Comparison of the nematode fauna from the Weddell Sea Abyssal Plain with two North Atlantic abyssal sites

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Abstract

This study provides for the first time data on the nematode community composition from the Weddell Sea Abyssal Plain. In addition, new data on the nematode communities from the Cape Verde Abyssal Plain and the Porcupine Abyssal Plain are provided. Three stations along an east–west transect in the Weddell Sea were sampled during the ANDEEP II campaign and compared with two north-east Atlantic abyssal sites, characterized by a contrasting food supply, in terms of densities, community structure and biodiversity. Local total nematode densities on the Weddell Sea Abyssal Plain (station 138) rank among the highest values recorded from abyssal plains worldwide, pointing to a locally high availability of food for meiofauna. Minor differences in the proportion of dominant genera were observed between the Weddell Sea Abyssal Plain and both North Atlantic sites. The nematode communities at the Weddell Sea Abyssal Plain were dominated by Thalassomonhystera and Acantholaimus, which is comparable to the North Atlantic abyssal plains. No endemic genera for the Southern Ocean were found. However, the higher abundance of the genera Microlaimus and Dichromadora seems to be typical for the Southern Ocean deep-sea, and might be related to the availability of fresh food.

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1. Introduction

In comparison with temperate areas such as the north-east (NE) Atlantic (Vincx et al., 1994 and references therein), studies on deep-sea meiofauna community structure at higher latitudes are scarce. Some information is available from the Arctic (Pfannkuche and Thiel, 1987; Vanaverbeke et al., 1997; Schewe and Soltwedel, 1999; Soltwedel et al., 2000, 2003; Vanreusel et al., 2000), but the number of studies dealing with Antarctic (either high Antarctic or subantarctic) meiobenthos is still very limited. Moreover, most of these studies have focused on shelf and slope sediments (Herman and Dahms, 1992; Vanhove et al., 1995, 1999; Fabiano and Danovaro, 1999), while one study dealt with the hadal environment of the South Sandwich Trench (Vanhove et al., 2004). Only the study of Gutzmann et al. (2004) has considered densities and composition of abyssal meiofauna at higher taxon level in the Weddell Sea. The present study is the first to provide information on meiofauna and nematode communities from the central and east part of the Weddell Sea Abyssal Plain (WAP).

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Vanhove et al. (1995) observed that the bathyal meiofauna (500–2000 m) of the Weddell Sea shows many features similar to those of deep-sea assemblages elsewhere in the world. In the present paper, we compare the nematode communities of the WAP with two Atlantic abyssal sites. Here, the focus will be on nematodes, as they are generally the most abundant taxon in deep-sea sediments (Vincx et al., 1994; Vanhove et al., 1995, 2004) and in Antarctic sediments (Gutzmann et al., 2004) both in terms of densities and biomass. Moreover, nematodes become relatively more abundant with increasing water depth (Shirayama, 1984; Soltwedel, 2000; Gutzmann et al., 2004).

In 1995, Vanreusel et al. (1995) compared two abyssal sites in the NE Atlantic (Porcupine Abyssal Plain (PAP) and the oligotrophic site of the French EUMELI program on the Cape Verde Abyssal Plain (CAP)) with a contrasting food supply. These sites were compared in terms of nematode density, biomass in the upper centimeter and biomass spectra. The present paper provides information on community composition (nematode genera) and biodiversity at these two sites. Moreover, we will compare these data with those from three abyssal stations in the Weddell Sea (subantarctic), sampled during the ANDEEP II Cruise in 2002. All stations at these three locations are located at depths between 4540 and 4995 m.

The main aim of this study is to compare information on nematode densities, community composition and biodiversity from the WAP, PAP and CAP. In this way, we will assess the extent of difference between the Antarctic abyssal nematode fauna and the North Atlantic abyssal nematode fauna, which are characterized by differences in phytodetritus deposition.

2. Materials and methods

2.1. Sampling locations and procedure

The current study compares abyssal nematode communities from two locations in the North Atlantic and three locations in the Weddell Sea (Fig. 1). The northern most site is located in the PAP. At this location, samples were taken from one station (48° 50’N 16° 30’W) during the RRS Challenger Cruise 79 in May 1991, at a depth of 4850 m. At this time of year, the site is known to be subject to a high seasonal input of aggregated phytodetritus. In contrast, the second North Atlant-
Sampling occurred between 29 September and 11 October 1993, during the RRS Discovery Cruise 204. Samples were also taken at three abyssal stations of the WAP, during the ANDEEP II Cruise of the FS Polarstern (ANT-XIX/4) between 28 February and 1 April 2002: station 136 (64° 1'S 39° 6'W; depth: 4732–4737 m), station 137 (63° 45'S 33° 48'W; depth: 4747–4995 m) and station 138 (62° 58'S 27° 54'W; depth: 4540–4541 m). These stations are situated along a southwest-to-northeast transect, near the southern bent of the Scotia Arc (Fig. 1). They are, on average, 378.5 km apart from each other.

All samples were taken with a multiple corer (MUC) (Barnett et al., 1984). At both North Atlantic locations, the MUC was deployed three times, and from each of these deployments one 25.52 cm² core (internal diameter 57 mm) was kept for meiofauna analysis. Three replicate cores of the same size were also collected at each of the WAP stations. Due to a restriction in sampling time, the three cores at stations 136 and 137 were obtained from two different MUC deployments only. As a result, two pseudo replicates (i.e. an extra core from one of the two deployments) had to be used for these stations. At station 138, replicate samples were obtained from three independent drops.

Each core taken at the North Atlantic sites was sliced into five horizons of 1 cm. The cores from the WAP stations were sliced as follows: 0–1, 1–3 and 3–5 cm. For reasons of comparability, only the three upper cm were considered in the community analysis, without subdivision into horizons. Densities were based on the upper 5 cm of sediment. All samples were fixed with 4% buffered formalin.

2.2. Laboratory analyses

The meiofauna fraction was separated from the macrofauna fraction by means of a 1-mm and 32-μm sieve. Meiofauna was extracted from the sediment by density gradient centrifugation with Ludox as a flotation medium (Heip et al., 1985; Vincx, 1996). A minimum of 300 nematodes were randomly picked out from the upper 3 cm of each replicate sediment core for identification. The animals were mounted onto glass slides using the formalin–ethanol–glycerol technique described by Seinhorst (1959) and Vincx (1996), and identified to the genus level under the microscope.

2.3. Statistical analyses

The PRIMER5 software (Plymouth Marine Laboratory; Clarke and Gorley, 2001) was used to calculate Bray–Curtis similarities and produce a test statistic R, which reflects within-group as well as between-group similarities. The obtained similarity matrix was used to produce a non-metric multidimensional scaling two-dimensional plot (nMDS). The stress value gives a measure for goodness-of-fit of the nMDS ordination; a low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke, 1993). One-way analysis of similarities (ANOSIM) was performed to test for significant differences (p<0.05) in the nematode community structure between the different stations. Relative data were used to carry out these analyses. A similarity of percentages (SIMPER) analysis was carried out on arcsin-transformed relative data to identify which taxa primarily account for the observed assemblage differences.

A selection of relevant biodiversity indices was calculated. Hill’s diversity numbers (Hill, 1973) gradually change from indices of species richness to indices of evenness with increasing number, with \( N_0 \), number of genera; \( N_1 \), exp(\( H^0 \)); and \( N_{\infty} \), reflecting evenness. \( H^0 \) is the Shannon–Wiener index (log base = e).

Parametric (one-way ANOVA, with indication of the \( F \)-statistic and d.f.) and non-parametric (Kruskal–Wallis ANOVA by ranks, with indication of the \( H \)-statistic) analysis of variance was performed using the STATISTICA6 software. Cochran’s C, Hartley’s \( F \) and Bartlett’s chi-square tests were used to verify homogeneity of variances prior to the analysis. Tukey’s HSD test was used to produce post hoc results.

3. Results

3.1. Nematode densities and community composition

Densities are plotted in box and whisker plots (Fig. 2). Highest values were found at station 138 of the WAP and at the PAP station. The CAP station was characterized by significantly lower densities than these two stations (\( F = 9.5; \) d.f. = 4 and 10; \( p = 0.002 \)). The two remaining WAP stations showed intermediate values, not significantly different from any other station.
A total of 109 genera from 33 families was found. Sixteen families and 25 genera were present at all three sites. Except for the PAP station, which was dominated by Chromadoridae, all stations were dominated by Monhysteridae. Highest degree of dominance was found for the WAP 138 station (35.10%) and the CAP station (33.64%). Moreover, the five most abundant nematode families were quite similar at all stations; they include Monhysteridae, Chromadoridae, Microlaimidae, Xyalidae, Oxystominidae and Diplopeltidae. These families took up more than 80% of the total nematode community. Chromadoridae and Xyalidae were most diversified, as they were both represented by 13 genera.

An overview of the 20 most abundant genera per station (first 3 cm) is given in Table 1. All stations were dominated by Thalassomonhystera, with highest relative abundances at WAP station 138 (35.10%) and on the CAP (33.48%). Thalassomonhystera, Acantholaimus and Daptonema were the three most abundant genera for both the PAP and CAP station. Compared to these, the WAP stations (especially stations 136 and 138) were characterized by much higher relative abundances of Microlaimus (\(H = 9.389; p = 0.002\)) and much lower relative abundances of Daptonema (\(H = 8.014; p = 0.005\)). The WAP stations were also characterized by significantly higher relative abundances of Dichromadora compared to the North Atlantic sites (\(H = 4.33; p = 0.04\)). This genus was even absent in the CAP station. Acantholaimus was very abundant at stations WAP 136 and WAP 137, making up 44–48% of the total community together with Thalassomonhystera and Microlaimus. Station 138 differed from the other two WAP stations by a significantly higher relative abundance of Southerniella (\(H = 4.27; p = 0.04\)).

Although the dominant genera were similar at all stations, the nematode communities from the three abyssal locations were well separated from each other, as shown in the nMDS plot (Fig. 3). This is confirmed by a cluster dendrogram (not shown) and the high \(R\)-value (\(R = 0.719; p = 0.001\)) generated by a one-way ANOSIM analysis. Highest \(R\)-values were found between the WAP and CAP stations (\(R = 0.815\)), and between the WAP and PAP stations (\(R = 0.852\)). Indeed, highest dissimilarity was found between the three WAP stations on the one hand and both North Atlantic locations on the
other (46–62%), while the dissimilarity between WAP stations varies between 41% and 44%. There was a dissimilarity of 45% between both North Atlantic locations. Differences were mainly explained by higher abundances of *Microlaimus* and *Dichromadora* at the WAP stations, and higher abundances of *Acantholaimus* at the North Atlantic locations. There was a relatively high similarity (SIMPER) between samples from the same area. Lowest similarity was found at the PAP site (56.70%), while the highest similarity was found at the CAP site (70.15%). Average similarity within each WAP station varied between 60.30% and 65.75%.

### Table 2

Average values (with standard deviation) of several biodiversity indices, calculated for all stations

<table>
<thead>
<tr>
<th></th>
<th>N₀</th>
<th>N₁</th>
<th>H'</th>
<th>N∞</th>
</tr>
</thead>
<tbody>
<tr>
<td>WAP 136</td>
<td>31.67 ± 3.21</td>
<td>15.60 ± 1.28</td>
<td>2.74 ± 0.08</td>
<td>4.82 ± 1.38</td>
</tr>
<tr>
<td>WAP 137</td>
<td>32.00 ± 2.00</td>
<td>14.94 ± 3.35</td>
<td>2.69 ± 0.24</td>
<td>4.07 ± 1.31</td>
</tr>
<tr>
<td>WAP 138</td>
<td>21.67 ± 1.53</td>
<td>9.04 ± 0.92</td>
<td>2.20 ± 0.10</td>
<td>2.96 ± 0.67</td>
</tr>
<tr>
<td>PAP</td>
<td>32.67 ± 6.81</td>
<td>14.34 ± 3.01</td>
<td>2.65 ± 0.23</td>
<td>4.21 ± 0.56</td>
</tr>
<tr>
<td>CAP</td>
<td>29.00 ± 5.29</td>
<td>11.54 ± 1.61</td>
<td>2.44 ± 0.14</td>
<td>3.00 ± 0.26</td>
</tr>
</tbody>
</table>

3.2. Biodiversity

WAP station 138 was characterized by the lowest diversity in terms of different biodiversity indices (Table 2). Both the Shannon–Wiener index ($F = 5.24$; d.f. $= 4$; $p = 0.02$) (Fig. 4) and Hill's $N_1$ ($F = 4.45$; d.f. $= 4$; $p = 0.03$) were significantly
different between stations. The other WAP stations were characterized by the highest diversity values for both \( N_1 \) and \( H' \). Shannon–Wiener diversity was significantly lower at station WAP 138 compared to both other WAP stations \( (F = 5.2; \text{d.f.} = 4 \text{ and } 10; \ p = 0.015) \). The PAP station was characterized by intermediate values for the Shannon–Wiener diversity index, whereas the CAP samples showed the second lowest average diversity of all stations, although this difference was not significant.

4. Discussion

Abyssal nematode communities have been studied regularly in the past, but most of the studies focused on temperate to tropical oceans (Tietjen et al., 1989; Vincx et al., 1994; Bussau et al., 1995; Vopel and Thiel, 2001; Lambshead et al., 2002), while little attention has been given to polar seas.

Nematode densities in the WAP show a high degree of spatial variation: from high numbers at the most northeastern station south from the South Sandwich Forarc (WAP 138) to lower densities in the more central part, which is situated more to the southwest. These local differences within the WAP are difficult to be explained by the observed sedimentation regime, as described by Howe et al. (2004), based on sediment samples and video footage taken during the same sampling campaign. According to these authors, WAP station 137 was characterized by large phytodetritus patches on the seafloor, while WAP station 138 shows obvious feeding traces, but no phytodetritus aggregates. Macrofauna densities (Blake and Narayanaswamy, 2004) were also twice as high at station 138 compared to stations 136 and 137, pointing to a higher food availability for the endofauna at station 138. The presence of feeding traces at this station might be related to a higher food input and consequently higher feeding activity, quickly removing freshly deposited phytodetritus, which explains its absence on the video-footage. However, as environmental variables were not measured for the three Weddell Sea sampling stations, it is impossible to confirm this hypothesis with real data.

Not only local differences in densities within the Weddell Sea Abyssal Plain are striking; the discrepancy with the CAP is also remarkable. Both
Vanhohe et al. (2004) and Gutzmann et al. (2004) observed locally higher meiofauna densities in the Southern Ocean compared to other areas worldwide, from similar depths. When plotting worldwide estimates of meiofaunal densities against water depth, the values obtained in our study for the WAP stations as well as for the PAP station were situated above the World Ocean’s regression line provided in Soltwedel (2000). Meiobenthic communities in the abyssal plain of many other oceans are rather impoverished and, on average, count less than 150 ind. 10 cm$^{-2}$ (Bussau et al., 1995; Vopel and Thiel, 2001). Lowest densities were found in the central Arctic Ocean, which was due to the low organic food input in this ice-covered and thus oligotrophic region (Vanreusel et al., 2000).

Low meiofaunal densities at the CAP compared to the more eutrophic PAP was explained before by the low surface primary productivity estimations of about 50 mg C m$^{-2}$ day$^{-1}$ (Aufret et al., 1992) and the absence of any seasonality in the deposition of phytodetritus in the former region. The high abundances at the PAP site, from the same order of magnitude as the highest WAP densities (station 138), seem to be associated with a strong seasonal pulse of phytodetritus to the deep-sea floor in spring and early summer each year (Billett et al., 1983), although the average annual surface primary production is estimated to be in the same order of magnitude as for the Cape Verde area (Campbell and Aarup, 1992). The strong seasonal pulse at the PAP is likely a feature in common with the WAP. Jennings et al. (1984) estimated an average primary productivity in the Weddell Sea in springtime to be 220–420 mg C m$^{-2}$ day$^{-1}$, while phytoplankton production under the winter pack ice appears to be minimal (Fischer et al., 1988). However, according to Vinogradova et al. (1993), sedimentation of organic matter from the euphotic zone in the Southern Ocean is often in the form of faecal pellets, originating from zooplankton feeding activities. Such pellets often enclose fresh diatoms. Fast sinking rates in combination with slow decomposition rates in cold water can keep the organic material free from degradation or scavenging (Beaulieu, 2002). Such fresh food may rapidly be utilized by nematodes through an opportunistic behavior (Vanhohe et al., 2004). In contrast, at the PAP site it was estimated that the organic carbon content of phytodetritus was surprisingly low: 0.56–1.28% (Rice et al., 1986). Such differences in sedimentation processes were expected to generate more pronounced differences in nematode densities between the Atlantic PAP site and the WAP. However, other biota of the benthic ecosystem should also be included in order to fully understand the relation between organic C input and benthic standing stock.

Deep-sea nematode community composition seems extremely comparable worldwide, including slopes (Vanhohe et al., 1999, 2004) and abyssal plains in Antarctica, despite some small differences in abundance of dominant and subdominant genera, which have been observed. The dominance of Thalassomonhystera, Microlaimus and Acantholaimus, and the subdominance of the genera Theristus and Halalaimus in the central Weddell Sea is in accordance with bathyal nematode communities from other parts of the world: the NE Atlantic (Vincx et al., 1994; Soetaert and Heip, 1995), the NW Atlantic (Tietjen, 1971, 1976, 1989; Thistle and Sherman, 1985), the Central Arctic (Vanreusel et al., 2000), the Indian Ocean (Muthumbi, 1998) and the Pacific (Bussau et al., 1995; Vanreusel et al., 1997; Vopel and Thiel, 2001; Lambshede et al., 2002; Gambi et al., 2003). A similar genus list has been reported from the nearby South Sandwich Trench (Vanhohe et al., 2004). Also, no endemic deep-sea nematode genera have been found in Antarctica so far.

Nematode community composition was similar at all WAP stations, although variation in relative abundances was evident. Thalassomonhystera, Microlaimus and Acantholaimus were dominant or subdominant at all these stations, but at station WAP 138 the relative abundance of Thalassomonhystera and Microlaimus was, on average, much higher than at both other stations. Together, they made up more than 50% of the total nematode community. Both genera are known to be opportunistic (Van Gaever et al., 2004), and might as such have reacted to the somewhat higher food availability at this station. Both genera are indeed to a large extent responsible for the increased densities at this station. Next to Thalassomonhystera and Microlaimus, Acantholaimus also showed a high abundance at stations WAP 136 and 137, with these three genera making up 44–48% of the total nematode community.

Genus biodiversity estimations point to a more diverse nematode community at stations WAP 136 and 137 compared to WAP 138. In some studies, it was observed that nematode diversity related positively to primary production and food supply.
in the deep sea (Boucher and Lambshead, 1995). The relatively low genus diversity at the CAP station and relatively high genus diversity at the PAP station fit well with this observation. However, the opposite is true for the WAP stations: the station characterized by the highest densities (WAP 138) yielded a nematode community with a low diversity. The lower genus diversity at WAP 138 might be a consequence of the high abundance of the opportunistic genera *Thalassomonhystera* and *Microlaimus*, which resulted in high total densities and lower genus diversity and evenness. A high dominance of *Thalassomonhystera* was also observed at the CAP station. Moreover, both WAP station 138 and the CAP station were characterized by the lowest values for genus richness ($N_0$) and evenness ($N_\infty$).

Our knowledge about global latitudinal (species) diversity gradients in the deep-sea is in an early and inductive phase (Rex et al., 2000). Research showed that Antarctic diversity was not remarkably different from Atlantic or Mediterranean diversity, even though a distinct contrast was obvious between the North (Arctic) and South (Antarctic) polar seas (Vanhove et al., 1999). Although still a matter of debate, primary productivity might be one of the many driving forces contributing to this striking difference in diversity between the polar seas (Stromberg, 1996). Other factors that might have influenced the high Antarctic diversity include higher age, greater environmental constancy and longer isolation (Brey et al., 1994).

Compared to the WAP, slightly higher nematode diversity estimates were recorded from the Weddell Sea shelf and slope by Vanhove et al. (1999) and in the Ross Sea by Manachini (1997). This is in accordance with the earlier described parabolic trend in diversity with depth, with decreasing diversity from mid-slope depths towards the abyss.

The average high abundance of epistrate feeders sensu Wieser (1953) at WAP station 138, due to high abundances of the small tooth-bearing genera *Microlaimus* (18.55%), *Chromadorita* (5.80%) and *Dichromadora* (3.40%), seems to be associated with higher densities and thus an expected higher input of organic matter. Similar observations were made before in the Weddell Sea (Vanhove et al., 1995, 1999, 2004). Taking into consideration the rapid deposition of relatively fresh material, this can be explained as a functional adaptation of nematode communities to short-term events of fresh food supply. The high abundance of these genera seems to be the main difference between the Antarctic deep-sea nematode fauna and the fauna in the North Atlantic, and might support the idea of a higher fresh food supply to the WAP compared to the PAP.

In general, the meiofaunal community composition in the central deep Weddell Sea is highly comparable to similar deep-sea areas elsewhere in the world, both on higher taxonomic and nematode generic level. There is no clear evidence for an Antarctic autochthonous nematode community, as the community is dominated by several genera also typical for other deep abyssal plains. This confirms earlier findings that deep-water nematode communities are comparable on a broad geographic level. The mechanism suggested for this broad geographic similarity of meiofauna (nematodes in particular) includes (1) vertical transport of sediments down the shelf to greater depths and (2) accompanying horizontal movement by bottom currents. Such a phenomenon might also be present in the Southern Ocean. However, one should not only focus on the similarities between the WAP stations and the North Atlantic locations. Although the dominant genera at the WAP are similar to those at the PAP and CAP, our multivariate analyses showed a clear separation of the nematode communities from the Southern Ocean and the two North Atlantic locations. Moreover, spatial variability at the WAP was high, which could be due to small-scale patchiness, possibly related to a patchy food deposition on the abyssal plain. The present study is the first to provide data on genus level nematode community composition for the WAP. Nevertheless, further study is required at species level to understand the community structure and ecology of Antarctic deep-water meiofauna.

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