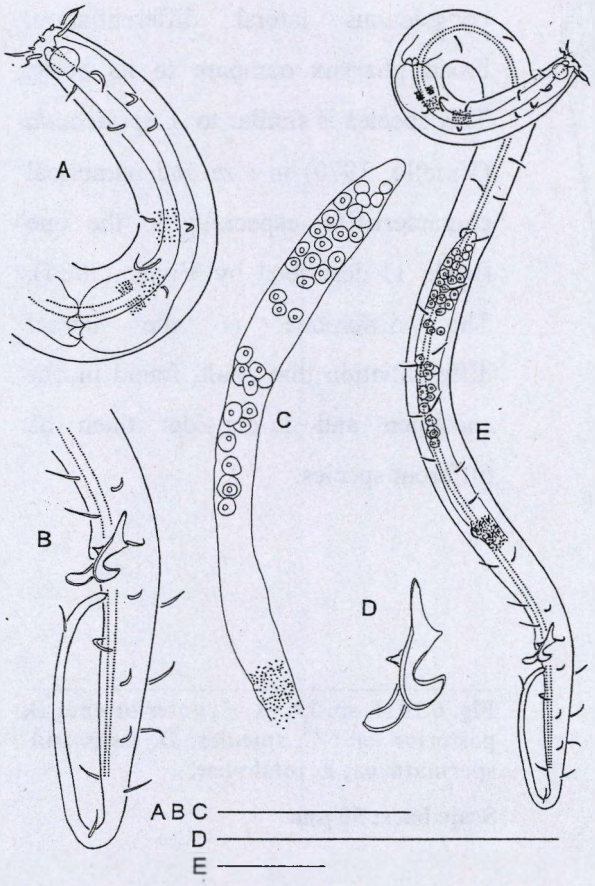
Scale bars: 50 µm.

***Acantholaimus* sp. 15 (n. sp.)**

Holotype: A-0408-10 (δ_1), from st. K4

$$\delta_1 = \frac{-}{10}\ \frac{101}{24}\ \frac{M}{24}\ \frac{456}{15}\quad 607.1\mu m;\ a = 25.8;\ b = 6.0;\ c = 4.0$$

Description; Small nematode. **Cuticle** is finely punctuated with distinct lateral differentiation. Anterior to pharyngeal bulb, the lateral differentiation is larger and scarce dots and posteriorly it becomes two parallel longitudinal rows of dots that end in the mid part of tail. **Head** is truncated. **Amphids** are round (*l*, 6.5 µm; *w*, 6.5 µm; 57.1% corresponding body diameter), located at 4.7 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are also papilliform. **Cephalic setae** are 5.9 µm long. **Amphidal setae** are pair in one subdorsal and the other in subventral position (9.4 µm long). **Somatic setae** are arranged along both side of lateral field (8.2 µm long). **Stoma** is small, armamented with small teeth. **Pharynx** is cylindrical (101.2 µm), posteriorly expanded to form the strongly muscularised round terminal bulb. **Spermatozoa** are small and rather round in shape (about 6 µm in diameter). **Spicules** are typical shape. **Tail** is gradually tapered, relatively short representing 25.0% of body length.



Diagnosis; *Acantholaimus* sp. 15 is characterised by small body with distinct lateral differentiation, brunt anterior end, papilliform outer labial sensilla, strong round pharyngeal end bulb and small round spermatozoa. There are two species which have a lateral difference with two longitudinal rows. One is *A. calathus* (Gerlach *et al.*, 1979) which is larger. *A. calatus* also have longer somatic setae more densely distributed along the body. Spermatozoa are also larger and different in shaple. The other one is *A. ewensis* (Platt and Zhang, 1982) that even have more hairy setae that are longer.

Fig. 6.9 *A.* sp. 15. A, δ_1 anterior end; B, posterior end; C, testis and spermatozoa; D, spicule; E, total view.

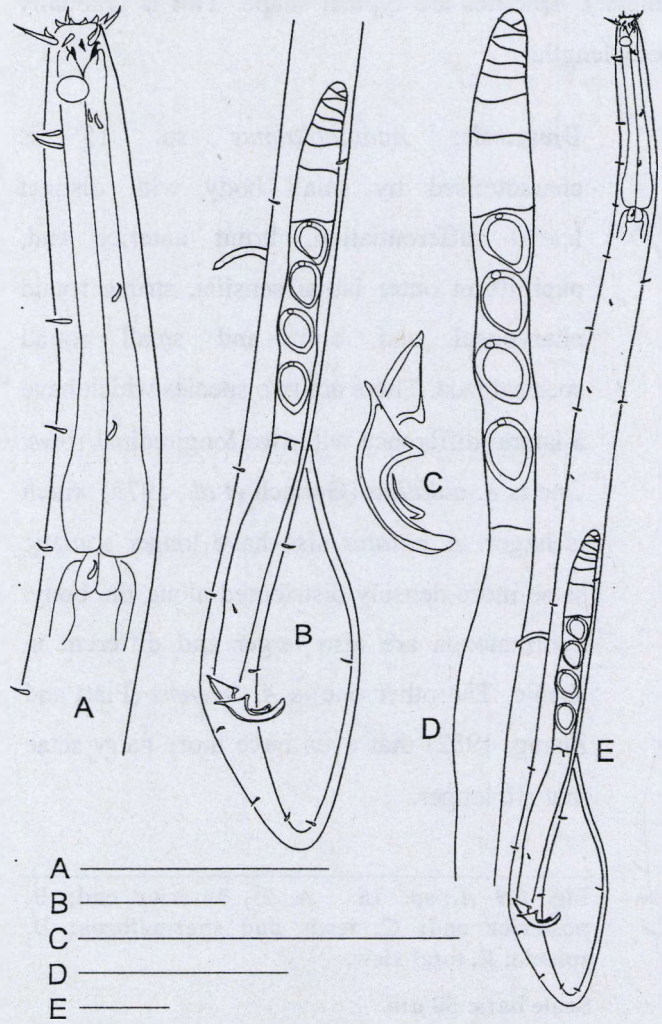
Scale bars: 50 µm.

Acantholaimus sp. 19 (n. sp.)

Holotype: A-0408-10 (δ_1), from st. K6

$$\delta_1 = \frac{-}{11}\ \frac{107}{22}\ \frac{M}{25}\ \frac{514}{22}\quad 796.5\,\mu m;\ a = 32.2;\ b = 7.4;\ c = 2.8$$

Description; Small nematode. **Cuticle** is finely punctuated. Lateral differentiation is a longitudinal band consisting of larger does. **Amphids** are rather small and transversely elongated oval shape (*l*, 5.3 µm; *w*, 6.5 µm; 45.8% corresponding body diameter), located at 10.6 µm from the anterior end. **Inner labial sensilla** are conspicuous papillae. **Outer labial sensilla** are setae form (2.9 µm long). **Cephalic setae** are 7.1 µm long. **Amphidal setae** are two pairs in two longitudinal subdorsal rows (5.9 µm long). **Somatic setae** are about 5.3 µm long). Stoma is relatively spacious and armamented with three teeth. **Pharynx** is cylindrical (109.4 µm), posteriorly swollen to form the round terminal bulb. **Spermatozoa** are oval and relatively large (*l*, 18.8 µm; *w*, 11.8 µm). **Spicules** are typical shape, 30.6 µm long in the outer arc length. **Tail** is gradually tapered and becomes filiform, representing 35.5% of body lenth.



Diagnosis; *Acantholaimus* sp. 19 is characterised by small body, conspicuous lateral differentiation, broad pharynx compare to its body. This species is similar to *A. spinicauda* (Vitiello, 1970) in size and numerical characteristics, especially to the one (Male 1) described by Vivier (1985). The difference is the lateral differentiation that could found in our specimen and I consider them as different species.

Fig. 6.10 *A.* sp. 19. A, δ_1 anterior end; B, posterior end; C, spicules; D, testis and spermatozoa; E, total view.

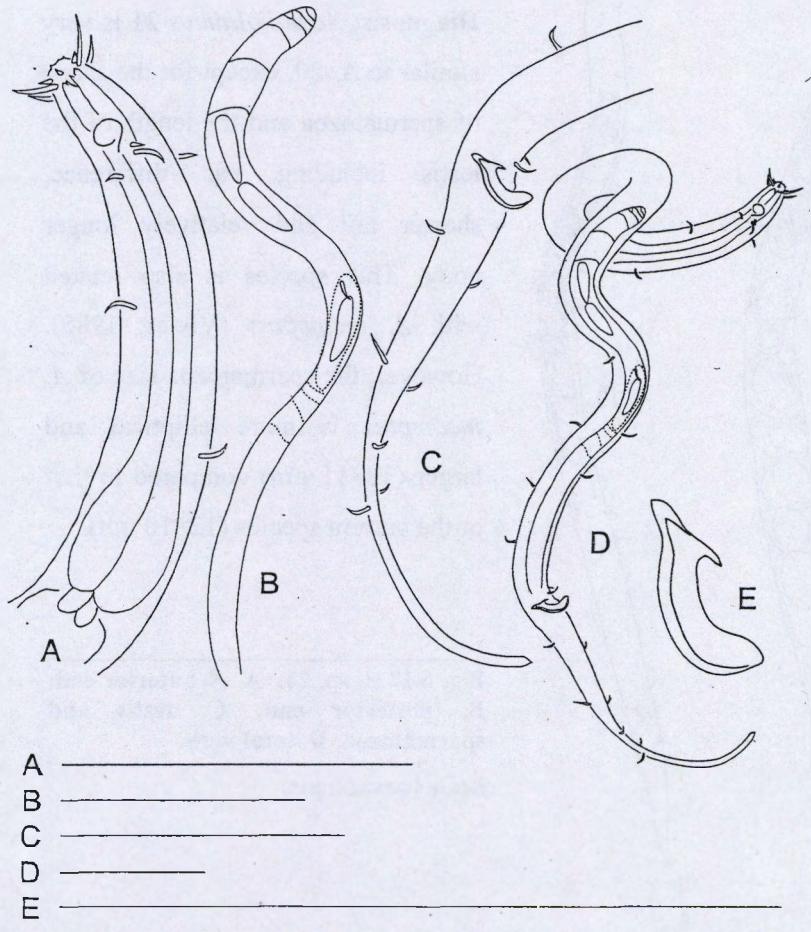
Scale bars: 50 µm.

***Acantholaimus* sp. 20 (n. sp.)**

Holotype: A-0408-10 (δ_1), from st. K4

$$\delta_1 = \frac{-\quad 79 \quad M \quad 313}{6 \quad 13 \quad 14 \quad 11} \quad 416.5\,\mu m;\ a = 30.8;\ b = 5.3;\ c = 4.0$$

Description; Small nematode. **Cuticular** punctations is almost not visible. No conspicuous lateral differentiation is observed through out the body. **Amphids** are round and rather small (*l*, 2.9 µm; *w*, 3.5 µm; 37.5% corresponding body diameter), located at 9.4 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are also papilliform. **Cephalic setae** are 7.1 µm long. **Amphidal setae** are probably two pairs in two longitudinal rows (4.7 µm long). **Somatic setae** are scarce and 4.7 µm long. Stoma is small, armamented with small teeth. **Pharynx** is cylindrical (79 µm long), posteriorly expanded to form an elongated oval terminal bulb. **Spermatozoa** are elongated oval in shape (*l*, 14.1 µm; *w*, 3.5 µm). **Spicules** are typical shape, 15.3 µm long in the outer arc length. **Tail** is conico-cylindrical and becomes filiform, representing 24.9% of body length.



Diagnosis; *Acantholaimus* sp. 20 is characterised by small body, small amphids that are located relatively posteriorly, elongated oval spermatozoa, rather short tail. This species is very similar to *A. incomptus* (Vivier, 1985) in most characteristics. However, the current species has longer spermatozoa and longer conical part of tail than *A. incomptus*.

Fig. 6.11 *A.* sp. 20. A, δ_1 anterior end; B, testis and spermatozoa; C, posterior end; D, total view; E, spicule.

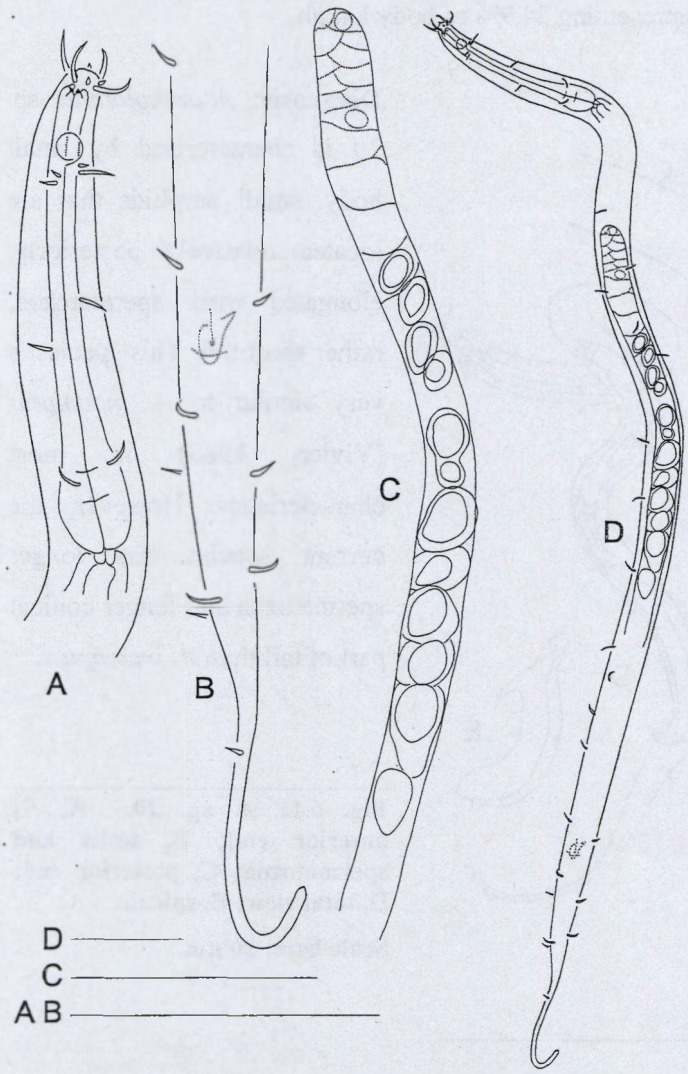
Scale bars: 50 µm.

***Acantholaimus* sp. 21 (n. sp.)**

Holotype: A-0280-1 (δ_1), from st. K7

$$\delta_1 = \frac{-\quad 79 \quad M \quad 429}{6 \quad 15 \quad 16 \quad 13} \quad 542\ \mu m;\ a = 32.9;\ b = 6.9;\ c = 4.8$$

Description; Small slender nematode. **Cuticle** is finely punctuated. No lateral differentiation is visible. **Amphids** are rather small and longitudinally elongated oval shape (*l*, 4.1 µm; *w*, 4.1 µm; 41.2% corresponding body diameter), located at 11.2 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are also papilliform. **Cephalic setae** are 7.1 µm long. **Amphidal setae** are two in two longitudinal rows and their length are various (long one, 7.1 µm long). **Somatic setae** are similar to cervical setae in length. Stoma is small, weekly armamented. **Pharynx** is cylindrical (78.8 µm), posteriorly expanded to form an oval terminal bulb. **Spermatozoa** are oval in shape (*l*, 11.8 µm; *w*, 10.0 µm). **Spicules** are typical shape. However, length could not measure due to the bad position. **Tail** is rather short, conico-cylindrical, representing 20.8% of body length.



Diagnosis; *Acantholaimus* 21 is very similar to A. 20, except for the shape of spermatozoa and the length of the testis including vas difference, shorter tail and relatively longer body. This species is also related with *A. incomptus* (Vivier, 1985). However, the spermatozoa size of *A. incomptus* is more elliptical and larger (18×11 µm) compared to that of the current species (12×10 µm).

Fig. 6.12 *A.* sp. 21. A, δ_1 anterior end; B, posterior end; C, testis and spermatozoa; D, total view.

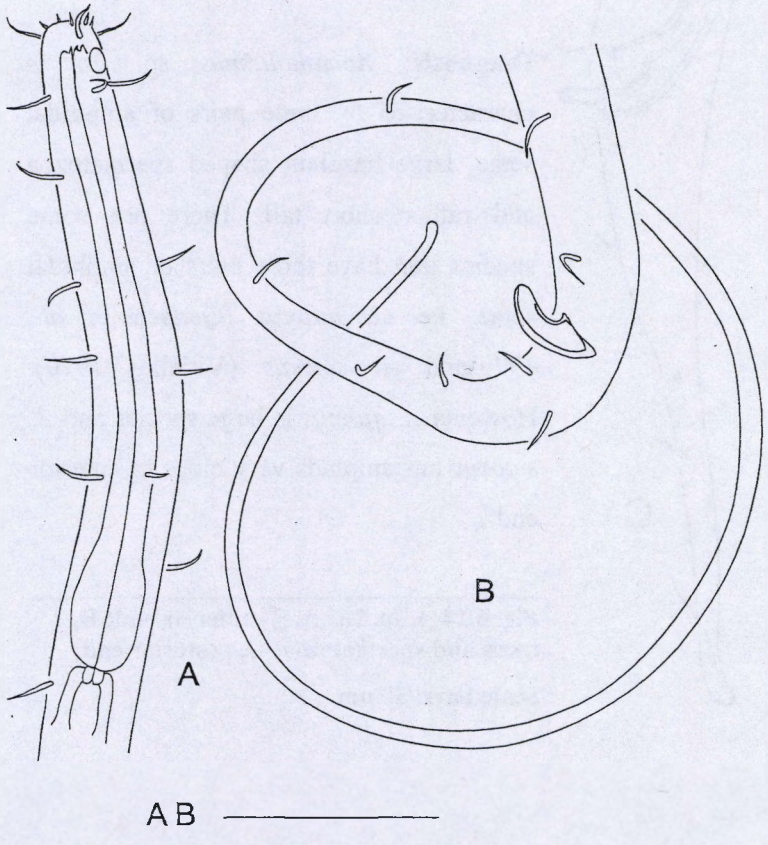
Scale bars: 50 µm.

***Acantholaimus* sp. 23 (n. sp.)**

Holotype: A-1225-2 (δ_1), from st. V2

$$\delta_1 = \frac{-}{12}\ \frac{154}{20}\ \frac{M}{21}\ \frac{665}{19}\ 1227.1\mu m;\ a = 57.9;\ b = 8.0;\ c = 2.2$$

Description; Slender nematode. **Cuticle** is finely punctuated. Lateral differentiation is present. **Amphids** are round and rather small (diameter, 5.9 μm; 40.0% corresponding body diameter), located at 12.5 μm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are also papilliform. **Cephalic setae** are 10.6 μm long. **Amphidal setae** are a pair (11.2 μm long). **Somatic setae** are more or less the same with Amphidal and cervical setae. Stoma is medium sized, armamented with three small teeth. **Pharynx** is cylindrical (154.1 μm), posteriorly it is expanded to form an oval terminal bulb. **Spermatozoa** are not piriform, but oval and rather small (*l*, 11.8 μm; *w*, 7.1 μm). **Spicules** are typical shape, 29.4 μm long in the outer arc length. **Tail** is gradually tapered and becomes filiform, representing 45.8% of body length.



Diagnosis; *Acantholaimus* sp. 23 is characterised by slender body, truncated head end, small amphids, rather long somatic setae, small oval spermatozoa. This species is somewhat related with *A. calathus* (Gerlach *et al.*, 1979) in cervical and somatic setae arrangement. However this species is much smaller and tail is longer. The size of spermatozoa is also different.

Fig. 6.13 *A.* sp. 23. A, δ_1 anterior end; B, tail and spicule.

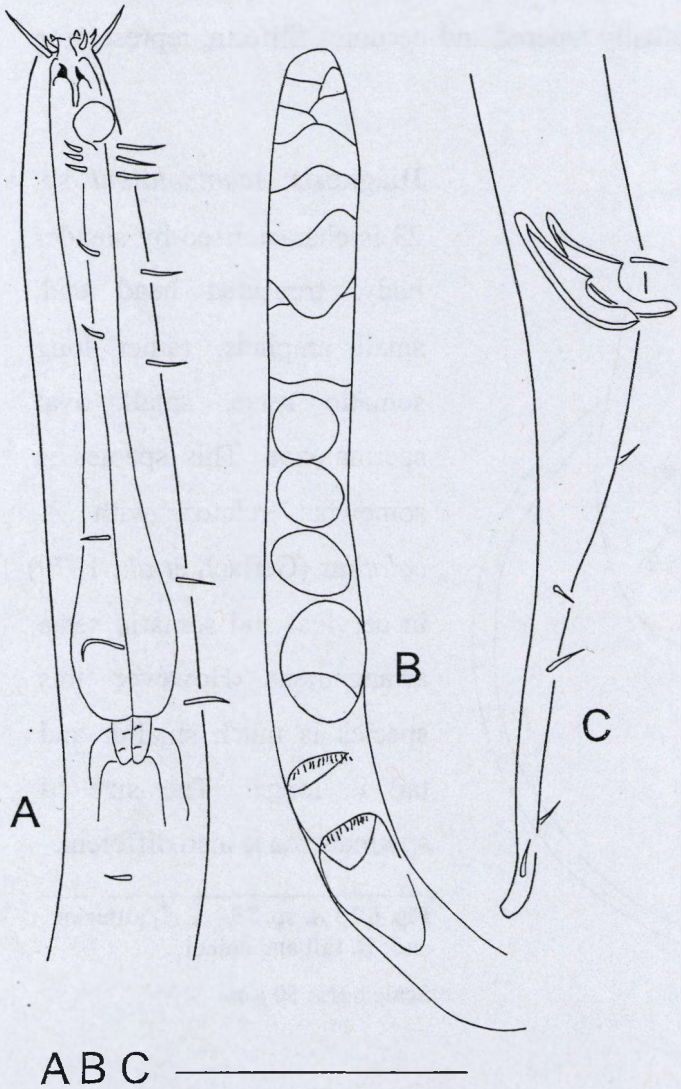
Scale bars: 50 μm.

***Acantholaimus* sp. 26 (n. sp.)**

Holotype: A-1225-2 (δ_1), from st. V2

$$\delta_1 = \frac{-}{11}\ \frac{118}{25}\ \frac{M}{26}\ \frac{648}{21}\ 755.3\,\mu m; a = 29.2; b = 6.62; c = 7.1$$

Description; Ordinarily shaped nematode. **Cuticle** is clearly punctuated, in anterior pharyngeal region, 4 rows of hypodermal pores are arranged along the both side of lateral differentiation together with cervical setae. Lateral differentiation is obvious. **Amphids** are round (*l*, 7.1 µm; *w*, 7.1 µm; 46.2% corresponding body diameter), located at 11.2 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are also papilliform. **Cephalic setae** are 8.8 µm long. **Amphidal setae** are three pairs in two longitudinal rows (7.6 µm long). **Somatic setae** are about the same length with cervical setae (7.1 µm long). Stoma is small, but armamented with three strong teeth. **Pharynx** is cylindrical (117.6 µm), posteriorly it is expanded to form an oval terminal bulb. **Spermatozoa** are large piriform (*l*, 25.9 µm; *w*, 14.1 µm). **Spicules** are typical shape, 30.6 µm long in the outer arc length. **Tail** is conico-cylindrical, rather short, representing 14.2% of body length.



Diagnosis; *Acantholaimus* sp. 26 is characterised by three pairs of amphidal setae, large hazelnut shaped spermatozoa and rather short tail. There are some species that have three pairs of amphidal setae, i.e. *A. quintus* (Gerlach *et al.*, 1979)and *A. setosus* (Vitiello, 1970). However *A. quintus* is large species and *A. setosus* has amphids very close to anterior end.

Fig. 6.14 *A.* sp. 26. A, δ_1 anterior end; B, testis and spermatozoa; C, posterior end; Scale bars: 50 µm.

***Acantholaimus* sp. 28 (n. sp.)**

Holotype: A-0408-10 (δ_1), from st. V2

$$\delta_1 = \frac{-}{8}\ \frac{153}{20}\ \frac{M}{20}\ \frac{614}{16}\ 1689.3\,\mu m;\ a = 84.5;\ b = 11.0;\ c = 1.57$$

Description; Slender nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are rather small and longitudinally elongated oval shape (*l*, 8.2 μm; *w*, 7.1 μm; 60% corresponding body diameter), located at 12.9 μm from the anterior. **Inner labial sensilla** are small papillae. **Outer labial** are setae form (5.9 μm long). **Cephalic setae** are very long (32.9 μm). **Amphidal setae** are two pairs in two longitudinal subdorsal rows (7.6 μm long). **Somatic setae** are scarce and similar with cervical setae in length (about 8 μm long). Stoma is small, teeth are sharp and long. **Pharynx** is cylindrical (109.4 μm), posteriorly it is expanded to form an elongaed oval terminal bulb, middle part is slightly narrower than other parts. **Spermatozoa** are elongated oval in shape (*l*, 24.7 μm; *w*, 7.1 μm). **Spicules** posteriorly widely inflated. **Tail** is gradually tapered, representing 63.6% of total body length.

Diagnosis; *Acantholaimus* sp. 28 is characterised by long cephalic setae, long tail. Such long cephalic setae can be found in *A. gigantasetosus* (Vivier, 1985). However *A. gigantasetosus* have longer outer labial setae and more round spermatozoa.

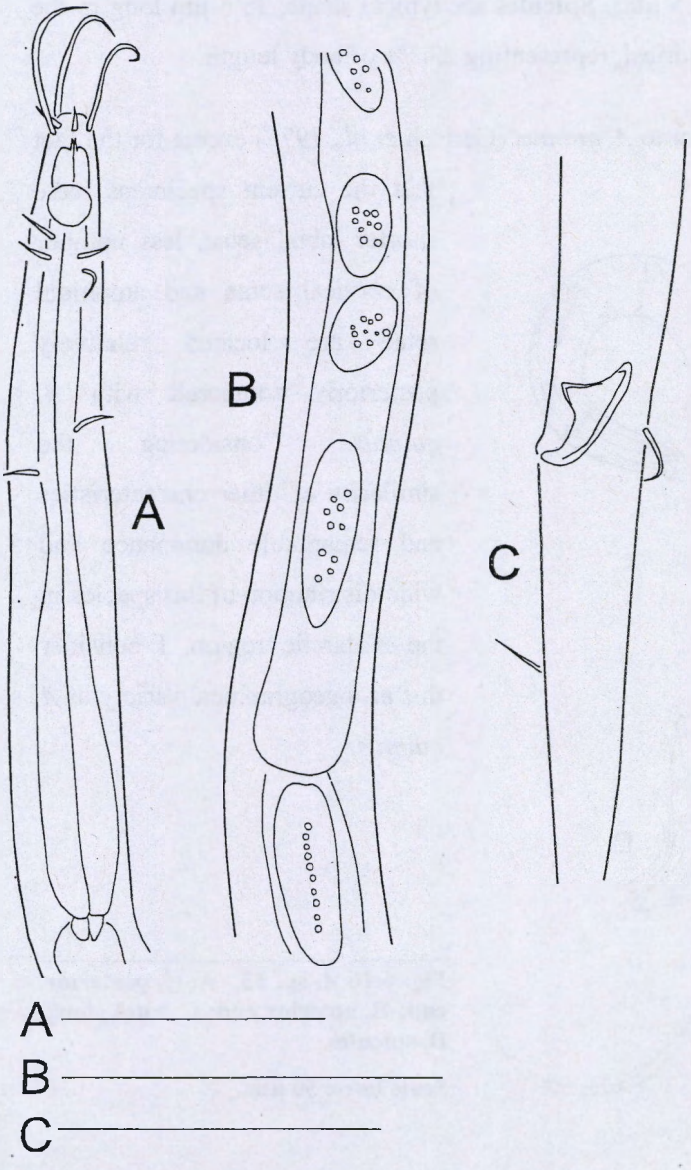


Fig. 6.15 *A.* sp. 28. A, δ_1 anterior end; B, testis and spermatozoa; C, posterior end; D, total view.

Scale bars: 50 μm.

***Acantholaimus* sp. 33 (*A. quintus*)** Fig. 6.16

Holotype: A-0002-5 (δ_1), from st. K2

$$\delta_1 = \frac{-\ 130\ \ M\ \ 741}{14\ \ 32\ \ 34\ \ 23}\ \ 965.9\,\mu m;\ a = 28.3;\ b = 7.5;\ c = 4.3$$

Description; Middle sized nematode with truncated head. **Cuticle** is punctuated. Lateral differentiation is wide longitudinal band that has larger and coarsely distributed dots. **Amphids** are round (*l*, 7.1 µm; *w*, 7.1 µm; 38.7% corresponding body diameter), located at 9.4 µm from the anterior end. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are about 3 µm long. **Cephalic setae** are 10.6 µm long. **Amphidal setae** are three pairs in two longitudinal sublateral rows (6 µm long). Cervical and **Somatic setae** are about the same length (7.6 µm). Stoma is armamented with three solid teeth. **Pharynx** is cylindrical (129.5 µm), posteriorly with oval terminal bulb. **Spermatozoa** are piriform (*l*, 29.5 µm; *w*, 11.4 µm). **Spicules** are typical shape, 35.6 µm long in the outer arc length. **Tail** is gradually conico-cylindrical, representing 23.3% of body length.

Diagnosis; *Acantholaimus* sp. 33 is very similar to *A. quintus* (Gerlach *et al.*, 1979) except for the fact that the current specimens have shorter labial setae, less number of cervical setae and amphidal setae are located relatively posteriorly compared with *A. quintus*. Considering the similarity of other characteristics and remarkable dominance and wide distribution of this species in the Antarctic region, I consider this as a geographical variety of *A. quintus*.

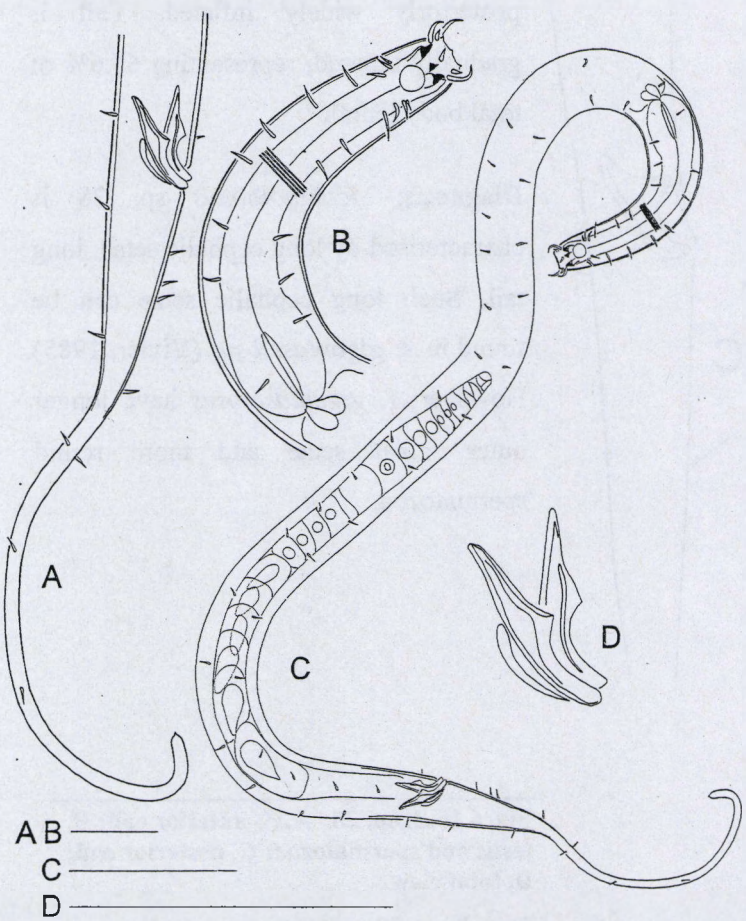


Fig. 6.16 *A.* sp. 33. A, δ_1 posterior end; B, anterior end; C, total view; D, spicules.

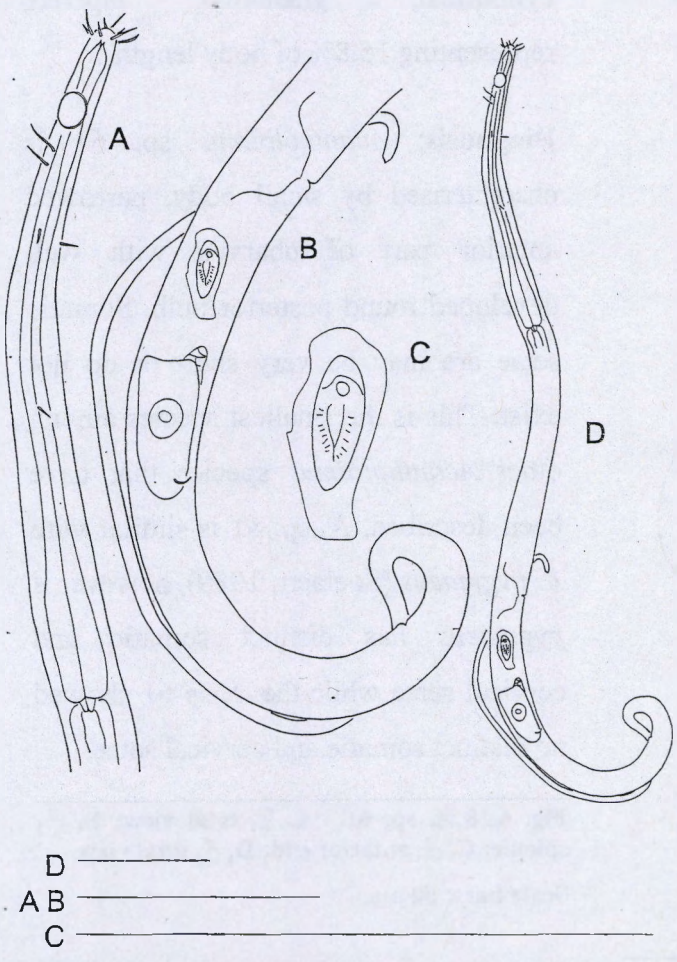
Scale bars: 50 µm.

***Acantholaimus* sp. 39 (n. sp.)**

Holotype: A-1162-1 (♀$_1$) from st.48/430; Paratype: A-1520-9 (♂$_1$) from st. 48/131

$$♀_1 = \frac{-\quad 142 \quad 280 \quad 434}{5 \quad 16 \quad 16 \quad 12} \quad 708.2\,\mu m;\ a = 43.0;\ b = 5.0;\ c = 2.6;\ V = 39.5\%$$

Description; Slender nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are large (*l*, 7.1 µm; *w*, 5.9 µm; 90.9% corresponding body diameter), located at 14.7 µm from the anterior.. **Inner labial sensilla** are small papillae. **Outer labial sensilla** are 3.5 µm long. **Cephalic setae** are 5.9 µm long. **Amphidal setae** are two in one longitudinal subdorsal row (7.1 µm long). **Somatic setae** are scarce and short (2.4 µm long). Stoma is small, weekly armamented. **Pharynx** is cylindrical (109.4 µm), posteriorly it is expanded to form an elongated oval terminal bulb. **Spermatozoa** are elongated oval in shape (*l*, 10.6 µm; *w*, 5.9 µm). **Spicules** are typical shape, 18.8 µm long in the outer arc length. **Tail** is filiform, representing 30.5% of body.



Diagnosis; *Acantholaimus* sp. 39 is characterised slender body, narrow elongated anterior pharyngeal region, two amphidal setae in one lateral row. This species is closely related with *A. verscheldi* (Muthumbi and Vincx, 1997), especially the De Man ratios and general features. The differences are that the current species is larger, amphidal setae are located in the lateral sector instead of sublateral, somatic setae are shorter and spicules seem to be different in shape.

Fig. 6.17 *A.* sp. 39. A, ♀$_1$ anterior end; B, posterior end; C, testis and spermatozoa; D, total view.

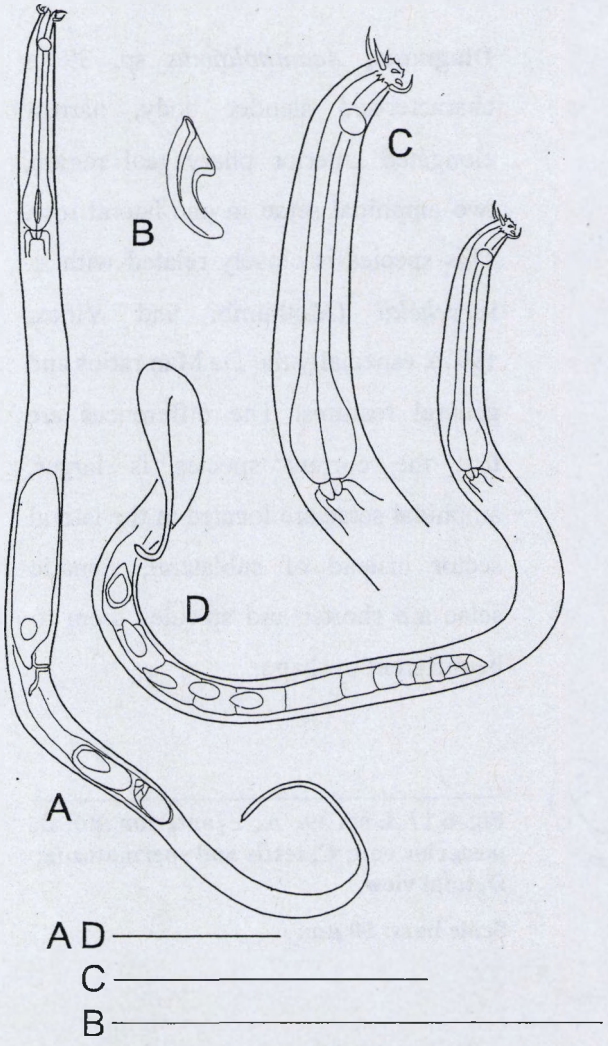
Scale bars: 50 µm.

***Acantholaimus* sp. 61 (n. sp.)**

Holotype: A-0867-8 (δ_1), from st. K1

$$\delta_1 = \frac{-}{5}\ \frac{68}{13}\ \frac{M}{13}\ \frac{302}{8}\ 363\,\mu m;\ a = 28.1;\ b = 5.3;\ c = 5.9$$

Description; Very small nematode. **Cuticle** is finely punctuated. No conspicuous lateral differentiation is observed through out the body. **Amphids** are small and transversely long (*l*, 3.5 µm; *w*, 4.1 µm; 50% corresponding body diameter), located at 8.2 µm from the anterior.. **Inner labial sensilla** are small papillae. **Outer labial** are also papilliform. **Cephalic setae** are 5.9 µm long. **Amphidal setae** are not observed. No **somatic setae** are visible. Stoma is small, weekly armamented. **Pharynx** is cylindrical (109.4 µm), posteriorly it is expanded to form an well developed oval terminal bulb. **Spermatozoa** are piriform (*l*, 12.9 µm; *w*, 7.1 µm). **Spicules** are typical shape, 14.1 µm long in the outer arc length. **Tail** is conico-cylindrical, gradually tapered, representing 16.8% of body length.



Diagnosis; *Acantholaimus* sp. 61 is characterised by small body, narrowed anterior part of pharynx with well developed round posterior bulb. Somatic setae are may be very short or do not exist. This is the smallest species among other *Acantholaimus* species that have been described. A. sp. 61 is similar with *A. pygmaeus* (Soetaert, 1989), however *A. pygmaeus* has distinct somatic and cervical setae while the *A.* sp 61 showed no distinct somatic and cervical setae.

Fig. 6.18 *A.* sp. 61. A, φ_1 total view; B, δ_1 spicule; C, δ_1 anterior end; D, δ_1 total view. Scale bars: 50 µm.

6.5. Discussion

6.5.1. Taxonomic position of *Acantholaimus*

There has been controversy on the position of Comesomatidae (see Lorenzen, 1994 for the different opinions). Lorenzen (1994), classified them as a group of Order Monhystera based on the fact that they have outstretched ovaries. On the other hand, in considering the evolutionary relationship of Comesomatidae with Monhysterida versus Chromadorida, Hope and Zhang (1995) conclude that mushroom-shaped and rod-like intracuticular punctations are character states of the same structure, and that the punctations in members of Comesomatidae are homologous with those in members of Achromadoridae, Cyatholaimidaes Ethmolaimidae, and Selachinematidae. Concerning the position of phylogenetic relationship of Acantholaimus with other nematodes, if the punctations of above nematodes are homologous, there is no reason to exclude *Acantholaimus* from those groups because this genus has punctations that are not distinguishable from that of Cyatholaimidae and Selachinematidae.

Acantholaimus is currently classified as a member of Family Chromadoridae within Order Chromadorida. This classification is based on the combination of holapomorphic characteristics: all males of Chromadoridae have a single outstretched testis and anterior gonad is always to the right and posterior one is to the left of intestine (Lorenzen, 1994). However, Wieser (1953) has reviewed on the problems of the taxonomic position of *Spiliphera* and temporally he classified as subfamily Ethmolaiminae within family Chromadoridae in order to separate this genus from other Chromadoridae genera suggesting more investigation to determine its exact status. *Spiliphera* is the most closely related nematode with *Acantholaimus* and the problem of *Spiliphera* is therefore applies to *Acantholaimus* as well.

Acantholaimus have some significant differences from other Chromadoridae genera in that that they have round amphids located far from the anterior end, conico-cylindrical tail can be very long, spermatozoa and spicules are unique, cuticular ornamentation is simple transverse rows of dots and tooth apophyses are often clearly visible.

Simple punctations and conico-cylindrical tail. Most species of *Acantholaimus* have simply punctuated cuticle and filiform tail that ends with a slightly bulbous tip. This character set is rather common in some genera of Cyatholaimidae and Selachinematidae whereas it is unique in Chromadoridae, except for *Spiliphera* that is closely related to *Acantholaimus*. The long

filiform tails are often found in many groups of nematodes and considered to be apomorphic because they are minor and do not represent the whole group they are belonging to. The fact that Acantholaimus species always have a certain degree of filiform tail implies that this group together with *Spiliphera* is probably monophyletic taxa.

Amphids. When the round amphids are concerned, I often found the nematode of which amphids are detached from the amphidal socket and unwound (Fig. 6.19). From such specimens it was observed that the amphid filaments are long and probably its original shape must be multispiral such as that of Cyatholaimidae or Selachinematidae. The difference of amphids between *Acantholaimus* and Cyatholaimidae or Selachinematidae is that the insertion of cuticle along the amphidal filaments does not occur in the case of *Acantholaimus* unlike those of Cyatholaimidae or Selachinematidae. Whether this is apomorphic or plesiomorphic character states for common multispiral amphids is unknown. However it might be proper to think that this is delivered from the common multispiral amphids rather than single spiral or slit shape of amphids that ordinary species of Chromadoridae have, because multispiral amphids are common in Chromadorid while slit like amphids are limited within Chromadoridae and even within this group simple spiral amphids can be found (*Karkinochromadora*, for instance). Therefore the simple spiral and slit like amphids in the family Chromadoridae and internal multispiral amphids of *Acantholaimus* are supposed to be evolved independently from multispiral amphids (Fig. 6.20).

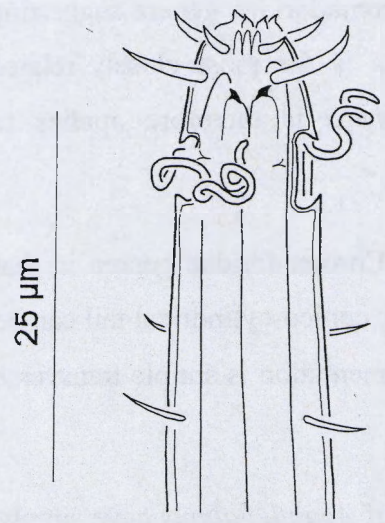


Fig. 6.19 A drawing of a specimen (*A.* sp. 42) of which amphids are detached and the amphidal corpus gelatum is uncoiled showing the evidence of multispiral form.

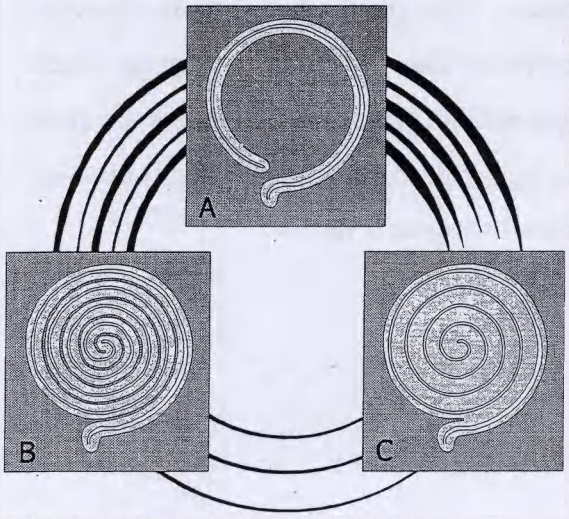


Fig. 6.20 A schematic drawing showing three different type of amphids. A, simple monospiral amphid; B, multispiral amphid; C, internal multispiral amphid. It is supposed that type C was evolved from type B rather than type A.

Buccal morphology. It is stated by Wieser (1953) that *Spiliphera* has tooth apophysis. This also can be seen from most *Acantholaimus* species especially the ones with strong buccal armament. *Acantholaimus* teeth are different from that of other Chromadoridae or Cyatholaimidae genera and seemed to have more closely related with Selachinematidae (Fig. 6.21). Cyatholaimidae and most Chromadoridae genera have hollow teeth that are originated probably from pharyngeal cuticle. In some case of Chromadoridae genera that have solid teeth seems to developed articulated teeth (*Atrochromadora*, for example). However, they never developed tooth apophysis and therefore it is unique within Selachinematidae, *Acantholaimus* and *Spiliphera*. The differences of buccal morphology between Selachinematidae and *Acantholaimus* are that *Acantholaimus* did not have strongly cuticularised vestibulum and teeth are only three. However, Acantholaimus seems to have more than three teeth, because there are cuticularised processes both side of teeth. Consequently *Acantholaimus* is distinguished from other Selachinematidae nematodes in buccal morphology, even though they must be most closely related.

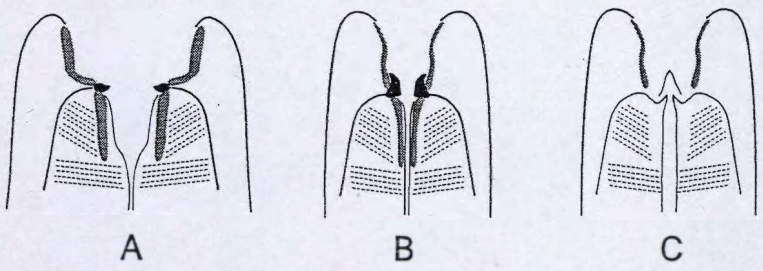


Fig. 6.21 Schematic illustrations showing phylogenetic relationship between different groups of nematode. A, typical buccal morphology of Selachinematidae; B, buccal morphology representing that of *Acantholaimus* and *Spiliphera*; C, buccal shape of Cyatholaimidae and Chromadoridae.

Considering above character status of *Acantholaimus*, this genus shares more common features with family Cyatholaimidae rather than Chromadoridae. However, this genus is still quite different from Cyatholaimidae and it has holapomorphic characteristics that is adequate to be considered as family characters. Therefore, it is suggested to separate this genus together with related genera from family Chromadoridae and establish a new family.

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