Macrofaunal nematodes of the deep Whittard Canyon (NE Atlantic): assemblage characteristics and comparison with polychaetes

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# Abstract

Large nematodes form an important component of deep-sea macrofaunal assemblages, but are often considered to be part of the meiobenthos and are rarely studied. We analysed the standing stocks, diversity, and functional group and genus-level composition of macrofaunal nematodes at lower bathyal depths (3500 m water depth) in the Whittard Canyon system (NE Atlantic) and on the adjacent continental slope. Five replicate sample sets were obtained using a Megacorer, at four locations (three canyon branches, one slope). Sediment samples were processed on a 500 μm mesh to provide both nematode and polychaete data from the same samples. The dominant nematode genera included *Paramesacanthion,* *Metacylicolaimus,* *Cylicolaimus* and *Phanodermopsis*. Nematode standing stocks (density and biomass) increased significantly from slope to canyon locations. Similarly, nematode dominance increased substantially (and diversity decreased) from slope to canyon locations. Nematode feeding groups and tail shape groups also appeared to exhibit common trends across study locations. Nematode genus-level faunal composition varied significantly between slope and canyon locations. We describe and discuss the broadly similar trends detected in the matching polychaete data, noting some differences in the polychaete density and diversity responses. We suggest that the similar trends in macrofaunal nematode and polychaete ecology across our four study locations reflects responses to both changing sedimentology and food availability.

# 1. Problem

The Nematoda is the most abundant and species-rich metazoan phylum living in deep-sea sediments ([Vincx *et al.* 1994)](#h.2afmg28), often representing 90 % or more of total metazoan meiofaunal numbers ([Thiel 1975)](#h.1jlao46). As part of the meiobenthos (passing through sieves with a mesh size in the range of 300-1000 μm and retained on 32-63 μm meshes; Giere 2009), their patterns of abundance and distribution are relatively well documented ([Thiel,](#h.1jlao46) 1983; [Vanreusel *et al.* 2010;](#h.2w5ecyt) [Pape *et al.* 2013; Moens *et al.* 2013)](#h.2zbgiuw). However, deep-sea nematodes are also found in the macrobenthic size fraction (retained on ≥ 300 μm meshes; [Thiel 1983)](#h.43ky6rz), although being considered meiobenthic animals they are often omitted from macrobenthic studies. Nevertheless, these large nematodes have sometimes been recorded in high densities (Giere, 2009). Specimens measuring up to 10 mm in length were reported from epibenthic sledge samples in the deep Rockall Trough, NE Atlantic ([Gage & Tyler 1991)](#h.3as4poj), where they made up about half of the total number of macrofaunal animals collected ([Gage 1979)](#h.qsh70q). On the Goban Spur (NE Atlantic), macrofaunal nematodes became relatively more important with increasing water depth, representing up to 20 % of total macrofaunal numbers at the deepest (4460 m) station sampled ([Flach *et al.* 1999)](#h.1ci93xb). In studies of the abyssal Pacific, nematodes comprised around half of all animals retained on 300 μm mesh sieves ([Hessler & Jumars 1974](#h.vx1227), [Hecker &Paul 1979)](#h.ihv636).

Despite sometimes being considered as part of the macrofauna, these large nematodes are rarely identified taxonomically. One of the few such studies is that of [Sharma *et al.* (2011),](#h.25b2l0r) who compared meio- and macrobenthic nematode assemblages from the deep Arctic (Canada Basin), Gulf of Mexico and the Bermuda slope. They concluded that the meio- and macrobenthic nematodes were distinct assemblages in terms of community structure, body size and functional groups, and that large nematodes should be included in macrobenthic studies. The study by Baldrighi & Manini (2015) of meio- and macrobenthic nematodes and polychaetes from six sites in the deep Mediterranean Sea reached a similar conclusion. Other studies that have identified macrofaunal nematodes to the species level are those of [Pavithran *et al.* (2009),](#h.3ygebqi) [Henry & Roberts (2007)](#h.2grqrue) and [Netto *et al.* (1999).](#h.3l18frh)

In a previous paper (Gunton *et al.* 2015a), we described the polychaete family-level assemblage composition and structure at sites located at 3500 m water depth in the Whittard Canyon system and on the continental slope adjacent to the canyon. Here, we focus on the community structure and functional traits of large nematodes from the same samples (> 500 μm fraction). Submarine canyons are conduits for the transport of organic matter and sediments, and often harbour an increased density of macrofauna ([Vetter & Dayton 1998)](#h.3vac5uf) and meiofauna ([Ingels *et al.* 2011c)](#h.28h4qwu). There are differences in the environmental conditions of the main branches of the Whittard Canyon and the adjacent slope. Sediments inside the canyon are organically enriched compared with the slope (Duineveld *et al.* 2001), and bathymetric derivatives (e.g. Bathymetric Position Index, slope angle, and rugosity) differ between branches (Gunton *et al.* 2015a). Benthic community composition also differs between the branches of the Whittard Canyon and adjacent slope (Amaro *et al.* 2016; [Duineveld *et al.* 2001;](#h.4i7ojhp) [Duros *et al.* 2011;](#h.2xcytpi) [Gunton *et al.* 2015a,b)](#h.3o7alnk).

The objectives of the present study were therefore as follows: 1) describe the standing stock, genus-level composition and diversity, and functional group composition of macrofaunal nematode assemblages; 2) compare these parameters among study locations (slope, and canyon branches) for the macrofaunal nematode assemblage; and 3) contrast them with comparable measures of the corresponding polychaete assemblages as recorded for the same samples.

# 2. Material and Methods

## 2.1 Sampling

Sediment cores for macrofauna were collected using a Megacorer (Gage & Bett, 2005) from three sites inside the Whittard Canyon system and one site on the adjacent continental slope (Fig. 1) during the RRS *James Cook* cruise 036 in June and July 2009 (Masson 2009). Samples were taken from 22 deployments, all located at a depth of around 3500 m (Table 1). In general, the Megacorer was fitted with eight large core tubes (100 mm internal diameter). Five deployments were carried out at the Slope and Western branch locations, and six at the Central branch and Eastern branch locations (the additional deployments at Central and Eastern sites represented repeats to improve sample size; see Table 1). The environmental characteristics of each study location are detailed in Gunton *et al.* (2015a) and summarised here as in Table 2. Briefly, locations were selected to target a common depth (c. 3500 m), seabed slope angle was 1° at Slope and 3° at canyon locations, mean sediment grain size was 72 μm at Slope and 30 μm at canyon locations, sediment mud content was 73 % at Slope and 88 % at canyon locations, total macrofaunal density (*sensu stricto* > 300 μm) increased from west to east in the canyon branches.

On deck, all the cores from a Megacorer deployment were sliced into five sediment layers (0-1, 1-3, 3-5, 5-10 and 10-15 cm) and each layer sieved, using filtered seawater, through 500 and 300 μm mesh screens. For each deployment, all of the 500 μm sieve residues from one layer were combined into a single residue and the same procedure performed for the 300-500 μm fraction. Thus, each deployment yielded ten sieve residues (five > 500 μm and five 300-500 μm). Samples were fixed with 10 % borax-buffered formalin. See Gunton *et al.* (2015a) for further details of Megacorer sample processing and preservation. For this study, only the pooled top three layers (0-5 cm) from the > 500 μm residues were analysed.

## 2.2 Macrofaunal Specimen identification

In the laboratory, samples were transferred from formalin onto a 300 μm mesh sieve, rinsed with fresh water, and sorted in 70 % ethanol. All nematodes were picked out under a stereomicroscope, transferred to glycerine ([Seinhorst 1959)](#h.3q5sasy), mounted on glass slides under cover slips sealed with paraffin wax, and identified to genus level using the pictorial key of [Warwick *et al.* (1998)](#h.1302m92). The body lengths of nematode specimens (excluding filiform tail when present) and their maximal body widths were measured using and Olympus BX 51 microscope, a Nixon Coolpix 500 camera and ImageJ software (Schneider *et al.* 2012). Nematode wet weight was then estimated using the formula provided by Andrassy (1956). Polychaete identification was as detailed by Gunton *et al.* (2015b), with the resultant species-level data aggregated to genus-level for the comparisons reported here.

## 2.3 Functional Groups Assessments

Individuals were assigned to four feeding groups based on buccal morphology ([Wieser 1953)](#h.haapch): buccal cavity absent or minimal - selective deposit feeders (1A); large but unarmed buccal cavity - non-selective deposit feeders (1B); buccal cavity with scraping tooth or teeth - epigrowth feeders (2A); buccal cavity with large jaws – omnivores / predators (2B). The index of trophic diversity (ITD) was then calculated as ITD = sum[Ø2], where Ø is the proportional representation of each trophic group ([Heip *et al.* 1998)](#h.32hioqz). Nematodes were also classified on the ‘coloniser to persister’ scale of [Bongers *et al.* (1991, 1995), and the](#h.35nkun2) maturity index (MI) calculated as MI = sum[*y(i)\*f(i)*]*,*where *v(i)* is the c-p value of the taxon and *f(i)* is the relative frequency of the taxon. Finally, nematodes were classified by tail shape, thought to be important in locomotion, feeding and reproduction (see Thistle & Sherman 1985), into four groups based on the scheme of [Thistle *et al.*](#h.2iq8gzs) (1995): type 1, “rounded” tails with a blunt end; type 2, “clavate-conicocylindrical” tails, initially conical with an extension to the tip; type 3, “conical” tails with a pointed tip and tail length less than five body widths; and type 4, “long”, a tail longer than five body widths.

Polychaetes were similarly classified into feeding groups using the scheme proposed by [Jumars *et al.* (2015):](#h.37m2jsg) microphagous (feeding on small particles), macrophagous (feeding on larger items), omnivorous (simultaneously feeding on more than one type of food). We also followed [Jumars *et al.* (*loc. cit*.) in classifying polychaetes into three motility groups:](#h.37m2jsg) motile (burrowing, crawling, swimming), discretely motile (burrow constructing, tube dwelling, able to rebuild or extend tube, portable tube) or sessile (unlikely to survive if removed from attachment site, tube or burrow).

## 2.4 Statistical Analysis

Faunal density was assessed by conventional oneway analysis of variance (ANOVA), by study location, of log transforms, using Tukey’s method for subsequent pairwise comparisons (5 % family-wise error rate) as implemented in the Minitab statistical software package (V17, Minitab Inc.) (see e.g. Sokal & Rohlf 2012). Results are reported as geometric means and corresponding 95 % confidence intervals (i.e. back-transforms of the log variables; see e.g. Elliot 1977). To estimate biomass, we first estimated geometric mean individual body weight for a statistically standardised sample of 100 individuals from each location. This was achieved by bootstrapping using ‘boot’ package (Canty & Ripley 2015) in the R programming environment (R Core Team 2015), using the adjusted bootstrap percentile (BCa) method to produce corresponding 95 % confidence intervals (see e.g. Davison & Hinkley 1997). A biomass estimate for each study location was then obtained as the product of geometric mean density and geometric mean individual body weight. All other univariate statistical comparisons were undertaken using Mood’s median test (see e.g. Siegel & Castellan 1988) as implemented in Minitab.

Multivariate analyses of faunal composition were carried out using non-metric multidimensional scaling (MDS) ordination and analysis of similarities (ANOSIM) in the PRIMER software package (V6, PRIMER-E; Clarke & Gorley 2006; for method detail see e.g. Clarke 1993). All results reported here (nematodes and polychaetes) refer to Bray-Curtis dissimilarity calculated from √*x* transforms of the faunal density data. Similarly, all results reported here (nematodes and polychaetes) concerning faunal diversity refer to rarefied estimates of genus richness, Fisher’s alpha, Shannon index, and Simpson’s index, as determined using EstimateS software (V9 Colwell 2013; for method details see e.g. Colwell *et al.* 2012).

# 3. Results

## 3.1 Nematodes Assemblages

### 3.1.1 Nematode Abundance and Biomass

In total, 410 macrofaunal nematodes were recorded from the samples and identified to genus level (supplementary Table 1). There was a statistically significant difference in macrofaunal nematode density between locations (ANOVA, F[3,16] = 6.26, p = 0.005). Pairwise comparison revealed a statistically significant (p < 0.05) difference between Slope and all canyon locations; no significant differences were detected among canyon locations (Fig. 2, Table 3). Estimated macrofaunal nematode biomass followed a similar pattern (Fig. 2, Table 3), with substantially higher biomass recorded at canyon locations than at the Slope location (the clear non-overlap in estimated confidence intervals was conservatively significant at p < 0.05).

### 3.1.2 Nematode Genus Composition

Nineteen nematode families and 48 genera were identified. *Paramesacanthion* was the most abundant genus overall (21 % total abundance) followed by *Metacylicolaimus* (20 %), *Cylicolaimus* (9 %), and *Phanodermopsis* (6 %). *Paramesacanthion* was the most abundant genus at Slope, *Metacylicolaimus* at Western and Central, and *Cylicolaimus* at Eastern (supplementary Table 1). Non-metric multidimensional scaling ordination (MDS) of the macrofaunal nematode fauna (Fig. 3D) revealed considerable similarity among canyon samples, and the relative distinctiveness of the Slope samples. Analysis of similarities (ANOSIM) indicated statistically significant moderate variation in faunal composition among sites (R = 0.299, p < 0.001), with Slope significantly different from all canyon locations (R = 0.404-0.644, p < 0.05), and no significant difference detected between any pair of canyon locations (Table 4). A similar trend is evident in macrofaunal nematode genus diversity (Table 5). For all comparative measures estimated (rarefied richness, Fisher’s alpha, Shannon and Simpson’s index), higher diversity was recorded at Slope than at any canyon location. This distinctiveness in diversity between slope and canyon areas appears to be largely driven by the dominance component of diversity (see Fig. 5).

### 3.1.3 Nematode Functional Group Composition

Macrofaunal nematode composition by feeding group and tail shape classification is illustrated in Fig. 4A and B. Slope exhibited a significantly higher percentage of nematodes belonging to feeding Group 1A (selective deposit feeders) than the canyon locations (Mood’s median test, p = 0.015), but no significant differences were detected for the other feeding groups. Nematodes from canyon locations were predominantly (77-88 %) either epigrowth feeders (2A, 34-45%) or omnivores/ predators (2B, 35-53 %) (Table 3). Nematode feeding group 1A represented 40 % of individuals at Slope site but only 12 % at canyon locations. Neither trophic diversity nor maturity index varied significantly between locations (Mood’s median test, Table 3). There was a significant difference in the percentage contribution of tail-shape type 4 (long) between locations (Mood’s median test, p = 0.034), all other tail types showed no significant differences between locations. Tail-shape type 2 (clavate-conicocylindrical) was the most abundant, and type 4 was the second most abundant, at all of the sites (Fig. 4C). Slope had a higher percentage of tail type 3 (conical, 24 %) than other the canyon locations (average 10 %).

## 3.2 Comparison with Polychaetes

An MDS analysis of polychaete genus-level data (Fig. 3C) suggested that all study locations were relatively distinct with regard to polychaete faunal composition. ANOSIM confirmed a substantial and statistically significant difference in composition among locations (R = 0.660, p < 0.001), and appreciable significant differences in all pairwise comparisons of locations (R = 0.432-0.964, p < 0.05; Table 4). In terms of polychaete generic diversity, all comparative measures estimated (rarefied richness, Fisher’s alpha, Shannon and Simpson’s index; Table 5) produced the same ordering of study locations: Slope > Western > Central > Eastern, with canyon branches having similar levels of rarefied polychaete genus richness. The dominance component of diversity appears to be the main driver of this consistent west-east variation in polychaete diversity (see Fig. 5).

Variations in polychaete feeding group composition were observed across the study location (Fig. 4B). Microphages were consistently the most abundant trophic group (> 50 %), although their contribution decreased from Slope (62%) to Eastern (56 %). The proportion of macrophages was relatively consistent between locations (25-26 %), while the proportion of omnivores increased from 11 % at Slope to 19 % at Eastern. These proportional shifts were statistically significant in the case of the omnivorous (Mood’s median test p = 0.015), but not the micro- or macrophages. There were also changes in the proportions of polychaete motility groups between study locations (Fig. 4D). Motile taxa were most abundant, and increased from Slope, site (54 %) to Eastern (78 %). The proportion of discretely motile polychaetes declined in a corresponding manner (Slope 33 % to Eastern 14 %). The changes between locations were statistically significant in the case of motile taxa (Mood’s median test p = 0.004), but not for the discretely motile and sessile types.

# 4. Discussion

## 4.1 Prior Studies of Macrofaunal Nematodes

Although the occurrence of macrofaunal nematodes in deep-sea samples is well documented, less is known about their taxonomic composition. Perhaps the most relevant genus-level study is that of Sharma *et al.* (2011), who described meio- and macrobenthic nematodes from the deep Arctic (Canada Basin), Gulf of Mexico (GOM) and Bermuda slope (212-3961 m water depth). In the GOM, Sharma *et al.* (2011) concluded that the meio- and macrobenthic nematode assemblages were taxonomically distinct. In all three areas, the macrobenthic assemblages were dominated by *Enoploides*, *Crenopharynx*, *Micoletzkyia* and *Phanodermella*. In our material, *Enoploides* was not recorded and the other three genera were present only in relatively low numbers. The dominant genera in the Whittard Canyon system and adjacent slope, *Paramesacanthion* and *Metacylicolaimus,* were not abundant in Sharma *et al.*’s (2011) material. *Sabatieria* and *Viscosia* were the dominant genera in a related study of macrobenthic nematodes from the Arctic deep sea (Canada Basin; 640-3848 m water depth; [Sharma & Bluhm 2011)](#h.kgcv8k). These two genera were recorded in the present study but were not abundant, while *Paramesacanthion* and *Metacylicolaimus* were not reported by Sharma & Bluhm (2011). The latter authors used a 250 μm mesh sieve; the genera *Sabatieria* and *Viscosia* are typically smaller in body size than *Paramesacanthion* and *Metacylicolaimus* and may not have been retained on the 500 µm mesh used in the present study. The genus *Sabatieria* is often associated with organic-rich muddy sediments that are anoxic just below the sediment surface ([Vincx *et al.* 1990;](#h.pkwqa1) [Vanreusel 1991)](#h.4h042r0). Although oxygen profiles were not available for our study locations, our core samples appeared to be well oxygenated to a depth below 5 cm, and showed no evidence for reducing conditions in the form of darkened sediments or a hydrogen sulphide smell.

Macrofaunal nematode species have been reported in a number of other studies. Dense aggregations of *Metoncholaimus* were observed in a South Atlantic atoll by Netto *et al.* (1999). In the abyssal Indian Ocean (4500-5500 m water depth), *Viscosia* was the most abundant genus, followed by *Halalaimus*, *Dolicholaimus*, *Polygastrophora* and *Phanoderma* (Pavithran *et al.* 2009). Two large nematodes, *Synonchus* cf. *acuticaudata* and *Cylicolaimus* cf. *magnus,* were abundant among macrofaunal species in coarse sediments adjacent to cold-water coral mounds in the Porcupine Seabight (NE Atlantic, 900 m water depth; [Henry & Roberts 2007)](#h.2grqrue). *Synonchus* and *Cylicolaimus* were among the top 10 genera in the present study, Henry & Roberts (2007) also recorded *Metacylicolaimus* a key taxon in our study.

Little is known about the biology of our two top-ranked genera, *Paramesacanthion* and *Metacylicolaimus.* The formerwas a moderately common component of the meiofaunal nematode assemblage at 4970 m water depth in the Nazaré Canyon ([Garcia *et al.* 2007)](#h.1pxezwc), and both genera occurred occasionally in meiofaunal samples from the same canyon (Ingels *et al.* 2011b). Soetaert & Heip (1995) note that some Mediterranean canyons are characterised by predatory nematodes, including *Paramesacanthion.* These large nematodes appear to be common inhabitants of at least some canyons, possibly linked to their role as predators, although the reasons for this association remain unclear.

## 4.2 Comparison with Meiofaunal Nematodes

Most of the macrofaunal nematode genera identified in the present study are comparatively rare in meiofaunal assemblages. Only four taxa (*Sabatieria, Aegialoalaimus, Sphaerolaimus, Oxystomina*) listed by Pape *et al.* (2013) as dominant (> 3 %) at sites around the southern European margin (Mediterranean and Iberian) were present in our samples. Similarly, only three of the genera (*Syringolaimus, Sabatieria* and *Cervonema*) reported as abundant in a study by [Ingels *et al.* (2011c)](#h.28h4qwu) of meiofaunal nematodes from the Whittard Canyon and Gollum Channel (700 and 1200 m water depths) were recorded in our samples, and they were relatively uncommon. Ingels *et al.* (2011c) did record our two top-ranked genera, *Metacylicolaimus* and *Paramesacanthion,* but they were not abundant. The use of completely different sieve fractions (> 500 µm vs. > 32 µm) probably accounts for these faunal differences, but different sampling depths (3500 m this study vs. 762 and 1160 m in Ingels *et al.* 2011c) may be an additional factor.

The most abundant nematode genera among the meiofauna from a group of Mediterranean canyons were *Sabatieria, Sphaerolaimus* and *Synonchiella* ([Soetaert & Heip 1995)](#h.34g0dwd); *Paramesacanthion* was uncommon and *Metacylicolaimus* not recorded. The latter two generawere not listed among the most abundant meiofaunal nematode genera (> 3 %) between 3200 and 4500 m water depth in Casçais and Sebútal Canyons ([Ingels *et al.* 2011a)](#h.4f1mdlm), where the dominant genus was *Acantholaimus.* *Metalinhomoeus* and *Sabatieria* were the dominant genera in the Nazaré Canyon (300-4970 m water depth); *Paramesacanthion* and *Metacylicolaimus* were present but were not common (Garcia *et al.* 2007). Again, these differences most likely result from the use of much finer size fractions compared with the present study. Most free-living meiobenthic marine nematodes span a body length range of 0.5 – 3 mm (Giere 2009), whereas the nematodes in our samples reached lengths of up to 13 mm. Mesh size is therefore likely to have a strong influence on the species that are recorded (LeDuc *et al*. 2010).

## 4.3 Standing Stock of Macrofaunal Nematodes

[Hunter *et al.* (2013),](#h.1v1yuxt) who studied samples from sites close to ours, reported that nematodes represented a higher proportion of the macrofauna (> 250 µm mesh) at Eastern (55 %, 487 ind 0.1 m-2) than at Western (35 %, 165 ind 0.1 m-2). We also found that Eastern had the highest relative and absolute abundances of macrofaunal nematodes (15 %, 47 ind 0.1 m-2), our much lower density reflecting the use of a 500 μm mesh sieve. Hunter *et al.* (2013) suggested that the high densities of nematodes, and cirratulid and spionid polychaetes at Eastern might indicate either organic-matter enrichment (combined with oxygen limitation), or disturbance of the sedimentary environment. Hunter *et al.* also provide direct estimates of sediment organic matter content for the Western (particulate organic carbon 0.53 %, total nitrogen 0.08 %) and Eastern (0.70 %, 0.10 %) locations.

[Vanreusel *et al.* (1995)](#h.1baon6m) suggested that mean nematode body size may be linked to food availability, reporting that a more eutrophic site on the Porcupine Abyssal Plain (4850 m water depth) yielded a higher number of large nematodes than an oligotrophic site on the Cap Verde Abyssal Plain (4600 m water depth). Similarly, nematodes represented 71 % of the macrofauna at a eutrophic site (5250 m) compared with 36 % at an oligotrophic site (4280 m) in the western North Pacific ([Alves *et al.* 2015)](#h.30j0zll). [Bett & Moore (1988)](#h.lnxbz9) reported very high densities of a large(20 mm), nematode (*Pontonema alaeospicula)* at an extremely eutrophic sublittoral site off the Scottish coast (82 m water depth). High numbers of macrofaunal nematodes (> 300 μm) in the Baltimore Canyon (NW Atlantic) were linked to increased food availability inside the canyon ([Bourque *et al.* 2015)](#h.44sinio). More generally, high levels of organic enrichment are thought to result in dramatic increases in the abundance and dominance of the largest species of the meiobenthos, mainly nematodes in the family Oncholaimidaeand harpacticoid copepods ([Warwick *et al.* 1986; Moore & Bett 1989)](#h.39kk8xu).

A similar relationship between the quantity and quality of available organic matter and the standing stocks of macrofaunal nematodes may also apply in the Whittard Canyon system, where both density and biomass were significantly higher (Fig. 2) at canyon locations than the Slope location. Similarly, numerical dominance was markedly increased (Fig. 5), and diversity decreased (Table 5), at canyon locations relative to the Slope location. Canyons are thought to represent preferential funnels or conduits through which organic matter of terrestrial and shelf-sea origin is transported to the deep sea (Vetter & Dayton 1998), such that enhanced benthic stocks may be expected. It is also possible that canyons may act to trap laterally advecting organic material, a mechanism that possibly occurs in the deeper Whittard Canyon (Whittard Channel) and maybe responsible for the enhanced local abundance of megabenthos (elpidiid holothurians)(Amaro *et al.* 2015). More generally, organic matter entrained by the North Atlantic slope current, which flows east to west across our study area (Pingree & Le Cann, 1989), possibly results in higher food availability in the Eastern branch, leading to an enhanced abundance of macrofaunal nematodes (Table 3) as well as of macrofauna generally (Table 2; Gunton *et al.* 2015a; Amaro *et al.* 2016). As noted in 4.3 above, Hunter *et al.* (2013) measured increased levels of sedimentary organic carbon and total nitrogen at the Eastern location than the Western location.

## 4.4 Macrofaunal Nematode Trait Analyses

Feeding type 2B (omnivore/ predator) nematodes are generally rare in deep-sea meiobenthic assemblages ([Jensen 1988;](#h.nmf14n) [Thistle *et al.* 1995;](#h.2iq8gzs) [Pape *et al.* 2013)](#h.2zbgiuw). However, they were more abundant at canyon locations than at the Slope location (Fig. 4A) and particularly abundant (53 %) at the Eastern location. These taxa tend to be of larger body size, and consequently more likely to be encountered in the macrofaunal size fraction. Pavithran *et al*. (2009) reported that 2B-taxa (*Viscosia*, *Polygastrophora*, *Dolicholaimus*) made up 62 % of macrobenthic nematodes in the abyssal Indian Ocean. Sharma *et al*. (2011) noted an increase with water depth in members of feeding group 2B (Oncholaimidae, Enchelidiidae), as well as group 1A (selective deposit feeders), among macrofaunal nematode assemblages. These authors proposed that the increase with depth could be linked to decreased competition from other macrobenthic predators. This is unlikely to explain the trend observed in the present study as the densities of the total macrofauna ([Gunton *et al.* 2015a)](#h.3o7alnk), as well as macrophagous and omnivorous polychaetes, increased in parallel with nematode density across the study locations.

Group 2B nematodes exploit a range of possible food sources (Moens & Vincx, 1997). [Warwick *et al.* (1986)](#h.39kk8xu) suggested that in organically enriched settings, larger meiofaunal organisms that are generalist feeders will be more successful than smaller species with highly specialised feeding behaviours. This is consistent with the high abundance of group 2B at canyon locations. Meiofaunal group 2B nematodes were more common in the Nazaré Canyon compared with the open slope ([Ingels *et al.* 2009)](#h.3tbugp1). In a feeding experiment in Nazaré Canyon (3500 m water depth), predatory nematodes were found to have a higher total biomass than other trophic groups ([Ingels *et al.* 2011b)](#h.2u6wntf). Soetaert & Heip (1995) linked the high relative abundance (20 %) of group 2B meiobenthic nematodes in Mediterranean canyons, compared with the non-canyon settings to an increased supply of organic matter and therefore increased populations of the smaller nematodes on which the predatory species may feed (Soetaert & Heip, 1995). Indeed, a positive relationship exists between the biomass of predatory nematodes and other nematode feeding groups ([Danovaro & Gambi 2002)](#h.1y810tw). Thus, the abundance of predatory nematodes may be higher in organically enriched settings, such as canyons that harbour higher nematodes densities. Among the Whittard Canyon macrofauna, the genus *Paramesacanthion* is largely responsible for the high abundance of predatory nematodes*.* This genus likely preys on nematodes, oligochaetes, and other meiofauna ([Moens & Vincx 1997)](#h.2lwamvv). Given the above, we consider it likely that the abundance of predatory nematodes in our samples is linked to enhanced food availability, and hence an increased density of prey organisms.

'Clavate-conicocylindrical' and 'long' were the most abundant tail shapes in our study, the Eastern location yielded the highest proportion of long tail forms (Fig. 4C). It has been suggested that long-tailed nematodes are disproportionately abundant in high-energy settings ([Thistle & Sherman 1985)](#h.xvir7l). These authors speculated that individuals may use their tails to escape into deeper sediment layers in order to avoid resuspension by erosive flows in hydrodynamically-active regions. Riemann (1974) observed that individuals with long flagelliform tails were able to anchor the tip of the tail with mucus from the caudal gland to sediment particles. This allowed them to move forward from the anchor by extending their tails, or to quickly pull the body into the sediment by coiling the tails. Long tails might also allow tube-dwelling nematodes to quickly retreat into their tubes if disturbed ([Riemann 1974)](#h.sqyw64). Since the four tail shapes groups were originally designated by Thistle et al. (1995), few studies ([Tita *et al.*](#h.3hv69ve)1999*;* [Fleeger *et al.* 2006;](#h.3whwml4) [Armenteros *et al.* 2009;](#h.2et92p0) [Fleeger *et al.* 2010;](#h.2bn6wsx) [Alves *et al.* 2014)](#h.1fob9te) have reported the presence of clavate-conicocylindrical tails in nematode assemblages, and none has linked this tail type to a particular ecological function. Like ‘long’ tails, the 'clavate-conicocylindrical’ tail shape is possibly used for anchorage in the sediment.

## 4.5 Macrofaunal Nematode and Polychaete Trends

**4.5.1. Previous studies**

As far as we are aware, faunal trends between macrofaunal nematodes and polychaetes have never been compared directly, although there are previous studies comparing macrofauna and meiofauna in which nematodes were included in both size fractions ([Netto *et al.* 1999;](#h.3l18frh) [Renaud *et al.* 2006;](#h.2dlolyb) [Sharma *et al.* 2011)](#h.25b2l0r). In particular, Baldrighi & Manini (2015) reported a significant eastward decrease in the density of meio- and macrofauna, as well as a positive relationship between the diversity of total macrofauna and meiofauna, macro- and meiofaunal nematodes, and meiofaunal nematodes and macrofaunal polychaetes, from six continental slope areas in the western and eastern Mediterranean Sea (1200-2800 m water depth). The trophic structure of macrobenthic nematodes and polychaetes exhibited a significant change along the continental slope from west to east, with the percentage of carnivores / scavengers / predators increasing for both groups in the central-eastern basin. Baldrighi & Manini (loc. cit.) concluded that these changes reflected a similar response to food inputs decreasing west to east. However, they believed that the abundance of meio- and macrofauna was influenced by different environmental factors; the macrofauna (polychaetes and nematodes) by organic matter quality and sediment grain size, and the meiofauna (nematodes) by particulate organic carbon flux.

**4.5.2. Diversity and density**

Trends in generic diversity were broadly similar for polychaetes and nematodes (Table 5; Fig. 5). In both cases, canyon locations had a reduced diversity relative to the Slope location, this pattern is evident in both the richness and dominance components of diversity in both taxa. The two taxa, however, do vary in the detail of their diversity response; nematode diversity exhibits a clear dichotomy between Slope and canyon locations that is particularly marked in the dominance component of diversity, while polychaete diversity exhibits a gradational change (Slope > Western > Central > Eastern) in all diversity components. Set against the available environmental parameters (Table 2) the nematode diversity response is well matched to the change in sedimentary environment between Slope and canyon locations (i.e. mean grain size 72 vs. 29 µm, sand fraction 27 vs 12 %). The polychaete response is perhaps best matched to the total density of macrofauna (*sensu stricto* > 300 µm), a potential proxy for organic matter availability that represents gradational change among canyon locations (Slope = Western < Central < Eastern). Macrofaunal nematode and polychaete densities exhibit very similar trends, in both cases increasing continuously from west to east (Tables 2 and 3, Fig. 2). However, whereas nematode density varies markedly between Slope and canyon locations, but does not vary significantly between canyon locations, polychaete density changes gradually, such that there is no significant difference (Tukey 5 % test) between adjacent locations (e.g. Slope < Central and Eastern; Western < Eastern).

**4.5.3. Functional groups**

Polychaete and nematode feeding groups appeared to display broadly similar changes across the study locations. This is best illustrated by combining the groups into deposit (1A and 1B) feeders and ‘larger particle’ (2A and 2B) feeders in the case of nematodes, and ‘smaller particle’ (microphage) feeders and ‘larger particle’ (macrophage and omnivore) feeders in the case of polychaetes. In the case of both taxa, the proportion of the latter to the former exhibits the same pattern: Slope < Western < Central < Eastern. We might tentatively ascribe this change to corresponding variations in the quantity and nature of organic matter present at each location. A similar approach is possible for nematode tail shape and polychaete motility. When ‘elongate’ (long and clavate-conicocylinderical) tail tips and ‘non-elongate’ (rounded and conical) tail tips are grouped in the case of nematodes, and ‘more motile’ (motile) and ‘less motile’ (discretely motile and sessile) in the case of polychaetes - the proportion of the latter to the former exhibits the same pattern (Slope < Western < Central < Eastern) in both taxa. Again, we might speculate that this change corresponds with variation in the sedimentary environment and / or the potential frequency of sediment disturbance.

**4.5.4. Assemblage composition**

The substantial disparity in samples size (number of specimens identified, c. 400 nematodes vs. c. 2000 polychaetes) makes a ‘fair’ comparison of trends in genus-level composition between the macrofaunal nematodes and polychaetes difficult. Consequently, the greater ecological resolution achieved with polychaetes (compare Fig. 3C and 3D) is inevitable. Combining the nematode and polychaete data (Fig. 3B) did not alter or degrade the ecological interpretation, indeed the distinction of Slope from all three canyon locations was marginally improved by the addition of the nematode data (Table 4). We interpret this as the result of a stronger response by the nematodes than the polychaetes to the change in sediment grade between Slope and canyon locations (Table 2). When the combined nematode and polychaete data are edited to only common taxa (present in ≥ 5 samples) it seems clear (Fig. 3A, Table 4) that all four of our study locations are ecologically distinct, with the distinctions probably being driven by related trends in sedimentology and organic matter availability (Fig. 6).

**4.6. Concluding remarks**

It is not surprising that common ecological trends seem to be apparent among nematodes and polychaetes, since ‘useful’ synecology is only possible through the degree of commonality in the distributions of distinct taxa in response to environmental drivers. Redundancy is a well-established feature of ecological datasets concerning the marine benthos (see e.g. Warwick 1988a, b). Our data do suggest that there is some value in combining the analysis of macrofaunal nematodes with the assessment of macrofauna *sensu strictu,* an issue of recent debate (Bett 2014; Warwick 2014). However, our data also suggest some difference between the responses of nematodes and polychaetes in terms of standing stocks and diversity (dominance).

Overall, it seems likely that the broadly similar trends in nematode and polychaete density, diversity, and functional group and genus-level faunal composition observed during the present study are related to the combined (and probably related) influences of sediment type and food availability, the latter likely maximal at our Eastern location ([Duineveld *et al.* 2001;](#h.4i7ojhp) [Gunton *et al.* 2015a; Hunter *et al.* 2013)](#h.3o7alnk). It seems clear that the analysis of ‘macrofaunal’ nematodes is of appreciable ecological value, and that more information is needed on their ecology, life history, and potential interactions with more ‘conventional’ macrofaunal taxa.

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# References

Alves, A., Ramos, S., Nomaki, H., Amaro, T. (2015) Benthic macrofaunal communities differences between oligotrophic and eutrophic abyssal habitats: a case study of the west Pacific *14th Deep-Sea Biology Symposium* Aveiro, Portugal. 320pp.

Alves, A.S., Veríssimo, H., Costa, M.J., Marques, J.C. (2014) Taxonomic resolution and Biological Traits Analysis (BTA) approaches in estuarine free-living nematodes. *Estuarine, Coastal and Shelf Science*, **138**, 69-78.

Amaro, T., de Stigter, H., Lavaleye, M., Duineveld, G. (2015) Organic matter enrichment in the Whittard Channel (northern Bay of Biscay margin, NE Atlantic); its origin and possible effects on benthic megafauna. *Deep Sea Research Part I* **102**, 90-100.

Amaro, T., Huvenne, V.A.I., Allcock, A.L., Aslam, T., Davies, J.S., Danovaro, R., De Stigter, H.C., Duineveld, G.C.A., Gambi, C., Gooday, A.J., Gunton, L.M., Hall, R., Howell, K.L., Ingels, J., Kiriakoulakis, K., Kershaw, C.E., Lavaleye, M.S.S., Robert, K., Stewart, H., Van Rooij, D., White, M., Wilson, A.M. (2016) The Whittard Canyon – A case study of submarine canyon processes. *Progress in Oceanography* **146**, 38-57.

Andrassy, I. (1956) The determination of volume and weight of nematodes. *Acta Zoologica* **2**, 1-15.

Armenteros, M., Ruiz-Abierno, A., Fernández-Garcés, R., Pérez-García, J.A., Díaz-Asencio, L., Vincx, M., Decraemer, W. (2009) Biodiversity patterns of free-living marine nematodes in a tropical bay: Cienfuegos, Caribbean Sea. *Estuarine, Coastal and Shelf Science*, **85**, 179-189.

Baldrighi, E., Manini, E. (2015) Deep-sea meiofauna and macrofauna diversity and functional diversity: are they related? *Marine Biodiversity* **45**, 469-488.

Bett, B.J. (2014) Macroecology and meiobenthos: Reply to Warwick (2014). *Marine Ecology Progress Series* **505**, 299-302.

Bett, B.J., Moore, C.G. (1988) The taxonomy and biology of a new species *Pontonema* (Nematoda, Oncholaimidae) dominant in organically polluted sublittoral sediments around Scotland, with a review of the genus. *Journal of Natural History* **22**, 1363-1377.

Bongers, A.M.T., Alkemade, R., Yeates, G.W. (1991) Interpretation of disturbance-induced maturity decrease in marine nematode assemblages by means of the Maturity Index. *Marine Ecology Progress Series* **76**, 135-142.

Bongers, T., De Goede, R., Korthals, G., Yeates, G. (1995) Proposed changes of cp classification for nematodes. *Russian Journal of Nematology* **3**, 61-62.

Bourque, J., Demopoulos, A., Stamler K.M., Robertson, C., Davies, A., Ingels, J., Mienis, F., Duineveld, G. (2015) Meiofaunal community structure and function in relation to sediment biogeochemistry and canyon morphology in Baltimore Canyon, western Atlantic *14th Deep Sea Biology Symposium*, Aveiro, Portugal. 178pp.

Canty, A., Ripley, B. (2015). boot: Bootstrap R (S-Plus) Functions. R package version 1.3-16.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117-143.

Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual / Tutorial. PRIMER-E, Plymouth, 192pp.

Colwell, R.K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C. X., Chazdon, R.L., Longino, J.T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *Journal of Plant Ecology* **5**, 3-21.

Danovaro, R., Gambi, C. (2002) Biodiversity and trophic structure of nematode assemblages in seagrass systems: evidence for a coupling with changes in food availability. *Marine Biology* **141**, 667-677.

Davison, A.C., Hinkley, D.V. (1997) Bootstrap Methods and Their Applications. Cambridge University Press, Cambridge. ISBN 0-521-57391-2.

Duineveld, G., Lavaleye, M., Berghuis, E., de Wilde, P. (2001) Activity and composition of the benthic fauna in the Whittard Canyon and the adjacent continental slope (NE Atlantic). *Oceanologica Acta* **24**, 69-83.

Duros, P., Fontanier, C., Metzger, E., Pusceddu, A., Cesbron, F., de Stigter, H.C., Bianchelli, S., Danovaro, R., Jorissen, F.J. (2011) Live (stained) benthic foraminifera in the Whittard Canyon, Celtic margin (NE Atlantic). *Deep-Sea Research Part I* **58**, 128-146.

Elliot, J.M. (1977) Some methods for the statistical analysis of samples of benthic invertebrates, 2nd edn. Freshwater Biological Association, Ambleside.

Flach, E., Vanaverbeke, J., Heip, C. (1999) The meiofauna : macrofauna ratio across the continental slope of the Goban Spur (north-east Atlantic). *Journal of the Marine Biological Association of the United Kingdom* **79**, 233-241.

Fleeger, J.W., Carman, K.R., Weisenhorn, P.B., Sofranko, H., Marshall, T., Thistle, D., Barry, J.P. (2006) Simulated sequestration of anthropogenic carbon dioxide at a deep-sea site: Effects on nematode abundance and biovolume. *Deep Sea Research Part I* **53**, 1135-1147.

Fleeger, J.W., Johnson, D.S., Carman, K.R., Weisenhorn, P.B., Gabriele, A., Thistle, D., Barry, J.P. (2010) The response of nematodes to deep-sea CO2 sequestration: A quantile regression approach. *Deep Sea Research Part I* **57**, 696-707.

Gage, J. (1979) Macrobenthic community structure in the Rockall Trough. *Ambio Special Report* **6**, 43-46.

Gage, J.D., Bett, B.J. (2005) Deep-sea benthic sampling. In Eleftheriou, A. & A. McIntyre (eds) Methods for the study of marine benthos 3rd ed. Blackwell Publishing, Oxford, 273-325.

Gage, J., Tyler, P. (1991). *Deep-Sea Biology*. Cambridge University Press, Cambridge.

Garcia, R., Koho, K.A., De Stigter, H.C., Epping, E., Koning, E., Thomsen, L. (2007) Distribution of meiobenthos in the Nazare canyon and adjacent slope (western Iberian Margin) in relation to sedimentary composition. *Marine Ecology-Progress Series* **340**, 207-220.

Giere, O. (2009). *Meiobenthology: the microscopic motile fauna of aquatic sediments*. Springer-Verlag, Berlin.

Gunton, L.M., Gooday, A.J., Glover, A.G., Bett, B.J. (2015a) Macrofaunal abundance and community composition at lower bathyal depths in different branches of the Whittard Canyon and on the adjacent slope (3500m; NE Atlantic). *Deep Sea Research Part I* **97**, 29-39.

Gunton, L.M., Neal, L., Gooday, A.J., Bett, B.J., Glover, A.G. (2015b) Benthic polychaete diversity patterns and community structure in the Whittard canyon system and adjacent slope (NE Atlantic). *Deep Sea Research Part I* **106**, 42-54.

Hecker, B., Paul, A. (1979) Abyssal Community Structure of the Benthic Infauna of the Eastern Equatorial Pacific: DOMES Sites A, B, and C. In: J. Bischoff & D. Piper (Eds). *Marine Geology and Oceanography of the Pacific Manganese Nodule Province*. Springer US: 287-308.

Heip, C., Herman, P., Soetaert, K. (1998) Indices of diversity and evenness. *Oceanis* **24**, 61-87.

Henry, L.-A., Roberts, J.M. (2007) Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep Sea Research Part I* **54**, 654-672.

Hessler, R.R., Jumars, P.A. (1974) Abyssal community analysis from replicate box cores in central north Pacific. *Deep-Sea Research* **21**, 185-209.

Hunter, W., Jamieson, A., Huvenne, V., Witte, U. (2013) Sediment community responses to marine vs. terrigenous organic matter in a submarine canyon. *Biogeosciences* **10**, 67-80.

Ingels, J., Billett, D.S.M., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A. (2011a) Structural and functional diversity of Nematoda in relation with environmental variables in the Setubal and Cascais canyons, Western Iberian Margin. *Deep Sea Research Part II* **58**, 2354-2368.

Ingels, J., Billett, D.S.M., Van Gaever, S., Vanreusel, A. (2011b) An insight into the feeding ecology of deep-sea canyon nematodes — Results from field observations and the first in-situ 13C feeding experiment in the Nazaré Canyon. *Journal of Experimental Marine Biology and Ecology* **396**, 185-193.

Ingels, J., Kiriakoulakis, K., Wolff, G.A., Vanreusel, A. (2009) Nematode diversity and its relation to the quantity and quality of sedimentary organic matter in the deep Nazare Canyon, Western Iberian Margin. *Deep-Sea Research Part I* **56**, 1521-1539.

Ingels, J., Tchesunov, A.V., Vanreusel, A. (2011c) Meiofauna in the Gollum Channels and the Whittard Canyon, Celtic Margin-How Local Environmental Conditions Shape Nematode Structure and Function. *Plos One* **6**, e0094 http://dx.doi.org/10.1371/journal.pone.0020094

Jensen, P. (1988) Nematode assemblages in the deep-sea benthos of the Norwegian Sea. *Deep Sea Research Part A* **35**, 1173-1184.

Jumars, P.A., Dorgan, K.M., Lindsay, S.M. (2015) Diet of Worms Emended: An Update of Polychaete Feeding Guilds. *Annual Review of Marine Science* **7**, 497-520.

Leduc, D., Probert, P.K., Nodder, S.D. (2010) Influence of mesh size and core penetration on estimates of deep-sea nematode abundance, biomass, and diversity. *Deep Sea Research I***57**, 1354-1362.

Masson, DG, (2009). RRS *James Cook* cruise 036, 19 Jul-28 Jul 2009. The Geobiology of Whittard Submarine Canyon. National Oceanography Centre Southampton Cruise Report, No. 41. National Oceanography Centre, Southampton.

Moens, T., Braeckman, U., Derycke, S., Fonseca, G., Gallucci, F., Gingold, R., Guilini, K., Ingels, J., Leduc, D., Vanaverbeke, J., Van Colen, C., Vanreusel, A., Vincx, M., (2013). Ecology of free-living nematodes. In: Schmidt-Rhaesa, A. (Ed.), Handbook of Zoology, Vol. 2 Nematoda. De Gruyter, pp. 109-152.

Moens, T., Vincx, M. (1997) Observations on the Feeding Ecology of Estuarine Nematodes. *Journal of the Marine Biological Association of the United Kingdom* **77**, 211-227.

Moore, C.G., Bett, B.J. (1989) The use of meiofauna in marine pollution impact assessment. *Zoological Journal of the Linnean Society* **96**, 263-280. doi:10.1111/j.1096-3642.1989.tb02260.x

Netto, S.A., Warwick, R.M., Attrill, M.J. (1999) Meiobenthic and Macrobenthic Community Structure in Carbonate Sediments of Rocas Atoll (North-east, Brazil). *Estuarine, Coastal and Shelf Science* **48**, 39-50.

Pape, E., Jones, D.O.B., Manini, E., Bezerra, T.N., Vanreusel, A. (2013) Benthic-pelagic coupling: effects on nematode communities along southern European continental margins. *Plos One* **8**, e59954.

Pavithran, S., Ingole, B.S., Nanajkar, M., Raghukumar, C., Nath, B.N., Valsangkar, A.B. (2009) Composition of macrobenthos from the Central Indian Ocean Basin. *Journal of Earth System Science* **118**, 689-700.

Pingree, R.D., LeCann, B. (1989) Celtic and Armorican slope and shelf residual currents. *Progress in Oceanography* **32,** 303-338.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Renaud, P.E., Ambrose Jr, W.G., Vanreusel, A., Clough, L.M. (2006) Nematode and macrofaunal diversity in central Arctic Ocean benthos. *Journal of Experimental Marine Biology and Ecology* **330**, 297-306.

Riemann, F. (1974) On hemisessile nematodes with flagelliform tails living in marine soft bottoms and on microtubes found in deep sea sediments. *Mikrofauna des Meeresbodens* **40**, 1-15.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* **9**, 671-675.

Seinhorst, J.W. (1959) A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. *Nematologica* **4**, 67-69.

Sharma, J., Baguley, J., Bluhm, B.A., Rowe, G. (2011) Do Meio- and Macrobenthic Nematodes Differ in Community Composition and Body Weight Trends with Depth? *Plos One* **6**, e14491. doi: 10.1371/journal.pone.0014491

Sharma, J., Bluhm, B. (2011) Diversity of larger free-living nematodes from macrobenthos (>250 μm) in the Arctic deep-sea Canada Basin. *Marine Biodiversity* **41**, 455-465.

Siegel, S., Castellan, N.J., (1988). Nonparametric Statistics for the Behavioural Sciences. New York: McGraw-Hill.

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.

Sokal, R.R., Rohlf, F.J. (2012) Biometry: the principles and practice of statistics in biological research. 4th edition. W. H. Freeman and Co.: New York. 937 pp. ISBN: 0-7167-8604-4

Thiel, H. (1975) The size structure of the deep-sea benthos. *Internationale Revue Der Gesamten Hydrobiologie* **60**, 575-606.

Thiel, H. (1983) Meiobenthos and nanobenthos of the deep sea. In: G. Rowe (Ed). *Deep-sea biology. The Sea*. Wiley-Interscience, New York. Pp. 167-230.

Thistle, D., Lambshead, P.J.D., Sherman, K.M. (1995) Nematode tail-shape groups respond to environmental differences in the deep sea *Vie et Milieu* **45**, 107-115.

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.

Tita, G., Vincx, M., Desrosiers, G. (1999) Size spectra, body width and morphotypes of intertidal nematodes: an ecological interpretation. *Journal of the Marine Biological Association of the United Kingdom* **79**, 1007-1015.

Vanreusel, A. (1991) Ecology of free-living marine nematodes in the Voordelta (Southern Bight of the North Sea). II. Habitat preferences of the dominant Species. *Nematologica* **37**, 343-359.

Vanreusel, A., Fonseca, G., Danovaro, R., Da Silva, M.C., Esteves, A.M., Ferrero, T., Gad, G., Galtsova, V., Gambi, C., Da Fonsêca Genevois, V., Ingels, J., Ingole, B., Lampadariou, N., Merckx, B., Miljutin, D., Miljutina, M., Muthumbi, A., Netto, S., Portnova, D., Radziejewska, T., Raes, M., Tchesunov, A., Vanaverbeke, J., Van Gaever, S., Venekey, V., Bezerra, T.N., Flint, H., Copley, J., Pape, E., Zeppilli, D., Martinez, P.A., Galeron, J. (2010) The contribution of deep-sea macrohabitat heterogeneity to global nematode diversity. *Marine Ecology* **31**, 6-20.

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 der gesamten Hydrobiologie und Hydrographie* **80**, 287-296.

Vetter, E.W., Dayton, P.K. (1998) Macrofaunal communities within and adjacent to a detritus-rich submarine canyon system. *Deep-Sea Research Part II* **45**, 25-54.

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**, 1-88.

Vincx, M., Meire, P., Heip, C. (1990) The distribution of nematodes communities in the Southern Bight of the North Sea. *Cahiers de Biologie Marine* **31**, 107-129.

Warwick, R.M. (1988a) Analyses of community attributes of the macrobenthos of Frierfjord / Langesundfjord, Norway, at taxonomic levels higher than species. *Marine Ecology Progress Series* **46**, 167-170.

Warwick, R.M. (1988b) The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin* **19**, 259-268.

Warwick, R.M. (2014) Meiobenthos and macrobenthos are discrete entities and not artefacts of sampling a size continuum: Comment on Bett (2013). *Marine Ecology Progress Series* **505**, 295-298.

Warwick, R., Collins, N., Gee, J., George, C. (1986) Species size distributions of benthic and pelagic Metazoa: evidence for interaction. *Marine Ecology Progress Series* **34**, 63-68.

Warwick, R.M. (2014) Meiobenthos and macrobenthos are discrete entities and not artefacts of sampling a size continuum: Comment on Bett (2013). *Marine Ecology Progress Series* **505**, 295-298.

Warwick, R.M., Platt, H.M., Somerfield, P.J. (1998) *Free-living marine nematodes. Part III: Monhysterids*. Pictorial key to world genera and notes for the identification of British species. Synopses of the British Fauna (New Series) No. 53. Field Studies Council, London.

Wieser, V.W. (1953) Die Beziehung zwischen Mundhohlengestalt, Ernahrungsweise und Vorkommen bei freilebenden marinen Nematoden. *Arkiv Zoologie* **2**, 439-484.

**Table 1.** Sampling sites in three branches of the Whittard Canyon and on the adjacent slope. (Area, total seafloor area sampled by pooled cores).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Location** | **Deploy -ment** | **Latitude (N)** | **Longitude (W)** | **Depth (m)** | **Area (m2)** |
| Slope | S016 | 47° 56.79' | 10° 46.85' | 3511 | 0.063 |
| S017 | 47° 56.78' | 10° 46.85' | 3512 | 0.055 |
| S018 | 47° 56.81' | 10° 46.91' | 3514 | 0.047 |
| S019 | 47° 56.74' | 10° 46.94' | 3505 | 0.063 |
| S020 | 47° 56.78' | 10° 46.85' | 3514 | 0.055 |
|  |  |  |  |  |
| Western | W002 | 48° 09.18' | 10° 33.70' | 3670 | 0.063 |
| W003 | 48° 09.17' | 10° 33.70' | 3661 | 0.055 |
| W011 | 48° 09.22' | 10° 32.36' | 3582 | 0.047 |
| W026 | 48° 09.18' | 10° 33.73' | 3670 | 0.039 |
| W043 | 48° 09.15' | 10° 33.76' | 3657 | 0.047 |
|  |  |  |  |  |
| Central | C063 | 48° 16.89' | 10° 18.74' | 3375 | 0.047 |
| C064 | 48° 16.97' | 10° 18.65' | 3382 | 0.063 |
| C065 | 48° 17.04' | 10° 18.89' | 3373 | 0.055 |
| C067 | 48° 16.98' | 10° 18.72' | 3376 | 0.055 |
| C066 | 48° 16.83' | 10° 18.72' | 3381 | } 0.063 |
| C068 | 48° 17.01' | 10° 18.83' | 3375 |
|  |  |  |  |  |
| Eastern | E093 | 48° 15.89' | 10° 09.56' | 3424 | 0.063 |
| E094 | 48° 15.78' | 10° 09.57' | 3429 | 0.053 |
| E095 | 48° 15.78' | 10° 09.58' | 3429 | } 0.063 |
| E096 | 48° 15.76' | 10° 09.60' | 3424 |
| E097 | 48° 15.89' | 10° 09.54' | 3425 | 0.039 |
| E098 | 48° 15.76' | 10° 09.60' | 3432 | 0.031 |

**Table 2.** Environmental characteristics of sampling sites in three branches of the Whittard Canyon and on the adjacent slope. Parameters are summarised from Gunton et al (2015a) as median values. (au, arbitrary units; BPI, bathymetric position index; macrofaunal density, refers to macrofauna sensu stricto > 300 µm). Also given in polychaete density from the present study (> 500 µm), as geometric mean, with corresponding 95% confidence intervals in parentheses.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Location** | **Water depth (m)** | **Seabed slope angle (°)** | **Local rugosity (au)** | **Fine- scale BPI (au)** | **Mean grain size (µm)** | **Sand fraction (%)** | **Mud fraction (%)** | **Macrofauna density (ind 0.1 m-2)** | **Polychaete density (ind 0.1 m-2)** |
| Slope | 3512 | 0.9 | 14 | -20 | 72 | 27 | 73 | 273 | 113 (89, 143) |
| Western | 3661 | 2.4 | 138 | 3 | 29 | 13 | 87 | 271 | 127 (100, 161) |
| Central | 3376 | 2.8 | 239 | -106 | 27 | 10 | 90 | 480 | 196 (155, 249) |
| Eastern | 3427 | 3.4 | 92 | -23 | 33 | 14 | 86 | 649 | 305 (240, 386) |
| Canyon (all sites) | 3425 | 2.8 | 140 | -23 | 29 | 12 | 88 | 461 | 196 (154, 251) |

**Table 3.** Macrofaunal nematode density, biomass, feeding types, trophic diversity, and maturity index at the Whittard Canyon (Western, Central and Eastern branches) and adjacent slope study sites. (Feeding types 1A, selective deposit feeder; 1B, non-selective deposit feeder; 2A, epigrowth feeder; 2B, predator / scavenger). Values given in parentheses are 95% confidence intervals.

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Location** | **Density  (ind 0.1 m-2)** | **Biomass (ng wwt 0.1 m-2)** | **Feeding type (%)** | | | | **Trophic diversity index** | **Maturity Index** |
| **1A** | **1B** | **2A** | **2B** |
| Slope | 16.1 (10.7, 24.4) | 0.70 (0.44, 1.13) | 39.8 | 4.9 | 20.0 | 35.3 | 0.42 | 3.36 |
| Western | 37.6 (24.8, 56.8) | 3.90 (2.49, 6.08) | 13.2 | 6.6 | 45.1 | 35.2 | 0.40 | 3.27 |
| Central | 42.0 (27.8, 63.5) | 9.58 (6.17, 14.9) | 14.8 | 8.8 | 34.1 | 42.4 | 0.34 | 3.03 |
| Eastern | 47.0 (31.1, 71.0) | 5.39 (3.45, 8.41) | 7.7 | 4.6 | 34.3 | 53.4 | 0.44 | 3.23 |

**Table 4.** Variations in apparent faunal composition assessed by analysis of similarities (ANOSIM), global and pairwise statistics are reported, for macrofaunal nematodes, polychaetes, combined nematodes and polychaetes, and combined common (present in ≥5 samples) nematodes and polychaetes, among study sites (SL, Slope; WE, Western; CE, Central; EA, Eastern; ns, not significant; \* p<0.05; \*\* p<0.01).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Taxa** | **Global R** | **Pairwise R** | | | | | |
| **SL-WE** | **SL-CE** | **SL-EA** | **WE-CE** | **WE-EA** | **CE-EA** |
| Common nematodes and polychaetes | 0.728 (p<0.001) | 0.740\*\* | 0.968\*\* | 0.984\*\* | 0.608\*\* | 0.796\*\* | 0.424\*\* |
| All nematodes and polychaetes | 0.671 (p<0.001) | 0.768\*\* | 0.944\*\* | 0.984\*\* | 0.492\* | 0.704\*\* | 0.428\*\* |
| Polychaetes | 0.660 (p<0.001) | 0.572\*\* | 0.860\*\* | 0.964\*\* | 0.600\* | 0.772\*\* | 0.432\* |
| Nematodes | 0.299 (p<0.001) | 0.540\*\* | 0.644\*\* | 0.404\* | ns | ns | ns |

**Table 5.** Macrofaunal nematode and polychaete genus diversity measures at the Whittard Canyon (Western, Central and Eastern branches) and adjacent slope study sites. (G, number of genera; N, number of individuals; EG, rarefied number of genera for n individuals; F, Fisher’s alpha index; H', standard and exponential form of Shannon diversity [log2]; 1/D, inverse form of Simpson’s index).

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
|  | **G** | **N** | **EG** | **F** | **H'** | **exp(H')** | **1/D** |
| **Nematodes** |  |  | (n = 46) |  |  |  |  |
| Slope | 19 | 46 | 19.0 | 12.1 | 2.59 | 13.4 | 10.1 |
| Western | 27 | 100 | 17.2 | 10.2 | 2.34 | 10.5 | 7.0 |
| Central | 28 | 124 | 16.4 | 9.1 | 2.21 | 9.3 | 6.0 |
| Eastern | 25 | 140 | 15.4 | 8.4 | 2.32 | 10.3 | 7.6 |
| **Polychaetes** |  |  | (n = 318) |  |  |  |  |
| Slope | 45 | 322 | 44.7 | 14.2 | 2.89 | 18.0 | 11.0 |
| Western | 35 | 318 | 35 | 10.0 | 2.67 | 14.5 | 9.6 |
| Central | 41 | 568 | 33.3 | 9.4 | 2.47 | 11.8 | 6.6 |
| Eastern | 40 | 751 | 30.4 | 8.2 | 2.30 | 10.0 | 5.2 |

**Figure captions**

Fig. 1. Study area. (A) General location of the Whittard Canyon system (contours illustrated: 200, 1000, 2000, 3000, 4000 m, adapted from the General Bathymetric Chart of the Oceans; PAP, Porcupine Abyssal Plain; PSB, Porcupine Seabight; UK, United Kingdom). (B) Detailed bathymetry of, and location of sampling sites within, the canyon system (SL, Slope; WE, Western; CE, Central; EA, Eastern; contours illustrated are 200-4500 m in 100 m intervals). Both maps are presented in the projected coordinate system: WGS1984 UTM zone 29N.

Fig 2. Macrofaunal nematode standing stocks at Slope (SL), Western (WE), Central (CE), and Eastern (EA) study sites. (A) Density (geometric mean and 95% confidence interval) and life stage proportions (juve., juvenile; indet., indeterminate). (B) Corresponding estimates of biomass (see text for detail; wwt, wet weight).

Fig. 3. Non-metric multidimensional scaling ordinations of macrofaunal assemblage variation: (A) common (present in ≥5 samples) nematodes and polychaetes, (B) all nematodes and polychaetes, (C) all polychaetes, and (D) all nematodes. In all cases based on √x-transformation of faunal density and Bray-Curtis dissimilarity. (SL, Slope; WE, Western; CE, Central; EA, Eastern).

Fig. 4. Macrofaunal functional group composition. (A) Nematode feeding groups (SD, selective deposit; ND, non-selective deposit; EP, epigrowth; OP, omnivore / predator). (B) Polychaete feeding groups (MI, microphage; MA, macrophage; OM, omnivore). (C) Nematode tail shape (RO, rounded; CO, conical; CC, clavate-conicocylindrical; LO, long). (D) Polychaete motility (MO, motile; DM, discretely motile; SE, sessile). (SL, Slope; WE, Western; CE, Central; EA, Eastern).

Fig. 5. Genus rank abundance distributions of macrofaunal (A) nematodes and (B) polychaetes (selected key taxa are indicated by letter coding). (SL, Slope; WE, Western; CE, Central; EA, Eastern).

Fig. 6. Ecological summary interpretation of macrofaunal nematode and polychaete data from the Whittard Canyon system study area (SL, Slope; WE, Western; CE, Central; EA, Eastern).



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