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Nematode beta diversity on the continental slope of New Zealand: spatial patterns and environmental drivers

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ABSTRACT: The management of marine biodiversity relies on sound knowledge of beta (or turnover) and gamma (or regional) diversity patterns, but such knowledge is largely lacking for continental slope environments. Here, we used free-living nematodes to investigate spatial and environmental patterns of beta and gamma diversity on 2 major seabed features of the New Zealand continental slope, Chatham Rise and Challenger Plateau. Species gamma diversity on Chatham Rise was about twice that observed on Challenger Plateau, which likely reflected the greater number of sites sampled and greater range of environmental conditions encompassed by our sampling on the former. Mean Bray-Curtis dissimilarity in community structure/composition (i.e. beta diversity) between Chatham Rise and Challenger Plateau, though high (>80%), was only marginally greater than within-region dissimilarity, and the beta diversity patterns we observed were mainly driven by factors acting at smaller (i.e. among-site) spatial scales. Sediment physico-chemical characteristics (i.e. microhabitat heterogeneity) were the main environmental driver of nematode species and genus beta diversity, and explained about a fifth of the variability. Spatial structure explained a similar proportion of species beta diversity, which, because our sampling strategy was designed to maximise the range of environments sampled across the study areas, may suggest an influence of environment at scales beyond that of the individual cores. A similarity profile test (SIMPROF) identified 9 sample groups based on species data, suggesting a relatively high level of heterogeneity on the open slope of New Zealand.

KEY WORDS: Chatham Rise · Challenger Plateau · Community structure · Sediment characteristics · Organic matter input · Habitat heterogeneity · Taxonomic resolution

INTRODUCTION

Describing and understanding beta diversity patterns (i.e. change in community composition/structure along spatial and environmental gradients; Anderson et al. 2011) is an important component of community ecology (e.g. Ellingsen & Gray 2002, Thrush et al. 2010). Lack of independence between sites due to geographical proximity (i.e. spatial autocorrelation/structure), however, is thought to be common in natural communities and poses problems for the interpretation of ecological patterns (Legendre 1993). In particular, failure to take into account the spatial component of ecological variation may affect tests of statistical significance when investigating relationships between diversity and environmental para-

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meters (Legendre & Troussellier 1988), but few beta diversity studies in the marine environment have considered the intrinsic spatial component of community composition (but see Merckx et al. 2009, Proches et al. 2010).

There has been increased interest in better quantifying spatial patterns of marine beta diversity in the last decade because of the pivotal role of beta diversity in relation to population connectivity and resilience (Thrush et al. 2009), environmental classification (Hooper et al. 2002) and conservation (Thrush et al. 2010). Defining community boundaries in the deep sea poses considerable challenges not only due to the difficulties in obtaining the required biological information, but also in relation to the interpretation of such data (Ricklefs 2008, Rex & Etter 2010). Clustering techniques that use resemblance measures (e.g. dissimilarity among samples of species) have helped provide objective methods for the delimitation of 'natural' communities, but they are less useful (or even misleading) when there is a gradual change in community composition between sites (Clarke & Warwick 2001), or impractical when they identify more communities than can be represented by a workable conservation/management scheme. Moreover, biogeographical subdivisions based on community composition patterns of different taxa are rarely consistent (e.g. Cartes et al. 2003). Thus, some degree of subjectivity is difficult to avoid when delimiting community boundaries for management purposes.

Our knowledge of the drivers of beta diversity in the marine environment, and in the deep sea in particular, is limited relative to terrestrial and freshwater ecosystems (Rex & Etter 2010). The majority of deep-sea studies of community composition have focused on depth-related patterns, with species turnover rates usually directly related to differences in water depth, and only weakly or not related at all to distance (Rex & Etter 2010). The rate of species replacement for mega-, macro- and meiofauna is usually greater on the continental slope, particularly at upper to mid-bathyal depths, than in the abyss, i.e. >4000 m; see Rex & Etter 2010 and references therein). This pattern probably reflects the relatively steep environmental gradients, complex topography and high environmental heterogeneity associated with bathyal zones (both vertically and horizontally) relative to deeper regions. Environmental factors such as organic matter input (Hecker 1990), input of terrestrial material (Galéron et al. 2009), currents (Blake & Grassle 1994), macrohabitat heterogeneity (Gooday et al. 2010), temperature (Howell et al. 2002), oxygen concentration (Levin et al. 2000) or a combination thereof are likely to be involved in determining beta diversity patterns in bathyal habitats. Thus, the continental slope is the ideal system for studying spatial patterns of deep-sea beta diversity and their potential environmental causes.

Nematodes are the most abundant (Giere 2009), and arguably the most diverse, animals in the deep-sea benthos (Lambshead & Boucher 2003). They also make a substantial contribution to deep-sea ecosystem functioning (e.g. Baguley et al. 2008). The majority of beta diversity studies in the deep sea, however, focus on the larger mega- and macrofauna (Rex & Etter 2010). A recent review of the ~640 deep-sea (>200 m depth) nematode species known to date shows that 100 species have wide bathymetric ranges (>1000 m), and 46 are likely to be cosmopolitan (Miljutin et al. 2010), suggesting that species turnover in the deep sea may be limited. On the other hand, studies on continental margins have found high levels of nematode beta diversity across and within ocean basins (Fonseca et al. 2007, Danovaro et al. 2009). Macrohabitat heterogeneity (e.g. canyons, coral degradation zones) in the deep sea influences nematode beta diversity patterns at regional to global scales (Raes & Vanreusel 2006, Vanreusel et al. 2010), but little is known about the potential influence of sediment characteristics (i.e. microhabitat heterogeneity; Fonseca & Soltwedel 2009). This lack of information is somewhat surprising given the strong links between sediment physical and chemical characteristics and the composition of benthic communities in shallow habitats (e.g. Vanaverbeke et al. 2011).

Many studies of deep-sea community composition are based on genus or family rather than species data. The paucity of data on the distribution of deep-sea species probably reflects the highly labour-intensive nature of species identification. Obtaining nematode species distribution data is particularly demanding in deep-sea investigations due to the high abundance, high diversity and the high proportion of undescribed species (Miljutin et al. 2010). These difficulties have led some researchers to explore the use of higher taxonomic levels (i.e. genus, family) as surrogates for species-level information for the study of meiofaunal diversity patterns in shallow marine habitats (e.g. Heip et al. 1988). Several nematode studies have shown that there is minimal loss of ecological information when using genus-level data (e.g. Heip et al. 1988, Somerfield & Clarke 1995), but few studies have been conducted in the deep sea (Muthumbi et al. 2011).

Elsewhere we have described patterns of nematode alpha diversity (Leduc et al. 2012b) on the continental slope of New Zealand. Here we compared nematode gamma diversity between 2 regions within the New Zealand Exclusive Economic Zone (Chatham Rise and Challenger Plateau) and investigated patterns of beta diversity within them. In doing so, we aimed to: (1) determine the influence of environmental factors (i.e. sediment characteristics and food availability) on nematode beta diversity; (2) describe spatial patterns in nematode community structure/composition; and (3) evaluate the effect of using lower taxonomic resolution (i.e. specific vs. generic) on these patterns.

MATERIALS AND METHODS

Sampling and laboratory methods

We focussed on 2 main bathymetric features of the New Zealand region, Challenger Plateau and Chatham Rise (SW Pacific Basin; Fig. 1). Challenger Plateau encompasses water depths from ca. 400 to 3000 m in an area of low biological productivity (Murphy et al. 2001) and low current activity (Heath 1985) to the northwest of the South Island, New Zealand. Chatham Rise is a submarine ridge extending eastwards from the South Island of New Zealand. It encompasses water depths from ca. 250 to 3000 m and lies beneath the Subtropical Front (STF), a region associated with heightened primary productivity (Murphy et al. 2001) and high levels of mixing and current activity (Nodder et al. 2007). Productivity is highest on the southern flank of the rise where the STF appears to be bathymetrically locked (Uddstrom & Oien 1999). Productivity over both Chatham Rise and Challenger Plateau is generally highest in areas closest to the mainland of New Zealand (i.e. eastern Challenger Plateau and western Chatham Rise) and lowest in areas farther offshore (i.e. western Challenger Plateau and eastern Chatham Rise; Murphy et al. 2001). The study area encompassed a wide range of environmental parameters (Table 1) and was well-suited for examining patterns of turnover beta diversity (sensu Anderson et al. 2011).

Sample sites and sampling methods are described by Leduc et al. (2012b). Briefly, samples were collected along a north–south transect at 178° 30′ E across Chatham Rise (9 sites, 350 to 3100 m water depth) in austral spring (September to October) 2001 during National Institute of Water and Atmospheric Research (NIWA) cruise TAN0116. This transect crossed contrasting productivity regimes on either

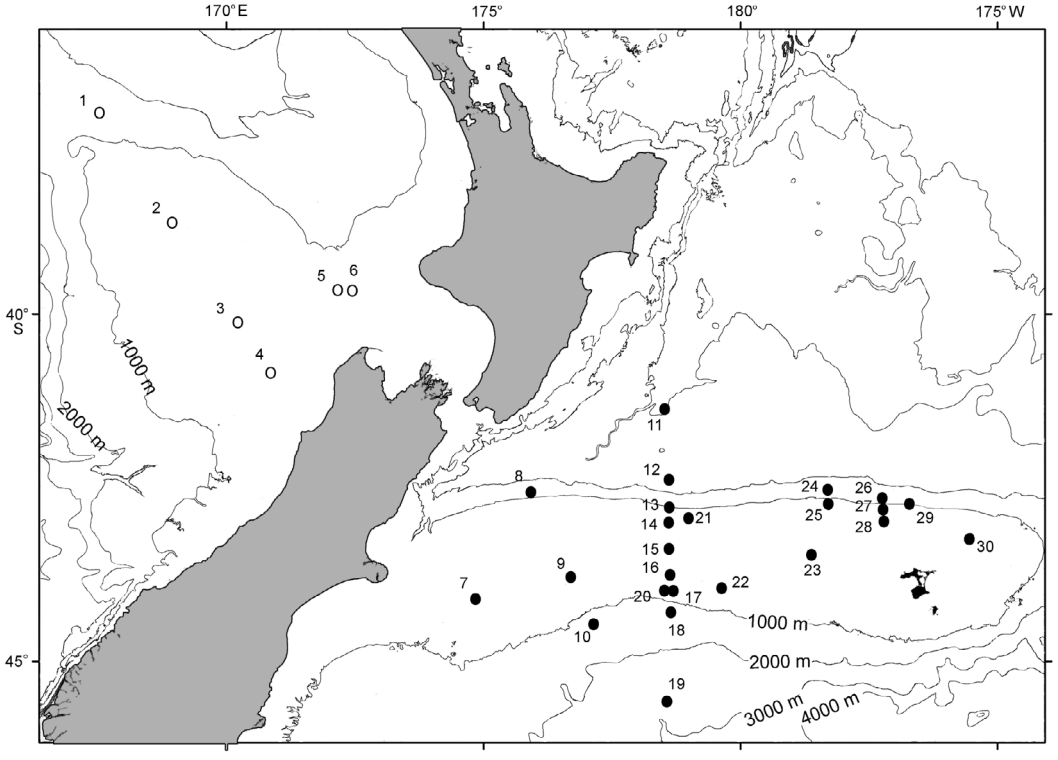

Fig. 1. New Zealand, showing 1000 m isobaths and location of study sites on the Chatham Rise (bottom right, ●) and Challenger Plateau (top left, ○)

Table 1. Number of sites, samples, individuals, species and genera identified on Chatham Rise and Challenger Plateau, range of environmental conditions and estimates of gamma species and genus diversity. The 3 deepest sites (2300–3100 m water depth) sampled on the Chatham Rise are not included in the Chatham Rise column to keep depth ranges comparable between regions. Numbers in brackets are standard deviations of the mean. CPE: chloroplastic pigment equivalents; DW: dry weight; TOM: total organic matter. Chao1 and ACE are abundance-based estimators; Chao2 and ICE are incident-based estimators

	Chatham Rise (350–1250 m)	Challenger Plateau (237–1213 m)	Chatham Rise & Challenger Plateau (237–3100 m)
No. of sites	21	6	30
No. of samples	23	11	38
% silt/clay range	6–94	35–90	6–97
% $CaCO_3$ range	10–80	26–90	10–100
% H_2O range	35–54	45–55	35–63
% chlorophyll *a* range	0–14	0–2	0–14
CPE range (µg g^{-1} DW sediment)	650–8348	832–3038	594–8348
%TOM range	1–6	2–4	1–7
No. of individuals identified	2845	1241	4546
Singletons (species)	218	136	283
Doubletons (species)	93	52	130
Recorded species richness	564	307	775
Recorded genus richness	146	102	162
Chao1 (species)	820 (46)	480 (40)	1080 (48)
Chao2 (species)	899 (55)	528 (46)	1183 (58)
ACE (species)	810	487	1082
ICE (species)	979	601	1281
Chao2 (genera)	156 (6)	161 (28)	181 (9)
Chao1 (genera)	156 (6)	129 (14)	185 (13)
ACE (genera)	154	128	175
ICE (genera)	162	141	183

side of the rise and provided the opportunity to sample communities under different trophic conditions at comparable depths (Berkenbusch et al. 2011). Twenty-one additional sites (6 on Challenger Plateau and 15 on Chatham Rise, 240 to 1300 m water depth) were sampled in austral autumn to early winter (March to April and May to June) 2007 (NIWA cruises TAN0705 and TAN0707, respectively). Sampling sites were determined based on the subdivision of Chatham Rise and Challenger Plateau into strata derived from multivariate classification of environmental data (Bowden 2011), thereby providing samples from a wide range of environments. The greater number of sites sampled on Chatham Rise relative to Challenger Plateau reflect the greater number of environments thought to exist on the former feature (Nodder et al. 2012). All the sites sampled in the present study were located on the open slope.

Sediment samples were collected using an Ocean Instruments MC-800A multicorer (MUC; core internal diameter = 9.52 cm). One to 3 replicates (i.e. samples from different MUC deployments) per site were obtained for faunal analyses. Each sample consisted of 1 subcore (internal diameter: 26 mm) taken to a depth of 5 cm. Samples were fixed in 10% formalin and stained with Rose Bengal. Samples were subsequently rinsed on a 1 mm sieve to remove large particles and on a 45 µm sieve to retain nematodes. Nematodes were extracted from the remaining sediments by Ludox flotation and transferred to pure glycerol (Somerfield & Warwick 1996). Extracted samples were mounted onto slides, and between 110 and 150 randomly chosen nematodes (or all individuals if fewer were present in the sample) were identified to genus and putative species using the descriptions in Warwick et al. (1998), as well as the primary literature. *Monhystrella* and *Thalassomonhystera* were treated as 1 genus ('Monhysteridae') because they are sometimes difficult to distinguish based on morphology (Fonseca & Decraemer 2008).

Physical and biogeochemical parameters were measured at the scale of individual MUC cores at all study sites. Methods for the analyses of sediment parameters were given by Nodder et al. (2003) and Grove et al. (2006). These parameters were: chloroplastic pigment equivalents (CPE), proportion of chlorophyll *a* (chl *a*) relative to chloroplastic pigment equivalents (% chl *a*), total organic matter content (%TOM), carbonate content (%$CaCO_3$) and water content (%H_2O). Sediment granulometry was quantified using the percent dry weight of 5 size classes (i.e. <63, 63–125, 125–250, 250–500, >500 µm).

Statistical analyses

Gamma diversity

We determined gamma (regional) diversity for Chatham Rise and Challenger Plateau separately by computing estimates of total species and genera richness using non-parametric estimators. We used both abundance- (i.e. Chao1 and ACE) and incidence-based estimators (Chao2 and ICE) because these

have been shown to perform well in comparative studies (e.g. Foggo et al. 2003) and because agreement between different estimators would suggest a robust result (e.g. Labrune et al. 2006). Estimates of species and genera richness using these estimators were computed using the EstimateS software v8.2.0 (Colwell 1997). Only 3 sites >1300 m water depth were sampled (11, 12, 19), all on Chatham Rise. These sites were omitted from comparisons to ensure comparable depth ranges between regions. Result from species and genus data were compared by plotting randomised, cumulative species richness estimates against number of samples.

Beta diversity

Beta diversity was calculated as the Bray-Curtis similarity between samples (e.g. Anderson et al. 2011) and represented as percentage similarity. Similarity matrices were computed using both square-root transformed abundance data and presence/absence data because the choice of transformation can have a substantial impact on beta diversity patterns (Anderson et al. 2011). Correlations between the matrices based on square-root and presence/absence data were determined using the RELATE function in PRIMER (Clarke & Warwick 2001) to examine differences between beta diversity patterns derived from abundance and presence/absence data. The relationship between species and genus similarity matrices was determined in the same way. Preliminary analyses showed no significant differences in community structure and composition between the 2 sampling years (i.e. 2001 and 2007; analysis of similarity [ANOSIM], $p > 0.05$); therefore, data from both years were combined in the final analyses.

The SIMPER function in PRIMER was used to quantify Bray-Curtis dissimilarity between sites (Clarke & Warwick 2001) and to provide a basis for comparisons with other studies of nematode beta diversity. Dissimilarities were quantified both within and across the 2 study regions. This analysis was based on 1 replicate per site only to avoid biases arising from the uneven number of replicates per site.

Relationships between spatial and environmental parameters and nematode beta diversity were investigated using distance-based linear models (DistLMs) in PERMANOVA+ (Anderson et al. 2008). The DistLM routine is based on an approach called distance-based redundancy analysis (dbRDA) first developed by Legendre & Anderson (1999). It is a semi-parametric, permutation-based method that does not rely on the assumption of normally distributed data and is a form of multivariate multiple regression that can be performed directly on a distance or dissimilarity matrix of choice (Anderson et al. 2008). The analyses conducted in DistLM are based on the individual samples, thereby allowing straightforward interpretation of partial regression tests (Anderson et al. 2008). In contrast, other approaches, which treat the individual distances as a single univariate response, are problematic for the interpretation of multiple regression analyses (e.g. the Mantel approach, Anderson et al. 2011). As for the SIMPER analyses, all DistLM analyses were conducted using 1 randomly chosen replicate per site to avoid biases arising from the uneven number of replicates per site. DistLM analyses are not affected by differences in the number of sites between regions (Anderson et al. 2008).

The spatial structure of nematode communities was modelled by building a matrix including the coordinates of each site on an arbitrary grid (X and Y), as well as their quadratic (X^2, Y^2) and cubic components (X^3, Y^3). The inclusion of quadratic and cubic terms allows us to model features such as gaps or patches instead of being limited to simple linear gradients (Borcard et al. 1992). These variables were analysed in a single set (hereafter referred to as 'spatial structure'; Anderson et al. 2008). Because connectivity between Chatham Rise and Challenger Plateau may be limited, we included the factor 'region' as an additional (but separate) spatial variable.

Variability in nematode beta diversity was partitioned according to 2 sets of environmental parameters, i.e. food availability and sediment physicochemical characteristics. Three environmental variables, i.e. CPE, % chl *a*, and %TOM, were considered food-related and were analysed together as a single set ('food availability'). The 7 remaining variables, i.e. $\%CaCO_3$, $\%H_2O$ and the percentage contribution of the different size classes (i.e. <63, 63–125, 125–250, 250–500, >500 µm) were analysed together in another set ('sediment characteristics'). Two variables were highly correlated (i.e. % 63–125 and 125–250 µm, $R^2 > 0.9$); therefore, one of these variables (% 125–250 µm) was removed from the analysis to avoid co-linearity (Quinn & Keough 2009).

Water depth is usually considered an environmental variable because it is often correlated with other parameters such as food availability and sediment characteristics. Here we considered water depth as an additional spatial variable (i.e. the third spatial dimension) because more direct proxies of food availability and sediment characteristics were included in the analyses (see above).

Relationships between spatial and environmental parameters and nematode beta diversity were initially examined by analysing each of the 5 predictors (i.e. spatial structure, region, water depth, food availability and sediment characteristics) separately (marginal tests). We then examined the relationship between beta diversity and the 2 environmental parameters (sediment characteristics and food availability) given the effect of the spatial variables by entering spatial structure, region and water depth as starting terms (Anderson et al. 2008). The step-wise selection procedure was applied for the 2 environmental parameters using adjusted (R^2_{adj}) as a selection criterion in order to take into account the different number of variables within each parameter (Anderson et al. 2008). We then investigated the relationship between spatial parameters and nematode beta diversity given the effect of environmental parameters by using the same approach (i.e. by entering sediment characteristics and food availability as starting terms, followed by a step-wise selection procedure for the 3 spatial parameters using R^2_{adj} as selection criterion). The p-values for individual predictor variables were obtained using 9999 permutations of raw data (Anderson et al. 2008).

To determine the proportion of total variation explained by the each predictor parameter to the overall model of beta diversity (and to produce a simple illustrative figure), the variability in species and genus beta diversity was partitioned into: (1) 'pure' environmental variation, or the fraction of variation explained by environmental parameters independently of spatial parameters; (2) 'pure' spatial variation, or the fraction of variation explained by spatial parameters independently of environmental parameters; (3) spatially structured environmental variation, or the fraction of variation explained by the combination of environmental and spatial parameters; and (4) unexplained variation, or the fraction of variation not explained by either environmental or spatial parameters in the DistLM models (for details see Borcard et al. 1992). The number of variables we used for spatial (8) and environmental (9) parameters were similar, which allowed meaningful comparisons of explained variation between the 2 parameters (Borcard et al. 1992).

Community composition/structure

We described the spatial patterns in community composition and structure using hierarchical cluster analysis in PRIMER (Clarke & Warwick 2001). Similarity matrices were built using Bray-Curtis similarity of square-root transformed abundance data and presence/absence data, and all samples (including replicates) were included in the analyses. A similarity profile test (SIMPROF) was performed to identify natural group structure in the samples (Clarke et al. 2008). The SIMPROF routine conducts a series of permutation tests to find clusters of samples with statistically significant internal structure (p set at 0.05; Clarke & Warwick 2001). Results of the SIMPROF analysis were superimposed on a map of the study area for graphical representation. The SIMPER routine in PRIMER was used to identify the taxa contributing most to within-group similarity and between-group dissimilarity (Clarke & Warwick 2001).

RESULTS

Gamma diversity

A total of ca. 4550 individuals belonging to 775 species and 162 genera were identified from the 38 samples taken on Chatham Rise and Challenger Plateau (Table 1). Over half (53%) of the species were represented by only 1 or 2 individuals, and about a quarter (23%) were recorded from both regions. The number of recorded species and genera were higher for Chatham Rise than Challenger Plateau (Table 1). Abundance-based estimators (i.e. Chao1 and ACE) consistently yielded lower estimates of total species richness than incidence-based estimators (Chao2 and ICE) (Table 1). Estimates were broadly consistent, however, with Chao2 estimates usually in the middle range of values. Estimates of total species richness for Chatham Rise (350 to 1250 m water depth), for example, ranged from 810 to 979 species (Chao2 estimate of 899 species), whilst estimates for Challenger Plateau (237 to 1213 m) ranged from 480 to 601 species (Chao2 estimate of 528 species). Plots of randomised, cumulative Chao2 estimates against number of samples show that species curves for each region, and for both regions combined, approached an asymptote, whereas the curve for genera (both regions combined) flattened out at 181 genera after 34 samples (Fig. 2).

Beta diversity

Comparison between abundance and presence/absence similarity matrices showed very high correlation for species (RELATE; $\rho = 0.98$, $p = 0.001$) and, to

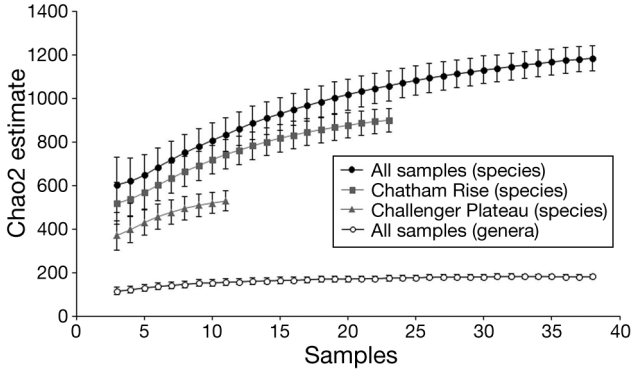

Fig. 2. Plot of randomised, cumulative Chao 2 species and genus richness estimates (±SD) against number of samples. The species curve for Chatham Rise excludes samples from the 3 deepest (2300–3100 m water depth) study sites (Sites 11, 12 and 19 in Fig. 1)

a lesser extent, genus data (ρ = 0.92, p = 0.001). Similarity matrices of species and genus data based on abundance (RELATE, ρ = 0.73, p = 0.001) and presence/absence data (ρ = 0.69, p = 0.001) were also significantly correlated. Bray-Curtis dissimilarity (square-root transformed data) was slightly greater between the 2 regions (84%) than within regions (Chatham rise: 83%; Challenger Plateau: 78%) The same pattern was found based on the presence/absence data (82, 81 and 76% dissimilarity, respectively).

Results of DistLM analyses on the influence of spatial and environmental parameters on nematode beta diversity showed similar results for species and genus data (Table 2). Results based on the abundance and presence/absence data were virtually identical; therefore, only the results based on the abundance data are reported and shown. All spatial and environmental parameters were significantly correlated with nematode species and genus beta diversity in marginal tests ($p < 0.05$). The strongest relationships were found for sediment characteristics and spatial structure (R^2 = 0.30–0.35), followed by food availability (R^2 = 0.17–0.18), region (R^2 = 0.06) and water depth (R^2 = 0.06).

The influence of sediment characteristics remained significant in sequential tests after the effect of spatial parameters was taken into account, but food availability was no longer significantly correlated with nematode species and genus beta diversity. Sediment characteristics explained 21 to 23% of the variability in species and genus beta diversity once the effect of spatial parameters was taken into account (see Table 2). In sequential tests with environmental parameters as starting terms, the effect of spatial structure remained significant for species

Table 2. Result of distance-based linear model (DistLM) analyses showing the influence of spatial (region, spatial structure, water depth) and environmental parameters (sediment physicochemical characteristics, food availability) on nematode species and genus beta diversity (Bray-Curtis similarity of square-root transformed abundance data between sites). Results of the marginal tests show the influence of each parameter in isolation, whereas results of the sequential tests show the effect of environmental parameters on nematode beta diversity in the combined model (stepwise selection with adjusted R^2 [R^2_{adj}] criterion). Prop.: proportion of total variation explained; Prop (cumul.): Prop. cumulative; Region: Chatham Rise vs. Challenger Plateau; Spatial structure: spatial coordinates and their quadratic and cubic components; Sediment: carbonate content, water content and percentage contribution of 4 different size classes; Food availability: chloroplastic pigment concentration, chlorophyll *a* content and total organic matter content. –: not applicable; $^{*}p < 0.05$; $^{**}p < 0.01$

Parameter	Prop.	Prop. (cumul.)	R^2_{adj} (cumul.)
Species			
Marginal			
Region**	0.06	–	–
Spatial structure**	0.30	–	–
Water depth**	0.06	–	–
Sediment characteristics**	0.30	–	–
Food availability**	0.17	–	–
Sequential (spatial first)			
Region + Spatial structure +			
Water depth**	0.38	0.38	0.14
+ Sediment characteristics*	0.21	0.59	0.21
+ Food availability	0.06	0.68	0.23
Sequential (environmental first)			
Sediment characteristics +			
Food availability**	0.42	0.42	0.16
+ Spatial structure*	0.20	0.62	0.22
+ Region	0.03	0.65	0.22
+ Water depth	0.03	0.68	0.23
Genera			
Marginal			
Region*	0.06	–	–
Spatial structure**	0.31	–	–
Water depth*	0.06	–	–
Sediment**	0.35	–	–
Food availability**	0.18	–	–
Sequential (spatial first)			
Region + Spatial structure +			
Water depth**	0.40	0.40	0.17
+ Sediment characteristics**	0.23	0.63	0.29
+ Food availability	0.07	0.70	0.27
Sequential (environmental first)			
Sediment characteristics +			
Food availability**	0.45	0.45	0.20
+ Spatial structure	0.18	0.63	0.24
+ Region	0.04	0.67	0.26
+ Water depth	0.03	0.70	0.27

beta diversity, but not genus beta diversity. Region and water depth were not significantly correlated with either species or genus beta diversity after the effect of environmental parameters was taken into account. Variation in nematode species and genus beta diversity in models combining all variables was partitioned as follows: (1) pure environmental variation: 30%; (2) pure spatial variation: 25–26%; (3) spatially structured environmental variation: 12–15%; (4) unexplained variation: 30–32% (Fig. 3).

Community composition/structure

Hierarchical cluster analysis based on abundance and presence/absence of species showed the same patterns and revealed 9 significant groups (SIMPROF, $p < 0.05$, Fig. 4); the following describes results based on the abundance data only. The 9 SIMPROF groups can be categorised into 5 broader, mainly location-based, 'communities' (CP, CR1, CR2, CR3) and 1 independent site (Site 19). CR1 was separated from the other communities at the 11% similarity level, and comprised 3 adjacent sites situated on the north-eastern Chatham Rise (799–980 m water depth, Fig. 5). These sites were characterised by the lowest silt/clay content of all the sites we sampled (6–7%, compared to 23–97% at the other sites). CR2 was separated from CP and CR3 at the 17% similarity level and consisted of the 2 deepest sites (2300 and 3100 m water depth) on the northern flank of the Chatham Rise. These sites were characterised by the finest sediments of the sites we sampled (95–97% silt/clay). CP and CR3 were separated at the 19% similarity level, and included the remaining sites from the Challenger Plateau and Chatham Rise, respectively, except for Site 10 (Chatham Rise), which was classified with the Challenger Plateau sites. CR3 was divided into an east (CR3E, 422–1200 m) and west sub-community (CR3W, 350–1210 m). Similarly, CP was divided into east (CPE, 237–804 m) and west sub-community (CPW, 480–1240 m).

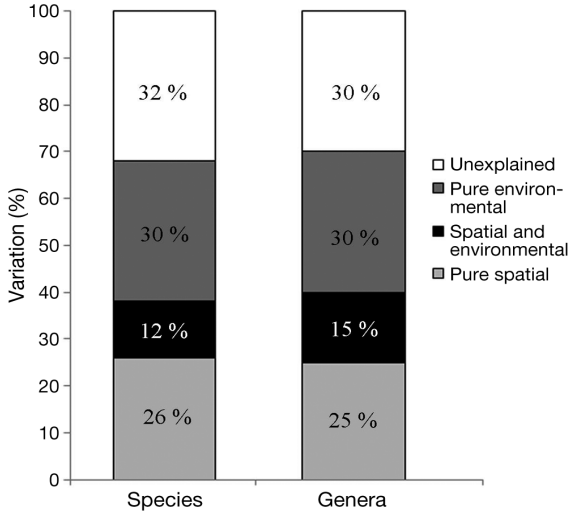

Fig. 3. Variation partitioning of nematode species and genus beta diversity similarity matrices computed using Bray-Curtis similarity of square-root transformed abundance data. See Table 2 for results of distance-based linear model (DistLM) analyses

Analysis of genus data showed some differences with the results of the species analysis, and contrasting results depending on the type of data used. The SIMPROF procedure based on the abundance data revealed 5 genera groups, which were categorised into 4 genera communities. Two of these communities corresponded to CR1 and CR2 identified from the species data, whereas the other 2 both represented a mixture of sites from CP and CR3 (Fig. 4). In contrast, only 2 SIMPROF groups were identified based on presence/absence data (not shown). One group corresponded to CR1 identified from the species data, and the other group included all other sites (except Site 18, which was not grouped).

The 5 species contributing the most to the faunal similarity of each species-based community are shown in Table S1 in the Supplement; www.int-res.com/articles/suppl/m454p037_supp.pdf. CR1 was the most distinct group identified from the hierarchical cluster analyses; about a third of the overall similarity within this group was accounted for by the species *Actinonema* sp. 3, *Calomicrolaimus* spp. 2 and 4, and *Microlaimus* sp. 17. *Diplopeltula* sp. 2, *Greeffiella* sp. 3 and *Halalaimus* sp. 7 accounted for much of the similarity of CR2. *Paramonohystera* sp. 1 contributed to the similarity of the sub-communities CR3W, CR3E and CPE, whereas *Theristus* sp. 9 was the highest contributor to the similarity sub-community CPW. The dissimilarity between CR1 and all other communities could be partly explained by the absence in the former of *Paramonohystera* sp. 1 and *Sabatieria bitumen* (Table S2 in the Supplement). Low abundance of these species within CR2 also contributed to the dissimilarity between this community and CP and CR3. The CP community could be distinguished from CR3 based on the relatively high abundance of *S. bitumen*, *Theristus* sp. 9 and *Sabatieria* sp. 16 in the former. The same species also accounted for much of the dissimilarity between CPW and CPE. High abundance of *Molgolaimus* sp. 6, *Gammanema* sp. 1, *S. bitumen* and *Vasostoma* sp. 1 in CR3E relative to CR3W contributed to the dissimilarity between these communities.

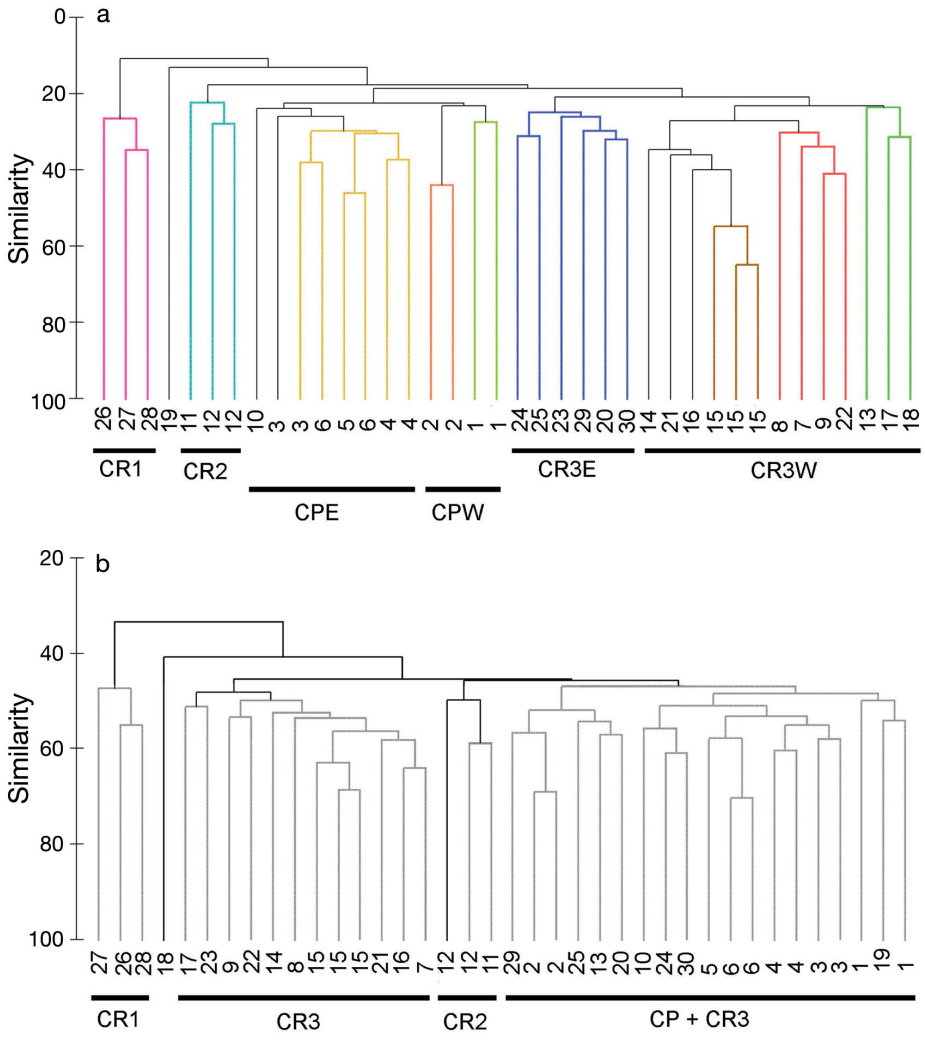

Fig. 4. Results of cluster and SIMPROF analyses of (a) species and (b) genus similarity matrices computed using Bray-Curtis similarity of square-root transformed abundance data. Significant groups ($p < 0.05$) are shown by (a) coloured (species groups) and (b) grey vertical bars (genera groups). Ungrouped samples are shown in black. Communities and sub-communities are identified by the thick horizontal lines below each cluster diagram. Numbers refer to sites shown in Fig. 1. CP: Challenger Plateau; CR: Chatham Rise; E: east; W: west

The 5 genera contributing the most to the faunal similarity of the CR1 and CR2 communities are shown in Table S3 in the Supplement. About a third of the overall similarity within CR1 was accounted for by the genera *Calomicrolaimus*, *Theristus* and *Monhystrella/Thalassomonhystera* ('Monhysteridae'). *Monhystrella/Thalassomonhystera*, *Acantholaimus* and *Desmoscolex* accounted for a similar proportion of the similarity of CR2. The dissimilarity between CR1 and the other communities could be partly explained by the low abundance of *Sabatieria* and *Monhystrella/Thalassomonhystera* in the former (Table S4 in the Supplement). We also noted the presence of the typically shallow water genera *Rynchonema*, *Xyala* and *Gonionchus* at CR1 (2–4% of total abundance); these were absent from all other sites we sampled. Low abundance of *Sabatieria*, as well as high abundance of *Monhystrella/Thalassomonhystera* and *Acantholaimus* within CR2 contributed to the dissimilarity between this and the other communities.

DISCUSSION

Gamma diversity

The number of species recorded from the study areas on the continental slope of New Zealand appears to be relatively high, although comparison with other continental margins is difficult due to differences in sampling effort and processing methods (Table 3). The number of species recorded on Chatham Rise, for example, is higher than recorded from other regions such as the North Atlantic, but this difference probably reflects the limited depth range sampled in the latter (Fonseca & Soltwedel 2009). In addition, sediment depth can have a major influence on nematode community composition (Giere 2009), and studies limited to surface sediments (e.g. Danovaro et al. 2009) are likely to substantially underestimate diversity relative to studies sampling deeper into the sediments (Leduc et al. 2010).

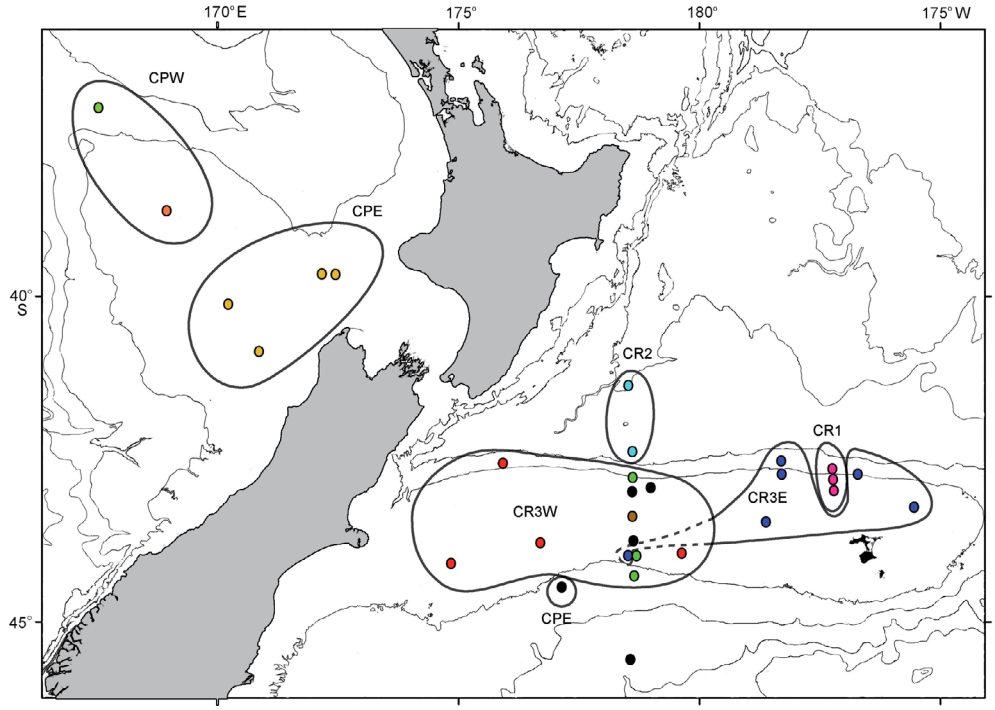

Fig. 5. Study sites, showing significant species groups ($p < 0.05$) identified from a similarity profile test (SIMPROF) analysis. Each group is identified by a colour, and ungrouped sites are shown in black. Species communities and sub-communities identified from cluster diagrams (CR1, CR2, CR3E, CR3W, CPE and CPW) are also shown. See Fig. 4 for abbreviations and details of cluster analysis

Our estimates of total species richness (gamma diversity) based on the Chao2 method are likely to be conservative because species accumulation curves did not quite reach an asymptote. Ellingsen & Gray (2002) also showed that this method can underestimate species richness by a factor of 2.5. Total nematode species richness in the study areas on the continental slope of New Zealand may, therefore, be considerably higher than our estimate of 1183 species. Total species richness on Chatham Rise (350–1250 m depth; 899 species) was almost twice that of Challenger Plateau (237–1213 m; 528 species). This difference is probably the result of the greater range of environmental conditions encompassed by Chatham Rise (see Table 1) and the greater number of sites sampled there (21 sites) relative to Challenger Plateau (6 sites). In contrast, Chao2 estimates of total genus richness reached an asymptote at 181 genera, and were similar between the 2 regions, suggesting similar levels of generic gamma diversity. This lack of

Table 3. Total nematode species richness in bathyal habitats. *N*: number of individuals identified; *S*: observed number of species; NS: not specified

Region	Water depth (m)	No. sites	No. samples	*N*	*S*	Source
Mediterranean	196–2342	23	69	NS (<6900)	255[a]	Danovaro et al. (2009)
NE Atlantic	416–4987	21	63	NS (<6300)	355[a]	Danovaro et al. (2009)
North Atlantic	2000	8	24	NS	406	Fonseca & Soltwedel (2009)
Rockall Trough	545–1474	3	9	304	80[a]	Lambshead et al. (1994)
Mediterranean	990	1	2	808	190	Soetaert & Heip (1990)
San Diego Trough	1050	1	6	1355	116[a]	Lambshead et al. (1994)
Fram Strait	2500	1	12	~1360	202[b]	Gallucci et al. (2008)
Fram Strait	1300	1	3	~3430	176[a]	Gallucci et al. (2009)
Chatham Rise	1240	1	6	1500	247	Leduc et al. (2010)
Chatham Rise	350–3100	24	38	3305	645	Present study
Challenger Plateau	237–1213	6	11	1241	307	Present study

[a]Only top 1 cm of sediment was analysed; [b]only top 2 cm of sediment were analysed

difference between regions may reflect the wide distribution of most deep-sea nematode genera and their generally low level of environmental specificity (Vanreusel et al. 2010).

Lambshead & Boucher (2003) suggested that, whilst deep-sea nematode diversity may be very high at the local scale, diversity at the regional scale is relatively limited. The information available to date appears to support this suggestion. Several studies have shown high nematode species richness (116 to 202 species) at single bathyal sites, although these are likely to be underestimates since only surface (≤2 cm) sediments were analysed (Lambshead et al. 1994, Gallucci et al. 2008, 2009). On the Chatham Rise, a comprehensive survey of nematode species at 1 site yielded 247 species (0–5 cm sediment depth, Leduc et al. 2010), which is equivalent to more than a third of all species recorded from 24 sites in the region (see Table 3). Low or comparable levels of regional diversity in bathyal relative to coastal habitats (despite the greater local diversity in the former) may be related to the lack of dispersal barriers and/or relatively low macrohabitat heterogeneity in deeper waters (Lambshead & Boucher 2003). The contribution of macrohabitat heterogeneity to regional diversity of deep-sea nematodes, however, may have been underestimated (Zeppilli et al. 2011).

Beta diversity

Our analyses based on nematode species and genus data yielded very similar relationships between environmental parameters and nematode beta diversity. Nematode genus beta diversity, however, was not significantly correlated with spatial parameters after the effect of environmental parameters was taken into account, suggesting that, unlike species data, genus beta diversity primarily reflects environmental influences and is not spatially structured. As noted above, most deep-sea genera have low environmental specificity and tend to be widely distributed (Vanreusel et al. 2010), which may explain this discrepancy. These results suggest that genus data can be used to determine environmental drivers of deep-sea nematode beta diversity without noticeable loss of information. In contrast, a study on the Kenyan margin found differences in patterns of nematode genus and species diversity (Muthumbi et al. 2011). The latter study, however, was restricted to 3 nematode families, which could explain this discrepancy.

Partitioning of variation in nematode species beta diversity showed that a substantial proportion of the variation was explained by pure spatial variation (26%), indicating that some unmeasured underlying processes are affecting nematode species beta diversity patterns. Much of this pure spatial variation was accounted for by spatial structure, which explained 20% of the variability in nematode species beta diversity in sequential tests (see Table 2). While these results do not tell us anything about the underlying mechanisms (Anderson et al. 2011), they indicate that a sizeable proportion of the variation in species beta diversity is associated with processes at the scale of our spatial structure variable. To some extent, these findings may reflect our sampling strategy for NIWA cruises TAN0705 and TAN0707 (see 'Materials and methods'), which was developed to maximise the range of environments sampled based on oceanographic data layers and parameters from multi-beam echo-sounder transects (Bowden 2011, Nodder et al. 2012). The relationship between spatial structure and nematode species beta diversity could, therefore, suggest an influence of environment at scales beyond that of the individual sediment cores at which detailed environmental measurements were made here. Irrespective of what the underlying mechanisms may be, our results suggest that future studies should focus on nematode diversity in relation to processes operating across a range of wider scales.

Our results showed high mean Bray-Curtis dissimilarity between the Chatham Rise and Challenger Plateau (82–84%, depending on whether abundance or presence/absence data were used). A study by Danovaro et al. (2009) on deep-sea nematode species communities found high levels of dissimilarity between the western and central Mediterranean (83%), and between the Portuguese and Mediterranean margins (90%); another study also found high dissimilarity between the eastern and western Mediterranean (75%; Danovaro et al. 2008). Mean Bray-Curtis dissimilarity between regions in the present study, however, was only marginally (1–6%) greater than within-region dissimilarity. In addition, results of DistLM analyses showed that the spatial factor 'region' explained only a small proportion (R^2 = 0.06) of the variability in nematode beta diversity. Deep-sea nematode species can disperse over large distances (i.e. 100–1000 km) despite their limited ability to swim and lack of pelagic larvae, and the limited evidence available to date suggests that some species are widely distributed across continental margins (Fonseca & Soltwedel 2009) and ocean basins (Miljutin et al. 2010). Potential for passive dispersal is

likely to be high on the Chatham Rise, where tidally driven currents are strong enough to regularly resuspend recently settled phytodetritus (Nodder et al. 2007), and in the vicinity of Cook Strait (which separates the 2 study regions), where very strong tidally generated currents can presumably transport individuals between the 2 regions. The high dissimilarity observed between the Chatham Rise and Challenger Plateau, therefore, was not related to regional differences in nematode species composition but to factors acting at smaller (i.e. among-site) spatial scales.

When taking into account the spatial structure of nematode communities, our findings indicate that the physicochemical characteristics of the sediments were the main environmental drivers of both species and genus beta diversity on the continental slope of New Zealand. Several studies have shown the strong influence of sediment characteristics on nematode community structure in shallow marine habitats (e.g. Merckx et al. 2009, Vanaverbeke et al. 2011). However, few studies have investigated the relationship between sediment physico-chemical characteristics and nematode beta diversity in the deep sea (e.g. Fonseca & Soltwedel 2009). The potential influence of sediment granulometry on nematodes, in particular, is seldom investigated, perhaps because variation in sediment grain size is (or is assumed to be) lower in the deep sea than in shallower environments. In the present study, a wide range of sediment grain sizes was sampled, which probably increased the likelihood of finding significant relationships relative to studies limited to a narrower range of grain sizes. Similarly, a large-scale study on the Norwegian continental shelf spanning a wide range of grain sizes showed that sediment granulometry was a major driver of macroinfaunal beta diversity (Ellingsen & Gray 2002). These findings suggest that variation in the physico-chemical structure of soft sediment habitats (i.e. microhabitat heterogeneity) is an important factor influencing beta diversity of the benthos. The key influence of larger features at the ≥ m scale (i.e. macrohabitat heterogeneity) on diversity has repeatedly been demonstrated (see review by Rosenzweig 1995); quantifying microhabitat heterogeneity and its influence on community composition or structure in the apparently homogeneous expanses of marine soft sediments, however, is challenging. The main impediment to quantifying microhabitat heterogeneity in soft sediments is the usually gradual nature of change in sediment characteristics, making any clear distinction between habitats difficult on the open slope or vast expanses of the abyss. Our results show that gradual variation in sediment characteristics over a sufficiently wide range can lead to distinct faunal communities (see next section) in soft-substratum environments. Assessing levels of microhabitat heterogeneity in deep-sea habitats should, therefore, be considered in addition to more easily observed macrohabitat heterogeneity.

In contrast, food availability did not appear to play a significant role in determining patterns of beta diversity at the study areas on the continental slope of New Zealand. This result may seem surprising given the gradients in productivity encompassed by the sampling, and a previous finding for the same areas suggests a significant unimodal relationship between productivity and nematode alpha diversity (Leduc et al. 2012a, this volume). Patterns of beta diversity, however, describe the variation in community composition/structure rather than the number of co-existing species. Thus, alpha and beta diversity trends are not necessarily influenced by the same environmental factors. In addition, highly oligotrophic habitats (e.g. abyssal plain) were not included in our analyses, which may have affected our results. Some authors, however, have observed different genus assemblages in deep-sea areas characterised by similar productivity (i.e. the abyssal NE and NW tropical Atlantic), suggesting that productivity is not always the primary driver of deep-sea nematode beta diversity (Vanreusel et al. 2010).

Community composition/structure

The number of communities identified by the hierarchical cluster analyses and SIMPROF depended on taxonomic resolution and, for the genus data, on the type of data used (abundance vs. presence/absence). All analyses identified the CR1 community as being distinct from the rest, while the CR2 community was identified in all analyses except that of genus presence/absence data. Thus, although there was some degree of consistency between the different methodologies, species data yielded a greater number of communities relative to genus data, indicating that species-level information allows greater discrimination between communities. Consequently, we suggest that species-level information is preferable for identifying communities for management and conservation purposes.

CR1 was the most distinct group identified from the hierarchical cluster analyses. Species of some genera, such as *Rynchonema*, *Xyala* and *Gonionchus*, were relatively common in CR1, but were absent everywhere else. These genera are usually found in

Fig. 6. Seabed photo taken at Site 27 on northeastern Chatham Rise (895 m water depth) showing presence of sand ripples. Scale bar = 20 cm

exposed intertidal or subtidal sandy sediments (e.g. Vincx & Furstenberg 1988, Ellis et al. 2011), and their presence in deep-sea sediments was unexpected. Conversely, genera that were dominant at most other sites (i.e. *Sabatieria*, *Monhystrella*/*Thalassomonhystera*) were relatively rare at CR1. Sediments at the 3 sites comprising the CR1 community were characterised by coarse grain size (93–94% sand), and seabed photographs of these sites show the presence of sand ripples, suggesting strong hydrodynamic conditions (Fig. 6). These findings indicate that the environmental conditions at the CR1 sites may be similar to those more typically found in shallow habitats, which may explain why the CR1 community is so distinct from all other sites we sampled.

The CR2 community was characterised by the relatively low abundance of species of the genus *Sabatieria*, a genus usually most abundant in fine sediments with high organic matter content (e.g. Soetaert & Heip 1995, Vanaverbeke et al. 2011). On the other hand, species of *Acantholaimus* and *Monhystrella*/*Thalassomonhystera* were more abundant in this community than at the other sites. These genera dominate abyssal nematode communities where organic matter input is much lower than on the continental slope (Vanreusel et al. 2010). In addition, the relative abundance of *Acantholaimus* typically increases with water depth and is inversely correlated with organic matter input (Soetaert & Heip 1995, De Mesel et al. 2006). Thus, the distinction between CR2 and the other communities probably reflects the environmental conditions typical of lower slope environments (i.e. low productivity and fine sediments).

Differences in the composition of nematode taxa between sub-communities identified from species data are more difficult to interpret due to the general lack of information on the ecology of deep-sea species. Distinctions between sub-communities were also more subtle than between communities, reflecting the greater faunal similarity of the former. Some tentative inferences, however, may be made based on the distribution of closely related species. The relatively high abundance of *Hopperia* and *Paramonohystera* spp. in the CPE sub-community relative to CPW on the Challenger Plateau, for example, may reflect the generally shallow water depth preferences of these genera (i.e. coastal and upper slope; Chen & Vincx 1998, 2000, Miljutin et al. 2010). *Theristus*, in contrast, has been described as a deep-sea genus (e.g. Soetaert & Heip 1995). Thus, the greater abundance of *Theristus* sp. 9 at CPW than at CPE may reflect the lower productivity at sites farther offshore (Murphy et al. 2001).

The distribution of the nematode communities identified by the present study can be compared with the results of previous studies for macrofauna. Probert et al. (1996) identified 2 infaunal polychaete communities on the Chatham Rise: a deep (802–1394 m) community that occurred on the northern and southern flanks of the central part of the rise, and a shallower (244–1048 m) community that occurred between the deep flanks. A more recent study by Probert et al. (2009) identified an infaunal polychaete community on the crest of Chatham Rise and another community at 750 m on the southern flank of the rise, whilst polychaete assemblages at deeper sites (981–2330 m) on either flank of the rise were highly heterogeneous. Three epibenthic macrofauna communities were distinguished on the Chatham Rise by McKnight & Probert (1997); the spatial pattern was similar to that for infaunal polychaetes. The most homogeneous of these communities occurred on the muddy sands of the crest and shallower flanks (237–602 m) of the rise. The other 2 generally depth-stratified communities were found both sides of the rise, but at deeper depths on the northern flank (625–1693 m, 462–665 m) than on the southern flank (1491–2039 m, 799–1963 m). Where the area covered by these 2 macrofauna studies overlaps with the present study (the central transect on the Chatham Rise), the spatial distribution of nematode communities is broadly similar to that of the macrofauna. A recent study of the hyperbenthic macrofauna by Lörz (2010), using data from some of the same sites as the present study from both Chatham Rise and Challenger Plateau, found that assemblages from the 2 regions were not different. This result contrasts with the weak but significant difference we described between these regions for nematode species and genus

communities. This discrepancy may reflect the relatively coarse taxonomic resolution (order, class, phylum) used by Lörz (2010).

SIMPROF results based on nematode species data yielded 9 distinct groups, suggesting a relatively high level of heterogeneity in nematode community composition/structure at our study sites. The western and central Chatham Rise areas were particularly heterogeneous and included 5 of these groups. This pattern may reflect a greater turnover of species within the western and central Chatham Rise areas than elsewhere or may have resulted from the greater density of sampling sites in these areas. The presence of 5 distinct and interspersed groups in these areas, however, would be difficult to accommodate in a workable conservation/management scheme. The more subjective grouping of the study sites into 6 broad communities and sub-communities would provide a more practical basis for spatial management of the seabed, but ignores much of the heterogeneity in the western/central Chatham Rise areas. The usefulness of the present subdivision of the study area based on nematode species data for management/conservation purposes is currently being assessed by comparing it to results of analyses based on data for other faunal groups (i.e. macrofauna, epibenthic megafauna) from the majority of the same sites (e.g. Knox et al. 2012). This study will include an evaluation of the representation of different seafloor communities by the current benthic protected areas on the Chatham Rise and Challenger Plateau (Helson et al. 2010), and the distribution of communities relative to areas covered by prospecting permits for mining of phosphorite nodules on the Chatham Rise (www.nzpam.govt.nz/cms/minerals/permits) and exploration permits for petroleum and gas on the edge of the Challenger Plateau (www.nzpam.govt.nz/cms/petroleum/permits-content).

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