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The biodiversity and biogeography of the free-living nematode genera *Desmodora* and *Desmodorella* (family Desmodoridae) at both sides of the Scotia Arc

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Abstract Samples taken at two stations in the northern and southern parts of the Scotia Arc, at depths of 277 and 307 m, respectively, were analysed for metazoan meiofauna with special attention to the nematodes. Identification to species level was performed for two closely related subdominant nematode genera (*Desmodora* and *Desmodorella*) in samples from the two Scotia Arc stations and in other available samples from adjacent areas (Magellan Region, Drake Passage, Weddell Sea). Seven *Desmodora* species and three *Desmodorella* species were found, of which, respectively five and two species are new to science. The Scotia Arc stations show relatively high densities and average diversity on meiofauna and nematode level compared to adjacent areas. The distribution patterns of the various *Desmodora* and *Desmodorella* species suggest the Scotia Arc as a shallow bridge and a possible exchange route for meiofauna between the Antarctic and South America, especially since these species seem to be constrained by water depth.

Introduction

Separated from other continents by at least 1,000 km (South America), and surrounded by some of the deepest and coldest seas of the world, Antarctica is without doubt the most isolated continent on this planet. In Paleozoic times, however, Antarctica was part of the Gondwana supercontinent, the climate of which was considerably warmer than that of today's southern continents. Rifting between the Eastern (comprising Antarctica, Australia and India) and Western

Gondwana (comprising South America and South Africa) started in the Early Jurassic (208–178 Ma) (Crame 1999) and eventually led to the complete disconnection of South America and the Antarctic continent by means of a middle- to deep-water passage somewhere in the Oligocene epoch (23–32 Ma) (Lawver and Gahagen 2003; Thomson 2004; Barker and Burrell 1982). Further opening of the Drake Passage eventually led to a complete Antarctic Circumpolar Current (ACC) around 22–17 Ma (Barker 2001), driven by the west wind drift and further isolating Southern Ocean biota (Crame 1999).

The cold, deep waters around Antarctica, the strong ACC and the steep gradients in temperature, phytoplankton abundance, distribution of zooplankton and climatic conditions at the Antarctic Convergence contribute to the isolation of Antarctica and are therefore considered as important biological barriers (Knox 1994). These factors, along with the long period of isolation and the occurrence of succeeding glacial and interglacial periods, drove evolution, leading to the present-day diversity and biogeography (Clarke and Crame 1992; Brey et al. 1996) in which the Southern Ocean benthic fauna is characterised by endemism on different taxonomic levels (Knox 1994; Clarke and Johnston 2003). However, continuing exchange through remaining migration routes may lead to characteristic faunistic links between Antarctica and the surrounding continents. Of particular interest is the Scotia Arc, which represents the remains of the last land bridge that connected Antarctica with another continent and now comprises different archipelagos creating a unique shallow chain between Antarctica and South America.

Meiobenthos (32–1,000µm) is the most abundant eukaryotic size class in marine sediments and the small, relatively easily collectable samples of seabed sediments yield thousands of individuals of many different species. Nematodes form the most abundant taxon within the metazoan meiobenthos, usually comprising more than 90% and displaying a tremendous diversity with over 4,000 free-living marine species described worldwide (Heip et al. 1982; Lamshead 1993) and a vast number

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of undescribed species. Yet in spite of their high abundances and species diversity, and their importance in marine ecosystems (Heip et al. 1982), nematodes have received relatively little attention in Antarctic research and consequently little is known about their biodiversity and biogeography. Only a few studies have dealt with ecological and biogeographical information on Antarctic nematodes at species level (Vermeeren et al. 2004; De Mesel et al. 2006; Fonseca et al. 2006).

By identifying all species within two closely related subdominant genera (*Desmodora* and *Desmodorella*) in samples collected from the Scotia Arc and adjacent areas (Magellan Region, Drake Passage, Weddell Sea), we present information about nematode biodiversity and biogeography at the species level. The aims of this study are to: (1) investigate both local and regional biodiversity at the genus level and (2) study the distribution of species within the two subdominant genera along and at both sides of the Scotia Arc. In addition, the effect of sample-size on diversity measures is evaluated.

Materials and methods

Sampling and sampling area

During the Latin AMerican POLarstern Study (LAMPOS, from 3 April 2002 to 5 May 2002) campaign along the Scotia Arc on board of the German research vessel Polarstern (Arntz and Brey 2003), meiofauna samples were taken using a multicorer (MUC), equipped with 12 core tubes with an internal diameter of 57 mm, equivalent to a 25.5 cm² cross-sectional area. Two stations on opposite sides of the Scotia Arc were sampled: station PS61-177 (277 m depth), near South Georgia on the northern part of the Scotia Arc (NSA) and station PS61-242 (307 m depth), in the vicinity of Signy Island in the southern part of the Scotia Arc region (SSA) (Table 1, Fig. 1). The distance between the stations is ca. 960 km. Stations PS61-177 and PS61-242 are hereafter referred to as NSA 177 and SSA 242, respectively.

In addition to the two samples processed in this study, the presence of species belonging to the genera *Desmodora* and *Desmodorella* was verified in several other samples from Subantarctic and Antarctic regions in the Atlantic sector of the Southern Ocean, near Rothera on the Pacific side of the Antarctic Peninsula, and in the Ross Sea. Samples for these areas were taken with

a boxcorer or multicorer and sometimes subsampling took place (this information is integrated in Table 2). These samples were already analysed to genus level in previous unpublished and published studies (Chen 1999; H.J. Lee, unpublished; Manachini 1997; Vanhove 1997; Vermeeren 2002; Luyten 1999; Vanhove et al. 2004; Table 2).

Meiofauna and nematode analysis

At the two Scotia Arc stations, three pseudo-replicate (different cores from the same MUC deployment) sediment samples were sliced (0–1 cm, 1–3 cm, 3–5 cm, 5–10 cm) and fixed in buffered 4% formalin solution. Afterwards, the samples were passed through a 1,000- μ m mesh and then sieved on a 32- μ m mesh to retrieve the meiofauna size class, which was then resuspended and centrifuged with LUDOX HS 40% as described by Heip et al. (1985) and Vincx (1996). After staining with Rose Bengal, all metazoan meiobenthic organisms were classified at higher taxon level and counted under a stereoscopic microscope using the work of Higgins and Thiel (1988). The samples taken at the additional stations were sliced at variable sediment depths and treated similarly to the NSA 177 and SSA 242 samples prior to analysis. However, sometimes the minimum mesh width was 38 μ m instead of 32 μ m. The number of nematodes identified to genus level and the used mesh width were mentioned per station in Table 2.

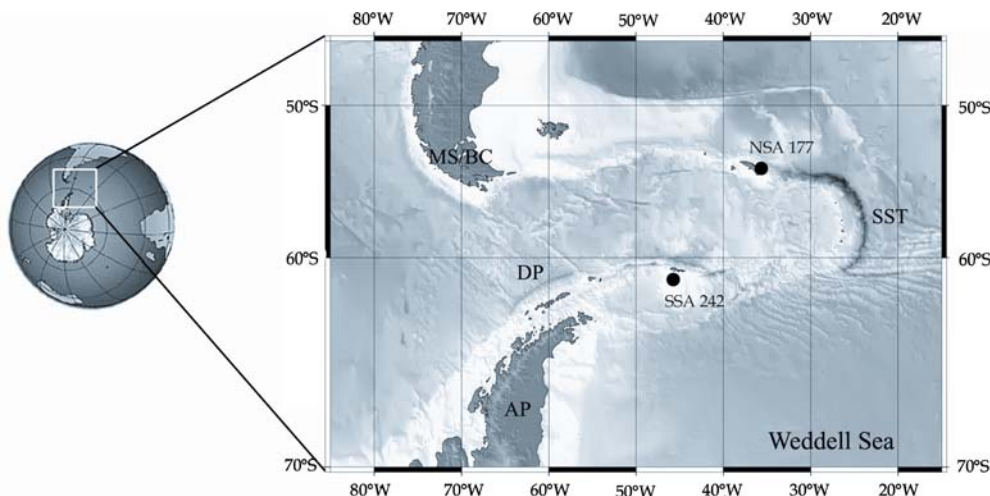
Six sets of 50 nematodes were picked out randomly from the top 0–1 cm slice of one pseudoreplicate for both Scotia Arc stations. They were transferred first to an alcohol–glycerine solution and then to glycerine and mounted on Cobb slides (Cobb 1917). The total number of nematodes identified was always lower than 300 due to, e.g., damaged specimens, juveniles. Nematodes were identified to genus level using the pictorial key to nematode genera of Platt and Warwick (1998), relevant taxonomic literature (Bussau 1993; Jensen 1978; Platt and Warwick 1998; Vermeeren et al. 2004; Verschelde et al. 1998) and reference drawings of the Department of Marine Biology of Ghent University. Identification to species level of the genera *Desmodora* and *Desmodorella* was done by comparing detailed morphological drawings (made with a camera lucida on a Leica DMLS microscope) and measurements of adult specimens with relevant literature concerning these genera in the

Table 1 Detailed information on the two Scotia Arc stations analysed in this study

Stations	Campaign	Station number	Coordinates		Sampling gear	Sediment texture
			Lat. S	Long. W		
NSA 177	LAMPOS 2002 (RV Polarstern)	PS61/177	54°25.5'	35°39'	MUC	Clay (> 10%), silt (> 85%), very fine sand (< 5%)
SSA 242	LAMPOS 2002 (RV Polarstern)	PS61/242	61°11.4'	45°46'	MUC	Clay (\approx 10%), silt (> 85%), very fine sand (< 5%)

Sediment fractions from 0.4 to 900 μ m were classified according to Wentworth (1922) and are very similar in both stations

Fig. 1 Location of the two stations: *NSA 177* (South Georgia) and *SSA 242* (Signy Island). *MS/BC* Magellan Strait/Beagle Channel; *DP* Drake Passage; *AP* Antarctic Peninsula



nematode library of Ghent University and the NeMys database (Deprez et al. 2005).

As a measure of diversity we used Hill's indices (Hill 1973) and applied them to genus level. Hill's indices or diversity numbers are variably sensitive to sample size and are commonly used to probe different aspects of the community, i.e. with increasing order they become more sensitive to dominant taxa and vice versa. Another advantage is that they are mathematically related to commonly used diversity indices such as Shannon–Wiener diversity index and Simpson's index (Heip et al. 1998; Soetaert and Heip 1990).

- N_0 = number of genera,
- $N_1 = \exp(H')$ with $H' = \text{Shannon Wiener index} = -\sum_{i=1}^n p_i \ln p_i$ and $p_i = \text{relative abundance of the } i\text{th genus}$,
- $N_2 = \frac{1}{D}$ with $D = \sum_{i=1}^n p_i^2 = \text{Simpson's index}$,
- $N_{\text{inf}} = \frac{1}{p_1}$ with $p_1 = \text{the proportional abundance of the most common genus}$.

Results

Meiofauna

Although a high diversity of major taxa was observed at both stations, the total number of taxa was higher at station NSA 177 (21 taxa) than at station SSA 242 (15 taxa). Other regularly occurring taxa, in addition to the Nematoda (ca. 90%), were harpactoid copepods and nauplii (3–5%), Kinorhyncha (ca. 1%), Polychaeta (0.8%, station NSA 177) and Ostracoda (0.6%, station SSA 242). Total meiofauna density was higher at station NSA 177 (8,804 ind./10 cm²) compared to station SSA 242 (3,409 ind./10 cm²).

At station NSA 177, nearly 40% of all meiofauna was situated in the upper centimetre of the sediment and 78.2% in the upper 3 cm. At station SSA 242, the

density decrease with increasing depth is even clearer; 55.3% and more than 90% of the meiofauna resided in the first centimetre and the upper 3 cm of the sediment, respectively. Between 5 and 10 cm depth, the total meiofauna fraction is reduced to less than 1% (Fig. 2).

Nematode diversity

Both stations are characterised by a relatively high generic nematode diversity. Hill's indices (especially N_2 and N_{inf} ; Fig. 3) showed a higher generic nematode diversity at station NSA 177. At this station, nematodes belonged to 44 different genera and 16 families, while at station SSA 242, 43 genera were found, belonging to 15 different families. The two stations have 27 genera and 13 families in common and show a similar dominance pattern (Table 3). Nine of the most abundant genera (> 1%) are common for both stations. The most abundant of these nine genera are *Microlaimus* and *Daptonema*, followed by *Monhystera*, *Desmodorella* and *Desmodora* of which the latter two belong to the family Desmodoridae. For station NSA 177 and station SSA 242, respectively 90.8% and 73.5% of the individuals that could not be identified to genus-level, almost exclusively juveniles, belonged to the family Desmodoridae (most likely to the genera *Desmodora* and *Desmodorella*), resulting in a very high Desmodoridae abundance. This observation (Table 3) provides a logical basis for choosing the genera *Desmodora* and the closely related *Desmodorella* for a more detailed biodiversity and biogeography study.

Taxonomical considerations for *Desmodora* and *Desmodorella* species

The genera *Desmodora* and *Desmodorella* have only recently been raised to the genus level. Before, the two genera were considered as subgenera within the genus *Desmodora* (Verschelde et al. 1998). The adult *Desmo-*

Table 2 Details concerning stations of which the available samples were checked for *Desmodora* and *Desmodorella* species

Region, campaign and reference	Station number	Depth (m)	Coordinates		Gear	Nematode density (ind./10 cm ²)/n _g .	Desmodoridae abundance (%)
			Lat. S	Long. W			
MS	1-818	8	53°03'	70°17'	MUC ^{a,c}	1,425/249	0
Magellan Campaign 1994 (RV Victor Hensen)	2-840	123	53°09'	70°38'	MUC ^{a,c}	980/219	15.6
Chen (1999)	3-846	195	53°22'	70°43'	MUC ^{a,c}	1,664/266	2.3
	4-864	550	53°43'	70°49'	MUC ^{a,c}	2,038/238	1.7
	5-866	440	53°42'	70°55'	MUC ^{a,c}	1,368/218	0.3
	6-872	351	53°43'	70°56'	MUC ^{a,c}	1,887/205	5.8
	7-877	227	53°42'	70°57'	MUC ^{a,c}	3,138/277	9.6
	8-954	79	53°00'	70°33'	MUC ^{a,c}	1,568/223	7.1
	9-956	80	53°00'	70°33'	MUC ^{a,c}	1,030/84	2.4
	10-971	90	53°29'	70°22'	MUC ^{a,c}	1,475/-	-
	11-977	459	53°33'	70°39'	MUC ^{a,c}	2,498/289	0
BC	12-1033	309	54°53'	69°55'	MUC ^{a,c}	2,418/193	7.1
Magellan Campaign 1994 (RV Victor Hensen)	13-1076	346	54°54'	69°30'	MUC ^{a,c}	3,548/266	0
Chen (1999)	14-1123	219	54°59'	69°02'	MUC ^{a,c}	3,692/227	12.1
	15-1135	257	54°55'	68°50'	MUC ^{a,c}	2,246/243	6.1
	16-1139	255	54°55'	68°39'	MUC ^{a,c}	4,427/-	-
	17-1144	110	55°08'	66°55'	MUC ^{a,c}	5,582/425	0.3
	18-1159	32	55°08'	67°02'	MUC ^{a,c}	2,536/-	-
	19-1181	110	55°07'	66°55'	MUC ^{a,c}	5,100/427	1
	20-1234	100	55°00'	66°54'	MUC ^{a,c}	8,552/327	3.8
South Georgia Island (NSA) LAMPOS 2002 (RV Polarstern)	PS61/177	277	54°25'	35°39'	MUC ^b	8,804/208	35.2
SST	21-199	747	57°38'	26°28'	MG ^{a,b}	932/150	24.15
LAMPOS 2002 (RV Polarstern) Vermeeren (2002) Vanhove et al. (2004)	22-211	1095	57°36'	26°24'	MUC ^b	4,272/150	13.01
SST	23-139	3981	58°15'	24°21'	MUC ^b	1,319/150	3.42
ANDEEP 2 2002 (RV Polarstern)	24-140	2949	58°16'	24°54'	MUC ^b	2,180/150	4.34
Vermeeren (2002) Vanhove et al. (2004)	25-141	2285	58°25'	25°00'	MUC ^b	1,776/150	11.75
	26-142	6319	58°51'	23°59'	MUC ^b	1,569/150	4.19
Signy Island (SSA) LAMPOS 2002 (RV Polarstern)	PS61/242	307	61°11'	45°45'	MUC ^b	3,409/199	25.7
DP	27-48/299	207	62°16'	58°43'	MG ^{a,b}	4,268/963	14.3
EASIZ 2 1998 (RV Polarstern)	28-48/300	423	62°17'	58°42'	MG ^{a,b}	2,872/923	8.3
H.J. Lee (unpublished)	29-48/330	2009	61°21'	58°15'	MG ^{a,b}	574/628	0.5
	30-48/334	1028	61°27'	58°07'	MG ^{a,b}	1,928/959	5.4
	31-48/341	429	61°35'	58°07'	MG ^{a,b}	3,268/905	4.5
	32-48/345	218	61°35'	59°07'	MG ^{a,b}	3,494/880	6.7
Rothera Summer visit 1998	33-N. Cove	31	67°34'	68°08'	PC ^c	2,250/277	7.9
Luyten (1999)	34-N. Cove	11	67°34'	68°08'	PC ^c	13,042/205	2.4
	35-Gr. Pipe	5	67°34'	68°08'	PC ^c	677/193	13.1
KN	36-48/047	243	70°52'	10°29'	MG ^{a,b}	2,120/857	12.4
EASIZ 2 1998 (RV Polarstern)	37-48/187	255	71°32'	13°32'	MG ^{a,b}	1,316/783	2.2
H.J. Lee (unpublished)	38-48/225	278	70°50'	10°35'	MG ^{a,b}	123/218	0
	39-48/227	332	70°50'	10°39'	MG ^{a,b}	1,775/885	5.8
	40-48/228	298	70°50'	10°38'	MG ^{a,b}	1,348/954	2.2
KN	41-14/274	211	71°37'	12°11'	MG ^{a,c}	2,721/181	10.3
EPOS 1989 (RV Polarstern)	42-14/277	405	71°40'	12°35'	MG ^{a,c}	2,507/194	18.7
Vanhove (1997)	43-14/278	537	71°29'	12°32'	MG ^{a,c}	4,151/162	17.3
	44-14/292	561	71°04'	12°42'	MG ^{a,c}	949/136	10.7
	45-14/294	1199	71°06'	13°04'	MUC ^{a,c}	818/183	28.4
	46-14/295	2080	71°08'	13°48'	MUC ^{a,c}	1,064/180	2.4
KN	47-D002a	182	71°20'	12°25'	MG ^{a,b}	578/1111	1.5
EASIZ 1 1996 (RV Polarstern)	48-D005c	216	71°40'	12°47'	MG ^{a,b}	3,285/917	2.9
H.J. Lee (unpublished)							

Table 2 (Contd.)

Region, campaign and reference	Station number	Depth (m)	Coordinates		Gear	Nematode density (ind./10 cm ²)/n _g	Desmodoridae abundance (%)
			Lat. S	Long. W			
HB	49-14/226	582	75°16'	25°49'	MUC ^{a,c}	2,138/172	6.1
EPOS 1989 (RV Polarstern)	50-14/229	502	75°14'	26°15'	MUC ^{a,c}	2,114/170	5
Vanhove (1997)	51-14/230	247	75°13'	26°59'	MG ^{a,c}	1,784/179	3.6
	52-14/235	399	75°11'	27°35'	MUC ^{a,c}	3,122/185	4.3
	53-14/241	458	75°06'	28°00'	MUC ^{a,c}	2,424/179	7
	54-14/245	492	74°40'	29°42'	MUC ^{a,c}	1,524/164	6.1
	55-14/248	633	74°38'	29°40'	MUC ^{a,c}	842/171	10.9
	56-14/249	681	74°37'	29°42'	MUC ^{*a,c}	794/171	2.3
	57-14/250	806	74°35'	29°40'	MUC ^{a,c}	1,020/164	15.6
	58-14/252	1183	74°32'	29°18'	MUC ^{a,c}	1,429/170	11.5
	59-14/253	1958	74°08'	30°40'	MG ^{a,c}	1,402/185	7.6
VK	60-48/092	993	73°34'	22°38'	MG ^{a,c}	1,947/904	13.4
EASIZ 2 1998 (RV Polarstern)	61-48/131	1944	73°24'	22°49'	MG ^{a,c}	1,138/833	1.2
H.J. Lee (unpublished)							
VK	62-E022	220	73°29'	20°41'	MG ^{a,b}	1,293/811	6
EASIZ 1 1996 (RV Polarstern)	63-B	570	74°00'	175°00'	BC ^c	1,463/690	12.3
H.J. Lee (unpublished)							
RS	64-C	460	72°30'	175°00'	BC ^c	230/408	1.1
ROSS-MIZE (RV Italica)							
Manachini (1997)							

MS Magellan Strait; BC Beagle Channel; SST South Sandwich Trench; DP Drake Passage; KN Kapp Norvegia; HB Halley Bay; VK Vestkapp; RS Ross Sea

Nematode density (n_g) stands for number of nematodes identified to genus level

Gear: MUC multiple corer, 12 core tubes with 57 mm internal diameter; MG multiple box corer, 9 individual boxes, 240 cm² each; PC push cores with 3.6 cm diameter; BC USNEL box corer

^a Subsampling took place

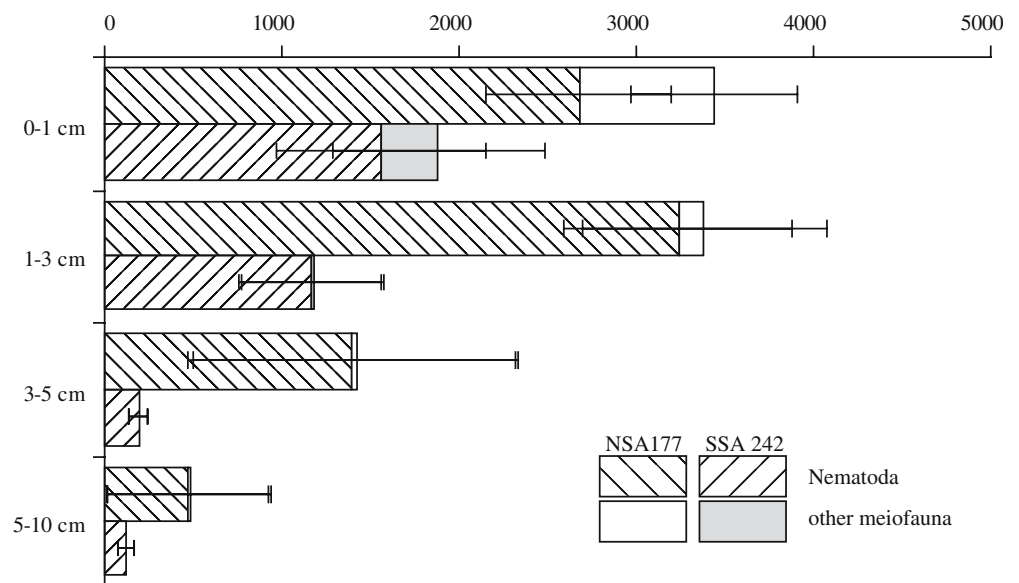
^b Minimum mesh width of 32 µm

^c Minimum mesh width of 38 µm

dora specimens encountered at stations NSA 177 and SSA 242 are identified as *Desmodora campbelli* Allgén, 1932 due to the characteristic morphology of the head, setae, cuticle and the structure of the spicules and the precloacal supplements of the males (Fig. 4f, g). Although *D. campbelli* bears the genus name *Desmodora*,

its characteristics are not fully consistent with the genus description according to Verschelde et al. (1998) and Pastor de Ward (1988); *D. campbelli* carries subcephalic setae like all *Desmodora* species, excluding it from *Pseudochromadora* which does not possess such setae, but it is also equipped with lateral alae on the cuticle, a

Fig. 2 Vertical gradient of meiofauna and nematode abundances (ind./10 cm² with st. dev.) for stations NSA177 and SSA242



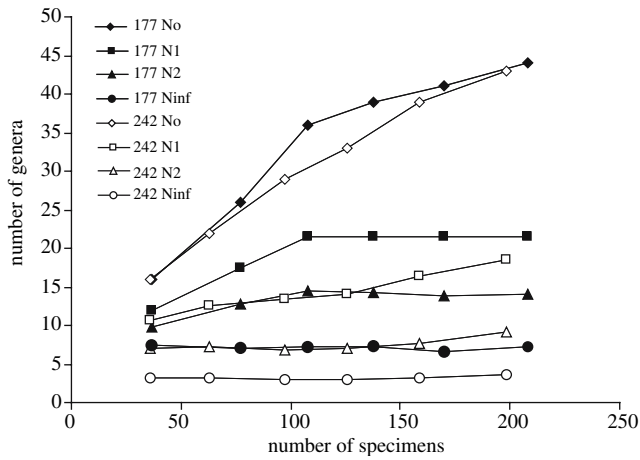


Fig. 3 Rarefaction curves of Hill's diversity indices for both Scotia Arc stations and for various sample sizes. Based on nematode specimens identified to genus level ($n_{g177} = 208$, $n_{g242} = 199$)

typical characteristic for the genus *Pseudochromadora*. Because of these conflicting characteristics, Verschelde et al. (1998) regarded this species as *incertae sedis*. For convenience, we continue to refer to it as *D. campbelli*.

Five new *Desmodora* species (sp. A, sp. B, sp. C, sp. D, sp. E) (Fig. 4a–e) could be distinguished. *Desmodora* sp. A and *Desmodora* sp. B are morphologically very similar and differentiated from the other *Desmodora* species, mainly by their body shape and small size. *Desmodora* sp. C shows an affinity with *Desmodora* sp. D and *Desmodora* sp. E but does not appear to have the numerous denticles in the buccal cavity and the distinct longitudinal rows of short, stout somatic setae

which characterise these species. There is a striking similarity between *Desmodora* sp. D and *Desmodora* sp. E which could only be distinguished from each other by the long somatic setae in the tail region (present with *Desmodora* sp. D) and the number of amphid turns.

The adult *Desmodorella* specimens from stations NSA 177 and SSA 242 are identified as *Desmodorella* aff. *balteata* (After *Desmodorella balteata* Verschelde, Gourbault and Vincx 1998) (Fig. 5c). They are distinguished from *Desmodorella tenuispiculum* (Allg n 1928) by the dimensions of the amphid and tail morphology and show striking resemblance with *D. balteata*. Yet, small variations in morphological characteristics (stoutness of precloacal setae, amphid dimensions) are observed. These are, however, not obtrusive enough to classify the specimens as new species. Interesting is the presence of cuticular rings which did not originate from the animal itself, resembling the trapping rings of nematophagous fungi (Barron 1977) and the presence of small Suctorina attached to the cuticle as was observed by Verschelde et al. (1998). However, these rings are not encountered not only with *Desmodorella* and are therefore unlikely to be species-specific.

In addition to *Desmodorella* aff. *balteata*, two new *Desmodorella* species (sp. A, sp. B) (Fig. 5a, b) occurred in the samples. *Desmodorella* sp. A has an amphid coiling only 1.5 times (vs. 2.6 turns with *D. balteata*) and the males have extremely long spicules, clearly distinguishing them from *D. balteata*. The body morphology, head structures and conspicuously long spicules of this species resemble the characteristics of *Desmodorella filispiculum* Lorenzen 1976 (description based on specimens from

Table 3 List of the most abundant (> 1%) nematode genera (totalling ca. 60% of the nematode communities) together with their abundances (%) based on total number of identified nematodes (n) for stations 177 and 242

Sta. NSA 177 ($n = 284$, $n_g = 208$)		Sta. SSA 242 ($n = 268$, $n_g = 199$)	
Genus	Abundance (%)	Genus	Abundance (%)
Fam. Desmodoridae	24.30	<i>Microlaimus</i>	21.35
<i>Daptonema</i>	10.21	Fam. Desmodoridae	18.66
<i>Microlaimus</i>	10.21	<i>Daptonema</i>	7.12
<i>Paranticoma</i>	5.99	<i>Monhystera</i>	6.74
<i>Actinonema</i>	5.63	<i>Desmodorella</i>	4.49
<i>Desmodorella</i>	5.63	<i>Halalaimus</i>	2.25
<i>Monhystera</i>	5.63	<i>Calomicrolaimus</i>	2.25
<i>Desmodora</i>	3.87	<i>Metadesmolaimus</i>	2.25
<i>Halalaimus</i>	2.82	<i>Leptolaimus</i>	2.25
<i>Dichromadora</i>	2.46	<i>Paramonohystera</i>	2.25
<i>Desmoscolex</i>	1.41	<i>Actinonema</i>	1.87
<i>Euchromadora</i>	1.41	<i>Desmodora</i>	1.87
<i>Anticoma</i>	1.06	<i>Acantholaimus</i>	1.87
<i>Calomicrolaimus</i>	1.06	<i>Dichromadora</i>	1.50
<i>Chromadorita</i>	1.06	<i>Campylaimus</i>	1.50
<i>Rhps</i>	1.06	<i>Ammotheristus</i>	1.12
<i>Trochamus</i>	1.06	<i>Chromadorina</i>	1.12
		<i>Eleutherolaimus</i>	1.12

n total number of identified nematodes per station, including problematic specimens (juveniles, damaged, etc.) not identified to genus level; n_g total number of identified nematodes to genus level; Fam. *Desmodoridae* the specimens not identified to genus level but belonging to the family Desmodoridae

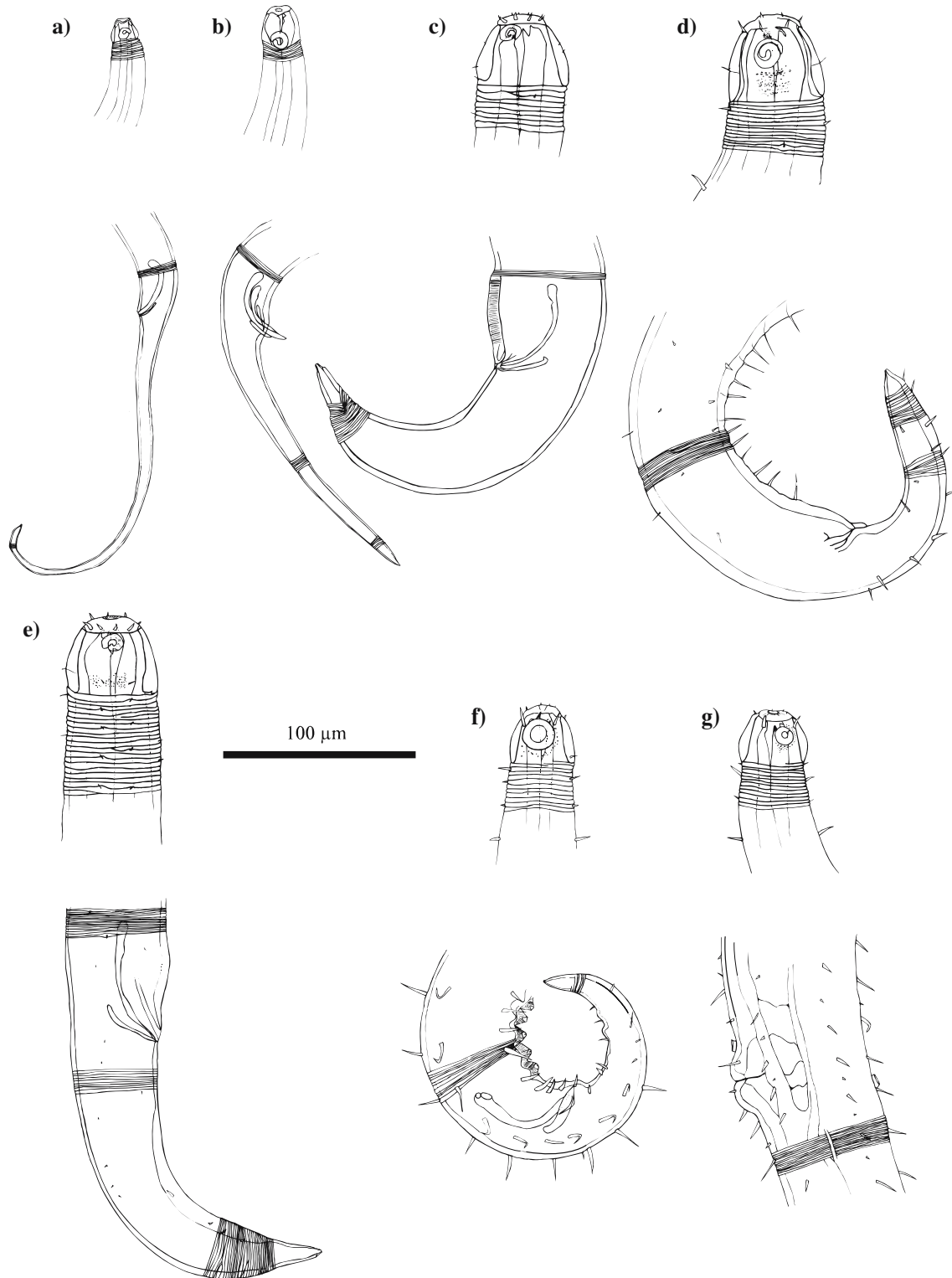


Fig. 4 Morphological drawings of the cephalic region and the tail (with spicules when male specimens were available) of *Desmodora* species: (a) *Desmodora* sp. A (♂), (b) *Desmodora* sp. B (♂), (c) *Desmodora* sp. C (♂), (d) *Desmodora* sp. D (♀), (e) *Desmodora* sp. E

(♂), (f) *Desmodora campbelli* (♂) (note the preloacal supplements), (g) *Desmodora campbelli* (♀) (drawing of the vulva region instead of the tail; note the lateral alae)

Southern Chile). However, *Desmodorella* sp. A has less regular and smaller somatic setae, a shorter and narrower, conical-shaped tail and the males are equipped

with a row of short preloacal setae. *Desmodorella* sp. B was characterised by a long and slender body shape, a spiral amphid (1.5 turn) and a relatively large tail.

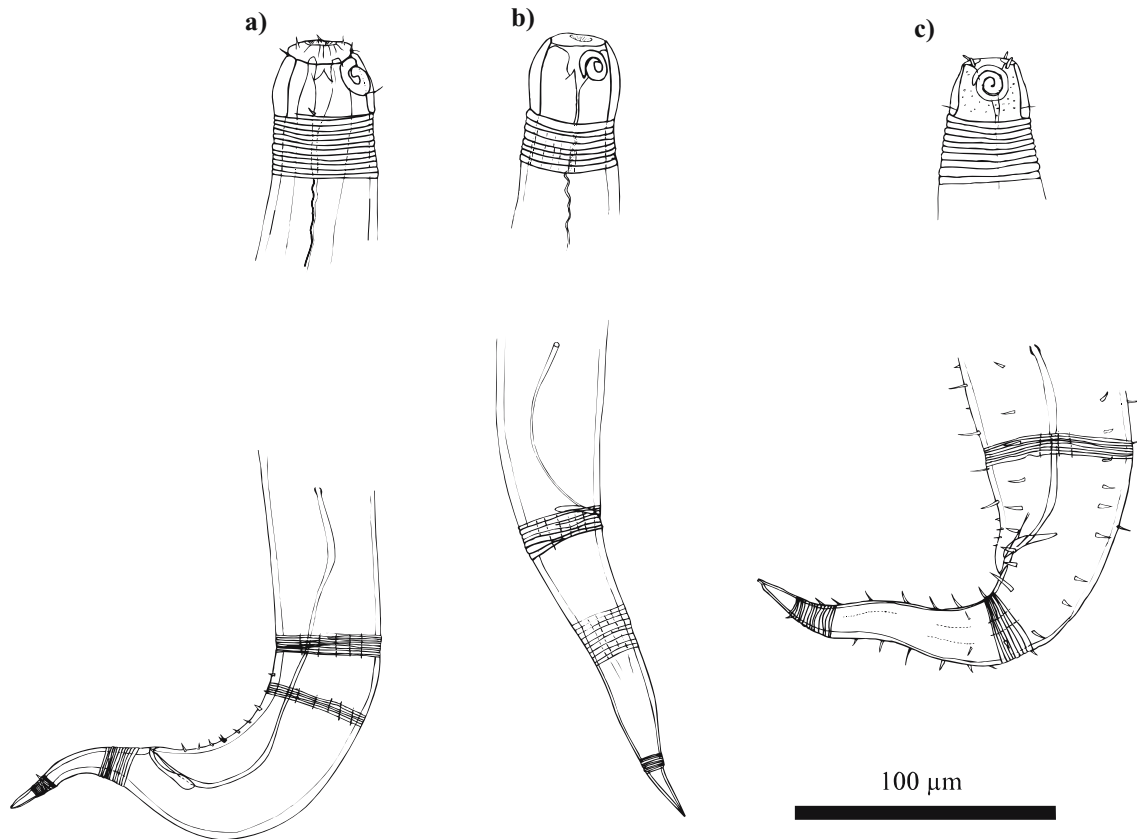


Fig. 5 Morphological drawings of the cephalic region and the tail of *Desmodorella* species: (a) *Desmodorella* sp. A (♂) (note the long spicules), (b) *Desmodorella* sp. B (♂), (c) *Desmodorella* aff. *balteata* (♂)

Biogeography of *Desmodora* and *Desmodorella*

From the 64 Antarctic and Magellanic stations analysed, 25 stations were characterised by the presence of the genera *Desmodora* and/or *Desmodorella* (Table 4). In total, ten different species were identified: seven *Desmodora* species and three *Desmodorella* species. Fifteen out of the 25 stations contained only one species of *Desmodora* or *Desmodorella* while the maximum number of species per station was three. The stations NSA 177 and SSA 242 were each characterised by two species: *Desmodora campbelli* (type material from Campbell island, ca. 700 km South of New Zealand, Pacific) and *Desmodorella* aff. *balteata* (similar to *D. balteata* which was described based on specimens from hydrothermal vents in the East Pacific Rise, Guyamas, at 2,000 m depth). These two species were each present in 12 of the 25 stations while the other species were restricted to 1 or 2 stations.

At station NSA 177, 11 adult specimens (5 males, 6 females) belonged to the species *D. campbelli* and 8 adult *Desmodorella* aff. *balteata* specimens (5 males, 3 females) were found. At station SSA 242, 5 adult specimens (3 males, 2 females) belonged to the species *D. campbelli* and 2 adult females were classified as *Desmodorella* aff. *balteata*.


Desmodora campbelli is relatively widely spread over the shallowest stations (100–405 m) investigated and was completely absent in the deeper samples, including the South Sandwich Trench, Drake Passage and Ross Sea. *Desmodorella* aff. *balteata* was present in all areas (even the Ross Sea) except for the South Sandwich Trench and the Magellan Region. The maximum depth observed for *Desmodorella* aff. *balteata* was 1,028 m in the Drake Passage. *Desmodora* sp. A, sp. B and sp. C were only observed in the South Sandwich Trench samples at depths between 747 and 6,315 m, while only *Desmodora* sp. D was found in the Weddell Sea as well as in the South Sandwich Trench. *Desmodora* sp. E, *Desmodorella* sp. A and *Desmodorella* sp. B are characteristic for the Weddell Sea. Finally, *Desmodora minuta* Wieser 1954 was found in the Magellan region. Distribution patterns are given in Table 4 and Fig. 6.

Discussion

Scotia Arc meiofauna

Antarctic benthic fauna is characterised by a high diversity which has been formed under the influence of the combined effects of speciation and extinction, abiotic

Table 4 Overview of the distribution of adult *Desmodora* and *Desmodorella* species

Region	N  S																									
	South America					Scotia Arc					DP	Weddell Sea					S									
	MS	BC				NSA	SST				SSA	DP	KN					HB					VK	RS		
Station number	2	14	15	19	20	177	21	23	24	26	242	30	36	37	39	41	42	48	50	52	53	55	56	62	63	
Depth (m)	123	219	257	110	100	277	747	3981	3000	6315	307	1028	243	255	332	211	405	216	502	399	458	633	681	220	570	
Adult/ Juvenile																										
<i>Desmodora</i> & <i>Desmodorella</i>	2/3	3/4	1/-	1/-	4/2	19/77	1/4	1/-	2/3	2/3	7/60	1/4	8/15	1/2	4/8	3/21	6/26	2/19	2/5	1/4	3/1	2/-	2/2	7/24	2/4	
<i>Desmodora minuta</i>	1																									
<i>Desmodora campbelli</i>	1	3	1	1	4	11					5		2		1		5	1	2							
<i>Desmodora</i> sp. A									1																	
<i>Desmodora</i> sp. B									1	2																
<i>Desmodora</i> sp. C							1																			
<i>Desmodora</i> sp. D									1						1											
<i>Desmodora</i> sp. E																1						2				
<i>Desmodorella</i> aff. <i>balteata</i>						8					2	1		1	2		1	1		1	3		2	7	2	
<i>Desmodorella</i> sp. A													6													
<i>Desmodorella</i> sp. B																2										

MS Magellan Strait; BC Beagle Channel; NSA northern Scotia Arc; SST South Sandwich Trench; SSA southern Scotia Arc; DP Drake Passage; KN Kapp Norvegia in the Weddell Sea; HB Halley Bay in the Weddell Sea; VK Vestkapp; RS Ross Sea

environmental conditions and biotic interactions (Arntz et al. 1994, 1997; Brey et al. 1994, 1996; Clark and Crame 1992). The metazoan meiofauna is a prominent member of the Antarctic benthic fauna as indicated by Heip et al. (1982). However, this group remains less studied in polar regions compared to macrofauna. Moreover, little is known about their biodiversity in the Antarctic.

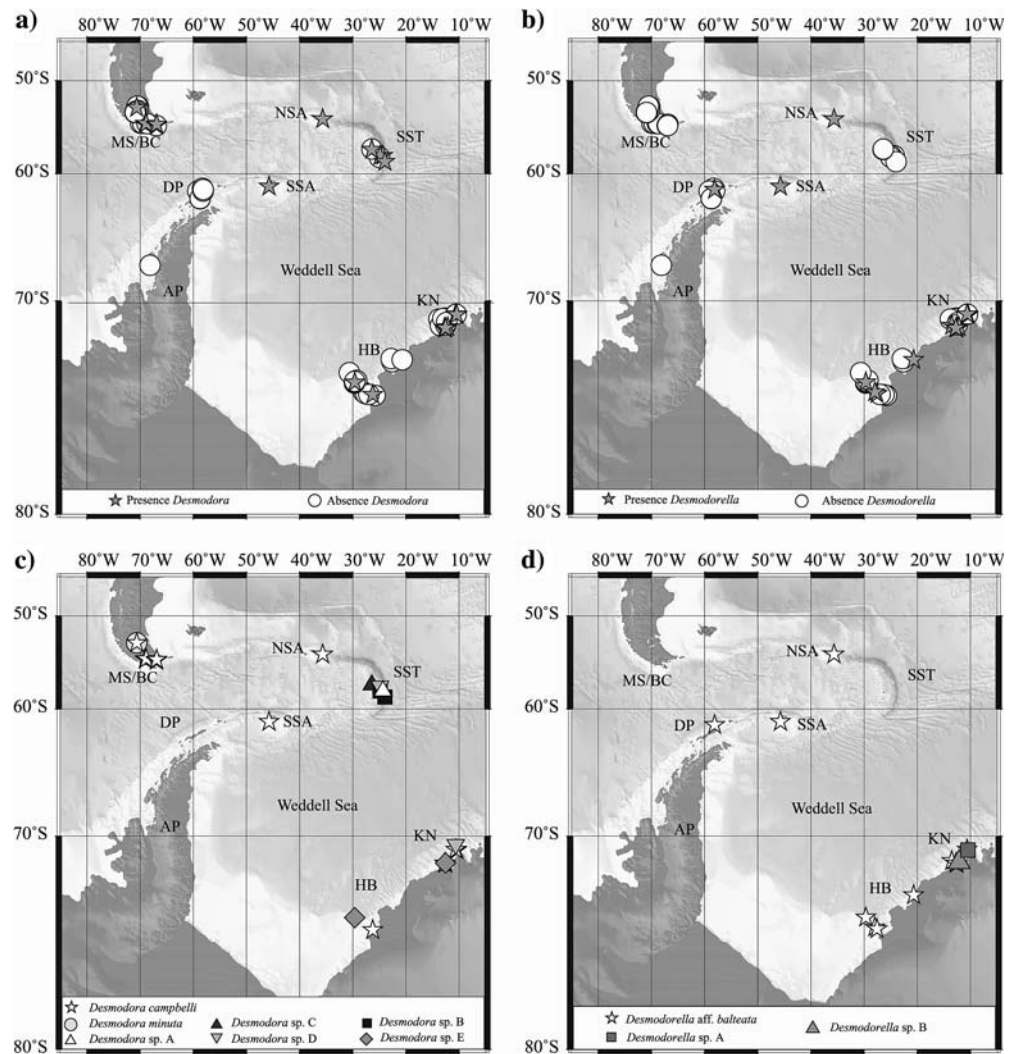
For stations NSA 177 and SSA 242, respectively 21 and 15 (total 22) higher meiofauna taxa were found, showing a high but not exceptional diversity compared to what was found in previous studies in the Atlantic sector of the Southern Ocean (Herman and Dahms 1992; Vanhove 1997; Vanhove et al. 1995, 1998, 1999, 2000, 2004). In the two stations studied, meiofauna densities were higher (8,804 ind./ 10 cm² for NSA 177 and 3,409 ind./ 10 cm² for SSA 242) than in other oceans at comparable depths (Soltwedel 2000). The previous Antarctic studies mentioned above demonstrated that meiofauna can be very abundant in the Southern Ocean. This might be a consequence of the

very high Antarctic primary production during the short but intensive summer bloom (Bathman et al. 1991; von Bodungen et al. 1986; von Bröckel 1985; Figueiras et al. 1998; Korb and Whitehouse 2004; Vanhove et al. 1995). The results show that densities decrease fast with increasing sediment depth (down to 1% between 5 and 10 cm depth), illustrating the importance of the topmost sediment layer. The spatial distribution of meiobenthos within the sediment shows a classic vertical decreasing pattern, and corresponds with a similar trend in food availability.

Scotia Arc nematodes

The nematode community of the two stations studied is dominated by the genera *Microlaimus* and *Daptonema*, followed by *Monhystera*, *Desmodorella* and *Desmodora*. The first three genera are similarly dominant in other oceans, across comparable depth ranges, whilst the latter two are much less abundant in oceans all over the world

Fig. 6 Distribution of (a) genus *Desmodora*, (b) genus *Desmodorella*, (c) *Desmodora* species, (d) *Desmodorella* species. *MS/BC* Magellan Strait/Beagle Channel; *DP* Drake Passage; *NSA* Northern Scotia Arc; *SST* South Sandwich Trench; *SSA* Southern Scotia Arc; *KN* Kapp Norvegia; *HB* Halley Bay; *AP* Antarctic Peninsula



(Jensen 1988; Vanreusel et al. 1992; Soetaert and Heip 1995; Vanaverbeke et al. 1997; Vanhove et al. 2004) and in the Magellan Region (0–3.8%) and the Weddell sea (0–4.12%). Perhaps the high Desmodoridae abundance can be explained by the very fine sediment structure (a higher percentage of silt-clay than stations at Kapp Norvegia, Halley Bay and Magellan Strait which clearly contained higher percentages of sand) providing preferential habitats for large burrowers (Tita et al. 1999; Wieser 1959; Coull 1988) such as *Desmodora* and *Desmodorella*. Thus, although the genera of the family Desmodoridae are widely distributed, their densities show a distinct variation on a global and local Antarctic scale.

Hill's indices (N_0 , N_1 , N_2 , N_{inf}) (Hill 1973), were calculated for the nematodes for both stations and represented in a rarefaction curve (Fig. 3). They are generally lower than for the Weddell Sea stations (Kapp Norvegia and Halley Bay; Vanhove et al. 1999), and higher than for the Rothera stations (Luyten 1999). The sample size dependency of many diversity indices is a well-known problem for nematode diversity studies and asks for specific methodological considerations. The

question of whether sample size is large enough to estimate real diversity has an ambiguous answer because both community type variability and the large variety of available diversity indices must be considered, a problem clearly pointed out by Heip et al. (1998) and Soetaert and Heip (1990). For station NSA 242, doubling the amount of identified nematodes from ca. 100 to 200 resulted in an increase of 48% of the number of genera (N_0). A similar trend is found for station NSA 177, where an increase of 93% of identified nematodes resulted in an increase of 22% in genera numbers. After identification of ca. 100 nematodes, the rarefaction curve of N_0 is flattening, making the identification of more nematodes relatively unimportant for estimating genus diversity. Except for N_0 (both stations) and N_1 (station SSA 242), an imaginary asymptote is reached within the ca. 200 nematodes identified. When analysing more than 200 specimens, new genera will be found but their low abundances in most cases will hardly influence higher order Hill's indices. In stations NSA 177 and SSA 242 there are respectively 22 and 25 single-individual genera or singletons, covering more than half of the total

number of genera in these stations (respectively, 44 and 43).

The Scotia Arc as possible migration route for interstitial meiofauna

The origin of Antarctic benthic biota has fascinated scientists for a long time and several hypotheses have been put forward. It may (a) represent a relict autochthonous fauna, or consist of (b) eurybathic species derived from adjacent deep-water basins, (c) abyssal species and sub-Antarctic species of predominantly northern origin, (d) species of Magellanic origin which have migrated to Antarctica via the Scotia Arc and vice versa (Knox 1994). Knox (1994) summarised some major distribution patterns observed for Antarctic fauna (Circumpolar distribution, Circum-Antarctic and Circum-sub-Antarctic). Of specific interest for this study is the role of the Scotia Arc as a migration path to and from the Antarctic.

The genus *Desmodora* occurred in all areas except for the Antarctic Peninsula (Drake Passage and Rothera), while *Desmodorella* was not recorded in the South Sandwich Trench area. In general *Desmodora* and *Desmodorella* specimens occurred mainly at shallow depths, except *Desmodora* sp. A, sp. B and sp. C which are confined to the deeper stations at the South Sandwich Trench.

Desmodora campbelli was found in the Atlantic and Pacific sector (Campbell Island) suggesting a circumpolar distribution. However, this species only occurred at shallower depths and was absent in deeper samples (South Sandwich Trench), presumably excluding its dispersion through the deep sea. It was also absent around the Peninsula, possibly due to low food availability or sediment characteristics: samples from the Rothera area were characterised by a relatively low silt-clay fraction. However, the absence of *D. campbelli* in a few samples does not necessarily mean that it is completely absent in the general sampling area. The Scotia

Arc may very well have served as a migration path from or to the Antarctic for this species. Its dispersion could be influenced by hydrodynamics (Palmer 1990) since dispersal of nematodes is assumed to be primarily by passive transport in the bedload and water column. Epigrowth-feeders such as *Desmodora* and *Desmodorella* prefer the surficial sediment and are most susceptible to erosion and transport (Commito and Tita 2002 and references therein). Although the nematodes are assumed to be permanent sediment inhabitants, their occurrence in the water column is not exceptional in high-energy areas (Ullberg and Ólafsson 2003). Considering that Antarctic waters are characterised by a complex current system (ACC, East Wind Drift, Weddell Sea gyre, eddies, etc.) and movement of vast water masses (Antarctic Bottom Water, Circumpolar Deep Water, Antarctic Surface Water, Sub Antarctic Surface Water, etc.), the dispersion of benthic meiofauna cannot be excluded since turbulent water masses are encountered at considerable depth and have enough energy to transport small animals (Angel and Fasham 1983; Clarke et al. 2005). Another explanation for the distribution of *D. campbelli* could be that it inhabited parts of South America and Antarctica before the two continents drifted apart, and remained unaltered ever since, partly due to a slow evolution rate which is typical in very cold conditions. This view is consistent with the assumption that the Antarctic fauna is very old. Preliminary molecular results based on ten partial COI-gene sequences (primers JB2 and JB5) of *D. campbelli* from NSA 177 and SSA 242 show little genetic divergence between populations from these stations, which again could point to either a very slow “evolver” or an extremely high gene flow. Considering the large distance (ca. 960 km) between both stations, the latter may seem very improbable, but the complex hydrodynamic situation around the Scotia Arc leaves scope for discussion.

Desmodorella aff. *balteata* occurs at all areas studied except for the Magellan region and South Sandwich Trench. Based on these records, which include the Ross Sea, we assume that its distribution is circum-Antarctic.

Table 5 Overview of the distribution of the *Dichromadora* species encountered in various regions of the Antarctic [table from Vermeeren et al. (2004) adjusted with *Dichromadora* findings of this study]

<i>Dichromadora</i> species	South Georgia (Scotia Arc)	Signy Island (Scotia Arc)	South Sandwich Trench		Halley Bay		Kapp Norvegia		Vestkapp		Drake Passage	
	277 m	307 m	1,000 m	2,000 m	1,000 m	2,000 m	1,000 m	2,000 m	1,000 m	2,000 m	1,000 m	2,000 m
<i>D. quadripapillata</i>				+								
<i>Dichromadora</i> sp. A						+						
<i>Dichromadora</i> sp. B	+	+				+		+				
<i>D. aff. weddellis</i>	+	+									+	
<i>D. weddellis</i>			+	+	+	+		+				
<i>D. southernis</i>						+	+	+			+	+
<i>D. parva</i>					+			+	+	+	+	+
<i>D. polarsternis</i>						+	+	+	+	+	+	+
<i>D. polaris</i>	+	+				+	+	+	+	+	+	+

Although this species is mainly observed at shallower depths, the type specimens of *D. balteata* were found at a hydrothermal vent at a depth of 2,000 m (Verschelde et al. 1998).

While both *D. campbelli* and *Desmodorella* aff. *balteata* show a wider distribution, most of the *Desmadora* and *Desmodorella* species seem to be confined in their distribution because of geographical or environmental barriers. However, evidence drawn from the distributions of *D. campbelli* and other species should be carefully assessed since, in addition to the real turn-over, environmental variables (e.g. sediment structure, food availability) may limit small-scale distribution of species. Moreover, we should keep in mind the possible effect of undersampling on species distribution patterns, especially when considering absence data. The maximum number of *Desmadora* and/or *Desmodorella* species occurring at one station was three out of a total of ten observed, leading to a high turn-over of species within these genera between stations and suggesting that regional diversity may increase significantly compared to local diversity.

The South Sandwich Trench is characterised by a very distinctive *Desmadora* assemblage and the absence of the genus *Desmodorella*. Three of the four *Desmadora* species found here, were apparently confined to this area; the fourth (*Desmadora* sp. D) also occurred at Kapp Norvegia. Environmental conditions (depth, sediment properties, food availability) peculiar for this area could explain the distinct and characteristic deep-sea nematode fauna observed.

Desmadora minuta is restricted to the Magellan Strait, an area characterised by a very different ecosystem. The different environmental conditions linked to this ecosystem may prevent its dispersion southward. Observation by Clasing (1980) off the coast of Puerto Mont, Chile suggests that this species is distributed around the southern part of South America.

Vermeeren et al. (2004) did a similar study of the distribution of the genus *Dichromadora* without including the Scotia Arc. Therefore, both Scotia arc stations were also checked on the presence of *Dichromadora* species. Vermeeren et al. (2004) came to the conclusion that nearly all Antarctic *Dichromadora* species were new to science. All the *Dichromadora* species encountered in the Scotia Arc samples (*Dichromadro* sp. B, *Dichromadro* aff. *weddellis*, *Dichromadro polaris*) are identified as species described by Vermeeren et al. (2004). We identified specimens as *Dichromadro* aff. *weddellis* because of a slight difference in tail length and spicule thickness compared to the type specimens, traits not distinct enough to regard them as a new species. An overview of the *Dichromadora* species distributions is given in Table 5. Assemblages of *Dichromadora* in NSA 177 and SSA 242 are similar and resemble those found in the SE Weddell Sea. *Dichromadora* sp. B and *D. polaris* are widely distributed over all areas at different depths (277–2,000 m) suggesting migration unaffected by bathymetry along deeper and shallower routes.

Conclusions

The Scotia Arc stations show high densities and average diversity on meiofauna and nematode level, compared to adjacent areas. In addition, the identification of ca. 200 nematodes provides a relatively accurate estimate of diversity at the generic level using Hill's diversity indices.

In this study the species level turn-over between different stations did not reflect regional diversity, due to the restricted distributions of some species. Bathymetrical and sedimentary constraints were observed, transcending biogeographical confinements, hence shaping these species' distributions.

The distribution patterns of *Desmadora campbelli* and *Desmodorella* aff. *balteata* which are present across the Scotia Arc, suggest either (1) that this shallow island chain serves as a possible migration path between South America and the Antarctic, or (2) that under the cold Antarctic conditions the evolution of these species is extremely slow.

Nematode species data for the Antarctic region are very scarce, despite the valuable information they can yield on biodiversity and biogeography. The development of molecular techniques combined with intensive morphological study of deep-sea nematodes may provide a solution for the lack of taxonomic knowledge for the Antarctic, and especially the deep sea.

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