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Distribution and environmental drivers of macrofaunal nematode communities across gradients of methane seepage at cold seeps on Hikurangi Margin (New Zealand) and potential implications of disturbance from gas hydrate extraction

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Cold seeps are areas characterised by specialized biological communities that rely on chemosynthesis for their nutrition. To date, research conducted on New Zealand's Hikurangi Margin seep communities has focused on communities at 650–1200 m water depth. Here, we characterize the macrofaunal nematode communities of New Zealand cold seeps for the first time, and at deeper (> 1200 m) seep locations (Maungaroa, Glendhu and Uruti South). There were no significant difference in nematode abundance, species richness, diversity and evenness among the seep areas, which may reflect the lack of difference in most sediment variables. However, a consistent spatial pattern in nematode abundance was observed within all the seep areas on the Hikurangi Margin: abundance was highest at or near the seep centre, decreased steeply away from the centre and was low in the periphery. These spatially consistent patterns reflect the influence of methane seepage, which appears limited to the inner 150–200 m radius of each area, on nematode abundance via input of chemosynthetic food sources. We found significant differences in nematode community structure among all three areas, with most of the heterogeneity in community structure between the shallow Uruti South area and deeper Maungaroa and Glendhu areas, and differences among nematode communities of high, medium and low abundance associated with site-specific gradients in methane seepage. Within area variability in nematode community structure was mainly correlated with food availability and sediment grain size. Consistent with previous investigations of seep nematodes, we did not find evidence of seep endemics. Although deposit feeders were generally the most

abundant feeding group, there were differences in the relative abundances of different feeding groups such as microvores and epigrowth feeders among the seep areas, and as a function of distance from the centre of the seep areas. Impact on seep communities from gas hydrate extraction processes may occur via reduction or potentially cessation of free-gas methane supply to the seafloor, 'sand' production at the seafloor due to the physical degradation of the substrate structure, or alteration of the structural integrity of the seafloor substrate. Any spatial management options considered for managing these impacts should reflect the differences in benthic community structure between depths and locations on the Hikurangi Margin.

KEYWORDS

macrofauna, infauna, community ecology, continental slope, nematode species

Introduction

Cold seeps are areas of where methane-rich fluids emerge from the seafloor, leading to the establishment of specialized biological communities that rely on chemosynthesis for their nutrition (Paull et al., 1984; Paull et al., 1985). To date, most of the research on cold seep faunal communities has focused on mega-epifaunal taxa (Levin, 2005; Cordes et al., 2009). This megafauna is typically dominated by vestimentiferan tube worms, bathymodiolin mussels and vesicomid clams hosting sulphide-oxidising and/or methanotrophic symbionts (Childress et al., 1986; Fiala-Medioni et al., 1993), with biomass far exceeding that of surrounding non-seep sediments. Macro-infaunal abundance in seep sediments also tends to be greater than in non-seep sediments, but in some cases the pattern is absent or even the reverse (Levin, 2005). Macrofauna are more likely to exhibit greater abundance in seep than non-seep sediments at greater water depths, presumably because food becomes more limiting in deeper environments (Levin and Michener, 2002). Seep macrofauna is typically dominated by polychaetes (e.g., dorvilleids, hesionids and ampharetids) and bivalves (e.g., vesicomid, solemyid, nuculanid clams). Some of these deep-sea seep-associated macro-infaunal taxa are endemic to seeps, in particular the chemoautotrophic taxa, but most also occur in non-seep sediments (Sahling et al., 2002; Sahling et al., 2003; Bernardino et al., 2012). Geochemical characteristics of the sediments such as seepage rate and sulphide concentration are key determinant of macro-infaunal community structure at seeps (Sahling et al., 2003; Levin et al., 2003; Demopoulos et al., 2018), as well as the presence of megafauna (Menot et al., 2010; Portail et al., 2015). Macro-infaunal communities associated with mats of sulphur bacteria are usually characterised by low diversity and are often dominated by a few highly abundant species (Dando et al., 1994; Levin, 2005; Menot et al., 2010).

Nematodes are among the most abundant metazoan taxon in deep-sea sediments (Zeppilli et al., 2018). They are particularly abundant in meiofaunal samples processed using a mesh size of 20–63 μm , often comprising >90% of metazoan abundance (Heip

et al., 1985). Nematodes are also common, and sometimes dominant, in deep-sea macrofaunal samples (usually processed using a 250–500 μm mesh) (Hessler and Jumars, 1974; Hecker and Paul, 1979; Pavithran et al., 2009; Sharma et al., 2011), but they are seldom included in studies of macro-infauna. Studies have shown macrofaunal nematode communities to be distinct from meiofaunal nematode communities, as well as exhibiting different functional response to environmental factors compared to their meiofaunal counterparts (Sharma et al., 2011; Baldrighi and Manini, 2015; Charrier et al., 2023). Macrofaunal nematode communities, on the other hand, appear to exhibit broadly similar trends to macrofaunal polychaete communities (Gunton et al., 2016).

In their review of nematodes associated with deep-sea chemosynthetic environments, Vanreusel et al. (2010a) found that nematodes are sometimes substantially more abundant in cold seep sediments than at nearby background sites, and that nematode communities at cold seeps are typically characterized by low diversity and are often dominated by a single species. Whilst studies of meiofaunal communities associated with shallow seeps have found high abundance of nematode species with endo- or ectosymbiotic bacteria (Dando et al., 1991; Jensen et al., 1992), symbiont-bearing nematode taxa have not been documented from deep-sea seeps. Unlike what has been observed for seep macro and megafaunal communities, there does not appear to be any nematode taxon endemic to seeps in the deep sea, and the available data show high variability in community structure among geographical locations (Vanreusel et al., 2010a). Investigations conducted since the review by Vanreusel et al. (2010a) largely confirm these observations (e.g., Hauquier et al., 2011; Pape et al., 2011; Portnova et al., 2011; Guilini et al., 2012).

Sites of active seepage have been identified on the Hikurangi Margin of New Zealand at depths of 600 to 2000 m (Greinert et al., 2010; Watson et al., 2020). Similar to seeps in other parts of the world, the mega-epifaunal communities at these Hikurangi Margin sites are dominated by vesicomid clams, siboglinid worms and bathymodiolin

mussels (Baco et al., 2010; Jones et al., 2010; Klaucke et al., 2010). The infaunal communities, however, are characterised by unusually high abundance and biomass of tube-building ampharetid polychaetes; the ampharetids are heterotrophic and derive most of their carbon from aerobic methanotrophy, probably by direct consumption of methane-oxidising bacteria (Thurber et al., 2010; Thurber et al., 2013). It is likely that ampharetids play a part in the early stages of seep community development on Hikurangi Margin by increasing the availability of sulphide and methane at the seabed (Bowden et al., 2013). Macro-infaunal seep communities on Hikurangi Margin were found to be distinct from slope, canyon and seamount communities in the region, largely due to a greater abundance of virtually all taxa, in particular spionid, ampharetid, glycerid and dorvilleid polychaetes as well as amphipods and cumaceans (Leduc et al., 2016). Rosli et al. (2016) showed that meiofauna abundance at the Opouawe Bank seep on Hikurangi Margin was similar to that of meiofauna from slope and seamount habitats at similar depths (ca. 1000 m), and lower than meiofauna from canyon habitats. Meiofaunal community structure differ between seep and all other deep-sea habitats, mainly due to a greater abundance of nauplii and amphipods in the seep samples relative to slope, canyon and seamount samples (Rosli et al., 2016). No data have yet been obtained, however, on nematode communities at seep sites on the Hikurangi Margin (Rosli et al., 2018).

Although seep sites have been identified at depths from 600 to 2000 m on the Hikurangi Margin, the bulk of the research conducted on the seep communities in the region to date has focused on seeps shallower than 1200 m water depth (Thurber et al., 2010; Thurber et al., 2013; Bowden et al., 2013; Leduc et al., 2016; Rosli et al., 2016; Rosli et al., 2018). These communities are exposed to varying degrees of trawling disturbance from fisheries, with some sites exposed to 100 or more trawls in a fifteen-year period, with signs of disturbance including areas of broken fragments of corals, abandoned gear and scour marks (Bowden et al., 2013). While no clear correlation between trawl intensity and benthic community structure has been quantified, tubeworm populations were found to be sparse, highly localised or absent at sites where trawling was most intense (Bowden et al., 2013). The Hikurangi Margin is an area where gas hydrates occur, and these deposits are a potentially extractable energy resource for New Zealand (Pecher and Henrys, 2003; Pecher et al., 2022). Shallow and deep seep communities may be vulnerable to the disturbance from large-scale extraction of seabed gas hydrates through direct physical impacts, smothering by resuspended sediments, modification of fluid flows, and large-scale destabilisation of slope sediments (Oluwunmi et al., 2023).

In July 2019, a research voyage to New Zealand's Hikurangi Margin took place as part of the research programme "Gas hydrates: Economic opportunities and environmental implications" (HYDEE). The goal of this voyage was to obtain biological and biogeochemical data to investigate the potential impact of disturbances from any future gas-hydrate extractions to the marine ecosystems. This voyage provided an opportunity to characterize the nematode species communities of New Zealand cold seeps, which had not been investigated previously, and to study deeper (> 1200 m) seep locations unimpacted by current anthropogenic disturbance (i.e., trawling). Here, we describe the

macrofaunal nematode communities at three seeps on Hikurangi Margin (Maungaroa, Glendhu and Uruti South) and investigate relationships with environmental variables. The results of this study are discussed in relation to the potential environmental effects of gas hydrate extraction for the nematode communities. Results of analyses conducted on the broader macro-infaunal communities, as well as meiofaunal and mega-epifaunal communities, as part of the HYDEE research programme will be presented elsewhere.

Methods

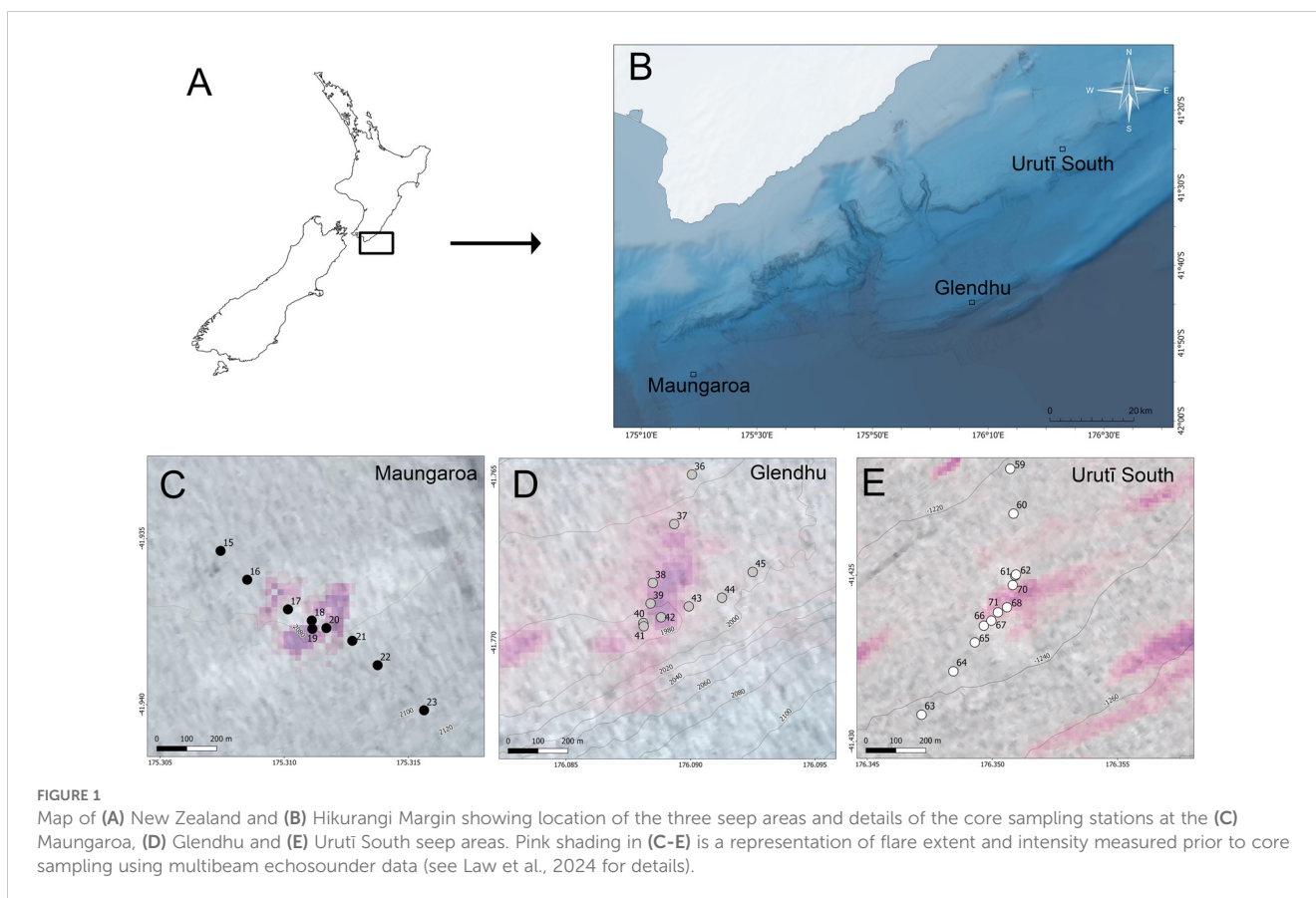
Sampling

Samples were obtained from the southern end of the Hikurangi subduction margin, off the east coast of New Zealand's North Island, in a region where the Pacific Plate subducts obliquely beneath the Australian Plate, and where potentially economically viable gas hydrate deposits are known to occur. Based on information from the geological/geophysical-focused research voyage HYDEE I (TAN1808) (Crutchley et al., 2018), three cold seeps were targeted during the biological/biogeochemical-focused research voyage HYDEE II (TAN1904) in July 2019: Maungaroa and Glendhu at ca. 2000 m depth, and Uruti South at ca. 1250 m depth (Law et al., 2024; Figure 1). Each seep area was approximately 1 km in diameter, at the centre of which was an active cold seep of approximately 200-300 m in diameter as determined by the extent of the seafloor backscatter signal for the carbonate rock that forms at the main seepage location. At each area, several transects were conducted using a deep-towed imaging system (DTIS) equipped with still and video camera (Bowden et al., 2013) and a methane sensor (Franatech, Oslo, Norway; Law et al., 2024). These transects were used to characterise the mega-epifauna and the substrate across gradients of seepage, obtain *in situ* measurements of methane concentrations, and help determine suitable coring location (Law et al., 2024, Bowden et al. in prep.). Methane readings closest to each core site were used for the analyses.

At each seep area, a video-guided multicorer was deployed once at each of 9-12 locations along a transect spanning the outer periphery of the area, the edge of the seep, and the centre of the seep (Table 1). The Ocean Instruments MC-800A multicorer was equipped with cores of 9.5 cm internal diameter. At most locations, two cores from the same deployment (station) were used for analyses of macro-infauna, with the exception of stations 42 and 71 where only one core was obtained. One core for analyses of sediment physicochemical characteristics was obtained from nine locations at each seep area (Table 1). The top 5 cm of sediment was sliced for analyses of macrofauna. The sediment was sieved using a 300 µm mesh, then fixed in 10% formalin and stained with Rose Bengal. Cores for analyses of sediment characteristics were sliced at one centimetre intervals.

Sediment and nematode analyses

The following sediment variables were determined: mean grain size (µm), proportion of silt/clay particles (%silt/clay), particle



skewness, kurtosis and sorting. Biogeochemical parameters were also determined, including porewater methane and sulphide concentrations, total organic matter (%TOM) as a measure of food availability, chlorophyll *a* (Chl *a* ($\mu\text{g/g}$ of dry weight sediment)) as a measure of 'fresh' phytodetrital organic matter, phaeopigments (Phaeo ($\mu\text{g/g}$ of dry weight sediment)) as a measure of degraded phytodetrital organic matter, and their ratio (Chl *a*: Phaeo) as a measure of the 'freshness' of the phytodetrital organic matter, with higher values being 'fresher'. Physical variables were determined by laser diffraction, while %TOM were determined by loss-on-ignition (4 h at 500°C) (Eleftheriou and Moore, 2005). Calcium carbonate percentages were determined using a gasometric technique. Chlorophyll *a* and phaeopigments were determined by standard spectrophotometric techniques subsequent to freeze-drying and extraction in 90% acetone (Sartory, 1982). Methane was measured from sediment via the headspace equilibration method (Magen et al., 2014). In brief, 5 mL of sediments were subsampled with a syringe into a glass vial with 2.5% NaOH and vials were capped and sealed. Headspace methane concentration was measured onshore using gas chromatography and a flame ionisation detector. Sulphide was measured from sediment porewater, sampled with Rhizons from sediment cores following retrieval, preserved with zinc acetate and measured via the methylene blue assay (Cline, 1969). Sediment grain size variables were measured based on the 0-1 cm, 1-2 or 2-3 cm, and 4-5 cm layers, and data shown here are shown as average of these three layers. Pigment and %TOM data were derived from the top five cm

layers, and carbonate data were obtained from the 0-1 and 4-5 cm layers (presented here as average of both).

Nematodes were counted under a stereomicroscope, transferred to pure glycerol and mounted on slides (Sommerfield and Warwick, 1996). All nematodes were identified to putative species (whenever possible) using the descriptions in Warwick et al. (1998) and Schmidt-Rhaesa, 2014), as well as the primary taxonomic literature. Nematodes were classified into feeding types following Moens and Vincx (1997). This scheme divides nematodes into six feeding types, i.e., microvores, ciliate feeders, deposit feeders, epigrowth feeders, facultative predators, and predators.

Statistical analyses

Analyses of univariate and multivariate data were conducted using the statistical routines in the multivariate statistical analysis software PRIMER v7 (Clarke and Gorley, 2015). PERMANOVA was used for analyses of nematode univariate and multivariate data as it does not rely on normally distributed data or balanced designs (Anderson et al., 2008). The following univariate parameters were quantified for each coring station: abundance (individuals 0.1 m^{-2}), species richness (core^{-1}), species diversity (Shannon diversity, $H'10$) and species evenness (J'). Univariate parameters were derived by averaging values of the two cores that were processed at each station, except for stations 42 and 71 where only one core was processed. Multivariate data were derived in the same way.

TABLE 1 Details of the Hikurangi Margin study areas sampled in July 2019 during NIWA voyage TAN1904.

| Seep area | Station | Distance from centre of seep area (m) | Water depth (m) | Latitude (S) | Longitude (E) | Number of macrofauna cores | Core for sediment analyses? |
|-------------|---------|---------------------------------------|-----------------|--------------|---------------|----------------------------|-----------------------------|
| Maungaroa | 15 | 386 | 2070 | 41.9354 | 175.3076 | 2 | Yes |
| | 16 | 253 | 2068 | 41.9363 | 175.3087 | 2 | Yes |
| | 17 | 87 | 2070 | 41.9372 | 175.3103 | 2 | Yes |
| | 18 | 17 | 2075 | 41.9376 | 175.3110 | 2 | Yes |
| | 19 | 0 | 2075 | 41.9376 | 175.3112 | 2 | Yes |
| | 20 | 55 | 2076 | 41.9378 | 175.3118 | 2 | Yes |
| | 21 | 149 | 2077 | 41.9382 | 175.3128 | 2 | Yes |
| | 22 | 266 | 2082 | 41.9390 | 175.3138 | 2 | Yes |
| | 23 | 479 | 2091 | 41.9403 | 175.3157 | 2 | Yes |
| Glendhu | 36 | 537 | 2000 | 41.7650 | 176.0902 | 2 | No |
| | 37 | 361 | 2003 | 41.7665 | 176.0895 | 2 | Yes |
| | 38 | 148 | 1994 | 41.7683 | 176.0886 | 2 | Yes |
| | 39 | 82 | 1985 | 41.7689 | 176.0885 | 2 | Yes |
| | 40 | 11 | 1993 | 41.7695 | 176.0882 | 2 | Yes |
| | 41 | 0 | 1989 | 41.7696 | 176.0882 | 2 | Yes |
| | 42 | 67 | 2003 | 41.7693 | 176.0889 | 1 | Yes |
| | 43 | 164 | 2010 | 41.7690 | 176.0900 | 2 | Yes |
| | 44 | 277 | 1985 | 41.7687 | 176.0913 | 2 | Yes |
| | 45 | 407 | 1996 | 41.7680 | 176.0926 | 2 | Yes |
| Uruti South | 59 | 467 | 1207 | 41.4218 | 176.3508 | 2 | Yes |
| | 60 | 312 | 1210 | 41.4232 | 176.3509 | 2 | Yes |
| | 61 | 105 | 1227 | 41.4251 | 176.3510 | 2 | No |
| | 62 | 116 | 1226 | 41.4250 | 176.3510 | 2 | Yes |
| | 63 | 455 | 1237 | 41.4292 | 176.3472 | 2 | Yes |
| | 64 | 275 | 1245 | 41.4279 | 176.3485 | 2 | Yes |
| | 65 | 164 | 1236 | 41.4271 | 176.3493 | 2 | Yes |
| | 66 | 101 | 1230 | 41.4266 | 176.3497 | 2 | Yes |
| | 67 | 67 | 1232 | 41.4264 | 176.3500 | 2 | Yes |
| | 68 | 0 | 1237 | 41.4260 | 176.3506 | 2 | Yes |
| | 70 | 82 | 1235 | 41.4253 | 176.3509 | 2 | No |
| 71 | 50 | 1224 | 41.4260 | 176.3500 | 1 | No | |

Similarity matrices for univariate variables were built using Euclidean distance of untransformed data, and similarity matrices for multivariate data (nematode community structure) were built using the Bray-Curtis similarity measure of square root-transformed abundance data (Anderson et al., 2008; Anderson et al., 2011). The PERMANOVA was conducted using the single fixed factor “area” and distance from centre of seep area as covariate. P-values were obtained by 999 permutations. Pairwise PERMANOVA comparisons were conducted to identify which pair

(s) of areas were responsible for the significant factor effect and the PERMDISP routine was used to test for differences in multivariate dispersion between the seep areas (Anderson et al., 2008). The SIMPER routine in PRIMER was used to identify the species contributing most to within-area similarity (75% similarity cut-off) and to among-area dissimilarity (40% dissimilarity cut-off) (Clarke and Warwick, 2001). Patterns in nematode community structure were visualised using a multidimensional (MDS) scaling ordination plot (Clarke and Warwick, 2001). In order to assess the level of

heterogeneity in the structure of nematode communities among and within areas, the CLUSTER and SIMPROF routines in PRIMER were used to identify natural community groupings, with *P* set at 0.01 (Clarke et al., 2008). The SIMPER routine was then used to identify species responsible for within-group similarity (75% similarity cut-off).

Environmental variables (including sediment characteristics and methane concentrations) were compared among areas using PERMANOVA. The similarity matrix was built using Euclidean distance of normalised multivariate environmental data. As per the nematode analyses, the PERMANOVA was conducted using the single fixed factor “area”, *P*-values were obtained by 999 permutations, and SIMPER was used to identify the variables contributing most to among area dissimilarity.

Relationships between predictor variables and univariate and multivariate nematode community parameters were investigated using distance-based linear models (DistLMs) (Anderson et al., 2008). Because preliminary PERMANOVA with pairwise comparisons showed significant differences in nematode community structure among all three seep areas, separate DistLM analyses were conducted for each area. Predictor variables were checked for multicollinearity, which led to the removal of particle kurtosis, particle sorting, sand content and mud content from the list of predictor variables as they were highly correlated with other variables ($r \geq 0.9$; Anderson et al., 2008). The remaining predictor variables were: mean particle size, particle skewness, %TOM, chl *a*, phaeo, chl *a*:phaeo, carbonate content, porewater sulphide concentration, porewater methane concentration and water column methane concentration. Water column methane concentration data from the nearest reading to the multicorer station were used (based on DTIS-mounted methane sensor), at a distance of 4–72 m away from the core location. As for the PERMANOVA, similarity matrices for univariate variables were built using Euclidean distance of untransformed data, and similarity matrices for multivariate data (nematode community structure) were built using the Bray-Curtis similarity measure of square root-transformed abundance data.

Results

Environment and sediment characteristics

There was a significant difference in environmental variables among the areas (PERMANOVA, $P = 0.001$). Pairwise comparisons were significant between all three areas ($P = 0.05$). Most (>50%) of the dissimilarity in environmental characteristics among the areas was due to sediment organic matter concentrations, water column and porewater methane concentrations, carbonates and pigment concentrations as well as sediment mean grain size (SIMPER, Supplement A). Methane concentrations in the water column decreased from the centre of each seep area towards the periphery (Figure 2). Methane concentrations in the water column were markedly greater at the Maungaroa (70–950 nmol L⁻¹) and Uruti South areas (39–688 nmol L⁻¹) than at the Glendhu area (4–208 nmol L⁻¹) (Supplement B). Porewater methane concentrations were markedly lower than water column methane

concentrations but showed the same general pattern of decreasing concentrations away from the centre of each seep area; the highest porewater methane concentrations were observed at Uruti South. Porewater sulphide concentrations decreased away from the centre of the Maungaroa seep area but peaked closer to the periphery at Glendhu and Uruti South. Sediment grain size characteristics were relatively similar across the three seep areas, consisting mostly of fine, medium and coarse silt particles (%silt = 87–97%, mean grain size = 12–27 μm) with relatively small proportions of sand particles (1–12%) (Supplement B). There was no obvious trend in grain size characteristics with distance from the seep centre at the Maungaroa area, however, mean grain size and particle sorting tended to be greater at or near the centre of the Glendhu and Uruti South areas (Figure 2); overall, mean grain size was slightly higher at the Glendhu area than at the other two areas. Sediment organic matter content (%TOM) was high and similar across all three areas (ca. 8–10%) but tended to be slightly higher at the Glendhu area and did not show any consistent trend with distance from the seep centres. Variability in carbonate content in the sediments was limited but tended to be lowest at the Maungaroa area, and to be slightly higher at or near the seep centres (Figure 2). Sediment chlorophyll *a* and phaeopigment concentrations were both markedly more elevated at the Maungaroa area than at the other two areas, but there was no trend in sediment pigment concentrations with distance from seep centres at any of the areas. The ratio of chlorophyll *a* to phaeopigment concentrations showed limited variability among the areas and no clear spatial trend was observed within areas (Figure 2).

Nematode communities

Values of univariate nematode community parameters were similar at all three study areas, and no significant difference in nematode abundance, species richness, diversity and evenness was observed among areas (PERMANOVA, $P > 0.05$; Supplement C). High nematode abundance values (> 1000 ind. 0.1 m²) were observed at (Maungaroa, Glendhu) or near (Uruti South) the centre of each of the seep area, with a steep decline away from the centre and uniformly low abundances in the seep periphery (>150–200 m away from seep centre; 190–681 ind. 0.1 m²; Figure 3). Despite the similar trends at the three areas, nematode abundance in the seep periphery was noticeably greater at the Maungaroa area (421–681 ind. 0.1 m²) than at the Glendhu and Uruti South areas (190–379 ind. 0.1 m²), and the peak in nematode abundance at or near the seep centre was ca. 45% higher at the Maungaroa and Uruti South areas (maximum abundance ca. 2300 ind. 0.1 m² at both areas) compared to the Glendhu area (ca. 1600 ind. 0.1 m²).

Species richness ranged from 5 to 18 species per core across the study areas. No clear within-area trend in species richness was observed at the Maungaroa and Glendhu areas, however, values tended to be more variable near the seep centre (Figure 3). At the Uruti South area, species richness values were elevated near the seep centre relative to values in the seep periphery. Species diversity (*H'*) and evenness (*J'*) showed a different trend, with the lowest values observed near the seep centres but with substantial variation among

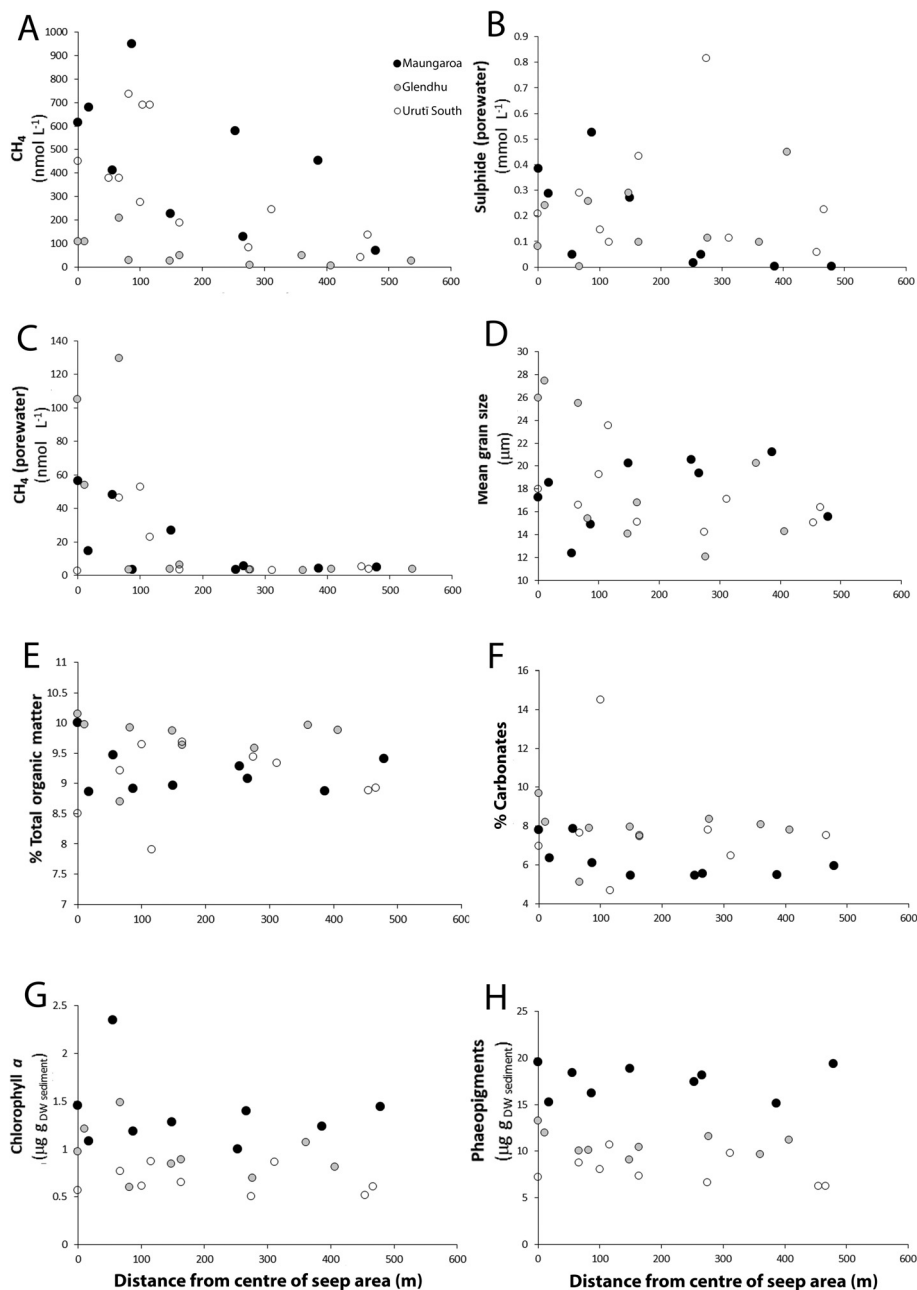


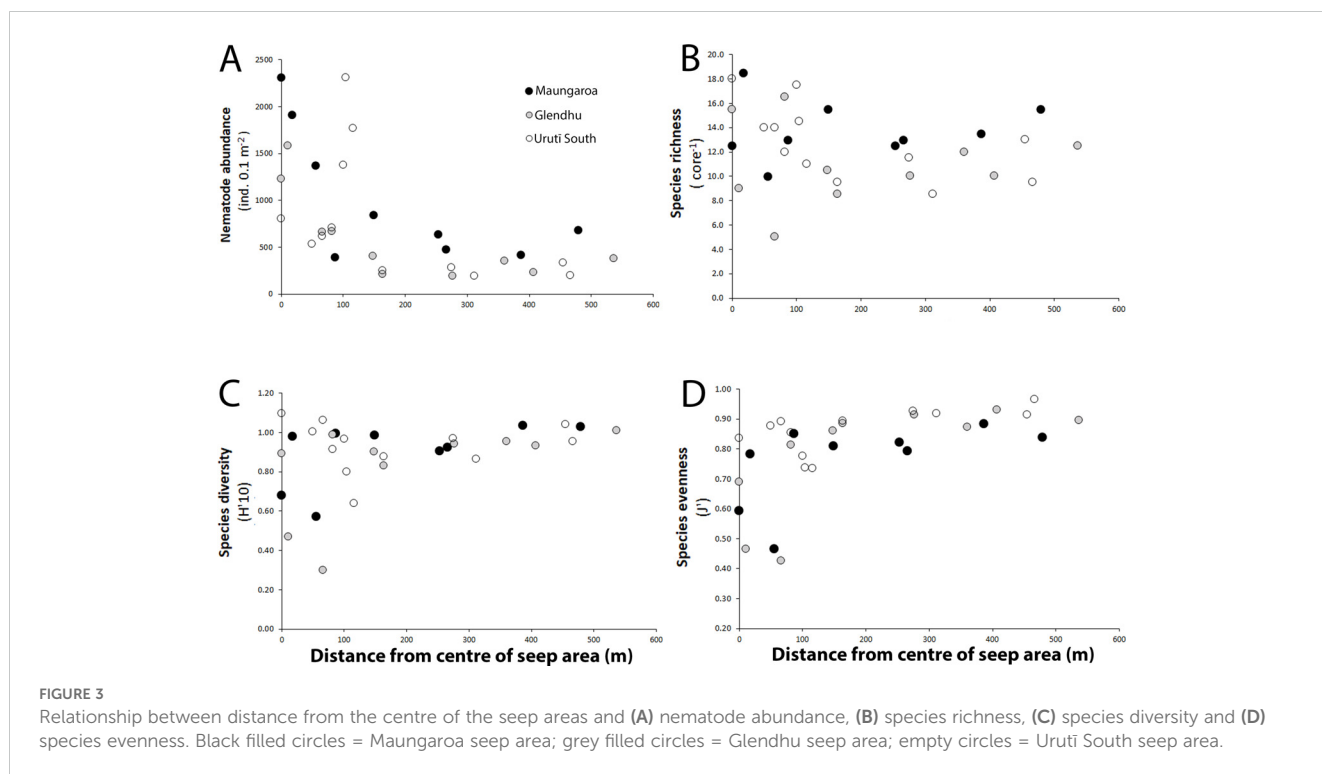
FIGURE 2

Relationship between distance from the centre of the seep areas and (A) dissolved methane concentration (seawater), (B) porewater sulphide concentration, (C) dissolved methane concentration (porewater), (D) sediment mean grain size, (E) organic matter content, (F) carbonate content, (G) chlorophyll a concentration, and (H) pheopigment concentrations. Black filled circles = Maungaroa seep area; grey filled circles = Glendhu seep area; empty circles = Uruti South seep area.

locations, whereas values were uniformly high in the seep periphery of all areas (Figure 3).

A total of 3374 nematode specimens were identified. Of these, 96% were identified to species or morphospecies, while the rest of the specimens was identified to genus or family due to poor preservation or because they were juveniles. Overall, 56 genera were identified with *Sabatieria* the most common genus by far (accounting for 28% of all nematodes), followed by *Rhabdodemanina* (10%), *Paramesacanthion* and *Oncholaimus* (8% each), *Odontophora* (6%) and *Halalaimus* (5%). All other genera

represented 4% or less of the total. A total of 103 nematode species comprising 17 named species and 86 morphospecies were identified (Supplement D). A total of 56, 60 and 67 species were identified from the Maungaroa, Glendhu and Uruti South areas, respectively, with 26 species present across all three areas, 29 species found at two of the three areas and 48 species found at only one area. Thirteen species were only found at the Maungaroa area, including *Odontophora* B, the most common species at that area. A similar number of species (14) were found only at the Glendhu area, all of which were relatively uncommon or rare (average abundance



< 3 ind. 0.1 m⁻²). Twenty-one species were found exclusively at the Uruti South area, including the relatively abundant *Oncholaimus A*, *Dorylaimopsis nodderi* and *Deontostoma tridentum* (average abundance > 10 ind. 0.1 m⁻²).

There was a significant difference in nematode species community structure among the seep areas (PERMANOVA, $P = 0.0001$), with all areas significantly different from each other (pairwise PERMANOVA, $P < 0.02$; Figure 4). The similarity between the nematode communities at the shallower Uruti South area and the two deeper Maungaroa and Glendhu areas was low (average similarity = 26% between each pair) relative to the similarity between the Maungaroa and Glendhu communities (35%). There was no significant difference in multivariate dispersion among the areas (PERMDISP, $P > 0.1$). A number of species accounted for a substantial proportion of within-area similarity across all areas, including *Paramesacanthion A*, *Rhabdodemanina zealandiaensis*, *Oncholaimus adustus* and *Odontanticoma A* (Table 2). Among-area dissimilarity was mostly due to differences in the abundances of species, although as noted above some species were found only at one or two of the areas (Table 3). For example, *Sabatieria bathycopia* was present at all three areas, being most common at Glendhu, followed by Maungaroa then Uruti South, while *Sabatieria articulata* and *Sabatieria balbutiens* were most abundant at Uruti South, less abundant at Maungaroa, and absent from Glendhu.

The Cluster and SIMPROF analyses identified six groupings, leaving one sampling location (Glendhu area, station 42, represented by one core) unclustered (Figure 4). This sample was unusual in that only five species were found there (species richness ranged from 8.5 to 18.0 per core at the other locations), with most (82%) specimens identified as *Sabatieria A*. Three of the SIMPROF

groups comprised samples from the Uruti South area, with the remaining three groups comprising a combination of Maungaroa and Glendhu samples or samples from Glendhu only. The Uruti South groups were: “U-High”, comprising samples with high nematode abundance (702–2310 ind. 0.1 m⁻²), “U-Med”, comprising samples with medium nematode abundance (534–801 ind. 0.1 m⁻²), and “U-Low”, comprising samples with low nematode abundance (190–330 ind. 0.1 m⁻²) (Table 4; Figure 5). The Maungaroa/Glendhu groups were: “MG-High” (1369–2310 ind. 0.1 m⁻²), “MG-Med” (232–1919 ind. 0.1 m⁻²) and “MG-Low” (190–211 ind. 0.1 m⁻²). The U-High group comprised samples located relatively near (67–116 m) to the centre of the Uruti South area, whereas the corresponding group MG-High comprised samples located at the centres (0–55 m) of the Maungaroa and Glendhu areas. These high abundance groups were characterised by low species evenness ($J' = 0.46$ – 0.89) relative to the medium and low abundance groups at their respective areas (Table 4). Both U-Low and MG-Low comprised samples taken at least 164 m away from the centres of their respective areas and were characterised by relatively high species evenness ($J' = 0.89$ – 0.96). Some species such as *Rhabdodemanina zealandiaensis* and *Oncholaimus adustus* were relatively common across all or most of the groups, whereas others such as *Metacylicolaimus catherinae* and *Linhomoeus pycnocricus* characterised only one or two groups. Within-group similarity for group U-High was mainly due to high relative abundance of *Sabatieria articulata*, *Rhabdodemanina zealandiaensis* and *Desmodora parapilosa*, whereas the MG-High group was mainly characterised by *Sabatieria bathycopia*, *Paramesacanthion A* and *Odontophora B*. The groups U-Med and GM-Med were both characterised by high abundance of *Oncholaimus adustus* and

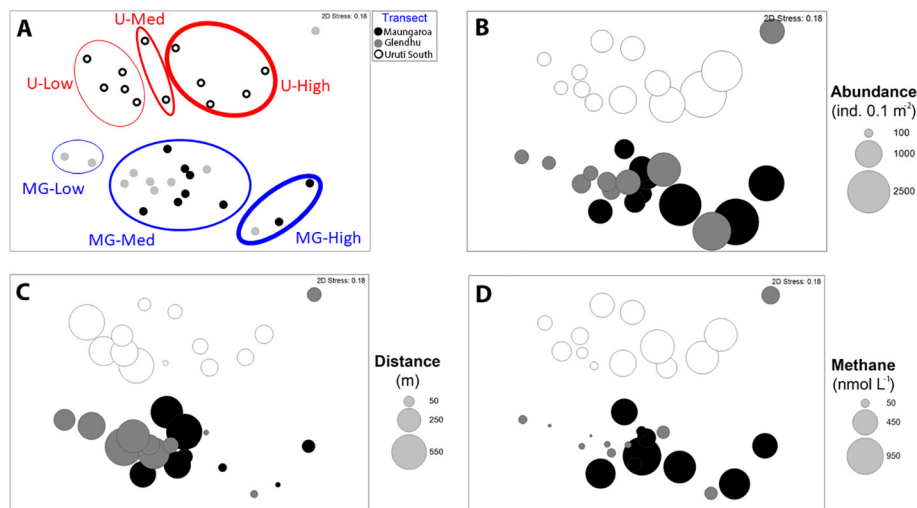


FIGURE 4

Two-dimensional multidimensional scaling (MDS) plot of square root-transformed nematode species abundance data at the Maungaroa (black filled circles), Glendhu (grey filled circles) and Uruti South (empty circles). The groups identified by SIMPROF are circled with blue (Uruti South groups) and blue lines (Maungaroa and Glendhu groups) (A). The size of the bubbles on (B), (C) and (D) indicate total nematode abundance, distance from the centre of the seep area, and methane concentration, respectively. U-High = Uruti South high abundance group; U-Med = Uruti South medium abundance group; U-Low = Uruti South low abundance group; Mg-High = Maungaroa & Glendhu high abundance group; MG-Med = Maungaroa and Glendhu medium abundance group; MG-Low = Maungaroa and Glendhu low abundance group.

Rhabdodemanina zealandiaensis, however the remaining characterising species differed between the groups. Group U-Low was characterised by high relative abundance of *Sabatieria balbutiens*, *Linhomoeus pycnocricus* and *Oncholaimus adustus* whereas group MG-Low was mainly characterised by *Oncholaimus adustus*, *Rhabdodemanina zealandiaensis* and *Halalaimus C.*

Nematode communities were dominated by deposit feeders and facultative predators, which together comprised over 70% of the community overall. There was substantial variability in the relative abundance of nematode feeding groups among the groups identified by the Cluster and SIMPROF analyses (Figure 6). Microvores, which include the common genus *Halalaimus*, tended to be more abundant at the deep Maungaroa and Glendhu areas than at the shallower Uruti South area. Average relative abundance of microvores was lowest (0-5% of total) in the high abundance groups (U-High and MG-High) but substantially higher (5-31%) in the U-Low, MG-Low and MG-Med groups. Deposit feeders, which included the highly abundant genus *Sabatieria*, were relatively abundant in all communities, averaging 33-59% of total abundance in the Uruti South communities, and 23-24, 10-46 and 13-82% in the MG-Low, MG-Med and MG High communities, respectively. Epigrowth feeders were present in low abundances in all the groups but tended to be somewhat more abundant in the Uruti South groups (0-16%) than in the deeper Mungaroa-Glendhu groups (0-6%, except for station 18, where epigrowth feeders represented 21% of total). Ciliate feeders were absent in 18 of the 30 cores we analysed and were relatively unimportant (348%) in most groups except for stations 19 and 20 (MG-High group) where they represented 22 and 65% of total abundance due to elevated abundances of *Dorylaimopsis nodderi* and *Odontophora* sp. B, respectively. Facultative predators were common in all groups,

averaging 11-38% of total nematode abundance in the Uruti South samples. Among the Mungaroa-Glendhu groups, facultative predators were most abundant in the MG-Low group (52-62%), followed by the MG-Med (27-46%) and Mg-High groups (10-19%). Relative abundances of predators were relatively low (<10%) at most sites but reached values of 15-35% at some U-High, MG-High and MG-Med sites.

Some trends were observed in the distribution of feeding groups in relation to distance from the centre of the seep areas (Figure 7). Deposit feeders, and to a lesser extent epigrowth feeders and ciliate feeders, tended to be most abundant at or near the centre of the seep areas, whereas microvores showed the opposite trend. No consistent trend was seen in the relative abundance of facultative predators and predators.

The results of DistLM analyses showed that nematode abundance was significantly and negatively correlated with distance from the centre of the seep areas at the Maungaroa and Glendhu areas ($P < 0.05$, $R^2 = 0.48-0.59$), but not at the Uruti South area where abundance was highest some distance away from the centre ($P < 0.05$; Table 5; see Figure 3). Nematode abundance was also positively correlated with mean grain size at the Glendhu and Uruti South areas ($P < 0.01$, $R^2 = 0.68-0.83$), positively correlated with sediment carbonate content at the Maungaroa area ($P < 0.05$, $R^2 = 0.58$) and positively correlated with porewater methane concentrations at the Maungaroa and Uruti South areas ($P < 0.05$, $R^2 = 0.37-0.60$). Nematode species richness was not significantly correlated with any of the predictor variables at the Maungaroa and Uruti South areas (DistLM; $P > 0.05$). At the Glendhu area, species richness was positively correlated with sediment organic matter content and sediment carbonates content ($P < 0.05$, $R^2 = 0.54-0.57$). Species evenness (J') and diversity (H') were significantly and negatively correlated with proxies of food availability at all three

TABLE 2 Result of SIMPER analyses showing nematode species accounting for most of the within-site similarity at the Maungaroa, Glendhu and Uruti South seep areas.

| Seep areas and species | Av.Abund (0.1 m ²) | Av.Sim | Sim/SD | Contrib% | Cum.% |
|------------------------------------------|--------------------------------|--------|--------|----------|-------|
| Maungaroa (Av.Sim = 42.5%) | | | | | |
| <i>Paramesacanthion</i> A | 95.2 | 6.93 | 6.40 | 16.32 | 16.32 |
| <i>Rhabdodemia</i> <i>zealandiaensis</i> | 86.6 | 5.39 | 1.14 | 12.69 | 29.02 |
| <i>Oncholaimus</i> <i>adustus</i> | 74.1 | 4.30 | 1.07 | 10.13 | 39.14 |
| <i>Halalaimus</i> C | 53.8 | 4.15 | 1.31 | 9.76 | 48.91 |
| <i>Sphaerolaimus</i> A | 20.3 | 3.11 | 2.70 | 7.33 | 56.24 |
| <i>Sabatieria</i> <i>bathycopia</i> | 136.5 | 2.13 | 0.92 | 5.01 | 61.25 |
| <i>Odontanticoma</i> A | 61.6 | 1.89 | 1.06 | 4.45 | 65.70 |
| <i>Oxystomina</i> A | 14.0 | 1.87 | 1.08 | 4.41 | 70.11 |
| <i>Micoletzkyia</i> A | 14.0 | 1.86 | 1.12 | 4.37 | 74.48 |
| <i>Sabatieria</i> B | 22.6 | 1.67 | 0.75 | 3.92 | 78.41 |
| Glendhu (Av.Sim = 36.2%) | | | | | |
| <i>Rhabdodemia</i> <i>zealandiaensis</i> | 68.1 | 6.73 | 2.90 | 18.57 | 18.57 |
| <i>Oncholaimus</i> <i>adustus</i> | 44.2 | 5.02 | 1.05 | 13.84 | 32.41 |
| <i>Halalaimus</i> C | 21.8 | 3.41 | 1.17 | 9.41 | 41.81 |
| <i>Paramesacanthion</i> A | 45.0 | 3.03 | 0.87 | 8.37 | 50.18 |
| <i>Odontanticoma</i> A | 11.9 | 2.78 | 1.19 | 7.68 | 57.86 |
| <i>Sabatieria</i> <i>bathycopia</i> | 161.5 | 2.30 | 0.57 | 6.34 | 64.20 |
| <i>Sphaerolaimus</i> A | 9.1 | 1.76 | 0.87 | 4.87 | 69.07 |
| <i>Oxystomina</i> A | 11.2 | 1.31 | 0.66 | 3.62 | 72.69 |
| <i>Sabatieria</i> B | 15.4 | 1.23 | 0.68 | 3.40 | 76.09 |
| Uruti South (Av.Sim = 38.2%) | | | | | |
| <i>Oncholaimus</i> <i>adustus</i> | 45.6 | 4.39 | 1.41 | 11.50 | 11.50 |
| <i>Rhabdodemia</i> <i>zealandiaensis</i> | 84.3 | 4.16 | 1.48 | 10.89 | 22.40 |
| <i>Linhomoeus</i> <i>pyncrocris</i> | 36.3 | 3.73 | 3.16 | 9.76 | 32.15 |
| <i>Sabatieria</i> <i>balbutiens</i> | 29.8 | 3.64 | 1.08 | 9.53 | 41.68 |
| <i>Sabatieria</i> <i>articulata</i> | 110.6 | 3.06 | 0.90 | 8.02 | 49.70 |
| <i>Paranticoma</i> A | 30.4 | 2.93 | 1.23 | 7.67 | 57.38 |
| <i>Paramesacanthion</i> A | 48.0 | 2.88 | 1.24 | 7.53 | 64.91 |
| <i>Odontanticoma</i> A | 21.1 | 2.24 | 1.27 | 5.86 | 70.77 |
| <i>Desmodora</i> <i>parapilosa</i> | 31.0 | 1.51 | 0.65 | 3.94 | 74.71 |
| <i>Dorylaimopsis</i> <i>nodderi</i> | 15.2 | 1.31 | 0.64 | 3.44 | 78.15 |

Av.Abund, average abundance; Av.Sim, average similarity; Sim/SD, similarity divided by standard deviation; Contrib%, percentage contribution; Cum%, cumulative percentage contribution.

areas, i.e., chlorophyll *a* and phaeopigment concentrations and sediment organic matter content, as well as sediment carbonates ($P < 0.05$, $R^2 = 0.45-0.83$). Significant negative correlations were also observed with the ratio of chlorophyll *a* to phaeopigment (proxy for food quality, $P < 0.05$, $R^2 = 0.44-0.62$) and porewater and water column methane concentrations ($P < 0.05$, $R^2 = 0.62-0.83$). Nematode community structure was significantly correlated with

a number of food availability proxies (porewater and water column methane concentration, pigment and organic matter concentrations, and/or distance from seep centre) and particle size variables (mean grain size and/or particle skewness), and/or carbonate content at all three areas. These significant correlations, however, were weaker ($R^2 = 0.21-0.44$) than for the univariate variables ($R^2 = 0.45-0.83$).

TABLE 3 Result of SIMPER analyses showing nematode species accounting for among-area dissimilarity among the Maungaroa, Glendhu and Uruti South seep areas.

| Seep areas and species | Av.Abund (0.1 m ²) | Av.Abund (0.1 m ²) | Av.Diss | Diss/SD | Contrib% | Cum.% |
|------------------------------------------------------|--------------------------------|--------------------------------|---------|---------|----------|-------|
| Maungaroa & Glendhu (Av.Diss = 64.3%) | | | | | | |
| | Maungaroa | Glendhu | | | | |
| <i>Sabatieria bathycopia</i> | 136.5 | 161.5 | 4.93 | 1.00 | 7.66 | 7.66 |
| <i>Odontophora</i> B | 170.1 | 0.0 | 4.05 | 0.68 | 6.30 | 13.96 |
| <i>Paramesacanthion</i> A | 95.2 | 44.9 | 3.05 | 1.33 | 4.75 | 18.70 |
| <i>Rhabdodemia zealandiaensis</i> | 86.6 | 68.1 | 2.90 | 1.86 | 4.51 | 23.21 |
| <i>Oncholaimus adustus</i> | 74.1 | 44.2 | 2.70 | 1.37 | 4.20 | 27.41 |
| <i>Halalaimus</i> C | 53.8 | 21.8 | 2.35 | 1.36 | 3.65 | 31.06 |
| <i>Metacycolaimus catherinae</i> | 67.9 | 2.1 | 2.29 | 0.65 | 3.55 | 34.61 |
| <i>Odontanticoma</i> A | 61.6 | 11.9 | 2.05 | 0.95 | 3.18 | 37.79 |
| <i>Sabatieria</i> B | 22.6 | 15.4 | 1.95 | 1.27 | 3.04 | 40.83 |
| Maungaroa & Uruti South (Av.Diss = 75.5%) | | | | | | |
| | Maungaroa | Uruti South | | | | |
| <i>Odontophora</i> B | 170.1 | 0.0 | 3.68 | 0.67 | 4.87 | 4.87 |
| <i>Sabatieria articulata</i> | 3.9 | 110.6 | 3.31 | 1.27 | 4.39 | 9.26 |
| <i>Sabatieria bathycopia</i> | 136.5 | 5.3 | 3.22 | 0.84 | 4.26 | 13.52 |
| <i>Halalaimus</i> C | 53.8 | 1.2 | 3.17 | 1.59 | 4.20 | 17.71 |
| <i>Rhabdodemia zealandiaensis</i> | 86.6 | 84.3 | 2.92 | 1.42 | 3.86 | 21.58 |
| <i>Paramesacanthion</i> A | 95.2 | 48.0 | 2.76 | 1.55 | 3.66 | 25.24 |
| <i>Oncholaimus adustus</i> | 74.1 | 45.6 | 2.39 | 1.43 | 3.17 | 28.40 |
| <i>Sabatieria balbutiens</i> | 2.3 | 29.8 | 2.30 | 1.36 | 3.05 | 31.45 |
| Glendhu & Uruti South (Av.Diss = 74.2%) | | | | | | |
| | Glendhu | Uruti South | | | | |
| <i>Sabatieria bathycopia</i> | 161.5 | 5.3 | 4.14 | 0.76 | 5.57 | 5.57 |
| <i>Sabatieria articulata</i> | 0.0 | 110.6 | 4.00 | 1.26 | 5.38 | 10.95 |
| <i>Sabatieria balbutiens</i> | 0.0 | 29.8 | 3.08 | 1.42 | 4.14 | 15.10 |
| <i>Rhabdodemia zealandiaensis</i> | 68.1 | 84.3 | 3.00 | 1.58 | 4.04 | 19.14 |
| <i>Paramesacanthion</i> A | 44.9 | 48.0 | 2.79 | 1.53 | 3.76 | 22.89 |
| <i>Sabatieria</i> A | 52.0 | 39.8 | 2.72 | 0.50 | 3.67 | 26.56 |
| <i>Paranticoma</i> A | 1.4 | 30.4 | 2.48 | 1.61 | 3.34 | 29.90 |
| <i>Halalaimus</i> C | 21.8 | 1.2 | 2.27 | 1.41 | 3.06 | 32.97 |
| <i>Oncholaimus adustus</i> | 44.2 | 45.6 | 2.27 | 1.21 | 3.05 | 36.02 |

Av.Abund, average abundance; Av.Sim, average similarity; Sim/SD, similarity divided by standard deviation; Contrib%, percentage contribution; Cum%, cumulative percentage contribution.

Discussion

The present work was undertaken as part of a wider study to characterise the marine ecosystem of an area where gas hydrate extraction could occur in the future. This study is the first to characterise macrofaunal nematode communities of cold seeps and provides the first insight into the distribution of nematode species

in deep-sea cold seep habitats of the New Zealand region. Our analyses have uncovered significant heterogeneity in the species structure and trophic make up of nematode communities across the three Hikurangi Margin seep areas, as well as within each of the areas, and show that this variability was linked to a range of proxies of food availability and sediment grain size variables. These results could be used for assessing the potential effects that could arise from

TABLE 4 Result of SIMPER analyses showing nematode species accounting for within-group similarity for each of the communities identified by SIMPROF analysis at the Uruti South (left-hand side columns) and Maungaroa and Glendhu areas (right-hand side columns).

| Uruti South | | | | | Maungaroa & Glendhu | | | | |
|--------------------------------------------------------------------------------------------------|----------|--------|----------|-------|-------------------------------------------------------------------------------------------------|----------|--------|----------|-------|
| Species | Av.Abund | Sim/SD | Contrib% | Cum.% | Species | Av.Abund | Sim/SD | Contrib% | Cum.% |
| Group U-High (Av.Sim = 50.7%; five locations) | | | | | Group MG-High (Av.Sim = 36.1%; two Maungaroa & one Glendhu locations) | | | | |
| Nem.Abund = 702-2310 ind. 0.1 m ² ; J' = 0.73-0.89; Dist. from seep centre = 67-116 m | | | | | Nem.Abund = 1369-2310 ind. 0.1 m ² ; J' = 0.46-0.47; Dist. from seep centre = 0-55 m | | | | |
| <i>Sabatieria articulata</i> | 245.8 | 5.11 | 17.43 | 17.43 | <i>Sabatieria bathycopia</i> | 632.0 | 0.77 | 27.64 | 27.64 |
| <i>Rhabdodemia zealandiaensis</i> | 151.7 | 5.86 | 13.59 | 31.02 | <i>Paramesacanthion</i> A | 145.1 | 4.06 | 19.82 | 47.47 |
| <i>Desmodora parapilosa</i> | 49.2 | 3.99 | 8.78 | 39.80 | <i>Odontophora</i> B | 456.4 | 0.58 | 17.62 | 65.09 |
| <i>Paramesacanthion</i> A | 96.9 | 1.15 | 7.86 | 47.66 | <i>Metacycolaimus catherinae</i> | 201.3 | 1.09 | 14.93 | 80.01 |
| <i>Paranticoma</i> A | 40.7 | 3.43 | 6.67 | 54.33 | | | | | |
| <i>Oncholaimus adustus</i> | 40.7 | 1.57 | 5.85 | 60.17 | | | | | |
| <i>Linhomoeus pycnocricus</i> | 63.2 | 2.02 | 5.67 | 65.84 | | | | | |
| <i>Deontostoma tridentum</i> | 26.7 | 1.04 | 4.74 | 70.58 | | | | | |
| <i>Odontanticoma</i> A | 40.7 | 0.94 | 4.02 | 74.59 | | | | | |
| <i>Crenopharynx</i> B | 22.5 | 1.07 | 3.72 | 78.31 | | | | | |
| Group U-Med (Av.Sim = 52.7%; two locations) | | | | | Group MG-Med (Av.Sim = 49.7%; seven Maungaroa & six Glendhu locations) | | | | |
| Nem.Abund = 534-801 ind. 0.1 m ² ; J' = 0.84-0.88; Dist. from seep centre = 0-50 m | | | | | Nem.Abund = 232-1910 ind. 0.1 m ² ; J' = 0.69-0.93; Dist. from seep centre = 0-537 m | | | | |
| <i>Oncholaimus</i> B | 108.5 | N/A | 18.80 | 18.80 | <i>Rhabdodemia zealandiaensis</i> | 95.1 | 2.94 | 14.72 | 14.72 |
| <i>Rhabdodemia</i> A | 108.5 | N/A | 17.41 | 36.21 | <i>Oncholaimus adustus</i> | 78.9 | 2.62 | 14.64 | 29.36 |
| <i>Dorylaimopsis nodderi</i> | 49.2 | N/A | 12.31 | 48.52 | <i>Paramesacanthion</i> A | 67.0 | 4.51 | 13.39 | 42.75 |
| <i>Linhomoeus pycnocricus</i> | 28.1 | N/A | 10.05 | 58.58 | <i>Halalaimus</i> C | 51.3 | 2.89 | 11.58 | 54.33 |
| <i>Sabatieria balbutiens</i> | 70.2 | N/A | 10.05 | 68.63 | <i>Sphaerolaimus</i> A | 18.9 | 3 | 7.09 | 61.42 |
| <i>Crenopharynx crassipapilla</i> | 28.1 | N/A | 7.11 | 75.73 | <i>Odontanticoma</i> A | 47.5 | 1.4 | 5.22 | 66.64 |
| | | | | | <i>Oxystomina</i> A | 15.7 | 1.35 | 5.1 | 71.73 |
| | | | | | <i>Micoletzkyia</i> A | 14.6 | 1.08 | 4.51 | 76.24 |

(Continued)

TABLE 4 Continued

| Uruti South | | | | | Maungaroa & Glendhu | | | | |
|--------------------------------------------------------------------------------------------------|----------|--------|----------|-------|--------------------------------------------------------------------------------------------------|----------|--------|----------|-------|
| Species | Av.Abund | Sim/SD | Contrib% | Cum.% | Species | Av.Abund | Sim/SD | Contrib% | Cum.% |
| Group U-Low (Av.Sim = 45.4%; five locations) | | | | | Group MG-Low (Av.Sim = 50.4%; two Glendhu locations) | | | | |
| Nem.Abund = 190-330 ind. 0.1 m ² ; J' = 0.89-0.96; Dist. from seep centre = 164-467 m | | | | | Nem.Abund = 190-211 ind. 0.1 m ² ; J' = 0.89-0.91; Dist. from seep centre = 164-277 m | | | | |
| <i>Sabatieria balbutiens</i> | 29.5 | 10.28 | 18.46 | 18.46 | <i>Oncholaimus adustus</i> | 42.1 | N/A | 24.83 | 24.83 |
| <i>Linhomoeus pycnocricus</i> | 12.7 | 5.96 | 10.94 | 29.40 | <i>Rhabdodemia zealandiaensis</i> | 38.6 | N/A | 20.28 | 45.11 |
| <i>Oncholaimus adustus</i> | 25.3 | 1.14 | 10.86 | 40.25 | <i>Halalaimus C</i> | 14.0 | N/A | 14.34 | 59.45 |
| <i>Paramesacanthion A</i> | 12.7 | 4.38 | 10.48 | 50.74 | <i>Halalaimus A</i> | 7.0 | N/A | 10.14 | 69.59 |
| <i>Odontanticoma A</i> | 8.4 | 10.32 | 9.78 | 60.52 | Oncholaimidae B | 10.5 | N/A | 10.14 | 79.72 |
| <i>Rhabdodemia zealandiaensis</i> | 7.0 | 1.15 | 5.70 | 66.21 | | | | | |
| <i>Paranticoma A</i> | 16.7 | 0.59 | 3.95 | 70.16 | | | | | |
| <i>Halalaimus A</i> | 5.6 | 0.62 | 3.28 | 73.44 | | | | | |
| <i>Paramicrolaimus hohonuicola</i> | 5.6 | 0.62 | 3.11 | 76.55 | | | | | |

A cut-off value of 75% was used. Communities are listed from top to bottom in order of decreasing total nematode abundance. Av.Abund, average abundance; Av.Sim, average similarity; Dist., distance; Nem.Abund, nematode abundance; Sim/SD, similarity divided by standard deviation; Contrib%, percentage contribution; Cum%, cumulative percentage contribution.

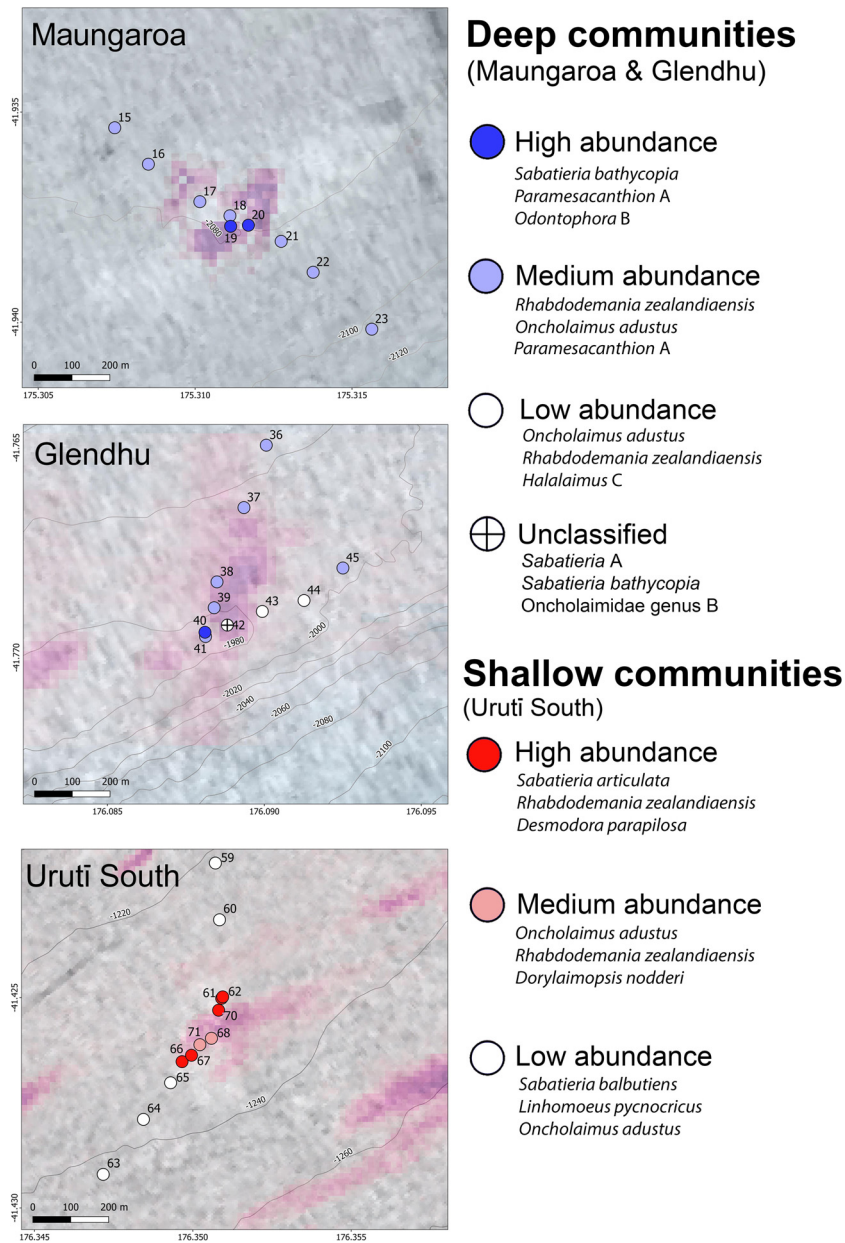


FIGURE 5

Spatial distribution of the six nematode communities (and one unclassified sample) identified by SIMPROF analysis at the Maungaroa, Glendhu and Uruti South seeps. The three species accounting for most of the within-community similarity (based on SIMPER analysis) are listed on the right. See Table 4 for detailed description of each group.

disturbances that might relate to future gas hydrate extraction in the region.

Variability in environmental variables

The three seep areas on the Hikurangi Margin shared some similarities in environmental conditions despite one area (Uruti South at 12000 m) being substantially shallower than the other two (Glendhu and Maungaroa at ca. 2000 m), while also exhibiting some significant differences. One difference was the almost one order of magnitude lower methane concentrations in the water

overlying the sediments at the Glendhu area relative to the Maungaroa and Uruti South areas. This trend among the three areas was also noted by Law et al. (2024) who suggested that the lower dissolved methane maximum at Glendhu may reflect that this area is characterised by a number of smaller dispersed seeps (Turco et al., 2022). Porewater methane concentrations showed the opposite pattern with the highest values observed at Glendhu. Estimated gas fluxes at the study areas overlap considerably and do not indicate substantially lower fluxes at Glendhu ($1.6\text{--}4.3 \times 10^6 \text{ kg yr}^{-1}$) compared to Maungaroa ($0.3\text{--}7.2 \times 10^6 \text{ kg yr}^{-1}$) or Uruti South ($1.3\text{--}3.6 \times 10^6 \text{ kg yr}^{-1}$), with fluxes likely to be stable over time, although current estimates are likely affected by a range of

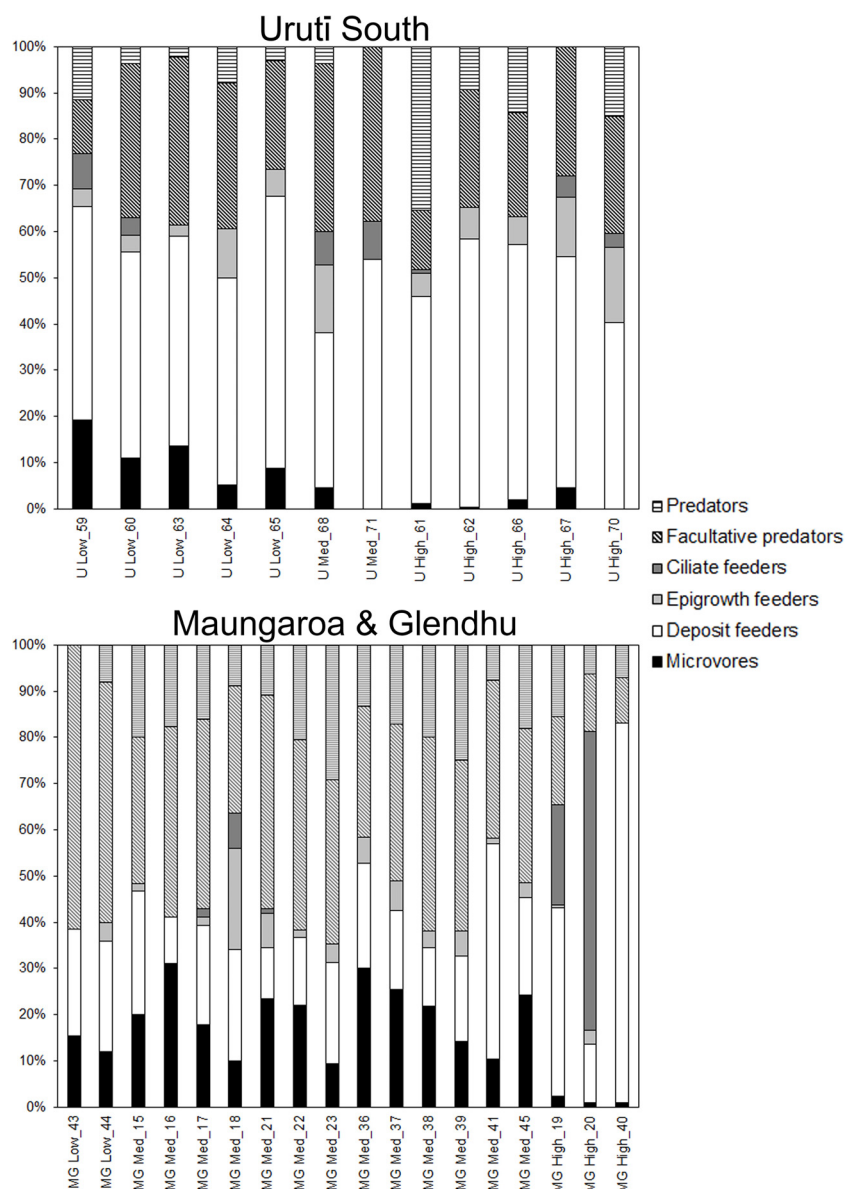


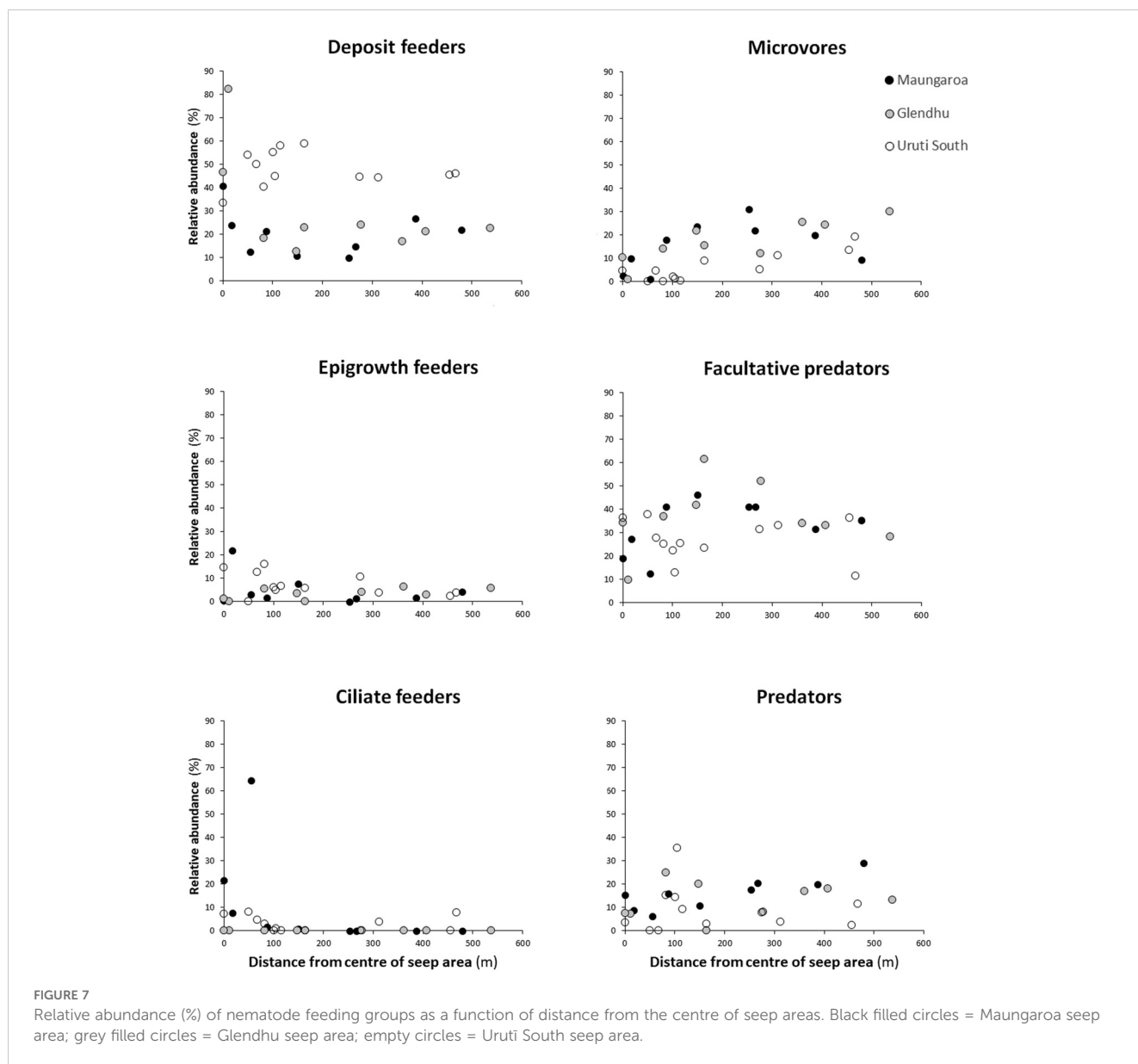
FIGURE 6

Relative abundance of nematode feeding groups at the Uruti South (top) and Maungaroa and Glendhu seep areas (bottom). U-High, Uruti South high abundance group; U-Med, Uruti South medium abundance group; U-Low, Uruti South low abundance group; Mg-High, Maungaroa & Glendhu high abundance group; MG-Med, Maungaroa and Glendhu medium abundance group; MG-Low, Maungaroa and Glendhu low abundance group.

methodological assumptions and uncertainties (Turco et al., 2022; Law et al., 2024). It is possible that the low methane concentrations in the overlying water observed at the Glendhu area reflects the effect of local currents or variation in the position of the samples relative to the areas of most active seepage rather than among-area difference in gas fluxes.

Despite the observed differences in methane concentrations observed among the study areas, we did not observe any obvious difference in sediment organic content among areas, indicating that sediment food availability for benthic fauna was similar. The three seep areas were all characterised by elevated organic matter concentrations ranging from 7.9 to 10.1% without obvious within-area trends. Similar elevated values of sediment organic matter content have been observed at other seeps (e.g., Seabrook

et al., 2024), but values in Kaikōura Canyon, located south of Hikurangi Margin and characterised by the highest benthic biomass of any known non-chemosynthetic deep-sea environment (De Leo et al., 2010), are relatively low, ranging from 2.2 to 6.8% (Leduc et al., 2014). These high organic matter concentrations were observed across all seep areas we sampled, and as far as 250 m away from the seep centre, suggesting that the influence of methane seepage on organic matter availability extends to the edge of the areas and likely beyond. It is not clear how methane seepage may influence sediment organic matter concentrations at the edge of the areas up to 250 m or more away. Studies have found little if any difference in proxies of food quantity or quality (e.g., %C, %N, C:N) between seeps and adjacent non-seep sediments, perhaps due to high variation among seep



macrohabitats (Levin et al., 2010; Ritt et al., 2012). Inputs of chemosynthetic carbon may not necessarily be reflected in sediment organic matter concentrations due to high turnover and consumption rates by infauna (Nascimento et al., 2012). The ratio of chlorophyll *a* to phaeopigment concentration, which gives an indication of the freshness (i.e., lability) of phytodetrital food sources, did not show any clear within-area spatial patterns, but this is not unexpected as pigment concentrations reflect inputs from surface primary productivity rather than *in situ* chemosynthesis. Among-area variability in pigment concentrations was observed, with elevated chlorophyll *a* and phaeopigment concentrations at the Maungaroa area relative to the Glendhu and Uruti South areas, indicating greater supply of phytodetrital food sources at the former. The Maungaroa area is located to the southwest of the other two areas, and is the area closest to the Subtropical Front, a region associated with heightened primary productivity (Bradford-Grieve et al., 1997; Murphy et al., 2001).

Sediments at the three seep areas were characterised by similar grain size distributions dominated by fine, medium and coarse silt particles. At Glendhu and Uruti South, however, mean sediment particle size tended to be highest at or near the centre of the area and was significantly and positively correlated with methane concentrations in the water column (DistLM, $P < 0.05$, $R^2 = 0.71$ and 0.78 , respectively). Seepage can affect sediment grain size distribution through mechanical disturbance by bubbling gas which may remove the finer particles or reduce their deposition (Luth et al., 1999; Dando and Hovland, 1992). Coarser particles may also result from microbially mediated authigenic carbonate production via *in situ* production of relatively large carbonate accretions or through the erosion of nearby carbonate mounds (Bourque et al., 2017). Carbonate concentrations tended to be most elevated at or near the seep centres, which aligns with localised precipitation of authigenic carbonates from anaerobic methane oxidation.

TABLE 5 Result of DistLM analyses showing the relationships between environmental variables and nematode community parameters.

| Nematode community parameters | Maungaroa | | | Glendhu | | | Uruti South | | |
|---------------------------------------|---------------------------|-------|----------|---------------------------|-------|----------|---------------------------|-------|----------|
| | Variables | P | Prop. | Variables | P | Prop. | Variables | P | Prop. |
| Abundance | Porewater CH ₄ | 0.023 | 0.60 (+) | Mean grain size | 0.004 | 0.68 (+) | Mean grain size | 0.002 | 0.83 (+) |
| | Carbonates | 0.027 | 0.58 (+) | Distance | 0.019 | 0.59 (-) | CH ₄ | 0.015 | 0.63 (+) |
| | Distance | 0.042 | 0.48 (-) | | | | Porewater CH ₄ | 0.043 | 0.37 (+) |
| Species richness | - | - | - | %TOM | 0.014 | 0.57 (+) | - | - | - |
| | | | | Carbonates | 0.030 | 0.54 (+) | | | |
| Species evenness (J') | Carbonates | 0.012 | 0.83 (-) | CH ₄ | 0.003 | 0.83 (-) | Mean grain size | 0.005 | 0.76 (-) |
| | Porewater CH ₄ | 0.014 | 0.79 (-) | Mean grain size | 0.005 | 0.75 (-) | CH ₄ | 0.015 | 0.62 (-) |
| | Chl a | 0.022 | 0.69 (-) | Porewater CH ₄ | 0.024 | 0.70 (-) | Particle skewness | 0.046 | 0.49 (+) |
| | Particle skewness | 0.010 | 0.67 (-) | Chl a | 0.040 | 0.67 (-) | Distance | 0.045 | 0.46 (+) |
| | | | | Particle skewness | 0.006 | 0.67 (+) | | | |
| | | | | Distance | 0.031 | 0.51 (+) | | | |
| Species diversity (H' ₁₀) | Carbonates | 0.008 | 0.77 (-) | Chl a | 0.004 | 0.78 (-) | Phaeopigments | 0.036 | 0.45 (-) |
| | Porewater CH ₄ | 0.017 | 0.74 (-) | CH ₄ | 0.008 | 0.76 (-) | | | |
| | Particle skewness | 0.007 | 0.70 (-) | Chl a:Phaeo | 0.020 | 0.62 (-) | | | |
| | Chl a | 0.038 | 0.59 (-) | Particle skewness | 0.006 | 0.61 (-) | | | |
| | %TOM | 0.030 | 0.53 (-) | Porewater CH ₄ | 0.042 | 0.53 (-) | | | |
| | | | | Mean grain size | 0.023 | 0.49 (-) | | | |
| Community structure | Carbonates | 0.002 | 0.44 | CH ₄ | 0.004 | 0.27 | Mean grain size | 0.003 | 0.29 |
| | Porewater CH ₄ | 0.008 | 0.41 | %TOM | 0.023 | 0.25 | CH ₄ | 0.017 | 0.26 |
| | Particle skewness | 0.022 | 0.30 | Mean grain size | 0.004 | 0.25 | Porewater CH ₄ | 0.028 | 0.25 |
| | Chl a | 0.023 | 0.30 | Porewater CH ₄ | 0.026 | 0.24 | Distance | 0.049 | 0.23 |
| | Chl a:Phaeo | 0.037 | 0.27 | Chl a | 0.020 | 0.23 | | | |
| | Distance | 0.043 | 0.26 | Particle skewness | 0.043 | 0.21 | | | |

Only environmental variables significantly correlated with nematode community parameters are shown. Positive and negative correlations are shown by a '+' or '-', respectively, following the proportion of variability explained by the predictor variable (Prop.). CH₄, methane concentration in overlying water in vicinity of coring station; Chl a, sediment chlorophyll a concentration; Chl a:Phaeo, ratio of chlorophyll a to phaeopigment concentration; Distance, distance from centre of seep area; Prop., proportion of variability explained by predictor variable; %TOM, sediment total organic matter content.

Nematode abundance, species richness and diversity

There were no significant difference in nematode abundance, species richness, diversity and evenness among the three study areas, which may reflect the lack of any obvious difference in sediment organic matter, carbonate content or sediment grain size among them. However, a consistent spatial pattern in nematode abundance was observed within all the study seep areas on the Hikurangi Margin: abundance was highest at or near the seep centre, decreased steeply away from the centre and was low in the periphery (> 150-200 m from the centre). These spatially consistent patterns clearly reflect the influence of methane seepage, which appears to be limited to the inner 150-200 m radius of each area on Hikurangi Margin, on nematode abundance via input of

chemosynthetic food sources. However, sediment organic matter concentrations were elevated both in the centres and peripheries of all three study areas, similar levels of food availability across the methane seepage gradient. This seemingly contradictory observation, both in the present study and previous studies (Levin et al., 2010; Ritt et al., 2012), could indicate that organic matter quality (lability) rather than quantity is the most important factor influencing nematode abundance (e.g., Cook et al., 2000). Areas of methane seepage at or near the seep centres were associated with nematode abundance up to ca. 6, 8 and 12 times higher at the Maungaroa, Glendhu and Uruti South areas, respectively, compared to values at their respective peripheries. Similar differences in macro-infaunal abundance have been found in several studies of continental slope seeps and adjacent non-seep sediments, with 2 to 10-fold greater macroinfaunal abundance in the former relative to

the latter (Robinson et al., 2004; Bernardino and Smith, 2010; Levin et al., 2010; Menot et al., 2010; Ritt et al., 2012; Bourque et al., 2017; Campaña-Llovet and Snelgrove, 2018; Washburn et al., 2018).

Although the same spatial trend was observed at all three areas, we also saw somewhat elevated nematode abundances in the periphery of the Maungaroa seep area (421–681 ind. 0.1 m^2) compared to the nematode abundance in the periphery of the other two areas (190–379 ind. 0.1 m^2). This contrast is consistent with the elevated pigment concentrations observed throughout the Maungaroa area, which likely reflects its proximity to the highly productive Subtropical Front (Bradford-Grieve et al., 1997; Murphy et al., 2001). Among-area difference in peak nematode abundance at or near the centres of the seep areas were also observed, with a low value observed at Glendhu (1580 ind. 0.1 m^2) relative to Maungaroa and Urutū South (2310 ind. 0.1 m^2 at both areas). It is not clear whether this difference reflects small-scale spatial patchiness in nematode abundance or lower food availability of photo- and/or chemosynthetic origins at the Glendhu area. There were no clear indications of low sediment food availability at the former area, although relatively low water column methane concentrations may reflect lower flux rates and therefore less chemosynthetic primary production.

Species richness did not exhibit clear patterns at any of the areas but tended to be most variable near the seep centres, whereas species diversity and evenness were lowest at or near the seep centres and elevated in the periphery. Elevated infaunal abundance in seeps is often associated with lower diversity and/or evenness relative to adjacent non-seep sediments (Dando et al., 1991; Bernardino and Smith, 2010; Menot et al., 2010; Ritt et al., 2012; Bourque et al., 2017; Campaña-Llovet and Snelgrove, 2018; Macheriotou et al., 2021) although this pattern is not always clear (Shirayama and Ohta, 1990; Levin et al., 2010). Decreased infaunal diversity and dominance by one or a few species in seeps is often observed and is likely a function of competitive displacement by species able to exploit the abundant food resources and increased stress from low oxygen and toxic sulphides, which only a limited number of taxa are able to withstand (Sahling et al., 2002; Levin et al., 2003; Levin, 2005). Among the infauna, nematodes appear to be particularly well-adapted to cope with high sulphide and low oxygen conditions, with a small number of opportunistic species able to exploit the abundant food resources present at seeps (Steichen et al., 1996; Van Gaever et al., 2006; Vanreusel et al., 2010a). It is not entirely clear how some nematode species cope with the toxic seep conditions, but some documented adaptations include ovoviviparous reproduction, storage of sulphur in intracellular inclusions, and a distribution restricted to the topmost layer of sediments (Thiermann et al., 2000; Van Gaever et al., 2006). Unlike macro- and megafauna associated with seeps, there is limited evidence of associations with ecto- or endosymbiotic bacteria in nematodes of deep-sea cold seep environments, although they have been documented in shallow water seeps (Dando et al., 1991; Jensen et al., 1992).

Comparisons between our results and published data are limited by the relatively small number of studies on deep-sea macrofaunal nematodes and the range of mesh sizes used by different authors (250 to 500 μm). The impact of mesh size on

estimates of macrofaunal nematode abundance was demonstrated in a study of macrofaunal nematodes of cold seeps on the Norwegian margin (732–1263 m depth) by Decker et al. (2012), who found nematode abundances ranging from 4 to 1015 ind. 0.1 m^2 when using a 250 μm mesh, which are similar, though not as high, as our estimates of nematode abundance at the Hikurangi margin seep sites based on a 300 μm mesh. The latter authors, however, found much lower abundances (0 to 56 ind. 0.1 m^2) when using a 500 μm mesh. In the eastern Mediterranean, macrofaunal nematode abundance based on a 250 μm mesh reached 928 ind. 0.1 m^2 at the Napoli mud volcano and 2612 ind. 0.1 m^2 at the Amsterdam mud volcano, respectively (Ritt et al., 2012), which is similar to the peak abundances (1580–2310 ind. 0.1 m^2) we observed in at our study sites. The nematode abundances we observed are high relative to abundances reported by Sharma and Bluhm, (2011) from the Arctic deep-sea Canada Basin. The latter authors used a 250 μm mesh to quantify the abundance of macrofaunal nematodes in box-corer samples. Mean nematode abundance was highest at their Chukchi Sea slope sites (898–1945 m depth; 400 to 515 ind. 0.1 m^2), which is within the range of values we observed in samples from the periphery of the seeps at similar depths. However, mean nematode abundances at the other twelve sites sampled by Sharma and Bluhm, (2011) at 640 to 3850 m depth were much lower and did not exceed 110 ind. 0.1 m^2 . A study by Gunton et al. (2016) on the macrofaunal nematodes of the deep Whittard Canyon and adjacent slope (3500 m depth, NE Atlantic) found relatively low mean abundances ranging from ca. 15 to 45 ind. 0.1 m^2 at slope and canyon sites. These low values likely reflect the relatively coarse mesh size (500 μm) used by the latter authors. Hunter et al. (2013) found higher macrofaunal abundance (ca. 190 ind. 0.1 m^2) at two sites in the Whittard Canyon at similar depths, which likely reflects the use of a finer (250 μm) mesh size than Gunton et al. (2016). The nematode abundances observed by Hunter et al. (2013) are at the lower end of values we observed at the periphery of our Hikurangi Margin seep areas, which is likely due to our seep sites being located at shallower depths (ca. 1225–2100 vs 3500 m). A study on Black Sea shelf cold seeps and adjacent non-seep sites based on box-corer samples (60–150 m water depth, 250 μm mesh size) showed nematodes to be the most dominant macrofaunal taxon with similar abundance at both seep and non-seep sites ranging from 129 to 653 ind. 0.1 m^2 (Luth et al., 1999), which is within the range of nematode abundances we observed at the periphery of the Hikurangi Margin seep areas. Considering the water depth of the seep sites investigated in the present study, the macrofaunal nematode abundances we observed appear to be relatively high even at the periphery of the seeps where the influence of methane seepage is expected to be negligible. To our knowledge, the peak in abundance observed at the centres of the Maungaroa and Urutū South areas (ca. 2300 ind. 0.1 m^2) are higher than any published values for macrofaunal nematode. These peak macrofaunal nematode abundance values are of similar magnitude to total macrofaunal abundance (macrofauna *sensu stricto* Hessler and Jumars, 1974) from some of the most abundant deep-sea seep infaunal communities documented to date (Levin et al., 2003; Levin, 2005; Levin and Mendoza, 2007; Robinson et al., 2004). The macrofaunal ampharetid polychaete communities described by

Thurber et al. (2013) from Hikurangi Margin at 662–1172 m depth are characterised by some of the highest seep macrofaunal densities recorded anywhere (300 μm mesh, 5700 ind. 0.1m^2 ; see Figure 5 in Thurber et al., 2013) but nematodes were not included in their faunal counts. Our findings provides further evidence for the presence of a highly abundant macrofaunal community associated with Hikurangi Margin seep environments; our data, as well as data from deep-sea cold seep habitats on the Norwegian margin (Decker et al., 2012) and mud volcanoes in the deep eastern Mediterranean Sea (Ritt et al., 2012), also show that macrofaunal nematode abundances can be of similar magnitude or greater than all other macrofaunal taxa combined (macrofauna *sensu stricto*) when a relatively fine mesh is used (250 or 300 μm).

Nematode communities

While there were no differences in univariate community metrics among the Hikurangi Margin seep areas, we found significant differences in nematode community structure among all three areas. However, the SIMPROF results showed that most of heterogeneity in community structure was due to (1) differences between the shallow Urutū South area and deeper Maungaroa and Glendhu areas, and (2) differences among nematode communities of high, medium and low abundance associated with area-specific gradients in methane seepage. The Maungaroa and Glendhu areas shared the same high and medium abundance nematode communities. This high abundance community was located at the centre of both seep areas and was characterised by a small number of dominant species, i.e., *Sabatieria bathycopia*, *Paramesacanthion* A, *Odontophora* B and *Metacylicolaimus catherinae*. The genus *Sabatieria* is often associated with organic-rich muddy sediments low in oxygen (Vanreusel, 1991; Vincx et al., 1990) and has been reported as a common or dominant genus in studies of meiofauna associated with cold seeps (Dando et al., 1991; Van Gaever et al., 2009a) and mud volcanoes (Van Gaever et al., 2006). This genus, however, is also found in less food-rich environments and is common or dominant in meio- and macrofaunal samples from open slope environments (Soetaert and Heip, 1995; Muthumbi et al., 2004; Sharma and Bluhm, 2011). *Sabatieria bathycopia* is a relatively large species (>2 mm body length) originally described from an organic matter-rich site at 1240 m depth on Chatham Rise, located southeast of Hikurangi Margin (Leduc, 2013). The dominance of this species at the centres of the Maungaroa and Glendhu seep areas is consistent with a preference for sediments rich in organic matter. *Paramesacanthion* and *Metacylicolaimus* are typically less abundant or absent in meiofauna samples. These genera were not abundant in the macrofaunal nematode material from the deep Arctic and Gulf of Mexico (Sharma et al., 2011; Sharma and Bluhm, 2011) but each represented about 20% of total nematodes identified in a study of macrofaunal nematodes of the Whittard Canyon (Gunton et al., 2016). Very little is known about the ecology of *Metacylicolaimus*, however, like other species of the genus, *M. catherinae* is among the largest free-living marine nematode taxa (body length 15–19 mm) and is equipped with a spacious buccal cavity with teeth and is likely able to prey on other

nematodes or other meiofauna (Leduc, 2023a). *Paramesacanthion* is a more common genus, and like other genera of the family Thoracostomopsidae, is thought to have predatory feeding habits (Jensen, 1987). *Odontophora* is a nematode genus characterised by a spacious buccal cavity with eversible teeth and has been classified as a non-selective feeder (Wieser, 1953) and ciliate feeder (Moens and Vincx, 1997). Representatives of this genus are mostly found in coastal sediments but also occurs in continental slope environments (Vitiello, 1971). *Odontophora* was recorded in Canadian Basin of the Arctic Ocean (Sharma and Bluhm, 2011) but to our knowledge no association between this nematode genus and seep habitats has been documented to date. High abundance of this typically shallow water genus at 2000 m depth could reflect the atypically high food availability characterising the Hikurangi Margin seep environments. It should be noted that although this species accounts for a substantial proportion of within-group similarity for the high nematode abundance found at the Maungaroa and Glendhu sites, it was only present at the Maungaroa area.

The medium abundance communities found at both Maungaroa and Glendhu areas, and the low abundance community found at the Glendhu area, were characterised by the same two species, i.e., *Rhabdodemania zealandiaensis* and *Oncholaimus adustus*, which together accounted for 30–45% of within group similarity. These two species were common at all three areas and present in all but three and five of the Hikurangi Margin cores we examined, respectively. The presence of these species across a relatively wide range of conditions spanning low to high food availability at both shallow and deep locations suggests that these are generalist species able to thrive in a wide range of environments. *Rhabdodemania zealandiaensis* also occurs on Chatham Rise, a submarine ridge southeast of Hikurangi Margin, hinting at wide distribution of this species in the region (Leduc, 2023a). Both *R. zealandiaensis* and *O. adustus* are characterised by large buccal cavity with teeth and have been classified as omnivores-carnivores in the scheme of Wieser (1953) and as facultative predators by Moens and Vincx (1997), meaning that they can potentially exploit a wide range of food sources ranging from detrital material to microalgae and nematode prey. The predator species *Paramesacanthion* A and *Sphaerolaimus* A are also important components of the medium abundance nematode community at Maungaroa and Glendhu, likely reflecting the still sufficiently high abundance of nematode and other prey some distance away from the centre of the highly productive seep areas. Two species of *Halalaimus*, a microbial feeding genus most commonly found on the lower continental slope and abyssal plain, are characteristic of the low abundance nematode community at the Glendhu area, and are indicative of more typical, lower productivity deep-sea conditions.

The high abundance community at Urutū South was dominated by *Sabatieria articulata*, a species belonging to the same genus as the dominant species characterising the high abundance community at Glendhu and Maungaroa (*Sabatieria bathycopia*). *Sabatieria articulata* was recently described by Fu et al. (2019) from subsurface (1–5 cm) sediments in the Conway Trough at 491–570 m water depth. The Conway Trough is a sedimentary basin immediately adjacent to the highly productive Kaikoura Canyon

(ca. 260 km to the south of the study seep areas), and like the latter is thought to be characterised by high food availability. Thus both *S. bathycopia* and *S. articulata* appear to have a preference for organically rich environments, but with *S. bathycopia* typically occurring at somewhat deeper locations (ca. 1200–2100 m water depth) than *S. articulata* (ca. 500–1200 m). *Desmodora parapilosa* was another species characterising the high abundance nematode community at Urutī South. Species of this genus are known to be associated with cold seep and mud volcanoes where they can be highly abundant (Van Gaever et al., 2009a; Vanreusel et al., 2010b; Pape et al., 2011; Zeppilli et al., 2011; Macherioutou et al., 2021). *Desmodora* species, including *Desmodora parapilosa*, are often characterised by the presence of ectosymbiotic bacteria and/or protists on their cuticle (Blome and Riemann, 1987; Bernhard et al., 2000; Leduc, 2023b), however, the nature of this symbiosis has not yet been investigated. *Desmodora* is characterised by a buccal cavity with teeth and is classified as an epistrate/epigrowth feeder (Wieser, 1953; Moens and Vincx, 1997), meaning that they can feed on freshly settled microalgae or bacteria attached on the surface of sediment particles or potentially their own cuticle. *Rhabdodemia zealandiaensis* and *Oncholaimus adustus* were common species characterising the three communities at Urutī South, with the former species most common in the high and medium abundance communities, and the latter species most common at the medium and low abundance communities. As noted earlier, these species were widely distributed at all three Hikurangi Margin areas where they can potentially exploit a wide range of food sources. *Dorylaimopsis nodderi*, another common species in the medium abundance community at Urutī South, was originally described from Chatham Rise at 350 m water depth (Leduc et al., 2012). This species possesses a spacious buccal cavity with eversible teeth and has been classified as a non-selective feeder (Wieser, 1953) and ciliate feeder (Moens and Vincx, 1997). *Linhomoeus pycnocricus*, a non-selective deposit feeder, was a characterising species of the low abundance community. This species, like others in the family Linhomoeidae, is characterised by sometimes abundant dark inclusions in the intestine wall (Leduc, 2023b). These inclusions have been found in a number of marine nematode taxa living in organic rich and low oxygen environments and may act to sequester toxic compounds such as H₂S from the environment (Nicholas et al., 1987; Thiermann et al., 1994). The high abundance of this species in the low abundance community found on the periphery of the Urutī South seep area could suggest the presence of reducing conditions. This species has also been found at a shallow (54 m) continental shelf site in the same region (D. Leduc, unpublished data).

Halalaimus and *Sabatieria* were the most species-rich genera with each represented by six species. The average abundance of *Halalaimus*, which is generally considered a deep-sea genus particularly abundant in abyssal plains (Miljutin and Miljutina, 2016), was higher at the deeper Maungaroa and Glendhu areas (67 and 39 ind. 0.1 m⁻²) than at the shallow Urutī South area (14 ind. 0.1 m⁻²). In contrast, the average abundance of *Sabatieria*, a genus most commonly found in coastal, shelf and continental slope

environments (Soetaert and Heip, 1995), was very similar across the areas (196–245 ind. 0.1 m⁻²); however, as noted above there were marked differences in the composition and relative abundances of the different *Sabatieria* species. Two of the *Sabatieria* species were present at all three areas (*Sabatieria* sp. A and *S. bathycopia*) but with marked differences in relative abundance, and the other species present at Maungaroa and one of the other two areas. These results show that an analysis focusing on nematode genera, as is commonly done in ecological studies of deep-sea nematodes, would have underestimated the heterogeneity in community structure we observed in our species level analyses. However, despite our focus on species, we did not find evidence of seep endemics with the majority of common species occurring at both the centre and periphery of the areas and/or in other deep-sea environments, which is consistent with previous investigations of seep nematodes (Vanreusel et al., 2010b).

Differences in the relative abundance of nematode feeding groups among the SIMPROF-identified communities suggest that there are functional differences in addition to the structural differences discussed above. The shallower Urutī South communities were characterised by greater relative abundances of epigrowth feeders (e.g., *Desmodora parapilosa*) than the deeper Mungaroa and Glendhu communities, perhaps reflecting greater availability of fresh microalgal detritus at shallower depths. Deposit feeders (e.g., *Sabatieria* species., *Linhomoeus pycnocricus*) were generally more abundant at Urutī South while microvores (e.g., *Halalaimus* species) and facultative predators (e.g., *Oncholaimus adustus*) were more abundant at the Maungaroa and Glendhu areas, suggesting that seep food webs may vary depending on water depth. The high abundance communities at Urutī South- and Maungaroa/ Glendhu were both characterised by low relative abundances of microvores (<2%), indicating that few nematodes specialise in exploiting bacterial food sources at Hikurangi Margin seeps. The high relative abundance of deposit feeders (50–58%) in these communities suggests instead that a broader diet, which may include detritus, bacteria and/or small protists (Moens and Vincx, 1997), is a more successful strategy. Facultative predators, predators and ciliate feeders were also relatively abundant in the high abundance communities, suggesting that macrofaunal nematodes exploit a wide range of food sources at seeps. Overall, our findings are consistent with previous studies of nematode communities at deep-sea cold seeps, which typically find that deposit feeders are the most abundant feeding group (Vanreusel et al., 2010b; Pape et al., 2011). Stable isotope studies suggest that deposit feeding nematodes associated with cold seeps feed on chemosynthetically derived carbon via either direct consumption of sulphur-oxidising bacteria in the sediment (Spies and Des Marais, 1983; Van Gaever et al., 2006; Van Gaever et al., 2009b) or consumption of dissolved organic matter released upon bacterial lysis (Jensen, 1987). However, in contrast to previous studies (Vanreusel et al., 2010b), we have found that predators can be relatively abundant at seeps (up to 17% of total), which may be due to differences in ecology between the macrofaunal (this study) and meiofaunal nematode size fractions (previous studies).

Within area variability in nematode community structure was mainly correlated with food availability variables and also sediment grain size. These results are consistent with the SIMPROF results which identified communities characterised by low, medium and high abundances distributed along gradients in methane seepage. Sediment grain size variables may directly affect nematode community structure through their influence on habitat heterogeneity or food source partitioning (Etter and Grassle 1992; Leduc, 2012). Alternatively, the relationship between community structure and sediment granulometry may reflect within-area variability in grain size associated with gradients in methane seepage, with coarser mean grain size in areas with high methane flux due to authigenic carbonate production or mechanical disturbance by bubbling gas removing finer particles (Luth et al., 1999; Bourque et al., 2017).

Implications of potential disturbance from gas hydrate extraction

Impacts on the abundance, diversity and structure of benthic communities by conventional oil/gas exploratory drilling and production have been demonstrated for the deep sea, although these impacts are typically observable over relatively small spatial extents (see review by Cordes et al., 2016). Drilling for gas hydrate is likely to take place directly above the hydrate resource, but because extraction can be via directional drilling, the well-head can and will most likely be located away from active seep areas on the seafloor surface. Therefore, while drilling will locally impact ‘background’ benthic communities on the Hikurangi Margin, there is no expectation that drilling infrastructure and products (well-head, cables, drilling rig/platform anchors if used, drilling cutting, etc.) will directly physically disturb the seep habitat and associated communities. However, gas hydrate extraction processes could impact these communities indirectly.

If effective gas production is established, it may reduce or potentially cause cessation of

free-gas methane supply to the seafloor seep (Oluwunmi et al., 2023). The correlation observed in this study between the abundance of nematodes and methane seepage, and associated organic matter, at the centre of the seep areas suggests that any reduction in fluid flux resulting from future hydrate extraction would lead to changes in community structure at seep areas. A potential reduction in the observed elevated levels of abundance could also have implications for nematode communities elsewhere if these high abundance sites act as a ‘hotspot’ source of new recruits and help maintain population connectivity on the margin (Edmunds, 2021). Drilling may also cause free gas to flow through alternative outlets on the seafloor (Oluwunmi et al., 2023). In this case, it is possible that new seep locations with potentially different magnitude of methane supply will cause the development of new seep-

related communities. However, while there are indications that seep-related megafaunal communities may take a potentially long time to reach a fully ‘mature’ structure on initiation of new seepage (Bowden et al., 2013), nematode communities will likely establish relatively quickly given that relative abundance, not species composition (including no seep-endemic species), is the primary structural component of the nematode communities observed at the centre of seep areas on the Hikurangi Margin. Abundance in deep-sea nematode communities has been shown to respond to alterations in organic matter availability within weeks to months (e.g., Soltwedel et al., 2018).

The depressurisation involved in the extraction of gas hydrate can cause ‘sand’ production at the seafloor due to the physical degradation of the substrate structure (Moridis and Reagan, 2007). There are means by which this ‘sand’ production can be reduced, for example, downhole sand screens/filters. However, some sediment will necessarily build up as an unconsolidated formation around the screens, and the use of screens may lead to formation of ‘wormholes’, which increase substrate permeability and can act as sites of erosion (Kurihara et al., 2008). Physical disturbance from the deposition of sediment in the vicinity of the well-head will affect ‘background communities’ but not seep communities if the well-head is located away from the seep habitat. The results of this study showed that nematode community structure across the study areas was related to sediment grain size, and therefore it is likely that any changes in sediment structure caused by hydrate extraction will result in concomitant changes in community structure. Studies elsewhere in the deep sea have shown that disturbance-related changes in sediment grain size do affect nematode community structure (e.g., Hasemann et al., 2020). Furthermore, depending on the physical characteristics of the produced ‘sand’, this sediment could be mobilised by local bottom currents and be dispersed from the well-head area to nearby active seafloor seepage areas. Elevations of suspended sediment above background levels can have detrimental effects for benthic fauna, and the ultimate deposition of these dispersed sediments, if above particular depths, can also impact benthic communities (Hendrick et al., 2016). Thus, it is reasonable to predict that any sediment mobilised by the drilling and transported to seep areas will similarly affect the abundance and diversity of nematode communities, although such impacts may be short term for nematodes (Schratzberger et al., 2000).

Extraction of hydrates will alter the structural integrity of the seafloor substrate, leading to subsidence around the well and compression of substrate in immediate region of the well (Jin et al., 2019; Lin and Hsieh, 2020; Zhu et al., 2023). ‘Background’ communities in the vicinity of the well-head will be impacted by such substrate alterations. Up to 8 m subsidence has been observed in large gas reservoirs with no aquifer support (Jin et al., 2019; Lin and Hsieh, 2020; Zhu et al., 2023). However, aquifer support is expected in the configurations investigated for the potential gas hydrate extraction on the Hikurangi Margin (Oluwunmi et al., 2023). Nonetheless, if subsidence does occur, it could cause lateral displacement if the geometry of the slope and sediments were

disposed to it. Such lateral displacement could, considering the location of the hydrate deposits on the Hikurangi Margin, trigger slope failure, submarine landslides and turbidity flows (Crutchley et al., 2016). Such disturbance would occur downslope and therefore is unlikely to impact seep-related communities. Physical disturbance from the consequences of slope failure will initially negatively impact the 'background' communities, causing major initial losses of benthic fauna followed by a period of community recovery that could take years to decades or potentially cause a shift to an alternative stable state if the disturbance is significant enough (Hecker, 1982). However, studies of meiofaunal response to turbidity flow disturbance indicates that nematode communities are likely to recover from even these large-scale disturbances within a few years (Bigham et al., 2024).

In addition to the most obvious potential impacts from gas hydrate drilling to benthic ecosystems noted above, there is also the possibility of other effects. For example, water is produced from the degradation of hydrate (Moridis and Reagan, 2007; Mery and Longinos, 2018; Zhang et al., 2023) and, depending on the chemical characteristics of this water, could have an impact on benthic communities if this water is disposed of at site and near the seabed. Heating at the well-head and of the extraction pipes could potentially be implemented to counter the freezing that occurs from secondary hydrate formation. The use of inhibitors, such as ethanol, can also be used to counter the freezing (Oluwunmi et al., 2015; Koh et al., 2016). The freezing, heating and/or use of inhibitors could potentially cause local impacts to benthic communities. In addition, there is always the possibility of a 'blow-out' event, although a hydrate gas blow-out is considered unlikely, as the reaction is endothermic and would act to shut-off the flow. A free-gas well blow-out is also considered a low-risk event, but it is possible. Sampling to date shows that very limited liquid hydrocarbons are produced during free-gas production, so an oil blow-out would not happen on the scale of and impact to benthic communities of the Horizon Deepwater at Macondo in the Gulf of Mexico (Schwing et al., 2020).

Clearly, the above is a very limited qualitative assessment of the likely impacts to benthic ecosystems that could result from gas hydrate exploitation. A full, and ideally quantitative, ecological risk assessment would need to be followed should the decision be made to proceed towards commercial extraction of gas hydrate on the Hikurangi Margin (Kaikkonen et al., 2018). Such a risk assessment should include the assessment of potential impacts from other human-related activities in the region. For example, assessing the potential cumulative impact from fishing within bottom trawling depth (e.g., Uruti South area) will be necessary given the indications of chronic impact to seep-associated communities by trawling disturbance on the Hikurangi Margin (Bowden et al., 2013). Following risk assessment, management options to mitigate the potential environmental effects from gas hydrate extraction will need to be identified (Ellis et al., 2017). Such mitigation measures can include the implementation of protected areas. In this regard it is worth finally noting that the results of this study showed that the macrofaunal nematode communities at the three different seep areas were different, principally varying with water depth. These

differences in community structure will need to be reflected in any spatial management options considered (i.e., have protected sites at different depths and locations on the Hikurangi Margin).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

Author contributions

DL: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. AR: Conceptualization, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing. SS: Data curation, Methodology, Writing – original draft, Writing – review & editing. DB: Data curation, Methodology, Writing – original draft, Writing – review & editing. AT: Investigation, Writing – original draft, Writing – review & editing. JH: Data curation, Methodology, Writing – original draft, Writing – review & editing. CL: Conceptualization, Data curation, Investigation, Methodology, Writing – original draft, Writing – review & editing. OP: Writing – original draft, Writing – review & editing. BW: Writing – original draft, Writing – review & editing. AM: Formal analysis, Methodology, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2024.1486305/full#supplementary-material>

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