Mar Biodiv (2015) 45:349–356
DOI 10.1007/s12526-014-0271-y

SENCKENBERG

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Effect of core surface area and sediment depth on estimates of deep-sea nematode genus richness and community structure

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Received: 2 June 2014 / Revised: 3 September 2014 / Accepted: 10 September 2014 / Published online: 7 October 2014

Abstract A variety of core sizes are used for sampling deep-sea nematodes but little is known about the potential effects of core dimensions on estimates of diversity and community structure. We investigated the effects of core surface area (subcores vs. cores; 6.6 vs. 66.4 cm^2) and depth (shallow vs. deep subcores; 0–1 vs. 0–5 cm) on estimates of nematode genus diversity and community structure at six sites on the continental slope of New Zealand. We found that cores yielded significantly higher genus richness [expected number of genera in a sample of 51 individuals; EG(51)] than the smaller subcores (by up to a third), but found no significant difference between shallow and deep subcores. Conversely, nematode community structure was influenced by core depth but not surface area, reflecting a consistent shift in nematode community structure between surface and subsurface sediment layers among study sites. Average dissimilarity between shallow and deep subcores (45.2 %) was only slightly greater than average dissimilarity between subcores and cores (41.3 %); thus, the lack of a significant difference between subcores and the larger cores was likely due to the random (i.e., unpredictable) nature of horizontal variability in nematode community structure. Estimates of nematode diversity and community structure derived from subcores and the cores from which they were taken were not significantly correlated, suggesting that: (1) shifts in these attributes are not consistent between sites, and (2) patterns in nematode diversity and community structure are influenced by the choice of core size. The present study shows that a difference of a few centimetres in the physical dimensions of a core can have a substantial influence on estimates of deep-sea nematode diversity and community structure. Studies on spatial and temporal patterns of nematode diversity and/or community structure should therefore be based on cores with the same or similar dimensions. Meaningful comparisons of nematode diversity and community structure between environments should ideally take into consideration any potential differences in horizontal and vertical patchiness at small (cm) scales, and ensure that core surface area and penetration depths are sufficient to allow representative samples to be obtained across the entire range of environmental conditions sampled.

Keywords Sampling methodology · Small-scale variability · Meiofauna · Canyon · Hikurangi margin

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Introduction

One of the most firmly established rules about the diversity of organisms states that larger areas contain more species (Arrhenius 1921; Rosenzweig 1995. and references therein). This pattern is found at all spatial scales, from small patches where individuals may interact directly to regions with separate evolutionary histories. As a consequence, diversity patterns are dependent on the scale at which observations are made (e.g., Huston 1999; Chase and Leibold 2002). Choosing at which scale(s) to conduct observations may be relatively straight-forward when studying organisms living in well-defined habitat patches (e.g., fish in lakes or watersheds, insects in trees or forests), but this choice is much less obvious when studying small invertebrates living in vast, seemingly homogeneous, expanses of deep-sea sediments (Andrew and Mapstone 1987).

Meiofauna, and nematodes in particular, are the most abundant and diverse group of metazoans living in the deep-sea

floor (Giere 2009). They are renowned for their patchy distribution at small (cm) spatial scales, both vertically and horizontally (e.g., Eckman and Thistle 1988; Gallucci et al. 2009), and recent evidence suggests that small-scale variability in community structure is more pronounced than variation at larger scales (Ingels and Vanreusel 2013). Small-scale horizontal patchiness may be driven by factors such as biotic interactions, variation in microtopography, disturbance, or food availability (Gallucci et al. 2009), whereas vertical patchiness is likely driven by strong vertical gradients in biogeochemical conditions (e.g., Jorissen et al. 1995; Soetaert et al. 2002), or the presence and activity of macrofauna (Braeckman et al. 2011a).

The size of cores in soft sediment studies needs to be at least one order of magnitude larger than the target organisms (Andrew and Mapstone 1987), but not so large as to unduly increase sample processing times and efficiency (e.g., Borg et al. 2002). For the latter reason, smaller cores are often used in highly productive areas with high meiofaunal densities (e.g., estuaries), whereas larger cores are commonly used where meiofaunal densities are expected to be lower (e.g., exposed beaches) (Somerfield et al. 2005). Core depth also differs between environments, with deeper cores often used in coarse, well-oxygenated sediments where meiofauna has a wide vertical distribution, compared with shallow cores used in fine sediments with low oxygen permeability, where meiofauna are restricted to the surface sediment (Giere 2009). In deep-sea studies, shallow (c. 1 cm depth) and deep cores (c. 5 cm), with surface areas ranging from c.1 to 100 cm^2 are used (e.g., Gallucci et al. 2009; Leduc et al. 2010; Danovaro et al. 2008), but the choice of the core dimensions is rarely justified. For sediment depth, cores that penetrate deeper into the sediment are likely to include animals from a wider range of biogeochemical conditions and may therefore yield higher estimates of diversity than shallow cores (Leduc et al. 2010). Similarly, cores that sample a greater surface area are likely to include a greater number of patches relative to smaller cores, so that the size of the core could impact estimates of diversity and community structure (e.g., Warwick and Clarke 1996; Borg et al. 2002).

Whilst there may not be a "correct" core size for sampling deep-sea meiofauna/nematodes, because optimal core dimensions may vary between habitats and/or the community metrics of interest, it is important to quantify the magnitude of any effects core size may have on estimates of community attributes. This kind of assessment is particularly relevant for studies aiming to compare communities sampled by different researchers with different core dimensions (e.g., Soltwedel 2000; Udalov et al. 2005; Leduc et al. 2012). In deep-sea nematode studies, Hurlbert's (1971) rarefaction method [expected number of species/genera for a sample of X individuals; ES(X) or EG(X)] has become the most widespread method for estimating species/genus richness (e.g., Danovaro et al. 2008; Vanreusel et al. 2010). This metric offers two main advantages: it (1) allows the samples of different sample sizes to be compared (both within and among studies), and (2) does not require all individuals in a sample to be identified (a subsample of at least 100 individuals is typically identified), thus reducing sample processing time. Estimates of richness based on the rarefaction method are, however, expected to vary depending core surface area, but the magnitude of this effect remains unknown.

Estimates of community structure are also likely to be affected by the physical dimensions of sampling units. Consistent shifts in community structure estimates could be expected between shallow and deep cores due to the presence of vertical gradients in the abundance of nematode genera in deep-sea sediments (e.g., Ingels et al. 2011). Strong shifts in species/genus abundance are also commonly observed horizontally at similar (cm) scales, but these shifts arise due to presence of small patches that do not vary in a predictable fashion (unlike vertical shifts in taxon abundance). Any effect of core surface area on estimates of community structure would therefore be difficult to predict. Spatial and/or temporal patterns in community structure, however, may not be substantially affected as analyses of multivariate community data are typically based on rank measures (e.g., Clarke and Warwick 2001). The physical dimensions of sampling units may also influence the variability of community attribute estimates. Larger samples would include a greater number of species aggregations, thereby smoothing out much of the small-scale variability (Gray 1971). Among-core variability should therefore be less for large cores relative to smaller cores, but no deep-sea data are available to test this hypothesis.

The aims of the present study were to evaluate the potential effects of core surface area (6.6 vs. 66.4 cm^2) and depth (0–1 vs. 0–5 cm) on estimates of nematode genus diversity and community structure at six sites on the continental slope of New Zealand.

Methods

The study sites were located on the southern Hikurangi margin to the east of North Island, New Zealand (Fig. 1). Three sites were located on the continental slope (670–1,350 m water depth), and three were located inside canyons (985–1,121 m). Samples were collected in April 2010 (NIWA voyage TAN1004) using an Ocean Instruments MC-800A multicorer (MUC; core internal diameter = 9.52 cm). One core was obtained from each site. From the centre of each of these cores, one subcore of internal diameter 2.9 cm was taken to a depth of 5 cm. Each subcore was divided into 0–1 and 1–5 cm sediment depth layers. The remaining sediment surrounding the subcore was also sampled to a depth of 5 cm.

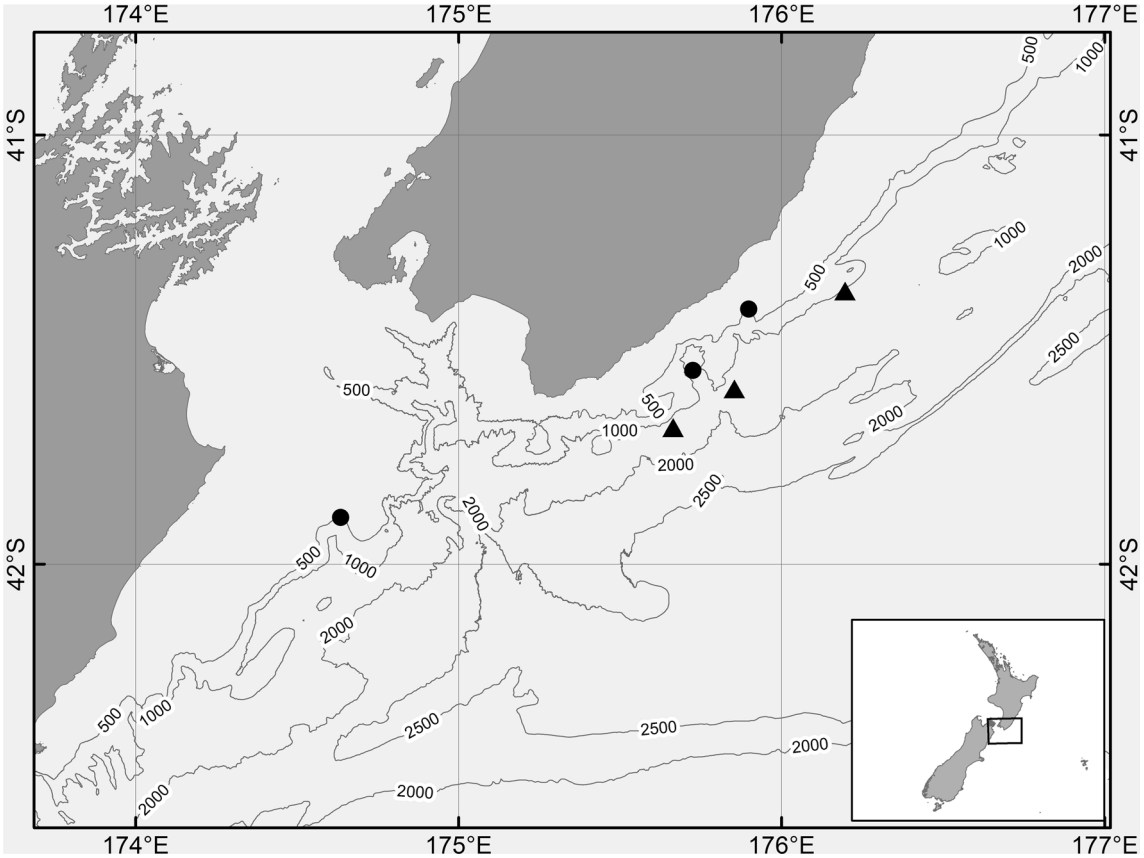

Fig. 1 Southern Hikurangi margin, east of New Zealand's North Island, showing canyon (*circles*) and slope (*triangles*) sampling locations

Each core was thus split into three portions: Subcore surface (0–1 cm sediment depth), Subcore subsurface (1–5 cm), and Core (remaining sample without the subcore, 0–5 cm sediment depth) (Fig. 2). Data from Subcore surface and Subcore subsurface were subsequently combined into one depth-integrated sample (Deep subcore) to allow comparisons between samples differing in surface area but not sediment depth (Deep subcore vs. Core). The surface area of the subcore (6.6 cm^2) was approximately ten times smaller than the surface area of the surrounding core (64.6 cm^2).

Samples were preserved in 10 % buffered formalin and stained with Rose Bengal, and subsequently washed through a 1-mm sieve to remove macrofauna and through a 45-μm mesh to retain nematodes. Nematodes were extracted from the sieved sediment by Ludox flotation (Somerfield and Warwick 1996). Nematodes from the Subcore surface and Subcore subsurface fractions were counted using a binocular microscope (×50 magnification) to determine their relative abundance and allow combining of the surface and subsurface fractions into whole subcores using the right proportions of individuals (see below).

One hundred nematodes (or all nematodes if fewer than 100 were present in the sample) from each of the Subcore surface, Subcore subsurface, and Core fractions were haphazardly selected, transferred to pure glycerol, and mounted on slides (Somerfield and Warwick 1996). Nematodes were identified to genus using the descriptions in Warwick et al. (1998), as well as the primary literature. *Monhystrella* and *Thalassomonhystera* were treated as one genus ("Monhysteridae") because they are sometimes difficult to distinguish based on morphology (Fonseca and Decraemer 2008).

To allow comparisons between Deep subcore and Core (i.e., samples differing in surface area but not sediment depth), nematodes from the 0–1 and 1–5 cm sediment depth layers were combined in proportions reflecting their respective abundance in each layer. If, for example, nematodes in a given subcore were found in proportion 0.4 and 0.6 in the 0–1 and 1–5 cm layers, respectively, then a sample of 100 individuals was assembled by combining the first 0.4(100) and 0.6(100) individuals identified from each sediment depth layer (i.e., 40+60=100). Nematode genus richness was quantified using the expected number of genera in a sample of 51 individuals [EG(51); Hurlbert 1971].

The PERMANOVA routine in PRIMER was used for the analysis of univariate and multivariate data (Anderson et al. 2008). PERMANOVA is a semi-parametric, permutation-based routine for analysis of variance based on any similarity measure (e.g., Euclidean, Bray–Curtis). Because samples were obtained from different habitats (three slope and three

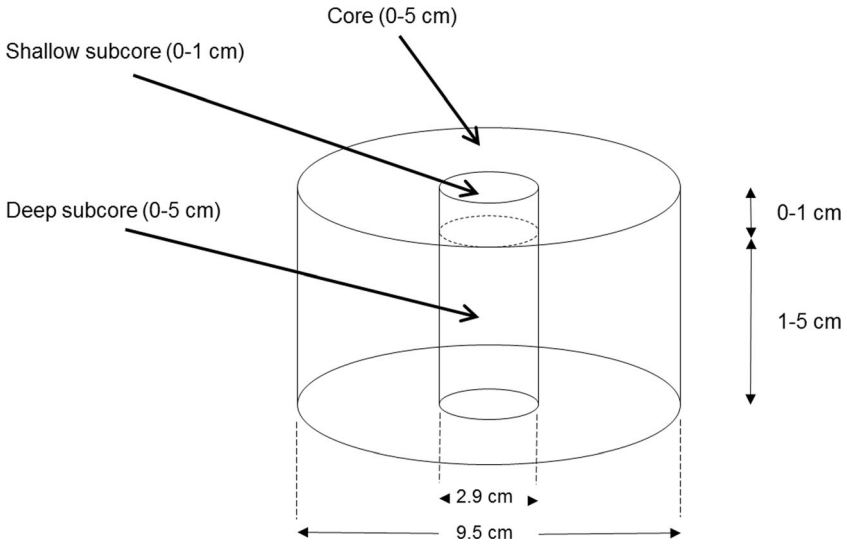

Fig. 2 Schematic representation of sampling methodology

canyon sites), habitat was included as a factor in the PERMANOVA analyses to take into account potential effects of habitat on nematode diversity and community structure (Leduc et al. 2014). The potential effect of water depth was accounted for by entering this variable as a covariate prior to significance testing. Analyses were conducted using a repeated measure design (to take into account the lack of independence between samples taken within the same MUC tube) using the fixed factor Core Size (three levels: Shallow subcore, Deep subcore, and Core), the fixed factor Habitat (two levels: Slope vs. Canyon), and with the random effect Site nested within Habitat but not Core Size (Quinn and Keough 2009). Pairwise comparisons were used to test for the effect of core depth (i.e., Shallow subcore vs. Deep subcore) and surface area (i.e., Deep subcore vs. Core) when a significant main effect of Core Size was found. No pairwise comparison was conducted between Shallow subcore and Core because any difference between these two levels could be due to variation in surface area, core depth, or a combination of the two. The PERMDISP routine was used to compare multivariate dispersion between core sizes (Anderson et al. 2008). The SIMPER routine in PRIMER was used to identify the taxa contributing most to significant pairwise differences between core sizes.

Correlation between estimates of genus richness in deep subcores and the corresponding cores (i.e., the core from which each subcore was taken) was investigated using distance-based linear models (DistLMs) in PERMANOVA+ (Anderson et al. 2008). The DistLM routine is a semi-parametric, permutation-based method that does not rely on the assumption of normally distributed data (Anderson et al. 2008). Similarly, correlation between similarity matrices of community structure inside deep subcores and cores was determined using the RELATE function in PRIMER (Clarke and Warwick 2001).

Similarity matrices for nematode diversity were built using Euclidean distance of untransformed data, and similarity matrices for multivariate data (nematode community structure) were built using the Bray–Curtis similarity measure of square root-transformed data (Anderson et al. 2008). *P* values for individual predictor variables were obtained using 999 permutations (Anderson et al. 2008).

Results

A total of 1,783 nematodes belonging to 98 genera were identified. The most common genera were *Mudwigglus* (6 % of depth-integrated total abundance), *Sabatieria* (6 %), *Halalaimus* (5 %), *Microlaimus* (5 %), *Cervonema* (4 %), and *Paramonohystera* (4 %).

There was no significant difference in nematode diversity or community structure between slope and canyon habitats (PERMANOVA, $P>0.05$; Table 1). Core size had a significant effect on all response variables, but pairwise comparisons showed different patterns in community structure and diversity. Community structure was significantly affected by core depth (Shallow subcore vs. Deep subcore; $P<0.05$) but not by core surface area (Deep subcore vs. Core; $P>0.05$) (Fig. 3). There was no significant difference in multivariate dispersion between core sizes (PERMDISP $P>0.05$). Results of SIMPER show that, of the species contributing most to the dissimilarity between core depths, *Acantholaimus*, *Desmoscolex*, and *Linhystera* were more common in shallow (0–1 cm) than in deep sediment (1–5 cm), whereas *Laimella*, *Molgolaimus*, *Mudwigglus*, *Sabatieria*, and *Sphaerolaimus* showed the opposite pattern. Community structure of deep subcores was not significantly correlated community structure in the cores from which they were taken (RELATE, $P>0.05$).

Table 1 Results of PERMANOVA analyses testing for the effects of core volume (fixed factor with three levels: Shallow subcore, Deep subcore, and Core), habitat (fixed factor with two levels: Slope vs. Canyon), site (random factor nested within the factor habitat), and the interaction of core volume and habitat on nematode genus richness and community structure after accounting for the effect of water depth (covariate)

	df	MS	Pseudo-*F*	*P*	Pairwise comparisons
EG(51)					
Water depth (covariate)	1	4.2	1.06	0.398	Shallow subcore = Deep subcore
Core volume	2	35.7	10.92	0.007	Deep subcore < Core
Habitat	1	21.3	5.35	0.128	
Site (Habitat)	4	4.0	1.22	0.354	
Core volume × Habitat	2	7.0	2.15	0.162	
Residual	8	3.3			
Total	17				
Community structure					
Water depth (covariate)	1	1,639	1.27	0.314	Shallow subcore ≠ Deep subcore
Core volume	2	1,807	3.01	0.004	Deep subcore = Core
Habitat	1	1,489	1.16	0.444	
Site (Habitat)	4	1,288	2.15	0.003	
Core volume × Habitat	2	659	1.10	0.383	
Residual	8	600			
Total	17				

Factors with significant effects ($P<0.05$) are shown in bold. Pairwise comparisons between levels of the factor core volume are shown when a significant main effect was found

Genus richness showed the opposite pattern to community structure and only differed between cores of different surface areas (PERMANOVA, $P<0.05$; Table 2; Fig. 4). Values of EG(51) were on average 12 (range: 4–33 %) higher in cores relative to the smaller deep subcores. The range of diversity values in deep subcores was also wider than in cores. Values of EG(51) ranged from 20.0 to 30.3 (range of 10.3) in deep subcores and from 26.8 to 30.6 in cores (range of 3.8). There were no significant correlations between diversity values in deep subcores and those of the cores from which the subcores were taken (DistLM, $P>0.05$).

Fig. 3 Two-dimensional multidimensional scaling configuration for nematode species abundance (square root-transformed data) showing differences in community structure between shallow subcores (0–1 cm sediment depth), deep subcores (0–5 cm), and cores (0–5 cm). See Table 1 for results of PERMANOVA

Discussion

The findings from the present study demonstrate that core surface area can have a significant influence on estimates of deep-sea nematode diversity. Larger cores yielded higher genus richness estimates (by up to a third) than those derived from smaller subcores. This effect probably stems from the larger number of nematode species aggregations included in the larger cores relative to small ones; a study by Gallucci et al. (2009), for example, showed high within-core (c. 80 cm^2) heterogeneity in deep-sea nematode community structure due to the small size of nematode species aggregations (<4 cm^2). Lack of correlation between diversity estimates based on subcores and cores showed that this shift in diversity associated with core surface area was not consistent among sites, suggesting that observed diversity patterns may vary depending on core size. This lack of a consistent shift in diversity between core sizes is likely to be a reflection of the high within-core variability in nematode community structure, a phenomenon that probably adds a considerable amount of noise in estimates of local (or alpha) and turnover (beta) nematode diversity (Ingels and Vanreusel 2013).

We did not find any consistent influence of core depth on estimates of nematode diversity. This finding is in contrast with previous results showing significantly higher species richness in deep subcores (0–5 cm sediment depth) relative to shallow subcores (0–1 cm) in the same region (Leduc et al. 2010). This difference could be due to contrasting methodologies; Leduc et al. (2010) sampled a single site, whereas the present study was based on samples from six sites across two different habitats types (slope and canyon). Among-site variability in nematode vertical distribution patterns (possibly due

Table 2 Nematode genus richness [EG(51)] at the southern Hikurangi margin study sites

	Slope			Canyon		
	670 m	683 m	1,350 m	985 m	1,046 m	1,121 m
Shallow subcore	24.8	24.1	22.4	23.7	26.2	24.6
Deep subcore	20.0	26.4	24.1	27.6	27.2	30.3
Core	26.8	29.1	29.7	29.5	30.6	28.9

to differences in organic matter supply and/or sediment characteristics) could explain the discrepancy between the two studies. In addition, the number of individuals identified by Leduc et al. (2010) was greater in deep than in shallow subcores (250 vs. 110 individuals), which may have inflated estimates of richness [ES(51)] in the former relative to the latter (Gray 2000). Lastly, the effects of core depths may be more easily detected when conducting species- than genus-level analyses.

Nematode community structure was influenced by core depth but not surface area. Average dissimilarity between shallow and deep subcores (45.2 %), however, was only slightly greater than average dissimilarity between deep subcores and cores (41.3 %). Thus, the presence of a significant core depth effect reflected the consistent shift in nematode community structure between sediment layers observed among study sites. Cores of different depths showed consistent shifts in the abundance of genera that have a preference for either surface or subsurface sediment layers (e.g., *Acantholaimus*, *Desmoscolex*, *Laimella, Sabatieria*). These genera show the same preference for the respective sediment depth layers across regions and ocean basins and are largely responsible for the pronounced community structure differences with sediment depth found in studies around the globe (e.g., Braeckman et al. 2011b; Leduc et al. 2010; Soetaert et al. 2002; Ingels and Vanreusel 2013). Shifts of similar magnitude were observed horizontally (i.e., between cores and deep subcores), but were not consistent among sites (as they were caused by shifts in the presence and/or abundance of different genera). The lack of correlation in community structure estimates between deep subcores and the cores from which they were taken mean that patterns in community structure are dependent on core surface area. Investigation of nematode community structure patterns should therefore be based on cores of fixed depth and surface area to avoid any core size effects.

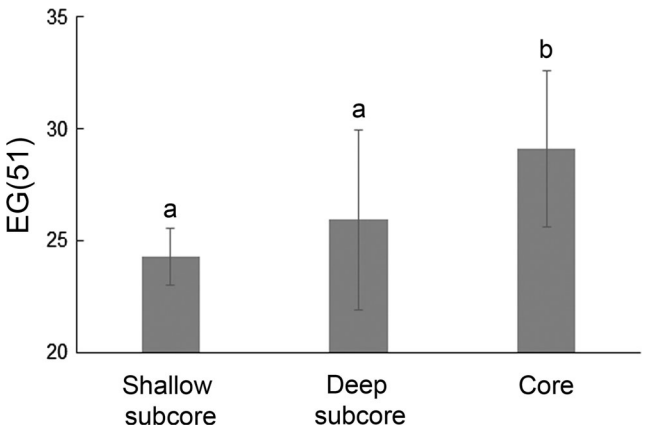

Fig. 4 Mean of nematode diversity (n=6) estimated from shallow subcores (0–1 cm sediment depth), deep subcores (0–5 cm), and cores (0–5 cm). *Error bars* standard deviations from the mean. *EG(51)* expected number of genera for a sample of 51 individuals. *Lower case letters above the bars* show the results of pairwise comparisons, with different letters indicating a significant difference between core sizes (PERMANOVA, P<0.05; see Table 1)

One weakness of the present study is that 100 nematodes were analysed for all samples irrespective of the dimensions of sampling units and total nematode abundance. This approach means that a smaller proportion of the total population was subsampled in the physically larger cores relative to the small ones (e.g., core vs. shallow and deep subcores). A better approach would have been to analyse a constant proportion (e.g., 20 %) of the total nematode population in each sample, because subsamples that are small relative to the sample may lead to increase variability in estimates of community attributes (i.e., lower precision; Andrew and Mapstone 1987; Gray 2000). This discrepancy in the proportion of the population represented in subsamples could explain why estimates of community structure were not more variable in subcores relative to cores (as would be expected since larger cores smooth out small-scale variability; Gray 1971). Consequently, any potential advantages that may be associated with obtaining large cores (i.e., lower variability in community attribute estimates) would likely be counter-balanced by the increased effort required to identify greater numbers of individuals (to ensure a suitable proportion of the total population is represented), even if only subsample are required for estimating diversity or community structure. It may be more informative to process a larger number of smaller cores, which, for the same number of individuals subsampled, would also provide information on species/genus turnover between sampling units.

There is no "correct" core size for sampling deep-sea nematodes; core dimensions only need to be appropriate for the particular environment and hypothesis(es) being investigated. However, the degree of horizontal and vertical patchiness in nematode distribution can vary considerably depending on local environmental conditions, and this variability should be taken into account when choosing core dimensions. For example, nematodes tend to be more strongly concentrated in the surface layer of sediment in areas characterised by fine sediments and high organic matter input than in coarse sediments with low organic matter input (Heip et al. 1985). Cores that penetrate only the top sediment layer sample the majority of the nematode community in the former environment (since most nematodes have a shallow distribution) but only a small fraction of the community in the latter environment (where most nematodes live deeper). Some samples are therefore more representative of the total nematode community than others. Studies comparing deep-sea nematode communities across regions and/or productivity gradients based on the top one cm layer of sediment, may therefore be biased (Danovaro et al. 2008, 2009). The same argument is also valid for horizontal patchiness and core surface area: nematode communities that are highly patchy horizontally are less adequately sampled by small cores (i.e., samples are less representative of the total community) than communities that are more uniform.

In conclusion, we have shown that a difference of a few centimetres in the physical dimensions of a core can have a substantial influence on estimates of deep-sea nematode diversity (by up to a third) and community structure. This effect stems from the well-known relationship between surface area and diversity, and the highly patchy distribution of nematodes at small spatial scales. Studies on spatial and temporal patterns of nematode diversity and/or community structure should be based on cores with the same or similar dimensions; also, meaningful comparisons of nematode diversity and community structure between environments should ideally take into consideration any potential differences in horizontal and vertical patchiness at small (cm) scales, and ensure that core surface area and penetration depths are sufficient to allow representative samples to be obtained across the entire range of environmental conditions sampled.

Acknowledgments This research was funded by research projects under the Marine Biological Resources and Marine Physical Resources programmes of NIWA's Coasts and Oceans Science Centre (2013/14 SCI), and the programme 'Impact of resource use on vulnerable deep-sea communities' (CO1X0906) and "Consequences of Earth-Ocean Change" (C01X0702). We thank Norliana Rosli (NIWA and University of Otago) for processing the subcores, the scientific team of voyage TAN1004, and the officers and crew of RV *Tangaroa*. We are grateful to two anonymous reviewers for providing constructive criticisms on the manuscript.

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