Progress in Oceanography xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas

Gustavo Fonseca [a,b,*], Thomas Soltwedel [a], Ann Vanreusel [c], Mats Lindegarth [d]

[a] Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen, 12, Bremerhaven 27570, Germany
[b] Centro de Biologia Marinha da Universidade de São Paulo, Rod. Manoel Hipólito do Rego Km 131.5, 116000-000 São Sebastião, Brazil
[c] Ghent University, Department of Biology, Marine Biology Section, Krijgslaan 281 S8, 9000 Gent, Belgium
[d] Department of Marine Ecology, Göteborg University, Tjärnö Marine Biological Laboratory, S-452 96 Strömstad, Sweden

ARTICLE INFO

Article history:
Received 26 June 2009
Received in revised form 6 November 2009
Accepted 13 November 2009
Available online xxxx

ABSTRACT

Although the comparison of relevant scales of variation is a prerequisite for understanding processes structuring benthic communities, deep-sea studies have traditionally examined spatial patterns of distribution of assemblages along a single scale or environmental gradient. A multiple-scale approach identifying which spatial-scale and associated environmental gradient is the most important in structuring the deep-sea benthos has never been attempted. To answer this question this study merged three independent data sets of nematodes from the Arctic deep seas. The data set included 300 samples and covered both margins of the Arctic Seas (Greenland and Norway–Spitsbergen, ca. 10^3 km distant apart), seven degrees of latitude (72–79°N), 2700 m depth differences (656–3350 m), horizontal distances between cores (20 cm) and vertical distances within the uppermost sediment layers (1–5 cm). Results showed that for abundance (N) and generic composition, differences between margins (M) and between cores (C) were the most important sources of variability, followed by water depth (D), vertical distribution within the sediment (VD) and latitude (*L*). For species and genera diversity, measured as ES(50) and EG(50), the order was slightly different. For species, *C* was the most important source of variability, followed by *D*, *M* and *L*, while for genera VD was the most important. Relationships between environmental variables and the fauna were highly dependent on scale indicating that, at least for the deep-sea environment, we cannot predict the structure of nematode assemblages by scaling up or down results obtained on one or another scale. The only consistent pattern across different spatial scales was that higher abundances were associated with higher number and lower turnover of species. This raises the hypothesis that the most abundant species are also the most widespread and that abundance is the best predictor of nematode diversity patterns in deep-sea ecosystems.

1. Introduction

Patterns in nature are scale dependent (Andrew and Mapstone, 1987). The scales on which patterns emerge depend upon the ecological factors structuring them (Wiens et al., 1993); i.e. factors that structure assemblages at the small scale are not necessarily the same as those structuring assemblages at larger scales. For instance, at small scales (<1 m), deep-sea faunal distribution is assumed to depend primarily on oxygen availability, biogenic disturbances, and interactions between organisms or between organisms and their micro-habitat (Eckman and Thistle, 1988; Snelgrove et al., 1992; Schaff and Levin, 1994). In contrast on larger scales, physical parameters (e.g. hydrodynamic regimes and near-bottom currents; Thistle and Sherman, 1985) as well as input of food from the euphotic zone and adjacent margins have been suggested to be relevant (Schaff et al., 1992; Vanreusel et al., 1995; Galerón et al., 2000). The identification of relevant scales of variation is therefore a necessary prerequisite for understanding processes structuring ecological communities and the scales at which these processes act (Underwood and Chapman, 1996; Chapman and Underwood 2008). Moreover, it helps in determining the extent to which a process operating at one scale can be generalised to other scales (Thrush et al., 1997).

Due to resource and logistic constrains, deep-sea studies have traditionally examined spatial patterns of distribution of populations and assemblages along a single scale or environmental gradient. The two most studied environmental gradients structuring deep-sea benthic organisms are water depth, which varies in the scale of hundreds of meters to kilometres (Soetaert and Heip, 1995; Soetaert et al., 1997; Vanaverbeke et al., 1997; Muthumbi et al., 2004; Hoste et al., 2007) and sediment depth at the scale

* Corresponding author. Address: Centro de Biologia Marinha da Universidade de São Paulo, Rod. Manoel Hipólito do Rego Km 131.5, 116000-000 São Sebastião, Brazil. Tel.: +55 12 38628402; fax.: +55 12 38628454.
E-mail address: fonseca_gfc@hotmail.com (G. Fonseca).

0079-6611/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.pocean.2009.11.001

of centimetres (Vincx et al., 1994; Soetaert et al., 1997). Particularly for meiofauna and nematodes, the number of individuals tends to decrease towards the deeper sites, while diversity peaks at intermediate water depths (Lambshead and Boucher, 2003). In the sediment layers, abundance and diversity dramatically decrease vertically with each centimetre layer (Vincx et al., 1994). Small scale (<1 m) horizontal heterogeneity is another important source of variability, although less studied (Gallucci et al., 2009). Variability of meiofauna assemblages in the horizontal small scales and between sediment layers is believed to be more important than changes along larger-scale gradients (Soetaert et al., 1997; Vanaverbeke et al., 1997).

Recent studies covering large-scale patterns in the deep sea showed that meiofauna may also change significantly over latitudes (Lambshead et al., 2002; Mokievsky and Azovsky 2002) and longitudes (Danovaro et al., 2008). Furthermore, variability at such large-scales is more pronounced than at smaller scales in the order of kilometres and meters (Gambi and Danovaro, 2006). Despite different sampling designs and different outcomes, a general agreement among these studies was that a single scale could not explain the entire variability of meiofauna assemblages. However, which spatial scale and associated environmental gradient is the most important in structuring the deep-sea meiofauna is still poorly understood.

Quantifying which spatial scale of variation is most important in structuring the fauna requires a proper sampling design and multiple spatial scales need to be analysed simultaneously (Archambault and Bourget 1996; Underwood and Chapman 1996; Kendall et al. 2003). However, differently from shallow-water and intertidal environments, multiple scale assessment in the deep-sea is logistically difficult. To address this issue, the present study merged three data sets with comparable methodologies from the Arctic Seas. The main aim was to investigate distributional patterns of deep-sea nematodes over five spatial scales (i.e. western and eastern margin of the Arctic Seas [ca. 1000 km apart from each other], seven degrees latitude [72°N–79°N], 2700 m depth differences [656–3350 m], horizontal distances between cores [ca. 20 cm] and the vertical distances within the sediment [1–5 cm]). Nematodes are the most abundant and one of the most specious metazoans in deep-sea sediments (Lambshead, 1993). Their diversity patterns at the small and larger scales appear to be related to that of other benthic components such as Foraminifera (Gooday et al., 1998) and macrofauna (Levin et al., 2001; Lambshead and Boucher, 2003). Nematodes are therefore considered to be good surrogates of spatial patterns of other benthic organisms in the deep sea (Danovaro et al., 2008). Specifically, the first hypotheses being tested was that deep-sea nematode assemblages, in terms of abundances, species and genera diversity and composition, varied significantly at the different spatial scales and that each scale contributed differently to the total variability. The second hypothesis being tested was that deep-sea nematode assemblages correlated significantly with environmental variables (organic matter, sediment water content, chloroplastic pigments equivalents and percentage of chlorophyll-a) at the different spatial scales. The main objective of this second hypothesis is to unravel whether there is a consistent pattern between fauna and the environment across different spatial scales in the Arctic deep seas.

2. Materials and methods

2.1. Study area

The margins of the Arctic Seas (here defined as Greenland Sea, Norwegian Sea and Fram Strait) are characterized by two major water currents with contrasting oceanographic conditions: the warm West Spitsbergen Current (WSC) along the eastern side flowing poleward and the ice-infested East Greenland Current (EGC) on the western margin flowing southward (Saloranta and Haugan, 2001; Fig. 1). The WSC is the polar limb of the North Atlantic circulation containing source waters of the Norwegian Atlantic Current and keeps the high latitudes, up to 78°N, ice-free most of the year (Aagaard et al., 1987). The EGC surface waters have constant temperatures close to the freezing point, low salinities (30 psu), and transport >90% of the sea ice formed in the Arctic Mediterranean which keeps the coastal areas ice covered seasonally to varying extents (Rudels et al., 2005). At lower latitudes, when approaching the Greenland and Iceland Seas, the EGC is also fed by warm and saline water from the south via the Norwegian Atlantic current (Aagard et al., 1985) which suppresses ice formation. These marked hydrographical differences between the EGC and WSC have direct effects on pelagic processes, primary production and sedimentation rates to the deep seafloor (Bodungen et al., 1995). Both margins differ largely in respect to the amounts and composition of exported particles as well as the seasonality in vertical particle fluxes (Bodungen et al., 1995). On average, mass flux as wells as carbonate and particulate organic carbon fluxes are generally higher in the Norwegian Sea than in the Greenland Sea (Hebbeln and Berner, 1993).

2.2. Sampling design and sample processing

Data from three independent studies from the Arctic deep seas (Fonseca and Soltwedel, 2007, 2009; Hoste et al., 2007) were merged to indentify the spatial scales that contributed most to the variability in abundance, species richness, species diversity and nematode species composition. The samples covered both margins of the Arctic Seas, four degrees of latitude (72°, 74°, 76° and 79°) and two bathymetrical transects (Fig. 1). Bathymetrical transects were restricted to latitude 74°N at the western margin (water depths: 656, 1198, 1560, 2129, 2735, 3033 m) and to latitude 79°N at the eastern margin (water depths: 1246, 1495, 1929, 2385, 2805, 3350 m). Latitudinal transects were restricted to 2000 m water depth. At each station, three samples from the same multiple corer were taken (ca. 20 cm apart from each other) and vertically sliced at one centimetre interval down to the 5th layer (Fig. 1). A total of 300 samples were analysed.

The applied methodological procedures were for each sample the same. Sub-sampling of the multiple-core (MUC) was performed with syringes with cut-off ends (5 cm in length and 1.2 and 2 cm in diameter for environmental variables and faunal parameters, respectively). Each sub-sample was taken from different cores, at least 20 cm apart from each other. To characterize the sedimentary environment, sediment water content and organic matter were determined. Sediment water content (H_2O), indicating the porosity of the sediments, was assessed by weight loss of wet sediment samples dried at 60 °C. The total organic matter (OM) content within the sediments was estimated by determining the ash-free dry weight after combusting sediment samples for 2 h at 500 °C. The input of phytodetritus, representing the main food source for benthic organisms, was estimated by determining sediment-bound pigments. Chloroplastic pigments (chlorophyll-a [Chl-a] and its degradation products, i.e. phaeopigments [Phaeo]) were extracted in 90% acetone and measured with a Turner fluorometer according to Yentsch and Menzel (1963) and Holm-Hansen et al. (1965). The bulk of pigments registered with this method (Chl-a + Phaeo) are termed chloroplastic pigment equivalents (CPE). The percentage contribution of Chl-a to the total pigment content (Chl-a%) is used to indicate the 'freshness' of the phytodetrital matter in the sediments.

Sediment samples for meiofauna investigation were fixed in 10% formalin immediately after sampling. In the laboratory, samples were washed through a 32 μm sieve, centrifuged (900 rpm)

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001

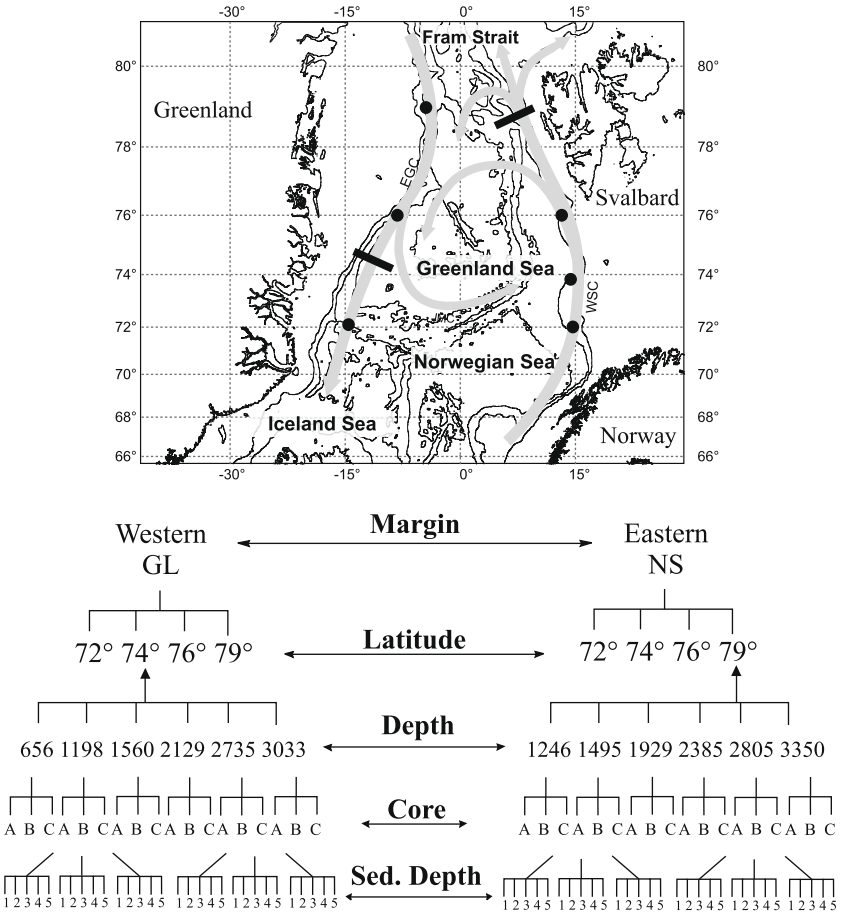

Fig. 1. Map of the sampling sites and schematic view of the sampling design. Dots represent the sampling stations and lines the bathymetrical transects. WSC, West Spitsbergen Current; EGC, East Greenland Current.

in a solution of colloidal silica (LUDOX TM-50) with density of 1.18 g cm^{-3}, stained with Rose Bengal and sorted under a low power stereo microscope (Heip et al., 1985). Nematodes were picked out, transferred to anhydrous glycerol, and mounted on permanent slides. Nematodes were identified to genus level (Warwick et al., 1998) and separated into putative species. Species were only used as univariate descriptor of the fauna. For the multivariate analysis (see data analysis) we used the data at generic level, since the separation into putative species from the different data sets was done by different people. Genera belonging to Monhysteridae were considered as one group in the uni- and multivariate analysis, since this family has been recently reviewed and modified by Fonseca and Decraemer (2008).

2.3. Data analysis

This study investigates primarily the contribution of each spatial scale or gradient in explaining the variability in nematode assemblages and the environmental factors which determine this variability. Descriptive information of the current data including nematode species composition was published elsewhere and it is out of the scope of this study (Fonseca and Soltwedel, 2007; Hoste et al., 2007; Fonseca and Soltwedel, 2009). Since bathymetrical transects were restricted to one latitude at each margin (Fig. 1), we split the entire data set into two sub-groups. One data set consisted of 120 samples and included the factors: margin, latitude and vertical distribution in the sediment. The second data set was based on 180 samples and included the factors: margin, bathymetrical gradient and vertical distribution in the sediment. Although replicates were taken from the same MUC and regarded as dependent samples (i.e. technically pseudo-replication), we considered in the analysis as independent samples since nematodes assemblages are most likely to vary on scales that the sub-cores of a MUC are significantly different from each other (Gallucci et al. 2009). Both data sets were therefore analyzed in the same way by means of analysis of variance (ANOVA) using mixed model designs (Table 1). Since in both designs the vertical layers in the sediment were not replicated within each core (zero degrees of freedom for the error term), the analyses were done using a

Table 1
Summary of the ANOVA mixed models designs used to analyse both data sets. *L*, latitude; *D*, water depth; *F*, fixed; *R*, random; *M*, margin; VD, vertical distribution; *C*, core; DF, degrees of freedom.

Model	Type	Effect term	Error term	DF
L	F	M	$C(M, L)$	1
	F	L	$C(M, L)$	3
	F	VD	VD $*$ $C(M, L)$	4
		$M * L$	$C(M, L)$	3
		$M *$ VD	VD $*$ $C(M, L)$	4
		$L *$ VD	VD $*$ $C(M, L)$	12
		$M * L *$ VD	VD $*$ $C(M, L)$	12
	R	$C(M, L)$	–	16
		VD $*$ $C(M, L)$	–	64
D	R	M	$D(M)$	1
	F	VD	$M *$ VD	4
		$M *$ VD	VD $*$ D(M)	4
	R	$D(M)$	C(M,D)	10
	R	$C(M, D)$	–	24
		VD $*$ $D(M)$	VD $*$ $C(M, D)$	40
		VD $*$ $C(D, M)$	–	96

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001

split-plot design. For all the calculations we used the Type-III sums of squares. The homogeneity of variances was tested by Cochran's test and when necessary data was Log(x + 1) transformed. All these tests were conducted with STATISTICA v7.0.

ANOVA further allows a quantitative measure of the variation associated with each factor in the analysis and the respective interaction effects from the mean squares estimates to be determined (Quinn and Keough, 2002). For the fixed factors we calculated the effect sizes and for the random factors the component variance. These calculations were done in accordance with Quinn and Keough (2002, p. 217).

Peaks of effect sizes and variance components indicate scales at which the between-group differences are especially large, suggesting that this may represent the scale of natural aggregation or patchiness in the system. Furthermore, coincidence in the variance peaks of different features of the system (e.g. nematode abundance and sediment water content) may indicate common spatial scaling and the possibility of direct linkages (Wiens, 1989). Given this, correlation between effect sizes of the environmental variables and the fauna, and between components variances, were also calculated to test whether or not independent variables are varying in the same magnitude across the different spatial scales.

As univariate descriptors of the fauna we used abundance (N) and the expected number of species and genera after sampling 50 individuals randomly (ES(50) and EG(50), respectively). The two most traditional measures of diversity, the absolute number of species (S) and Shannon Wiener diversity (H') were not further considered in this study, since S was strongly correlated with N ($r > 0.88$) and ES(50) with H' ($r > 0.93$) in both data sets.

The analytical design used for the multivariate analyses of the fauna was the same used for the univariate measures (Table 1). The test of each term was done by means of multivariate multiple regression analysis with the software DISTLM (Anderson, 2004). The theoretical background of this analysis is given by McArdle and Anderson (2001). The main advantage of this software over others is that DISTLM allows the analysis of split-plot designs of multivariate data by entering a third matrix (*Xdenom*), which contains the codes for the denominator term for the individual test to be performed. In addition to the X_{denom} matrices, one must also provide the program with a coding matrix (X) corresponding to the term to be tested (i.e. main effects and interaction effects). Both types of matrices (X, *Xdenom*) were created with the software XMATRIX (Anderson, 2003). P-values were obtained using 999 permutations of residuals under the reduced model. All tests were applied on a Bray–Curtis similarity matrix underlying the classification of samples (factors). Prior to the analysis, data were standardized and Log(x + 1) transformed. Since our data set was characterized by many samples having few individuals or even no individuals, increasing significantly the variability of the data, we added a dummy variable (weight 1) to the matrix (Clarke and Gorley, 2006). Multi-dimension scaling (MDS) plots of the multivariate structure of the nematode assemblages (Multiv) were performed with PRIMER v6 (Clarke and Gorley, 2006).

Finally, to know whether correlations between environmental variables and the univariate parameters of the fauna were dependent on the scale analysed (e.g. LogN and H_2O could be strongly correlated at latitudes but not necessarily and the scale of vertical distribution in the sediment layers), we performed Spearman-rank correlations for each effect term presented in Table 1. For this we averaged and calculated the 95% confidence interval for each variable at each level of the analysis.

At this stage, we were especially interested in whether the environmental variables were positively or negatively correlated with the fauna and which variable was responsible for the highest correlation value.

3. Results

3.1. Nematode assemblages

From a total of 33,995 nematodes surveyed, 180 nematode genera were observed. The mean number of genera per core, regardless of sediment layers, was 15 (SD + 10). Along the GL margin, only the three most abundant taxonomic units, Monhysteridae, *Acantholaimus* and *Daptonema*, occurred in more than 50% of the samples, while along the NS margin, the ten most abundant genera (the previous three together with *Tricoma*, *Halalaimus*, *Dichromadora*, *Desmoscolex*, *Theristus*, *Sabatieria* and *Microlaimus*) occurred in more than 50% of the samples.

For the univariate measures of the fauna, Log N, ES(50) and EG(50), the results of both ANOVA models (L and D) pointed to significant differences for most of the main factors and interaction effects (Table 2). The analysis based on Model L showed that differences in abundances, species and genera diversity were dependent on the margin, latitude and vertical layer of the sediment analysed (significant interaction effect). Higher abundance, species and genera diversity values for the NS margin were only observed in the northern latitudes (76°N, 79°N) at the deeper layers of the sediment (Fig. 2). Abundance, genera and species diversity of the deeper layers of the sediment (<3 cm) along the GL latitudinal gradient decreased with increasing latitude, while along the NS margin latitudinal trends were less pronounced (Fig. 2). In relation to water depth (Model D), along the GL margin, the deeper stations (>2000 m water depth) had in average more individuals, species and genera diversity than shallower stations (not always significant), while along the NS margin these three parameters were in average higher at shallower stations (Fig. 3). At the upper sediment layers, standard deviations from all parameters in both models were overlapping indicating no differences between margins, latitude and water depth.

Analysis of effect sizes and variance components showed that for Log N, difference between margins in both ANOVA models (L and D) was the most important factor explaining the total variance (0.18 and 0.20, respectively; Table 2). Variability between cores was the second most important in both models. For ES(50), both models also showed similar patterns. In that case, the residuals of both analyses, which are the variability between cores and the interaction effect between cores and vertical distribution, explained most of the total variance, summing up to 68.26 in Model L and 58.01 in Model D. Apart from the residuals, in Model L differences in ES(50) between sediment layers (VD) was the second most important factor (23.8). In Model D differences between water depths (25.3) was more important than differences between sediment layers (16.95) in explaining the total variance. For EG(50), VD was the most important source of variability in both models followed by cores.

Results of the DISTLM analysis showed that for the Model L differences between nematodes assemblages were dependent on the margin, latitude and vertical sediment layer analysed (interaction effect, Table 2). For the Model D, significant interaction effects were also observed. In both models, the residuals explained most of the total variance (Table 2) followed by differences between margins. Differences between water depths were more important than differences between vertical layers in the Model D, and differences between vertical layers were more important than differences between latitudes in the Model L.

By plotting both data sets in independent MDS-plots using sediment vertical distribution as coding factor, a horizontal gradient along the X-axis with samples from the upper layers getting more aggregated towards to the right hand side of the graph becomes evident (Fig. 4). It is interesting to note that although we had per-

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001

Table 2
Results of the ANOVA for both data sets. MS: means squares; Var: variance components or effect sizes; Multiv: nematode genera composition; *N*: abundance; ES(50) and EG(50): expected number of species and genera after sampling randomly 50 individuals; OM: organic matter; H_2O: sediment water content; Chl-a%: percentage of chlorophyll-a; CPE: chloroplastic pigment equivalents. For further abbreviations see Table 1. Bold values stand for $p < 0.05$ and underlined values stand for the highest effect size or component variance.

Model	Factor	MS Log *N*	*F*	*p*	Var	MS ES(50)	*F*	*p*	Var	MS EG(50)	*F*	*p*	Var	MS Multiv	*F*	*p*	Var
L	*M*	10.62	124.88	**0.001**	0.18	897.96	17.09	**0.001**	14.09	149.63	4.40	**0.050**	1.93	23844.45	16.122	**0.001**	372.76
	L	1.83	21.52	**0.001**	0.02	327.53	6.23	**0.005**	3.06	113.57	3.34	**0.046**	2.65	6892.62	4.66	**0.001**	60.15
	VD	7.46	170.77	**0.001**	0.08	2300.97	146.50	**0.001**	23.80	1086.05	92.94	**0.001**	44.77	12073.66	8.72	**0.001**	111.35
	$M * L$	2.47	29.00	**0.001**	0.05	318.81	6.07	**0.006**	5.92	255.83	7.52	**0.002**	16.28	6856.15	4.64	**0.001**	119.49
	$M *$ VD	0.17	3.92	**0.007**	0.00	234.87	14.95	**0.001**	4.57	109.11	9.34	**0.001**	8.12	3578.52	2.59	**0.001**	45.71
	$L *$ VD	0.31	7.07	**0.001**	0.00	49.35	3.14	**0.001**	0.47	18.98	1.62	0.107	1.22	1813.42	1.31	**0.043**	5.96
	$M * L *$ VD	0.23	5.25	**0.001**	0.01	63.53	4.05	**0.001**	1.33	38.81	3.32	**0.001**	9.04	2382.61	1.72	**0.001**	27.73
	$C(M, L)$	0.09			0.09	52.55			52.55	34.01			34.01	1479.00			1479.00
	VD $* C(M, L)$	0.04			0.04	15.71			15.71	11.69			11.69	1384.22			1384.22
D	*M*	19.40	11.40	**0.007**	0.20	753.08	1.79	0.210	3.70	832.05	2.35	0.156	5.31	48050.86	6.06	**0.001**	445.79
	VD	7.52	29.94	**0.003**	0.05	2629.40	13.96	**0.013**	16.95	1250.16	22.06	**0.005**	33.15	15138.11	3.79	**0.001**	77.36
	$M *$ VD	0.25	1.87	0.134	0.01	188.33	3.92	**0.009**	7.79	56.68	1.79	0.149	1.39	3997.67	1.65	**0.015**	87.10
	$D(M)$	1.70	10.63	**0.001**	0.10	420.35	10.31	**0.001**	25.30	353.89	12.40	**0.001**	21.69	7929.90	3.80	**0.001**	389.37
	$C(M, D)$	0.16			0.16	40.79			40.79	28.53			28.53	2089.37			2089.37
	VD $* D(M)$	0.13	2.38	**0.001**	0.02	48.05	2.79	**0.001**	10.28	31.62	2.92	**0.001**	6.93	2429.79	1.67	**0.001**	325.32
	VD $* C$(BD, *M*)	0.06			0.06	17.22			17.22	10.83			10.83	1453.84			1453.84
		OM				H_2O				Chl-a%				CPE			
L	*M*	242.95	63.57	**0.000**	3.99	15.66	72.74	**0.000**	0.26	28.42	2.26	0.152	0.26	137.35	13.45	**0.00**	2.12
	L	46.51	12.17	**0.000**	0.47	5.31	24.66	**0.000**	0.06	356.07	28.33	**0.000**	3.82	310.15	30.38	**0.00**	3.33
	VD	2.23	1.85	0.131	0.01	17.02	167.17	**0.000**	0.18	6.29	1.03	0.399	0.00	552.66	152.27	**0.00**	5.72
	$M * L$	10.01	2.62	0.087	0.14	5.24	24.33	**0.000**	0.11	332.34	26.44	**0.000**	7.11	104.95	10.28	**0.00**	2.11
	$M *$ VD	1.70	1.40	0.243	0.01	1.79	17.61	**0.000**	0.04	10.09	1.65	0.172	0.08	6.73	1.86	0.13	0.06
	$L *$ VD	0.67	0.56	0.869	−0.01	0.61	5.99	**0.000**	0.01	10.86	1.78	0.071	0.07	59.00	16.26	**0.00**	0.77
	$M * L *$ VD	2.18	1.81	0.066	0.03	0.63	6.23	**0.000**	0.01	12.13	1.99	**0.040**	0.17	37.28	10.27	**0.00**	0.93
	$C(M, L)$	3.82			3.82	0.22			0.22	12.57			12.57	10.21			10.21
	VD $* C(M, L)$	1.21			1.21	0.10			0.10	6.11			6.11	3.63			3.63
D	*M*	420.21	7.01	**0.024**	4.00	18.06	3.62	0.086	0.15	5.09	0.98	0.345	0.00	501.27	14.76	**0.00**	5.19
	VD	1.59	2.10	0.245	0.01	23.70	28.26	**0.003**	0.16	10.84	10.30	**0.022**	0.07	48.00	14.29	**0.01**	0.31
	$M *$ VD	0.75	0.90	0.471	−0.01	0.84	0.17	0.950	0.01	1.05	0.92	0.460	0.00	3.36	1.96	0.12	0.09
	$D(M)$	59.94	41.85	**0.000**	3.90	4.99	10.47	**0.000**	0.30	5.19	9.02	**0.000**	0.31	33.97	25.23	**0.00**	2.17
	$C(M, D)$	1.43			1.43	0.48			0.48	0.58			0.58	1.35			1.35
	VD $* D(M)$	0.84	1.24	0.195	0.06	0.62	3.74	**0.000**	0.15	1.14	1.70	**0.019**	0.16	1.71	2.16	**0.00**	0.31
	VD $* C(D, M)$	0.67			0.67	0.17			0.17	0.67			0.67	0.79			0.79

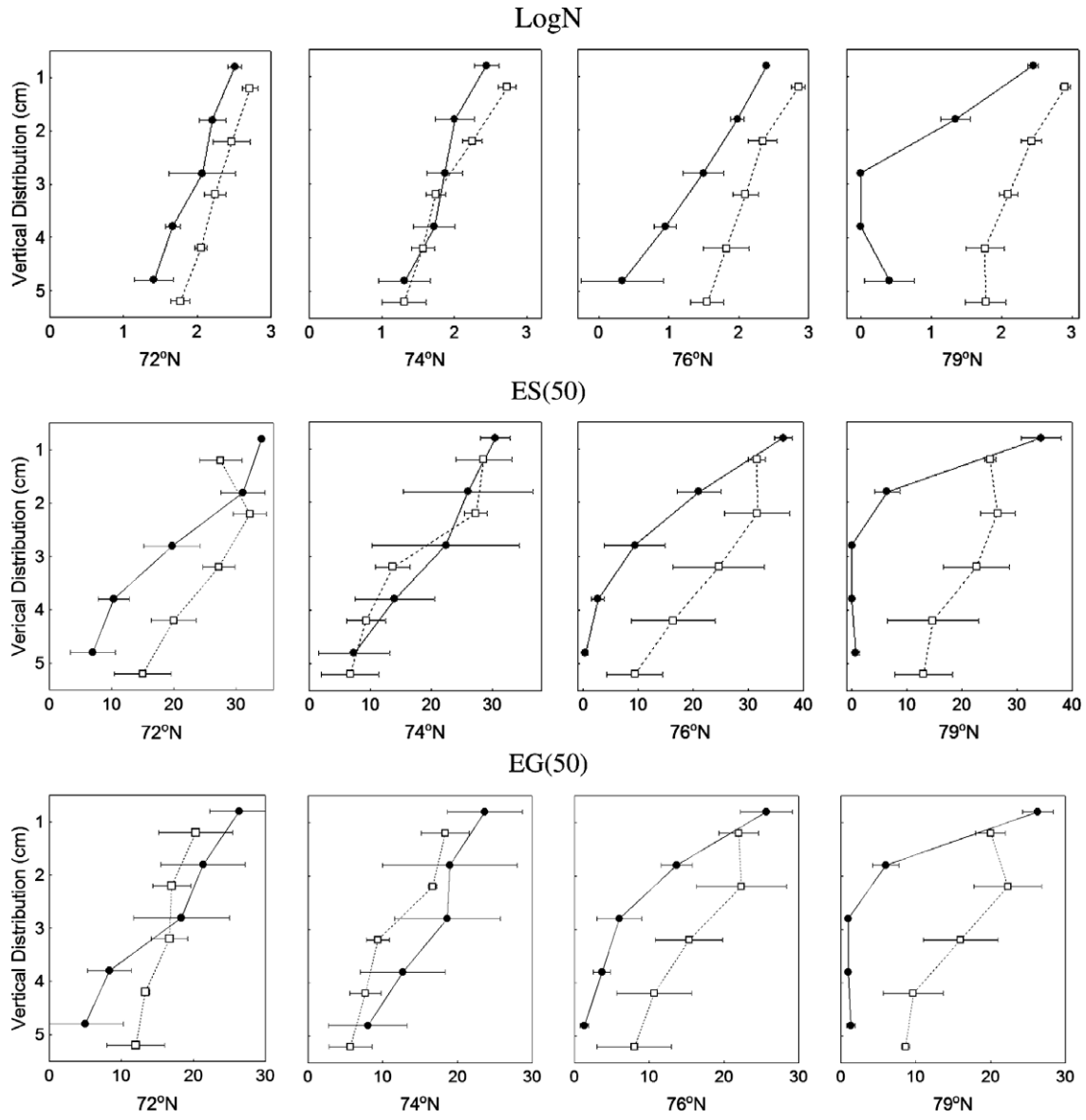

Fig. 2. Mean and standard deviation of the Log-transformed nematode abundances (Log *N*) and expected number of species and genera after sampling 50 individuals (ES(50) and EG(50), respectively) at each latitude and sediment layer. Greenland (GL): dots; Norway–Svalbard (NS): squares.

formed the analysis on the standardized data set, absolute abundance was the main variable predicting the multivariate structure of the assemblage. Results of a simple regression for the MDS coordinates along the *X*-axis using Log-transformed abundance as predictor showed that abundance predicted 88% or the variability along the MD1 (Fig. 5; $r^2 = 0.88$, $p < 0.01$). This means that higher abundances are associated with higher positive values of the *X*-axis and higher similarity between assemblages from different samples. In other words, samples characterized by lower abundances do not share the same species and were more spread in the MDS plots.

3.2. Environmental variables

Significant differences of organic matter (OM) in Model L were restricted to the factors *M* and *L*. OM was higher in the NS margin and at higher latitudes, 76°N and 79°N. Concerning Model D, OM also significantly differed between margins and water depths within margins (Table 2). The NS margin had higher values than GL and shallower stations along the NS margin had more material than the deeper stations, while along the GL margin mid-slope stations had the highest OM concentrations. In both models, the factor margin was the most important factor structuring OM concentrations.

Significant differences in sediment water content (H_2O), an indirect measure of sediment porosity, were dependent on the margin, latitude and vertical layer analysed (Model L, Table 2). Concentrations were higher along the NS margin at latitudes 74°, 76° and 79°N. In Model D, difference in sediment water content was dependent on the water depth and vertical sediment layer analyzed. Along the NS margin, sediment water content decreased with increasing depth at all layers, while at the GL margin significant changes were only observed at the uppermost layer at mid-slope stations. In both models when considering each factor individually, the residuals accounted for most of the total variability, followed by *M* in Model L and *D*(*M*) in Model D.

Differences in Chl-a% and CPE were dependent on the margin, latitude and vertical layer analysed (significant interaction effect, Model L). Significant differences in CPE and Chl-a% concentrations were restricted to the uppermost sediment layer. At the 79°N station CPE was higher at the GL margin, and at the 72° and 74°N CPE

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001

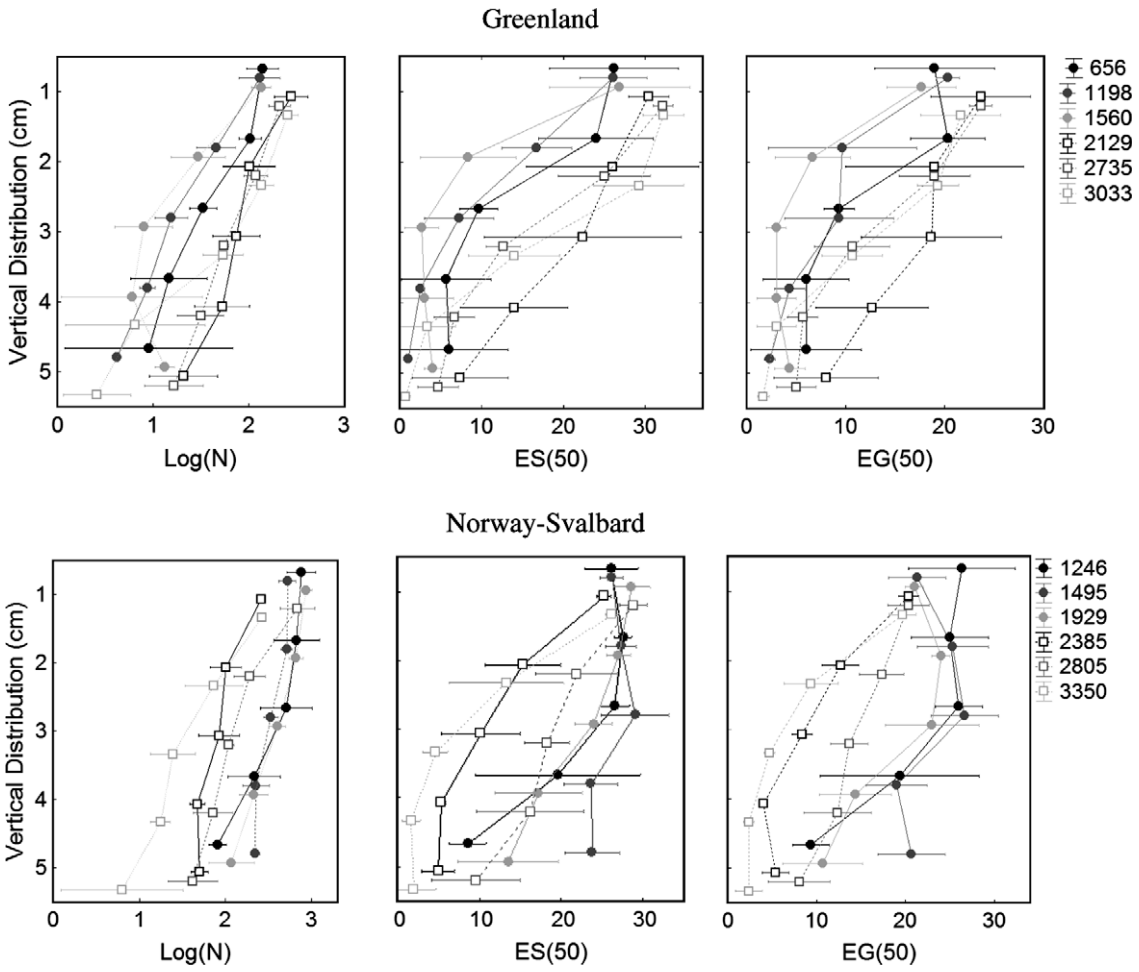

Fig. 3. Mean and standard deviation of the Log-transformed nematode abundances (Log *N*) and expected number of species and genera after sampling 50 individuals (ES(50) and EG(50), respectively) at each water depth and sediment layer.

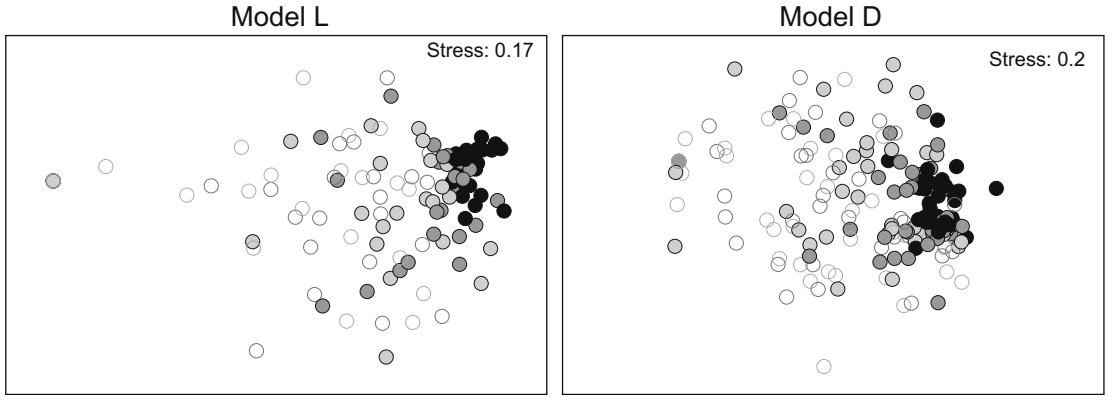

Fig. 4. MDS plots of the standardized, Log-transformed nematode assemblages for both models using sediment vertical distribution as coding factor. 1–5 cm: ● ● ● ○ ○.

was higher at the NS margin. Chl-a% followed a similar pattern, being higher at latitude 74 °N in GL and at 79°N in NS. Variability of CPE in Model L was mainly explained by the residuals followed by VD, while in Model D differences between margins and depths within margins were the two most important structuring factors. For Chl-a%, the residuals of both ANOVA models accounted for most of the variability, followed by the interaction $M * L$ and $D(M)$, respectively.

3.3. Nematodes versus environmental variables

3.3.1. Effect sizes and variance components

With the exception of EG(50), all effect sizes derived from the fixed factors of the ANOVA models of the fauna were significantly correlated to the effect sizes of sediment water content (Table 3). This means that fauna and water content were varying at similar magnitude at the different scales. The higher the difference of

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001

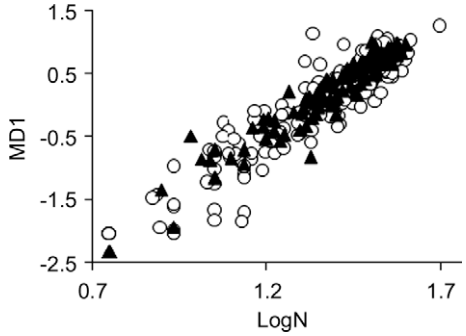

Fig. 5. Scatterplot between coordinates of the MD1 and Log *N* for the Model L (▲) and Model D (○).

sediment water content between two levels of a factor (e.g. Margins, Latitudes, etc.), the higher was the difference in abundance, species diversity and multivariate structure. Effect sizes and variance components of Log *N* were also highly correlated to OM ($r > 0.70$). Effect sizes of the multivariate structure of the nematodes were also significantly correlated to the effect sizes of OM (Table 3). Variance components of the fauna were positively correlated to the effect sizes of H_2O, although only significant for EG(50) (Table 3). Effect sizes and variance components of EG(50) were highly correlated with ES(50) (0.65 and 0.96, respectively).

3.3.2. Correlations at the different scales

Results of the Spearman Rank correlation showed that EG(50) and ES(50) are highly positively correlated ($r > 0.90$) at all the spatial scales and therefore only ES(50) will be analysed with the environmental variables. The correlation between Log *N* and ES(50) versus the environmental variables for both models (L and D) are presented in Appendix A and B. In both models, correlations between fauna and environmental variables were dependent on the scale (effect term) analysed. For instance, if we consider the relationship between Log *N* and OM in both models, the correlation was significantly high ($r > 0.98$) for the effect term margin (M), it was low and not significant (Model L: $r = 0.20$; Model D: $r = 0.15$) for VD and it was low and negative ($r = -0.17$) for the effect term $D(M)$, in the case of the GL margin, and highly positive ($r = 0.79$) along the NS margin (Fig. 6a). The relationship between Log *N* and OM for the effect term VD $*$ $D(M)$ varied from negative ($r = -0.20$, 1198 m water depth in the GL margin) to highly positive ($r = 0.77$, 2129 m, GL) (Fig. 6b).

With the exception of few cases, for both models, negative correlations between the univariate measures of the fauna and OM were mainly observed within cores, VD $*$ $C(M, L)$ and VD $*$ $C(M, D)$. This means that at larger scales OM had a positive correlation with abundance and diversity of nematodes, while at the smallest scale it had a negative or positive correlation depending on the station and replicate considered.

With few exception in both models, the results of ES(50) mirrored the results of Log *N*. For instance, for the factor M in both

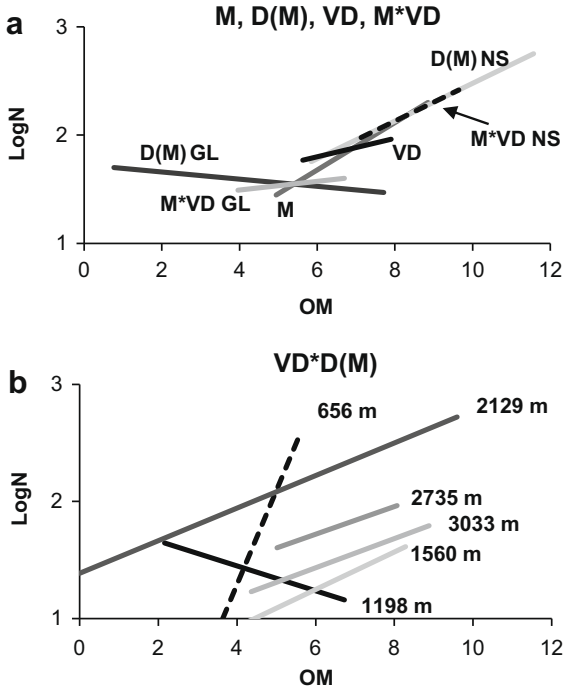

Fig. 6. Correlation between Log-transformed abundance (N) and organic matter (OM) for the effect terms M, $D(M)$, VD and $M * VD$ (a) and for the interaction effect term VD $*$ $D(M)$ along the Greenland margin (b) of the ANOVA Model D. Numbers indicate water depths in meters.

models, Log *N* and ES(50) were positively correlated to all environmental variables (Appendix A and B). For the factor L both variables were significantly positively correlated to H_2O and OM, while for the factor $D(M)$ along the GL margin they were significantly positively with CPE and Chl-a%. For most of the cases when the factor VD was included in the interaction effect (i.e. M $*$ VD, L $*$ VD, VD $*$ D(M), etc.), nematodes were significantly positively correlated with CPE and Chl-a% (Appendix A and B).

4. Discussion

The aim of this study was to understand differences in deep-sea nematode assemblages over five spatial scales representing different environmental gradients. Vertical distribution in the sediment (1 cm scale) and variability between cores from the same sampling station (ca. 20 cm scale) were the smallest scales, while water depth, latitude and differences between both margins of the Arctic Seas represented the larger scales (kilometres scale). The results of the component variances showed that within each of these scales the environmental conditions varied in a different way. For instance, chloroplastic pigments (CPE and Chl-a%) varied more at the smaller than at the larger scales. Among the larger scales, both variables changed more pronouncedly along the bathymetrical

Table 3
Correlation between effect sizes and variance components derived from the ANOVA of the fauna and the environmental variables. For abbreviations see Table 2. Bold values stand for significant correlation at $p < 0.05$.

Var	Effect-sizes				Variance components			
	Log *N*	ES(50)	EG(50)	Multiv	Log *N*	ES(50)	EG(50)	Multiv
OM	**0.72**	0.03	−0.44	**0.87**	**0.70**	0.37	0.57	0.02
H_2O	**0.91**	**0.90**	0.23	**0.80**	0.60	0.66	**0.76**	0.60
Chl-a%	−0.21	−0.32	−0.21	−0.11	−0.09	0.66	0.60	0.43
CPE	0.44	0.63	0.14	0.32	0.35	0.56	0.61	0.27

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001

gradients and between margins than along the latitudinal gradients. However, contrary to chloroplastic pigments, concentration of organic matter (OM) and sediment water content (H_2O) were more variable between margins and water depths rather than at the smallest scales. These findings suggest that while chloroplastic pigments are probably reflecting local processes, OM and H_2O are reflecting broad oceanographic processes. Small-scale processes causing different sedimentary characteristics in the Arctic deep seas are probably related to the patchy input of phytodetritus (Rice et al. 1994), seafloor microtopography as well as benthic biogenic structures (Jumars, 1976; Snelgrove and Smith, 2002). At the large scale, however, contrasting oceanographic currents between both margins (SWC and EGC, Fig. 1), presence of marginal ice zones and associated surface primary production (Schewe and Soltwedel, 2003; Fonseca and Soltwedel, 2007), and distance from the land (Soltwedel et al., 2005) should be the causes. The question now is which of these spatial scales and associated environmental conditions is more important in structuring deep-sea nematode assemblages.

By considering both ANOVA models together (Models D and L), we are able to draft a rough outline of importance for the effect terms structuring nematode abundance, diversity and generic composition. For abundance and generic composition, the analyses showed that variability between margins and between cores were the most important factors followed by water depth, vertical distribution in the sediment and latitude. For ES(50), the order is slightly different with variability between cores being the most important, followed by water depth, vertical distribution in the sediment, margin and latitude. For all these parameters, the small horizontal scale between cores was one of the most important scales of variability. As mentioned above, ANOVA results showed that chloroplastic pigments also varied more at the smallest scales suggesting it could be responsible for the small-scale variability of the fauna. Nevertheless, correlation analysis between the parameters of the fauna and chloroplastic pigments were not consistent among stations suggesting that other unmeasured environmental factors are responsible. Actually, small-scale patterns of deep-sea meiofauna are still poorly understood (Snelgrove and Smith, 2002). It is believed that like macrofauna organisms, meiofauna species are patchily distributed with patch sizes ranging around few centimetres to meters (Gallucci et al., 2009). However the processes shaping patchiness in deep-sea nematodes are highly speculative. According to the spatial–temporal mosaic theory (Grassle, 1989), such high small-scale variability is a result of different stages of succession and recolonization from discrete disturbance operating at both spatial and temporal scales. If Grassle's conclusion proves to be true for nematodes, then information on the natural history of species is essential to integrate studies across space and time scales. Reproductive rates, life cycles, scales of movement, dispersal abilities, behaviour and resource requirements for different life-stages all play important roles in how species respond to environmental heterogeneities at different scales (Thrush et al., 1997). Recent studies showed that basic information on body size, mobility and feeding mode can also be used to explain small-scale spatial arrangements of deep-sea nematodes (Gallucci et al., 2008, 2009).

Among the five spatial scales investigated, latitude was the least important scale in structuring all parameters of the fauna (abundance, species and genera diversity and composition). One might argue that the latitudinal range sampled in this study was relatively small (seven degrees between latitudes 72 and 79°N) and did not encompass enough variability. Nevertheless, previous studies covering larger latitudinal gradients also noticed that changes in deep-sea nematode assemblages along bathymetrical gradients prevailed over latitudinal gradients (Rex et al., 2001 and references therein). Moreover, both bathymetrical transects studied here were also limited in depth (656–3350 m) and certainly more variability would be added when extending the bathymetry from intertidal areas to abyssal plains. Probably, even over larger scales, changes in nematode assemblages along latitudes will be less pronounced than changes along bathymetrical gradients. It is important to remark that latitude and depth are not the causes of macroecological patterns; they are merely geographic gradients that define environmental patterns (Hawkins and Diniz-Filho, 2004). The results of the ANOVA also showed that all the environmental variables were less variable between latitudes than at any other scale. Moreover the correlations between the environmental variables and the fauna at the latitudinal scale were not consistent between both margins. At the western margin, nematode abundance and diversity were more positively correlated with interstitial space (H_2O), while at the eastern margin they were with chloroplastic pigments. This difference might be related to the contrasting oceanographic conditions and extent of sea-ice between both margins (Fonseca and Soltwedel, 2009).

In contrast to latitude, depth related patterns along both margin were rather consistent. Nematodes were stronger correlated with CPE than any other variable along both margins. In the deep sea, environmental changes along water depths, in comparison to elevation gradients in terrestrial systems, generate strong changes in short distances (Rex et al., 2005), while latitudinal trends are more smooth and easily interrupted by regional processes which are not covarying with latitude. Bathymetry was also more important than sediment layers in structuring deep-sea nematode species diversity, abundance and composition in the Arctic deep seas but not in structuring genera diversity. For nematode genera, vertical distribution in the sediment was the most important source of variability as previously observed in the North Atlantic (Soetaert et al., 1997; Vanaverbeke et al., 1997). This discordance between taxonomic levels is probably related to the fact that nematode genera are widespread at different water depths, while species are more restricted in their distribution.

The importance of sediment interstitial space, organic matter and phytodetritus in structuring deep-sea benthic communities has been extensively discussed (Heip et al., 1985; Levin et al., 2001; Snelgrove and Smith, 2002). The positive relationship between benthic communities and OM and CPE is probably a direct result of more food availability (Vincx et al., 1994; Vanreusel et al., 1995). Yet the relationship between fauna and sediment water content, an indirect measure of interstitial space, could be a direct cause of more physical space available for nematodes from different species to coexist (Heip et al., 1985), or indirect causes such as higher oxygen availability at deeper layers and higher rate of organic carbon burial within the sediment (Levin et al., 2001). Independently of the causes, the most interesting aspect of the present analysis is that the relationships between these variables and the fauna changed according to sample resolution. This means that deep-sea nematodes do not respond evenly to changes in OM or any other environmental variable that we analysed for across different spatial gradients or even between cores along the same gradient. A general trend observed was that stations where the average concentration of phytodetritus and organic matter was low (e.g. stations deeper than 3000 m along the NS margin), these two variables were positively correlated with the fauna factors. On the other hand, when food resources were abundant (e.g. shallower stations in the NS margin), sediment water content was highly correlated with the fauna indicating that once food is not limiting other variables from becoming the structuring factor (Gray, 2002). In practice, it suggests that, at least for the deep-sea environment, we cannot predict the structure of nematode assemblages by scaling up or down results obtained from one or another scale. It also implies that broad scale relationships emerge from additive or interactive responses to processes operating

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001

across scales rather than local responses to a certain environment factor being dominant and limiting species distribution (Thrush et al., 2005). Like for other taxa and biotopes, nematodes may respond to ecological processes operating simultaneously over a variety of scale, thus different factors may be limiting at different scales (Wiens, 1989; Chapman and Underwood, 2008). As a result, there is no single right scale of sampling to determine species–environment relationships. Therefore, testing for the scale-dependence of relationships becomes essential (Thrush et al., 2005).

The only consistent relationship observed over a variety of spatial scales at the Arctic deep-seas was that between nematode abundance, species richness and generic composition. Independent of the scale considered here, any two samples with higher abundances shared more genera in common than samples with lower abundances. Data based on species level achieved similar conclusions (Fonseca and Soltwedel, 2009). These results raise an attractive hypothesis for predicting biodiversity patterns in deep-sea benthic ecosystems. The hypothesis is that both local richness and turnover of nematode species (or genera) in the deep-sea are closely associated with number of individuals. When population sizes are small, local extinctions are more prompt to occur increasing regional rareness and turnover of species. However, when population sizes are large enough to maintain its reproductive levels, species become more widespread reducing the turnover at the larger scales. Based on this hypothesis, we may also expect that widely distributed deep-sea species tend to occur at higher densities at the local scale, while restricted species appear at lower densities at the local scale. Such positive relationship between occurrence and local abundance has already been observed for deep-sea nematodes (Gallucci et al., 2009) and macrofauna (Gray et al., 2005). Moreover, it seems to govern biodiversity patterns in terrestrial systems (Hubbel, 2001). Yet if this hypothesis is valid across different deep-sea oceans is matter of further research.

When evaluating the results of our analyses, it is important to remember that some caveats apply. Questioning complex multiple-scale interaction effects between the fauna and the environment requires proper sampling designs, preferably orthogonal designs where all effect terms are analysed simultaneously. The lack of samples taken in the Arctic deep seas did not allow us to compare variances along water depths and latitudes in one model, nor to integrate spatial variability in the order of centimetres, meters to hundreds of meters at the horizontal scale. Another restriction of the present study is the lack of additional environmental variables in the analyses, such as grain size and oxygen availability, which would help the interpretation of the data. These reflect the practical limitations of sampling effort present in marine benthic studies, particularly in deep-sea studies. Large-scale studies in the marine realm will always face an important trade-off between extent and resolution, which means that increasing extent, is generally associated with a decrease in resolution (Hewitt, 1998). Hopefully, in the near future, we solve these problems by merging larger data sets or by performing multiple-scale nested sampling designs as already done in shallower marine systems (e.g. Thrush et al., 1997, 2005; Hewitt, 1998; Kendall et al., 2003). Although multiple-scale sampling design might be difficult to achieve in the deep seafloor, it has to become priority in future studies.

Acknowledgments

The authors acknowledge the comments made by F. Gallucci and two anonymous reviewers, as well as the linguistic improvement of P. Hutchings. G.F. is sponsored with a PhD scholarship by the Brazilian national council for scientific and technological development (CNPq). This study was achieved after the workshop on large scale patterns in bathyal free-living nematodes funded by the Continental Margin Ecosystem (COMARGE) and census of marine life (CoML). Many thanks go for the Bea Merckx and Eveline Hoste for helping with the data set. This is Publication No. awi-n18067 of the Alfred Wegener Institute for Polar and Marine Research.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.pocean.2009.11.001.

References

Aagard, K., Swift, J.H., Carmack, E.C., 1985. Thermohaline circulation in the Arctic Mediterranean seas. Journal Geophysical Research 90, 4833–4846.
Aagaard, K., Foldvik, A., Hillman, S.R., 1987. The west spitsbergen current: disposition and water mass transformation. Journal Geophysical Research 92, 3778–3784.
Anderson, M.J., 2003. XMATRIX: a FORTRAN computer program for calculating design matrices for terms in ANOVA designs in a linear model. University of Auckland.
Anderson, M.J., 2004. DISTLM v.5: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model. University of Auckland.
Andrew, N.L., Mapstone, B.D., 1987. Sampling and description of spatial patterns in marine ecology. Oceanography and Marine Biology: An Annual Review 25, 39–90.
Archambault, P., Bourget, E., 1996. Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. Marine Ecology Progress Series 36, 111–121.
Bodungen, B., Antia, A., Bauerfeind, E., Haupt, O., Koeve, W., Machado, E., Peeken, I., Peinert, R., Reitmeier, S., Thomsen, C., Voss, M., Wunsch, M., Zeller, U., Zeitzschel, B., 1995. Pelagic processes and vertical flux of particles: an overview of a long-term comparative study in the Norwegian Sea and Greenland Sea. Geologische Rundschau 84, 11–27.
Chapman, M.G., Underwood, A.J., 2008. Scales of variation of gastropod densities over multiple spatial scales: comparison of common and rare species. Marine Ecology Progress Series 354, 147–160.
Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
Danovaro, R., Gambi, C., Lampadariou, N., Tselepides, A., 2008. Deep-sea nematode biodiversity in the Mediterranean basin: testing for longitudinal, bathymetric and energetic gradients. Ecography 31, 231–244.
Eckman, J.E., Thistle, D., 1988. Small-scale spatial pattern in meiobenthos in the San Diego Trough. Deep-Sea Research 35, 1565–1578.
Fonseca, G., Decraemer, W., 2008. State of the art of the free-living marine Monhysteridae (Nematoda). Journal of the Marine Biological Association of the UK 88, 1371–1390.
Fonseca, G., Soltwedel, T., 2007. Deep-sea meiobenthic communities underneath the marginal ice zone off Eastern Greenland. Polar Biology 30, 607–618.
Fonseca, G., Soltwedel, T., 2009. Regional patterns of nematode assemblages in the Arctic deep seas. Polar Biology 32, 1345–1357.
Galerón, J., Sibuet, M., Mahaut, M.L., Dinet, A., 2000. Variation in structure and biomass of the benthic communities at three contrasting sites in the tropical northeast Atlantic. Marine Ecology Progress Series 197, 121–137.
Gallucci, F., Moens, T., Vanreseul, A., Fonseca, G., 2008. Active colonization of disturbed sediments by deep-sea nematodes: evidence for the patch mosaic model. Marine Ecology Progress Series 367, 173–183.
Gallucci, F., Moens, T., Fonseca, G., 2009. Small scale spatial patterns of meiobenthos in the Arctic deep sea. Marine Biodiversity 39, 9–25.
Gambi, C., Danovaro, R., 2006. A multiple-scale analysis of metazoan meiofaunal distribution in the deep Mediterranean Sea. Deep-Sea Research I 53, 1117–1134.
Gooday, A.J., Bett, B.J., Shires, R., Lambshead, P.J.D., 1998. Deep-sea benthic foraminiferal species diversity in the NE Atlantic and NW Arabian Sea: a synthesis. Deep-Sea Research I 45, 165–201.
Grassle, J.F., 1989. Species diversity in deep-sea communities. Trends in Ecology and Evolution 4, 12–15.
Gray, J.S., 2002. Species richness of marine soft sediments. Marine Ecology Progress Series 244, 285–297.
Gray, J.S., Bjørgesæter, A., Ugland, K.I., 2005. The impact of rare species in natural assemblages. Journal of Animal Ecology 74, 1131–1139.
Hawkins, B.A., Diniz-Filho, J.A.F., 2004. 'Latitude' and geographic patterns in species richness. Ecography 27, 268–272.
Hebbeln, D., Berner, H., 1993. Surface sediment distribution in the Fram Strait. Deep-Sea Research 40, 1731–1745.
Heip, C., Vincx, M., Vranken, G., 1985. The ecology of marine nematodes. Oceanography and Marine Biology: An Annual Review 23, 399–489.
Hewitt, J.E., 1998. The effect of changing sampling scales on our ability to detect effects of large-scale processes on communities. Journal of Experimental Marine Biology and Ecology 227, 251–264.
Holm-Hansen, O., Lorenzen, C.J., Holmes, R.W., Strickland, J.D.H., 1965. Fluorometric determination of chlorophyll. Journal du Conseil Permanent International pour l'Exploration de la Mer 30, 3–15.

Hoste, E., Vanhove, S., Schewe, I., Soltwedel, T., Vanreusel, A., 2007. Spatial and temporal variations in deep-sea meiofauna assemblages in the Marginal Ice Zone of the Arctic Ocean. Deep-Sea Research I 54, 109–129.

Hubbel, S.P., 2001. The Unified Theory of Biodiversity and Biogeography. Princeton University Press.

Jumars, P.A., 1976. Deep-sea species diversity: does it have a characteristic scale? Journal of Marine Research 34, 217–246.

Kendall, M.A., Widdicombe, S., Weslawski, J.M., 2003. A multi-scale study of the biodiversity of the benthic infauna of the high-latitude Kongsfjord, Svalbard. Polar Biology 26, 383–388.

Lambshead, P.J.D., 1993. Recent developments in marine benthic biodiversity research. Oceanis 19, 5–24.

Lambshead, P.J.D., Boucher, G., 2003. Marine nematode deep-sea biodiversity – hyperdiverse or hype? Journal of Biogeography 30, 475–485.

Lambshead, P.J.D., Brown, C.J., Ferrero, T.J., Mitchell, N.J., Smith, C.R., Hawkins, L.E., Tietjen, J., 2002. Latitudinal diversity of deep-sea marine nematodes and organic fluxes: a test from the central equatorial Pacific. Marine Ecology Progress Series 236, 129–135.

Levin, L.A., Etter, R.E., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. Annual Review of Ecology and Systematics 32, 51–93.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297.

Mokievsky, V., Azovsky, A., 2002. Re-evaluation of species diversity patterns of free-living marine nematodes. Marine Ecology Progress Series 238, 101–108.

Muthumbi, A.W., Vanreusel, A., Duineveld, G., Soetaert, K., Vincx, M., 2004. Nematode community structure along the continental slope off the Kenyan Coast, western Indian Ocean. International Review of Hydrobiology 89, 188–205.

Rex, M.A., Stuart, C.T., Etter, R.J., 2001. A comment on whether deep-sea nematodes show a positive latitudinal gradient of species diversity: the potential role of depth. Marine Ecology Progress Series 210, 297–298.

Rex, M.A., Crame, J.A., Stuart, C.T., Clarke, A., 2005. Large-scale biogeographic patterns in marine molluscs: a confluence of history and productivity? Ecology 86, 2288–2297.

Rice, A.L., Thurston, M.H., Bett, B.J., 1994. The IOSDL DEEPSEAS programme: introduction and photographic evidence for the presence and absence of a seasonal input of phytodetritus at contrasting abyssal sites in the northeastern Atlantic. Deep-Sea Research I 41, 1305–1320.

Rudels, B., Björk, G., Nilsson, J., Winsor, P., Lake, I., Nohr, C., 2005. The interactions between waters from the Arctic Ocean and the Nordic Seas north of Fram Strait and along the East Greenland Current: results from the Arctic Ocean-02 Oden Expedition. Journal of Marine Systems 55, 1–30.

Quinn, G.P., Keough, M., 2002. Experimental Design and data Analysis for Biologists. Cambridge University Press, Cambridge.

Saloranta, T.M., Haugan, P.M., 2001. Interannual variability in the hydrography of Atlantic water northwest of Svalbard. Journal of Geophysical Research 106, 13931–13943.

Schaff, T.R., Levin, L.A., 1994. Spatial heterogeneity of benthos associated with biogenic structures on the North Carolina continental slope. Deep-Sea Research II 41, 901–918.

Schaff, T.R., Levin, L.A., Blair, N., De Master, D., Pope, R., Bohme, S., 1992. Spatial heterogeneity of benthos on the Carolina continental slope: large (100 km)-scale variation. Marine Ecology Progress Series 88, 143–160.

Schewe, I., Soltwedel, T., 2003. Benthic response to ice-edge induced particle flux in the Arctic Ocean. Polar Biology 26, 610–620.

Snelgrove, P.V.R., Smith, C.R., 2002. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. Oceanography and Marine Biology: An Annual Review 40, 311–342.

Snelgrove, P.V.R., Grassle, J.F., Petrecca, R.F., 1992. The role of food patches in maintaining high deep-sea diversity: field experiments with hydrodynamically unbiased colonization trays. Limnology and Oceanography 37, 1543–1550.

Soetaert, K., Heip, C., 1995. Nematode assemblages of deep sea and shelf break sites in the North Atlantic and Mediterranean Sea. Marine Ecology Progress Series 125, 171–183.

Soetaert, K., Vanaverbeke, J., Heip, C., Herman, P.M.J., Middelburg, J.J., Sandee, A., Duineveld, G.C.A., 1997. Nematode distribution in ocean margin sediments of the Goban Spur (north-east Atlantic) in relation to sediment geochemistry. Deep-Sea Research 44, 1671–1683.

Soltwedel, T., Hasemann, C., Quéric, N.-V., von Juterzenka, K., 2005. Gradients in activity and biomass of the small benthic biota along a channel system in the deep Western Greenland Sea. Deep-Sea Research I 52, 815–835.

Thistle, D., Sherman, K.M., 1985. The nematode fauna of a deep-sea site exposed to strong near-bottom currents. Deep-Sea Research 32, 1077–1088.

Thrush, S.F., Schneider, D.C., Legendre, P., Whitlatch, R.B., Dayton, P.K., Hewitt, J.E., Hines, A.H., Cummings, V.J., Lawrie, S.M., Grant, J., Pridmore, R.D., Turner, S.J., McArdle, B.H., 1997. Scaling-up from experiments to complex ecological systems: where to next? Journal of Experimental Marine Biology and Ecology 216, 243–254.

Thrush, S.F., Hewitt, J.E., Herman, P.M.J., Ysebaert, T., 2005. Multi-scale analysis of species–environment relationships. Marine Ecology Progress Series 302, 13–26.

Underwood, A.J., Chapman, M.G., 1996. Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107, 212–224.

Vanaverbeke, J., Soetaert, K., Heip, C., Vanreusel, A., 1997. The metazoan meiobenthos along the continental slope of the Goban Spur (NE Atlantic). Journal of Sea Research 38, 93–107.

Vanreusel, A., Vincx, M., Bett, B.J., Rice, A.L., 1995. Nematode biomass spectra at two abyssal sites in the NE Atlantic with a contrasting food supply. Internationale Revue des Gesamten Hydrobiologie 80, 287–296.

Vincx, M., Bett, B.J., Dinet, A., Ferrero, T., Gooday, A.J., Lambshead, P.J.D., Pfannkuche, O., Soltwedel, T., Vanreusel, A., 1994. Meiobenthos of the deep Northeast Atlantic. Advances in Marine Biology 30, 2–88.

Warwick, R.M., Platt, H.M., Somerfield, P.J., 1998. Free living marine nematodes: part III. Monhysterids. In: Barnes, R.S.K., Crothers, J.H. (Eds.), Synopses of the British Fauna (new series), vol. 53. Field Studies Council, pp. 1–303.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3, 385–397.

Wiens, J.A., Stenseth, N.C., Van Horne, B., Ims, R.A., 1993. Ecological mechanisms and landscape ecology. Oikos 66, 369–380.

Yentsch, C.S., Menzel, D.W., 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Research 10, 221–231.

Please cite this article in press as: Fonseca, G., et al. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. Prog. Oceanogr. (2010), doi:10.1016/j.pocean.2009.11.001