# ECOLOGY OF MEIOFAUNA FROM THE NEW ZEALAND CONTINENTAL MARGIN

**BY**

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# Abstract

Deep-sea meiofaunal communities vary at a range of spatial scales. However, identifying which scale(s) account for most of the variability in deep-sea communities remains difficult, as few studies have been designed in such a way as to allow meaningful comparisons across more than two spatial scales. Moreover, deep-sea studies have largely focused on particular (macro) habitats in isolation, with few studies considering multiple habitats simultaneously in a comparable manner.

In the present study, meiofaunal and nematode community attributes (abundance, diversity, community structure and trophic structure) were investigated at different spatial scales (sediment depth (cm), habitat (slope, canyon, seamount, and seep: 1–100 km), and region (100–10000 km)) in two regions on the continental slope of New Zealand (Hikurangi Margin and Bay of Plenty), while accounting for the effects of water depth (700, 1000, 1200 and 1500 m). Nematode species new to science encountered during sampling on the continental margin of New Zealand were also described.

A consistent pattern for each meiofaunal community attribute was observed. The greatest variability was found between sediment depth layers and between regions, which explained 2–4 times more variability than habitats. Meiofaunal abundance and diversity were higher at surface than subsurface sediment. High abundance of meiofauna was also found in the higher productivity region of Hikurangi Margin than in the Bay of Plenty region, but not diversity, which was slightly higher in the Bay of Plenty region. The variability pattern among spatial scales was not the same in each region. In the Bay of Plenty region, nematode diversity, community structure and trophic structure consistently showed increased variability from habitat and water depth to sediment depth. However, no consistent pattern was observed in Hikurangi Margin.

The findings in this study suggest that meiofaunal community attributes are mostly influenced by sediment characteristics and food availability, but that disturbance (fishing activity and bioturbation) also accounts for some of the variability. These findings provide new insights into the relative importance of processes operating at different spatial scales in regulating meiofaunal communities in the deep-sea, and their potential vulnerability to anthropogenic activities.

Two new species and one new species record of the family Comesomatidae from the Hikurangi Margin were described: *Vasostoma hexodontium* **n. sp.**, *Sabatieria dispunctata* **n. sp.**, and *Laimella subterminata* Chen & Vincx, 2000. A total of 159 species have been recorded/described from the New Zealand region, of which 37% are deep-sea species. This study improves understanding of meiofaunal biodiversity and their distribution patterns on the New Zealand continental region, which will help underpin effective management of New Zealand's continental margin communities in the future.

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a = body length/maximum body diameter

abd = anal body diameter

b = body length/pharynx length

c = body length/tail length

cbd = corresponding body diameter

hd = head diameter

L = body length

%V = vulva distance from anterior end of body × 100/total body length

# Chapter 1

# Review of recent trends in ecological and taxonomic studies of deep-sea meiofauna, with an emphasis on the New Zealand region

## 1.1 Introduction

The deep seafloor (> 200 m water depth) is the largest ecosystem on Earth, but remains largely unexplored due to the high costs and technological challenges associated with working in this environment. To date, only 5% of the deep-sea has been explored with remote instruments, and less than 0.01% of the deep seafloor has been sampled and studied in detail (Ramirez-Llodra et al. 2010). Advances in technology, such as multibeam echosounders for high resolution bathymetry mapping, Remotely Operated Vehicles (ROVs), Autonomous Underwater Vehicles (AUVs), and permanent seafloor observatories have increased the capability for exploring, sampling and experimentation in the deep-sea (Ramirez-Llodra et al. 2010). At the same time, new deep-sea technologies have increased interest in deep-sea exploration for mineral and biological sources as the deep-sea becomes more accessible. However, relatively little information is available on how human activities may impact deep-sea communities, and it is therefore important to obtain a better knowledge about the nature of deep-sea benthic communities and the forces that shape and control their structure and function.

Meiofauna, which are defined as benthic metazoans that pass through a 500–1000 µm mesh but retained on a 20–63 µm mesh, are the most abundant and diverse animals in deep-sea sediments (Giere 2009). Nematodes are typically the most abundant meiofaunal group, and often constitute more than 90% of all sediment metazoans, followed by harpacticoid copepods, nauplii, and annelids (Grove et al. 2006, Giere 2009). Meiofauna play an important role in the sediment as they serve as food for higher trophic levels such as macrofauna (e.g. shrimps and demersal fishes) (Coull 1990, Service et al. 1992, Feller and Coull 1995), contribute to bioturbation, thus enhancing nutrient exchange (Cullen 1973, Alkemade et al. 1992, Green and Chandler 1994, Meadows and Meadows 1994), and also contribute to remineralization processes in the sediment by stimulating microbial activity through grazing and by enhancing assimilation of detritus by larger deposit feeders (Findlay and Tenore 1982, Montagna et al. 1995, Moens et al. 2007, Pape et al. 2013a). Meiofauna also indirectly influence biogeochemical cycles through their contribution to mineralization of carbon and nitrogen (Findlay and Tenore 1982, Ingham et al. 1985, Alkemade et al. 1992, Heip et al. 1992). Moreover, several studies have demonstrated the usefulness of meiofauna as bio-indicators of pollution, disturbance and climate change (Coull and Chandler 1992, Balsamo et al. 2012, Pusceddu et al. 2014a, Zeppilli et al. 2015a). However, compared to larger benthic fauna, meiofauna often receive less attention in deep-sea studies (Rex and Etter 2010). Although deep-sea expeditions began in the late-1860s (Ramirez-Llodra et al. 2010), the first study of deep-sea meiofauna was only carried out a century later (Wigley and McIntyre 1964). Since meiofauna play an important role in sediment ecosystems as well as being a useful proxy for responses of benthic communities to environmental changes, more studies on meiofauna are needed so they can be incorporated into global change impact research (Zeppilli et al. 2015a).

### 1.1.1 Previous reviews of the ecology of deep-sea meiofauna

Thiel (1983) first summarised the quantitative studies available for deep-sea meiofauna up to the early 1980s, and a decade later Tietjen (1992) provided another review of deep-sea meiofauna studies focusing on the information collected during the 1980s. More recently Soltwedel (2000) provided an overview of meiofaunal studies from the 1970s to the late-1990s. These authors focused on summarising patterns of benthic standing stock (abundance and biomass) along bathymetric gradients, horizontal and vertical distribution in the sediments, and seasonal patterns in the Atlantic, north-west Indian, north- and south-west Pacific Ocean and Mediterranean Sea, and across polar, temperate, subtropical, tropical and arid regions (Figure 1.1). Overall, these pre-2000 studies show that meiofaunal standing stocks decrease with increasing water depth, both at the scale of ocean basins and globally (Thiel 1983, Tietjen 1992, Soltwedel 2000). These patterns are closely related to declines in food availability with depth (Tietjen 1992, Soltwedel 2000); however, abiotic factors such as hydrographic regime and varying sediment types can also influence these general patterns (Soltwedel 2000). The negative relationship between meiofauna standing stock and water depth is primarily related to the abundance and biomass of two dominant meiofauna taxa, i.e. nematodes and harpacticoid copepods.

In his review, Thiel (1983) noted the relation between productivity levels and meiofauna standing stock along bathymetric gradients in different oceans (Atlantic, Indian Ocean, Mediterranean Sea) and central oceanic regions (seamount plateau, abyssal and hadal region). Three studies from seamount plateau showed abundances as low as the nearby deep-sea plain (5000 m) and suggested the influence of strong anticyclonic currents reducing sedimentation rate and leading to low organic matter concentrations on the plateau (Thiel 1970, Rachor 1975, Thiel 1975). No clear seasonal pattern was observed in meiofauna abundance but he noted the high small-scale (< 15 cm) variability in meiofaunal abundance and diversity between samples. Small-scale variability was suggested to be related to the small size of meiofaunal organisms, sediment heterogeneity, small-scale biological disturbance, and also the relative stability of the physical environment. He argued that comparing meiofaunal communities at larger scale should therefore be done with caution. Thiel (1983) also noted shifts in the vertical distribution of meiofauna with sediment depth. Meiofauna were generally concentrated in the upper 5 cm and showed a consistent decreased from surface to subsurface sediment, which he related to trends in food availability; however, he noted that deviation from this pattern can occur due to processes such as bioturbation.

Tietjen (1992) summarised trends in meiofaunal abundance and biomass along bathymetric gradients in the Atlantic, Pacific and Indian Oceans, relationships between meiofaunal abundance and biomass, and relationships between standing stocks of meiofauna and other benthic size groups. He noted a significant decrease in meiofaunal abundance and biomass with water depth in the Atlantic Ocean, but not in the Pacific and Indian Oceans. This observation was probably due to the low number of studies (seven), conducted in the latter regions and including different habitats such as hydrothermal vents. However, he found that meiofauna benthic standing stocks generally showed a positive relationship with various indices of surface-derived organic matter flux and surface productivity. He noted a positive correlation between meiofauna abundance and macrofauna abundance in the Atlantic Ocean. Tietjen (1992) observed that the abundance ratios of bacteria, and meio-, macro-, and megafauna varied relatively little across ocean basins, with bacterial abundance seven to eight orders of magnitude greater than meiofauna abundance, and meiofaunal abundance about three and seven orders of magnitude greater than macrofaunal and megafaunal abundances, respectively.

Soltwedel (2000) summarised regional differences in meiofaunal standing stocks associated with differences in surface productivity along bathymetry gradients. The highest abundances occurred in upwelling regions off the north-western and south-western African coast (Thiel 1982, Kamenskaya and Galtsova 1996), while the lowest abundance was observed off north-eastern Australia (Alongi and Pichon 1988). Food availability was identified as the most important factor influencing meiofaunal abundance and higher taxa diversity. Soltwedel (2000) explored the relationship between meiofauna abundance and food availability (measured using chloroplastic pigment equivalents concentrations in the sediments) and argued that large variation in these relationships resulted from the influence of abiotic factors (pressure, temperature, oxygen level and sediment granulometry), biological process in the water column (degradation process of organic matter), and competitive and predatory interactions with other faunal groups.

Overall these literature reviews show that relationships between meiofaunal benthic standing stocks and food availability and along bathymetry gradients are not always consistent across regions due to the influence of other abiotic and biotic factors. Therefore, each region needs to be investigated separately in order to describe patterns and environmental variables that influences these patterns (Soltwedel 2000). This realisation likely helped to stimulate further investigations of deep-sea meiofauna in other parts of the globe, where meiofaunal communities remained either incompletely undescribed or poorly known.

### 1.1.2 Ecological studies of deep-sea meiofauna since 2000

Since Soltwedel's (2000) review, the focus of deep-sea meiofauna studies has widened to include the eastern and southwest Pacific Ocean, the Sea of Japan, the central Indian Ocean, the south Atlantic, and areas off the Antarctic Peninsula (Figure 1.1). Further studies have been conducted in habitats such as seamounts and hydrothermal vents, with the exploration of new habitats such as canyon and cold seep. In addition to focussing on patterns related to water depth (Vanreusel et al. 2000, Hughes and Gage 2004, Sevastou et al. 2013), regions (Lambshead et al. 2002, Tselepides et al. 2004), vertical gradients in the sediment (Neira et al. 2001, Van Gaever et al. 2004) and seasons (Danovaro et al. 2000, Shimanaga et al. 2004), meiofaunal studies conducted since 2000 have also concentrated on the effect of deep-sea habitat (Vanreusel et al. 2010b), the relative importance of different spatial scales (Gambi and Danovaro 2006, Bianchelli et al. 2013, Danovaro et al. 2013, Ingels and Vanreusel 2013, Gambi et al. 2014), meiofauna colonisation pattern in the deep-sea (Gallucci et al. 2008b, Guilini et al. 2011, Zeppilli et al. 2015b), and disturbance on meiofaunal communities (Pusceddu et al. 2014a). Habitat studies have been mainly directed on one particular habitat (e.g. cold seep; Robinson et al. 2004, Van Gaever et al. 2004, or seamount; Pusceddu et al. 2009, Covazzi Harriague et al. 2014), or comparisons between two habitats (e.g. canyon and adjacent slope habitat; Soltwedel et al. 2005, Baguley et al. 2006a, Garcia et al. 2007, Bianchelli et al. 2008). The complex settings of these habitats with different topographic and hydrodynamic regimes, or contrasting geochemistry or physical substrates, also provide an opportunity to investigate and compare the importance of environmental variables in structuring meiofaunal communities at within-habitat scales (Van Gaever et al. 2004, Ingels et al. 2011b).

Meiofaunal dispersal and colonisation processes also play an important role in structuring meiofaunal species diversity. Meiofauna may passively disperse over large distance through the water column caused by hydrodynamic forces (Boeckner et al. 2009), even though their ability to actively disperse in the water column is limited. This passive dispersal can promote recolonisation of more distant locations and may explain their widespread geographic distribution (Bik et al. 2010). Sediments rich in organic matter have been shown to enhance nematode colonisation in the deep-sea (Gallucci et al. 2008b), but another study has shown the opposite pattern where either the presence of organic matter or type of organic matter did not affect nematode colonisation (Guilini et al. 2011). Other studies on marine nematodes have shown that type of substratum, reduced chemical exposure (Zeppilli et al. 2015b), variability in microhabitats, and biological interactions (Cuvelier et al. 2014) can influence nematode colonisation.

Disturbance can play an important role in shaping the distribution of meiofaunal communities (Schratzberger et al. 2009), and has been the focus of several studies since the review of Soltwedel (2000). Physical disturbance can occur at various of spatial and temporal scales including events induced by physical (i.e. erosion, sediment deposition, turbidity current, glacial fjord, benthic storm, earthquakes; Lambshead et al. 2001, Canals et al. 2006, Somerfield et al. 2006, Schratzberger et al. 2009), or biological (i.e. bioturbation and predation; Hughes and Gage 2004, Kristensen and Kostka 2013), or anthropogenic sources (i.e. fishing and mining; Schratzberger et al. 2009, Hein et al. 2013, Martín et al. 2014, Ramirez-Llodra et al. 2015). Physical disturbance can be beneficial, by stimulating bacterial activity and helping to distribute organic matter into deeper sediment from resuspension events (Olafsson 2003, Hughes and Gage 2004). However, physical disturbance can also negatively impact meiofauna communities directly or indirectly. The transport of surface sediments along with strong bottom currents can lead to an unstable sediment substrate, while frequent resuspension with high sedimentation rates can also cause meiofauna to be buried by sediment, all of which can lead to lower diversity and higher dominance of certain disturbance-tolerant species (Garcia et al. 2007, Martín et al. 2014, Pusceddu et al. 2014a). In addition, anthropogenic disturbance caused by bottom trawling or deep-sea mining can have pronounced effects on deep-sea soft sediment communities, where the rates and magnitudes of these alterations often greatly exceed those of natural disturbance occurrences (Schratzberger et al. 2009, Miljutin et al. 2011, Martín et al. 2014).

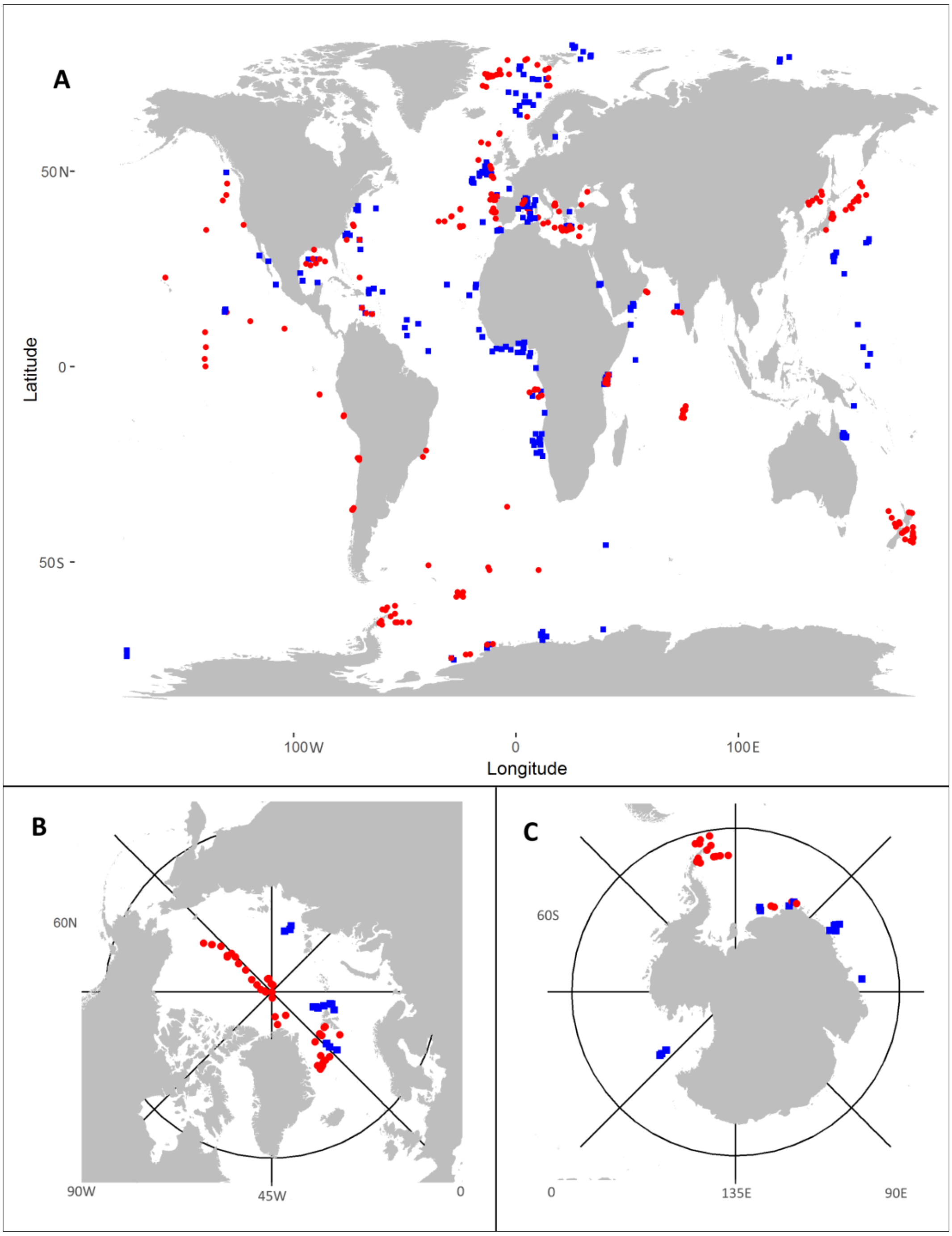

Figure 1.1. Map showing the distribution of ecological studies of deep-sea meiofauna before (blue squares) and after (red circles) the review by Soltwedel (2000) in (A) the world oceans, (B) Arctic region, and (C) Antarctic region. The circle in (B) and (C) shows the position of latitude 60°.

### 1.1.3 Changes in mesh size and sampling approaches over time

The lower mesh size limit used to sample meiofauna has differed widely between studies. Wigley and McIntyre (1964) carried out the first deep-sea meiofauna study and used a 74 µm lower mesh size. Later, Thiel (1966), Dinet (1973), and Thiel (1971) reduced the lower limit to 65, 50 and 42 µm respectively for their investigation of deep-sea meiofauna, in order to collect smaller abundant meiofauna as well. In Soltwedel's review, just over half of the cited papers used lower mesh sizes of 40–45 µm, about one-quarter used larger (50–74 µm) mesh sizes, and the rest used a smaller (32–38 µm) mesh size. Studies conducted since 2000 are based on mesh sizes of 20–63 µm, with almost two-thirds of studies using a mesh size smaller than 40 µm (Table 1.1). For upper limit mesh size, little change occurred between pre- and post-2000 studies. In both periods, a 1000 µm mesh size is most commonly used, with about a third of post-2000 studies using 150–500 µm mesh sizes.

The progression from a coarser to a finer lower mesh size in deep-sea meiofauna sampling is due to the increasing awareness of the smaller size of meiofauna in deep-sea sediments relative to coastal ecosystems (Soltwedel 2000, Mokievskii et al. 2007). However, relatively few studies have evaluated the effects of different mesh sizes on meiofauna extraction efficiency. A study by Rodrigues et al. (2007) indicated that the smaller mesh sizes result in higher retention of meiofaunal individuals rather than more species. In contrast, Leduc et al. (2010b) showed that use of a coarse mesh (63 µm) led to significantly lower abundance and diversity estimates, loss of resolving power in multivariate community analyses, and required greater sampling effort to detect significant changes in diversity indices compared to a smaller mesh size. Therefore, the use of a relatively fine (45 µm) mesh for accurate characterization of deep-sea nematode abundance and diversity was recommended (Leduc et al. 2010a, Leduc et al. 2010b).

There was a shift in the sampling gear used to obtain meiofauna samples between pre- and post-2000 studies. More than 50% of the papers cited in Soltwedel's review used box-corers and various grabs, with the remainder using multicorers. In post-2000 studies, 62% of the papers cited used multicorers, 27% used box-corers, and the rest used automated push corers (1%) and grabs (<1%). Multicorers have been used widely in deep-sea sampling in recent years because they allow sediment samples to be collected with minimal disturbance of the sediment-water interface, thereby decreasing this sampling artefact, whilst grabs and spade corers produce a pressure wave that tends to blow away light surficial materials from the sediment surface (Bett et al. 1994).

### 1.1.4 Ecological and taxonomic studies of deep-sea meiofauna in the New Zealand region

In the New Zealand region, ecological research on deep-sea meiofauna began only recently; to date, thirteen papers investigating deep-sea meiofaunal abundance, diversity and community structure have been published from the New Zealand Exclusive Economic Zone, all since 2000 (Table 1.1). Studies were conducted mainly on the Chatham Rise, but also in other regions including Kaikoura Canyon, Challenger Plateau, and Hikurangi Margin down to a depth of about 3600 m (Figure 1.2). Studies have included comparisons of meiofaunal community distribution between regions (Leduc et al. 2012b, Leduc et al. 2012c, Leduc et al. 2013), and variation in communities along bathymetric gradients (Nodder et al. 2003, Grove et al. 2006, Leduc et al. 2010a, Berkenbusch et al. 2011, Leduc et al. 2012c). Meiofaunal communities have also been compared between different habitats, such as between canyon and slope (Leduc et al. 2012c, Leduc et al. 2014), among the sediment depth layers (Grove et al. 2006, Leduc et al. 2010b, Leduc and Pilditch 2013, Leduc et al. 2015), as well as seasonally (Nodder et al. 2003, Grove et al. 2006). The meiofaunal communities of the New Zealand region are relatively well studied compared to those of the Australian region, where only two studies were conducted (both before 2000; Alongi and Pichon 1988, Alongi 1992). Nonetheless, we know little about how the environmental variability among the deep-sea habitats of the New Zealand continental margin, and the potential impacts of human activities on meiofaunal abundance, diversity and community structure.

Studies on the taxonomy of marine nematodes in New Zealand are still in their early stages, with only a few taxonomic studies conducted in New Zealand until recent years (Ditlevsen 1921, Allgén 1927, Ditlevsen 1930, Allgén 1932, Allgén 1947, 1950, Wieser 1956). Recent interest in the taxonomy of nematodes in the region has led to the description of several new species and genera in both shallow (e.g. *Desmolaimus courti*, *Setosabatieria australis*) and deep-sea environments (e.g. *Mudwigglus patumuka*, *Vasostoma hexodontium*). Since the early 1900s, a total of 159 valid species have been recorded/described from New Zealand, ninety-one of which were described in the early studies of Ditlevsen (1921, 1930), Allgén (1927, 1932, 1947, 1950) and Wieser (1956). However, the majority of the marine free-living nematode species in New Zealand remain to be described (Yeates 2010). The deep-sea nematode fauna of the New Zealand region is thought to be diverse, with an estimated ~1200 species present on Chatham Rise and Challenger Plateau alone (Leduc et al. 2012b). Much of this diversity, both in New Zealand and worldwide, is likely to be new to science, and it is therefore important to keep describing species in order to generate as complete an understanding of meiofauna ecology as possible (Miljutin et al. 2010, Abebe et al. 2011).

Understanding interactions between biodiversity and ecological functioning requires a thorough knowledge of the nematode species diversity in the context of species functionality, which however is still limited (Danovaro et al. 2008a, Abebe et al. 2011). Nematodes are often used to investigate ecological patterns and relationships with environmental factors because they are: (1) sensitive to stressful conditions and show potentially genus-specific responses to different environmental factors (Danovaro et al. 1995, Austen and McEvoy 1997, Mirto et al. 2000), (2) have easily recognizable feeding types making it possible to identify functional diversity traits (Moens and Vincx 1997), (3) have high turnover rates which makes them respond more quickly to environmental change (short generation time, ranging from 4-63 days) (Vranken et al. 1986), and (4) lack larval dispersal and are therefore expected to have limited dispersal abilities and therefore cannot avoid changes in environmental conditions (Palmer 1988).

### 1.1.5 Review aim

The aim of this review is to describe spatial distribution patterns of deep-sea meiofaunal communities at regional (~100–10,000 km), habitat (~0.1–100 km), local (~0.1–100 m) and small scales (~0.1–10 cm), with reference to the effects of environmental variables and disturbance (biological and human) that control these patterns. Particular emphasis is placed on ecological studies published since Soltwedel’s review in 2000, and from the New Zealand region (including also taxonomic studies) up to but not including 2016. Studies that describe patterns for foraminiferans only were excluded from the review because live foraminiferans cannot be accurately quantified using techniques such as elutriation or Ludox extraction, meaning that comparisons with findings for other meiofauna are questionable (Thiel 1983, Tietjen 1992, Soltwedel 2000). A total of 135 papers published after Soltwedel's (2000) review, based on samples from over fifty deep-sea sites, were reviewed (Table 1.1).

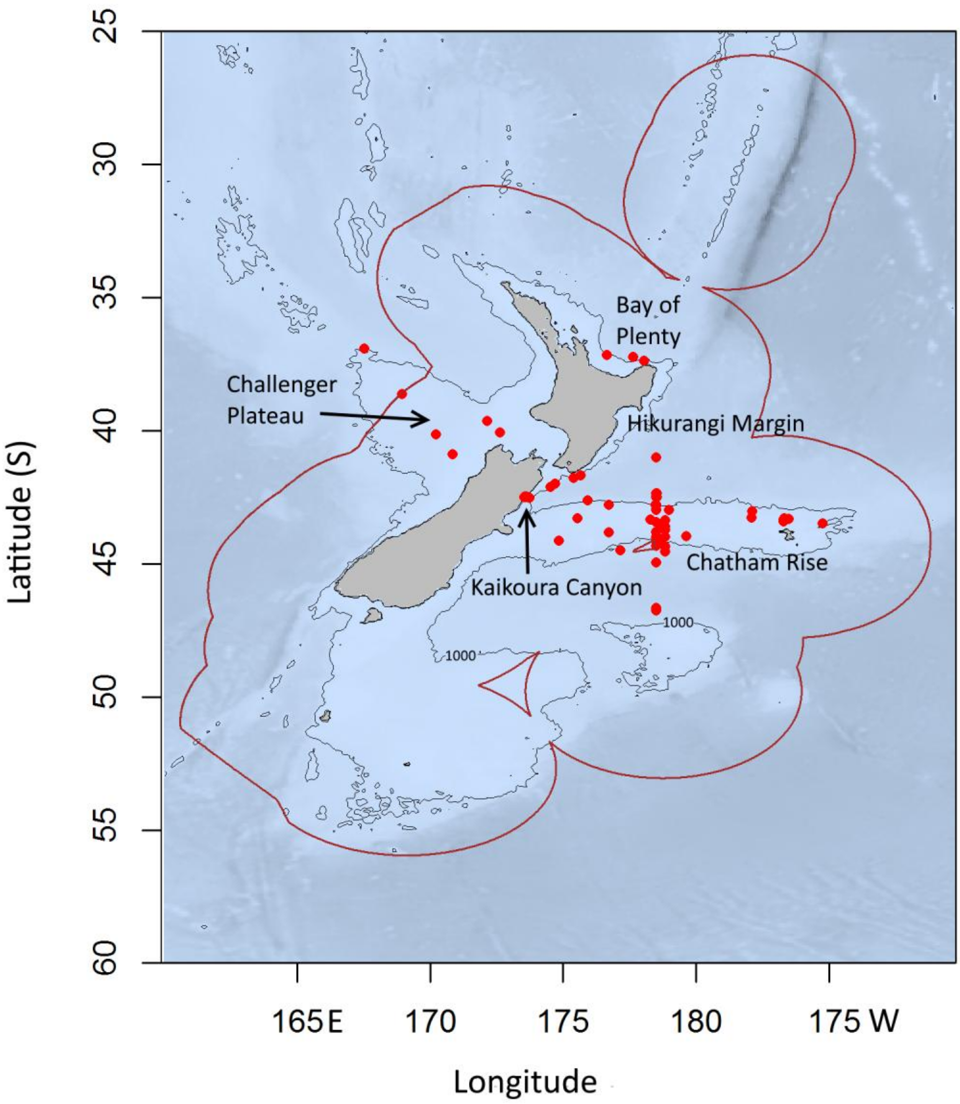

Figure 1.2. Map showing pre-2016 studies of deep-sea meiofauna in and adjacent to the New Zealand Exclusive Economic Zone (red line) (see Table 1.1). Black line indicates 1000 m isobaths.

Table 1.1. Summary of deep-sea meiofauna studies (>200 m water depth) conducted across all oceans and in the New Zealand Exclusive Economic Zone since the review of Soltwedel (2000) and up to 2016. Spatial scale: small-scale (small): 0.001–0.1 m, local-scale (local): 0.1–100 m, habitat-scale (habitat): 0.1–100 km, regional-scale (region): 100–10,000 km. Abbreviations: BC = Box corer; Gr = grab; MUC = Multicorer; Pac = Programme auto-corer; Pc = ROV Push corer; Submersible = Sm; A = abundance; B = biomass; CS = community structure; D = diversity; Bact = bacteria; Copep = copepods; Foram = foraminiferans; Lori = loriciferans; Ostra = ostracods; Nema = nematodes; Meio = meiofauna; Macro = macrofauna; Mega = megafauna; n/a = not applicable; n/s = not specified.

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| **Around the world** |  |  |  |  |  |  |  |  |  |  |
| Central Indian Ocean | Meio | n/s | 5000–5200 | BC, Gr | 63 | 500 | Abyssal plain | Small | A | Ansari (2000) |
| Arabian Sea, NW Indian Ocean | Nema | Oct–Nov 1994 | 400–3400 | MUC | 45 | n/s | Slope | Habitat | A | Cook et al. (2000) |
| Cretan Sea, Mediterranean Sea | Meio | Aug 1994–Sep 1995 | 40–1500 | MUC | 37 | 500 | Slope | Habitat | A, B | Danovaro et al. (2000) |
| Central Indian Ocean | Meio | n/s | 5300 | BC | 45 | n/s | Abyssal plain | Small | A | Ingole et al. (2000) |
| Adriatic Sea, Mediterranean Sea | Meio | Apr-May 1995 | 15–1000 | BC | 38 | n/s | Slope | Small | A, B, CS, D | Moodley et al. (2000) |
| Sagami Bay Japan, North Pacific Ocean | Meio | Dec 1996–Aug 1998 | 1400–1500 | MUC | 31 | 1000 | Slope | Small | A, CS | Shimanaga et al. (2000) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Arctic Ocean | Meio | Sep 1991,<br>July– Aug 1994 | 540–4300 | MUC, BC | 32 | 1000 | Slope | Habitat | A, B, CS | Vanreusel et al. (2000) |
| Peru Margin, SE Pacific Ocean | Copep | Feb–Mar 1989, Jan 1996 | 4000–4100 | MUC | 63 | n/s | Abyssal plain | Small, habitat | CS | Ahnert and Schriever (2001) |
| North Atlantic Ocean | Nema | n/s | 3500–5400 | MUC, BC | n/s | n/s | Slope | Region | D | Lambshead et al. (2001) |
| Peru Margin, SE Pacific Ocean | Meio | Dec 1997–Jan 1998 | 300–1200 | MUC | 40 | 500 | Slope | Small, habitat | A, CS | Neira et al. (2001) |
| Peru Margin, SE Pacific Ocean | Nema | Feb 1996 | 4000–4100 | MUC | 63 | n/s | Abyssal plain | Habitat | CS, D | Vopel and Thiel (2001) |
| Acatama Trench, SE Pacific Ocean | Meio | Sep 1997 | 1050–7800 | BC, Pac | 20 | 1000 | Trench | Habitat | A, B, CS | Danovaro et al. (2002) |
| Pacific Ocean | Nema | July–Aug, Nov–Dec 1992 | 4300–5000 | MUC, BC | 45 | n/s | Abyssal plain | Habitat | D | Lambshead et al. (2002) |
| NE Pacific Ocean | Meio | 1995–1997 | 4380–4430 | MUC | 32 | 500 | Abyssal plain | Small | A, CS | Radziejewska (2002) |
| Galician Margin, NE Atlantic | Nema | Jun–July 1997,<br>May–June 1998,<br>May 1999 | 130–4900 | MUC, BC | 32 | n/s | Canyon, slope, seamount, abyssal plain | Small, habitat | A, B, CS | Soetaert et al. (2002) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Clarion-Clipperton Fracture Zone, NE Pacific Ocean | Nema | July–Aug, Nov–Dec 1992 | 4300–4900 | MUC, BC | 45 | n/s | Abyssal plain | Region | CS, D | Lambshead et al. (2003) |
| Acatama trench, SE Pacific Ocean | Nema | Sep 1997 | 1050–7800 | BC, Pac | 20 | 1000 | Trench, slope | Habitat | CS, D | Gambi et al. (2003) |
| Cretan & Aegean Sea, Mediterranean Sea | Meio | Sep 1989, 1994, Mar, May, Sep 1995, Sep 1997, Sep 1998 | 900–2400 | MUC, BC | 20 | 1000 | Slope | Local, habitat, region | D | Danovaro et al. (2004) |
| NW Atlantic Ocean | Meio<br>Macro<br>Mega | Apr– May, June– July 1998 | 1100–3500 | MUC, BC | 45 | 250 | Slope | Small, habitat | A, B, CS | Hughes and Gage (2004) |
| Kenyan Margin, Western Indian Ocean | Nema | June–July, Nov–Dec 1992 | 20–2000 | BC | 32 | 1000 | Slope | Habitat | A, CS, D | Muthumbi et al. (2004) |
| NE Atlantic Ocean | Meio | Aug 2000 | 900–1000 | MUC, BC | 32 | 1000 | Cold seep | Small, habitat | A, CS, D | Van Gaever et al. (2004) |
| Gulf of Mexico & Blake Ridge, Atlantic Ocean | Meio<br>Foram<br>Macro | Oct 2000, Sept 2001 | 690–2240 | Pc | 63 | 300 | Cold seep | Small, habitat, region | A, CS | Robinson et al. (2004) |
| Sagami Bay Japan, North Pacific Ocean | Copep | Dec 1996, 1997, June 1997, May 1998, Aug 1997, 1998 | 1400 | MUC | 63 | n/s | Slope | Local | CS, D | Shimanaga et al. (2004) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Balearic & Ionian Sea, Mediterranean Sea | Meio<br>Foram | Jun–July 2001 | 600–1700 | MUC | 32 | 500 | Slope | Habitat, region | A | Tselepides et al. (2004) |
| South Sandwich Trench, South Atlantic Ocean | Meio | Mar–Apr 2002 | 750–6300 | MUC, BC | 32 | 1000 | Slope, abyssal plain, trench | Habitat | A, B, CS | Vanhove et al. (2004) |
| Campos Basin, SE Brazil, SW Atlantic Ocean | Meio | n/a | 200–900 | BC | 63 | n/s | Slope | Region | A, CS, D | Netto et al. (2005) |
| West Greenland Sea, North Atlantic Ocean | Meio<br>Bact<br>Foram | Summers 1999–2002 | 600–3700 | MUC | 32 | 500 | Canyon, slope | Small, habitat | A, B | Soltwedel et al. (2005) |
| Central Indian Ocean | Meio | Apr 2001 | 520–5300 | BC | 45 | 500 | Abyssal plain | Small, habitat | A, CS | Ingole et al. (2005) |
| Monterey Canyon, NE Pacific Ocean | Copep | Oct 2002 | 3250 | Pc | 32 | n/s | Canyon | Small, local | D | Thistle et al. (2005) |
| Gulf of Mexico, North Atlantic Ocean | Meio | May–June 2000 | 200–3800 | BC | 45 | n/s | Canyon, slope | Habitat | A | Baguley et al. (2006a) |
| Gulf of Mexico, North Atlantic Ocean | Copep | May–June 2000 | 200–3000 | BC | 45 | n/s | Canyon, slope | Habitat, region | CS, D | Baguley et al. (2006b) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| North east Pacific Rise | Nema | Nov 1999 | 2400–2700 | Sm | 63 | n/s | Vent | Local, habitat | A, D | Flint et al. (2006) |
| Aegean Sea, NE Mediterranean Sea | Meio | Aug–Sep 1997, Mar–Apr 1998 | 150–1800 | MUC | 30 | 500 | Slope | Habitat, region | A, B, CS, D | Lampadariou and Tselepides (2006) |
| Mediterranean Sea | Meio | Mar–Apr, Oct–Nov 2001 | 2700–2900 | MUC, BC | 20 | 1000 | Slope | Local, habitat, region | A, B, CS, D | Gambi and Danovaro (2006) |
| Arctic Ocean | Nema<br>Macro | Sep 1991, July–Aug 1994 | 1000–4300 | MUC, BC | 32 | 1000 | Slope | Habitat, region | CS, D | Renaud et al. (2006) |
| Arctic Ocean | Nema<br>Macro | Sep 1997 | 80–360 | BC, Gr | 63 | n/s | Glacial fjord | Habitat | CS, D | Somerfield et al. (2006) |
| Hakon Mosby Mud Volcano, Barents Sea, Arctic Ocean | Meio | June–July 2003 | 1300–1900 | MUC | 32 | n/s | Cold seep | Small, habitat | A, B, CS, D | Van Gaever et al. (2006) |
| East Pacific Rise | Nema | Dec 2001, 2002 | 2500 | Sm | 63 | 1000 | Vent | Habitat | A, CS, D | Zekely et al. (2006a) |
| Mid-Atlantic Ridge & east Pacific Rise | Meio | July, Dec 2001 | 2500, 3500 | Sm | 63 | 250 | Vent | Habitat | A, CS | Zekely et al. (2006b) |
| Porcupine Seabight, NE Atlantic Ocean | Nema | June 2000, May 2001 | 970–1000 | BC | 32 | 1000 | Slope | Habitat | A, CS, D | Raes and Vanreusel (2006) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| North & east Pacific Rise | Meio | Feb, Nov 1999 | 2450–2700 | Sm | 62 | n/s | Vent | Habitat | A, CS, D | Copley et al. (2007) |
| Southern Ocean & western Indian Ocean | Nema | July–Dec 1992, Dec–Feb 1989, 2002 | 200–2000 | MUC, BC | 32 | n/s | Slope | Local, habitat, region | D | Fonseca et al. (2007) |
| Nazaré Canyon, NE Atlantic Ocean | Meio<br>Foram | May 2004 | 300–5000 | MUC | 48 | 150 | Canyon, slope | Habitat | A, B CS, D | Garcia et al. (2007) |
| East Pacific Rise | Meio | Dec 2001, 2001 | 2500 | Sm | 63 | 1000 | Vent | Habitat | A, CS | Gollner et al. (2007) |
| Axial Volcano Juan de Fuca Ridge, NE Pacific Ocean | Meio<br>Macro | July 2002 | ~1500 | Sm | n/s | n/s | Vent | Local | CS | Limén et al. (2007) |
| Black Sea | Meio | Oct 2004 | 180–250 | MUC | 64 | 1000 | Cold seep | Small, local | A, CS | Sergeeva and Gulin (2007) |
| HAUSGARTEN, Arctic Ocean | Meio | 2000–2004 | 1200–5500 | MUC | 32 | 1000 | Slope | Habitat | A, CS | Hoste et al. (2007) |
| Adriatic Sea, Mediterranean Sea | Meio | May 2006 | 200–900 | BC | 32 | n/s | Canyon, slope | Habitat | A | Bianchelli et al. (2008) |
| Mediterranean Sea | Nema | June– July 1999 | 1290–4000 | MUC | 20 | 1000 | Slope | Habitat | D | Danovaro et al. (2008b) |
| Arctic Ocean | Meio | Summer 1999– July 2003 | 2500 | Pc | 32 | n/s | Slope | Local | A, CS, D | Gallucci et al. (2008a) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) | | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Lower | Upper | | | | |
| Arctic Ocean | Nema | Summer 2006 | 1300 | MUC | 32 | n/s | n/a | Small | A, B, CS, D | Gallucci et al. (2008b) |
| NE Atlantic Ocean, Mediterranean Sea | Meio | Oct 2005<br>May, Sep 2006 | 200–5000 | MUC, BC | 20 | 1000 | Canyon, slope | Habitat, region | D | Danovaro et al. (2009) |
| Greenland Sea, North Atlantic Ocean | Nema | July 2000,<br>Aug 2006,<br>Aug 2007 | 2000 | MUC | 32 | n/s | Slope | Habitat, region | A, CS, D | Fonseca and Soltwedel (2009) |
| Arctic Ocean | Meio | June–Aug 2006 | 1300 | MUC | 32 | n/s | Slope | Small, local | A, D | Gallucci et al. (2009) |
| Norwegian Sea, North Atlantic Ocean | Meio<br>Macro | May–June 2006 | 700–1300 | MUC, Pc, BC | 32 | n/s | Cold seep | Habitat, region | A, CS, D | Van Gaever et al. (2009b) |
| Gulf of Guinea, South Atlantic Ocean | Meio | Nov–Dec 2001<br>Dec 2003-Jan 2004 | 3150–4800 | Pc, MUC | 32 | n/s | Canyon, cold seep | Small, habitat, region | A, B, CS, D | Van Gaever et al. (2009a) |
| Nazaré Canyon, NE Atlantic Ocean | Meio | July–Aug 2005 | 3400–4300 | MUC | 32 | 1000 | Canyon, slope | Small, habitat | A, B, CS, D | Ingels et al. (2009) |
| Tyrrhenian sea, Mediterranean Sea | Meio | July 2005 | 3500 | MUC | 20 | 1000 | Seamount | Local, habitat | A, B, CS, D | Pusceddu et al. (2009) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Chile Margin, SE Pacific Ocean | Meio | Apr 2001 | 120–360 | MUC | 40 | n/s | Slope | Habitat | A, CS | Veit-Kohler et al. (2009) |
| Mediterranean Sea | Meio | Oct 2005<br>May 2006<br>Sep 2006 | 200–5000 | MUC, BC | 20 | 1000 | Canyon, slope | Habitat | A, B, CS, D | Bianchelli et al. (2010) |
| Deep anoxic hypersaline L'Atalante basins, Mediterranean Sea | Meio<br>Lori | Dec 1998, Aug 2005, June 2008 | 3200–3600 | BC | 20 | 1000 | Hypersaline anoxic sediment | n/a | CS | Danovaro et al. (2010b) |
| East Pacific Rise | Meio | 2001–2004 | 2500 | Sm | 63 | 1000 | Vent | Habitat | A, CS, D | Gollner et al. (2010) |
| Clarion-Clipperton Fracture Zone, NE Pacific Ocean | Nema | June 2004 | 4800–5000 | MUC, BC | 40 | n/s | Slope | Habitat | A, CS, D | Miljutina et al. (2010) |
| Eastern Antarctic Peninsula | Nema | Jan 2007 | 240–40 | MUC | 32 | 1000 | Slope | Habitat | A, CS, D | Raes et al. (2010) |
| Norwegian Sea, North Atlantic Ocean | Nema | Jun–July 2003, May–June 2006 | 720–1900 | MUC, Pc | 32 | n/s | Cold seep | Local, region | CS, D | Van Gaever et al. (2010) |
| Eastern Antarctic Peninsula, Southern Ocean | Nema | Jan 2007 | 820 | MUC | 32 | 1000 | Cold seep | Small, local | A, CS, D | Hauquier et al. (2011) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| HAUSGARTEN, Arctic Ocean | Nema | Summer 2001 | 2300 | Pc | 32 | 500 | Slope | Small | A, CS, D | Hasemann and Soltwedel (2011) |
| Clarion-Clipperton Fracture Zone, NE Pacific Ocean | Nema | Jun 2004 | 5000 | MUC, BC | 40 | n/s | Slope | Habitat | A, CS, D | Miljutin et al. (2011) |
| Kenyan Margin, Western Indian Ocean | Nema | Jun–July, Nov–Dec 1992 | 20–2000 | BC | 32 | 1000 | Slope | Habitat, region | CS, D | Muthumbi et al. (2011) |
| Eastern Antarctic Peninsula, Southern Ocean | Meio<br>Macro<br>Mega | Jan 2007 | 150–300 | MUC | 32 | 1000 | Slope | Habitat | A, CS, D | Gutt et al. (2011) |
| Mediterranean Sea | Meio | Feb–Mar, July 2007 | 140–220 | BC | 20 | 1000 | Cold seep, slope | Small, habitat | A, CS, D | Zeppilli et al. (2011) |
| Setúbal and Cascais Canyon, NE Atlantic Ocean | Nema | Apr– May 2006 | 3200–4500 | MUC | 32 | 1000 | Canyon | Small, habitat | A, B, CS, D | Ingels et al. (2011a) |
| Gollumn Channels and Whittard Canyon, NE Atlantic | Meio | June 2006 | 700, 1000 | MUC | 32 | 1000 | Canyon | Small, habitat | A, B, CS, D | Ingels et al. (2011b) |
| Gulf of Cadiz, NE Atlantic | Meio | May 2007 | 1100 | MUC, Pc | 32 | n/s | Cold seep | Local, habitat | A, B, CS, D | Pape et al. (2011) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| West Mediterranean Sea | Meio | Oct 2005, 2007 | 260–430 | MUC | 20 | 1000 | Cold seep, slope | Small, habitat | A, B, CS, D | Zeppilli et al. (2012) |
| Ionian Sea, Mediterranean Sea | Meio<br>Bact<br>Macro | May 2009 | 1200–2100 | BC | 20 | 300 | Slope | Habitat | A, B, CS, D | Baldrighi et al. (2013) |
| Mediterranean Sea | Nema | Sep 1989, July 1998, Oct 2005, May 2006 | 600–1300 | BC, MUC | 20 | 1000 | Canyon, slope, coral rubble | Habitat region | D | Bianchelli et al. (2013) |
| SW Adriatic Margin, Mediterranean Sea | Nema | Mar 2009 | 200–1200 | BC | 20 | 1000 | Slope | Small, local | A, CS, D | Danovaro et al. (2013) |
| East Pacific Rise | Nema | Nov-Dec 2006, Dec 2007, Oct 2009 | 2500 | Sm | 32 | 1000 | Vent | n/a | A, D | Gollner et al. (2013) |
| Blanes Canyon, NW Mediterranean Sea | Nema | Nov 2003, May 2004 | 300–1600 | MUC | 32 | 250 | Canyon, slope | Habitat | A, B | Ingels et al. (2013) |
| East Mediterranean Sea | Meio | Oct 2007 | 1900–2200 | Pc, BC, MUC | 32 | n/s | Cold seep | Small, habitat, region | A, B, CS, D | Lampadariou et al. (2013) |
| Central Chile margin, SE Pacific Ocean | Meio | Mar–Apr 1999 | 100–1000 | MUC | 40 | n/s | Slope | Small, habitat | A, B, CS, D | Neira et al. (2013) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (μm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Gulf of Mexico, North Atlantic Ocean | Meio<br>Macro | Oct 2010 | 76–2767 | MUC | 42 | n/s | Slope | n/a | A, D | Montagna et al. (2013) |
| Galicia Bank, NE Atlantic & Mediterranean Sea | Nema | Jun, Oct 2008, Jun, Nov 2009 | 1000–3000 | MUC, BC | 32 | n/s | Slope | Habitat, region- | B, D | Pape et al. (2013a) |
| Galicia Bank, NE Atlantic & Mediterranean Sea | Nema | Jun, Oct 2008, Jun, Nov 2009 | 1000–3000 | MUC, BC | 32 | n/s | Seamount, slope | Habitat | A, B, CS | Pape et al. (2013b) |
| Gulf of Lions, Mediterranean Sea | Meio | May 2004, Apr, Oct 2005, Aug 2006, Apr 2008, 2009 | 940–2100 | MUC, BC | 20 | 1000 | Canyon, slope | Habitat | A, B, D | Pusceddu et al. (2013) |
| NW Mediterranean Sea | Meio | Autumn 2003, Spring 2004 | 400–1500 | MUC | 32 | 250 | Canyon, slope | Small, habitat | A, CS | Romano et al. (2013) |
| Japan Sea, NW Pacific Ocean | Meio | Aug– Sep 2010 | 450–3370 | MUC | 40 | 1000 | Slope | Habitat | A, CS, D | Trebukhova et al. (2013) |
| Azores, NE Atlantic Ocean | Meio | July 2010 | 200–1700 | MUC | 20 | 1000 | Seamount, slope | Small, habitat | A, B, CS, D | Zeppilli et al. (2013) |
| Tyrrhenian Sea, Mediterranean Sea | Meio<br>Macro | May 2009 | 100–2700 | BC | 45 | 500 | Seamount | Habitat | A, B, CS, D | Covazzi Harriague et al. (2014) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Mid-Atlantic Ridge | Meio<br>Macro | 2006, 2008 | 1700 | Sm | 63 | 1000 | Vent | n/a | CS, D | Cuvelier et al. (2014) |
| Mediterranean Sea | Nema | Apr & Nov 2001 | 2760–2854 | MUC, BC | 20 | 1000 | Slope | Local, habitat, region | A, D | Gambi et al. (2014) |
| SE Atlantic Ocean | Copep | July– Aug 2000 | 5300–5500 | MUC | 40 | n/s | Abyssal plain | Habitat | A, CS, D | George et al. (2014) |
| Fram Strait, Arctic Ocean | Meio | Summer 2005–2009 | 1200–5500 | MUC | 32 | 500 | Slope | Small, habitat | A, CS, D | Górska et al. (2014) |
| Chukchi Sea, Arctic Ocean | Meio | July–Sep 2010 | 40–50,<br>400–2300 | MUC, BC | 32 | 500 | Slope | Small, region | A, CS, D | Lin et al. (2014) |
| La Fonera Canyon, NW Mediterranean Sea | Meio | May 2011 | 500–2000 | MUC | 20 | 1000 | Canyon | Small, habitat | A, D | Pusceddu et al. (2014a) |
| Nazaré Canyon, NE Atlantic Ocean | Meio | Spring–summer 2005–2007 | 3500, 4400 | MUC, Pc | 32 | 1000 | Canyon | Habitat | A, B, CS, D | Ramalho et al. (2014) |
| California, Pacific Ocean | Meio | n/s | 2700, 3700 | MUC | 30 | 300 | Slope | Habitat, region | A | Rohal et al. (2014) |
| Nyegga region Norwegian Sea, North Atlantic | Meio | July– Aug 2008 | 700 | Pc | 32 | 500 | Cold seep | Habitat | A, CS, D | Portnova et al. (2014) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Central Indian Ocean | Nema | Sep 2009 | 5000–5100 | BC | 32 | n/s | Abyssal plain | Habitat | A, B, CS, D | Singh et al. (2014) |
| Myojin Knoll, NW Pacific Ocean | Nema | Apr 2008 | 850–1400 | Pc | 63 | 1000 | Vent, seamount | Habitat | CS | Setoguchi et al. (2014) |
| Black Sea | Meio | April 2010 | 97–300 | MUC | 63 | 1000 | Slope, anoxic sediment | Local | A | Sergeeva et al. (2014) |
| Azores, NE Atlantic | Nema | July 2010 | 200–1900 | MUC | 20 | 1000 | Seamount, slope | Small, habitat | A, B, CS, D | Zeppilli et al. (2014) |
| Gulf of Mexico, North Atlantic Ocean | Meio | Oct 2010 | 76–2767 | MUC | 45 | n/s | Slope | n/a | A, D | Baguley et al. (2015) |
| Deep anoxic hypersaline L'Atalante basins, Mediterranean Sea | Meio | Nov–Dec 2011 | 3400–3600 | Pc | 63 | n/s | Hypersaline anoxic sediment | n/a | A, CS | Bernhard et al. (2015) |
| East Pacific Rise | Meio<br>Macro | 2001–2004 | 2500 | Sm | 32 | 1000 | Vent | Habitat | D | Gollner et al. (2015) |
| Antarctic Peninsula | Nema | Jan–Mar 2013 | 500 | MUC | 32 | 1000 | Slope | Small, region | A, CS, D | Hauquier et al. (2015) |
| Southern Ocean | Nema | Jan–Mar 2012 | 3700–4100 | MUC | 32 | 1000 | Slope | Small, habitat | A, B, CS | Lins et al. (2015) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) | | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Lower | Upper | | | | |
| Eastern Antarctic Peninsula & Weddel Sea, Southern Ocean | Meio | Mar 2002, Nov 2006–Jan 2007 | 240–4070 | MUC | 40 | 1000 | Cold seep, slope | Habitat, | A, CS, D | Rose et al. (2015) |
| Kuril-Kamchatka Trench, NW Pacific Ocean | Meio | July-Sep 2012 | 4800–5700 | MUC | 32 | n/s | Trench, abyssal plain | Small, habitat | A, CS, D | Schmidt and Martínez Arbizu (2015) |
| Mid-Atlantic Ridge | Meio<br>Macro | 2006 | 1700 | Sm | 63 | 1000 | Vent | Local | A, CS, D | Sarrazin et al. (2015) |
| Mid-Atlantic Ridge | Nema | Oct 2010 | 1700 | Sm | 20 | 1000 | Vent | n/a | A, B, D | Zeppilli et al. (2015b) |
| Deep anoxic hypersaline L'Atalante basins, Mediterranean Sea | Lori | Nov–Dec 2011 | 3400–3600 | Pc | 63 | n/s | Hypersaline anoxic sediment | Small | A, D | Danovaro et al. (2016) |
| Whittard Canyon, NE Atlantic Ocean | Meio | June 2007 | 1000–4000 | MUC | 20 | 1000 | Canyon, slope | Habitat | A, B, D | Gambi and Danovaro (2016) |
| Sanriku Japan, NW Pacific Ocean | Meio | July–Aug 2011, summer 2012 | 150–4000 | MUC | 63 | 500 | Slope | Habitat | A, CS | Kitahashi et al. (2016) |
| Western Iberian Margin | Nema | June 2013, 2014 | 294–1006 | MUC | 32 | 1000 | Slope | Habitat | CS, D | Lins et al. (2016) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Blanes Canyon, Mediterranean Sea | Meio | Spring 2012, 2013, autumn 2012, 2013 | 462–1998 | MUC | 32 | 1000 | Canyon, slope | Habitat | A, CS | Román et al. (2016) |
| Tohoku Japan, NW Pacific Ocean | Meio<br>Macro<br>Bact | Mar 2012 | 310–880 | MUC | 63 | 1000 | Slope | Small | A, CS | Nomaki et al. (2016) |
| Spitsbergen, Svalbard Archipelago | Meio | July 2010, 2011 | 600–2000 | BC | 20 | 1000 | Slope | Habitat | A, B, D | Pusceddu et al. (2016) |
| Arabian Sea, Indian ocean | Nema | Aug 2007 | 30–2500 | BC | 32 | 500 | Slope | Habitat | A, CS, D | Singh and Ingole (2016) |
| **New Zealand continental margin, SW Pacific Ocean** |  |  |  |  |  |  |  |  |  |  |
| Chatham Rise | Meio<br>Macro<br>Bact | Apr–May, Oct–Nov 1997, Jan–Feb 2000 | 350–2600 | MUC, BC | 63 | 425 | Slope | Habitat | B | Nodder et al. (2003) |
| Chatham Rise | Meio | Apr– May, Oct–Nov 1997, Jan–Feb 2000 | 350–2600 | MUC | 63 | 425 | Slope | Small, local, habitat | A, B | Grove et al. (2006) |
| Chatham Rise, Challenger Plateau | Nema | Sep–Oct 2001, Mar–Apr, May–Jun 2007 | 240–3100 | MUC | 32, 45, 63 | 1000 | Slope | Small | A, B | Leduc et al. (2010a) |
| Chatham Rise | Nema | Apr 2007 | 1240 | MUC | 32, 45, 63 | 1000 | Slope | Small | A, B, CS, D | Leduc et al. (2010b) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Chatham Rise | Meio<br>Macro | Sep–Oct 2001 | 350–3100 | MUC | 45 | n/s | Slope | Habitat | B | Berkenbusch et al. (2011) |
| Chatham Rise, Challenger Plateau | Nema | Sep–Oct 2001, March–Apr, May–June 2007 | 240–3100 | MUC | 45 | 1000 | Slope | Habitat, region | CS, D | Leduc et al. (2012b) |
| Chatham Rise, Challenger Plateau, Kaikoura Canyon, Ross Sea, Antarctic | Nema | Sep–Oct 2001, Mar–Apr, May–June 2007, Feb–Mar 2008, Feb 2009, May 2010 | 240–3600 | MUC | 45 | 1000 | Canyon, slope | Habitat | A, B, D | Leduc et al. (2012c) |
| Chatham Rise, Challenger Plateau | Nema | Sep–Oct 2001, March–Apr, May–June 2007 | 240–1300 | MUC | 45 | 1000 | Slope | Small | D | Leduc et al. (2012d) |
| Chatham Rise, Challenger Plateau | Nema | Sep–Oct 2001, March–Apr, May–June 2007 | 240–1250 | MUC | 45 | 1000 | Slope | n/a | D | Leduc et al. (2013) |
| Chatham Rise | Nema | Feb 2011 | 345 | MUC | 45 | 1000 | Slope | Small | A, CS, D | Leduc and Pilditch (2013) |
| Kaikoura Canyon, Chatham Rise | Nema | May 2010 | 400–1400 |  | 45 | 1000 | Canyon, slope | Habitat | A, B, CS, D | Leduc et al. (2014) |
| Hikurangi Margin | Nema | Apr 2010 | 670–1350 | MUC | 45 | 1000 | Canyon, slope | Small | CS, D | Leduc et al. (2015) |

| Area | Taxa | Sampling date | Depth range (m) | Method | Meiofauna mesh size limits (µm) |  | Habitat | Spatial scale | Community attribute(s) | Reference |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | Lower | Upper |  |  |  |  |
| Chatham Rise, Challenger Plateau | Meio<br>Macro | Mar–June 2007 | 260–1200 | MUC | 32 | 500, 1000 | Slope | Habitat, region | A, B, CS | Pilditch et al. (2015) |
| Chatham Rise, Challenger Plateau | Meio<br>Macro<br>Mega | Sep–Oct 2001, Mar–June 2007 | 240–1300 | MUC | 32–45 | 1000 | Slope | Habitat, region | A, B | Leduc et al. (2016a) |
| Bay of Plenty, Hikurangi Margin | Meio | Apr 2010, Nov2006, Apr 2012 | 700–1500 | MUC | 45 | 1000 | Canyon, seamount, seep, slope | Small, habitat, region | A, CS, D | Rosli et al. (2016b) |

## 1.2 Spatial distribution patterns

### 1.2.1 Regional scale

Regional scale studies are defined as studies conducted over a distance of ~100–10 000 km. In this review, a total of twenty-six papers have described patterns for meiofauna at regional scales, including four studies conducted in New Zealand waters (Table 1.1).

Deep-sea meiofaunal abundance can vary widely among regions. Differences in abundance at the regional scale are often associated with different productivity regimes (Gambi and Danovaro 2006, Lampadariou and Tselepides 2006, Fonseca and Soltwedel 2009, Gambi et al. 2014). High organic matter flux from the surface to the seafloor has been linked to higher food availability in the sediment, which in turn leads to greater abundance of sediment fauna (Lambshead et al. 2002, Tselepides et al. 2004, Lampadariou and Tselepides 2006, Ingels et al. 2009). A study by Tselepides et al. (2004) showed that proxies of surface productivity do not always predict the amount of food at the seabed accurately, which higher meiofaunal abundance observed in the low productivity western Ionian Sea than the comparatively high productivity eastern Ionian and Balearic seas at > 800 m depth. This study showed that local hydrodynamic regimes (e.g. convection and advection) and seabed topography greatly influence spatial variability in organic matter availability at deep sites (Tselepides et al. 2004).

Meiofaunal diversity typically shows high variability at regional scales (Lambshead et al. 2003, Gambi and Danovaro 2006, Lampadariou and Tselepides 2006, Fonseca et al. 2007, Danovaro et al. 2009, Van Gaever et al. 2010, Muthumbi et al. 2011, Bianchelli et al. 2013). Regional-scale studies have shown that areas with high availability of food in the sediment are typically characterised by greater total regional diversity (Gambi and Danovaro 2006, Lampadariou and Tselepides 2006). High productivity may promote species diversity, because large populations of species associated with high productivity are less prone to extinction, compared to sparser populations found in lower productivity regions (Rosenzweig 1995). However, high productivity is not always associated with high diversity. Other studies have shown a bell-shaped curve for productivity-diversity relationships where lower diversity has been observed at high productivity regions (Leduc et al. 2012c, Leduc et al. 2014). This lower diversity at high productivity was suggested to be due to elevated competitive exclusion rates (Rex 1983) and biochemical conditions such as low oxygen concentration (Levin 2003). The geological history of the region may also influence regional diversity. For example, high nematode diversity characterises the north Aegean, which was once completely isolated from the rest of the Mediterranean Sea (Lampadariou and Tselepides 2006). These authors suggest that this isolation may have resulted in higher speciation rates and consequently in a higher biodiversity of nematodes and various fauna groups in the north Aegean Sea (i.e. Kröncke et al. (2003)). However, the opposite pattern of low diversity was observed in the Norwegian Sea (Lambshead et al. 2000). The Norwegian Sea is a relatively small and shallow, partially isolated basin affected by Quaternary glaciation which may have led to higher extinction rates (Rex et al. 1997), which likely contributed to the low nematode diversity observed there. Difference in deep-water temperature can also influence meiofaunal diversity, which higher regional diversity usually observed in colder deep waters of the Mediterranean (Danovaro et al. 2004, Danovaro et al. 2009). Regions with greater local- and habitat-scale variability arising from steep environmental gradients and a wide range of habitats are likely to support more species and have higher regional diversity ((e.g. Robinson et al. (2004), Baguley et al. (2006b), Vanreusel et al. (2010b), Leduc et al. (2012b), Lampadariou et al. (2013))). Some studies showed a lack of differences in meiofaunal local diversity between regions (Renaud et al. 2006, Pape et al. 2013a), however low number of samples is thought to account for the lack of any obvious environmental controls on regional diversity patterns for some of these studies (Renaud et al. 2006). Disturbance also can play an important role in influencing diversity at regional scales. Natural disturbances, which include erosion, sediment deposition, benthic storms, icebergs, and turbidity currents, can be concentrated in particular regions (Somerfield et al. 2006). A study by Lambshead et al. (2001) at the HEBBLE (High Energy Benthic Boundary Layer Experiment) site suggested that a large-scale natural event may have caused low nematode diversity. The HEBBLE site was associated with repetitive exposure to turbidite events caused by benthic storms, and low diversity at this site was thought to be caused by insufficient time for meiofauna to recolonize the impacted area.

Meiofaunal community structure can vary greatly between regions (Lampadariou and Tselepides 2006, Danovaro et al. 2009, Gambi et al. 2014). Dissimilarity in community structure between regions can reflect differences in the abundance of taxa (Danovaro et al. 2009, George et al. 2014), or the presence/absence of particular taxa (Lampadariou and Tselepides 2006, Gambi et al. 2014). Differences in the structure/composition of communities may be explained by a number of factors. Large geographic distances between regions may limit the dispersal of meiofauna since they lack pelagic larvae, and have no or limited active dispersal capabilities (Lambshead and Inst 1993, Leduc et al. 2012b, Bianchelli et al.

2013). Geological history may also play a role, where a region is isolated by boundaries that restrict the dispersal of meiofauna (Lampadariou and Tselepides 2006, Fonseca et al. 2007). Oceanographic boundaries, such as temperature differences which may influence water mass circulation patterns, are also thought to account for regional differences in community composition (Danovaro et al. 2009). Some studies, however, found no (Gambi and Danovaro 2006, Renaud et al. 2006), or only limited regional differences in community structure (Fonseca and Soltwedel 2009). Similarity in meiofaunal communities probably resulted from low taxonomic resolution (Gambi and Danovaro 2006), or from sampling artefact; Renaud et al. (2006) suggested that limited sampling effort could explain the failure to detect regional-scale patterns of nematode community structure in the Arctic Ocean. On the other hand, the high similarity in nematode communities in the Arctic Ocean observed by Fonseca and Soltwedel (2009) was thought to be the result of the passive dispersal of nematodes by currents.

In the New Zealand region, two studies have compared meiofaunal communities at a regional scale between the Chatham Rise and Challenger Plateau (Leduc et al. 2012b, Pilditch et al. 2015). The Chatham Rise and Challenger Plateau are large topographic features separated by ~200 km, situated on opposite sides of the two main islands of New Zealand (Figure 1.2). Leduc et al. (2012b) found that Chatham Rise had greater total nematode species diversity than the Challenger Plateau, which is probably because it is more productive overall or because it has a greater range of environmental conditions (e.g. sediment physical characteristics). However, they observed no difference in community structure between the regions, despite regional differences in environmental factors, and considered that community structure variation was related to factors that act at smaller scales (Leduc et al. 2012b). In contrast, Pilditch et al. (2015) found strong regional differences in the abundance and community structure of major meiofaunal taxa, but not diversity, between the Chatham Rise and Challenger Plateau. Differences in community structure were driven by the elevated abundance of some taxa on Chatham Rise (i.e. ostracods, kinorhynchs, annelids, copepods and nematodes), which likely reflects regional differences in primary production between the two regions (Pilditch et al. 2015).

### 1.2.2 Habitat scale

Habitat-scale studies are here defined as those that examine meiofauna community patterns between different macro-habitats, typically at scales of ~0.1–100 km. Studies that examine meiofauna along bathymetric gradients are, in effect, studies at the habitat scale, because environmental conditions can change substantially and in a predictable away along large bathymetric gradients. Bathymetric gradient studies post-2000 are not reviewed here because in general they largely confirmed the findings of earlier similar studies (e.g. Romano et al. 2013, Sevastou et al. 2013, Lin et al. 2014), rather than provide additional ecological insights concerning habitat-scale patterns. However, a review of recent bathymetric studies of meiofauna in the New Zealand region is included for completeness of the literature for the focus area. In this review, a total of ninety-six papers have described patterns for meiofauna at habitat scales, including nine studies conducted in New Zealand waters (Table 1.1).

The presence of macro-habitats plays an important role in influencing patterns of meiofauna abundance, diversity and community structure. Macro-habitats can be characterized by their unique topographic and/or biogeochemical characteristics. Topographic features can influence the hydrodynamic regime of the environment and thus affect sediment heterogeneity, food, and oxygen availability in the sediment (i.e. canyons and seamounts) (Baguley et al. 2006a), and hence the meiofauna. Habitats with different biogeochemical properties, such as cold seeps and hydrothermal vents, can support unique meiofauna (e.g. the mouthless nematode *Astomonema southwardorum* and the tolerant opportunistic species *Halomohystera disjuncta*) that depend directly or indirectly on chemoautotrophic bacteria and/or are tolerant of the extreme environmental conditions that occur at such habitats (Austen et al. 1993, Olu-Le Roy et al. 2004, Levin 2005, Olu et al. 2009, Van Gaever et al. 2009b). Meiofauna studies of macro-habitats have mainly focussed on single habitats such as canyon (Garcia et al. 2007, Ingels et al. 2011a), seamount (Pusceddu et al. 2009, Zeppilli et al. 2014), cold seep (Van Gaever et al. 2004, Portnova et al. 2014), and hydrothermal vent (Kamenev et al. 1993, Setoguchi et al. 2014). Only a few studies have compared two (e.g. canyon and slope (Baguley et al. 2006a, Ingels et al. 2009, Bianchelli et al. 2010)) or multiple habitats (Soetaert et al. 2002, Vanreusel et al. 2010b).

Canyons are complex topographic features that influence local hydrodynamic regimes, and thus sediment transport and accumulation (de Stigter et al. 2007, García et al. 2008). The majority of canyons, which are considered inactive, incise only the outer edge of continental shelves and are remote from abundant supply of coastal sediment, whereas active canyons typically incise more deeply and retain their abundant supply of coastal sediment (Harris and Whiteway 2011). Seamounts, which are defined as elevated features that include knolls, pinnacles and hills where the elevation can be as low as 100 m (Pitcher et al. 2007, Clark et al. 2010), can affect surrounding flow conditions resulting in enhanced currents, eddies, up- and down-welling and closed retention cells (White et al. 2007, Bashmachnikov et al. 2013). These modified flow conditions increase vertical mixing, spatial variation in sedimentation processes, and the distribution of food resources (Levin and Dibacco 1995, Bongiorni et al. 2013, Zeppilli et al. 2013). Cold seeps and hydrothermal vents are characterised by the flow of reduced chemical compounds (e.g. methane, sulphur) from the subsurface to the seafloor (Levin 2005, Van Gaever et al. 2009a, Lampadariou et al. 2013, Van Dover 2014). The emission of reduced fluids results in a broad range of geological, sedimentary and biological structures (e.g. gas seepage, microbial mat, pockmarks, authigenic reef structures, chimneys) (Judd et al. 2002, Levin 2005, Van Dover 2014), thus providing a variety of habitats for meiofauna that differ from 'background' habitats (Kamenev et al. 1993, Levin and Mendoza 2007, Setoguchi et al. 2014).

Meiofaunal abundance generally shows high variability between different habitats. Meiofaunal abundance has been found to be higher in canyons compared to adjacent slope and basin habitats (Baguley et al. 2006a, Bianchelli et al. 2008, Danovaro et al. 2009, Ingels et al. 2009, Ingels et al. 2011b, Romano et al. 2013). High food availability appears to be responsible for elevated abundance in canyons, and this is positively related with hydrodynamic disturbance in the canyon (Ingels et al. 2011b, Leduc et al. 2014). Hydrodynamic disturbance can help replenish food availability in the sediment through a cycle of resuspension and deposition of organic matter (Ingels et al. 2011b). However, each canyon is unique with a different topography and hydrodynamic regime, which influences patterns of meiofauna abundance between canyons (Bianchelli et al. 2010, Ingels et al. 2011a) and patterns of higher meiofauna abundance in canyons are not always observed. Lower abundance or no differences in abundance between canyon and adjacent slope have also been found. Lower meiofauna abundance was observed in the Nazaré Canyon compared to adjacent slope (Garcia et al. 2007), whilst no differences in abundance between canyon and slope were observed in Catalan, Portuguese, and South Adriatic Margin (Bianchelli et al. 2010). Lower meiofaunal abundance in canyons may be related to environmental stress caused by strong currents that result in frequent resuspension and transport of the surface sediment, or to the burial of meiofauna from high sedimentation rates, or being swept away by currents (Garcia et al. 2007).

Meiofauna of seamount habitat have received less attention than that of canyons, with only six ecological studies conducted at seamounts since 2000. A negative and/or positive influence of seamount habitat on meiofauna abundance patterns has been reported. Zeppilli et al. (2013, 2014) found higher abundance of meiofauna on the flank and base of Condor Seamount (NE Atlantic Ocean) compared to other parts of the seamount and an adjacent seamount. Covazzi Harriague et al. (2014) also found higher meiofaunal abundance on the flanks of Vercelli Seamount (NW Mediterranean Sea) compared to non-seamount areas. Higher abundance of meiofauna on the flanks of the seamount was positively correlated with water depth, food availability and sediment heterogeneity (Zeppilli et al. 2013, Covazzi Harriague et al. 2014).

The abundance of meiofauna is generally greater in seep habitats than adjacent deep-sea sediment (Van Gaever et al. 2006, Zeppilli et al. 2011, Lampadariou et al. 2013). A study by Van Gaever et al. (2009a) also showed meiofaunal abundance to be higher at seep than canyon habitats in the Gulf of Guinea, despite the high variability in abundance within seep habitat. Studies by

Zeppilli et al. (2011, 2012), however, found that seep habitat characterised by intensive seepage displayed the lowest meiofaunal abundance compared to non-seep area. The positive effect of seep habitats on meiofauna abundance is thought to be related to the presence of high structural complexity and microbial mats (Van Gaever et al. 2009b, Zeppilli et al. 2011, Lampadariou et al. 2013), whereas a negative effect has been associated with intense gas emissions that are too toxic for most meiofaunal taxa to survive, but which allows tolerant species to dominate (Giere 2009, Zeppilli et al. 2011). In contrast to seeps, deep-sea vents generally do not show high abundance of meiofauna (Vanreusel et al. 2010a). Meiofauna abundance has been shown to be lower or similar at vent habitats compared to adjacent non-vent habitats (Vanreusel et al. 1997, Flint et al. 2006, Zekely et al. 2006b, Copley et al. 2007, Gollner et al. 2007). Vanreusel et al. (2010a) suggest that lower abundance at vent habitats is probably related to the unsuitable substrate for meiofauna, because vents mainly consist of hard substrates (i.e. basalt or sulphide mineral precipitates) with no or little sediment (Vanreusel et al. 2010a). However, Zeppilli et al. (2015b) showed that nematodes can colonise hard substrates such as slate and wood panels. Depending on the period time of colonisation, abundance of nematode can be influence by the type of substrate and hydrothermal activity (Zeppilli et al. 2015b).

Meiofauna diversity patterns have also been investigated at different habitats (Gambi and Danovaro 2006, Danovaro et al. 2010a, Ramirez-Llodra et al. 2010). In contrast to abundance patterns, diversity is generally lower in canyons (Garcia et al. 2007, Bianchelli et al. 2008, Ingels et al. 2009, Van Gaever et al. 2009a) and seamounts (Pusceddu et al. 2009) compared to adjacent slope habitat. However, Ingels et al. (2011b) found a different pattern at Gollum Channel and Whittard

Canyon, where these canyons harboured high nematode diversity relative to nearby slope environments, whilst Danovaro et al. (2009) found that meiofauna and nematode diversity did not display significant differences between canyons and slope habitats within the same region. Comparable levels of nematode diversity between seamount and non-seamount sites was also observed in other studies (Zeppilli et al. 2013, Covazzi Harriague et al. 2014, Zeppilli et al. 2014). Habitat-related patterns in diversity may thus depend on which canyon or seamount is investigated, and where samples are obtained within these features, because canyons and seamounts are influenced by varying local hydrodynamic regimes, which affect sedimentation processes and the distribution of food resources (de Stigter et al. 2007, Bongiorni et al. 2013).

Meiofaunal diversity can be high at cold seep habitats compared to adjacent non-seep areas, a pattern that has been linked with the high micro-habitat heterogeneity and structural complexity of seeps (Zeppilli et al. 2011). However, other studies have found that low meiofauna diversity at seeps compared to non-seep sites may be more typical (Van Gaever et al. 2006, Van Gaever et al. 2009a, Zeppilli et al. 2012, Lampadariou et al. 2013). Extreme environmental conditions at seeps (i.e. presence of the gas in the sediment) can be hostile to a large fraction of meiofaunal taxa, and only certain taxa can tolerate and dominate seep habitats, such as nematodes belonging to the genera *Halomonhystera* and *Terschellingia* (Van Gaever et al. 2009b, Zeppilli et al. 2012). Meiofaunal diversity in hydrothermal vents has also been observed to be lower than at non-vents habitats, with only taxa capable of tolerating reduced chemical compounds and low oxygen dominating the low diversity vent communities (Vanreusel et al. 1997, Copley et al. 2007, Vanreusel et al. 2010a, Setoguchi et al. 2014).

Patterns of meiofaunal community structure are often highly variable between different habitats. Canyon communities can be highly distinct from slope communities because certain taxa can be exclusively present in canyons (i.e. Tanaidaceans) while others can be confined to the adjacent open slopes (i.e. priapulids) (Soltwedel et al. 2005, Van Gaever et al. 2009a, Bianchelli et al. 2010). Nematode communities have also been observed to be distinct between canyon and adjacent slope, with certain genera dominating canyon habitats compared to slope (Garcia et al. 2007, Ingels et al. 2009, Van Gaever et al. 2009a, Vanreusel et al. 2010b, Ingels et al. 2011a). For example, deposit-feeding species of the nematode genus *Sabatieria* can thrive in disturbed environments and near anoxic muddy sediments, conditions which may characterise canyon habitats with a complex hydrodynamic regime, and high sediment transport and organic matter accumulation rates. Canyon communities can also be characterised by high abundances of predatory/scavenging nematodes (e.g. *Sphaerolaimus*, *Pomponema*) which are typically associated with sediments with relatively large amounts of organic matter (Ingels et al. 2009), or 'chemosynthetic' *Astomonema* nematodes which indicate the presence of reduced environments (Ingels et al. 2011b). However, nematode community structure in canyons can also be similar to that of the adjacent slope (Danovaro et al. 2009, Ingels et al. 2013), indicating relatively similar environmental conditions between the two habitats (Ingels et al. 2009). Seamounts can harbour a distinct nematode community compared to non-seamount sites; for example, nematodes with a coarse ornamented cuticle (e.g. *Desmoscolex, Desmodora*, *Richtersia*, *Ceramonema*, Epsilonematidae, Draconematidae), whilst generally not abundant in bathyal sediments, can dominate seamount sites (Pusceddu et al. 2009, Vanreusel et al. 2010b, Zeppilli et al. 2014). A thick, coarsely ornamented cuticle may provide protection from physical damage and/or resuspension in constantly shifting sediments affected by strong hydrodynamic conditions (Raes et al. 2007, Vanreusel et al. 2010b, Zeppilli et al. 2014). Species belonging to the families Enchelididae, Ironidae, and Leptosomatidae have also been found exclusively on seamounts (Palinuro and Marsili seamounts) (Pusceddu et al. 2009). These findings suggest that differences in the biochemical composition of sediment at seamounts favour certain species of nematodes. Particular hydrodynamic conditions (e.g. eddies) that are typically associated with the presence of seamounts, increase the spatial variation in sedimentation processes and may affect the export of material to the deep-sea basin surrounding seamounts, which explain the differences in biochemical composition at seamounts.

Meiofaunal seep communities are generally characterised by high abundances of nematodes and annelids, and by reduced species richness (Van Gaever et al. 2009b). As already noted above, certain structurally complex sub-habitats (i.e. mud volcanoes, pockmarks, etc.) can host an abundance of otherwise rare taxa which can account for the difference in community structure observed between seep and non-seep habitats (Zeppilli et al. 2011, Zeppilli et al. 2012). Nematode species that are reported to dominate seep sediments belong to the genera *Sabatieria*, *Daptonema*, *Halomonhystera*, *Desmodora*, *Terschellingia, Aponema*, and the family Stilbonematinae (Van Gaever et al. 2004, Van Gaever et al. 2006, Van Gaever et al. 2009a, Van Gaever et al. 2009b, Lampadariou et al. 2013). *Sabatieria, Daptonema*, and *Terschellingia* for example, are adapted to sediment with high organic input and can tolerate low oxygen levels, whereas *Halomonhystera* is known to adopt an ovoviviparous reproductive mode as a strategy for protecting offspring from toxic environment conditions (Van Gaever et al. 2006). Species of Stilbonematinae have ectosymbiotic bacteria, which may act as protective layer or detoxification mechanisms against toxic hydrogen sulphide (Tchesunov et al. 2012). Meiofaunal communities at hydrothermal vents show similar patterns of community structure to seep habitats, but at vents the communities are generally composed mainly of nematodes and copepods (Vanreusel et al. 1997, Zekely et al. 2006b, Copley et al. 2007). Setoguchi et al. (2014) showed that nematode community structure differs significantly between vent and non-vent fields around Myojin Knoll. Differences in nematode community structure are typically due to the different abundance of genera between vent and non-vent habitats rather than the presence of unique nematode genera (Copley et al. 2007, Setoguchi et al. 2014). However, it is possible that at the species level there are vent endemic taxa (Copley et al. 2007). *Thalassomonhystera*, a typical bathyal genus and generally associated with low food input, was found to be abundant at vent habitats, which may indicate low food availability locally (Zekely et al. 2006b, Copley et al. 2007, Gollner et al. 2007, Sarrazin et al. 2015). An earlier study by Vanreusel et al. (1997) showed that nematode community structure of hydrothermal vents in the North Fiji Basin did not differ greatly from that of adjacent non-vent habitats at the genus level, although there were differences at the species level.

As well as the environmental differences that can account for differences in meiofaunal communities at the habitat scale, disturbance can also play an important role in structuring meiofaunal communities. Depending on the level of disturbance, meiofauna communities may show negative or no effect from the disturbance at the habitat scale. Where trawling may be targeted at particular habitats, such as canyons, meiofaunal abundance and diversity has been observed to be lower in trawled canyons than the non-trawled slope (Pusceddu et al. 2014a). However, other studies have shown no effect of disturbance at a habitat scale on meiofaunal abundance and diversity, but clear differences in the community structure (Somerfield et al. 2006, Kitahashi et al. 2016). Somerfield et al. (2006), in a study in Kongsfjord Fjord, where the fjord is heavily influenced by sediment deposition disturbance from the discharge of meltwater ice, found a significant difference in community structure with an increasing distance from the source of disturbance at the head of the fjord. Kitahashi et al. (2016) observed differences in meiofaunal community structure before and after the Tohoku earthquake, suggesting that turbidity currents caused by seismic activity may have influenced community structure.

In the New Zealand region, habitat-scale studies on meiofauna have mostly focused on bathymetric gradients on the continental slope (five papers), and two papers have described nematode community patterns between canyon and adjacent slope (Leduc et al. 2012c, Leduc et al. 2014). Meiofaunal abundance generally shows a negative relationship with water depth (350–2600 m) on the Chatham Rise slope (Grove et al. 2006). This pattern was related to different sediment physical and chemical properties which varied along the bathymetric gradients, and was more pronounced at the deepest sites on both the study transects (north and south of the Rise). Different sediment properties at the deepest sites between transects were thought to reflect the difference in productivity between transects (Grove et al. 2006). Pilditch et al. (2015) did not find any significant correlation between meiofauna abundance and water depth on the slope both on Chatham Rise and Challenger Plateau, but this might be explained by the narrow depth range (266–1241 m) used in the study which means that only one habitat was effectively sampled. Meiofaunal abundance at Chatham Rise sites tends to increase from east to west and with increasing distance from the mainland, following the productivity gradient, whereas the reverse longitudinal gradient was observed on Challenger Plateau, which probably also reflects diminishing organic matter fluxes further away from the New Zealand landmass (Pilditch et al. 2015). Higher nematode abundance, but lower species diversity, was observed in Kaikoura Canyon compared to the Chatham Rise (Leduc et al. 2012c, Leduc et al. 2014). High abundance observed in Kaikoura Canyon was attributed to the higher availability of food in Kaikoura Canyon compared to Chatham Rise. While abundance was influenced by food availability in Kaikoura Canyon, lower diversity may be due to increased competitive exclusion rates and challenging biogeochemical conditions such as low oxygen concentrations, which permit only a few species to persist. High dissimilarity of nematode community structure was observed at the habitat-scale in these same studies (Leduc et al. 2012b, Leduc et al. 2014). A difference in community structure between Kaikoura Canyon and Chatham Rise slope was mainly explained by the dominance of taxa such as *Sabatieria pulchra* and *Daptonema* spp. in the canyon (Leduc et al. 2014). Species of the genera *Sabatieria* and *Daptonema* are typically associated with high organic input of sediment and can tolerate low oxygen concentrations, which explains why they can thrive in canyon habitat compared to species of other genera. Nematode community structure was also observed to differ between a cluster of sites on the north-eastern edge of Chatham Rise and the rest of the rise; the community on north-eastern Chatham Rise comprised a highly distinct group of species belonging to the genera *Rhynchonema, Xyala* and *Gonionchus* which were absent everywhere else. This group of genera are generally found in exposed intertidal or subtidal sandy sediments (Vincx and Furstenberg 1988, Ellis et al. 2011), and their presence in deep-sea sediments may related to strong hydrodynamic conditions (inferred by the presence of ripples) and coarse sediment size that were observed at north-eastern Chatham Rise sites, which resemble shallow habitats where these genera usually found.

### 1.2.3 Local scale

Local scale is here defined as studies conducted within macro-habitats, typically over distances of ~0.1–100 m. In this review, a total of twenty-one papers describing patterns at local scales are included, with one study conducted in New Zealand waters (Table 1.1).

Local-scale variability in meiofaunal abundance is typically limited. For example, meiofaunal abundance did not display significant variability at local scales in the studies of Gambi and Danovaro (2006) and Gallucci et al. (2009). Other studies found significant but limited differences in abundance at the local scale (Pusceddu et al. 2009), or differences limited to certain taxa (i.e. nauplii) (Gallucci et al. 2009). The latter finding is probably related to the different locomotory abilities of meiofaunal groups. For example, copepods and nauplii have a higher mobility and can actively emerge into the water column and make use of bottom water flow for locomotion, compared to nematodes which are considered poor swimmers and are likely restricted to smaller areas (Gallucci et al. 2009). However, meiofaunal abundance has been shown to vary substantially at local-scales at seep (Hauquier et al. 2011, Pape et al. 2011) and vent habitats (Vanreusel et al. 1997, Flint et al. 2006). This local-scale variation at seeps was ascribed to variability in sub-habitat and the physical structure of seep habitats, as well as food patchiness and the influence of seepage (in term of pore-water geochemistry) (Hauquier et al. 2011). At vent habitats, temperature differences and food input have been suggested to affect meiofauna abundance variability at local scales (Flint et al. 2006).

Meiofaunal diversity showed no significant variation at local scales in the Mediterranean (Gambi et al. 2014), whereas other studies have found significant differences in diversity in other oceans (Gallucci et al. 2009, Van Gaever et al. 2010). Significant variability in diversity at local scales is thought to be influenced by the presence of food patches on the seafloor (Rice and Lambshead 1994), which are normally associated with elevated meiofauna diversity (Lambshead et al. 2000). High variability in local-scale diversity is also typically observed at cold seep and hydrothermal vent habitats. For example, diversity was higher in the siboglinid worm tube patches than in the *Beggiatoa* bacteria patches at the Håkon Mosby mud volcano (Van Gaever et al. 2010), while nematode genus diversity was lower at *Bathymodiolus* mussel fields near the centre of vents compared to a site located at the margin of a hydrothermal vent (Vanreusel et al. 1997). The well oxygenated surface sediments at siboglinid fields may favour a more diverse nematode community compared to anoxic and sulphidic *Beggiatoa* patches (Van Gaever et al. 2010). Low diversity at other sites in seeps and vents has been related to lower oxygen levels and presence of sulphide, resulting in dominance of single nematode species (Vanreusel et al. 1997, Van Gaever et al. 2010). Flint et al. (2006) found that nematode diversity exhibited low variability at a local scale within a vent habitat; however, this was possibly due to limited variability in environmental conditions.

Nematode community structure can be highly variable at local scales. High dissimilarity was observed in nematode communities of different sub-habitats at cold seeps (*Beggiatoa* mat versus siboglinid worm tubes) (Van Gaever et al. 2010), with *Beggiatoa* sub-habitats dominated by the genera *Halomonhystera* and *Microlaimus*, whereas siboglinid sub-habitats were dominated by *Sabatieria*, *Molgolaimus*, *Metalinhomoeus* and *Dichromadora* (Van Gaever et al. 2010). High dominance of *Halomonhystera disjuncta* at *Beggiatoa* bacteria patches was probably related to their ability to withstand low oxygen levels and the presence of sulphide, which are consider toxic to most other nematode taxa (Van Gaever et al. 2010). A study by Vanreusel et al. (1997) also showed different community structure at local scales within vent habitat, with the genus *Molgolaimus* particularly dominant at a central site within a hydrothermal vent compared to the sites located at the margin of vent. *Molgolaimus* is often common in reduced conditions such as the hypoxic bottom at Kilviken Bay (Hendelberg and Jensen 1993).

Disturbance has been shown to impact on meiofaunal communities at a local scale. A study of a 26-year-old experimental disturbance at an abyssal site targeted for manganese nodule mining showed lower abundance and diversity of nematodes within a dredge track than outside the track (Miljutin et al. 2011). The nematode community structure within the dredge track also differed significantly from that of undisturbed sites outside the track. *Oncholaimus* spp. were more abundant inside than outside of the track; species of the family Oncholaimidae can be very abundant in organically and chemically polluted littoral and shallow water sediments (Lorenzen et al. 1987). The slow rate of nematode recovery following the experimental disturbance is thought to be related to the physical modification of the sediment and slow sedimentation rate at abyssal depths (Miljutin et al. 2011).

In the New Zealand region, only one study has examined meiofauna community patterns at local scales. Grove et al. (2006) found high variation in meiofauna abundance between multicore deployments < 1 km apart at a deep site (2300 m), whereas at a shallower station (450 m), high variability was observed between cores < 1 m apart on individual multicore deployments. The local-scale pattern in abundance at the deep site was suggested to be related to the occasional presence of biogenic structures that act as sediment traps and provide food source for fauna. Food patchiness and selective food intake by meiofauna taxa other than nematodes was proposed to influence local-scale pattern at shallow site, since these taxa contributed to higher variation at this local scale. Patterns of meiofauna diversity and community structure were not examined by Grove et al. (2006).

### 1.2.4 Small scale

Small scale studies are defined as studies conducted over ~1–10 cm. In this review, a total of forty-seven papers have described patterns for meiofauna at small scales, including seven studies conducted in New Zealand waters (Table 1.1).

Small-scale variation in meiofauna communities has been observed at both horizontal (Gallucci et al. 2009) and vertical scales (Vanaverbeke et al. 1997b, Soltwedel et al. 2005, Van Gaever et al. 2006, Ingels et al. 2009). Meiofauna communities show a high degree of variability at small scales compared to other scales (Danovaro et al. 2013, Ingels and Vanreusel 2013), probably because of their smaller size, which means they tend to respond to small-scale variability in environmental conditions within the sediment (Soetaert et al. 1997, Vanreusel et al. 2010b, Ingels et al. 2011a, Ingels et al. 2011b). Compared to vertical scale, information on horizontal small scale variability in the deep-sea sediment is very limited. Horizontally, meiofauna show an aggregated distribution with patches smaller than 10 cm (Gallucci et al. 2009). Nematode patch sizes were generally smaller than 4 $cm^2$ compared to copepods and nauplii that showed patches size between 9–64 $cm^2$ (Gallucci et al. 2009). This differences in patch size between these groups is suggested to be related to their different locomotory abilities:

copepods and nauplii have a higher mobility and can actively emerge into the water column (Thistle et al. 2007), whereas nematodes cannot swim, and their dispersal is mainly through sinusoidal, active movement through the sediment (Giere 2009), and therefore limited to a smaller area. Patch size also differ among nematode species, with larger species typically showing larger patch sizes relative to smaller nematodes with filiform tail and minute buccal cavity. Gallucci et al. (2009) however, found no link between heterogeneity in potential food sources (i.e. phytodetritus and bacterial abundance) and aggregation patterns observed. Other factors such as presence of biogenic structures and biotic interactions may thus be more important in influencing meiofauna aggregation patterns. Vertically, meiofaunal abundance is generally higher in the surface sediment and declines with increasing sediment depth (Vanaverbeke et al. 1997b, Neira et al. 2001, Danovaro et al. 2002, Soltwedel et al. 2005, Van Gaever et al. 2006, Ingels et al. 2009). This pattern is mainly controlled by decreasing food and oxygen availability in subsurface sediments (Vanreusel et al. 1995, Vanaverbeke et al. 1997b, Giere 2009, Moens et al. 2014). Bioturbation by larger fauna also may influence meiofauna abundance pattern in subsurface sediment layers (Lambshead et al. 1995, Moodley et al. 2000) through increased downward transport of food (Heip et al. 2001, Hughes and Gage 2004).

Meiofaunal diversity also shows high variability at small scales within the sediment. Meiofaunal diversity is typically highest in surface sediment and decreases in deeper sediments where nematodes become highly dominant (Ingels et al. 2011b) (Danovaro et al. 2002, Schmidt and Martínez Arbizu 2015), and sometimes become more diverse than in surface sediment (Leduc et al. 2010b). Decline in nematode diversity with increasing sediment depth is mainly controlled by decreasing food availability in subsurface sediment (Moens et al. 2014), where increased food availability has been previously shown to enhance diversity (Lambshead et al. 2000). Local disturbance such as bioturbation activities by larger fauna can transport organic matter to deeper sediment depth, and stimulate biochemical processes along the burrow wall, thus promoting diversity in the subsurface sediment (Kristensen and Kostka 2013). Increased sub-habitat heterogeneity in relation to structural habitats at cold seep and vent habitats (e.g. authigenic carbonate reefs, tests of large agglutinated rhizopods, mussel beds) can result in high horizontal variability in environmental conditions at small scales and with concomitant changes in meiofaunal diversity (Van Gaever et al. 2009b, Vanreusel et al. 2010b). High variability of meiofauna diversity in relation to sub-habitat heterogeneity is evident in seeps (Van Gaever et al. 2004, Levin 2005, Bongiorni et al. 2013, Lampadariou et al. 2013); however, it is unproven for vent habitats since no small-scale study of meiofaunal diversity has been conducted at this habitat.

Meiofaunal community structure shows pronounced and consistent differences between surface and subsurface sediments. Copepods and kinorhynchs are often abundant in the well-oxygenated upper sediment layer, since both these taxa are more sensitive to low oxygen concentrations than nematodes (Vidaković 1984, Grego et al. 2014). Nematodes are more tolerant of low oxygen concentrations (Giere 2009), and certain nematode species (i.e. *Oncholaimus campylocercoides*) can tolerate high sulphide concentrations (Thiermann et al. 2000) typically associated with deeper sediments. Surface nematode communities are often characterised by high abundance of the genera *Acantholaimus*, *Daptonema*, *Desmoscolex*, and *Halalaimus*, whereas *Molgolaimus*, *Sabatieria*, *Sphaerolaimus*, and *Syringolaimus* are generally most abundant in the subsurface sediment (Vanaverbeke et al. 1997b, Leduc et al. 2010b, Leduc et al. 2015). Species of the genus *Sabatieria* are known to be well adapted to fine sediment environments, with high organic input, as well as areas with low oxygen levels and disturbed conditions. *Acantholaimus* has been shown to have restricted colonisation abilities (Lee et al. 2001) and their buccal morphology suggests that members of this taxon may feed on microalgal detritus (they are categorised as epigrowth feeders), which may explain their preference for surface sediment where fresh phytodetritus is likely to be most easily accessible. *Halalaimus*, a widespread deep-sea genus characterised by long and thin body shape, also showed a preference for surface sediments (Vanaverbeke et al. 1997b, De Mesel et al. 2006a, Leduc et al. 2010b, Vanreusel et al. 2010b, Ingels et al. 2011a, Leduc et al. 2015), which may reflect their inability to effectively burrow into more compacted subsurface sediment layers.

Macrofauna can rapidly mix fresh deposited organic matter into sediments, while burrowing megafauna can subduct phytodetritus from surface sediments to greater depths, and facilitate oxygen transport (Hughes and Gage 2004, Kristensen and Kostka 2013). Bioturbation activity can also create micro-habitats (e.g. broken polychaete tubes, sponge debris patches) and a wider range of particle size in the sediments (Etter and Grassle 1992, Zuhlke et al. 1998, Hughes and Gage 2004). All of these factors related to bioturbation have been shown to influence meiofaunal community attributes within the sediment at small scales (Zuhlke et al. 1998, Olafsson 2003, Hughes and Gage 2004). The presence of macro-infauna can also lead to the depletion of shared food sources (Olafsson 2003, Gallucci et al. 2008a), and predation by larger organisms can cause a significant reduction in meiofauna populations (Service et al. 1992, Gallucci et al. 2008a). However, whilst predation can cause reduction in meiofauna abundance, it can also promote diversity at small scales. An experimental study by Gallucci et al. (2008a) in the Arctic showed that excluding megafauna by a cage favoured nematode abundance, but not local diversity. Higher diversity at the control sites was observed compared to cage sites, where the sedimentary environment was more heterogeneous outside the cages, suggesting that megafauna play an important role in creating microhabitats in the sediment, hence promoting species coexistence. Other mechanisms to explain this observed pattern include pre-conditioning of food sources resulting from feeding activities by benthic megafauna that facilitate uptake for other components of the benthic community, such as nematodes (Karlson et al. 2016).

In the New Zealand region, six studies have examined meiofaunal patterns at small scales. A study by Grove et al. (2006) showed that meiofaunal abundance at small scales on the Chatham Rise follows the general pattern of decreasing abundance with increasing sediment depth. Nematode diversity has been observed to be lower in the surface sediment (0–1 cm) compared to subsurface sediment (1–5 cm) in another study (Leduc et al. 2010b). This unusual pattern may be due to the greater volume of the subsurface layer, which would likely include nematodes from a wider range of environmental conditions than the smaller surface sediment samples, thus yielding greater diversity than the surface layer samples (Leduc et al. 2010b). Meiofaunal community structure has also been shown to be significantly different between surface and subsurface sediments. This distinction is because most of the meiofauna groups are found concentrated in the top 1 cm of the sediment, while the deepest sediment layer (3–5 cm) is inhabited almost entirely by nematodes (Grove et al. 2006). Surface and subsurface sediments also are inhabited by different nematode species, where surface sediment is dominated by species belonging to

Desmoscolecidae, *Acantholaimus* and *Linhystera,* whereas subsurface sediment is dominated by species belonging to Comesomatidae, *Laimella*, *Molgolaimus*, *Mudwigglus*, *Sabatieria* and *Sphaerolaimus* (Leduc et al. 2010b, Leduc et al. 2015).

A disturbance experiment by Leduc and Pilditch (2013) showed that nematode abundance in surface sediment (0–1 cm) was significantly lower in disturbed experimental samples than in undisturbed samples, whereas the opposite trend was observed in the deepest sediment layer (3–5 cm). The same disturbance experiment showed nematode diversity to be higher in the two uppermost sediment layers (0–1 and 1–3 cm) than in the deepest layer (3–5 cm) in disturbed samples (Leduc and Pilditch 2013). This pattern is most likely due to the vertical mixing of nematodes between sediment layers as a result of the disturbance, which would lead to vertical homogenisation of species distributions (Leduc and Pilditch 2013). This result suggests that nematode communities are resilient to disturbance, with disturbance causing the movement of nematodes within the sediment column, instead of killing them (Leduc and Pilditch 2013).

## 1.3 Taxonomy of free-living marine nematodes in the New Zealand region

About 6900 species of free-living marine nematode species have been described to date (Appeltans et al. 2012), with only a total of 638 species described from the deep-sea (Miljutin et al. 2010). In New Zealand, the study of marine nematode taxonomy is in the early stages. To date, a total of only 159 species have been recorded or described from the New Zealand region, of which 65 species have been recorded or described since 2000. Of these, 37% (59 species) were recorded from the deep-sea (200–8000 m), mostly from Chatham Rise, Challenger Plateau, and the Kermadec Trench (Leduc 2013d, Leduc 2014, 2015), while the rest were recorded from shallow subtidal and intertidal habitats (Ditlevsen 1921, Allgén 1927, Ditlevsen 1930, Leduc and Gwyther 2008). Shallow-water nematodes have been recorded in association with stranded macroalgae, bryozoans and sponges, as well as sediments (Sudhaus 1974a, b, c) . The species described to date belong to eight orders, thirty families and 100 genera; so far, most of the described species belong to the Comesomatidae (nine genera and 25 species), followed by the Desmodoridae (fourteen genera and 15 species).

Leduc et al. (2012b) estimated that about 1200 nematode species are present on the Chatham Rise and Challenger Plateau at depths of 250–3000 m. Extensive sampling and taxonomic research is required to determine the true extent of nematode biodiversity in the New Zealand region. Nematodes are good indicators of environmental changes (e.g. pollution, disturbance and global changes) (Balsamo et al. 2012, Zeppilli et al. 2015a), as they are highly diverse and show potentially species-specific responses to different environmental stressors (Danovaro et al. 1995, Austen and McEvoy 1997, Mirto et al. 2000). Nematodes are also used in exploring relationships between biodiversity and ecosystem function (Danovaro et al. 2008a), since their feeding types are easily recognizable, making it possible to identify functional diversity traits (Moens and Vincx 1997). Moreover, morphologically similar cryptic species can have different functional traits as they showed different feeding behaviours, which in turn may have important implications for biodiversity-ecosystem function relationships (Derycke et al. 2016). Therefore, by focusing on genus-level information only, a loss of ecological information will inevitably occur.

## 1.4 Conclusion

Deep-sea meiofaunal abundance, diversity, and community structure vary across all spatial scales. Each community attribute can vary at different spatial scales, suggesting that different environmental and biotic processes acting at different scales influence these attributes. Meiofauna community attributes appear to vary most at regional and small scales, but studies have indicated that variation at habitat, local, and small scales are also important. Both environmental and disturbance processes (including those resulting from human activity such as bottom trawling) are important in controlling community distribution patterns. In order to better understand the reasons for the observed patterns in meiofauna community attributes, it is important to increase efforts to describe meiofauna species, particularly ecologically important nematode genera, and to include as many spatial scales in order to compare their relative importance.

## 1.5 Research objectives

This review was carried out to inform and shape the aims of my PhD thesis research. As a consequence of the review, and the samples and data available to me through a particular deep-sea research project, this study was carried out with the following aims and objectives:

1. Determine the influence of environmental parameters and disturbance on meiofauna and nematode community attributes at multiple spatial scales in the New Zealand region, with the objective of understanding what factors most influence meiofauna and nematode communities and how they may be vulnerable to anthropogenic activities.

2. Describe nematode species new to science encountered by recent sampling on the continental margin of New Zealand, with the objective of producing descriptions of species that will ultimately provide additional insight into the ecology of deep-sea meiofauna in the region.

## 1.6 Thesis outline

This thesis has been written as a series of manuscripts ready for submission to scientific journals. Two chapters have already been published. Thus, there is some repetition throughout the thesis, especially in the Introduction and the Method sections, mostly in the closely related Chapters Two and Three. All of the nematode identification, and the majority of meiofaunal taxa identification except for seep samples, all of data analysis, and manuscript preparation were done by myself. Additional contributions by co-authors to the final manuscripts are listed below.

Chapter 1: This introductory chapter reviews the development of deep-sea meiofauna studies and provides the thesis aims.

The review component of this chapter has been prepared for submission to Marine Biodiversity journal.

Chapter 2: This chapter has been published as a scientific paper and describes meiofauna community patterns and their relationship with environmental variables.

“**Differences in meiofauna communities with sediment depth are greater than habitat effects on the New Zealand continental margin: implications for vulnerability to anthropogenic disturbance**”

Rosli, N., Leduc, D., Rowden, A. A., Clark, M. R., Probert, P. K., Berkenbusch, K., and Neira, C. 2016. PeerJ 4:e2154.

- Daniel Leduc: provided material and analysis tools, guidance on the statistical analysis and reviewed drafts of the manuscript.
- Ashley A Rowden: involvement in the survey design and data collection and reviewed drafts of the manuscript.
- Malcolm R Clark: involvement in the survey design and data collection and reviewed final drafts of the manuscript.
- P Keith Probert: provided material and analysis tools, and reviewed drafts of the manuscript.
- Katrin Berkenbusch: processed a subset of samples and reviewed final drafts of the manuscript.
- Carlos Neira: reviewed final drafts of the manuscript.

Chapter 3: This chapter describes nematodes community patterns and their relationship with environmental variables. This chapter has been submitted for review to Progress in Oceanography journal.

“**Marked differences in deep-sea nematode communities between regions and sediment depths, but not habitats: implications for vulnerability to disturbance”**

Norliana Rosli, Daniel Leduc, Ashley A. Rowden, P. Keith Probert, Malcolm R. Clark

- Daniel Leduc: provided material and analysis tools, guidance on the statistical analysis and reviewed drafts of the manuscript.
- Ashley A Rowden: involvement in the survey design and data collection and reviewed drafts of the manuscript.
- P Keith Probert: provided material and analysis tools, and reviewed drafts of the manuscript.
- Malcolm R Clark: involvement in the survey design and data collection and reviewed final drafts of the manuscript.

Chapter 4: This chapter is a modified version of a published paper, which describes new nematode species and the status of nematode taxonomy studies in New Zealand.

“**Two new species and a new record of Comesomatidae (Nematoda, Araeolaimida) from Southern Hikurangi Margin, New Zealand**”

Rosli, N., Leduc, D., and Probert, P. K. (2014). Zootaxa 3900:505–525.

- Daniel Leduc: provided guidance on the nematode taxonomy identification and reviewed drafts of the manuscript.
- P Keith Probert: reviewed drafts of the manuscript.

Chapter 5: This is a conclusions chapter, which summarises the main findings and their significance.

# Chapter 2

# Differences in meiofauna communities with sediment depth are greater than habitat effects on the New Zealand continental margin: implications for vulnerability to anthropogenic disturbance

The ecological information in this chapter has been published in the following paper:

Rosli, N., Leduc, D., Rowden, A. A., Clark, M. R., Probert, P. K., Berkenbusch, K., and Neira, C. 2016. Differences in meiofauna communities with sediment depth are greater than habitat effects on the New Zealand continental margin: implications for vulnerability to anthropogenic disturbance. PeerJ 4:e2154.

## 2.1 Abstract

Studies of deep-sea benthic communities have largely focused on particular (macro) habitats in isolation, with few studies considering multiple habitats simultaneously in a comparable manner. Compared to mega-epifauna and macrofauna, much less is known about habitat-related variation in meiofaunal community attributes (abundance, diversity and community structure). Here, we investigated meiofaunal community attributes in slope, canyon, seamount, and seep habitats in two regions on the continental slope of New Zealand (Hikurangi Margin and Bay of Plenty) at four water depths (700, 1000, 1200 and 1500 m). We found that patterns were not the same for each community attribute. Significant differences in abundance were consistent across regions, habitats, water and sediment depths, while diversity and community structure only differed between sediment depths. Abundance was higher in canyon and seep habitats compared with other habitats, while between sediment layer, abundance and diversity were higher at the sediment surface. Our findings suggest that meiofaunal community attributes are affected by environmental factors that operate on micro- (cm) to meso- (0.1–10 km), and regional scales (>100 km). We also found a weak, but significant, correlation between trawling intensity and surface sediment diversity. Overall, our results indicate that variability in meiofaunal communities was greater at small scale than at habitat or regional scale. These findings provide new insights into the factors controlling meiofauna in these deep-sea habitats and their potential vulnerability to anthropogenic activities.

## 2.2 Introduction

Continental margins comprise a variety of topographically-defined habitats such as canyons, seamounts and slopes, as well as chemically-defined habitats such as cold seeps and hydrothermal vents (Levin et al. 2010). Canyons are complex topographic features that influence local hydrodynamic regimes, and thus sediment transport and accumulation (García et al. 2008). The resulting changes in physico-chemical characteristics and organic enrichment in the sediments have been linked to high variation in infaunal benthic community structure (Baguley et al. 2006a, de Stigter et al. 2007, García et al. 2008, Romano et al. 2013). Seamounts, which are defined as elevated features that include knolls, pinnacles and hills where the elevation can be as low as 100 m (Pitcher et al. 2007, Clark et al. 2010), can affect surrounding flow conditions resulting in enhanced currents, eddies, up- and down-welling and closed retention cells (White et al. 2007, Bashmachnikov et al. 2013). These modified flow conditions increase vertical mixing, spatial variation in sedimentation processes, and the distribution of food resources (Levin and Dibacco 1995, Bongiorni et al. 2013, Zeppilli et al. 2013). These and other factors can result in distinct benthic communities on seamounts (Bongiorni et al. 2013, Zeppilli et al. 2014). Cold seeps are characterised by the flow of reduced chemical compounds (e.g. methane, sulphur) from the subsurface to the seafloor (Levin 2005, Van Gaever et al. 2009a, Lampadariou et al. 2013). The emission of reduced fluids results in a broad range of geological and sedimentary structures (e.g. gas seepage, microbial mat, pockmarks) (Judd et al. 2002, Levin 2005), which increase small-scale variability in the sediment, thus providing a variety of habitats for infauna that differ from ‘background’ habitats (Levin and Mendoza 2007). Hydrothermal vents are localized areas of the seabed where heated and chemically modified seawater exits the seafloor as diffuse or focused flow (Van Dover 2014). Vent ecosystems are typically dominated by benthic invertebrate taxa that host symbiotic, chemoautotrophic microorganisms, and the infauna of hydrothermally ‘active’ sediments has been shown to differ from that of ‘inactive’ sediments (Levin et al. 2009).

Meiofauna are the most abundant infauna in deep-sea sediments, with nematodes being the most abundant taxon (Heip et al. 1985, Vanreusel et al. 2010b). Studies of meiofaunal communities in the deep sea have focused on canyon and adjacent slope habitats (Soetaert and Heip 1995, Soltwedel et al. 2005, Bianchelli et al. 2008, Danovaro et al. 2009), and few comparative studies have included seamount (Zeppilli et al. 2013) or cold seep habitats (Robinson et al. 2004, Pape et al. 2011). Vanreusel et al. (2010b) provided the first comprehensive comparison of nematode communities among multiple deep-sea habitats (e.g. canyon, seamounts, seep and vent), and showed that different habitats harbour distinct nematode communities and therefore contribute to overall deep-sea nematode diversity.

Although our understanding of meiofaunal community structure of deep-sea habitats is growing, there is remaining uncertainty as meiofauna are not considered in a number of biodiversity studies and are generally poorly studied (particularly in the deep sea) compared to larger macrofauna (Zeppilli et al. 2015a). In addition, a more rigorous test of habitat effects on meiofaunal communities requires comparisons that avoid the potential influence of geographical distance on community patterns. Knowledge of meiofaunal distribution and connectivity between different habitats is essential for understanding ecological processes, and for assessing the vulnerability of benthic communities to anthropogenic disturbance. There have been concerns about the potential threats of anthropogenic activities on the diversity and function of deep-sea ecosystems (Ramirez-Llodra et al. 2011, Pusceddu et al. 2014a, Van Dover 2014), as technological advances make these habitats more accessible (Benn et al. 2010, Levin and Sibuet 2012). For example, industrial fisheries are expanding and moving into deeper waters (Pitcher et al. 2010, Pusceddu et al. 2014a), and seabed mining in the deep sea is expected to begin in the near future (Hein et al. 2013, Ramirez-Llodra et al. 2015).

Physical disruption of habitat by bottom trawling can have pronounced effects on deep-sea soft sediment communities (Pusceddu et al. 2014a). Trawling generally has a negative impact on macro-infaunal communities (Hansson et al. 2000, Hinz et al. 2009), whereas studies of meiofauna reveal inconsistent results. To date, studies from shallow water habitats suggest that trawling may have a positive (Pranovi et al. 2000, Liu et al. 2011), negative (Schratzberger and Jennings 2002, Hinz et al. 2008), or only minor impact (Schratzberger et al. 2002, Lampadariou et al. 2005, Liu et al. 2009) on meiofaunal communities. The only meiofaunal study conducted in the deep-sea (Pusceddu et al. 2014a) showed a negative effect of trawling on meiofaunal communities. Meiofauna, and nematodes in particular, are generally considered to be more resilient to physical disturbance than larger organisms because they are less likely to be killed and can recover more quickly (Schratzberger et al. 2002, Whomersley et al. 2009, Leduc and Pilditch 2013). Nevertheless, bottom trawling can also have indirect impacts on sediment communities through the modification of sediment physical characteristics and distribution of organic matter, which can lead to potentially long-term changes in benthic communities (Martín et al. 2014, Pusceddu et al. 2014a).

Because of their smaller size, meiofauna tend to respond to micro-scale (cm) variability of environmental conditions in surface and subsurface sediment layers (Soetaert et al. 1997, Ingels et al. 2011a, Ingels et al. 2011b). Ingels and Vanreusel (2013) showed that most of the variability in nematode community structure occurs at micro (cm) rather than larger spatial scales (10–100 km). Decline in meiofaunal densities with sediment depth is probably the most pervasive gradient observed in marine sediments (Vanaverbeke et al. 1997b, Soltwedel et al. 2005, Van Gaever et al. 2006, Ingels et al. 2009), with the vertical distribution of meiofauna in the sediments mainly controlled by decreasing food and oxygen availability in subsurface sediments (Vanreusel et al. 1995, Vanaverbeke et al. 1997b, Giere 2009, Moens et al. 2014). Meiofaunal diversity is typically highest in surface sediment and decreases in deeper sediments where nematodes become dominant (Danovaro et al. 2002, Schmidt and Martínez Arbizu 2015). The more abundant and diverse meiofaunal communities of surface sediments are more exposed to disturbance than subsurface communities, and may therefore be affected more by physical disturbance. Studies aiming to uncover the processes driving the composition of deep-sea meiofaunal communities, including potential physical disturbance, should therefore include examination of variation at these smaller scales.

The main objectives of this study were to: (1) compare meiofaunal community attributes (abundance, diversity and community structure) in surface (0–1 cm) and subsurface (1–5 cm) sediment layers among deep-sea habitats; (2) describe relationships between environmental variables (i.e., water depth, sediment characteristics, topography, food availability), bottom trawling and community attributes of meiofaunal communities; (3) assess the relative vulnerability of meiofaunal communities among habitats, and between surface and subsurface sediment layers.

## 2.3 Material and Methods

### 2.3.1 Study area and sampling design

The study area comprised two regions: Hikurangi Margin and Bay of Plenty of New Zealand (Figure 2.1). These two regions were selected because each encompasses a range of benthic habitats within a restricted geographic area, thus facilitating comparisons between associated faunas that were not confounded by distance. The Hikurangi Margin study region is located to the north-east of the South Island, hosts many submarine canyons on its continental slope, and also includes other deep-sea habitats such as seamounts, and cold seeps (Mountjoy et al. 2009, Ruff et al. 2013). The Bay of Plenty study region, located to the north-east of North Island, also includes slope, canyon and seamount habitats, with hydrothermal vents on some seamounts (Wysoczanski and Clark 2012). The Hikurangi Margin hosts significant fisheries, including hoki (*Macruronus novaezelandiae*), alfonsino (*Beryx splendens*) and orange roughy (*Hoplostethus altanticus*) which occur across all habitats (Clark 1995). This area is also of potential interest for drilling gas hydrate deposits (Pecher and Henrys 2003). The Bay of Plenty region is subject to some deep-sea trawl fisheries, including orange roughy, black cardinal fish (*Epigonus telescopus*) and alfonsino (*Beryx decadactylus*) (Clark and O'Driscoll 2003), and is of potential interest for mining of seafloor massive sulphide deposits (Boschen et al. 2013).

Sampling sites have been previously described by Bowden et al. (2016). Sampling was conducted at slope, canyon and seamount sites from RV *Tangaroa* during National Institute of Water and Atmospheric Research (NIWA) voyage TAN1004 (April 2010) on the Hikurangi Margin, and voyage TAN1206 (April 2012) in the Bay of Plenty (Figure 2.1). The samples were collected under Special Permit (542) issued by the Ministry for Primary Industries pursuant to section 97(1) of the Fisheries Act 1996. Fishing intensity was included as a variable in the analysis (see below) to account for the possible influence of anthropogenic disturbance on the main analysis. Trawl effort data for the period July 1980 to March 2011 were sourced from the trawl database of the New Zealand Ministry for Primary Industries. Sampling was undertaken at four water depth strata (700, 1000, 1200 and 1500 m) at each habitat site to incorporate the effects of water depth in the statistical analyses and provide a more robust evaluation of any habitat effect on community structure. At Hikurangi Margin, meiofauna could not be sampled at some sites/depths, whereas in Bay of Plenty, the limited occurrence of soft sediment prevented the sampling on seamount and vent habitats. The limited data from these sites were not included in the analysis (Table 2.1). At each sampling station, a towed video camera frame was deployed along transects to ascertain the type of substratum and benthic megafauna before the water column and seafloor was disturbed by sampling gear. Deployment of the multicorer, which targeted soft sediment substrates, was directed based on information from multibeam echo-sounder (MBES) bathymetric maps and observations from the video transects.

Meiofauna samples from seep habitats in the Hikurangi Margin at two sites geographically close to the other habitats sites were obtained from a previous survey in 2006 (voyage TAN0616) (Table 2.1), and were used in a second-stage analysis comparing seep, canyon, seamount, and slope communities (see below).

Macrofaunal and mega-epifaunal communities were also sampled using towed cameras, corers, trawls, and epibenthic sled at the same depth strata at each habitat during the two main surveys, and the results of the analyses of data for these components of the benthos have and will be reported elsewhere (Bowden et al. 2016, Leduc et al. 2016b). Data on meiofauna are reported here for the first time.

### 2.3.2 Sampling and sample processing

Meiofauna and sediment samples were collected using an Ocean Instruments MC-800A multicorer (internal diameter core = 9.52 cm). At each station, one to three cores were used from each multicorer deployment for meiofaunal samples (refer Table 2.1), and one core for a sediment sample. Each meiofaunal core consisted of a subcore (26 mm internal diameter), was sliced into three vertical fractions: 0–1 cm, 1–3 cm and 3–5 cm sediment depth layers and preserved in 10% buffered formalin. Previous analysis showed there was no significant difference between 1–3 cm and 3–5 cm layers, therefore these layers were combined prior to sieving. Samples were rinsed on a 1 mm mesh sieve to remove macrofauna and on a 45 µm mesh to retain meiofauna. Meiofauna were extracted from the sieved sediment by Ludox flotation (Somerfield and Warwick 1996) and were identified to main taxa (e.g. nematodes, nauplii, copepods, annelids) (Higgins and Thiel 1988) under a stereomicroscope.

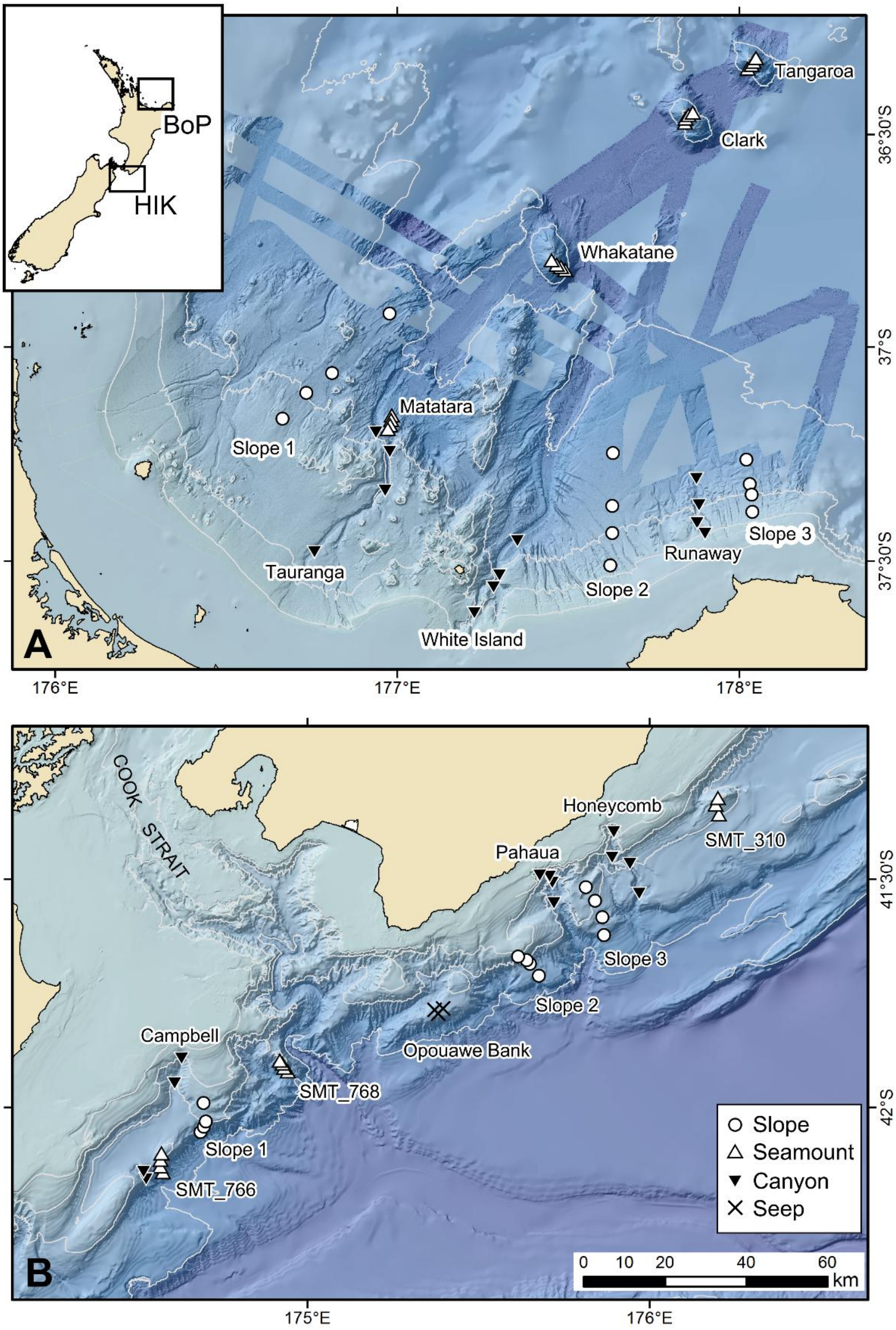

Figure 2.1. Map showing sampling sites and stations in the Bay of Plenty (BoP (A)) and Hikurangi Margin (HIK (B)) study regions and their relative locations in New Zealand (inset). Scale bar applies to both regional maps. Not all sites and stations could be sampled in the present study. Refer to Table 2.1 for a list of sites and stations where meiofaunal samples were obtained. The blue strips in the top panel show multibeam lines where bathymetry is more detailed than the underlying pale blue. Isobaths show 200, 500, 1000, and 2000 m depths.

The following physical and biogeochemical parameters were determined from the sediment samples: mean particle size (geometric), sorting, skewness, kurtosis, %silt/clay, particle size diversity (PSD; calculated using Shannon-Wiener diversity index of eleven particle size classes (after Etter and Grassle 1992)), calcium carbonate content (%$CaCO_3$), organic matter content (%OM), organic carbon content (%OC), nitrogen content (%N), chlorophyll *a* concentration (chl *a*) and phaeopigment concentration (phaeo) using methods described by (Nodder et al. (2003), Grove et al. (2006), Nodder et al. (2007)). The %$CaCO_3$ was determined from the top 5 cm of sediment, whereas organic matter (%OM, %OC and %N) was determined from the top 1 cm of sediment.

### 2.3.3 Additional environmental characterisation

The environmental data used in the present study were first published in Bowden et al. (2016). Surface water chlorophyll concentrations were determined using ocean colour estimates of surface chlorophyll concentrations as a proxy for long-term inter-station variability in primary production (NASA SeaWiFS Project: http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/8Day/9km/chlor_a). The 9 km composited data of surface chlorophyll were further composited to 90 × 90 km pixels centred on the location of each sample station. The mean value for the 1997–2010 period was computed for each station.

Seafloor habitats at the study sites were characterised using seafloor morphology derivatives from MBES data gridded at 25 m resolution. The following topographic variables were derived for each sampling station: depth, slope (steepest gradient to any neighbouring cell), curvature (change of slope), plan curvature (curvature of the surface perpendicular to the slope direction), and profile curvature

(curvature of the surface in the direction of slope) (see Appendix A). A further set of derivatives was calculated for the standard deviation of depth, depth range, standard deviation of the slope (a proxy measure for slope roughness), and terrain rugosity based on a 3, 5, 7, and 15 grid cell focal means. A total of eighteen topographic variables were used in the analysis. Methods for the determined topographic variables are provided by Nodder et al. (2013).

Trawl effort data were used to quantify the extent of commercial fishing intensity conducted on the seafloor in the study regions. Estimates of fishing intensity for a 5 km x 5 km cell grid covering the New Zealand Exclusive Economic Zone were derived using the number of tows and an estimate of swept area derived from the trawl width and either the distance between start and finish positions, or the tow duration (Black and Wood 2014). Fishing intensity at each of the study stations was estimated for the total trawled area within the corresponding 5 km x 5 km cell integrated over a period of ten years prior to sampling.

Table 2.1. List of sampling sites for Hikurangi Margin (TAN1004) and Bay of Plenty (TAN1206) (see Bowden et al. (2016)). Full names for named features are: Campbell Canyon, Honeycomb Canyon, Pahaua Canyon, Tauranga Canyon, White Island Canyon and Runaway Sea Valley. Unnamed seamount features are labelled according to the registration number of NIWA New Zealand seamounts database (e.g. 'SMT_310'). N = number of cores.

| Region | Voyage | Sampling date | Habitat | Site | Strata | Station | Depth (m) | Latitude (S) | Longitude (E) | N |
|---|---|---|---|---|---|---|---|---|---|---|
| Hikurangi Margin | TAN1004 | April 2010 | Slope | 1 | 700 | 124 | 690 | 41.9857 | 174.6982 | 2 |
| | | | | | 1500 | 128 | 1420 | 42.0485 | 174.7000 | 1 |
| | | | | 2 | 1000 | 4 | 1046 | 41.6837 | 175.6642 | 3 |
| | | | | | 1200 | 76 | 1282 | 41.6833 | 175.6500 | 2 |
| | | | | | 1500 | 10 | 1561 | 41.7170 | 175.6748 | 2 |
| | | | | 3 | 700 | 44 | 728 | 41.5258 | 175.8003 | 3 |
| | | | | | 1000 | 41 | 942 | 41.5475 | 175.8398 | 3 |
| | | | | | 1200 | 38 | 1121 | 41.5937 | 175.8532 | 3 |
| | | | | | 1500 | 17 | 1514 | 41.6288 | 175.8682 | 2 |
| | | | | | 1500 | 19 | 1553 | 41.6270 | 175.8637 | 1 |
| | | | Canyon | Pahaua | 700 | 31 | 730 | 41.4962 | 175.6828 | 3 |
| | | | | | 1000 | 27 | 1013 | 41.4983 | 175.7043 | 3 |
| | | | | | 1200 | 22 | 1188 | 41.5100 | 175.7187 | 3 |
| | | | | | 1500 | 12 | 1350 | 41.5508 | 175.7250 | 3 |
| | | | | Honeycomb | 700 | 58 | 670 | 41.4080 | 175.8977 | 3 |
| | | | | | 1000 | 53 | 948 | 41.4563 | 175.8970 | 1 |
| | | | | | 1200 | 62 | 1171 | 41.4760 | 175.9477 | 3 |
| | | | | Campbell | 700 | 92 | 683 | 41.8922 | 174.6347 | 2 |
| | | | | | 1000 | 97 | 1011 | 41.9458 | 174.6173 | 1 |
| | | | | | 1000 | 98 | 1012 | 41.9277 | 174.6165 | 2 |
| | | | | | 1200 | 127 | 1177 | 42.1228 | 174.5397 | 1 |

| Region | Voyage | Sampling date | Habitat | Site | Strata | Station | Depth (m) | Latitude (S) | Longitude (E) | N |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 1500 | 126 | 1495 | 42.1422 | 174.5492 | 3 |
| | | | Seamount | 310 | 700 | 69 | 670 | 41.3353 | 176.1882 | 3 |
| | | | | | 1000 | 72 | 985 | 41.3657 | 176.1958 | 3 |
| | | | | 766 | 1000 | 130 | 894 | 42.1363 | 174.5737 | 1 |
| | | | | | 1500 | 129 | 1456 | 42.1345 | 174.5860 | 1 |
| | | | | | 1500 | 132 | 1453 | 42.1345 | 174.5850 | 1 |
| South Tower | TAN0616 | Nov 2006 | Seep | Opouawe Bank | 1000 | 84 | 1053 | 41.7832 | 175.4007 | 2 |
| | | | | | 1000 | 86 | 1050 | 41.782 | 175.402 | 2 |
| | | | | | 1000 | 116 | 1049 | 41.7885 | 175.4075 | 2 |
| | | | | | 1000 | 118 | 1051 | 41.7893 | 175.4072 | 2 |
| North Tower | | | | | 1000 | 112 | 1054 | 41.0782 | 175.4013 | 2 |
| | | | | | 1000 | 123 | 1051 | 41.079 | 175.4075 | 2 |
| Bay of Plenty | TAN1206 | April 2012 | Slope | 1 | 700 | 2 | 699 | 37 ° 10.14 | 176 ° 39.58 | 3 |
| | | | | | 1000 | 5 | 998 | 37 ° 06.74 | 176 ° 43.86 | 3 |
| | | | | | 1200 | 9 | 1193 | 37 ° 03.48 | 176 ° 48.38 | 3 |
| | | | | | 1500 | 13 | 1501 | 37 ° 55.35 | 176 ° 58.74 | 3 |
| | | | | 2 | 700 | 52 | 710 | 37 ° 30.26 | 177 ° 37.19 | 3 |
| | | | | | 1000 | 49 | 1004 | 37 ° 25.90 | 177 ° 37.55 | 3 |
| | | | | | 1200 | 44 | 1202 | 37 ° 21.95 | 177 ° 37.57 | 3 |
| | | | | | 1500 | 42 | 1501 | 37 ° 14.50 | 177 ° 37.86 | 3 |
| | | | | 3 | 700 | 185 | 726 | 37 ° 22.84 | 178 ° 01.92 | 3 |
| | | | | | 1000 | 181 | 998 | 37 ° 20.56 | 178 ° 01.71 | 3 |
| | | | | | 1200 | 178 | 1196 | 37 ° 19.01 | 178 ° 01.42 | 3 |
| | | | | | 1500 | 175 | 1494 | 37 ° 15.66 | 178 ° 00.23 | 3 |
| | | | Canyon | Tauranga | 700 | 125 | 697 | 37 ° 28.48 | 176 ° 45.51 | 3 |

| Region | Voyage | Sampling date | Habitat | Site | Strata | Station | Depth (m) | Latitude (S) | Longitude (E) | N |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | 1000 | 118 | 1083 | 37 ° 20.00 | 176 ° 57.72 | 3 |
| | | | | | 1200 | 111 | 1221 | 37 ° 15.05 | 176 ° 58.02 | 2 |
| | | | | | 1200 | 113 | 1222 | 37 ° 15.06 | 176 ° 57.98 | 1 |
| | | | | | 1500 | 105 | 1486 | 37 ° 11.35 | 176 ° 56.59 | 3 |
| | | | | White Island | 700 | 154 | 700 | 37 ° 37.05 | 177 ° 13.46 | 1 |
| | | | | | 700 | 155 | 704 | 37 ° 37.04 | 177 ° 13.48 | 2 |
| | | | | | 1000 | 150 | 1017 | 37 ° 33.14 | 177 ° 16.21 | 1 |
| | | | | | 1000 | 151 | 1023 | 37 ° 33.20 | 177 ° 16.10 | 1 |
| | | | | | 1000 | 152 | 1031 | 37 ° 33.17 | 177 ° 16.05 | 1 |
| | | | | | 1200 | 142 | 1200 | 37 ° 31.75 | 177 ° 17.71 | 1 |
| | | | | | 1200 | 143 | 1202 | 37 ° 31.77 | 177 ° 17.69 | 2 |
| | | | | | 1500 | 135 | 1523 | 37 ° 26.59 | 177 ° 21.05 | 3 |
| | | | | Runaway | 700 | 55 | 705 | 37 ° 25.85 | 177 ° 53.62 | 3 |
| | | | | | 1000 | 60 | 900 | 37 ° 24.17 | 177 ° 52.65 | 2 |
| | | | | | 1000 | 61 | 870 | 37 ° 24.20 | 177 ° 52.67 | 1 |
| | | | | | 1200 | 65 | 1254 | 37 ° 21.86 | 177 ° 52.59 | 1 |
| | | | | | 1200 | 66 | 1254 | 37 ° 21.86 | 177 ° 52.59 | 2 |
| | | | | | 1500 | 70 | 1518 | 37 ° 18.13 | 177 ° 52.27 | 3 |

### 2.3.4 Statistical analysis

Statistical analyses were conducted to test the following main hypotheses: that there is no difference in meiofaunal community attributes (abundance, diversity and community structure) in surface (0–1 cm) and subsurface (1–5 cm) sediment layers among deep-sea habitats, water depths, and between regions, and that there is no relationship between bottom trawling or environmental variables and meiofaunal community attributes.

Analyses of meiofaunal community attributes (abundance, diversity, and community structure) were conducted using statistical routines in the multivariate software package PRIMER v6 with PERMANOVA (Clarke and Gorley 2006, Anderson et al. 2008). Meiofaunal taxon richness was used as the measure of meiofaunal diversity. All analyses were conducted on individual core data. Gamma diversity was calculated as the total diversity of the entire region.

Analysis of community structure was based on fourth-root transformed abundance data (abundance data per core at each station). Fourth-root transformation was used to reduce contributions to similarity by the numerically dominant nematodes (Somerfield and Clarke 1995). Similarity matrices for the community structure analysis were built using Bray-Curtis similarity (Clarke and Gorley 2006). Similarity matrices for meiofauna abundance and diversity were based on Euclidean distance similarity matrices of untransformed data.

The PERMANOVA routine in PRIMER was used to investigate the relative influences of survey region, habitat, water depth strata and sediment depth on community attributes (Anderson et al. 2008). Preliminary analysis showed a significant difference in the abundance of meiofauna between the two regions. Therefore, in addition to a single-factor test for the effect of region (Hikurangi Margin versus Bay of Plenty), and to avoid an overriding influence of abundance on patterns of community structure, analysis testing for the effects of habitat, water depth, and sediment depth were conducted for each region separately. Data were analysed using a four-factor design, with the factors habitat (fixed; canyon, seamount, slope), water depth (fixed; 700, 1000, 1200, 1500 m), sediment depth (fixed; 0–1 and 1–5 cm), and cores (random, nested within habitat and water depth strata). P-values for individual predictor variables were obtained using 9999 permutations. Lack of independence between stations due to geographical proximity (i.e. spatial autocorrelation/structure) is common in natural communities and poses limitations for the interpretation of ecological patterns (Legendre 1993). In particular, failure to take into account the spatial component of ecological variation may affect tests of statistical significance when investigating relationships between community structure and environmental parameters (Legendre and Troussellier 1988). Therefore, latitude and longitude were fitted first in the models of community structure to account for the effect of geographical proximity. The main factor test was followed by pair-wise tests when significant effects were found. The square-root value of estimates of components of variation (√ECV) was used to compare the relative strengths of significant factor effects. A non-metric multi-dimensional scaling plot (MDS) was used to visualise patterns in multivariate community structure. The SIMPER routine was used to identify which taxa were responsible for any habitat (i.e. beta diversity = measure of community similarity between habitats), region, water depth strata and/or sediment-related differences in community structure. SIMPER was also used to identify the main environmental variables responsible for differences between regions. This analysis was conducted on similarity matrices built using normalised environmental data and the Euclidean similarity measure; topographical variables were not included because slope, canyon, and seamount habitats are defined *a priori* as topographical features.

The DistLM routine was used to investigate the relationship between meiofaunal community attributes and environmental variables. The full set of environmental variables was partitioned into five sets, i.e., spatial (water depth), sediment characteristics (mean particle size, sorting, skewness, kurtosis, %silt/clay, PSD, %$CaCO_3$, %OM, %N, %OC, chl *a*, phaeopigment), primary productivity (surface chlorophyll concentration), fishing intensity, and topography variables (18 variables). Environmental variables that were strongly correlated ($r > 0.8$) were removed prior to analysis (Appendix B). Relationships between environmental parameters and community attributes were initially examined by analysing each predictor separately (marginal tests). Partial regressions were used to better characterise the relationships and to account for the effect of the remaining variables. Sequential tests were conducted using step-wise selection procedures and $R^2$ as the selection criterion. Latitude and longitude were fitted first in the models of community structure to account for the effect of geographical proximity. P-values for individual predictor variables were obtained using 9999 permutations.

Meiofaunal community data from slope, canyon, and seamount habitats in Hikurangi Margin (from TAN1004) were compared to those for seep meiofauna in a second-stage analysis. Stations from the two seep sites were available from 1049–1059 m water depths (Table 2.1), thus only data from the depth strata of, and closest in depth to, these sites were included in the analysis (i.e. the 1500 m stratum was excluded). The effects of habitat and sediment depth on meiofaunal community attributes were compared using PERMANOVA. MDS and SIMPER routines were conducted as described above.

## 2.4 Results

In total, fifteen meiofaunal taxa were identified from the samples. The most abundant taxon was nematodes (87.1% of total abundance), followed by copepods (6.0%), nauplii (4.2%) and annelids (1.4%). The abundance of each of the remaining taxa (e.g. ostracods, kinorhynchs, isopods, tanaidaceans, amphipods, gastrotrichs, loriciferans, tardigrades, bivalves, cumaceans, aplacophorans) was less than 0.8% of total meiofaunal abundance.

### 2.4.1 Comparison of Hikurangi Margin and Bay of Plenty regions

SIMPER analysis of environmental variables showed substantial variability between regions, mostly in surface water chlorophyll concentration, sediment phaeopigment concentration, organic carbon content of the sediment and fishing intensity (Appendix C). These four variables were substantially higher in the Hikurangi Margin than in the Bay of Plenty (Figure 2.2). Surface water chlorophyll concentrations and organic carbon content were two times higher, and sediment phaeopigment concentration five times higher, in the Hikurangi Margin than in the Bay of Plenty. Mean fishing intensity was thirty times greater in the former region, but among-site variability was high.

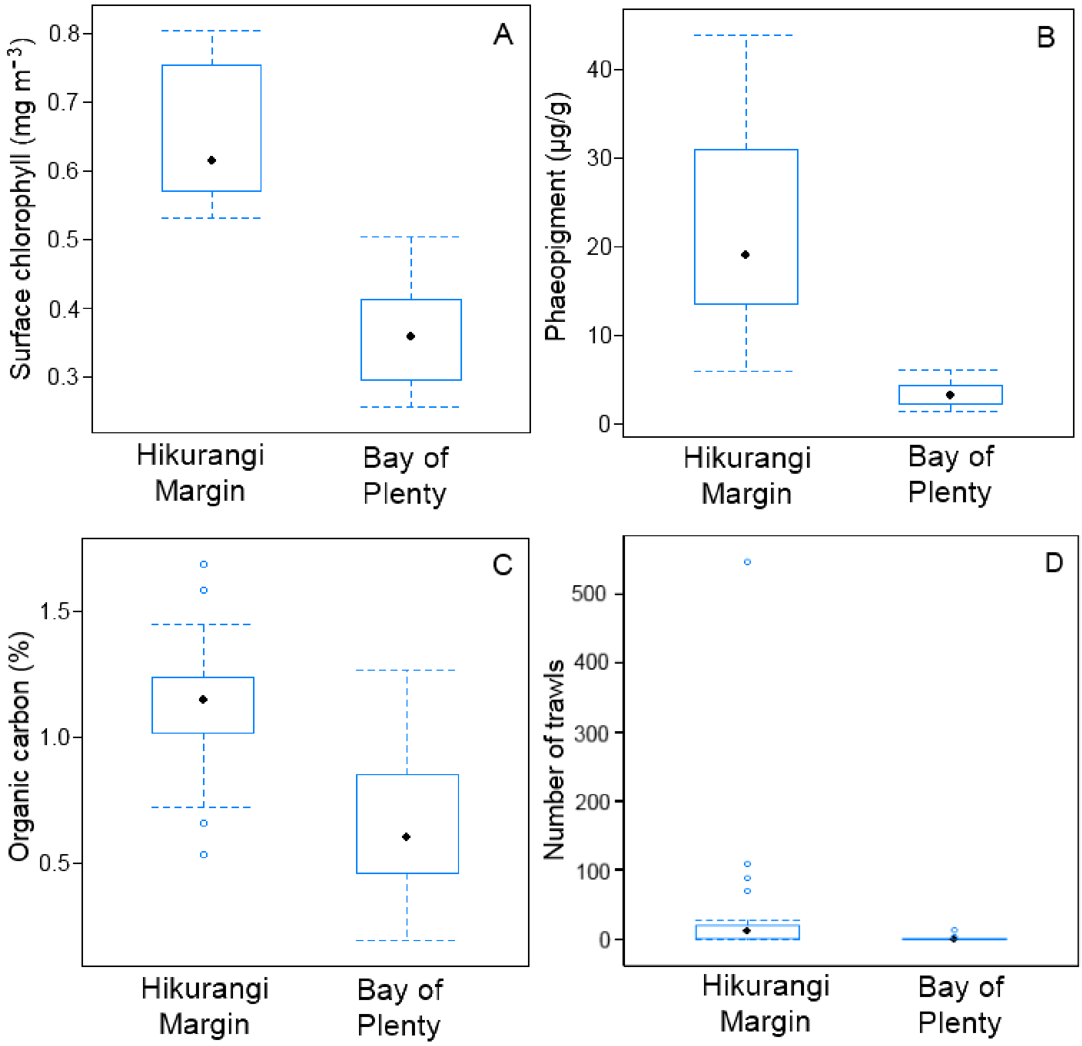

Figure 2.2. Comparison of variables responsible for most of environmental dissimilarity between the Hikurangi Margin and Bay of Plenty study regions. A. Mean surface chlorophyll concentration; B. Sediment phaeopigment concentration; C. Sediment organic carbon content; D. Fishing intensity. (Environmental data first published in Bowden et al. (2016)).

There was a significant difference in meiofaunal abundance between regions (PERMANOVA, P = 0.0001). Average meiofaunal abundance was about one and a half times higher in the Hikurangi Margin (1481 ± 538 individual 10 cm$^{-2}$) compared to the Bay of Plenty (929 ± 396). There was a small but significant difference in meiofaunal diversity (meiofaunal taxon richness) between regions (PERMANOVA, P = 0.04), with a total of twelve major taxa identified in the Hikurangi Margin region (average diversity: seven taxa per core), which was less than the fourteen major taxa identified in the Bay of Plenty region (average diversity: six taxa per core).

Meiofaunal community structure was significantly different between regions (PERMANOVA, P = 0.0001; Figure 2.3). Kinorhynchs were the greatest contributor to between-region dissimilarity, and like most other meiofaunal taxa, their average abundance was higher in the Hikurangi Margin region than in the Bay of Plenty (Table 2.2). Tardigrades, gastrotrichs and loriciferans were only recorded in the Bay of Plenty, whereas bivalves were only recorded in the Hikurangi Margin.

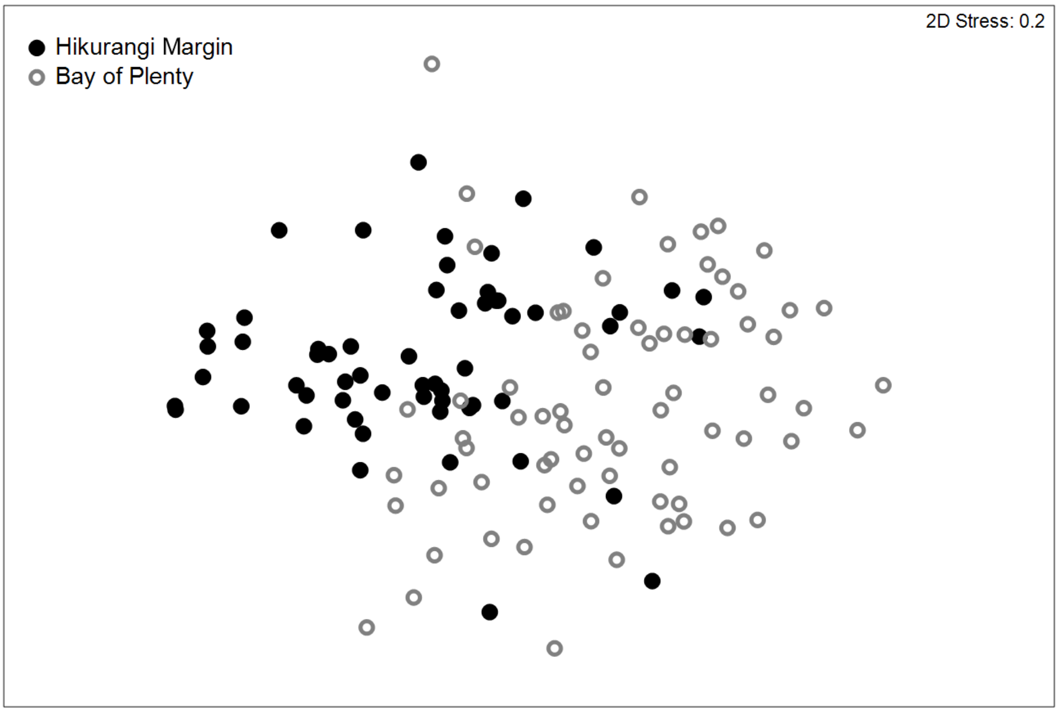

Figure 2.3. Two-dimensional MDS ordination plot of meiofaunal community structure at the Hikurangi Margin and Bay of Plenty study regions.

Table 2.2. SIMPER analysis results showing meiofaunal taxa accounting for community dissimilarity between the Hikurangi Margin and Bay of Plenty study regions (cut-off applied at 90% contribution).[Av.abund = average meiofauna abundance (individual 10 $cm^{-2}$), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold.

| Taxon | Av.Abund Hikurangi Margin | Av.Abund Bay of Plenty | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| Kinorhynchs | **6.6** | 1.5 | 2.96 | 1.31 | 13.25 | 13.25 |
| Ostracods | **2.9** | 0.9 | 2.66 | 1.25 | 11.89 | 25.15 |
| Nematodes | **663.4** | 446.5 | 2.32 | 1.5 | 10.39 | 35.54 |
| Copepods | **58.1** | 21.0 | 2.25 | 1.54 | 10.06 | 45.6 |
| Tanaidaceans | **1.1** | 0.4 | 2.18 | 1.11 | 9.75 | 55.36 |
| Nauplii | **38.4** | 16.6 | 2.18 | 1.39 | 9.74 | 65.1 |
| Tardigrades | 0 | **1.0** | 1.95 | 0.95 | 8.72 | 73.82 |
| Annelids | **14.0** | 4.4 | 1.84 | 1.53 | 8.25 | 82.06 |
| Isopods | **0.50** | 0.3 | 1.34 | 0.74 | 6.01 | 88.08 |
| Amphipods | **0.40** | 0.2 | 1.19 | 0.69 | 5.31 | 93.38 |

### 2.4.2 Hikurangi Margin

Meiofaunal abundance differed significantly among habitats, water depths, and sediment depths in the Hikurangi Margin study region (PERMANOVA, $P < 0.05$; Figure 2.4; Appendix D). Interactions between sediment depth and all the other factors were also significant, indicating that patterns were not consistent between surface and subsurface layers. Pairwise comparisons showed significantly lower abundance of surface (0–1 cm) meiofauna on seamounts relative to canyons, while subsurface (1–5 cm) meiofaunal abundance was significantly lower on seamounts than in both canyon or slope habitats. Pairwise comparisons also showed significantly higher abundance of surface and subsurface meiofauna at 700 m water depth than deeper depths (surface layer: 1200 and 1500 m, subsurface layer: 1000, 1200 and 1500 m). Comparing the estimates of components of variation showed that sediment depth (89.0) and habitat (86.8) explained similar proportions of variability in abundance, whilst water depth explained a smaller proportion (57.4) (Appendix

D). Diversity differed significantly between sediment depths, but not among habitats or water depths (PERMANOVA, P < 0.05; Appendix E), and higher in surface than in subsurface sediments.

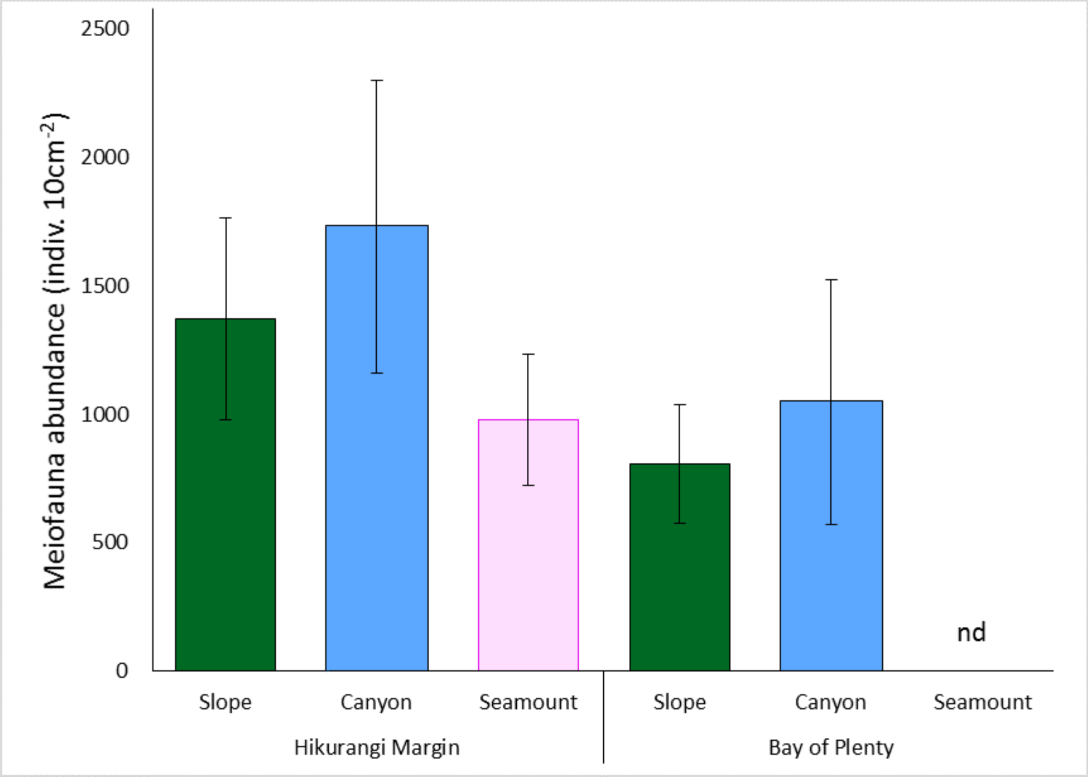

Figure 2.4. Comparison of average total meiofaunal abundance among habitats (slope, canyon and seamount) in Hikurangi Margin and Bay of Plenty. Data are means (±SD). nd = no data.

Meiofaunal community structure differed significantly between sediment depths, but not among habitats or water depths (PERMANOVA, P = 0.0001; Figure 2.5; Appendix F). SIMPER analysis showed average community dissimilarity between the 0–1 cm and 1–5 cm sediment depth was 24.2%; nauplii were the largest contributor to community dissimilarity (16.8% of total dissimilarity) (Table 2.3). Average abundance of nematodes, annelids, and isopods was higher in the 1–5 cm than the 0–1 cm sediment depth layer, whereas the other meiofaunal taxa showed the opposite trend.

Results of DistLM analyses showed that abundance in the 0–1 cm sediment layer was significantly correlated with profile curvature and water depth ($P < 0.05$; $R^2 = 0.12$; Table 2.4; Figure 2.6). Abundance in surface sediment was negatively correlated with profile curvature, indicating that abundance was greater in depressions than on elevated topography, whereas the relationship between abundance and water depth was positive. Meiofaunal abundance in the 1–5 cm layer was significantly and positively correlated with the standard deviation of the slope (15 grid cell focal mean; a proxy measure for slope roughness), and sediment phaeopigment concentration ($P < 0.05$; $R^2 = 0.24$–$0.41$). Abundance in subsurface sediment was also negatively correlated with water depth ($P < 0.05$; $R^2 = 0.19$; Table 2.4).

Meiofaunal diversity in the 0–1 cm sediment layer was significantly and negatively correlated with mean particle size, particle size diversity and fishing intensity ($P < 0.05$; $R^2 = 0.07$; Table 2.4; Figure 2.7). Diversity in the 1–5 cm sediment layer was significantly and negatively correlated with both curvature and profile curvature ($P < 0.05$; $R^2 = 0.13$–$0.16$), indicating that diversity was greater in depressions than on elevated topography.

Meiofaunal community structure in the 0–1 cm sediment layer was significantly correlated with profile curvature, curvature and water depth ($P < 0.05$; $R^2 = 0.05$–$0.08$; Table 2.4), whilst community structure in the 1–5 cm sediment layer was significantly correlated with curvature and phaeopigment concentration in the sediment.

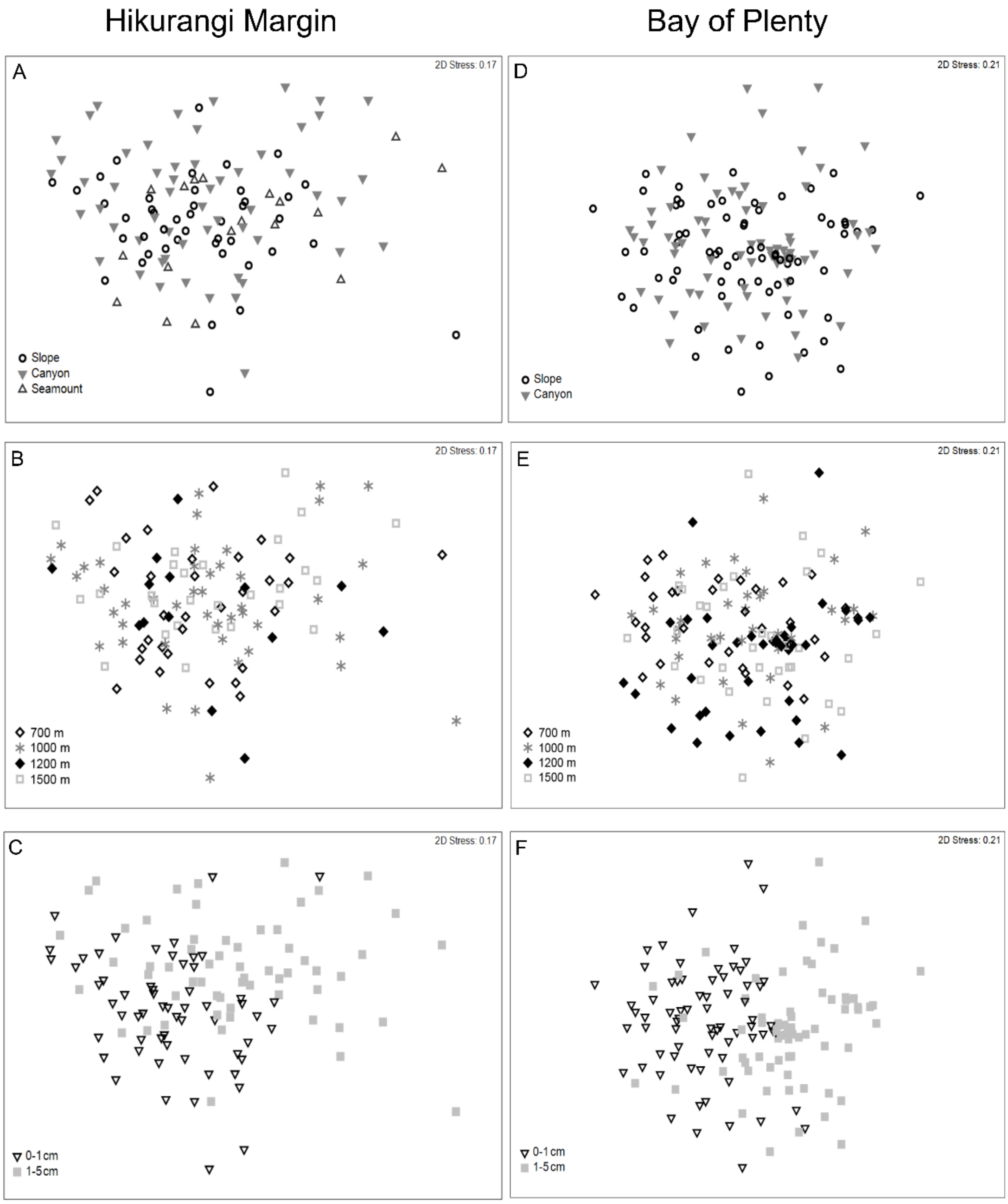

Figure 2.5. Two-dimensional MDS ordination of meiofaunal community structure at the study regions. Hikurangi Margin: A. Habitat; B. Water depth; C. Sediment depth; Bay of Plenty: D. Habitat; E. Water depth; F. Sediment depth.

Table 2.3. SIMPER analysis results showing meiofaunal taxa accounting for community dissimilarity between 0–1 and 1–5 cm sediment depth layers in the Hikurangi Margin study region (cut-off applied at 90% contribution). [Av.abund = average meiofauna abundance (individual 10 $cm^{-2}$), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold.

| Taxon | Av.Abund<br>0-1cm | Av.Abund<br>1-5cm | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| Nauplii | **28.7** | 9.7 | 4.06 | 1.23 | 16.78 | 16.78 |
| Kinorhynchs | **4.3** | 2.3 | 3.35 | 1.2 | 13.85 | 30.63 |
| Copepods | **39.1** | 19.0 | 3.21 | 1.08 | 13.26 | 43.89 |
| Ostracods | **2.2** | 0.7 | 3.07 | 1.17 | 12.67 | 56.56 |
| Nematodes | 248.3 | **415.2** | 3.02 | 1.34 | 12.48 | 69.05 |
| Tanaidaceans | **0.7** | 0.8 | 2.13 | 0.93 | 8.81 | 77.86 |
| Annelids | 4.9 | **9.1** | 2.09 | 1.03 | 8.62 | 86.48 |
| Isopods | 0.2 | **0.3** | 1.1 | 0.58 | 4.52 | 91.00 |

Table 2.4. DistLM analysis results showing correlations between environmental variables and meiofaunal attributes for the Hikurangi Margin region. [P = probablity, $R^2$ = proportion of explained variation attributable to each variable, $R^2$ (cum) = cumulative proportion of variation, rs.df = residual degrees of freedom, Slope STD = Standard deviation of slope based on 3, 5, 7, 15 grid cell focal mean, STD = Standard deviation of depth, Vrm = terrain rugosity, (+/-) = positive/negative relationship].

| Variable | P | R2 | Variable | P | $R^2$ | $R^2$ cum | rs.df |
|---|---|---|---|---|---|---|---|
| MARGINAL TESTS | | | SEQUENTIAL TESTS | | | | |
| **Abundance 0–1cm** | | | **Abundance 0–1cm** | | | | |
| (-) Profile curvature | 0.0073 | 0.12 | (-) Profile curvature | 0.0075 | 0.12 | 0.12 | 57 |
| (+) Water depth | 0.0074 | 0.12 | (+) Water depth | 0.0087 | 0.10 | 0.22 | 56 |
| (-) Curvature | 0.0124 | 0.11 | (-) %$CaCO_3$ | 0.0295 | 0.06 | 0.28 | 55 |
| **Abundance 1–5cm** | | | **Abundance 1–5cm** | | | | |
| (+) Slope STD15 | 0.0001 | 0.41 | (+) Slope STD15 | 0.0001 | 0.41 | 0.41 | 57 |
| (+) Vrm05 | 0.0012 | 0.25 | (-) %$CaCO_3$ | 0.0007 | 0.12 | 0.53 | 56 |
| (+) Phaeopigment | 0.0003 | 0.24 | (+) Vrm05 | 0.0013 | 0.11 | 0.64 | 55 |
| (-) Water depth | 0.0006 | 0.19 | (+) Slope STD03 | 0.0005 | 0.07 | 0.71 | 54 |
| (+) Skewness | 0.0022 | 0.14 | | | | | |
| (-) Curvature | 0.0209 | 0.09 | | | | | |
| (+) STD15 | 0.0363 | 0.07 | | | | | |
| (+) Particle size diversity | 0.0475 | 0.07 | | | | | |
| **Diversity 0–1cm** | | | **Diversity 0–1cm** | | | | |
| (-) Mean particle size | 0.0407 | 0.07 | (-) Mean particle size | 0.0418 | 0.07 | 0.07 | 57 |

| Variable | P | R2 | Variable | P | $R^2$ | $R^2$ cum | rs.df |
|---|---|---|---|---|---|---|---|
| MARGINAL TESTS | | | SEQUENTIAL TESTS | | | | |
| (-) Particle size diversity | 0.0444 | 0.07 | | | | | |
| (-) Fishing intensity | 0.0445 | 0.06 | | | | | |
| **Diversity 1–5cm** | | | **Diversity 1-5cm** | | | | |
| (-) Curvature | 0.0010 | 0.16 | (-) Curvature | 0.0019 | 0.16 | 0.16 | 57 |
| (-) Profile curvature | 0.0039 | 0.14 | | | | | |
| (+) Phaeopigment | 0.0068 | 0.13 | | | | | |
| (-) %$CaCO_3$ | 0.0073 | 0.12 | | | | | |
| **Community structure 0–1cm** | | | **Community structure 0-1cm** | | | | |
| Profile curvature | 0.0008 | 0.08 | Profile curvature | 0.0008 | 0.08 | 0.08 | 57 |
| Curvature | 0.0017 | 0.07 | %$CaCO_3$ | 0.0057 | 0.05 | 0.18 | 55 |
| Depth | 0.0145 | 0.05 | Depth | 0.0207 | 0.04 | 0.12 | 56 |
| Skewness | 0.0227 | 0.05 | Vrm05 | 0.0293 | 0.03 | 0.24 | 53 |
| %$CaCO_3$ | 0.0466 | 0.04 | | | | | |
| **Community structure 1-5cm** | | | **Community structure 1-5cm** | | | | |
| Curvature | 0.0020 | 0.09 | Curvature | 0.0021 | 0.09 | 0.09 | 57 |
| Phaeopigment | 0.0023 | 0.08 | Slope STD15 | 0.0025 | 0.08 | 0.16 | 56 |
| Slope STD15 | 0.0022 | 0.08 | %$CaCO_3$ | 0.0074 | 0.05 | 0.21 | 55 |
| %$CaCO_3$ | 0.0106 | 0.06 | | | | | |
| Profile curvature | 0.0123 | 0.06 | | | | | |
| Vrm05 | 0.0131 | 0.06 | | | | | |
| Depth | 0.0232 | 0.05 | | | | | |

### 2.4.3 Bay of Plenty

Meiofaunal abundance differed significantly among habitats, water depth, and sediment depths in the Bay of Plenty study region; there was also a significant interaction between habitat and water depth (PERMANOVA, $P < 0.05$; Appendix D; Figure 2.4). Pairwise comparisons only showed a significant interaction at 1200 m, but not at other water depths, where higher abundance of meiofauna were observed in canyons relative to slopes. Comparing the estimates of components of variation showed that habitat explained a greater proportion of the variability in abundance than sediment depth and water depth (Appendix D). Diversity differed significantly between sediment depth, but not among habitats or water depths (PERMANOVA, $P < 0.05$; Appendix E), and higher in surface than in subsurface sediments.

Meiofaunal community structure differed significantly among water depths and between sediment depths, but not among habitats (PERMANOVA, $P < 0.05$; Figure 2.5; Appendix F). Comparing the estimates of components of variation showed that sediment depth explained a greater proportion of the variability in abundance than water depth (Appendix F). Pairwise comparisons showed that community structure differed significantly between 700 m and 1200 m, and between 700 m and 1500 m. SIMPER analysis showed average community dissimilarity between 700 m and 1200 m, and between 700 and 1500 m depth, was ~24%. SIMPER results showed that nauplii were the main contributor to community dissimilarity, and that the average abundance of all meiofaunal taxa was higher at 700 m than at 1200 and 1500 m water depths (Table 2.5). Average community dissimilarity between 0–1 cm and 1–5 cm sediment depths was 26.3%. SIMPER results showed that nauplii were the main contributor to community dissimilarity, and that nematode average abundance was higher in the 1–5 cm than the 0–1 cm sediment depth, whereas the other meiofaunal taxa showed the opposite trend (Table 2.5).

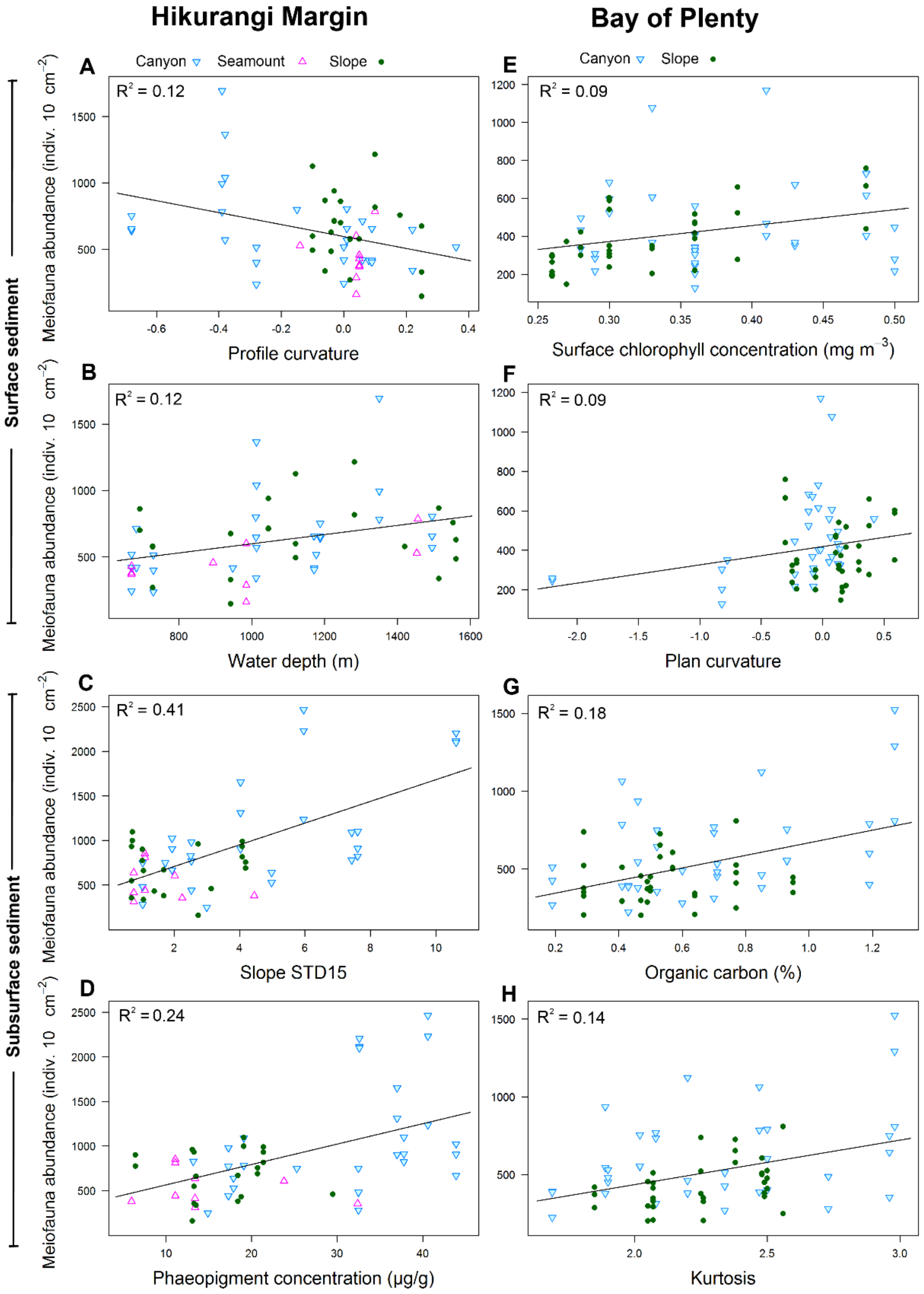

Figure 2.6. Selection of statistically significant ($P < 0.05$) correlations between environmental variables and meiofaunal abundance at different sediment layers in the Hikurangi Margin and Bay of Plenty regions. Hikurangi Margin, surface sediment (0–1 cm): A. Profile curvature; B. Water depth (m); Subsurface sediment (1–5 cm): C. Standard deviation of the slope (15 grid cell focal mean); D. Phaeopigment concentration (µg/g); Bay of Plenty, surface sediment (0–1 cm): E. Surface chlorophyll concentration (mg m$^{-3}$); F. Plan curvature; Subsurface sediment (1–5 cm): G. Organic carbon content (%OC); H. Kurtosis. (See Table 2.4 and Table 2.6 for results of DistLM analyses).

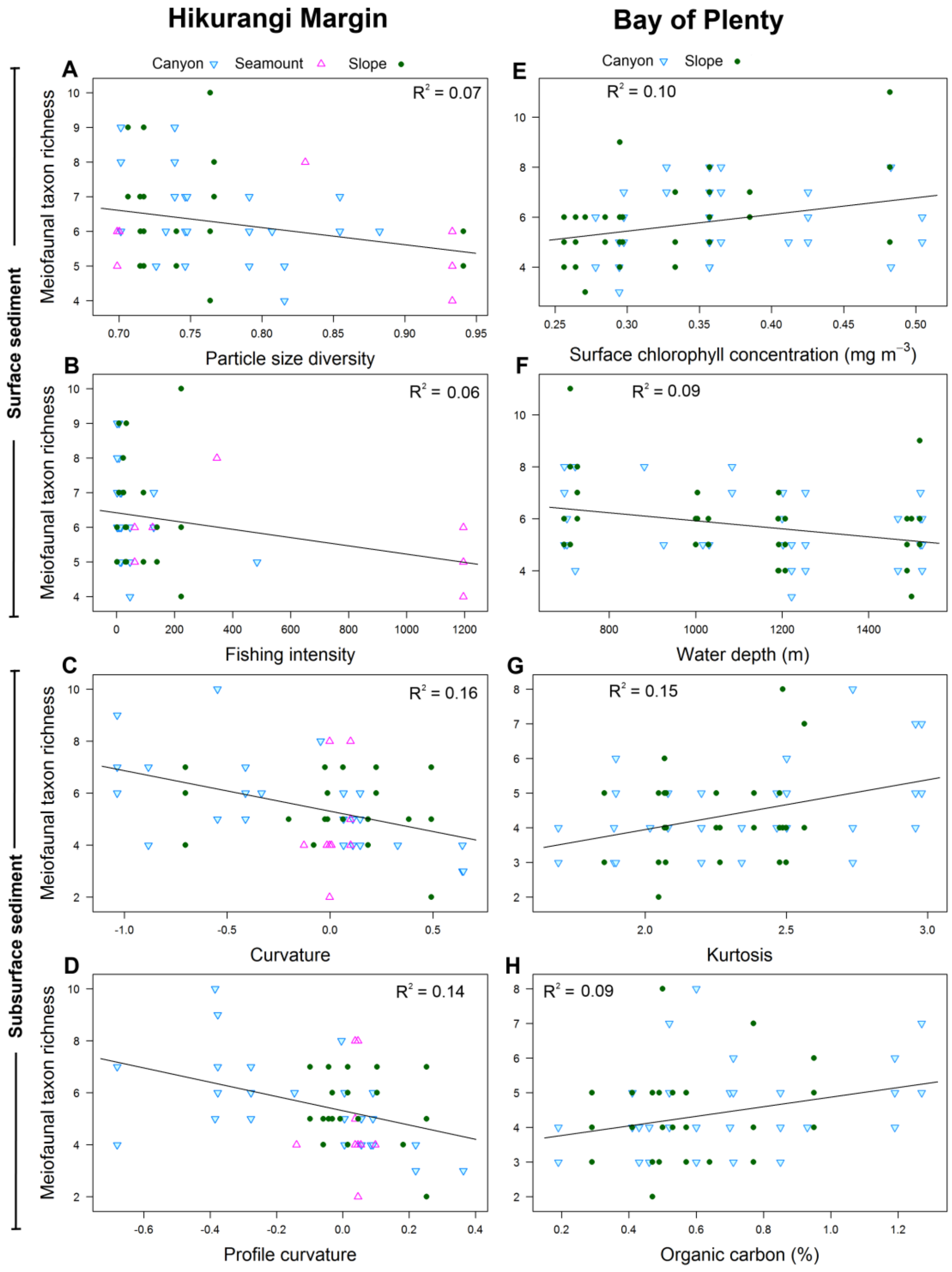

Figure 2.7. Selection of statistically significant ($P < 0.05$) correlations between environmental variables and meiofaunal diversity at different sediment layers in the Hikurangi Margin and Bay of Plenty study regions. Hikurangi Margin, surface sediment (0–1 cm): A. Particle size diversity; B. Fishing intensity (num. of trawls); Subsurface sediment (1–5 cm): C. Curvature; D. Profile curvature; Bay of Plenty, surface sediment (0–1 cm): E. Surface chlorophyll concentration (mg $m^{-3}$); F. Water depth (m); Subsurface sediment (1–5 cm): G. Kurtosis; H. Organic carbon content. (See Table 2.4 and Table 2.6 for results of DistLM analyses).

Results of DistLM analysis showed that abundance in the 0–1 cm sediment layer was significantly correlated with surface water chlorophyll concentration, sediment carbonate content and plan curvature ($P < 0.05$; $R^2 = 0.09$; Table 2.6). The relationship between abundance and sediment carbonate content was negative, whereas abundance was positively correlated with surface water chlorophyll concentration and plan curvature (Figure 2.6). The positive relationship between plan curvature and abundance indicated that abundance was greater in elevated topography perpendicular to the slope direction. Abundance in the 1–5 cm sediment layer was significantly and positively correlated with organic carbon content, kurtosis, and phaeopigment concentration in the sediment ($P < 0.05$; $R^2 = 0.07$–$0.18$; Table 2.6; Figure 2.6).

Meiofaunal diversity in the 0–1 cm sediment layer was significantly correlated with surface water chlorophyll concentration and water depth ($P < 0.05$; $R^2 = 0.09$–$0.1$; Table 2.6; Figure 2.7). The relationship between diversity and surface water chlorophyll concentration was positive, whereas diversity was negatively correlated with water depth. Diversity in the 1–5 cm sediment layer was significantly and positively correlated with kurtosis and organic carbon content ($P < 0.05$; $R^2 = 0.09$–$0.15$).

Meiofaunal community structure in the 0–1 cm sediment layer was significantly correlated with water depth and surface water chlorophyll concentration ($P < 0.05$; $R^2 = 0.04$; Table 2.6). Community structure in the 1–5 cm sediment layer was significantly correlated with kurtosis, silt and clay particle content, and particle skewness ($P < 0.05$; $R^2 = 0.05 – 0.06$).

Table 2.5. SIMPER analysis results showing meiofaunal taxa accounting for community dissimilarity between different water and sediment depths for the Bay of Plenty study region (cut-off applied at 70% contribution). [Av.abund = average meiofauna abundance (individual 10 cm$^{-2}$), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold.

| Taxon | Av.Abund | Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| *Water depths* | *700 m* | *1200 m* | | | | |
| Nauplii | **24.4** | 12.0 | 4.05 | 1.17 | 17.02 | 17.02 |
| Annelids | **5.8** | 3.2 | 3.19 | 1.08 | 13.4 | 30.42 |
| Kinorhynchs | **1.7** | 1.2 | 2.78 | 0.94 | 11.65 | 42.07 |
| Tardigrades | **1.6** | 0.6 | 2.57 | 0.89 | 10.81 | 52.89 |
| Nematodes | **441.6** | 385.1 | 2.52 | 1.31 | 10.59 | 63.48 |
| Copepods | **28.0** | 19.4 | 2.47 | 1.38 | 10.36 | 73.84 |
| | | | | | | |
| | *700 m* | *1500 m* | | | | |
| Nauplii | **24.4** | 14.1 | 3.94 | 1.17 | 16.52 | 16.52 |
| Copepods | **28.0** | 16.4 | 3.35 | 1.03 | 14.04 | 30.57 |
| Kinorhynchs | **1.7** | 1.5 | 2.88 | 0.97 | 12.08 | 42.65 |
| Nematodes | **441.6** | 431.3 | 2.73 | 1.31 | 11.44 | 54.08 |
| Tardigrades | **1.6** | 0.9 | 2.72 | 0.95 | 11.41 | 65.49 |
| Ostracods | **1.6** | 0.7 | 2.3 | 0.83 | 9.64 | 75.13 |
| | | | | | | |
| *Sediment depths* | *0–1 cm* | *1–5 cm* | | | | |
| Nauplii | **13.6** | 3.0 | 5.06 | 1.34 | 19.24 | 19.24 |
| Copepods | **15.2** | 5.8 | 3.28 | 1.23 | 12.49 | 31.73 |
| Kinorhynchs | **1.2** | 0.3 | 3.23 | 1.03 | 12.27 | 44 |
| Nematodes | 184.9 | **261.6** | 2.99 | 1.3 | 11.39 | 55.4 |
| Tardigrades | **0.8** | 0.2 | 2.74 | 0.94 | 10.42 | 65.82 |
| Annelids | **2.4** | 2.1 | 2.51 | 0.9 | 9.53 | 75.35 |

Table 2.6. DistLM analysis results showing correlations between environmental variables and meiofaunal community attributes in the Bay of Plenty region. [P = probablity, R2 = proportion of explained variation attributable to each variable, R2 (cum) = cumulative proportion of variation, rs.df = residual degrees of freedom, Slope STD = Standard deviation of slope based on 3, 5, 7, 15 grid cell focal mean, STD = Standard deviation of depth, (+/-) = positive/negative relationship].

| Variable | P | $R^2$ | Variable | P | $R^2$ | $R^2$ cum | rs.df |
|---|---|---|---|---|---|---|---|
| MARGINAL TESTS | | | SEQUENTIAL TESTS | | | | |
| **Abundance 0–1cm** | | | **Abundance 0–1cm** | | | | |
| (+) Surface chlorophyll concentration | 0.0125 | 0.09 | (+) Surface chlorophyll concentration | 0.0119 | 0.09 | 0.09 | 69 |
| (-) %$CaCO_3$ | 0.0140 | 0.09 | (+) Plan curvature | 0.0172 | 0.09 | 0.17 | 68 |
| | | | (+) %OC | 0.0170 | 0.07 | 0.24 | 67 |
| | | | (-) Skewness | 0.0356 | 0.05 | 0.29 | 66 |
| | | | (+) Slope STD07 | 0.0265 | 0.05 | 0.40 | 62 |
| **Abundance 1–5 cm** | | | **Abundance 1–5 cm** | | | | |
| (+) %OC | 0.0001 | 0.18 | (+) %OC | 0.0005 | 0.18 | 0.18 | 69 |
| (+) Kurtosis | 0.0012 | 0.14 | (+) Kurtosis | 0.0115 | 0.07 | 0.26 | 68 |
| (+) Phaeopigment | 0.0057 | 0.10 | (+) Range07 | 0.0212 | 0.05 | 0.53 | 53 |
| (+) %Silt/clay | 0.0141 | 0.08 | | | | | |
| (-) Sorting | 0.0163 | 0.08 | | | | | |
| **Diversity 0–1cm** | | | **Diversity 0–1cm** | | | | |
| (+) Surface chlorophyll concentration | 0.0053 | 0.10 | (+) Surface chlorophyll concentration | 0.0057 | 0.10 | 0.10 | 69 |
| (-) Water depth | 0.0107 | 0.09 | (-) Sorting | 0.0244 | 0.07 | 0.17 | 68 |
| (+) Phaeopigment | 0.0100 | 0.09 | | | | | |
| **Diversity 1–5 cm** | | | **Diversity 1–5 cm** | | | | |
| (+) Kurtosis | 0.0014 | 0.15 | (+) Kurtosis | 0.0013 | 0.15 | 0.15 | 69 |
| (+) %OC | 0.0106 | 0.09 | | | | | |
| (+) Skewness | 0.0220 | 0.07 | | | | | |
| (+) %Silt/clay | 0.0335 | 0.06 | | | | | |
| (+) %OM | 0.0369 | 0.06 | | | | | |
| **Community structure 0–1 cm** | | | **Community structure 0–1 cm** | | | | |
| Water depth | 0.0056 | 0.04 | Water depth | 0.0062 | 0.04 | 0.04 | 69 |
| Surface chlorophyll concentration | 0.0110 | 0.04 | Plan curvature | 0.0082 | 0.03 | 0.07 | 68 |
| Plan curvature | 0.0174 | 0.03 | %OM | 0.0220 | 0.03 | 0.14 | 66 |
| %Silt/clay | 0.0294 | 0.03 | Kurtosis | 0.0302 | 0.03 | 0.28 | 59 |
| Phaeopigment | 0.0306 | 0.03 | | | | | |
| Sorting | 0.0418 | 0.03 | | | | | |
| %OM | 0.0403 | 0.03 | | | | | |
| **Community structure 1–5 cm** | | | **Community structure 1–5 cm** | | | | |
| Kurtosis | 0.0003 | 0.06 | Kurtosis | 0.0004 | 0.06 | 0.06 | 69 |

| Variable | P | $R^2$ | Variable | P | $R^2$ | $R^2$ cum | rs.df |
|---|---|---|---|---|---|---|---|
| MARGINAL TESTS | | | SEQUENTIAL TESTS | | | | |
| %Silt/clay | 0.0030 | 0.05 | %OC | 0.0448 | 0.03 | 0.09 | 68 |
| Skewness | 0.0048 | 0.05 | Surface chlorophyll concentration | 0.0475 | 0.03 | 0.16 | 65 |
| %OC | 0.0091 | 0.04 | | | | | |
| Sorting | 0.0252 | 0.03 | | | | | |
| %OM | 0.0276 | 0.03 | | | | | |
| Phaeopigment | 0.0274 | 0.03 | | | | | |

### 2.4.4 Slope, canyon, and seamount habitats compared to seep habitat: Hikurangi Margin

The second-stage analysis of slope, canyon, seamount, and seep communities in the Hikurangi Margin showed a significant effect of habitat, sediment depth, and their interaction on abundance (PERMANOVA, $P < 0.05$). Pairwise comparisons only showed a significant interaction between canyons and seeps at subsurface sediment (1–5 cm), where abundance was higher in canyon than seep habitats (Appendix G). Diversity differed significantly among habitats and between sediment depths (PERMANOVA, $P < 0.05$). Differences in diversity were small, but overall diversity was significantly higher in seep habitat (average diversity = 7.2) compared to the other habitats (canyon = 5.9, slope = 6.0, seamount = 5.4), and was significantly higher in surface sediment (6.6) than in subsurface sediment (5.7).

Meiofaunal community structure differed significantly among habitats and between sediment depths (PERMANOVA, $P < 0.05$; Appendix H). Pairwise comparisons showed that meiofaunal communities differed significantly ($P < 0.05$) between seep and all of the other habitats, which did not differ significantly from each other (Figure 2.8). Nauplii and amphipods contributed the most to community dissimilarity (12–15% of total dissimilarity) between seeps and the other habitats (Table 2.7). Average abundance of meiofaunal taxa was higher in seep habitats than in the other habitats, except for kinorhynchs, ostracods and nematodes which were most abundant in canyon and slope habitats.

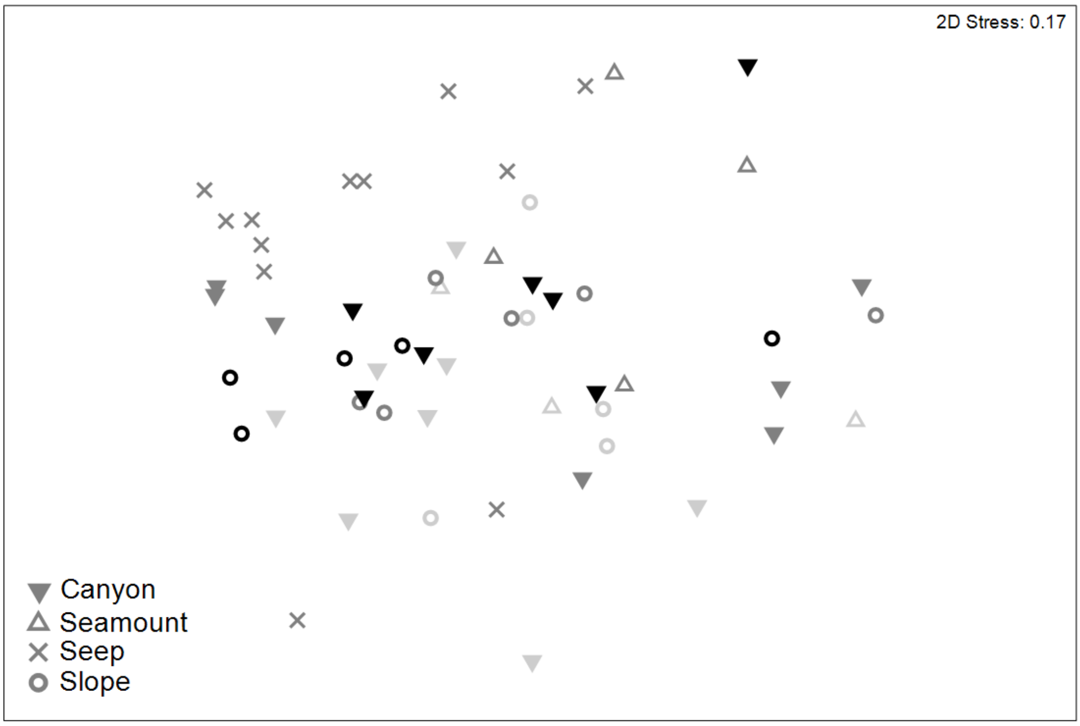

Figure 2.8. Two-dimensional MDS ordination of meiofaunal community structure for habitats in the Hikurangi Margin study region (water depth: 700–1200 m only). Depth strata are shown by shades of grey ranging from light grey (700 m) to black (1200 m).

Table 2.7. Results of the SIMPER analysis showing meiofauna taxa accounting for community dissimilarity between seep and other habitats for the Hikurangi Margin study region (cut-off applied at 90% contribution). [Av.abund = average meiofauna abundance (individual 10 cm$^{-2}$), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold.

| Taxon | Av.Abund | Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| | *Seamount* | *Seep* | | | | |
| Nauplii | 8.6 | **30.3** | 4.04 | 1.19 | 14.73 | 14.7 |
| Amphipods | 0.2 | **3.6** | 3.59 | 1.32 | 13.07 | 27.8 |
| Copepods | 16.9 | **36.8** | 3.3 | 1.13 | 12.01 | 39.8 |
| Tanaidaceans | 0.3 | **2.5** | 3.2 | 1.27 | 11.65 | 51.5 |
| Kinorhynchs | 2.4 | **2.6** | 3.06 | 1.15 | 11.15 | 62.6 |
| Ostracods | 0.6 | **1.5** | 2.74 | 1.13 | 9.98 | 72.6 |
| Bivalves | 0 | **1.0** | 2.46 | 1.04 | 8.97 | 81.6 |
| Nematodes | 213.4 | **268.2** | 2.36 | 1.39 | 8.6 | 90.2 |
| | *Canyon* | *Seep* | | | | |
| Nauplii | 19.8 | **30.3** | 3.8 | 1.21 | 14.28 | 14.3 |
| Amphipods | 0.2 | **3.6** | 3.4 | 1.35 | 12.76 | 27.0 |
| Kinorhynchs | **4.3** | 2.6 | 3.07 | 1.17 | 11.54 | 38.6 |
| Tanaidaceans | 0.5 | **2.5** | 2.87 | 1.24 | 10.8 | 49.4 |
| Copepods | 30.3 | **36.8** | 2.87 | 1.27 | 10.8 | 60.2 |
| Ostracods | **1.8** | 1.5 | 2.71 | 1.16 | 10.19 | 70.4 |
| Nematodes | **398.5** | 268.2 | 2.69 | 1.31 | 10.1 | 80.5 |
| Bivalves | 0.4 | **1.0** | 2.32 | 1.06 | 8.74 | 89.2 |
| Annelids | 9.1 | **9.3** | 1.66 | 1.11 | 6.25 | 95.5 |
| | *Slope* | *Seep* | | | | |
| Amphipods | 0.2 | **3.6** | 3.45 | 1.36 | 13.15 | 13.2 |
| Nauplii | 22.6 | **30.3** | 3.32 | 1.24 | 12.68 | 25.8 |
| Tanaidaceans | 0.5 | **2.5** | 3.01 | 1.28 | 11.47 | 37.3 |
| Kinorhynchs | **3.6** | 2.6 | 2.89 | 1.14 | 11.04 | 48.4 |
| Copepods | 34.9 | **36.8** | 2.89 | 1.17 | 11.01 | 59.4 |
| Ostracods | **1.7** | 1.5 | 2.65 | 1.16 | 10.1 | 69.5 |
| Nematodes | **315.5** | 268.2 | 2.38 | 1.27 | 9.07 | 78.5 |
| Bivalves | 0.03 | **1.0** | 2.28 | 1.04 | 8.7 | 87.2 |
| Annelids | 5.3 | **9.3** | 1.83 | 0.83 | 6.99 | 94.2 |

## 2.5 Discussion

Knowledge of the benthic communities associated with distinct habitats in the deep sea has increased significantly during the last decades, as we now have a better understanding of how substrate type and availability, biogeochemistry, nutrient input, productivity, hydrographic conditions and catastrophic events shape community patterns on regional scales (Levin et al. 2010, Vanreusel et al. 2010b). In this study, meiofaunal community attributes differed between regions and sediment depths, and between habitats and water depths for some community attributes. Relationships between environmental variables, trawling intensity, and community attributes also differed between surface and subsurface sediment communities. The patterns observed are discussed below in relation to potential environmental drivers, as is the relative vulnerability of meiofaunal communities to anthropogenic activities.

### 2.5.1 Regional differences in meiofaunal communities

The flux of organic matter from the surface to the seafloor is the main driver of meiofaunal benthic abundance (Soltwedel 2000, Lambshead et al. 2002). Meiofaunal density has often been linked to food availability in the sediment (Lampadariou and Tselepides 2006, Ingels et al. 2009, Leduc et al. 2014), with high food concentrations associated with high numbers of individuals. The greater abundance of meiofauna in the Hikurangi Margin relative to the Bay of Plenty appeared to be related to differences in surface water chlorophyll concentrations, which was two times greater in the Hikurangi Margin. The latter corresponded with phaeopigment concentrations and organic carbon content of the sediment, indicating increased food availability in the Hikurangi Margin than in the Bay of Plenty region. It is likely that this higher food availability led to the observed differences in meiofaunal abundance. There was a clear difference in meiofaunal community structure between regions. Most taxa were more abundant in the Hikurangi Margin compared to the Bay of Plenty, except for certain rare taxa (e.g. gastrotrichs, tardigrades, loriciferans, bivalves) that were only present in one of the regions. However, it is also possible that regional differences in food availability contributed to inter-annual variability since the samples were collected two years apart.

Trawling activity can have pronounced effects on meiofaunal communities (Schratzberger et al. 2009, Pusceddu et al. 2014a), and could also be responsible for regional differences in community attributes in the present study. Although there was only a weak correlation between trawling intensity and diversity in surface sediments, it is possible that trawling impacts on environmental variables may have affected diversity. For example, trawling has been shown to alter sediment physical characteristics and the distribution of organic matter in the sediment column, through continuous stirring of the upper sediments which leads to removal of recent organic-rich sediment and induced changes in the grain size distribution, as repeated resuspension of the remaining sediments favours the sorting of particles according to their settling speeds (Martín et al. 2014, Pusceddu et al. 2014a). In the present study, we found a negative relationship between mean particle size and particle size diversity and meiofaunal diversity in the surface sediment of the Hikurangi Margin, which contrasts with the findings of previous studies showing the opposite pattern (Etter and Grassle 1992, Leduc et al. 2012d). This discrepancy may be explained by the impacts of trawling, which could increase mean sediment particle size and sediment particle size diversity while at the same time decreasing diversity through increased dominance of opportunistic genera (Schratzberger et al. 2009, Pusceddu et al. 2014a). However, identifying potential impacts of trawling at the regional scale will require further research. Natural disturbance such as from currents could explain the increase in mean particle size and particle size diversity in the Hikurangi Margin. However, this region is also being disturbed by trawling activity, and a negative relationship between mean particle size and particle size diversity, and meiofaunal diversity were observed in this study, which suggest that this may be linked to the effect of trawling rather than currents. However, further studies are needed to examine this relationship.

### 2.5.2 Among-habitat differences in meiofaunal communities

Meiofaunal abundance differed among the deep-sea habitats studied, which was evident in both of the study regions. The first-stage analysis showed that abundance was higher in canyons than in other habitats of both regions. Abundance also differed between water depths in both study regions, with total meiofaunal abundance consistently higher in the shallower strata.

In the Hikurangi Margin region, profile curvature and water depth were the two factors most strongly correlated with abundance in the surface sediment. Greater meiofaunal abundance in seafloor depressions could be associated with greater settlement of meiofauna associated with slower near-bottom water currents in depressions (Fleeger et al. 1995, Giere 2009). Negative profile curvatures were mostly found in canyon habitat (see Figure 2.6), which is well known for their complex topography (Canals et al. 2006), and could partly explain the observed canyon habitat effect. In addition, abundances for surface sediments were positively correlated with water depth in all habitats. Higher abundance at deeper sites could result from high settlement of meiofauna that was passively transported downslope by currents; even weak currents can re-suspend meiofaunal organisms and transport them long distances down continental margins (Boeckner et al. 2009, Pusceddu et al. 2014a). Higher abundance could also be related to increase in food availability at deeper depths observed in this study, which may result from downslope transport of fine organic matter (Weaver et al. 2000, Pusceddu et al. 2014a).

In the Bay of Plenty region, other environmental variables influenced meiofaunal abundance. In the surface sediment, surface chlorophyll concentration and plan curvature were positively correlated with abundance. Surface water chlorophyll concentration can be considered an indicator of the flux of organic matter and phytodetritus to the sea floor, and thereby the availability of food to benthic organisms (Rex and Etter 2010). In the present study, surface water chlorophyll concentrations corresponded with higher meiofaunal abundance at the canyon sites, and previous studies support this finding (Soltwedel 2000, Baguley et al. 2006a, Ingels et al. 2009, Pusceddu et al. 2009). The positive relationship between plan curvature and abundance was contrary to the findings in the Hikurangi Margin which showed a negative relationship with curvature and profile curvature, and suggests that abundance is not always greatest in seafloor depressions. Sun and Fleeger (1994) showed that recolonization processes and abundance patterns of meiofauna depend on the interaction between the hydrodynamic regime associated with seafloor depressions and the life style of meiofauna (e.g. epibenthic or burrowers), and it is possible that similar interactions influence the abundance patterns of meiofauna in this study region, resulting in different patterns between regions. However, the lower level of taxonomic resolution used in this study prevented further analysis to confirm this result.

The second-stage analysis showed that meiofaunal abundance, diversity and community structure at seep habitats were significantly different from the other habitats in the Hikurangi Margin and the differences in community structure were due to variation in the relative abundances of a large number of taxa rather than the presence or absence of unique taxa. Overall abundance was higher at the seep habitat compared with the other habitats, with nauplii and amphipods contributing most to community dissimilarity. High densities at seep sites compared with the adjacent slope habitat have also been observed previously, and have mainly been due to elevated abundances of nematodes and copepods (Shirayama and Ohta 1990, Van Gaever et al. 2006, Vanreusel et al. 2010b, Pape et al. 2011). In the present study, the high abundance of copepods and nauplii at cold seeps was opposite to the pattern observed by Van Gaever et al. (2009a), where low abundances of copepods and nauplii were observed, and kinorhynchs, polychaetes, and gastrotrichs were more abundant. Similarly, the high abundance of nematodes, kinorhynchs and ostracods in canyon and slope habitat compared with seep habitat was different to patterns observed elsewhere (Van Gaever et al. 2006). Priapulid larvae were only observed in the seep habitat in the Hikurangi Margin, and the reason for this observed pattern remains unclear. In the present study, diversity was higher in the seep compared with other habitats, which were similar to each other. This finding is similar to Bianchelli et al. (2010), where canyons and slopes were equally diverse, but opposite to other studies where seep diversity was lower than canyon and slope habitats (Ingels et al. 2009, Van Gaever et al. 2009a).

Our results support the general findings that there is an effect of seeps on meiofaunal abundance, diversity and community structure (Lampadariou et al. 2013). Higher meiofaunal abundance at seeps has been attributed to high food availability, resulting from methane seepage fuelling bacterial productivity (Van Gaever et al. 2006); a number of nematode and copepod species are adapted to exploiting bacteria in sediment patches with high methane levels (Zeppilli et al. 2011). In addition, a broad range of geological and sedimentary structures (e.g. gas seepage, microbial mat, pockmarks), and seep epifauna generate habitat (e.g. tubeworms, mussels, clams), resulting in habitat heterogeneity, both above and below the sediment surface (Judd et al. 2002, Levin 2005). This habitat heterogeneity is likely to be a key reason for the relatively high diversity in seep habitats in the Hikurangi Margin, where microbial mats, sediment patches contained methane/hydrogen sulphide, clam beds, and carbonate structures have been observed (Baco et al. 2010). Increased microhabitat heterogeneity at seeps compared to other adjacent deep-sea habitats provides a broad array of geophysical environments including those that some fauna are particularly adapted to, such as nematodes that occur in the oxygenated sediment underneath siboglinid tubeworm patches (Vanreusel et al. 2010b). Each seep site is unique with different geophysical structure, and thus the influence of the seepages on benthic biodiversity is likely to be site-specific (Zeppilli et al. 2012). This proposition could explain the different responses of meiofaunal taxa in our study to those in previous studies (Van Gaever et al. 2006, Van Gaever et al. 2009a, Pape et al. 2011).

### 2.5.3 Meiofaunal community attributes in surface and subsurface sediment layers

The magnitude of sediment depth-related differences in meiofaunal community attributes was substantially greater than for habitats or water depths. This finding is consistent with Ingels and Vanreusel (2013) who observed that variability in meiofaunal communities between sediment depth layers was much greater than variability observed at larger geographical scales (10–100 km).

Meiofaunal abundances were much higher in the surface than the subsurface layer of the sediments, except for nematodes which showed the opposite trend. These results are comparable with findings from other meiofaunal studies, where abundance decreased with sediment depth, and where nematodes become the dominant taxon at subsurface depths (Neira et al. 2001, Danovaro et al. 2002, Ingels et al. 2009). In the Hikurangi Margin region, the differences in the abundance in surface and subsurface sediment layers were greater between canyon and seamount habitats, and between shallow and deep sites. This result may be explained by the complex hydrodynamic regime associated with canyons that can affect the deposition and accumulation rates of sediments and organic matter, resulting in a pronounced structuring of the sediment column within the canyon, with fine-grained suspended sediment being transported to lower parts of canyon leaving heavier-grained sediment, which indirectly changes the particle-size diversity in the affected area. Abundance in surface sediment increased with water depth, while abundance in subsurface sediment decreased with water depth, a pattern similar to that observed by Vanaverbeke et al. (1997b). These authors argued that the low input of organic matter at the deeper sites, as well as shallow penetration of organic matter in the sediment due to lower bioturbation, could explain this pattern (Vanaverbeke et al. 1997b).

Different factors may be driving variation in the abundance of surface and subsurface meiofaunal communities in different regions. In the Hikurangi Margin, seafloor depressions apparently contributed to higher abundance in surface sediment than on flat or elevated ground, by reducing current flow and helping deposition and meiofauna settlement (Fleeger et al. 1995, Giere 2009). Changes in hydrodynamic conditions around seabed features may also affect larval settlement and sediment grain size characteristics (Butman 1987, McClain and Barry 2010). In the subsurface sediments, abundance was positively correlated with sediment phaeopigment concentration and standard deviation of the slope (a proxy measure for slope roughness). Enhanced food availability in the sediment, as indicated by elevated phaeopigment concentrations derived from surface water productivity, has frequently been shown to support higher meiofaunal abundance (Ingels et al. 2009, Pusceddu et al. 2009). It remains unclear how slope roughness is likely to influence meiofaunal abundance in subsurface sediment.

In the Bay of Plenty, abundance was positively influenced by surface chlorophyll concentration and plan curvature in the surface sediments. In the subsurface sediment, abundance was positively related with both sediment organic carbon content and kurtosis. Increased organic carbon content in the sediment has been shown to favour elevated meiofaunal abundance (Morse and Beazley 2008, Ingels et al. 2009). Sediment kurtosis is a measure of the particle size distribution, and high values of kurtosis indicate that there are outliers in the distribution (heavy-tailed relative to normal distribution), and could therefore be interpreted as a measure of habitat heterogeneity. Similar proxies of sediment heterogeneity have been shown to influence meiofaunal abundance (Netto et al. 2005), because habitat heterogeneity increases the partitioning of food resources (Whitlatch 1981, Levin et al. 2001).

Meiofaunal diversity was higher in the surface than subsurface sediment layer in both regions. Similarly, Vanaverbeke et al. (1997b) and Danovaro et al. (2002) found diversity was typically highest in surface sediment and decreased in deeper sediments, where nematodes become the dominant taxon. In the Hikurangi Margin, diversity in surface sediments was negatively influenced by particle size diversity, mean particle size, and fishing. Negative relationship between these variables and diversity may be an indication of indirect effect of trawling, as noted earlier. The diversity of subsurface meiofauna was not correlated with trawling intensity, but was greater in seafloor depressions than on flat or elevated ground. As mentioned earlier, seafloor depressions may increase meiofauna settlement and deposition of organic matter due to reduced water flow, and increased food availability may enhance diversity (Lambshead et al. 2000). The different patterns observed between surface and subsurface sediment layers in the Hikurangi Margin may reflect the greater exposure of surface communities to the direct and indirect effects of trawling. In the Bay of Plenty surface sediment, surface chlorophyll concentration was positively correlated to diversity, while water depth was negatively correlated to diversity. Surface chlorophyll concentrations provide an indication of the flux of organic matter and phytodetritus to the sea floor, and diversity can increase with an increase in organic flux (Lambshead et al. 2000). A decrease in diversity with increased water depth is possibly related to decreased food availability with depth (Vanaverbeke et al. 1997b). In the Bay of Plenty subsurface sediment, kurtosis and sediment organic carbon content were positively correlated to diversity. As described above, these findings are consistent with increased habitat heterogeneity increasing the partitioning of food resources (Whitlatch 1981, Levin et al. 2001), and increased organic carbon content in the sediment has been shown to increase diversity (Lambshead et al. 2000). Thus, in the Bay of Plenty, meiofaunal diversity in both surface and subsurface sediments were positively linked with proxies of food availability. It remains unclear why a positive correlation between kurtosis and diversity was only found in subsurface sediments.

Meiofaunal community structure was different between surface and subsurface sediment in both Hikurangi Margin and Bay of Plenty. Nauplii, copepods and kinorhynchs were the highest contributors to community dissimilarity between sediment depths for both regions, where the abundance of these taxa was higher in the surface than in the subsurface sediment. Nauplii and copepods are generally the second most abundant taxa after nematodes in the sediment (Vanaverbeke et al. 1997b, Danovaro et al. 2002). Typically, copepods and kinorhynchs occupy the well oxygenated sediment layer and are more sensitive to low oxygen concentrations than nematodes (Vidaković 1984, Grego et al. 2014), which may be the reason for their higher abundance in the surface than subsurface sediment. The higher abundance of kinorhynchs may also be related to higher food availability in surface sediments, since kinorhynch abundance has a positive relationship with food availability (Shimanaga et al. 2000). In the Hikurangi Margin region, profile curvature was most highly correlated with meiofaunal community structure in the surface sediment, whilst curvature and phaeopigment were most correlated with community structure in the subsurface sediment. As already noted, seafloor depressions tend to accumulate organic matter and increased meiofaunal settlement from the water flow than elevated slope, and thus influence community structure. The greater importance of phaeopigment for the subsurface community compared to surface community may be due to the generally low food availability in subsurface sediment layers, where limited shifts may have relatively strong effects on communities (Giere 2009).

In the Bay of Plenty, surface chlorophyll concentration was correlated most to community structure in the surface sediment, while kurtosis (a measure of habitat heterogeneity) was correlated most to community structure in the subsurface sediment. These results largely reflect similar patterns observed for abundance and diversity in the region.

### 2.5.4 Relative vulnerability of meiofauna communities to anthropogenic disturbance

Clear differences in meiofaunal community attributes between the two study regions imply potential regional differences in vulnerability to disturbance caused by bottom trawling, and other physical disturbances that may impact upon the seafloor in the future, such as seabed mining. In this study, trawling activity was noted to be thirty times greater in the Hikurangi Margin region compared to the Bay of Plenty region. Bottom trawling have been associated with sediment physical characteristics modification, reducing the availability of food within the sediment and altering habitat characteristics (Martín et al. 2014, Pusceddu et al. 2014a). These impacts have been linked with changes in meiofauna abundance and diversity, although not necessarily declines in these community measures (Hinz et al. 2008, Pusceddu et al. 2014a). However, short-term microcosm experiment on the effect of disturbance on deep-sea nematode colonisation on enriched and unenriched sediments showed that nematode abundance and diversity were significantly higher in the enriched sediment, suggesting that the presence of food can enhances meiofaunal recolonization, and resilience to disturbance (Gallucci et al. 2008b). Thus, meiofauna communities in the Hikurangi Margin, which experience higher surface water productivity and related food availability in the sediment, could be less vulnerable to the effects of disturbance (from bottom trawling or seabed mining) than those in the lower food availability sediments of the Bay of Plenty (Leduc et al. 2016b).

Within regions, fishing intensity was relatively high in seamount habitat, with mean fishing intensity approximately three times that of canyon, and six times that of slope habitats (Leduc et al. 2016), which implies greater vulnerability in seamount habitat than canyon and slope habitats. However, there was no difference between seamount communities and slope communities, compared to the difference between seamount and canyon communities. Thus, seamount and slope communities should be presumed to be equally vulnerable to disturbance.

Abundance was the only community attribute that differed significantly among habitats. The higher abundance at canyon habitats implies that the vulnerability of canyon communities to anthropogenic disturbance may be different from that of other deep-sea communities. Canyon communities differed from seamount and slope communities due to differences in the abundance of a number of shared taxa, but the former communities also supported slightly more rare taxa than slope and seamount communities. The presence of rare taxa can make a community more susceptible to disturbance when they occur at low densities, as it reduces the chances for successful recolonization, making them potentially vulnerable to localised extinction events. Canyon communities might also be more vulnerable to bottom trawling than other communities because of the generally steep topography of canyon habitats, which makes them prone to slope instability and turbidity flows following trawling events (Puig et al. 2012). This instability can have direct negative impacts on canyon meiofauna, since increased turbidity and sedimentation rates may cause sudden burial of infauna, and slope instability can removed organic-rich sediment down-slope to deeper parts of the canyon (Puig et al. 2012, Pusceddu et al. 2014a). Conversely, this organic matter enrichment from the upper canyon might favour meiofauna at deeper locations. Nevertheless, other physical characteristics of canyons, such as the presence of hard substrates and complex topography may protect areas of soft sediment from physical disturbance, providing a source for faunal recolonization to disturbed areas of the canyon (Puig et al. 2012).

The inclusion of seep habitat in the among-habitat comparison in the Hikurangi Margin showed that community abundance, diversity and community structure in seeps were different compared with canyon, slope and seamount habitats. Meiofauna seep communities maybe more vulnerable to disturbance because seep habitats: (1) have complex geological morphology and biogenic structures that increase the microhabitat heterogeneity, which in turns supports a distinct and diverse meiofaunal community that includes temporary meiofauna (such as priapulid larvae that were observed only at the seep habitat in this study); (2) the relatively small and localized seep microhabitats and the sometimes large distances between habitat patches (Greinert et al. 2010), can reduce chances for successful recolonization following anthropogenic disturbance and make seep communities potentially vulnerable to localised extinction events; and (3) potential modification of fluid flow patterns resulting from future large-scale extraction of methane hydrates might affect the persistence or structure of seep communities (Baco et al. 2010, Bowden et al. 2013). Seep habitat and megafauna in the Hikurangi Margin are known to have already been subjected to fishing impacts, and could be subjected to drilling for hydrates in the future (Baco et al. 2010, Bowden et al. 2013).

Clear differences in meiofaunal communities between surface and subsurface sediment layers also imply a relative vulnerability to disturbance, such as from bottom trawling or seabed mining. Bottom trawling can cause widespread damage to sediment column by increased sediment resuspension and deposition, sediment particle size alteration and reduced food availability within the sediment, including changes in oxygen penetration depths (Martín et al. 2014). These habitat modifications can have an impact on infauna (Schratzberger et al. 2009, Pusceddu et al. 2014a), and likely to be greater for fauna inhabiting surface of the sediment. Copepods and kinorhynchs, for example, are generally more prevalent in surface than subsurface sediment (Shimanaga et al. 2000, Grego et al. 2014), making them vulnerable to disturbance that may only affect the sediment surface. In contrast, nematodes can penetrate deeper into the sediment (up to 50 cm depending on sediment types) as they are more tolerant of low oxygen concentrations (Grego et al. 2014, Moens et al. 2014) and may therefore avoid some of the impacts. However, previous studies also found large differences in sediment compaction between untrawled and trawled areas, where surface sediment at trawled areas are much denser, which may affect the nematodes abilities to penetrate deeper in the sediment column (Martín et al. 2014, Pusceddu et al. 2014a). Meiofauna may also be resuspended by physical disturbances, instead of being killed directly because of their smaller sizes, and can quickly recolonize the sediment column. Copepods can rapidly recolonise sediments via active dispersal in the water column, while nematodes can only recolonise sediment directly from adjacent undisturbed sediment or through suspended sediment transport (Schratzberger et al. 2004). Nematodes can withstand disturbance and recover faster than other sediment inhabiting meiofaunal groups subjected to disturbance, probably due to their high abundance and short generation time (Sherman and Coull 1980, Schratzberger et al. 2002), and may thus dominate surface sediment meiofauna communities following trawling (Schratzberger et al. 2000). Deep-sea mining when it occurs could also cause disruption to the seafloor, but this is likely to result in surface and subsurface sediment meiofauna being equally vulnerable to disturbance. While some deep-sea minerals are found predominantly on the seafloor surface (e.g. phosphate and manganese nodules), present designs for mining tools are expected to disturb at least the upper 5–10 cm layer of soft sediment, and impact the meiofauna to this depth (Miljutin et al. 2011). Similarly, impacts from certain types of trawling will penetrate well into the subsurface layer (Martín et al. 2014). Thus, it is clear that meiofaunal communities are vulnerable to disturbance, and living deeper in the sediment does not necessarily offer protection.

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# Chapter 3

# Marked differences in deep-sea nematode communities between regions and sediment depths, but not habitats on the New Zealand margin: implications for vulnerability to disturbance

This chapter has been submitted for review to Progress in Oceanography journal.

## 3.1 Abstract

Deep-sea community attributes have been shown to vary at a range of spatial scales. However, identifying which scale(s) account for most of the variability in deep-sea communities remains difficult, as few studies have been designed in such a way as to allow meaningful comparisons across more than two spatial scales. In the present study, we investigated nematode diversity, community structure and trophic structure at different spatial scales (sediment depth (cm), habitat (1–100 km), and region (100–10000 km), while accounting for the effects of water depth, in two regions on New Zealand's continental margin. The greatest variability in community attributes were found between sediment depth layers and between regions, which explained 2–4 times more variability than habitats. The variability pattern among spatial scales, however, was not the same in each region. In the Bay of Plenty region, nematode diversity, community structure and trophic structure consistently showed increased variability from habitat and water depth to sediment depth. However, no consistent pattern was observed in Hikurangi Margin. Analyses suggest that nematode communities are mostly influenced by sediment characteristics and food availability, but that disturbance (fishing activity and bioturbation) also accounts for some of the observed patterns. The results of the study provide new insight on the relative importance of processes operating at different spatial scales in regulating nematode communities in the deep-sea, and indicate differences in community vulnerability to anthropogenic disturbance.

## 3.2 Introduction

Deep-sea communities vary at a range of spatial scales, including regional (Grassle and Maciolek 1992, Levin et al. 2001, Gambi and Danovaro 2006, Fonseca and Soltwedel 2009), bathymetry gradient (Rex 1981, Etter and Grassle 1992, Garcia et al. 2007, Sevastou et al. 2013), and local scales (Eckman and Thistle 1988, Gallucci et al. 2009, Rex and Etter 2010, Van Gaever et al. 2010, Lampadariou et al. 2013). Different biotic and environmental processes are likely to be operating at each of these spatial scales (Levin et al. 2001, Rex and Etter 2010, Bianchelli et al. 2013, Ingels and Vanreusel 2013), therefore understanding the processes regulating deep-sea biodiversity and community structure requires investigating patterns across all scales. Identifying which scale(s) account for most of the variability in deep-sea communities remains difficult, as few studies have been designed in such a way as to allow meaningful comparisons across more than two spatial scales (Fonseca et al. 2010, Bianchelli et al. 2013, Ingels and Vanreusel 2013, McClain and Rex 2015).

The most well established pattern in studies of deep-sea benthic communities is the gradual change in community composition (i.e., turnover or beta diversity) with water depth (Rex and Etter 2010, McClain and Rex 2015). Horizontal gradients in community composition are also often present but are usually weaker than depth-related gradients, except at upper bathyal zones under coastal influences (McClain and Rex 2015). Few studies have compared variation in megafaunal communities across spatial scales, but the evidence available to date suggests that megafauna communities vary more strongly at regional (100 km) than local (km) scales (Taylor et al. 2016). In contrast, macro- and meiofaunal communities typically show high local scale variation, a pattern generally interpreted from species accumulation curves that rarely reach an asymptote (Snelgrove and Smith 2002, McClain and Rex 2015).

Nematodes receive less attention in deep-sea ecological studies because their high abundance, high diversity and high proportion of undescribed species makes processing samples labour intensive, and taxonomic expertise is limited (Miljutin et al. 2010, Rex and Etter 2010). However, nematodes often dominate benthic communities and typically constitute more than 90% of infaunal metazoans (Grove et al. 2006, Giere 2009). Studies on deep-sea nematode are usually restricted to a single scale, with a focus on patterns related to bathymetry (Vanreusel et al. 2000, Sevastou et al. 2013), or habitats (Garcia et al. 2007, Bianchelli et al. 2010); or two scales, such as between sediment depths and sites (Ansari 2000, Van Gaever et al. 2004).

A high degree of centimetre-scale variation has been observed for deep-sea nematodes communities both horizontally (Gallucci et al. 2009) and vertically into the sediments (Vincx et al. 1994, Leduc et al. 2010b), although horizontal patchiness in the deep sea remains under studied relative to vertical patchiness. Shallow water studies have shown that horizontal patchiness may result from the distribution of organic matter (Rice and Lambshead 1994), which can be generated by the interaction between small-scale topography and hydrodynamic regime (waves and currents), as well as biological activities such as bioturbation and construction of biogenic structures by other benthic organisms (Reise 2002). A study by Gallucci et al. (2009), however, did not find any correlation between food availability and nematode distribution at this scale in the deep sea. Vertically in the sediment, nematode diversity is generally higher in the surface sediment and decreases in subsurface sediments (Vincx et al. 1994, Ingels et al. 2011b). Vertical distribution in the sediment is mainly controlled by decreasing food and oxygen availability, and the presence of toxic sulphides in subsurface sediments. Nematode community structure typically shows a pronounced pattern between surface and subsurface sediments, with some genera such as *Acantholaimus*, *Desmoscolex,* and *Halalaimus* showing a preference for surface sediments, whereas genera tolerant of low oxygen conditions such as *Sabatieria* are generally most abundant in subsurface sediment layers (Vanaverbeke et al. 1997b, Leduc et al. 2010b, Leduc et al. 2015).

At larger scales, deep-sea habitats such as canyons and seamounts often contribute significantly to deep-sea nematode diversity (Vanreusel et al. 2010b, Ingels et al. 2011a). For example, canyons are characterized by genera such as *Daptonema*, a genus considered to be well adapted to fine sediment environments and hypoxic subsurface layers of organic rich sediments (Wetzel et al. 2002, Leduc et al. 2014), which probably reflects hydrodynamically active conditions and high sediment transport and accumulation rates (Vanreusel et al. 2010b, Ingels et al. 2011a). Seamount habitats, which are often characterized by strong current activity and coarse biogenic sediments composed of corals and mollusc shells, are generally characterised by relatively high abundances of desmoscolecid, epsilonematid and draconematid nematodes (Pusceddu et al. 2009, Vanreusel et al. 2010b, Zeppilli et al. 2014) which are adapted to attaching to different type of substratum and feeding on biofilms (Raes et al. 2007, Zeppilli et al. 2014). Upper continental slopes are generally characterised by relatively high abundance of *Sabatieria*, species of which are well adapted to fine sediment environments with high organic input and low oxygen levels (Vanreusel 1990, Schratzberger et al. 2009, Vanreusel et al. 2010b, Ingels et al. 2011a), whereas the genera *Acantholaimus* and *Thalassomonhystera* generally occur on the lower continental slope and abyssal plains, and are typically associated with low food input (De Mesel et al. 2006a, Vanreusel et al. 2010b, Ingels et al. 2011a).

Beyond habitat-related community patterns, regional differences can also account for some of the variation in nematode diversity and composition (Danovaro et al. 2009, Fonseca and Soltwedel 2009, Leduc et al. 2012b, Gambi et al. 2014). Large-scale variability of nematode communities is thought to be mainly controlled by a difference in productivity gradients, temperature, and hydrodynamic regimes (Levin et al. 2001, Danovaro et al. 2004, Danovaro et al. 2009, Fonseca and Soltwedel 2009). Geographical barriers (Lampadariou and Tselepides 2006, Fonseca et al. 2007) and large-scale natural disturbance (Lambshead et al. 2001) can also influence regional patterns of nematode distribution. Some studies have found variability in community patterns within a region to be similar to variability between regions, showing high similarity in the regional species pool between regions (Fonseca and Soltwedel 2009, Leduc et al. 2012b). This pattern is thought to derive from nematode passive dispersal by currents and also factors acting at smaller scales (i.e. among-site).

In one of the first multi-scale studies on deep-sea nematode communities, Fonseca et al. (2010) showed that variability in nematode genus diversity was highest among sediment layers, whilst genus community composition showed greater variability between margins and among cores than with depth, latitude or among sediment depths. More recently Ingels and Vanreusel (2013) showed that variability in nematode genus diversity was greater between sediment layers than between slope and canyon habitats or along a 700–4300 m depth gradient, whereas community composition showed greatest variability between stations. Other studies have shown significant differences in nematode community composition between regions, habitats, and along water depth gradients in the Mediterranean (Bianchelli et al. 2013, Danovaro et al. 2013, Gambi et al. 2014); these authors noted that although community dissimilarity is high across all scales, differences in community composition were greatest at the largest spatial scale investigated and no significant patterns were found at the metre to kilometre scales.

Nematode trophic structure can be a useful tool in exploring variation in benthic food webs across spatial scales. The multi-scale study by Ingels and Vanreusel (2013) has shown that greater variability in nematode functional diversity (which included trophic diversity) occurred between sediment depths, than between habitats or water depths. Deep-sea nematodes are typically dominated by microvores, which feed selectively on bacteria, and deposit feeders, which feed less selectively on detrital particles and associated microbiota (Moens and Vincx 1997, Vanaverbeke et al. 1997a, Giere 2009, Danovaro et al. 2013). Trophic group composition often varies between sediment layers, which can reflect available food sources and oxygen supply within sediment (Vanreusel et al. 1995, Neira et al. 2013). Predators and omnivores for example, are typically associated with sediments with relatively large amounts of organic matter, and can be found either on surface sediment or at deeper oxygenated sediment layer with higher food availability, whereas some deposit feeders (i.e. *Sabatieria*, *Theristus*) can dominate deeper layers of sediment since they can thrive in low oxygen conditions (Steyaert et al. 2003, Neira et al. 2013). Canyons are sometimes characterized by a higher abundance of facultative predators and predators compared to slope (Ingels et al. 2009). Facultative predators and predators are typically larger and longer compared to other feeding types, which makes them more agile in disturbed canyon sediments and enhances their survival rate (Ingels et al. 2009). A study by Pusceddu et al. (2009) showed that areas on seamounts with different sediment organic matter harbour different types of nematode trophic groups. Areas on seamounts characterized by high food availability were dominated by predators and omnivores, which suggests increased food availability will favour nematode abundance and hence increase the availability of prey in the area, whereas epigrowth feeders are more abundant in areas of seamounts characterized by low food availability. Epigrowth feeders are often prominent in deep-sea sediments where inputs of fresh and intact diatom cells is absent or limited, which suggests that they can obtain food by scraping microbes from sediment particles or mucus threads (Moens and Vincx 1997, Vanreusel et al. 2010b, Moens et al. 2014). Whilst the abundance of particular feeding groups may not always necessarily reflect the abundance of their presumed food sources, different trophic groups respond to environmental factors differently, and the presence of a trophically diverse community may allow persistence of the ecosystem function following disturbance (Walker 1995, Naeem 1998, De Mesel et al. 2006a).

Disturbance can play an important role in shaping nematodes communities (Schratzberger et al. 2009). Disturbance can occur at a variety of spatial and temporal scales and includes events induced by physical (i.e. turbidite, bottom trawling), or biological sources (i.e. bioturbation and predation) (Heip et al. 2001, Lambshead et al. 2001, Pusceddu et al. 2014a). Physical disruption by bottom trawling can have pronounced effects on deep-sea soft sediment communities (Pusceddu et al. 2014a), with generally negative impacts on macro-infaunal communities (Hansson et al. 2000, Hinz et al. 2009). However, shallow water habitat studies suggest that trawling may have a positive (Liu et al. 2011), negative (Schratzberger and Jennings 2002, Hinz et al. 2008), or only minor impact (Schratzberger et al. 2002, Lampadariou et al. 2005, Liu et al. 2009) on nematode communities. Nematodes are generally considered to be more resilient to physical disturbance than larger organisms because they are less likely to be killed and can recover more quickly (Schratzberger et al. 2002, Whomersley et al. 2009, Leduc and Pilditch 2013). At smaller scales, natural disturbance such as bioturbation and predation can influence vertical patterns of nematodes in the sediment (Lambshead et al. 1995, Moodley et al. 2000). Bioturbation plays a prominent role in structuring or altering the properties of the sediment column, where macrofauna can rapidly mix fresh deposited organic matter into the sediments, while burrowing megafauna can subduct phytodetritus to even greater depths (Heip et al. 2001, Hughes and Gage 2004). Studies have shown that bioturbation by macrofauna enhance nematode abundance in subsurface sediment layers through increased downward transport of food (Lambshead et al. 1995, Moodley et al. 2000). Biogenic structures produced by benthic macrofauna can also enhance nematodes species diversity by acting as traps for organic matter, thus promoting diversity in the subsurface sediments (Zuhlke et al. 1998, Olafsson 2003, Callaway 2006, Moens et al. 2014).

New Zealand's Exclusive Economic Zone (EEZ) is topographically diverse, and encompasses areas in which several seabed habitat types occur in close proximity to each other, which provides opportunity for direct comparisons between nematode communities among and within habitats, while minimising confounding factors introduced by spatial separation. The main aims of this study were to: (1) compare nematode community attributes (genus diversity, community structure and trophic structure) at different spatial scales (sediment depth (cm), habitat (1–100 km), and region (100–10000 km), while accounting for the effects of water depth; and (2) describe relationships between the patterns observed and environmental variables (i.e. sediment characteristics, topography variables, food availability), and disturbance from bottom trawling and bioturbation by macro-infauna and mega-epifauna. Nematode abundance is not included in the analysis of the present study because this community metric has been included in a previous analysis of meiofauna (Rosli et al. 2016a). Meiofauna abundance patterns generally reflect nematode abundance patterns, since nematode typically comprise more than 90% of the total abundance of metazoan meiofauna. An additional objective of the present study was to evaluate the relative vulnerability of nematode communities to anthropogenic activities such as trawling, and possible future seabed mining in the New Zealand EEZ.

## 3.3 Material and Methods

### 3.3.1 Study area and sampling design

The study areas comprise two regions: the Hikurangi Margin and Bay of Plenty in the waters off New Zealand (see Figure 2.1, p. 66). These two regions were selected because each encompasses a range of benthic habitats within a restricted geographic area, thus facilitating comparisons between their associated faunas that are unconfounded by distance. The Hikurangi Margin study region is located to the north-east of the South Island, hosts many submarine canyons on its continental slope, and also includes other deep-sea habitats such as seamounts, and cold seeps (Mountjoy et al. 2009, Ruff et al. 2013). The Bay of Plenty study region, located to the north-east of the North Island, also includes slope, canyon and seamount habitats, with hydrothermal vents on some of the latter (Wysoczanski and Clark 2012). The Hikurangi Margin hosts significant fisheries, including hoki (*Macruronus novaezelandiae*), alfonsino (*Beryx splendens*) and orange roughy (*Hoplostethus altanticus*) which occur across all habitats (Clark 1995). The Bay of Plenty region supports some deep-sea trawl fisheries, including orange roughy, black cardinal fish (*Epigonus telescopus*) and alfonsino (*Beryx decadactylus*) (Clark and O'Driscoll 2003).

Sampling was conducted at slope, canyon and seamount sites using RV *Tangaroa* during National Institute of Water and Atmospheric Research (NIWA) voyage TAN1004 (April 2010) in the Hikurangi Margin, and voyage TAN1206 (April 2012) in the Bay of Plenty (Figure 2.1). Sample sites were selected to avoid areas of high fishing intensity; however, bottom trawling is prevalent across the entire New Zealand margin and so fishing intensity was included as a variable in the analysis to examine the possible influence of any past anthropogenic disturbance on faunal patterns observed (see below). Sampling was undertaken at four water depth strata (700, 1000, 1200 and 1500 m) at each habitat site to allow for the control of water depth effects in the statistical analyses and provide a more robust evaluation of any scale effect on community structure. Sampling for nematodes was not successful at some sites/depths on the Hikurangi Margin, and from seamount and vent habitats in the Bay of Plenty (due to the limited occurrence of soft sediment), so data from these sites were not included in the analysis (Table 2.1, p. 69). While meiofauna have been sampled previously from seep sites on the Hikurangi Margin (Rosli et al. 2016a), there were no available data for nematodes at the genus level of identification to include in the present analysis. At each sampling station, a towed camera was deployed along transects to ascertain the type of substratum, benthic mega-epifauna, and bioturbation marks on the seafloor before the water column and seafloor was disturbed by sampling gear. Deployment of the multi-corer, which targeted soft sediment substrates, was directed based on information from multibeam echo-sounder (MBES) bathymetric maps and observations from the camera transects.

Macrofaunal and mega-epifaunal communities were also sampled using towed cameras, corers, trawls, and epibenthic sled at the same depth strata at each habitat during the two main surveys, and the results of the analyses of data for these components of the benthos have been and will be reported elsewhere (Bowden et al. 2016, Leduc et al. 2016b, Rowden et al. submitted). Data on meiofaunal taxa (at higher taxonomic group level – copepods, annelids, nematodes etc.) are reported in Rosli et al. (2016a).

### 3.3.2 Sampling and sample processing

Meiofauna and sediment samples were collected using an Ocean Instruments MC-800A multicorer (internal diameter core = 9.52 cm). At each station, one to three cores were used from 1–2 multicorer deployments for nematode samples (see Table 2.1), and one core for sediment analyses. Each nematode sample consisted of a subcore (26 mm internal diameter), was sliced into three vertical fractions: 0–1 cm, 1–3 cm and 3–5 cm sediment depth layers and preserved in 10% buffered formalin. Preliminary analyses showed there was a small difference between 1–3 cm and 3–5 cm layers, therefore these layers were combined prior to sieving. Samples were rinsed on a 1 mm sieve to remove macro-infauna and on a 45 µm mesh to retain nematodes. Nematodes were extracted from the sieved sediment by Ludox flotation (Somerfield and Warwick 1996) and 100–130 individuals (or all nematodes if nematode abundance was lower than 100 specimens per sample) were picked out from each sediment layer. Nematodes were transferred to glycerine and mounted onto permanent slides (Somerfield and Warwick 1996). Nematodes were identified to genus according to Platt & Warwick (1983, 1988) , Warwick et al. (1998), Schmidt-Rhaesa (2014) and the primary literature. Nematode individuals that could not be identified to genus were identified to family level. Each nematode genus was assigned to one of six feeding groups (microbial feeder, deposit feeder, ciliate feeder, facultative predator or predator) based on their buccal structures using the modified classification of Wieser (1953) proposed by Moens and Vincx (1997) (refer to Appendix I).

The following physical and biogeochemical parameters were determined from the sediment samples: mean particle size (geometric), sorting, skewness, kurtosis, %silt/clay, particle size diversity (PSD; calculated using Shannon-Wiener diversity index of eleven particle size classes (afterEtter and Grassle 1992)), calcium carbonate content (%$CaCO_3$), organic matter content (%OM), organic carbon content (%OC), nitrogen content (%N), chlorophyll *a* concentration (chl *a*) and phaeopigment concentration (phaeo) using methods described by (Nodder et al. (2003), Grove et al. (2006)) and Nodder et al. (2007). The %$CaCO_3$ was determined from the top 5 cm of sediment, whereas organic matter (%OM, %OC and %N) was determined from the top 1 cm of sediment.

### 3.3.3 Additional environmental characterisation

Surface water chlorophyll concentrations were determined using ocean colour estimates of surface chlorophyll concentrations as a proxy for long-term inter-station variability in primary production (NASA SeaWiFS Project: http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/8Day/9km/chlor_a). The 9 km composited data of surface chlorophyll were further composited to 90 × 90 km pixels centred on the location of each sample station. The mean value for 1997–2010 was computed for each station.

Seafloor habitats at the study sites were characterised using seafloor morphology derivatives from MBES data gridded at 25 m resolution. The following topographic variables were derived for each sampling station: depth, slope (steepest gradient to any neighbouring cell), curvature (change of slope), plan curvature (curvature of the surface perpendicular to the slope direction), and profile curvature (curvature of the surface in the direction of slope). A further set of derivatives was calculated for the standard deviation of depth, depth range, standard deviation of the slope (a proxy measure for slope roughness), and terrain rugosity based on a 3, 5, 7, and 15 grid cell focal means. A total of eighteen topographic variables were used in the analysis. Methods for the determined topographic variables are provided by Nodder et al. (2013).

Trawl effort data were used to quantify the extent of commercial fishing intensity conducted on the seafloor in the study regions. Estimates of fishing intensity for a 5 km x 5 km cell grid covering the New Zealand Exclusive Economic Zone were derived using the number of tows and an estimate of swept area derived from the trawl width and either the distance between start and finish positions, or the tow duration (Black and Wood 2014). Fishing intensity at each of the study stations was estimated for the total trawled area within the corresponding 5 km x 5 km cell integrated over a period of ten years prior to sampling. Trawl effort data were sourced from the period July 1980 to March 2011 from the trawl database of the New Zealand Ministry for Primary Industries.

The possible effects of biological disturbance (mega-epifaunal and macro-infaunal) in structuring nematode communities were investigated by including the following proxies of bioturbation: counts of bioturbation marks derived from camera transects (Bowden et al. 2016), total macro-infauna abundance, and abundance of macro-infaunal deposit feeders and grazers (Leduc et al. 2016b). Mega-epifaunal bioturbation marks (number of counts standardised to numbers per 1000 $m^{-2}$) were split into surface (i.e. tracks, faecal coils, hemichordate spirals, and total surface bioturbation) and subsurface (i.e. burrows, mounds, ring of burrows, pits, pepperpots, and total subsurface bioturbation) disturbance sources. Macro-infauna trophic group abundance (i.e. deposit feeder and grazer) and total macro-infauna abundance of all trophic groups were recorded as individuals core $^{-1}$ from 0–5 cm sediment layer and then averaged by sampling site. Only the trophic groups of deposit feeder and grazer were used as source of disturbance; since grazers feed on the surface sediment, while deposit feeders may feed on the surface as well as in deeper sediment, which disturbs the sediment column and may have an impact on nematode communities.

### 3.3.4 Statistical analysis

Statistical analyses were conducted to test the following main hypotheses: that there is no difference in nematode community attributes (diversity, community structure, and trophic structure) at different spatial scales (sediment layers, habitats, and regions), and that there is no relationship between disturbance or environmental variables and nematode community attributes.

Analyses of nematode community attributes were conducted using statistical routines in the multivariate software package PRIMER v6 with PERMANOVA (Clarke and Gorley 2006, Anderson et al. 2008). Nematode diversity was quantified using the rarefaction method (Hurlbert 1971) for a sample of forty individuals [EG (40)] since four stations (two in Hikurangi Margin, and two in Bay of Plenty) were characterised by lower numbers of nematodes (41–124 individuals). Gamma diversity was calculated as the total diversity of the entire region.

Analysis of community structure was based on square-root transformed abundance data, while trophic structure analysis was based on standardisation of abundance data. Similarity matrices for the community structure analysis were built using Bray-Curtis similarity (Clarke and Gorley 2006). Similarity matrices for nematode diversity were based on Euclidean distance similarity matrices of untransformed data (Anderson et al. 2008).

The PERMANOVA routine in PRIMER was used to investigate the relative influences of region, habitat, water depth strata and sediment depth on community attributes (Anderson et al. 2008). A first stage analysis was conducted to compare all the spatial scales and water depth in one analysis using a five factor design, with the factors region (random; Hikurangi Margin and Bay of Plenty), habitat (fixed; canyon, seamount, slope), water depth (fixed; 700, 1000, 1200, and 1500 m), sediment depth (fixed; 0–1 and 1–5cm), and cores (random, nested within habitat and water depth). Region was treated as a random factor because the effect of region was considered unpredictable. The two regions are just two possibilities among many possible regional effects, and region is therefore ‘random’ rather than ‘fixed’ (like habitats). Second stage analyses were conducted for each region separately to investigate the patterns in more detail within each region using a four factor design (factors as above but omitting region). P-values for individual predictor variables were obtained using 9999 permutations. Lack of independence between stations due to geographical proximity (i.e. spatial autocorrelation/structure) is common in natural communities and poses problems for the interpretation of ecological patterns

(Legendre 1993). In particular, failure to take into account the spatial component of ecological variation may affect tests of statistical significance when investigating relationships between structural community structure and environmental parameters (Legendre and Troussellier 1988). PERMANOVA is sensitive to differences in multivariate dispersion among groups, therefore the PERMDISP routine in PRIMER was used to test for homogeneity of dispersion when significant factors were found (Anderson et al. 2008). The main factor test was followed by pair-wise tests when significant effects were found. A square root of estimates of components of variation (√ECV) and percentage of estimates of components of variation (%ECV) were used to allow comparison among the factors (Anderson et al. 2008). Non-metric multi-dimensional scaling plots (MDS) were used to visualise multivariate patterns. The SIMPER routine was used to identify which genera were responsible for observed differences in community structure (i.e. beta diversity = measure of community similarity between habitats).

The DISTLM routine was used to investigate relationships between nematode community attributes, environmental variables and disturbance proxies. DISTLM analysis was conducted for surface (0–1 cm) and subsurface (1–5 cm) sediments separately. The full set of environmental variables was partitioned into five sets of variables, i.e., spatial (water depth), sediment characteristics (mean particle size, sorting, skewness, kurtosis, %silt/clay, PSD, %$CaCO_3$, %OM, %N, %OC, chl *a*, phaeopigment), primary productivity (surface chlorophyll concentration), disturbance (fishing intensity, macro-infauna trophic group abundance, total macro-infauna abundance and mega-epifaunal bioturbation marks), and topography variables (18 variables), and were tested for collinearity using a Draftsman plot. Environmental variables that were strongly correlated (r > 0.8) were removed prior to analysis (Appendix B). Relationships between environmental parameters and community attributes were initially examined by analysing each predictor separately (marginal tests). Partial regressions were used to better characterise the relationships and to account for the effect of the remaining variables. Sequential tests were conducted using step-wise selection procedure and the $R^2$ as selection criterion. Latitude and longitude were fitted first in the models of community structure to take into account the effect of geographical proximity. P-values for individual predictor variables were obtained using 9999 permutations.

## 3.4 Results

A total of 179 nematode genera belonging to thirty-nine families were identified from the samples. The most abundant genera in both regions were *Sabatieria* (12%), *Halalaimus* (8–11%) and followed by *Daptonema* (9%) in Hikurangi Margin and *Acantholaimus* (8%) in Bay of Plenty. The family Chromadoridae was the most diverse family in this study (nineteen genera), followed by Desmodoridae (fifteen), Comesomatidae (fourteen) and Xyalidae (fourteen).

### 3.4.1 First stage analyses

Results of the analysis of environmental data and disturbance proxy data have been published previously by Bowden et al. (2016), Leduc et al. (2016) and Rosli et al. (2016), but are included here for completeness. Analysis of environmental variables showed substantial variability between regions, mostly in surface water chlorophyll concentration, sediment phaeopigment concentration, organic carbon content of the sediment, and proxies for disturbance (Figure 3.1).

These five variables were substantially higher (2–30 times) in the Hikurangi Margin than the Bay of Plenty, except for burrows (mega-epifaunal bioturbation marks) which was four times higher in Bay of Plenty than Hikurangi Margin region.

There was a significant difference in nematode diversity between regions, habitats, water depth, sediment depths and their interactions (PERMANOVA, $P < 0.05$; Table 3.1). Diversity tended to be slightly higher in Bay of Plenty than in the Hikurangi Margin, both in surface and subsurface sediments. In the Hikurangi Margin region, diversity tended to increase with water depth in the subsurface sediment, except for slope habitat at deeper depth, and was also lower in subsurface sediment than surface sediment across all habitats (Figure 3.2). Percentage of estimates of components of variation (%ECV) showed that region (12%) explained higher proportions of variability in diversity, compared to habitat (9%), sediment depth (8%), and water depth (7%) which showed similar proportions (Table 3.1; Figure 3.3). Even though significant, the diversity difference between Bay of Plenty (mean 19.2) and Hikurangi Margin region (mean 18) was small.

Nematode community structure differed significantly between regions and sediment depths, but not among habitats or water depths (PERMANOVA, $P < 0.05$; Table 3.1; Figure 3.4). Interactions between region and all other factors were also significant. There was no significant difference in multivariate dispersion between regions (PERMDISP, $P > 0.05$). Percentage of estimates of components of variation showed that region (14%) and sediment depth (13%) explained relatively high proportions of variability in community structure, whereas habitat (4%) and water depth (3%) accounted for smaller proportions (Table 3.1). *Sabatieria* was the highest contributor to between-region dissimilarity, followed by *Acantholaimus* and

*Daptonema*. Average abundance of *Acantholaimus*, *Molgolaimus* and *Syringolaimus* was higher in the Bay of Plenty region than in Hikurangi Margin, while *Sabatieria*, *Daptonema*, and *Paramonohystera* showed the opposite trend (SIMPER; Table 3.2).

Nematode trophic structure differed significantly different between regions, habitats, and sediment depths, but not among water depths (PERMANOVA, $P < 0.05$; Table 3.1). Interactions between region and water depth, region and sediment depth, and region, habitat and water depth were also significant. Percentage of estimates of components of variation showed that sediment depth (32%) explained almost four times as much variability in trophic structure than region (8%), habitat (7%) or water depth (1%) (Table 3.1; Figure 3.3). Deposit feeders were the highest contributor to between-region dissimilarity, followed by microvores and epigrowth feeders. Average percentage abundance of epigrowth feeders and ciliate feeders were higher in the Bay of Plenty than in Hikurangi margin, while the rest of nematode trophic groups showed the opposite trend (SIMPER; Table 3.2; Figure 3.5).

Table 3.1. Results of PERMANOVA analysis test on nematode attributes for the effects of region between Hikurangi Margin and Bay of Plenty study region. Significant factors at the 5% level are shown in bold. [df = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistic, P = Probability, Unique perms = number of unique permutations, √ECV = square root of estimates of components of variation, Re = region, Ha = habitat, Wd = water depth, Sd = sediment depth].

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | √ECV | ECV% |
|---|---|---|---|---|---|---|---|---|
| **Diversity** | | | | | | | | |
| Re | 1 | 133.6 | 133.6 | 25.876 | **0.0002** | 9856 | 1.1 | 11.8 |
| Ha | 2 | 102.3 | 51.2 | 5.585 | **0.0205** | 9953 | 0.9 | 9.0 |
| Wd | 3 | 78.7 | 26.2 | 2.87 | **0.0470** | 9943 | 0.7 | 7.3 |
| Sd | 1 | 40.7 | 40.7 | 5.817 | **0.0332** | 9959 | 0.8 | 8.4 |
| Re x Ha | 1 | 6.9 | 6.9 | 1.345 | 0.3116 | 9848 | 0.2 | 2.0 |
| Re x Wd | 3 | 20.4 | 6.8 | 1.317 | 0.3163 | 9955 | 0.3 | 2.7 |
| Re x Sd | 1 | 8.7 | 8.7 | 2.998 | 0.1068 | 9834 | 0.3 | 3.5 |

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | √ECV | ECV% |
|---|---:|---:|---:|---:|---:|---:|---:|---:|
| Ha x Wd | 5 | 46.8 | 9.4 | 0.408 | 0.9465 | 9945 | -1.0 | -10.7 |
| Ha x Sd | 2 | 10.8 | 5.4 | 1.387 | 0.3604 | 9963 | 0.3 | 2.6 |
| Wd x Sd | 3 | 81.5 | 27.2 | 3.377 | **0.0247** | 9947 | 1.0 | 10.6 |
| Re x Ha x Wd | 3 | 97.6 | 32.5 | 6.302 | **0.0046** | 9951 | 1.5 | 15.4 |
| Re x Ha x Sd | 1 | 3.3 | 3.3 | 1.149 | 0.3019 | 9833 | 0.1 | 1.4 |
| Re x Wd x Sd | 3 | 22.9 | 7.6 | 2.631 | 0.0876 | 9950 | 0.6 | 6.4 |
| Ha x Wd x Sd | 5 | 25.2 | 5.0 | 0.766 | 0.6886 | 9941 | -0.5 | -5.1 |
| Re x Ha x Wd x Sd | 3 | 23.7 | 7.9 | 2.719 | 0.0866 | 9949 | 0.9 | 9.3 |
| Residuals | 151 | 909.5 | 6.0 |  |  |  | 2.5 | 25.4 |
| Total | 258 | 1848.5 |  |  |  |  |  | 100 |
|  |  |  |  |  |  |  |  |  |
| **Community structure** |  |  |  |  |  |  |  |  |
| Re | 1 | 34755 | 34755 | 27.696 | **0.0001** | 9941 | 18.4 | 13.9 |
| Ha | 2 | 8616.9 | 4308.5 | 1.506 | 0.0903 | 9904 | 5.4 | 4.1 |
| Wd | 3 | 8423.6 | 2807.9 | 1.133 | 0.2765 | 9885 | 3.3 | 2.5 |
| Sd | 1 | 17830 | 17830 | 5.578 | **0.0065** | 9944 | 16.9 | 12.8 |
| Re x Ha | 1 | 3257.5 | 3257.5 | 2.596 | **0.0034** | 9919 | 6.4 | 4.8 |
| Re x Wd | 3 | 8015 | 2671.7 | 2.129 | **0.0007** | 9882 | 7.6 | 5.7 |
| Re x Sd | 1 | 4936.6 | 4936.6 | 6.056 | **0.0002** | 9927 | 9.1 | 6.9 |
| Ha x Wd | 5 | 8975.4 | 1795.1 | 0.72 | 0.9803 | 9834 | -7.7 | -5.8 |
| Ha x Sd | 2 | 1997.7 | 998.86 | 0.763 | 0.8135 | 9880 | -3.9 | -2.9 |
| Wd x Sd | 3 | 5085.9 | 1695.3 | 1.232 | 0.1631 | 9863 | 4.6 | 3.5 |
| Re x Ha x Wd | 3 | 9478.6 | 3159.5 | 2.518 | **0.0001** | 9896 | 12.4 | 9.4 |
| Re x Ha x Sd | 1 | 1664.5 | 1664.5 | 2.042 | **0.0290** | 9942 | 5.9 | 4.4 |
| Re x Wd x Sd | 3 | 4132.9 | 1377.6 | 1.69 | **0.0207** | 9885 | 6.7 | 5.1 |
| Ha x Wd x Sd | 5 | 6012.4 | 1202.5 | 1.077 | 0.3521 | 9843 | 3.8 | 2.9 |
| Re x Ha x Wd x Sd | 3 | 3341.9 | 1114 | 1.366 | 0.1142 | 9896 | 6.9 | 5.3 |
| Residuals | 151 | 198720 | 1316 |  |  |  | 36.3 | 27.5 |
| Total | 258 | 435560 |  |  |  |  |  | 100 |
|  |  |  |  |  |  |  |  |  |
| **Trophic structure** |  |  |  |  |  |  |  |  |
| Re | 1 | 1548.4 | 1548.4 | 12.148 | **0.0004** | 9955 | 3.8 | 8.2 |
| Ha | 2 | 1223.2 | 611.6 | 5.060 | **0.0087** | 9950 | 3.1 | 6.6 |
| Wd | 3 | 955.2 | 318.4 | 0.959 | 0.5219 | 9938 | -0.7 | -1.4 |
| Sd | 1 | 11720 | 11720 | 26.406 | **0.0001** | 9947 | 14.8 | 32.1 |
| Re x Ha | 1 | -27.0 | -27.0 | Negative | n/a | n/a | -1.8 | -3.8 |
| Re x Wd | 3 | 988.2 | 329.4 | 2.584 | **0.0416** | 9953 | 2.9 | 6.2 |
| Re x Sd | 1 | 641.1 | 641.1 | 3.558 | **0.0279** | 9958 | 3.1 | 6.6 |
| Ha x Wd | 5 | 1964.7 | 392.9 | 0.732 | 0.7941 | 9916 | -3.2 | -6.9 |
| Ha x Sd | 2 | 232.6 | 116.3 | 0.963 | 0.5390 | 9944 | -0.5 | -1.1 |
| Wd x Sd | 3 | 481.3 | 160.4 | 0.831 | 0.6678 | 9947 | -1.7 | -3.6 |
| Re x Ha x Wd | 3 | 1834.3 | 611.4 | 4.796 | **0.0019** | 9955 | 6.2 | 13.6 |
| Re x Ha x Sd | 1 | 140.2 | 140.2 | 0.778 | 0.4963 | 9963 | -1.3 | -2.8 |

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | √ECV | ECV% |
|---|---|---|---|---|---|---|---|---|
| Re x Wd x Sd | 3 | 789.5 | 263.2 | 1.460 | 0.1988 | 9941 | 2.6 | 5.6 |
| Ha x Wd x Sd | 5 | 1214.6 | 242.9 | 0.988 | 0.5251 | 9925 | -0.7 | -1.5 |
| Re x Ha x Wd x Sd | 3 | 914.5 | 304.8 | 1.692 | 0.1520 | 9941 | 4.5 | 9.7 |
| Residuals | 151 | 33824 | 224 |  |  |  | 15.0 | 32.5 |
| Total | 258 | 83468 |  |  |  |  | 46.1 | 100 |

Table 3.2. SIMPER analysis results showing nematode genera accounting community dissimilarity between the Hikurangi Margin and Bay of Plenty study regions (cut-off applied at 25% contribution). [Av.abund = average nematode relative abundance (community structure = individual 10 cm$^{-2}$; trophic structure (%)), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance is shown in bold.

| Genera | Av.Abund | Av.Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
|  | Hikurangi Margin | Bay of Plenty |  |  |  |  |
| Community structure |  |  |  |  |  |  |
| *Sabatieria* | **48.2** | 40.6 | 2.33 | 1.3 | 3.9 | 3.9 |
| *Acantholaimus* | 9.7 | **27.7** | 1.82 | 1.54 | 3.0 | 6.9 |
| *Daptonema* | **34.9** | 14.1 | 1.75 | 1.3 | 2.9 | 9.8 |
| *Molgolaimus* | 11.0 | **17.2** | 1.48 | 1.17 | 2.5 | 12.3 |
| *Paramonohystera* | **20.0** | 9.2 | 1.47 | 1.31 | 2.5 | 14.7 |
| *Halalaimus* | **44.9** | 28.6 | 1.32 | 1.24 | 2.2 | 16.9 |
| *Dichromadora* | **13.8** | 5.8 | 1.26 | 1.37 | 2.1 | 19.0 |
| *Endeolophos* | **10.7** | 4.2 | 1.25 | 1.27 | 2.1 | 21.1 |
| *Sphaerolaimus* | **13.5** | 7.8 | 1.20 | 1.29 | 2.0 | 23.1 |
| *Syringolaimus* | 0.8 | **8.0** | 1.19 | 1.19 | 2.0 | 25.1 |
|  |  |  |  |  |  |  |
| Trophic structure |  |  |  |  |  |  |
| Deposit feeders | **31.1** | 29.3 | 7.06 | 1.34 | 30.3 | 30.3 |
| Microvores | **34.2** | 33.9 | 6.65 | 1.37 | 28.5 | 58.8 |
| Epigrowth feeders | 25.1 | **29.3** | 5.44 | 1.28 | 23.4 | 82.2 |
| Predators | **5.8** | 4.5 | 2.04 | 1.18 | 8.8 | 90.9 |
| Facultative predators | **2.7** | 1.8 | 1.36 | 0.91 | 5.8 | 96.8 |
| Ciliate feeders | 1.0 | **1.2** | 0.75 | 0.9 | 3.2 | 100.0 |

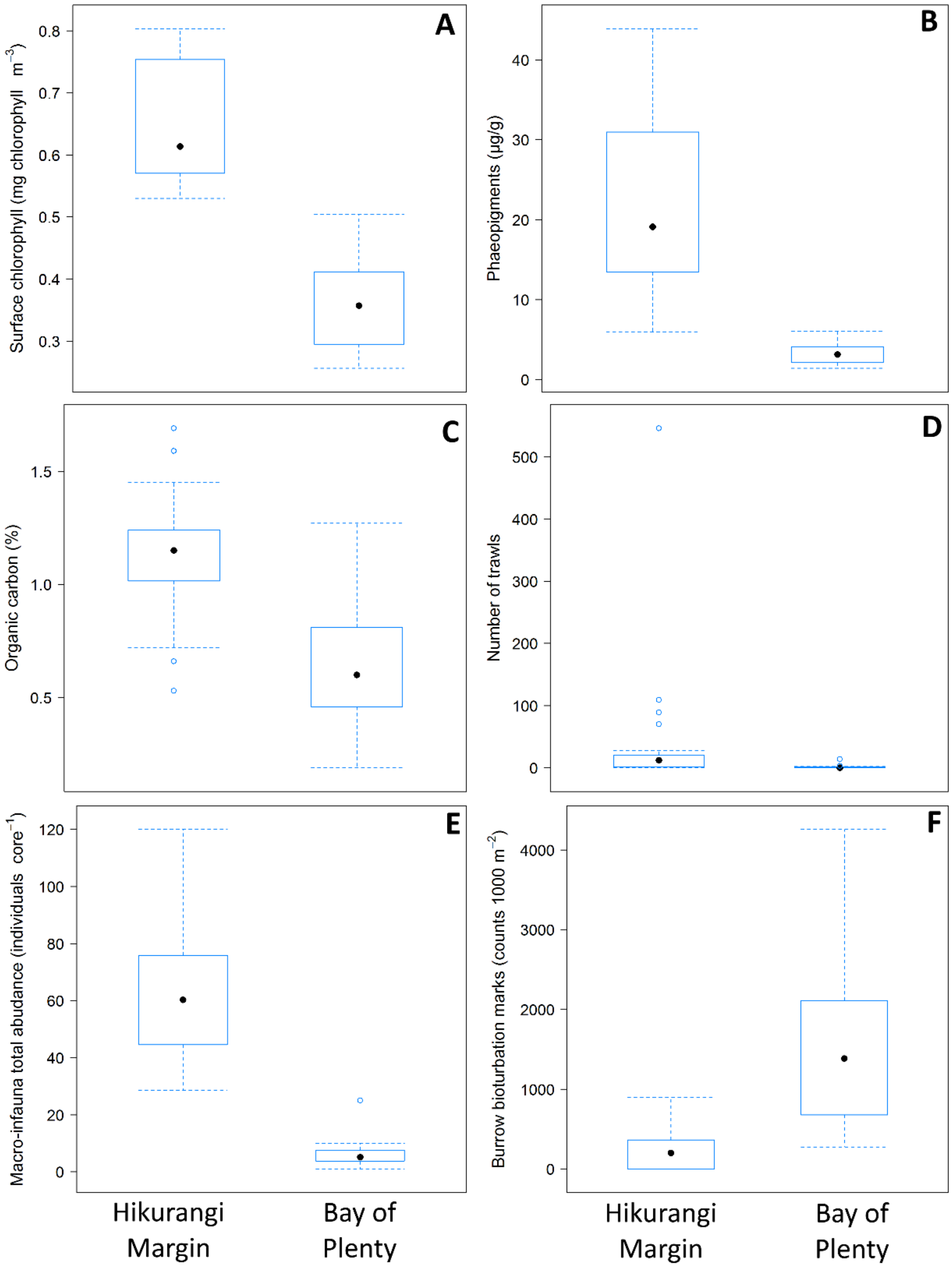

Figure 3.1. Box plot of variables responsible for most of environmental dissimilarity between the Hikurangi Margin and Bay of Plenty study regions. A. Mean surface chlorophyll concentration; B. Sediment phaeopigment concentrations; C. Sediment organic carbon content; D. Fishing intensity; E. Macro-infauna total abundance (individuals core$^{-1}$); F. Burrows (mega-epifaunal bioturbation marks 1000 m$^{-2}$). (Environmental data published in Bowden et al. (2016) and Rosli et al. (2016)).

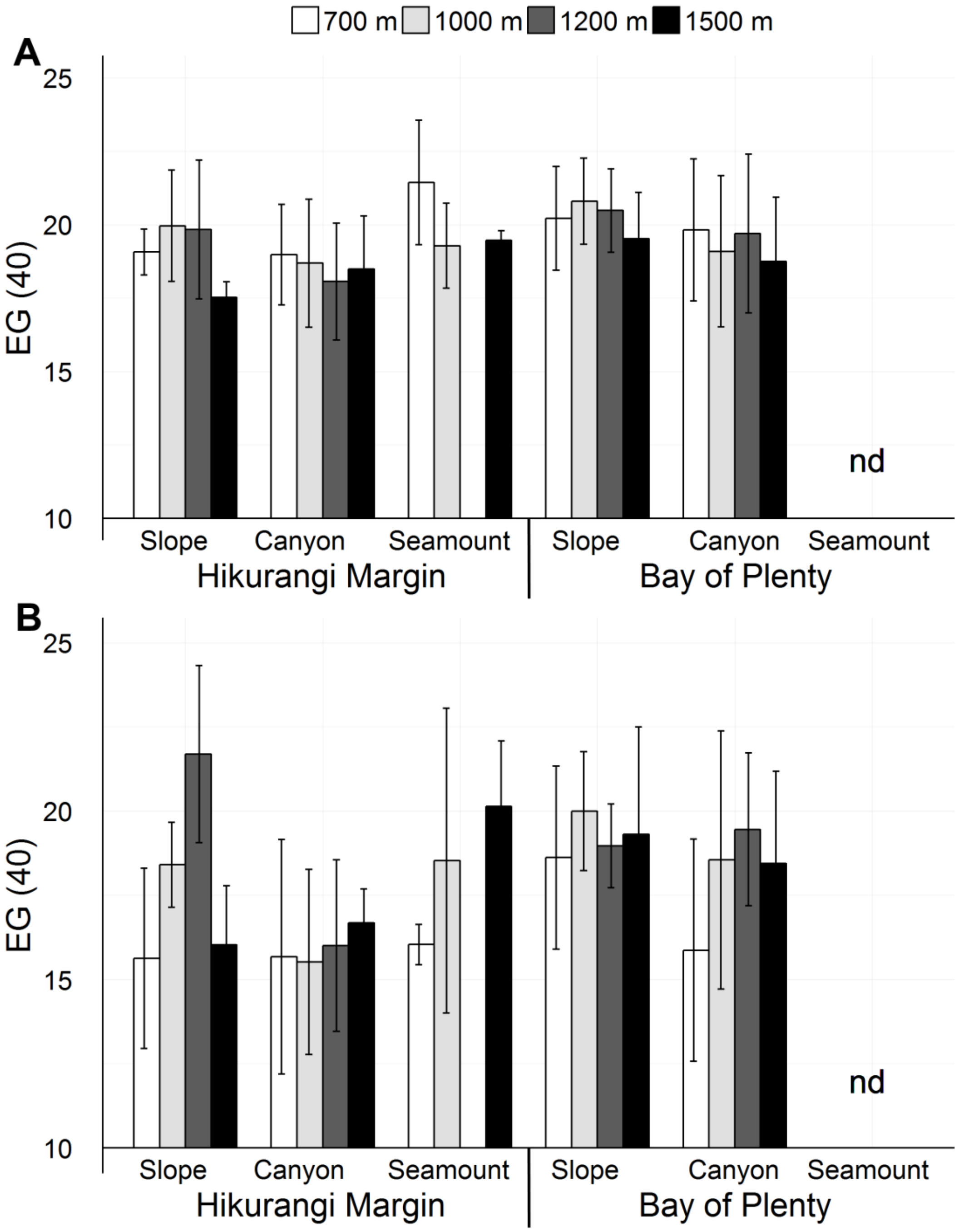

Figure 3.2. Average diversity of nematodes (EG [40]) at A. Surface sediment (0–1 cm); B. Subsurface sediment (1–5 cm); at different water depths (700 m, 1000 m, 1200 m, 1500) across different habitats (slope, canyon, seamount) in Hikurangi Margin and Bay of Plenty regions.

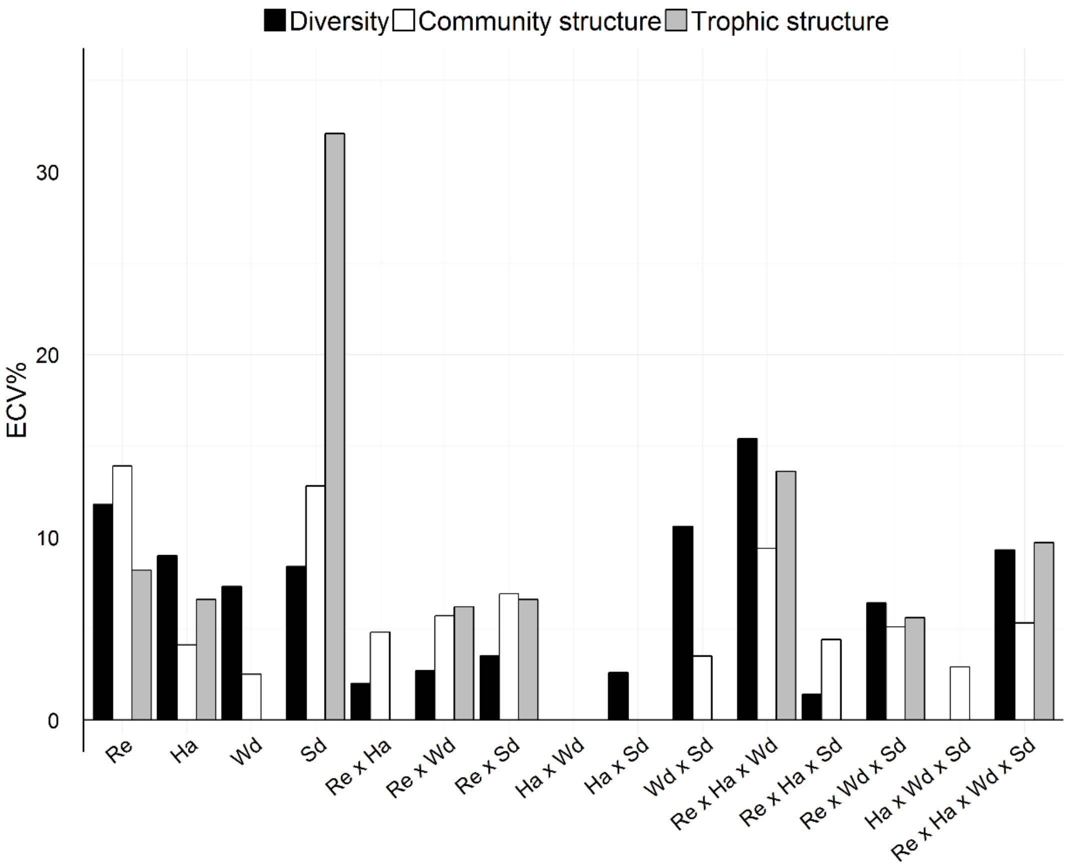

Figure 3.3. Percentage of estimates components of variation for each factor and interaction in PERMANOVA tests on nematode community attributes of Hikurangi Margin and Bay of Plenty. Negative values are showed as zero. [Re = region, Ha = habitat, Wd = water depth, Sd = sediment depth].

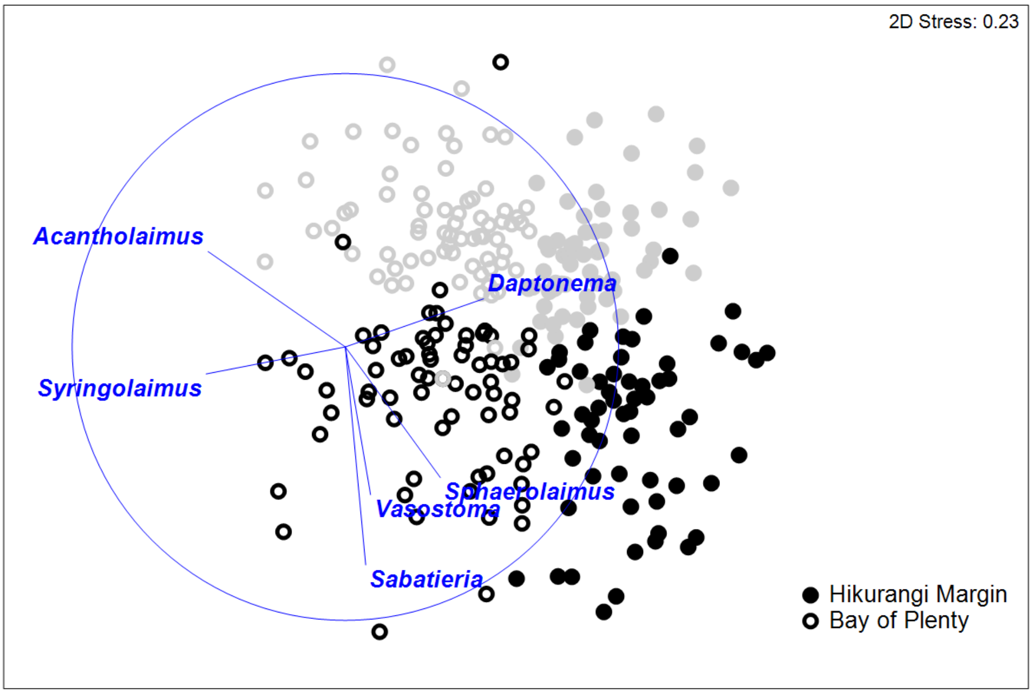

Figure 3.4. Two-dimensional MDS ordination plot of nematode community structure at the Hikurangi Margin and Bay of Plenty study regions at different sediment depths (cut-off applied at correlation > 0.5). Sediment layer are shown grey (surface sediment, 0–1 cm) and black (subsurface sediment, 1–5 cm).

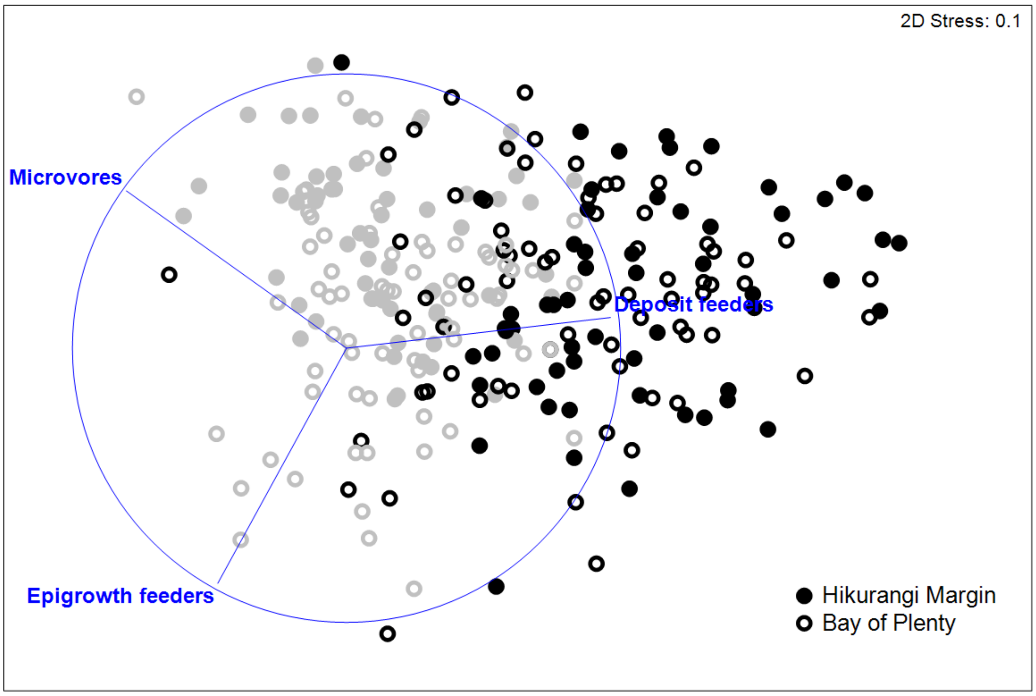

Figure 3.5. Two-dimensional MDS ordination of nematode trophic structure at the Hikurangi Margin and Bay of Plenty study regions at different sediment depths (cut-off applied at correlation > 0.5). Sediment layer are shown grey (surface sediment, 0–1 cm) and black (subsurface sediment, 1–5 cm).

### 3.4.2 Second stage analyses: Hikurangi Margin

Nematode diversity showed significant differences among habitats, water depths, sediment depths and their interactions (PERMANOVA < 0.05; Appendix J). There was no clear pattern of diversity between surface and subsurface sediments among habitats or water depths. Diversity tended to be lower in subsurface sediment than in surface sediment except for seamount and slope habitats where it showed the opposite pattern at 1500 and 1200 m depth respectively (Figure 3.2). Habitat (13%) and sediment depth (12%) explained similar proportions of variability in diversity, whereas water depth explained a smaller proportion (8%) (Appendix J, Figure 3.6).

Nematode community structure differed significantly among habitats, water depths, sediment depths and their interactions (PERMANOVA < 0.05, Appendix J, Appendix K). There were significant differences in multivariate dispersion among water depths and between sediment depths, but not among habitats (PERMDISP, P > 0.05). Multivariate dispersion was significantly different between the 700 m and 1500 m, 1000 m and 1500 m, and 1200 m and 1500 m water depth, but not in other comparisons (mean deviation from centroid: 700 m = 39.7; 1500 m = 34.0). Multivariate dispersion was significantly greater at subsurface (mean deviation from centroid = 37.0) than surface sediment layer (33.8) (P < 0.05). Sediment depth (19%) explained higher proportions of variability in community structure than habitat (11%) and water depth (5%) (Appendix J). Pairwise comparisons showed differences in community structure were significant between canyon and slope habitats for surface sediment nematodes at 700 and 1200 m water depth, while subsurface sediment nematodes only differed significantly at 1200 m between the same habitats. Surface sediment communities differed significantly between canyon and seamount at 1000 m, while subsurface sediment communities differed significantly between seamount and slope habitat at 1500 m. *Sabatieria* was the largest contributor to community dissimilarity among habitats, water and sediment depths (3–5% of total dissimilarity) (Table 3.3). *Sabatieria*, *Paramonohystera* and *Sphaerolaimus* were most abundant in subsurface sediment depth, whereas *Daptonema*, *Acantholaimus*, *Molgolaimus*, *Halalaimus*, *Leptolaimus*, *Endeolophos* and *Desmoscolex* were most abundant in the surface sediment layer.

Nematode trophic structure differed significantly among habitats, water depths, and sediment depths. Interaction between habitat and water depth was also significant (PERMANOVA $< 0.05$, Appendix J). Pairwise comparisons showed differences in trophic structure were significant between canyon and seamount habitats, between slope and seamount habitats and also between canyon and slope at 700 and 1500 m water depth. Sediment depth (34%) explained higher proportions of variability in community structure than habitat (7%) and water depth (6%) (Appendix J, Figure 3.6). Microvores, deposit feeders, and epigrowth feeders were the largest contributor to dissimilarity among habitats, water depths and between surface and subsurface sediment (17–34%) (Table 3.4). Average abundance of deposit feeders, predators and facultative predators were higher in the subsurface than surface sediment layers, whereas microvores, epigrowth feeders and ciliate feeders showed the opposite trend.

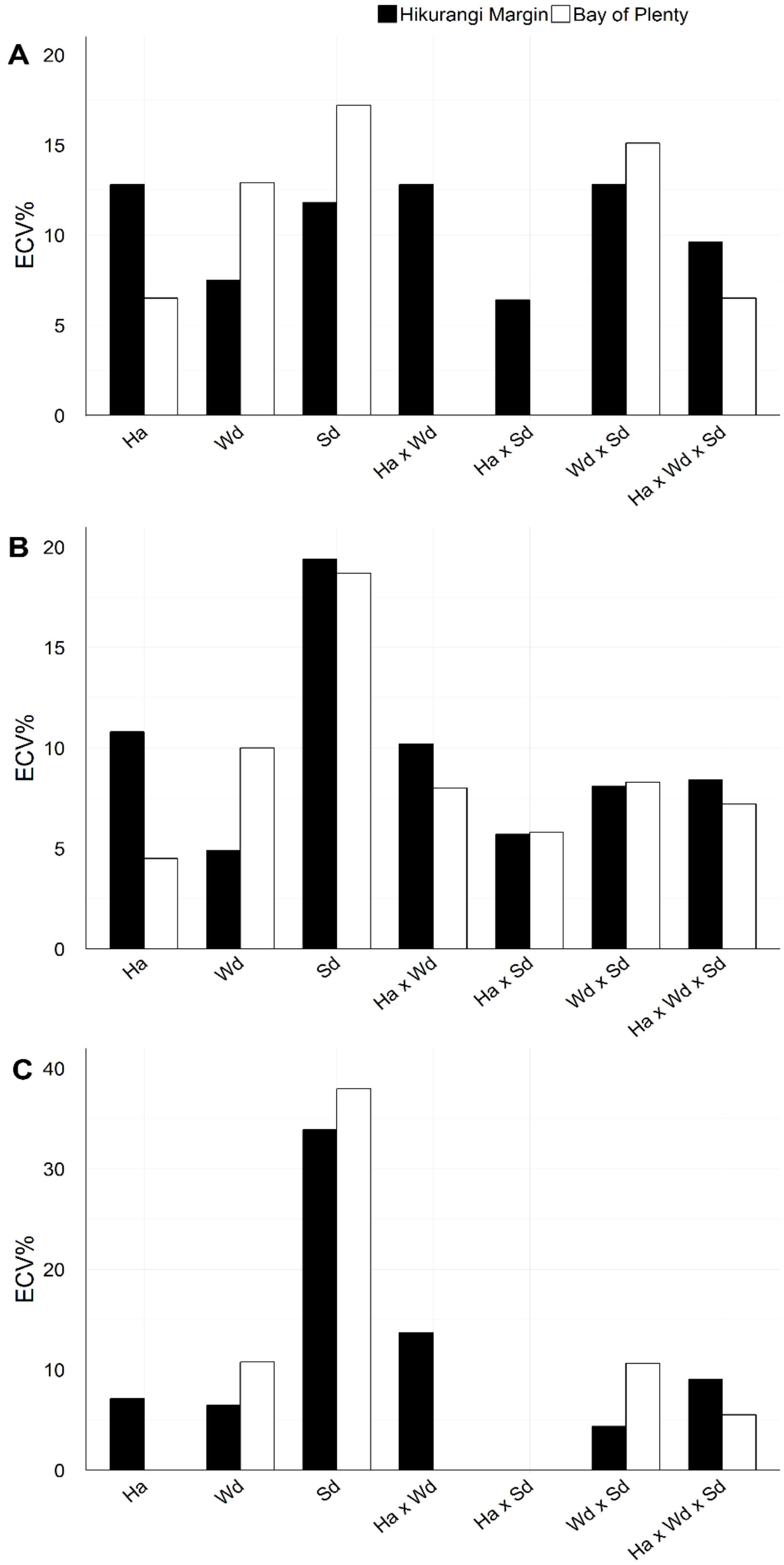

Figure 3.6. Percentage of estimates components of variation for each factor and interaction in PERMANOVA tests of Hikurangi Margin and Bay of Plenty on nematode: A. Diversity; B. Community structure; C. Trophic structure. Negative values are showed as zero. [Ha = habitat, Wd = water depth, Sd = sediment depth].

Table 3.3. SIMPER analysis results showing nematode genera accounting for community dissimilarity between different habitat, water and sediment depths for the Hikurangi Margin study region (cut-off applied at 25% contribution). [Av.abund = average nematode abundance (individual 10 cm$^{-2}$), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold. Only two depth strata were shown to display difference between shallow and deep site.

| Genera | Av. Abund | Av. Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| Habitat | *Canyon* | *Seamount* | | | | |
| Av. Dissimilarity: 56% | | | | | | |
| *Sabatieria* | 21.7 | **27.7** | 2.22 | 1.28 | 4.0 | 4.0 |
| *Daptonema* | **22.6** | 6.2 | 1.86 | 1.4 | 3.3 | 7.3 |
| *Vasostoma* | 2.4 | **7.7** | 1.43 | 1.0 | 2.6 | 9.8 |
| *Acantholaimus* | 3.2 | **6.8** | 1.41 | 1.34 | 2.5 | 12.3 |
| *Paramonohystera* | 8.3 | **10.9** | 1.34 | 1.3 | 2.4 | 14.7 |
| *Halalaimus* | **24.1** | 20.7 | 1.29 | 1.32 | 2.3 | 17.0 |
| *Molgolaimus* | **5.8** | 4.7 | 1.29 | 1.23 | 2.3 | 19.3 |
| *Desmoscolex* | 3.8 | **4.0** | 1.22 | 1.12 | 2.2 | 21.5 |
| *Cervonema* | **13.2** | 8.9 | 1.2 | 1.1 | 2.1 | 23.6 |
| *Laimella* | **4.7** | 2.4 | 1.17 | 0.91 | 2.1 | 25.7 |
| | | | | | | |
| Av. Dissimilarity: 54% | *Canyon* | *Slope* | | | | |
| *Sabatieria* | 21.7 | **25.1** | 2.05 | 1.31 | 3.8 | 3.8 |
| *Daptonema* | **22.6** | 15.6 | 1.41 | 1.22 | 2.6 | 6.4 |
| *Paramonohystera* | 8.3 | **11.9** | 1.38 | 1.28 | 2.5 | 8.9 |
| *Acantholaimus* | 3.2 | **6.4** | 1.37 | 1.37 | 2.5 | 11.5 |
| *Molgolaimus* | **5.8** | 5.5 | 1.30 | 1.28 | 2.4 | 13.9 |
| *Halalaimus* | **24.1** | 21.3 | 1.19 | 1.32 | 2.2 | 16.0 |
| *Endeolophos* | **6.0** | 5.1 | 1.19 | 1.29 | 2.2 | 18.2 |
| *Cervonema* | **13.2** | 7.9 | 1.17 | 1.15 | 2.2 | 20.4 |
| *Metacyatholaimus* | 2.8 | **5.8** | 1.15 | 1.10 | 2.1 | 22.5 |
| *Desmoscolex* | **3.8** | 3.4 | 1.12 | 1.12 | 2.1 | 24.6 |
| *Sphaerolaimus* | 7.0 | 7.0 | 1.11 | 1.30 | 2.1 | 26.7 |
| | | | | | | |
| Av. Dissimilarity: 54% | Slope | Seamount | | | | |
| *Sabatieria* | 25.1 | **27.7** | 2.18 | 1.25 | 4.0 | 4.0 |
| *Vasostoma* | 2.4 | **7.7** | 1.46 | 0.92 | 2.7 | 6.7 |
| *Daptonema* | **15.6** | 6.2 | 1.30 | 1.44 | 2.4 | 9.1 |
| *Acantholaimus* | 6.4 | **6.8** | 1.27 | 1.37 | 2.4 | 11.5 |
| *Paramonohystera* | **11.9** | 10.9 | 1.22 | 1.26 | 2.3 | 13.7 |
| *Metacyatholaimus* | **5.8** | 2.4 | 1.21 | 1.09 | 2.2 | 16.0 |
| *Halalaimus* | **21.3** | 20.7 | 1.21 | 1.32 | 2.2 | 18.20 |
| *Desmoscolex* | 3.4 | **4.0** | 1.16 | 1.19 | 2.1 | 20.3 |
| *Molgolaimus* | **5.5** | 4.7 | 1.13 | 1.28 | 2.1 | 22.4 |
| *Leptolaimus* | **4.1** | 3.4 | 1.03 | 1.27 | 1.9 | 24.3 |

| Genera | Av. Abund | Av. Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| *Sphaerolaimus* | **7.0** | 5.7 | 1.02 | 1.27 | 1.9 | 26.2 |
| | | | | | | |
| Water depth | *700 m* | *1500 m* | | | | |
| Av. Dissimilarity: 55% | | | | | | |
| *Sabatieria* | **26.8** | 18.8 | 2.11 | 1.30 | 3.8 | 3.8 |
| *Daptonema* | **19.0** | 18.5 | 1.52 | 1.24 | 2.7 | 6.5 |
| *Vasostoma* | **7.2** | 0.6 | 1.35 | 0.99 | 2.4 | 8.9 |
| *Endeolophos* | 3.8 | **7.2** | 1.35 | 1.28 | 2.4 | 11.3 |
| *Molgolaimus* | 6.2 | **6.8** | 1.32 | 1.25 | 2.4 | 13.6 |
| *Cervonema* | **10.4** | 9.6 | 1.29 | 1.12 | 2.3 | 15.9 |
| *Acantholaimus* | 3.0 | **6.2** | 1.28 | 1.19 | 2.3 | 18.2 |
| *Paramonohystera* | **10.2** | 7.9 | 1.23 | 1.28 | 2.2 | 20.4 |
| *Sphaerolaimus* | **7.7** | 7.3 | 1.16 | 1.31 | 2.1 | 22.5 |
| *Leptolaimus* | 2.4 | **3.0** | 1.16 | 1.29 | 2.1 | 24.5 |
| *Desmoscolex* | **4.7** | 1.9 | 1.13 | 1.07 | 2.0 | 26.6 |
| | | | | | | |
| Sediment depth | *0-1 cm* | *1-5 cm* | | | | |
| Av. Dissimilarity: 58% | | | | | | |
| *Sabatieria* | 8.7 | **39.4** | 2.83 | 1.62 | 4.9 | 4.9 |
| *Daptonema* | **20.0** | 14.9 | 1.51 | 1.29 | 2.6 | 7.5 |
| *Acantholaimus* | **7.7** | 2.1 | 1.45 | 1.38 | 2.5 | 10.0 |
| *Molgolaimus* | **7.5** | 3.6 | 1.43 | 1.38 | 2.5 | 12.5 |
| *Halalaimus* | **29.0** | 16.0 | 1.39 | 1.44 | 2.4 | 14.9 |
| *Leptolaimus* | **6.0** | 0.9 | 1.37 | 1.56 | 2.4 | 17.3 |
| *Endeolophos* | **8.3** | 2.4 | 1.37 | 1.44 | 2.4 | 19.6 |
| *Desmoscolex* | **6.2** | 1.1 | 1.37 | 1.25 | 2.4 | 22.0 |
| *Paramonohystera* | 9.6 | **10.4** | 1.33 | 1.28 | 2.3 | 24.3 |
| *Sphaerolaimus* | 3.6 | **10.0** | 1.3 | 1.46 | 2.2 | 26.5 |

Results of DistLM analyses showed that diversity in the surface sediment layer was significantly correlated with sediment particle kurtosis, sediment phaeopigment concentration, seafloor profile curvature and the abundance of macro-infaunal deposit feeders in marginal tests; in sequential tests, sediment particle kurtosis and seafloor profile curvature were the only variables significantly correlated with diversity ($P < 0.05$; $R^2 = 0.05–0.14$; Appendix L; Figure 3.7). Diversity in surface sediment was negatively correlated with sediment particle kurtosis and sediment phaeopigment concentration, whereas seafloor profile curvature and macro-infaunal deposit feeder abundance were positively correlated with diversity. A negative relationship between sediment particle kurtosis and diversity indicates that diversity was lower in sediments with a narrow range of particle sizes. Seafloor profile curvature was positively correlated with diversity, indicating that diversity was lower in depressions than on elevated topography. Nematode diversity in the subsurface sediment layer was significantly and negatively correlated with particle size diversity and terrain rugosity (5 grid cell focal mean) in marginal tests, whereas particle size diversity and sediment phaeopigment concentration were both significantly and negatively correlated with diversity in sequential tests ($P < 0.05$; $R^2 = 0.09$–$0.11$, Appendix L).

Nematode community structure in the surface sediment layer was significantly correlated with sediment phaeopigment concentration, seafloor profile curvature, sediment organic carbon content, particle kurtosis and mean particle size in marginal tests; in sequential tests the relationship was significant for sediment phaeopigment concentration and mean particle size only ($P < 0.05$; $R^2 = 0.03$–$0.07$; Appendix L). Nematode community structure in the subsurface sediment layer was significantly correlated with sediment organic carbon content, particle kurtosis, and phaeopigment concentration in marginal tests, whereas in sequential tests, community structure was significantly correlated with sediment organic carbon content and water depth ($P < 0.05$; $R^2 = 0.04$–$0.06$; Appendix L).

Table 3.4. SIMPER analysis results showing nematode trophic groups accounting for trophic dissimilarity between different habitat, water and sediment depths for the Hikurangi Margin study region. [Av.abund = average nematode relative abundance (%), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold. Only two depth strata were shown to display difference between shallow and deep site.

| Genera | Av. Abund | Av. Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| Habitat | *Canyon* | *Seamount* | | | | |
| Av. Dissimilarity: 24% | | | | | | |
| Microvores | 33.2 | **37.3** | 7.96 | 1.42 | 33.1 | 33.1 |
| Deposit feeders | **32.9** | 27.6 | 7.82 | 1.38 | 32.5 | 65.7 |
| Epigrowth feeders | 24.9 | **27.6** | 4.53 | 1.42 | 18.9 | 84.5 |
| Predators | **5.8** | 5.0 | 2.01 | 1.24 | 8.4 | 92.9 |
| Facultative predators | **2.6** | 1.7 | 1.12 | 0.97 | 4.7 | 97.6 |
| Ciliate feeders | 0.7 | **0.8** | 0.58 | 0.81 | 2.4 | 100 |
| Av. Dissimilarity: 23% | *Canyon* | *Slope* | | | | |
| Microvores | 33.2 | **34.2** | 7.04 | 1.37 | 30.9 | 30.1 |
| Deposit feeders | **32.9** | 30.3 | 6.83 | 1.36 | 29.2 | 59.3 |
| Epigrowth feeders | **24.9** | 24.4 | 4.93 | 1.42 | 21.0 | 80.3 |
| Predators | 5.8 | **6.3** | 2.38 | 1.27 | 10.1 | 90.4 |
| Facultative predators | 2.6 | **3.3** | 1.5 | 1.02 | 6.4 | 96.9 |
| Ciliate feeders | 0.7 | **1.5** | 0.74 | 0.97 | 3.2 | 100 |
| Av. Dissimilarity: 23% | *Slope* | *Seamount* | | | | |
| Microvores | 34.2 | **37.3** | 7.88 | 1.42 | 34.0 | 34.0 |
| Deposit feeders | **30.3** | 27.6 | 7.21 | 1.41 | 31.1 | 65.0 |
| Epigrowth feeders | 24.4 | **27.6** | 3.96 | 1.36 | 17.1 | 82.1 |
| Predators | **6.3** | 5.0 | 2.03 | 1.29 | 8.7 | 90.8 |
| Facultative predators | **3.3** | 1.7 | 1.33 | 0.98 | 5.8 | 96.6 |
| Ciliate feeders | **1.5** | 0.8 | 0.79 | 1.08 | 3.4 | 100 |
| Av. Dissimilarity: 23% | *700 m* | *1500 m* | | | | |
| Microvores | 31.9 | **34.7** | 7.05 | 1.37 | 30.0 | 30.0 |
| Deposit feeders | **32.6** | 27.3 | 6.83 | 1.38 | 29.9 | 59.1 |
| Epigrowth feeders | 24.6 | **28.3** | 4.99 | 1.32 | 21.2 | 80.4 |
| Predators | **6.3** | 6.2 | 2.34 | 1.31 | 10.0 | 90.3 |
| Facultative predators | **3.6** | 2.2 | 1.53 | 1.06 | 6.5 | 96.9 |
| Ciliate feeders | 0.9 | **1.3** | 0.74 | 0.91 | 3.1 | 100 |
| Av. Dissimilarity: 29% | *0-1 cm* | *1-5 cm* | | | | |
| Microvores | **43.7** | 24.6 | 9.81 | 1.78 | 34.3 | 34.3 |
| Deposit feeders | 22.3 | **40.0** | 9.24 | 1.67 | 32.3 | 66.6 |
| Epigrowth feeders | **26.7** | 23.6 | 4.86 | 1.4 | 17.0 | 83.6 |
| Predators | 4.2 | **7.5** | 2.47 | 1.3 | 8.6 | 92.2 |
| Facultative predators | 1.7 | **3.8** | 1.5 | 1.02 | 5.3 | 97.5 |
| Ciliate feeders | **1.5** | 0.6 | 0.73 | 0.95 | 2.5 | 100 |

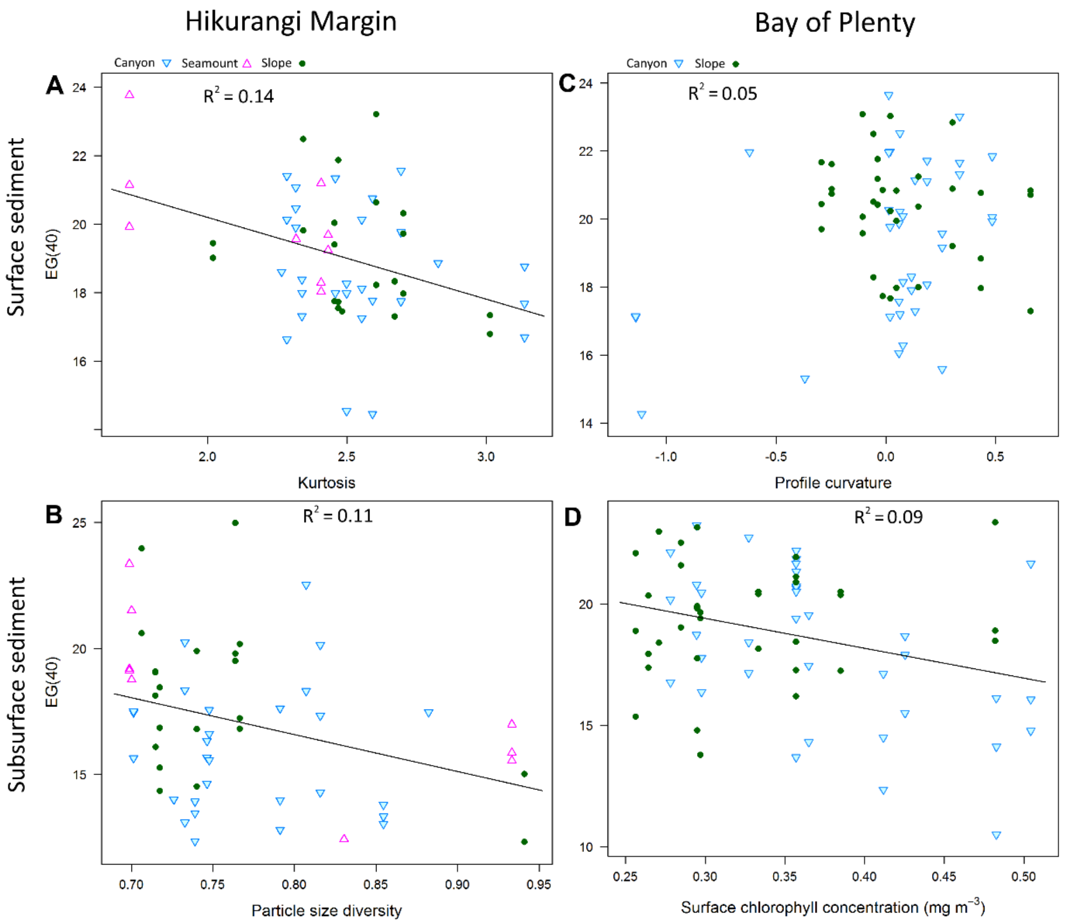

Figure 3.7. Selection of statistically higher significant correlations ($P < 0.05$) between environmental variables and nematode diversity at different sediment layers in the Hikurangi Margin and Bay of Plenty regions. Hikurangi Margin, surface sediment (0–1 cm): A. Kurtosis; subsurface sediment (1–5 cm): B. Particle size diversity; Bay of Plenty, surface sediment (0–1 cm): C. Profile curvature; subsurface sediment (1–5 cm): D. Surface chlorophyll concentration (mg $m^{-3}$).

Nematode trophic structure in the surface sediment layer was significantly correlated with terrain rugosity (5 grid cell focal mean), standard deviation of slope (3 grid cell focal mean), curvature, mega-epifaunal track marks and total surface bioturbation marks in marginal tests, whereas in sequential tests, only terrain rugosity (5 grid cell focal mean) and curvature were significantly correlated with nematode trophic structure ($P < 0.05$; $R^2 = 0.05$–$0.07$; Appendix L; Figure 3.8). Nematode trophic structure in the subsurface sediment layer was significantly correlated with water depth, carbonate content in the sediment, and terrain rugosity

(5 grid cell focal mean) in marginal tests, whereas in sequential tests, only water depth was significantly correlated with nematode trophic structure ($P < 0.05$; $R^2 = 0.05$; Appendix L; Figure 3.8).

### 3.4.3 Second stage analyses: Bay of Plenty

Nematode diversity showed significant differences between sediment depths, but not among habitats and water depths (PERMANOVA < 0.05; Appendix J). Even though significant, the diversity difference between surface (19.8) and subsurface sediments (18.6) was very small.

Nematode community structure differed significantly among habitats, water depths, sediment depths, and their interactions (PERMANOVA < 0.05; Appendix J; Appendix K). There was no significant difference in multivariate dispersion among water depths and sediment depths, but there was significant difference between habitats (PERMDISP, $P > 0.05$), where canyon (mean deviation from centroid = 40.6) difference was greater than slope habitat (36.2). Sediment depth (19%) explained higher proportions of variability in community structure than habitat (5%) and water depth (10%) (Appendix J). Pairwise comparisons showed differences in community structure were significant between canyon and slope habitats for surface sediment nematodes at 1000 m and 1200 m water depth. Pairwise comparisons also showed a significant difference between surface and subsurface sediment layers at all water depths strata. *Sabatieria* was the largest contributor to community dissimilarity between each pair of habitats, water and sediment depths tested (4–6% of total dissimilarity) (Table 3.5). *Sabatieria*, *Syringolaimus*, *Paramonohystera* and *Sphaerolaimus* were abundant in surface sediments, whereas *Acantholaimus*, *Halalaimus, Molgolaimus, Daptonema, Thalassomonhystera* and Xyalidae showed the opposite trend.

Table 3.5. SIMPER analysis results showing nematode genera accounting for community dissimilarity between different habitat, water and sediment depths for the Bay of Plenty study region (cut-off applied at 25% contribution). [Av.abund = average nematode abundance (individual 10 cm$^{-2}$), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold. Only two depth strata were shown to display difference between shallow and deep site.

| Genera | Av. Abund | Av. Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| Habitat | *Slope* | *Canyon* | | | | |
| Av. Dissimilarity: 55% | | | | | | |
| *Sabatieria* | **20.4** | 20.2 | 2.48 | 1.29 | 4.5 | 4.5 |
| *Molgolaimus* | 6.0 | **10.9** | 1.64 | 1.16 | 3.0 | 7.5 |
| *Daptonema* | **8.1** | 6.0 | 1.31 | 1.28 | 2.4 | 9.8 |
| *Paramonohystera* | 4.3 | **4.9** | 1.22 | 1.23 | 2.2 | 12.0 |
| *Syringolaimus* | 3.8 | **4.1** | 1.18 | 1.28 | 2.1 | 14.2 |
| *Thalassomonhystera* | 3.2 | **3.4** | 1.17 | 1.18 | 2.1 | 16.3 |
| Xyalidae | 4.0 | **4.1** | 1.16 | 1.21 | 2.1 | 18.4 |
| *Acantholaimus* | **15.3** | 12.4 | 1.14 | 1.21 | 2.1 | 20.4 |
| *Halalaimus* | 13.9 | **14.7** | 1.14 | 1.25 | 2.1 | 22.5 |
| *Sphaerolaimus* | **4.5** | 3.2 | 1.14 | 1.31 | 2.1 | 24.6 |
| *Cervonema* | 6.8 | **7.3** | 1.12 | 1.22 | 2.0 | 26.6 |
| Water depth | *700 m* | *1500 m* | | | | |
| Av. Dissimilarity: 55% | | | | | | |
| *Sabatieria* | **33.0** | 17.3 | 2.91 | 1.3 | 5.3 | 5.3 |
| *Molgolaimus* | 5.1 | **10.9** | 1.75 | 1.21 | 3.2 | 8.5 |
| *Daptonema* | **7.2** | 7.0 | 1.33 | 1.29 | 2.4 | 10.9 |
| *Sphaerolaimus* | **5.3** | 3.0 | 1.31 | 1.35 | 2.4 | 13.3 |
| *Halalaimus* | **18.8** | 13.2 | 1.3 | 1.29 | 2.4 | 15.6 |
| *Syringolaimus* | 3.4 | **6.0** | 1.27 | 1.35 | 2.3 | 17.9 |
| *Thalassomonhystera* | 2.6 | **4.3** | 1.26 | 1.22 | 2.3 | 20.2 |
| *Vasostoma* | **4.5** | 0.8 | 1.22 | 0.93 | 2.2 | 22.5 |
| *Metalinhomoeus* | 2.1 | **4.3** | 1.12 | 1.22 | 2.0 | 24.5 |
| *Cervonema* | 6.2 | **7.2** | 1.11 | 1.17 | 2.0 | 26.5 |
| Sediment depth | *0-1cm* | *1-5cm* | | | | |
| Av. Dissimilarity: 58% | | | | | | |
| *Sabatieria* | 4.9 | **35.6** | 3.38 | 1.7 | 5.8 | 5.8 |
| *Molgolaimus* | **9.8** | 7.5 | 1.68 | 1.2 | 2.9 | 8.8 |
| *Daptonema* | **8.5** | 5.7 | 1.32 | 1.31 | 2.3 | 11.0 |
| *Syringolaimus* | 2.8 | **5.1** | 1.23 | 1.32 | 2.1 | 13.2 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Paramonohystera* | 4.3 | **4.9** | 1.21 | 1.19 | 2.1 | 15.3 |
| *Halalaimus* | **17.3** | 11.3 | 1.2 | 1.23 | 2.1 | 17.3 |
| *Acantholaimus* | **16.8** | 10.9 | 1.2 | 1.19 | 2.1 | 19.4 |
| *Sphaerolaimus* | 2.3 | **5.5** | 1.19 | 1.28 | 2.1 | 21.5 |
| *Thalassomonhystera* | **4.0** | 2.6 | 1.17 | 1.17 | 2.0 | 23.5 |
| Xyalidae | **4.3** | 3.8 | 1.16 | 1.21 | 2.0 | 25.5 |

Nematode trophic structure differed significantly among water depths and sediment depths, but not among habitats (PERMANOVA < 0.05; Appendix J). Pairwise comparisons showed differences in trophic structure were significant between shallow (700 and 1000 m) and deeper depth strata. Sediment depth (38%) explained higher proportions of variability in trophic structure than water depth (11%), whereas habitat explained a small proportion (4%) (Appendix J; Figure 3.6). Deposit feeders, microvores and epigrowth feeders were the largest contributors to dissimilarity between shallow and deeper water depth strata and between surface and subsurface sediment (26–32%, and 25–34% respectively) (Table 3.6). Average abundance of epigrowth feeders was higher in the deeper than shallow water depth, whereas the rest of trophic groups showed the opposite trend. Average abundance of deposit feeders, predators, facultative predators, and ciliate feeders were higher in the subsurface than surface sediment layers, whereas microvores and epigrowth feeders showed the opposite trend.

Results of DistLM analyses showed that diversity in the surface sediment layer was correlated with seafloor profile curvature but was not significant, both in marginal and sequential tests ($P > 0.05$; $R^2 = 0.05$; Appendix M; Figure 3.7). Nematode diversity in the subsurface sediment layer was significantly and negatively correlated with surface water chlorophyll concentration and macro-infaunal total abundance in marginal tests, whereas in sequential tests, only surface water chlorophyll concentration was significantly and negatively correlated with diversity ($P < 0.05$; $R^2 = 0.06–0.09$; Appendix M; Figure 3.7).

Table 3.6. SIMPER analysis results showing nematode trophic groups accounting for trophic dissimilarity between different habitat, water and sediment depths for the Bay of Plenty study region. [Av.abund = average nematode relative abundance (%), Av.Diss = average dissimilarity, Diss/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average abundance are shown in bold. Only two depth strata were shown to display difference between shallow and deep site.

| Genera | Av. Abund | Av. Abund | Av.Diss | Diss/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| Habitat | *Canyon* | *Slope* | | | | |
| Av. Dissimilarity: 22% | | | | | | |
| Deposit feeders | 29.1 | **29.6** | 7.02 | 1.33 | 31.5 | 31.5 |
| Microvores | 33.5 | **34.2** | 5.87 | 1.32 | 26.4 | 57.8 |
| Epigrowth feeders | **30.0** | 28.6 | 5.75 | 1.31 | 25.8 | 83.6 |
| Predators | 4.1 | **4.9** | 1.67 | 1.10 | 7.5 | 91.1 |
| Facultative predators | **2.0** | 1.5 | 1.18 | 0.74 | 5.3 | 96.4 |
| Ciliate feeders | **1.3** | 1.2 | 0.81 | 0.9 | 3.6 | 100 |
| Av. Dissimilarity: 24% | *700 m* | *1500 m* | | | | |
| Deposit feeders | **33.3** | 28.2 | 7.45 | 1.28 | 31.6 | 31.6 |
| Microvores | **33.4** | 31.9 | 6.62 | 1.44 | 28.1 | 59.7 |
| Epigrowth feeders | 25.8 | **33.6** | 6.08 | 1.41 | 25.8 | 85.5 |
| Predators | **4.6** | 4.4 | 1.78 | 1.23 | 7.6 | 93.1 |
| Ciliate feeders | **1.6** | 0.8 | 0.82 | 1.18 | 3.5 | 96.6 |
| Facultative predators | **1.4** | 1.1 | 0.8 | 1.06 | 3.4 | 100 |
| Av. Dissimilarity: 25% | *0-1 cm* | *1-5 cm* | | | | |
| Deposit feeders | 22.2 | **36.5** | 8.40 | 1.48 | 33.6 | 33.6 |
| Microvores | **39.0** | 28.7 | 6.64 | 1.37 | 26.6 | 60.1 |
| Epigrowth feeders | **33.2** | 25.5 | 6.18 | 1.34 | 24.7 | 84.9 |
| Predators | 3.5 | **5.4** | 1.74 | 1.11 | 7.0 | 91.8 |
| Facultative predators | 1.0 | **2.6** | 1.24 | 0.76 | 5.0 | 96.8 |
| Ciliate feeders | 1.1 | **1.4** | 0.81 | 0.89 | 3.2 | 100 |

Nematode community structure in the surface sediment layer was significantly, but weakly correlated with water depth, carbonate content in the sediment and standard deviation of slope (5 grid cell focal mean) in marginal tests, whereas in sequential tests, depth and standard deviation of slope (7 grid cell focal mean) were weak, but significantly correlated with community structure ($P < 0.05$; $R^2 = 0.03–0.04$; Appendix M). Nematode community structure in the subsurface sediment layer was significantly correlated with sediment organic matter content, percentage of silt/clay, and particle kurtosis in marginal tests, whereas in sequential tests, sediment organic matter content and water depth were significant correlated with community structure ($P < 0.05$; $R^2 = 0.05–0.06$; Appendix M).

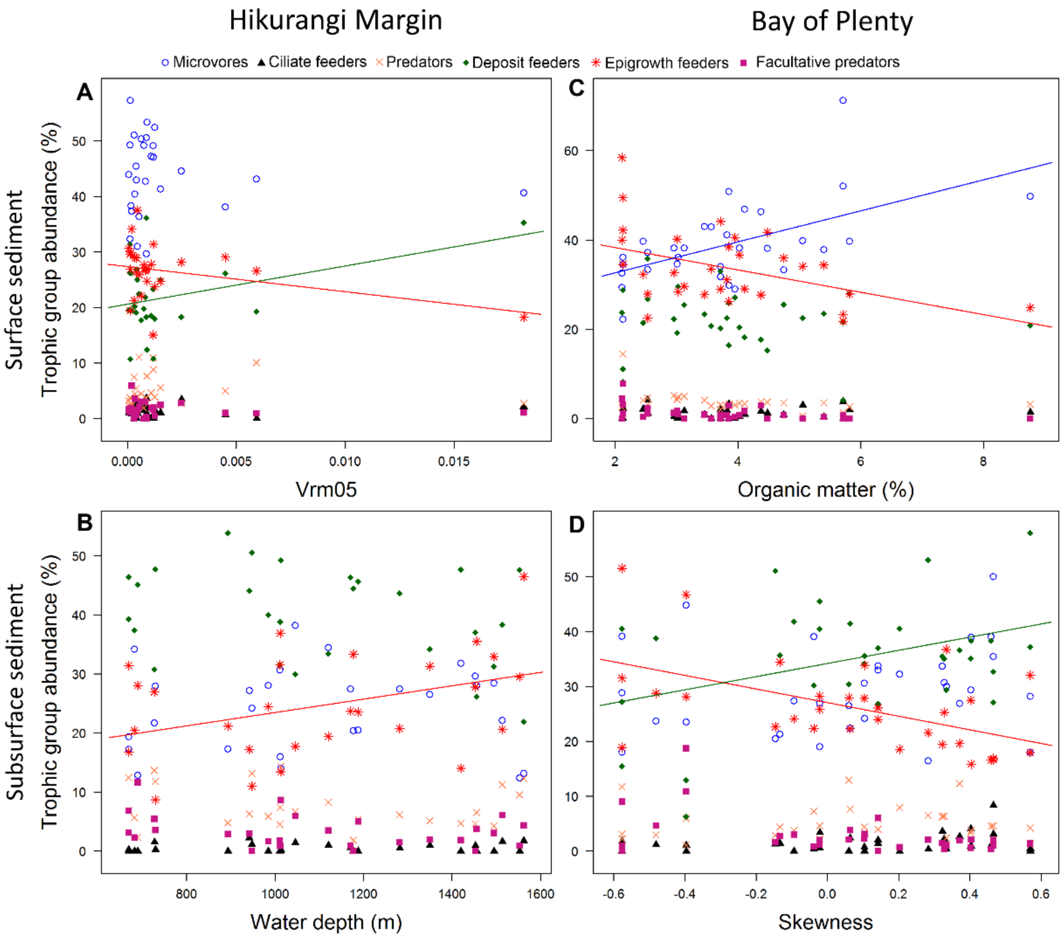

Figure 3.8. Selection of significant correlations ($P < 0.05$) between environmental variables and nematode feeding groups at different sediment layers in the Hikurangi Margin and Bay of Plenty regions. Hikurangi Margin, surface sediment (0–1 cm): A. Terrain rugosity based on 5 grid cell focal mean (Vrm05); Subsurface sediment (1–5 cm): B. Water depth (m); Bay of Plenty, surface sediment (0–1 cm): C. Organic matter (%); Subsurface sediment (1–5 cm): D. Skewness. Only significant relationships between nematode feeding groups and environmental variables are shown by the line(s).

Nematode trophic structure in the surface sediment layer was significantly correlated with organic matter content, sediment particle skewness, and percentage of silt/ clay in marginal tests, whereas in sequential tests, only organic matter content was significantly correlated with nematode trophic structure ($P < 0.05$; $R^2 = 0.08–0.09$; Appendix M; Figure 3.8). Nematode trophic structure in the subsurface sediment layer was significantly correlated with sediment particle skewness, sorting, and kurtosis in marginal tests, whereas in sequential tests, sediment particle skewness, terrain rugosity (5 grid cell focal mean), sediment organic carbon content and burrows (mega-epifaunal bioturbation marks) were significantly correlated with nematode trophic structure ($P < 0.05$; $R^2 = 0.04–0.09$; Appendix M; Figure 3.8).

## 3.5 Discussion

Knowledge of spatial patterns in deep-sea benthic communities across different spatial scales is still limited, because studies have traditionally examined patterns for nematode communities at a single scale or along bathymetric gradients. In this study, nematode community attributes mainly differed between regions and sediment depths, and to a lesser degree among habitats for some community attributes. Below we discuss the patterns we observed at each spatial scale in relation to the likely processes responsible for their existence, and the implications of the results for the vulnerability of nematode communities to anthropogenic disturbance.

### 3.5.1 Regional scale patterns and processes

Local nematode genus diversity differed significantly between the study regions. Regional patterns in nematode diversity have been observed in several studies, with high local diversity often found in regions with high productivity

(Gambi and Danovaro 2006, Bianchelli et al. 2013). In the present study, the highest diversity was observed in the low productivity region, the Bay of Plenty, which indicates that productivity was not low enough to limit local diversity of nematodes, as has been observed in the Eastern Mediterranean (Danovaro et al. 2009). However, despite the significant difference, mean local diversity was only slightly greater in the Bay of Plenty than the Hikurangi Margin (19 vs. 18 genera), which is unlikely to be ecologically meaningful.

Regional differences in nematode community structure have been observed in previous studies, which are usually associated with differences in the abundance of many genera rather than differences in genus composition (Lampadariou and Tselepides 2006, Danovaro et al. 2009, Gambi et al. 2014). Regional differences were also observed in the present study, where we found a clear difference in nematode community structure between Hikurangi Margin and Bay of Plenty. Several genera were characterised by higher relative abundance in the Hikurangi Margin than the Bay of Plenty region. *Sabatieria* and *Daptonema* are well adapted to fine sediment environments with high organic input (Wetzel et al. 2002, Vanreusel et al. 2010b, Ingels et al. 2011a), and were more abundant in the Hikurangi Margin than Bay of Plenty region. In contrast, *Acantholaimus,* which is a deep-sea genus typically associated with low food input, showed the opposite pattern (De Mesel et al. 2006a, Vanreusel et al. 2010b, Ingels et al. 2011a). The pattern of nematode community structure in the present study is consistent with the higher surface water chlorophyll and sediment pigment concentrations in the Hikurangi Margin than Bay of Plenty region, thus suggesting that food availability is an important driver of regional differences in nematode community structure.

Trophic structure of nematode communities also differed between regions, and largely reflected the difference in community structure described above, likely resulting from regional differences in food availability. Deposit feeders were the highest contributor to regional differences, followed by microvores and epigrowth feeders. All these trophic groups, except for epigrowth feeders and ciliate feeders, showed higher relative abundance in Hikurangi Margin than Bay of Plenty region. Greater abundance of deposit feeders and microvores is generally associated with organic rich sediments that occur in a high productivity region (Gallardo and Espinoza 2007), where these two trophic groups feed on bacteria, detrital particles and associated microbiota (Moens and Vincx, 1997). Higher abundance of predators and facultative predators in the Hikurangi Margin region also reflects greater food availability that help facilitates the energy transfer within nematode communities up to the predator level, which has been observed previously (Pusceddu et al. 2009). Epigrowth feeders are often prominent in low productivity deep-sea sediments despite low inputs of fresh and intact diatom cells (Pusceddu et al. 2009, Vanreusel et al. 2010b, Moens et al. 2014), which is consistent with their high relative abundance observed in the Bay of Plenty region.

Disturbance can play an important role in shaping nematodes communities in shallow waters (Schratzberger et al. 2009), and the presence of a significant positive correlation between trawling intensity and nematode diversity, and between trawling intensity and community structure on the Hikurangi Margin, indicates that disturbance could be responsible for regional differences in deep-sea nematode community attributes in the present study. Nematodes are thought to be relatively resilient to disturbance compared to larger organisms because they are less likely to be killed and can recover more quickly (Schratzberger et al. 2002, Whomersley et al.

2009, Leduc and Pilditch 2013). This apparent resilience to disturbance may help explain the positive impact of trawling on nematode communities abundance observed in some shallow water studies (Liu et al. 2011). A peak in nematode diversity at intermediate levels of physical disturbance has also been reported (Schratzberger and Warwick 1998), perhaps because moderate physical disturbance allows communities to diversify by preventing competitive exclusion (Connell 1978). Physical disturbance generally causes a shift in nematode community structure with a decline in the abundance of susceptible genera, and increased dominance of opportunistic genera such as *Sabatieria* (Schratzberger et al. 2009), which may explain the higher abundance of this genus in the Hikurangi Margin compared to the Bay of Plenty region.

Natural disturbance such as bioturbation can also influence nematode community patterns (Lambshead et al. 1995, Moodley et al. 2000), and may explain regional differences in nematode communities. There was a significant correlation between bioturbation activities and nematode diversity, community structure and trophic structure, even though relationship patterns varied between regions. Greater macro-infaunal total abundance was observed in Hikurangi Margin, and has been positively correlated with nematode diversity. This positive relationship has been observed previously (Zuhlke et al. 1998, Olafsson 2003, Callaway 2006, Moens et al. 2014), where bioturbation activities by larger fauna can help structure or alter the properties of the sediment column and increased downward transport of food into subsurface sediments (Lambshead et al. 1995, Moodley et al. 2000, Heip et al. 2001, Hughes and Gage 2004). In the Bay of Plenty region, the opposite pattern was observed, i.e., mega-epifaunal bioturbation was negatively correlated with diversity. This difference in pattern may be related to increased competition for food resources between nematodes and larger fauna communities in the low productivity Bay of Plenty region, leading to reduced nematode diversity (Olafsson et al. 1993).

### 3.5.2 Habitat scale patterns and processes

Nematode diversity differed among all habitats studied in the Hikurangi Margin region, but not in the Bay of Plenty. Diversity was higher at seamount habitats relative to canyon and slope habitats, with particularly low diversity observed in canyon habitats. Habitat pattern, however, was not consistent among water depths, but consistently showed lower diversity at canyon habitat at almost all water depths. High diversity in seamount habitats has been observed previously, and can be related to high hydrodynamic conditions which increase spatial variation in sedimentation process and food availability in the sediment (Zeppilli et al. 2014). Lower diversity has been observed in canyon habitats previously (Garcia et al. 2007, Bianchelli et al. 2008, Ingels et al. 2009). Canyons are generally associated with hydrodynamically active conditions and high sediment transport and accumulation rates, where only certain genera can tolerate challenging environmental conditions, which leads to higher dominance and lower diversity (Ingels et al. 2009). This situation is reflected by nematode communities in canyon habitats on the Hikurangi Margin. In this region, sediment particle kurtosis was negatively correlated with nematode diversity in the surface sediment, whereas in the subsurface sediment, particle size diversity was negatively correlated with diversity. High values of sediment particle kurtosis were mainly observed in canyon habitats. Sediment particle kurtosis is a measure of the particle size distribution, and high values of kurtosis indicate that there are outliers in the distribution (heavy-tailed relative to normal distribution). High or low values of kurtosis imply that part of the sediment achieved its sorting elsewhere in a high energy environment (Friedman 1962). The high kurtosis in canyons may reflect a past high energy disturbance event such as a turbidity flow, which has imposed a negative influence on nematode surface diversity. Particle size diversity showed a negative relationship with diversity; however, there was no clear habitat-scale pattern for particle size diversity that may influence subsurface diversity. No differences in diversity between habitats in the Bay of Plenty are probably related to the relative similarity of food concentrations and other environmental variables between these habitats in this region.

Community structure differed among all habitats in both study regions. Additional multivariate dispersion analysis showed significant differences between habitats in the Bay of Plenty region, where canyon communities were more variable than slope communities. The habitat effects differed among water depths, which indicates that the influence of habitat is not consistent across depth. *Sabatieria* was the greatest contributor to community dissimilarity among habitats, where this genus was found to be most abundant at seamount habitats, and least abundant in canyon habitats. *Sabatieria* is well adapted to the fine sediments with high organic input and low oxygen levels (Vanreusel 1990), and is generally found in high abundance in canyon habitats (Ingels et al. 2009, Ingels et al. 2011a, Ingels et al. 2011b), which was opposite to what was found in the present study. However, higher abundance of *Sabatieria* was observed in canyons at 1200 m water depth compared to seamount and slope habitats in Hikurangi Margin, whereas in Bay of Plenty, higher abundance was observed in canyons at 700 m and 1500 m water depths compared to slope habitats. This inconsistent pattern probably reflects different hydrodynamic conditions and the heterogeneous environment in canyon habitat among water depths and between canyons. Community structure of nematodes from surface and subsurface sediment layers was influenced by similar environmental proxy variables of food in both regions (i.e. phaeopigment, sediment organic carbon content), which mostly occurred at canyon habitats. This finding suggests that food availability in canyon habitat is higher compared to other habitats, which can influence nematode communities. However, the active hydrodynamic conditions typically found in canyons may have had an impact on the abundance of some taxa, including *Sabatieria*. Higher abundance of *Sabatieria* in seamount habitats might be related to presence of high organic input due to seamount flow conditions that help increase vertical mixing and sedimentation process (Bongiorni et al. 2013, Zeppilli et al. 2013). Seamounts are generally characterised by relatively high abundances of desmoscolecid nematodes (Pusceddu et al. 2009, Zeppilli et al. 2014), which has been observed in the present study. Desmoscolecids are adapted to strong current activity and coarse biogenic sediments composed of corals and mollusc shells by attaching to different type of substratum and feeding on biofilms, where these conditions generally occur in seamount habitats (Raes et al. 2007, Vanreusel et al. 2010b, Zeppilli et al. 2014).

Nematode trophic structure did not differ among habitats in the Bay of Plenty region. Trophic structure did differ among habitats in the Hikurangi Margin region, but habitat patterns were not the same for all water depths. In this region, greater differences in trophic structure were observed between canyon and seamount habitats, and also between canyon and slope at 700 and 1500 m water depth. Microvores were the highest contributor to the trophic group differences among habitats, followed by deposit feeders and epigrowth feeders. Relative abundance of microvores and epigrowth feeders were higher at seamount habitats, whereas deposit feeders were more abundant in canyons. Seamount hydrodynamic conditions may provide high inputs of fresh food, and thus favour bacteria assemblages, which may have contributed to higher abundance of microvores and epigrowth feeders observed in seamount habitat. High sedimentation rate can increase food availability in canyons and seems to favour deposit feeders, which feed less selectively on detrital particles and associated microbiota (Moens and Vincx 1997, Vanaverbeke et al. 1997a, Giere 2009, Danovaro et al. 2013), and might explain their high abundance in canyon habitats. In the Hikurangi Margin region, terrain rugosity was correlated with nematode trophic structure in the surface sediment, whereas water depth was correlated with trophic structure in the subsurface sediment. There was no clear habitat-scale pattern for these environmental variables that could be related to trophic structure differences.

Disturbance may also be a factor influencing nematode community patterns among habitats. Bottom trawling intensity in the Hikurangi Margin region tends to be greatest in seamount habitats, intermediate in slope habitats, and lowest at canyon habitats at 700–1000 m water depths, but shows no obvious habitat-related differences at 1200–1500 m depth (Bowden et al. 2016). However, no clear habitat-related differences in diversity were observed in this region, and community structure differences were found in both shallow (1000 m) and deep (1500 m) strata. In the Bay of Plenty region, trawl intensity shows similar patterns as Hikurangi Margin for slope and canyon habitats. However, there was no significant difference in nematode diversity between canyon and slope habitats, but there was a significant difference in community structure at shallow (1000 m) and deep (1200 m) water depth strata in this region. These observations suggest that trawl intensity is unlikely to be responsible for habitat-related differences in community attributes within the study regions, and this variable was not selected as important by the correlation analyses.

In the Hikurangi Margin region, the bioturbation proxy variables showed a positive relationship with nematode diversity. Burrow density was highest in seamount habitats and lowest at canyon habitats at 700–1000 m water depths, while at 1200–1500 m water depths, burrow density was greatest in slope habitats, intermediate in canyon habitat, and lowest at seamount habitats. Similarly, high diversity was observed at seamount habitats and was lowest in canyon habitats, which implies this high diversity at seamount habitat may be influenced by bioturbation activity by burrowing fauna. Total macro-infauna abundance however, was greatest in canyon habitats and lowest at seamount habitats, whereas at 1200–1500 m water depths, total macro-infauna abundance shows similar patterns as burrow density. These observed patterns suggest that even though bioturbation proxies showed a positive relationship with diversity, other factors may play important roles in influencing diversity, particularly in canyons and in deeper strata (1200–1500 m). Nematode community structure also was significantly correlated with bioturbation proxy variables, but these correlations were weak ($R^2 < 0.05$) and therefore of limited ecological significance in the habitat context.

### 3.5.3 Sediment depth scale patterns and processes

In the Bay of Plenty region, nematode diversity was slightly higher in surface than subsurface sediments, whereas differences in diversity between sediment layers were not consistent among habitats or water depths in the Hikurangi Margin region. Overall, differences in diversity between surface and subsurface sediment layers were limited, which contrasts with the finding of previous studies showing greater diversity in surface than subsurface sediments, a trend associated with the sharp declines of food and oxygen availability, and the presence of toxic sulphides in subsurface sediments (Vanaverbeke et al. 1997b, Ingels et al. 2011b). Relatively high diversity in the subsurface layer of sediment in the deepest strata in the Hikurangi Margin region suggests that these are not limiting factors in the present study, i.e., that subsurface sediment layers are generally characterised by sufficiently high food availability, and/or are well oxygenated. Combining the 1–5 cm depth layers is also likely to have obscured the lowest nematode diversity often observed in the deepest layers (e.g. 4–5 cm; Ingels et al. 2011b).

On the Hikurangi Margin, nematode diversity in surface sediment was negatively correlated with sediment particle kurtosis and sediment phaeopigment concentration, and positively correlated with the abundance of macro-infaunal deposit feeder and trawling intensity; in subsurface sediment, diversity was negatively correlated with particle size diversity, and positively correlated with mega-infaunal bioturbation proxies. Sediment particle kurtosis, as noted earlier, could be interpreted as a measure of past disturbance, with the negative relationship indicating a negative effect of disturbance on diversity (Lambshead et al. 2001), which may be most strongly reflected in surface nematode communities. The negative relationship between diversity and sediment phaeopigment concentration may result from high rates of competitive exclusion (Grime 1973, Huston 1979) and differences in the response of different species towards increased food resources (dos Santos et al. 2008). Macro-infaunal deposit feeders may enhance nematode surface diversity through their feeding activities, which can stimulate bacterial growth (Moens et al. 2014) or prevent single species from dominating small patches of sediment (Widdicombe and Austen 2005). Biogenic structures produced by benthic fauna can also enhance nematodes species diversity by acting as traps for organic matter (Zuhlke et al. 1998, Olafsson 2003, Callaway 2006, Moens et al. 2014). Burrowing infauna may influence subsurface nematode diversity through their bioturbation and bio-irrigation activities, which help to distribute phytodetritus to deeper sediment layers, alter microbial community distribution, and modify the physical-chemical gradients in the sediment, such as oxygen penetration, thus providing favourable conditions to subsurface nematode communities (Heip et al. 2001, Olafsson 2003, Hughes and Gage 2004, Callaway 2006, Moens et al. 2014). Fishing intensity was also positively correlated with nematode surface diversity. Disturbance from trawling may enhance surface diversity by mixing sediment and food particles, and resuspending nematode communities over large areas (Pranovi et al. 2000, Leduc and Pilditch 2013). In subsurface sediment, the negative relationship between particle size diversity and diversity contrasts with the findings of previous studies which described the opposite trend (Etter and Grassle 1992, Leduc et al. 2012d). However, studies have shown that the positive relationship between particle size diversity and deep-sea nematode diversity is not universal, and may be obscured by other environmental factors (Pape et al. 2013a). In the surface sediment of the Bay of Plenty, no environmental variable was significantly correlated with diversity, suggesting that factors not considered in this study may influence nematode surface diversity in this region, or that environmental variability was not sufficiently high to cause substantial changes. Bioturbation by macro-infauna was negatively correlated with nematode subsurface diversity in this region, which is the opposite pattern observed on Hikurangi Margin. This finding may indicate that in a lower productivity region, such as the Bay of Plenty, competition for shared food resources between nematode communities and other infauna may lead to the exclusion of some taxa (Olafsson et al. 1993). These results show that surface and subsurface diversity are influenced by similar environmental factors (i.e. sediment characteristics and bioturbation by larger fauna), even though relationship patterns might be different between regions.

There were pronounced and consistent differences in community structure between surface and subsurface sediment layers in both regions. *Sabatieria* was the highest contributor to sediment depth differences in community structure, and was found to be most abundant in the subsurface layers. *Sabatieria* was generally more abundant in subsurface sediment layers presumably because members of this genus can tolerate low oxygen levels and/or high sulphide concentrations (Vanreusel 1990, Vanaverbeke et al. 1997b, Schratzberger et al. 2009, Leduc et al. 2010b, Vanreusel et al. 2010b, Ingels et al. 2011a, Leduc et al. 2015). It is unclear whether such conditions were present in subsurface sediments at the study sites, particularly in the Bay of Plenty region where food availability is low and suboxic conditions are less likely to develop. It is possible that *Sabatieria*, a genus with relatively large body size and which is thus probably highly mobile,  may be better adapted to exploit food resources away from the surface than other deep-sea genera (Ingels et al. 2011a). *Daptonema* and *Paramonohystera* were also major contributors to differences in community structure between sediment layers in both regions, with *Daptonema* was more abundant in surface sediment, while *Paramonohystera* was abundant in subsurface sediment. *Daptonema*, and *Paramonohystera* are often common in shelf and upper slope environments, and may reach particularly high densities in fine, organic matter rich sediments (Vanreusel et al. 2010b). *Paramonohystera* species have been experimentally shown to survive extremes temperature in anoxic conditions (Wieser et al. 1974), which may explain their preference for subsurface sediment. *Daptonema* is thought to be an efficient colonizer, which can actively migrate or settle into new food patches (Wetzel et al. 2002), which may explain their high abundance in surface sediments (Wetzel et al. 2002, Leduc et al. 2014). *Halalaimus*, a widespread deep-sea genus characterised by long and thin body shape, also showed a preference for surface sediments in both regions (Vanaverbeke et al. 1997b, De Mesel et al. 2006a, Leduc et al. 2010b, Vanreusel et al. 2010b, Ingels et al. 2011a, Leduc et al. 2015), which may reflect their inability to effectively burrow into more compacted subsurface sediment layers. *Acantholaimus* has been shown to have restricted colonisation abilities (Lee et al. 2001) and members of this genus are considered as persisters (low production rate and colonisation ability, and long life cycle) rather than colonisers (Bongers et al. 1991, De Mesel et al. 2006b). The buccal morphology of *Acantholaimus* suggests that members of this taxon may feed on microalgal detritus (they are categorised as epigrowth feeders), which may explain their preference for surface sediment where fresh phytodetritus is likely to be most easily accessible.

On the Hikurangi Margin, community structure of both surface and subsurface sediment was most strongly correlated with food availability proxies. Disturbance proxies, trawling intensity and total surface and subsurface bioturbation were also correlated with community structure in both surface and subsurface sediment, but only weakly. Proxies of bioturbation by macro- and mega-epifauna were also correlated with community structure of both surface and subsurface sediment in the Bay of Plenty. Surface bioturbation marks such as tracks and faecal coils are generally produced by larger infaunal deposit-feeders, which indirectly enhance food resources along their feeding track by helping to stimulate bacterial growth or introduce bacteria along their tracks (Moens et al. 2014), thus influencing surface nematode communities. As noted above, the Bay of Plenty region is characterized by lower surface productivity, and therefore food availability may be more limiting in the subsurface compared to surface sediments, which could explain the presence of a link between sediment organic matter content to subsurface nematode community structure. Overall these results show that surface and subsurface community structure are influenced by broadly similar environmental factors (i.e., proxies of food availability and bioturbation by larger fauna), although the degree of consistency may vary regionally.

Trophic structure differed greatly between sediment layers, and consistently in both the Hikurangi Margin and Bay of Plenty regions. Microvores, deposit feeders and epigrowth feeders contributed most to sediment depth differences in both regions. Microvores and epigrowth feeders were most abundant in the surface sediments, whereas deposit feeders showed the opposite pattern. The high abundance of microvores and epigrowth feeders in surface sediments has been observed previously (Moens and Vincx 1997, Vanaverbeke et al. 1997a, Giere 2009, Neira et al. 2013) and may reflect the higher availability of fresh phytodetritus and associated bacteria in surface than subsurface sediments (Vanaverbeke et al. 2008, Ingels et al. 2010). Deposit feeder feed less selectively on detrital particles and associated microbiota (Moens and Vincx 1997, Vanaverbeke et al. 1997a, Giere 2009, Danovaro et al. 2013), and are typically more abundant in subsurface sediments (Steyaert et al. 2003). A study by Neira et al. (2013) showed that deposit feeding nematodes have high body length to body width ratios, which results in high surface area and may thus enhance cuticular uptake of dissolved organic matter in deeper sediment (Riemann et al. 1990).

In the Hikurangi Margin region, trophic structure of surface nematodes (and the abundance of deposit feeders and epigrowth feeder in particular) was mostly correlated with terrain rugosity, whereas in subsurface sediment, nematode trophic structure (the abundance of epigrowth feeders in particular) was correlated with water depth. Terrain geomorphology has been shown to strongly influence sedimentological distributions (Arzola et al. 2008). Terrain rugosity (a proxy measure of topographic roughness) may enhance sedimentation rate and accumulation of food, which may favour deposit feeders in surface sediment. However, increased fine sediment deposition may have an opposite effect for epigrowth feeders since they may require a wide range of particle size to feed effectively, rather than uniformly fine sediment (Giere 2009). It should also be noted that the relationship between rugosity and the abundance of feeding groups was influenced by outliers, and should therefore be interpreted with caution. In subsurface sediment, epigrowth feeders showed a positive relationship with increased water depth, which may be related to their abilities to survive in low food conditions (typically food availability decreases with increasing depth, (Tietjen (1992), Soltwedel (2000))) by scraping microbes from sediment particles or mucus threads (Moens and Vincx 1997, Vanreusel et al. 2010b, Moens et al. 2014).

In the Bay of Plenty region, trophic structure was correlated with organic matter in surface sediment, whereas in subsurface sediment, trophic structure was correlated with sediment particle skewness. Microvores showed a positive relationship with increased organic matter, whereas epigrowth showed the opposite pattern. Organic matter is generally utilised by bacteria assemblages, which then become a food source to microvores (Findlay and Tenore 1982), which is reflected in the positive relationship between microvores and organic matter. The negative relationship with organic matter observed for epigrowth feeders may related to their feeding preferences to fresh inputs of intact diatom cells (Moens and Vincx 1997, Moens et al. 2014). In subsurface sediment, the relative abundance of deposit feeders and epigrowth feeders were significantly correlated with sediment particle skewness. Skewness implies a state of sediment size distribution lacking in symmetry, where it can be positively skewed (tail of distribution points to the right) or negatively skewed (tail of distribution points to the right). Epigrowth feeder abundance was positively correlated with particle skewness, whereas deposit feeders showed the opposite pattern. In deep-sea sediment, epigrowth feeders may feed by scraping microbes from sediment particles or mucus threads (Moens and Vincx 1997, Vanreusel et al. 2010b, Moens et al. 2014), and therefore may feed more effectively in heterogeneous sediment, rather than uniformly fine sediment (Giere 2009), while deposit feeders are thought to select food particles largely based on particle size (Moens and Vincx 1997), and may thus feed more effectively in homogeneous fine sediment.

### 3.5.4 Multi-scale patterns

The first stage analysis showed that nematode diversity, community structure and trophic structure showed greater variability between regions and sediment depths, compared to among habitats and water depths. Nematode diversity and community structure showed highest variability between regions, followed by sediment depths, whereas nematode trophic structure showed the opposite pattern. Multi-scale studies by Fonseca et al. (2010) and Ingels and Vanreusel (2013) have shown similar results, where nematode diversity and functional diversity were highly variable between sediment depths, but not community structure, which was more variable between margins. Other studies have also noted that the highest variability in nematode community structure is greatest at the regional scale (Bianchelli et al. 2013, Danovaro et al. 2013, Gambi et al. 2014), although these studies were not conducted in the same manner and the relative importance of different scales is not easily interpreted (Barton et al. 2013). The present study also showed that within each region, variability in nematode community attributes varied differently at habitat and sediment depths scales, and was also influenced by water depth. At the habitat scale, all nematode community attributes showed greater variability in the Hikurangi Margin than the Bay of Plenty region. At the scale of sediment depth, only community structure showed highest variability in the Hikurangi Margin region, whereas diversity and trophic structure showed highest variability in the Bay of Plenty region. This finding that the patterns for nematode community attributes are not the same at each scale at each region, reflects the differences in the environmental variables that control nematode distribution.

The present study is one of only few studies designed to compare variability of deep-sea communities across several spatial scales (Fonseca et al. 2010, Ingels and Vanreusel 2013, Taylor et al. 2016), and demonstrates the power of such studies to reveal the relative importance of variation in environment and disturbance at regional and sediment depth scales in influencing nematode communities. The study also highlighted the relative unimportance of habitat effects on these communities, at least for nematodes found in soft sediments of seamount, canyon and slope habitats. That is not to say that habitat effects do not occur for such nematode communities, just that they are less significant than influences operating at larger and smaller spatial scales. It is clear that interactions by nematode communities with their surrounding environment are complex, and should not be interpreted by single-scale studies only, if we are to improve our understanding of the processes that control benthic community attributes in the deep sea, and the vulnerability of communities to anthropogenic disturbance.

### 3.5.5 Implications for vulnerability to anthropogenic disturbance

Nematode community attributes showed clear differences between the study regions, which may imply differences in vulnerability to disturbance from bottom trawling or seabed mining. Higher diversity in the low productivity region of Bay of Plenty compared to the high productivity Hikurangi Margin region could imply greater vulnerability towards less diverse communities in Hikurangi Margin since high diversity communities might be more resilient disturbance (McCann 2000). However, difference in diversity between these two regions was too small to be sufficiently dissimilar in vulnerability levels between each region. Marked differences in nematode community structure between Hikurangi Margin and Bay of Plenty regions were driven largely by the differences in particular genera and their relative abundance. Some of the most common genera found in the Bay of Plenty, such as *Acantholaimus*, are considered persisters and are thought to have limited colonisation abilities (Bongers et al. 1991, Lee et al. 2001, De Mesel et al. 2006b). In Hikurangi Margin, opportunistic genera such as *Sabatieria* were particularly abundant, which may imply lower vulnerability of nematode communities to disturbance in this region. Furthermore, high food availability has been shown to enhance nematode recolonization and overall resilience to disturbance (Gallucci et al. 2008b). Thus, it seems likely that nematode communities in the Bay of Plenty region are more vulnerable to physical disturbance than those on the Hikurangi Margin. However, the present data showed that trawling activity was thirty times greater in

Hikurangi Margin compared to Bay of Plenty region, and it is possible that the high abundance of *Sabatieria* reflects past disturbances from fishing and that communities in this region are therefore already in an altered state.

Habitat differences in nematode community structure were mainly driven by differences in the relative abundance of shared genera. However, some genera were present in certain habitats only. Habitats with high numbers of exclusive genera may be more vulnerable to disturbance because the risk of local extinctions may be greater and the lower chances of successful recolonization by these rare taxa following disturbance (Eskin and Palmer 1985). Genera with restricted distributions were found in all habitats, but canyons had a higher number of exclusive genera (17–28) compared to seamount (7) and slope (14–17) habitats in both regions. Even though canyon habitat was less heavily trawled than seamount habitat (Leduc et al. 2016b), a higher number of exclusive genera occurred at this habitat, suggesting that nematode communities in canyons could be more susceptible to disturbance than in other habitats. The steep topography of canyon habitats also makes nematode communities subject to slope instability and turbidity flows that can occur as a result of trawling events (Puig et al. 2012). This disturbance can cause sudden burial of infauna and can also remove organic-rich sediment down-slope to deeper depths, which can lead to changes in community structure. Although natural disturbance events in canyons could mean that nematode communities are already adapted to such events, canyon communities can still being affected by bottom trawling since anthropogenic disturbances can occur at a greater frequency than natural disturbances.

Bottom trawling can cause widespread changes to vertical gradients in sediment biogeochemistry by altering sediment particle size distribution, re-distributing food particles, and modifying oxygen penetration depths (Martín et al. 2014). Deep-sea mining may also cause long-term changes in sediment compaction (Van Dover 2011), which would severely limit the ability of nematodes to move between surface and subsurface layers. Nematode communities in surface and subsurface sediment are likely to be equally vulnerable to direct physical disturbance from bottom trawling or seabed mining because both trawls and mining tools disturb the sediment to depths > 5 cm. However, a study by Schratzberger et al. (2004) showed that following disturbance, nematodes can recolonise surface sediment through suspended sediment transport, suggesting a potentially more rapid recovery for surface communities than subsurface communities. Physical disturbance may thus accentuate differences between surface and subsurface nematode communities.

## 3.6 Acknowledgements

This study was part of NIWA’s research project ‘Impact of resource use on vulnerable deep-sea communities’ funded by the New Zealand Ministry of Business, Innovation and Employment (CO1X0906). We thank the scientific personnel of voyages TAN1004 and TAN1206, and the officers and crew of RV *Tangaroa*. We are also grateful to Lisa Northcote and Karen Thompson for sediment analyses, David Bowden for providing bioturbation data, and Andy McKenzie for help in R software (all NIWA). We acknowledge funding from the Department of Marine Science, University of Otago, New Zealand, and Universiti Pendidikan Sultan Idris through the Ministry of Higher Education, Malaysia.

# Chapter 4

# Addressing the taxonomic challenge for marine nematodes in the New Zealand region: description of new species and assessment of the state of systematics

The taxonomic information in this chapter has been published in the following paper:

Rosli, N., Leduc, D., and Probert, P. K. (2014). Two new species and a new record of Comesomatidae (Nematoda, Araeolaimida) from Southern Hikurangi Margin, New Zealand. Zootaxa 3900: 505–525.

## 4.1 Introduction

### 4.1.1 Taxonomy of deep-sea nematodes

Nematodes are the most abundant animals in marine sediments (Lambshead and Boucher 2003, Giere 2009, Moens et al. 2014) and display a high level of local and regional diversity (Miljutin et al. 2010, Leduc et al. 2012b). Approximately 6,900 species of free-living marine nematodes have been described to date, and it has been estimated, based on expert opinion, that about 50,000 species are still undescribed and undiscovered (Appeltans et al. 2012). In the deep sea, a total of 638 valid species belonging to 175 genera and forty-four families have been reported, mostly from the North Atlantic and the Mediterranean, with the rest of the world's deep oceans considered understudied (Miljutin et al. 2010).

Nematodes are often used to investigate patterns and relationships with environmental variables because they are considered good indicators of pollution, disturbance and global climate changes (Balsamo et al. 2012, Zeppilli et al. 2015a). Nematodes are good indicator taxa because they are highly diverse and show potentially species- or genus-specific responses to different environmental stressors (Danovaro et al. 1995, Austen and McEvoy 1997, Mirto et al. 2000). Nematode feeding groups are also easily recognizable, which makes it possible to identify functional diversity traits (Moens and Vincx 1997), and can be used in exploring relationships between biodiversity and ecosystem function (Danovaro et al. 2008a). However, a recent study by Derycke et al. (2016) has shown that morphologically similar cryptic species can have different food preferences. Genus-level information may therefore not be sufficient for fully understanding the ecology of nematodes in deep-sea ecosystems. Species-level information is also crucial for the investigation of biodiversity-function relationships (Danovaro et al. 2008a, Leduc et al. 2013), and therefore it is important that taxonomic studies of nematodes are undertaken.

### 4.1.2 Taxonomy of free-living marine nematodes in New Zealand

Studies on the taxonomy of free-living marine nematodes in New Zealand are still in the early stages, with only a few taxonomic studies conducted before the 21st century (Ditlevsen 1921, Allgén 1927, Ditlevsen 1930, Allgén 1932, Allgén 1947, 1950, Wieser 1956). Until recently, only two deep-sea nematode species, *Thoracostoma bruuni* Wieser, 1956 and *Synonchoides galatheae* Wieser, 1956, were known from the New Zealand region. Over the last few years, several new deep-sea nematode species have been described from the continental slope of Chatham Rise and Challenger Plateau (e.g. Leduc 2012, 2013b, Leduc and Verschelde 2013). The deep-sea nematode fauna in the New Zealand region is highly diverse with estimates of ~1200 species present on Chatham Rise and Challenger Plateau alone (Leduc et al. 2012b), with much of this diversity likely to be new to science. With so many species undescribed it is prudent to prioritise taxonomic efforts towards those taxa that are either common and/or are likely to provide ecological insight.

### 4.1.3 Taxonomy of the Family Comesomatidae in New Zealand

Comesomatids are among the most abundant nematodes in continental margin sediments (Jensen 1979, Netto et al. 2005, Muthumbi et al. 2011, Zeppilli et al. 2011, Danovaro et al. 2013). Comesomatids are generally most abundant in coastal, shelf and upper continental slope sediments and are less commonly recorded beyond the lower slope depths (Vanreusel 1990, Netto et al. 2005, Schratzberger et al. 2009, Vanreusel et al. 2010b, Ingels et al. 2011a, Muthumbi et al. 2011). *Sabatieria* is generally the most abundant comesomatid genus found on continental slopes, and may account for up to ~20% of total nematode abundance (Netto et al. 2005, Danovaro et al. 2013). *Laimella* and *Vasostoma* are less common on the continental slope compared to *Sabatieria* species; *Laimella* can been found from 250–3600 m water depth (Chen and Vincx 2000, Hong et al. 2016), whereas *Vasostoma* has been recorded at 670–1200 m water depth (Leduc et al. 2012a). *Sabatieria* is considered to be well adapted to fine sediment environments with high organic input, and can tolerate the low oxygen levels that characterise some subsurface sediments (Vanreusel 1990, Vanaverbeke et al. 1997b, Schratzberger et al. 2009, Leduc et al. 2010b, Vanreusel et al. 2010b, Ingels et al. 2011a, Leduc et al. 2015). *Sabatieria* is also sometimes associated with physically disturbed sediments, possibly due to their resilience to burial and ability to survive in low oxygen conditions (Vanreusel 1990, Schratzberger et al. 2009). *Sabatieria* is generally considered as indicator of disturbed conditions, such as in canyon habitats where active hydrodynamic regimes lead to high sediment transport and accumulation, or in the sediment underlying oxygen minimum zone (Ingels et al. 2009, Ingels et al. 2011a, Neira et al. 2013). A study by Mirto et al. (2002) on the impact of fish farming activities on nematode communities found that the comesomatid genus *Setosabatieria* was highly sensitive to biodeposition and disappeared almost completely in sediments beneath fish farms, whereas other comesomatid genera (*Sabatieria*, *Dorylaimopsis*) increased in dominance. This finding indicates that comesomatid genera are not equally tolerant to physical disturbance or pollution. Apart from *Sabatieria,* no information is available on the sensitivity of other genera to disturbance, either in shallow or deep waters in the New Zealand region.

Here, I describe two new species belonging to the genera *Vasostoma* Wieser, 1954 and *Sabatieria* De Rouville, 1903, and provide the first record of *Laimella* *subterminata* Chen & Vincx, 2000 from Hikurangi Margin, New Zealand. A new key of species identification for *Vasostoma* genera also has been constructed and modified from a previous key. The species descriptions are put in the context of an updated checklist for nematodes of the New Zealand region, and elsewhere in the Southern Hemisphere.

## 4.2 Material and methods

### 4.2.1 Species descriptions

Specimens for species descriptions were obtained from samples collected from two canyon sites (670 m and 1350 m) on the southern Hikurangi Margin during National Institute of Water and Atmospheric Research (NIWA) research cruise TAN1004 on 14–29 April 2010 (Figure 4.1). Samples were collected using an Ocean Instruments MC-800A multicorer (MUC), and three replicate cores were obtained from each site. Each subcore was divided into three vertical fractions: 0–1 cm, 1–3 cm and 3–5 cm depth (1–3 cm and 3–5 cm were later combined). Physical and biogeochemical parameters (i.e., sediment grain size, pigment concentrations, $CaCO_3$ content, total organic matter (TOM), water content) were determined for each sample using standard methods (Nodder et al. 2003, Grove et al. 2006) (see also Chapter 2 and 3).

Sediment samples were washed on a 1 mm mesh sieve to remove macrofauna and on a 45 µm mesh to retain nematodes and other meiofauna. Meiofauna were extracted from the sieved sediment by Ludox flotation (Somerfield and Warwick 1996). Nematodes were transferred to glycerine and mounted onto permanent slides (Somerfield and Warwick 1996).

All measurements are in µm, and all curved structures are measured along the arc. Type specimens are held in the NIWA Invertebrate Collection, Wellington. Anterior sense organs are defined as follows: papillae (<1 µm long), setiform papillae (1–2 µm), and setae (>2 µm) (Leduc and Wharton 2008). Abbreviations in the text are as follows:

a = body length/maximum body diameter
abd = anal body diameter
b = body length/pharynx length
c = body length/tail length
cbd = corresponding body diameter
hd = head diameter
L = body length
%V = vulva distance from anterior end of body × 100/total body length

The modified key of species identification was constructed by compiling all valid species for the specific genera. The characteristics and measurements of each species were listed to differentiate similarity and dissimilarity between each species. Then, a key is constructed of a series of couplets, each consisting of two separate statements, started from broad characteristics and progressing towards narrow characteristics until single option is remain, which lead to characteristics that are only present for that species.

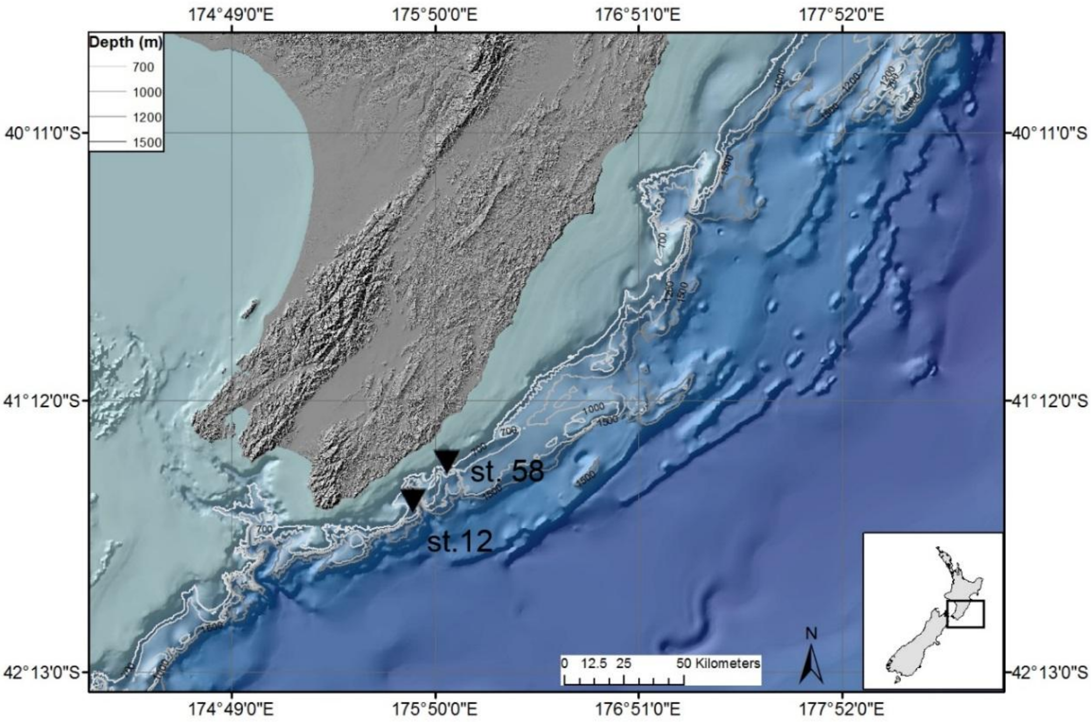

Figure 4.1. Map of study area showing location of sampling sites (inverted triangles, stations 12 and 58 from voyage TAN1004).

### 4.2.2 Species checklist for nematodes

The checklist for marine nematode species provided by Leduc and Gwyther (2008) was updated. This checklist was updated by searching the taxonomic literature that has been published after 2008, and also by checking the nematode database NeMys (Guilini et al. 2016). Species from both New Zealand and Southern Hemisphere localities were included in the checklist, and it was also noted if a species also occurred in the Northern Hemisphere. Details of water depth range were also recorded (“shallow”, 0–200 m depth range; “deep”, > 200 m depth).

## 4.3 Results

### 4.3.1 Systematics

**Family Comesomatidae Filipjev, 1918**

**Diagnosis (Modified from Platt and Warwick (1988) and Fonseca and Bezerra (2014)).**

Multi-spiral amphids. Cuticle with transverse rows of punctations, usually differentiated laterally. Buccal cavity without cheilorhabdia, in two compartments, with a globular, cup-shaped or shallow anterior portion, and either narrow, weakly cuticularized, collapsed tubes or dilated, cylindrical to conical portion with cuticularized walls and projections at the borders between the two portions. Pharynx gradually widens posteriorly but rarely has a true bulb. Gubernaculum with or without paired dorso-caudal apophyses. Pre-cloacal supplements present or absent. Testes paired, outstretched. Copulatory apparatus with weakly to strongly cuticularized spicules and gubernaculums, paired apophyses of variable position. Precloacal supplements mostly pore-like or papilloid, occasionally tubular. Ovaries didelphic, opposed and outstretched. Conico-cylindrical tail with three terminal setae.

**Subfamily Dorylaimopsinae De Connick, 1965**

**Diagnosis (Modified from Jensen (1979)).**

Cuticle punctated, with or without lateral differentiation. Anterior sensillae in three distinctly separated circles. Buccal cavity cuticularized, anterior portion shallow, posterior portion dilated, cylindrical or conical, with strongly cuticularized walls and three thorn-like projections (teeth) at the border between the two portions. Gubernacular apophyses usually directed caudally, occasionally dorso-caudally.

### Genus Vasostoma Wieser, 1954

### Diagnosis (modified from Wieser (1954), Jensen (1979) & Leduc et al. (2012a)).

Punctated cuticle without lateral differentiation. Outer labial papillae immediately anterior to cephalic setae. Posterior portion of buccal cavity cylindrical to conical, lightly to strongly cuticularized, provided with three, rarely six, acute projections (teeth) at border with anterior portion. Spicules usually short and arcuate, rarely long and slender. Gubernacular apophyses directed dorso-caudally. Supplements sometimes present.

**Type species**: *Vasostoma spiratum* Wieser, 1954

### List of valid *Vasostoma* species

(Note: *recorded from New Zealand).
*V. auratum* Leduc et al., 2012*
*V. articulatum* Huang & Wu, 2010
*V. brevispicula* Huang & Wu, 2011
*V. longicaudata* Huang & Wu, 2011
*V. longispicula* Huang & Wu, 2010
*V. spiratum* Wieser, 1954
*V. vietnamica* Tu et al., 2008

### *Vasostoma hexodontium* n. sp. (Figure 4.2–Figure 4.5)

Type material: Holotype male (NIWA 88371), collected on 20 April 2010, NIWA cruise TAN1004, station 58, Southern Hikurangi, (41.408 N, 175.8977 E), canyon axis. Characteristics of sediment layer (1–5 cm): muddy sediment (92.2%), calcium carbonate content: 2.3%; total organic matter content: 5.2%; chloroplastic pigment concentration: 4 µg/g. Paratype female (NIWA 88372), same data as holotype.

## Description

**Male**: Body cylindrical, gradually tapering towards both extremities. Head set off by constriction immediately posterior to cephalic setae. Cuticle with transverse rows of dots, no lateral differentiation. Somatic setae short and sparse (1–3 µm).

Inner labial sensillae indistinct; six outer labial papillae, and four cephalic setae, 0.3 cbd. Anterior portion of buccal cavity cup-shaped, cuticularized. Posterior portion of buccal cavity cylindrical and heavily cuticularized, six triangular, cuticularized teeth at border with anterior portion of buccal cavity, two of them are distinct and the other four are indistinct. Amphid spiral, three turns. Pharynx widens gradually towards posterior, no true bulb. Cardia small, oval-shaped. Nerve ring near half of the pharynx length from anterior. Secretory-excretory system not observed.

Reproductive system diorchic, with two outstretched testes. Anterior testis to the left of intestine, posterior testis to the right of intestine. Spermatozoa present, oblong or oval shaped (4–6 µm × 10–19 µm). Five rounded ejaculatory glands, situated on the anterior to the spicules (Figure 4.3A), may be paired, but only distinct on dorsal side. Spicules arcuate, strongly cuticularized, thickest at one third of spicule length from proximal end, 2.2 abd. Gubernaculum with small, cuticularized pointed structure at base of cuneus (Figure 3D). Long, straight caudal apophyses, constricted at the base. The gubernaculum and caudal apophyses strongly cuticularized along the posterior edge. Cloacal gland with complex shape, surrounding one-third of the spicules and gubernaculum. Pre-cloacal supplements indistinct. One pre-cloacal seta, 2 µm long.

Tail conico-cylindrical with slightly swollen tip. Scarce, short caudal setae (1–2 µm) and three short terminal setae, 3–5 µm. Three caudal glands.

**Female**: Similar to male, but with slightly larger maximum body diameter. Slightly shorter cephalic setae (0.2–0.3 cbd). Six triangular, cuticularized teeth, all distinct, unlike in the male. Secretory-excretory system present, excretory pore located posterior to nerve ring, ventral gland distinct, posterior to pharynx. Reproductive system didelphic, with two opposed and outstretched ovaries. Anterior ovary to the left of intestine, posterior ovary to the right of intestine. Vulva at mid-body. Granular vaginal glands and spermatheca present. Mature eggs 70–81 µm long, 51–58 µm wide. Terminal setae 2–3 µm in length.

### Diagnosis

*Vasostoma hexodontium* n. sp. is characterized by its amphideal fovea with three turns, posterior portion of buccal cavity deep, cylindrical, with six teeth at anterior edge, indistinct pre-cloacal supplements, arcuate spicules 2.2 abd long and strongly cuticularized, gubernaculum with small, cuticularized pointed structure at base of cuneus with long, straight caudal apophyses.

### Differential diagnosis

*Vasostoma hexodontium* n. sp. differs from all other *Vasostoma* species by having six cuticularized teeth. The gubernaculum of *V. hexodontium* n. sp. is distinguished from that of other *Vasostoma* species by having a cuticularized pointed structure at the base of cuneus. *Vasostoma hexodontium* n. sp. also has a deep buccal cavity similar to *V. longispicula* Huang & Wu, 2010 (35–36 *vs* 30–37 µm deep). Other *Vasostoma* species have relatively shallow buccal cavities (12–22 µm deep).

*Vasostoma longispicula* Huang & Wu, 2010 shares a similar name with *V. longispiculum* Timm (1961). The species names differ only in their endings (*-a vs –um*), presumably due to confusion as to the gender of *Vasostoma* (stoma is neutral). Hopper (1967) transferred *V. longispiculum* to *Paracomesoma*; according to Hopper, *V. longispiculum* is more similar to *Paracomesoma* because of its elongated spicules, gubernaculum without apophyses and small buccal cavity. *Vasostoma longispicula* also has long spicules but is characterised by a gubernaculum with dorso-caudal apophyses, and should therefore remain in *Vasostoma*.

*Paracomesoma* and *Vasostoma* are similar in the arrangement of the head sensillae and buccal cavity with three or six teeth, but differ in the length of spicule, structure of the gubernaculum and buccal cavity. *Paracomesoma* species usually have long and slender, unjointed spicules, small plate-like gubernaculum without dorsal apophyses, and small, conical buccal cavity, whereas *Vasostoma* species usually have short and bent spicules (some species have jointed spicules, *i.e., V. articulatum* Huang & Wu, 2010), gubernaculum always with conspicuous apophyses directed dorso-caudally, and cylindrical to conical buccal cavity. Some *Vasostoma* species are similar to *Paracomesoma* because they have long spicules (*i.e*., *V. articulatum, V. longispicula*), or a small buccal cavity (*i.e*., *V. articulatum, V. brevispicula* Huang & Wu, 2011) but differ from *Paracomesoma* because they possess conspicuous gubernacular apophyses.

## Etymology

The species epithet, derived from the Greek *hex* (six) and *odontos* (tooth), refers to the presence of six teeth.

**Note:** Article 34.2 of the International Code of Zoological Nomenclature states that "The ending of a Latin or Latinised adjectival or participial species-group name must agree in gender with the generic name with which it is at any time combined; if the gender ending is incorrect it must be changed accordingly (the author and date of the name remain unchanged). However, Article 31.2.2 states that "Where the author of a species-group name did not indicate whether he or she regarded it as a noun or as an adjective, and where it may be regarded as either and the evidence of usage is not decisive, it is to be treated as a noun in opposition to the name of its genus (the original spelling is to be retained, with gender ending unchanged)". Therefore, we propose that the endings of the following species names, which are best regarded as adjectives, be emended to reflect the neutral gender of the Greek *–stoma*: *V. articulata* Huang & Wu, 2010, *V. aurata* Leduc et al., 2012a, and *V. spirata* Wieser, 1954 (these species names should now end with the suffix *–um*). The names of the remaining *Vasostoma* species cannot decisively be regarded as adjectives, and should therefore remain unchanged.

**Key to all known species of *Vasostoma* (Modified from Huang and Wu (2011) and Leduc et al. (2012a))**

1. Pharyngeal bulb present ........................................................................... 2

Pharyngeal bulb absent ............................................................................. 4

2. Spicules jointed................................................*V. articulatum* Huang & Wu, 2010

Spicules without joints............................................................................. 3

3. Spicules short (< 2 abd long), pre-cloacal supplements less than 11 ...................... ...................................................................... *V. brevispicula* Huang & Wu, 2011

Spicules long (> 4 abd long), pre-cloacal supplements more than 11 ..................... ..................................................................... *V. vietnamica* Tu et al., 2008

4. Buccal cavity with six teeth.................................................. *V. hexodontium* **n. sp.**

Buccal cavity with 3 teeth........................................................................ 5

5. Spicules short (≤ 1.8 abd long) ................................................................ 6

Spicules long (> 2 abd long) ............................*V. longispicula* Huang & Wu, 2010

6. Tail long, filiform (> 7 abd), no terminal setae ......................................................

......................................................................*V. longicaudata* Huang & Wu, 2011

Tail short (≤ 5 abd), with terminal setae ...............................................................7

7. Conspicuous chords (outline of cells bodies golden-colored), pre-cloacal supplements indistinct..............................................*V. auratum* Leduc et al., 2012

Chords not conspicuous, pre-cloacal supplements conspicuous............................ ......................................................................... *V. spiratum* Wieser, 1954

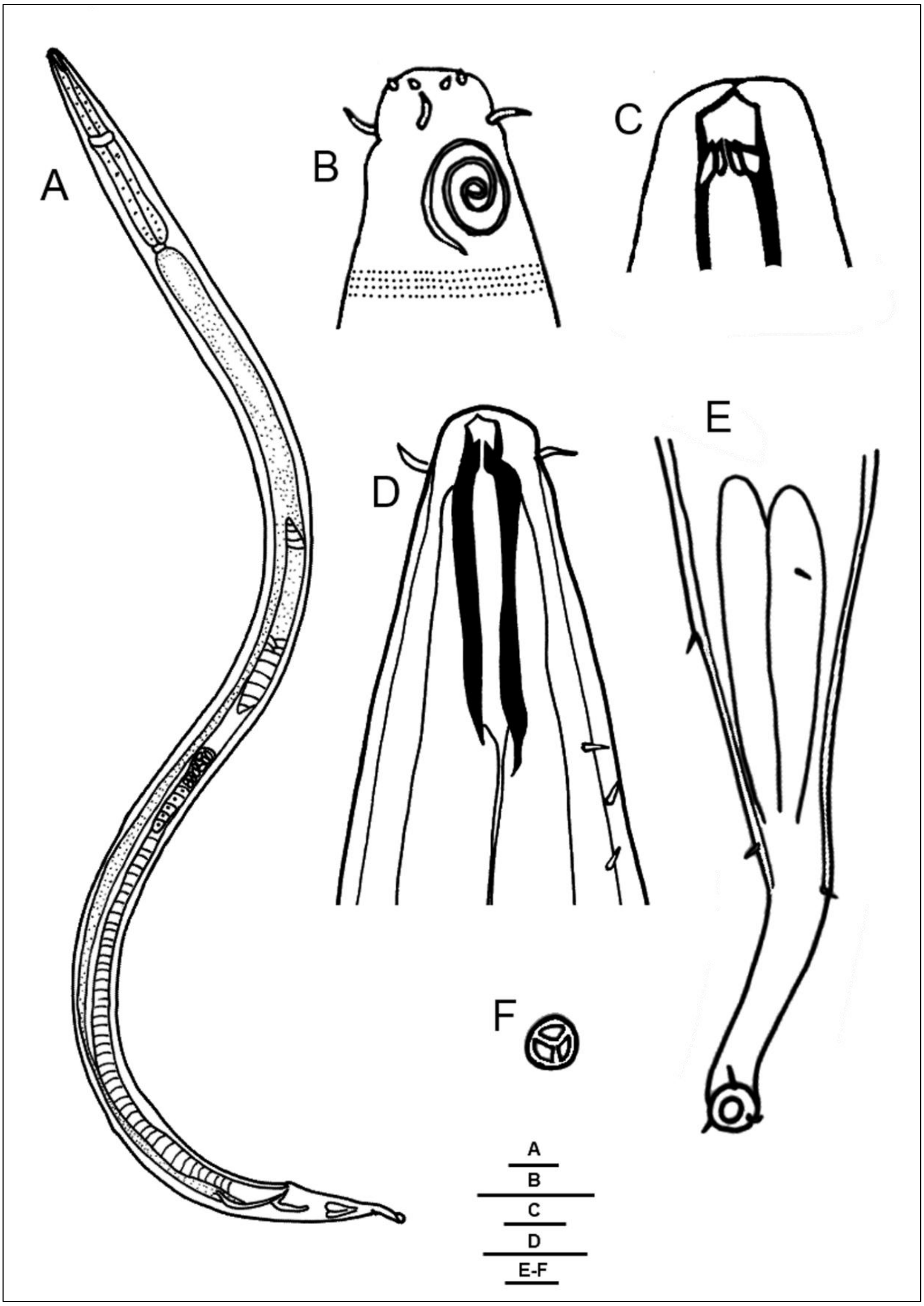

Figure 4.2. *Vasostoma hexodontium* n. sp. Male. A. Entire body; B. Lateral surface view of anterior end showing amphid and setae; C. Lateral view of anterior head showing teeth; D. Anterior head showing buccal cavity and teeth; E. Tail region; F. Cross-section of tail showing caudal glands. Scale bars: A: 64 µm; B, D: 12 µm; C: 3 µm; E–F: 8 µm.

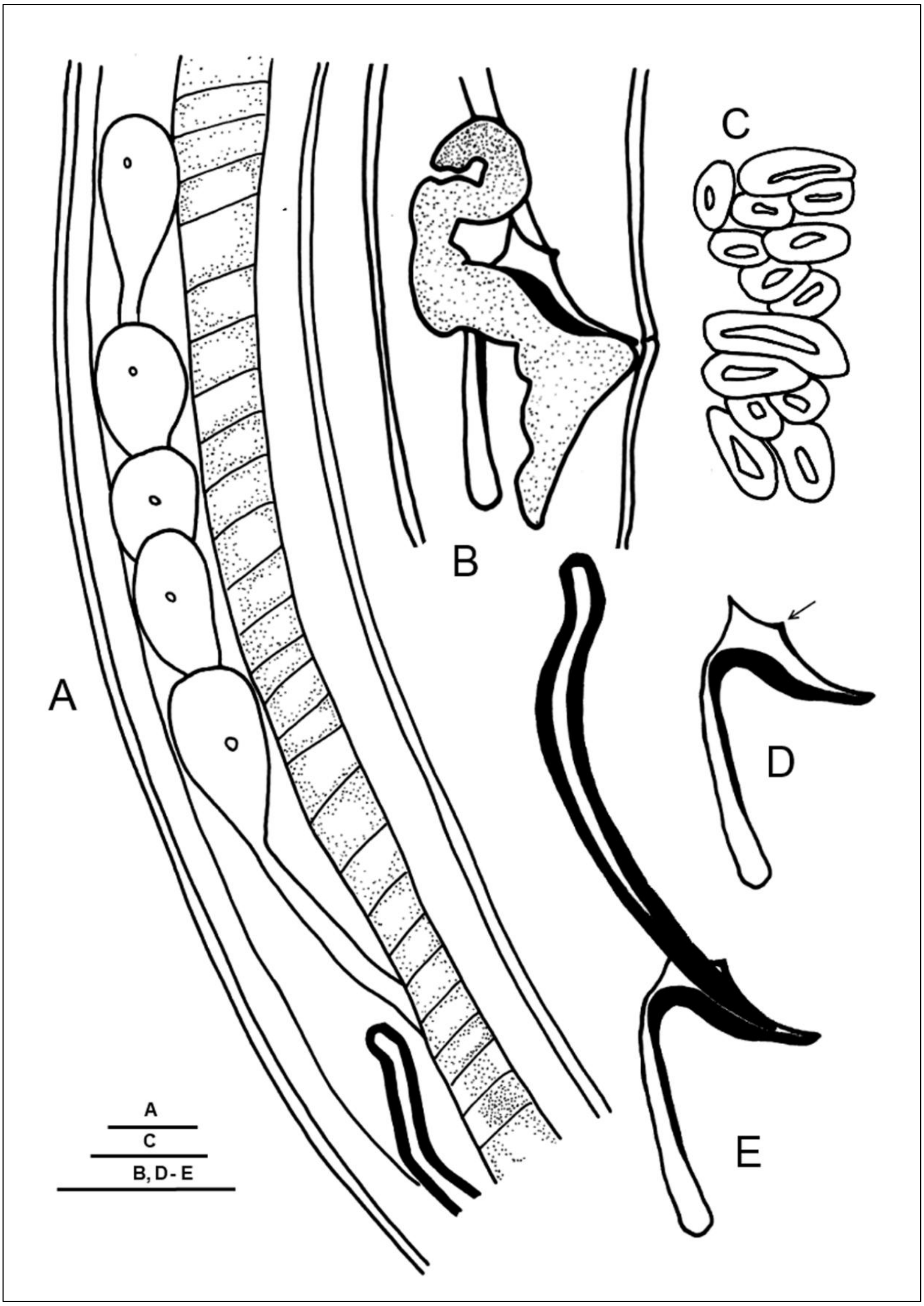

Figure 4.3. *Vasostoma hexodontium* n. sp. Male. A. Posterior body region showing ejaculatory glands; B. Cloacal gland with gubernaculum and spicule underneath; C. Spermatozoa; D. Gubernaculum (arrow pointing the pointed bits on the cuneus); E. Spicule with gubernaculum. Scale bars: A: 20 µm; B, D–E: 33 µm; C: 19 µm.

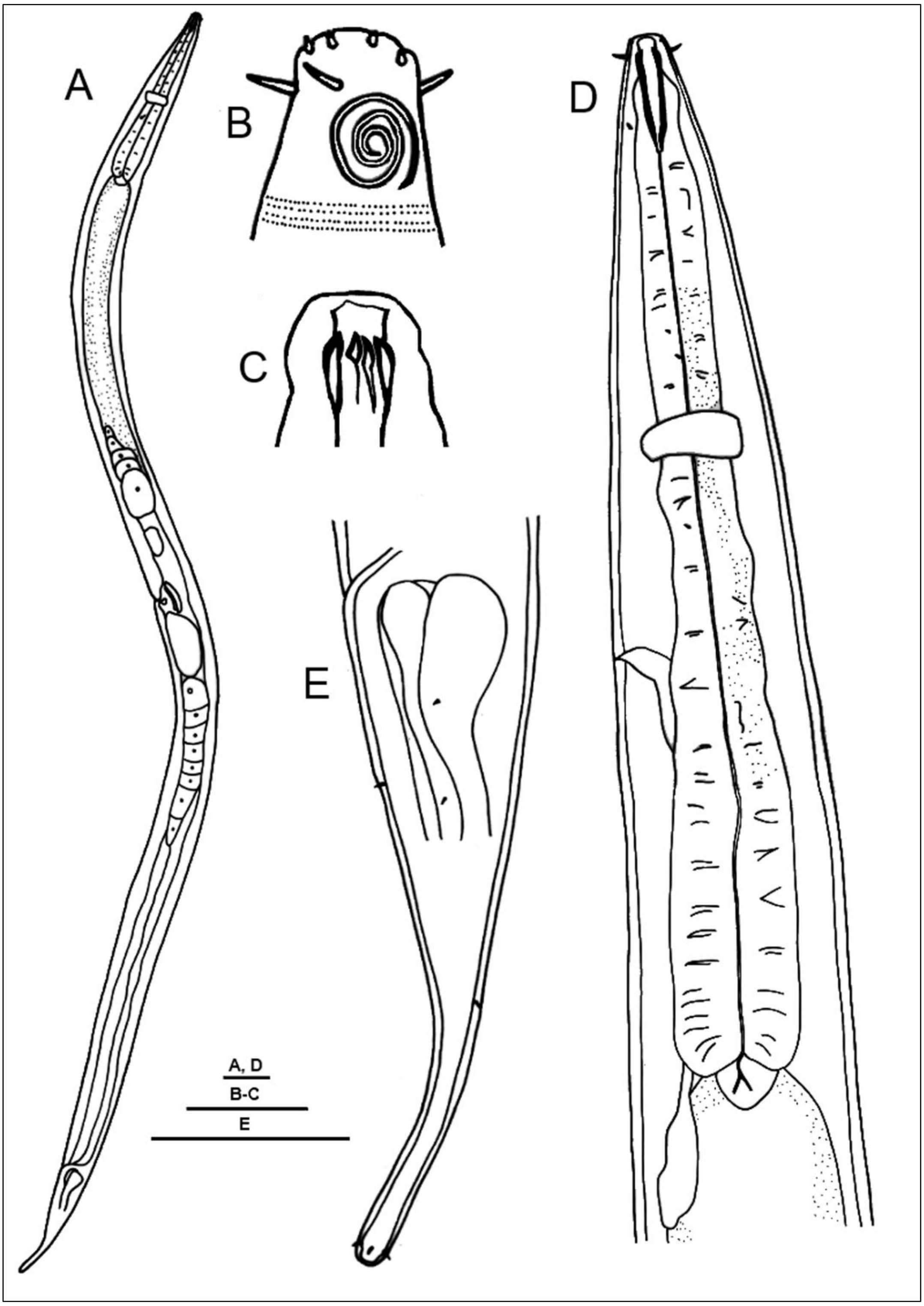

Figure 4.4. *Vasostoma hexodontium* n. sp. Female. A. Entire body; B. Lateral surface view of anterior end showing amphid and setae; C. Lateral view of anterior head showing buccal cavity and teeth; D. Pharynx region showing buccal cavity, nerve ring, excretory pore and ventral gland; E. Tail region. Scale bars: A, D: 73 µm; B–C: 14 µm; E: 55 µm.

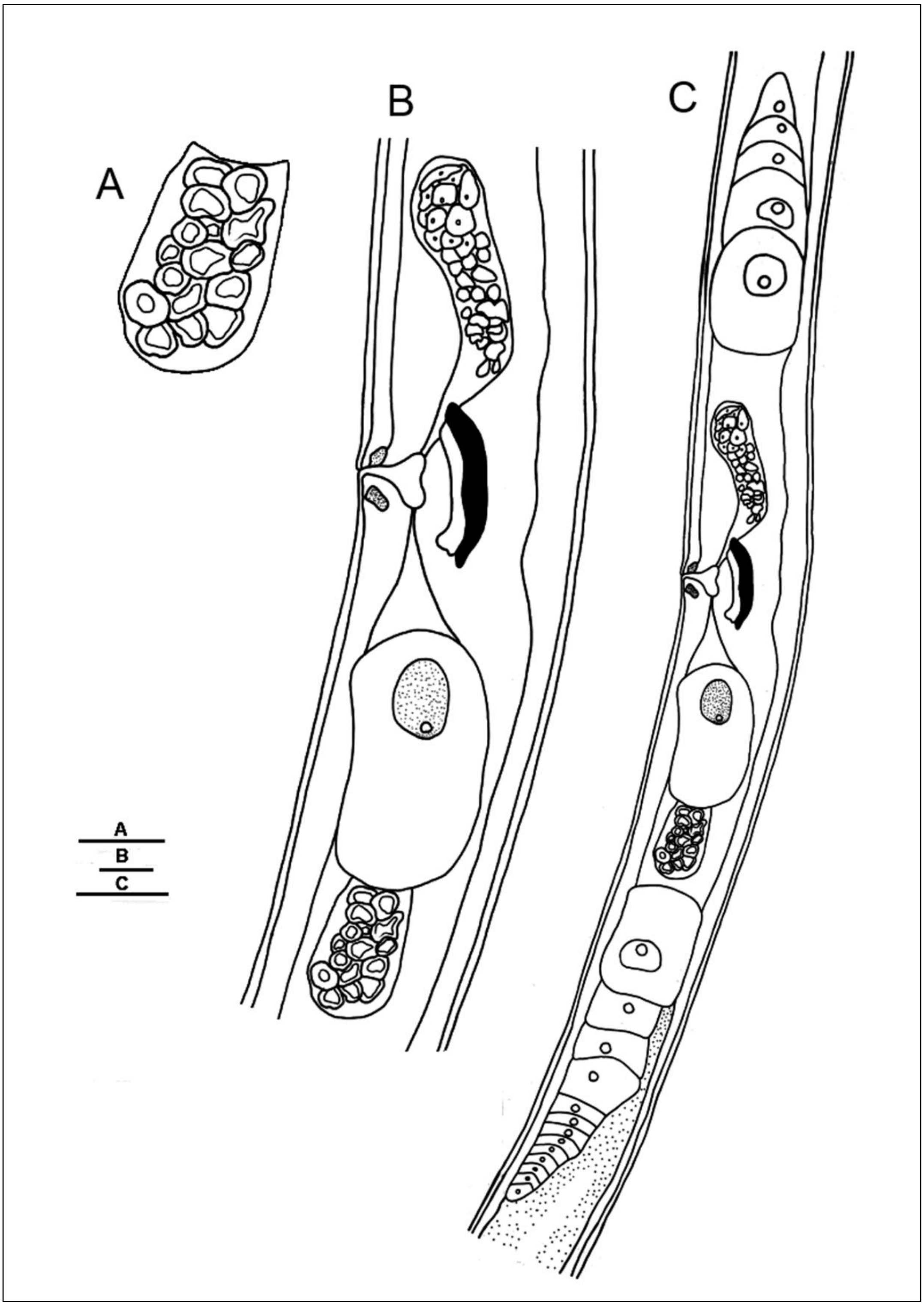

Figure 4.5. *Vasostoma hexodontium* n. sp. Female. A. Posterior spermathecal; B. Vulva with egg and spermathecal; C. Mid region of body showing vulva and genital branches. Scale bars: A–B: 20 µm; C: 64 µm.

Table 4.1. Morphometrics of *Vasostoma hexodontium* n. sp., *Sabatieria dispunctata* n. sp. and *Laimella subterminata* Chen & Vincx, 2000. All measurements are in µm.

| Species | *Vasostoma hexodontium* n. sp. | | *Sabatieria dispunctata* n. sp. | | *Laimella subterminata* | |
|---|---|---|---|---|---|---|
| | Male | Female | Male | Female | Male | Female |
| Length | 2183 | 2287 | 661 | 573 | 1439 | 1423 |
| a | 30 | 28 | 35 | 25 | 35 | 41 |
| b | 7 | 7 | 6 | 6 | 10 | 10 |
| c | 12 | 10 | 7 | 5 | 6 | 5 |
| Max. body diameter | 73 | 82 | 19 | 23 | 42 | 35 |
| Head diameter at amphid | 12 | 15 | 5 | 6 | 15 | 12 |
| Head diameter at cephalic setae | 12 | 14 | 5 | 6 | 15 | 12 |
| Depth of buccal cavity | 36 | 35 | - | - | - | - |
| Length of outer labial setae | - | - | - | - | 2–4 | 3–5 |
| Length of cephalic setae | 4 | 3–4 | 3–4 | 2–4 | 6–8 | 7–9 |
| Amphid height | 10 | 10 | 5 | 5 | 9 | 7 |
| Amphid width | 9 | 11 | 5 | 6 | 10 | 8 |
| Amphid width/cbd (%) | 59 | 65 | 83 | 92 | 61 | 56 |
| Amphid from anterior end | 7 | 8 | 3.31 | 3.01 | 6.35 | 6 |
| Nerve ring from anterior end | 130 | 132 | 52 | 50 | 81 | 57 |
| Nerve ring cbd | 50 | 55 | 13 | 14 | 34 | 29 |
| Nerve ring % | 42 | 39 | 48 | 51 | 54 | 41 |
| Excretory pore from anterior end | - | 207 | - | 57 | 99 | 86 |
| Pharynx length | 308 | 341 | 107 | 98 | 151 | 140 |
| Pharynx cbd | 64 | 73 | 15 | 16 | 39 | 34 |
| Pharyngeal diameter at base | 36 | 42 | 10 | 12 | 31 | 25 |
| Spicule length | 122 | - | 24 | - | 38 | - |
| Gubernacular apophyses length | 45 | - | 5 | - | 10 | - |
| Anal body diameter (abd) | 54 | 55 | 13 | 15 | 32 | 25 |
| Tail length | 177 | 220 | 101 | 114 | 246 | 288 |
| Tail length/abd | 3 | 4 | 8 | 8 | 8 | 12 |
| Vulva from anterior end | - | 1156 | - | 267 | - | 649 |
| Vulva body diam. | - | 82 | - | 22 | - | 32 |
| Vulva (%) | - | 51 | - | 47 | - | 46 |

### Subfamily Sabatieriinae Filipjev, 1934

**Diagnosis (modified from Jensen (1979) and Fonseca and Bezerra (2014)).**

Anterior sensillae in three separate circles, second and third circles very close together. Buccal cavity rather weakly cuticularized; anterior portion globular to cup-shaped, sometimes very small; posterior portion never strongly cuticularized and never cylindrical or conical, but always a narrow collapsed tube. Spicules bent, usually enlarged proximally. Apophyses usually directed dorso-caudally and paired; if directed dorsally, apophysis is single, small and rudimentary.

### Genus Sabatieria De Rouville, 1903

**Diagnosis (modified from Jensen (1979), Platt (1985) and Fonseca and Bezerra (2014)).**

Cuticle with transverse punctation, lateral differentiation of larger regular or irregular punctations may occur, or occasionally striated. Cephalic sensillae in three distinct circles, setae of third circle longer than those of second circle. Anterior buccal cavity cup-shaped, posterior buccal cavity narrow, weakly cuticularized. Amphid multi-spiral. Spicules short. Gubernaculum with dorso-caudal or caudal apophyses. Pre-cloacal supplements usually present.

**Type species:** *Sabatieria cettensis* De Rouville, 1903

**List of valid *Sabatieria* species by group (**modified from Leduc (2013d) and (Botelho et al. 2014))**.**

(Note:*recorded from New Zealand; **new record for New Zealand).

***S. praedatrix group:***

*S. alata* Warwick, 1973

*S. ancudiana* Wieser, 1954

*S. balbutiens* Leduc, 2013*

*S. bitumen* Botelho et al., 2007**

*S. bubulba* Leduc, 2013*

*S. challengerensis* Leduc, 2013*

*S. conicauda* Vitiello, 1970

*S. coomansi* Chen & Vincx, 1999

*S. curvispiculata* Gagarin, 2013

*S. demani* Bresslau & Stekhoven, 1940

*S. doancanhi* Tu et al., 2008

*S. dodecaspapillata* (Kreis, 1929)

*S. exculta* Leduc, 2013*

*S. falcifera* Wieser, 1954

*S. fidelis* Botelho et al., 2009

*S. finitima* Fadeeva & Belogurov, 1984

*S. flecha* Pastor de Ward, 2003

*S. foetida* Gagarin & Thanh, 2008

*S. granifer* Wieser, 1954

*S. granulosa* Vitiello & Boucher, 1971

*S. heipi* Chen & Vincx, 200

*S. intacta* Fadeeva & Belogurov, 1984

*S. intermissa* Wieser, 1954

*S. kolaensis* (Ssaweljev, 1912)

*S. labium* Botelho et al., 2014

*S. lawsi* Platt, 1983

*S. lucia* Muthumbi et al., 1997

*S. lyonessa* Warwick, 1977

*S. palmaris* Fadeeva & Belogurov, 1984

*S. parabyssalis* Wieser, 1954

*S. paracupida* Wieser & Hopper, 1967

*S. paradoxa* Wieser & Hopper, 1967

*S. parapraedatrix* Leduc, 2013*

*S. paraspiculata* Botelho et al., 2007

*S. parvula* Gagarin & Thanh, 2006

*S. praedatrix* De Man, 1907 syn. *S. dubia* (Ditlevsen, 1918), syn. *S. cobbi* Kreis, 1929, syn. *S. rugosa* Schuurmans, 1950

*S. sanjosensis* Pastor de Ward, 2003

*S. spiculata* Botelho et al., 2007

*S. stekhoveni* Vitiello, 1970

*S. subrotundicauda* Botelho et al., 2007

*S. triplex* Wieser, 1954

*S. vasicola* Vitiello, 1970

*S. verteris* Botelho et al., 2014

*S. wieseri* (Wieser, 1954)

***S. pulchra* group:**

*S. breviseta* Stekhoven, 1935

*S. maboyae* Gourbault & Vincx, 1990

*S. mortenseni* (Ditlevsen, 1921)* syn. *S. annulata* Leduc & Wharton, 2008*

*S. pisinna* Vitiello, 1970

*S. propisinna* Vitiello, 1976

*S. pulchra* (Schneider, 1906) syn. *S. vulgaris* (de Man, 1907), syn. *S. clavicauda* (Filipjev, 1918), syn. *S. punctata* (Kreis, 1924), syn. *S. trivialis* Tchesunov, 1978

*S. pumila* Leduc, 2013*

*S. punctata* (Kreis, 1924)** syn. *S. americana* Timm, 1952

***S. celtica* group:**

*S. bathycopia* Leduc, 2013*

*S. celtica* Southern, 1914 syn. *S. cupida* Bresslau & Schuurmans Stekhoven, 1940, syn. *S. longiseta* (Allgén, 1934)

*S. furcillata* Wieser, 1954

*S. kelleti* Platt, 1983

*S. strigosa* Lorenzen, 1971

***S. armata* group:**

*S. armata* Gerlach, 1952

*S. elongata* Jayasree & Warwick, 1977

*S. longispinosa* Lorenzen, 1972

*S. migrans* Jensen & Gerlach, 1977

*S. arcuata* Wieser, 1954

*S. supplicans* Gerlach, 1956

***S. ornata* group:**

*S. abyssalis* (Filipjev, 1918)

*S. longisetosa* (Kreis, 1929)

*S. macramphis* Lorenzen, 1972

*S. ornata* (Ditlevsen, 1918) syn. *S. proabyssalis* Vitiello & Boucher, 1971, syn. *S. similis* (Allgén, 1933)

*S. stenocephalus* Huang & Zhang, 2006

### *Sabatieria dispunctata* n. sp. (Figure 4.6–Figure 4.7)

Type material: Holotype male (NIWA 88373), collected on 20 April 2010, NIWA cruise TAN1004, station 58, Southern Hikurangi, (41.408 N, 175.8977 E), canyon axis. Characteristics of sediment layer (1–5 cm): muddy sediment (92.2%), calcium carbonate content: 2.3%; total organic matter content: 5.2%; chloroplastic pigment concentration: 4 µg/g. Paratype female (NIWA 88374), same data as holotype.

### Description

**Male**: Body cylindrical, tapering towards anterior and posterior extremities. Head small, slightly set off immediately posterior to cephalic setae. Cuticle finely striated, punctation not discernible. Short, sparse somatic setae, irregularly distributed along the body.

Inner labial and outer labial sensillae indistinct. Four cephalic setae, 0.6–0.7 cbd. Buccal cavity cup-shaped, not cuticularized, small, without teeth. Amphid large, spiral, 4.5 turns. Pharynx with posterior pyriform bulb. Cardia small. Nerve ring at middle of pharynx. Secretory-excretory system present; excretory pore not observed, ventral gland situated slightly posterior to pharynx.

Reproductive system diorchic, with two outstretched testes. Anterior testis to the left of intestine, posterior testis to the right of intestine. Sperm cells large, globular, 5–7 µm × 6–7 µm. No ejaculatory gland observed. Spicules strongly arcuate and cuticularized, with weak central lamella extending one quarter of spicule length from proximal end. Gubernaculum with short, straight, thin caudal apophyses, 5 µm long. Cloacal gland cells observed, surrounding almost half of the anterior spicule and gubernaculum. No pre-cloacal supplements. One pre-cloacal seta, 2 µm.

Conico-cylindrical tail with short, sparse setae, 1 µm. Three terminal setae, 3–4 µm. Three small caudal glands.

**Female**: Similar to male, but slightly larger maximum body diameter. Four cephalic setae, 0.4–0.7 cbd. Nerve ring at middle of pharynx. Excretory pore located slightly posterior to nerve ring. Reproductive system didelphic, with two opposed and outstretched ovaries. Anterior ovary to the left of intestine, posterior ovary to the right of intestine. Vulva located slightly pre-median. Vulva directed posteriorly (Figure 4.7D). Spermatheca indistinct. Granular vaginal glands present. One mature egg, 36 ×13 µm.

### Diagnosis

*Sabatieria dispunctata* n. sp. is characterized by the absence of cuticle punctations, cephalic setae 0.4–0.7 cbd long, indistinct inner and outer labial sensillae, large amphideal fovea with 4.5 turns, pharynx with posterior bulb, no ejaculatory glands, pre-cloacal supplements absent, strongly arcuate spicules, and simple gubernaculum with short, straight, thin apophyses directed caudally. Female is characterised by having vulva opening directed posteriorly.

### Differential diagnosis

*Sabatieria dispunctata* n. sp. is similar to several comesomatid genera. It resembles *Laimella* by lacking cuticle punctations, but it does not have a cuticularized pharyngeal lumen or teeth, and does not have outer labial setae close to the cephalic setae. *Sabatieria dispunctata* n. sp. is also similar to *Cervonema* in terms of cuticle without punctations, and small buccal cavity with no teeth, but it does not have setiform outer labial sensillae similar in length to the cephalic setae and possesses a gubernaculum with conspicuous apophyses.

*Sabatieria dispunctata* n. sp. is placed in the genus *Sabatieria* because it also has four cephalic setae, small cup-shaped buccal cavity without teeth, multi-spiral amphid, short spicules and gubernaculum with caudal apophyses, but lacks cuticle punctations. Several *Sabatieria* species, however, also lack cuticle punctations: *S. dodecaspapillata* Kreis, 1929, *S. longisetosa* Kreis, 1929, and *S. mortenseni*

Ditlevsen, 1921. *Sabatieria dispunctata* n. sp. differs from the latter species by not having pre-cloacal supplements, shorter body length (573–661 vs. 1312–2524 µm) and amphids with more turns (4.5 vs. ≤ 2.5). *Sabatieria dispunctata* n. sp. is also similar to *S. pisinna* Vitiello, 1970 and *S. propisinna* Vitiello, 1976, which lack pre-cloacal supplements and have similar body length (657–777; 670–780 µm). The presence of a bulb in *S. dispunctata* n. sp. is also similar to *S. bubulba* Leduc, 2013 and *S. foetida* Gagarin & Thanh, 2008, but the shape of the bulb is different; *S. dispunctata* n. sp. is characterized by having a pyriform bulb, while *S. bubulba* and *S. foetida* are characterized by elongated bulbs. The vulva opening in the female of *S. dispunctata* n. sp. is directed posteriorly, unlike all other *Sabatieria* species.

This new species cannot be satisfactorily classified with any of the *Sabatieria* groups (Platt, 1985). Most species in the *Praedatrix* group have cuticle punctations with lateral differentiation consisting of larger and widely spaced dots, spicules without a central list separating from the proximal projection and simple tubular or pore-like supplements. Species of the *Armata* group usually have elongate cephalic (>1.7 cbd) and cervical setae, and usually have slender bodies (a= >65), with simple tubular supplements, while *S. dispunctata* n. sp. has relatively short cephalic setae (0.6–0.7 cbd), a wider body (a= 25–35), and no pre-cloacal supplements. Again, *S. dispunctata* n. sp. does not fit under the *Pulchra* group because of the absence of paired cervical setae, pre-cloacal supplements, and median pieces of gubernaculum. *Sabatieria dispunctata* n. sp. cannot be placed in the *Celtica* group because it does not possesses curved apophyses on the gubernaculum, and lacks pre-cloacal supplements. Similarly to the *Ornata* group, *S. dispunctata* n. sp. does not have a posterior group of closely situated pre-cloacal supplements.

## Etymology

The species epithet, derived from the Latin *dis* (without, not) and *punctum* (small hole, dot, spot), refers to the absence of punctations on the cuticle.

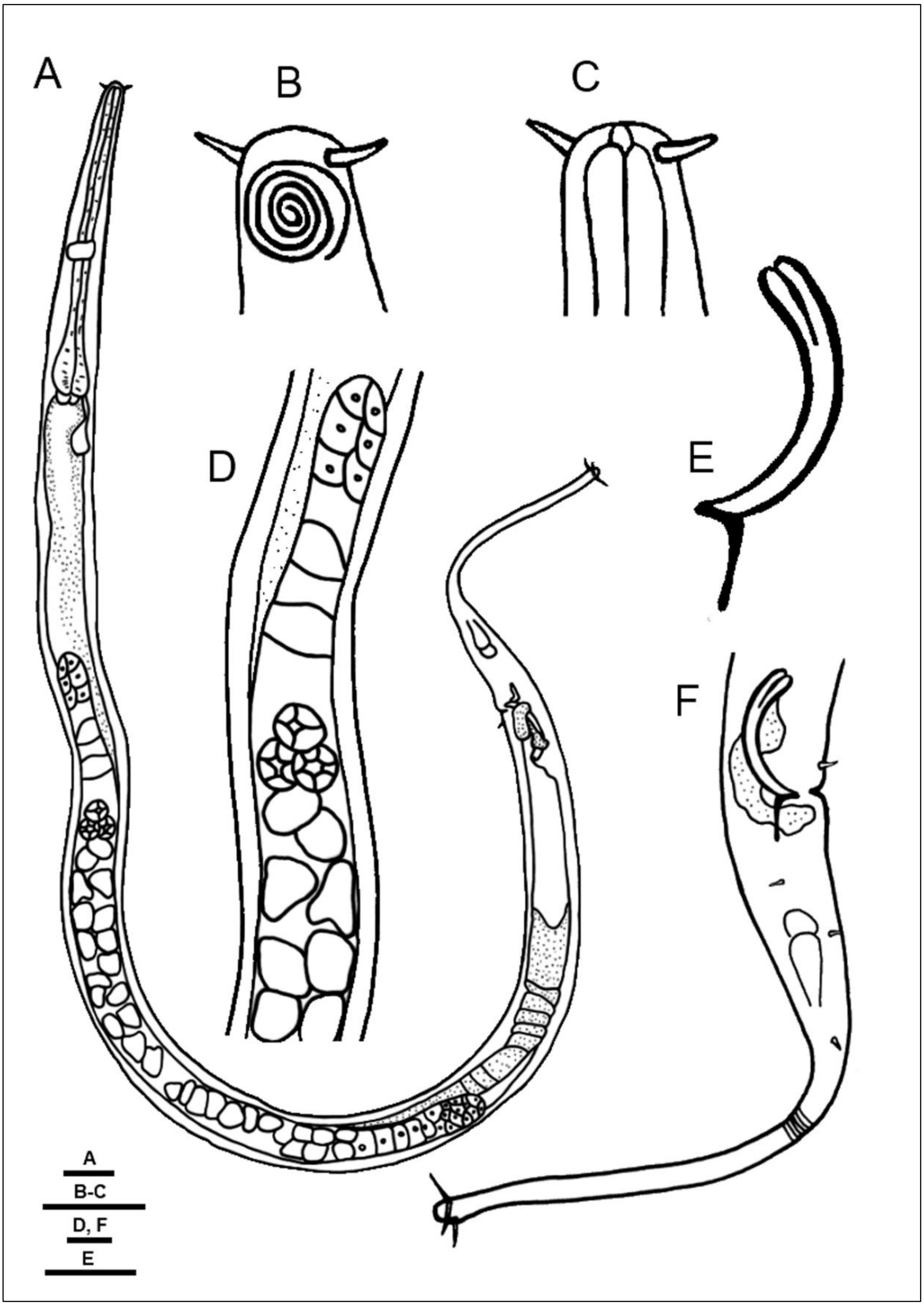

Figure 4.6. *Sabatieria dispunctata* n. sp. Male. A. Entire body; B. Lateral surface view of anterior end showing amphid and setae; C. Anterior head showing buccal cavity; D. Anterior testis with sperm cells; E. Spicule with gubernaculum; F. Tail region. Scale bars: A–C, E: 5 µm; D, F: 100 µm.

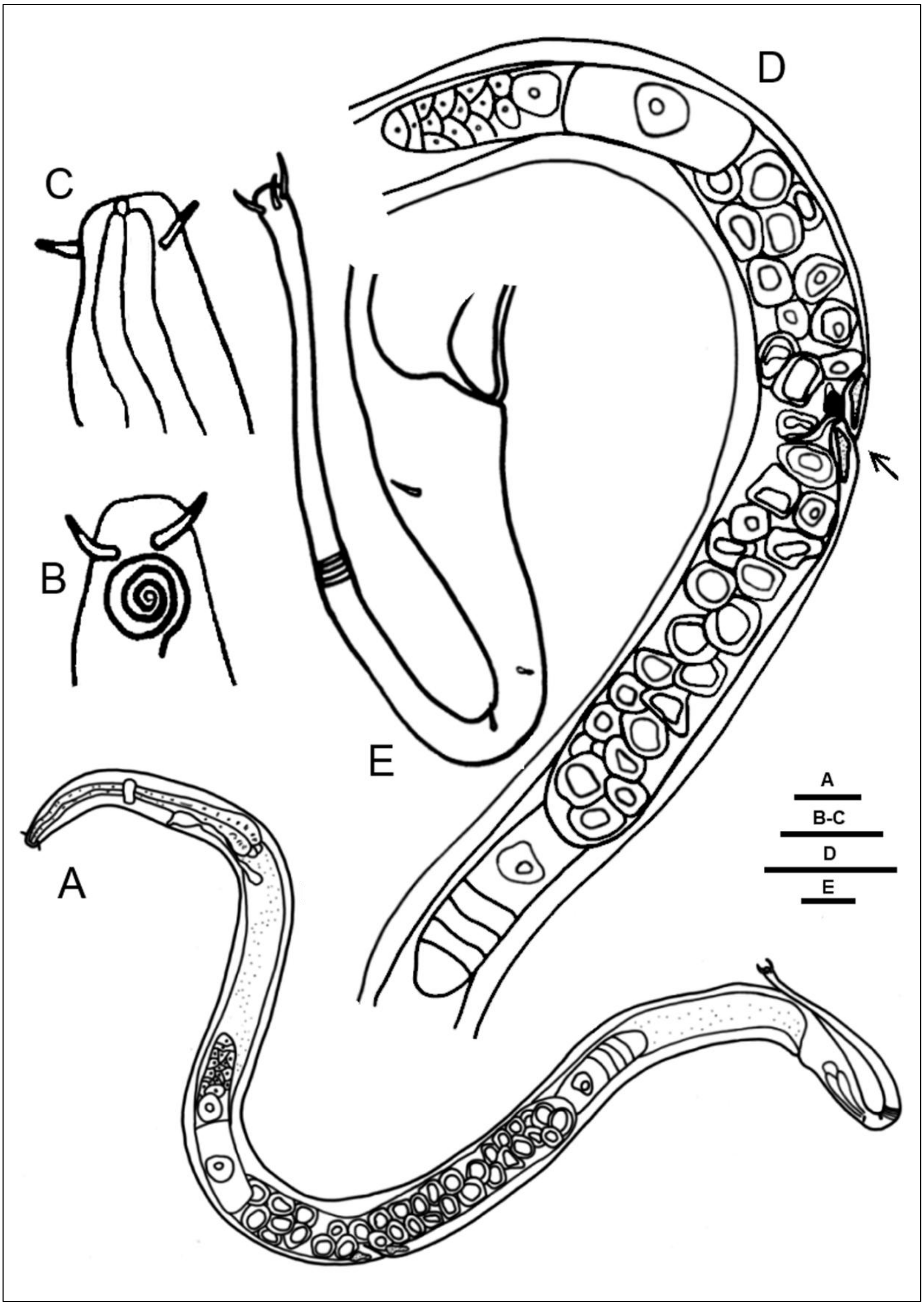

Figure 4.7. *Sabatieria dispunctata* n. sp. Female. A. Entire body; B. Lateral surface view of anterior end showing amphid and setae; C. Anterior head showing buccal cavity; D. Vulva region showing ovaries and egg; E. Tail region. Scale bars: A, D: 22 µm; B–C, E: 5 µm.

### Genus Laimella Cobb, 1920

**Diagnosis (modified from Hopper (1967), Jensen (1979)).**

Cuticle with striations or very fine dots. Anterior and posterior cephalic setae located close together. Buccal cavity small, with three small teeth. Spicules short, arcuate. Gubernaculum with caudally directed apophyses. Pre-cloacal supplements minute or absent. Tail with conical anterior portion and filiform posterior.

**Type species:** *Laimella longicauda* Cobb, 1920.

**List of valid *Laimella* species (**modified from Barnes et al. (2012)).
(Note: **new record for New Zealand).
*L. annae* Chen & Vincx, 2000
*L. ferreroi* Barnes et al., 2012
*L. filicaudata* Ward, 1974
*L. filipjevi* Jensen, 1979
*L. longicauda* Cobb, 1920
*L. minuta* Vitiello, 1970
*L. sandrae* Chen & Vincx, 2000
*L. socotris* Barnes et al., 2012
*L. subterminata* Chen & Vincx, 2000**
*L. tongyeongensis* Barnes et al., 2012
*L. vera* Vitiello, 1971

### *Laimella subterminata* Chen & Vincx, 2000 (Figure 4.8–Figure 4.10)

Specimens: Male (NIWA 88375), collected on 16 April 2010, NIWA cruise TAN1004, station 12, 1350 m depth, Southern Hikurangi, (41.5508 N, 175.725 E), canyon axis. Characteristics of sediment layer (1–5 cm): muddy sediment (99.8%), calcium carbonate content: 2.2%; total organic matter content: 5.6%; chloroplastic pigment concentration: 6 µg/g. Female (NIWA 88376), collected on 20 April 2010, station 58, 670 m depth, Southern Hikurangi (41.408 N, 175.8976 E), canyon axis. Characteristics of sediment layer (1–5 cm): muddy sediment (92.2%), calcium carbonate content: 2.3%; total organic matter content: 5.2%; chloroplastic pigment concentration: 4 µg/g.

### Re-Description

**Male**: Body cylindrical, tapering towards posterior extremity. Head slightly set off immediately posterior to cephalic setae. Cuticle with fine striations, punctation not discernible. Short somatic setae, 3–4 µm, irregularly distributed along body.

Inner labial papillae minute, six short outer labial setae close to four cephalic setae, 0.4–0.5 cbd. Subventral cephalic setae shorter than subdorsal cephalic setae. Buccal cavity narrow, and weakly developed, located subterminally and ventrally, with three small teeth. Amphid spiral, 3.5 turns. Pharynx with pyriform posterior bulb. Cardia small. Nerve ring at middle of pharynx length. Secretory-excretory system present; excretory pore located posterior to the nerve ring, ventral gland situated posterior to pharynx.

Reproductive system diorchic, with two outstretched testes. Anterior and posterior testes situated to the right of intestine. Sperm cells small, elongate, 6–13 µm in length. Three large, round ejaculatory glands, in pairs, situated dorsally anterior of the spicules. Spicules short, thick, slightly arcuate, pointed at distal end, strongly cuticularized. Gubernaculum with dorso-caudal apophyses, slightly bent at distal end. Cloacal gland cells present, surrounding almost half of spicules and gubernaculum. Ten minute pre-cloacal supplements. Pre-cloacal seta present.

Tail with conical anterior portion and filiform, gradually tapering posterior portion. Three caudal glands. Short, sparse caudal setae 1–3 µm. No terminal setae.

**Female**: Similar to male, but with slightly smaller maximum body diameter. Four cephalic setae, 0.6–0.8 cbd. Nerve ring at almost half of pharynx length from anterior. Reproductive system didelphic, with two opposed and outstretched ovaries. Anterior ovary to the left of intestine, posterior ovary to the right of intestine. Vulva position slightly pre-median. Granular vaginal glands and spermatheca present. Short, sparse caudal setae, 3–4 µm.

### Remarks

*Laimella subterminata* was first described by Chen and Vincx (2000) from the Beagle Channel and Magellan Strait, Chile, based on specimens collected from muddy sediment at 255–555 m water depth. The Hikurangi margin specimens were collected from muddy sediment but at greater depths (670–1350 m). This species is distinctive due to the presence of a subterminal mouth opening, a trait not found in any other *Laimella* species. The present specimens agree well with the description by Chen & Vincx (2000), but there are slight differences in body length (1162–1305 µm in the Chilean specimens *vs* 1423–1439 µm in present specimens), maximum body diameter (25–32 *vs* 35–42 µm), amphids (4.0 turns; 60–64.7% cbd *vs* 3.5 turns; 56–61% cbd), spicule length (1.7 *vs* 1.2 abd), gubernaculum apophyses length (14 *vs*10 µm), and number of pre-cloacal supplements (6 *vs* 10). The location of the testes is also different; in our specimen, the anterior and posterior testes are located to the right of the intestine, but in the Chilean specimens, the anterior testis is located to the left of intestine and the posterior testis to the right of the intestine.

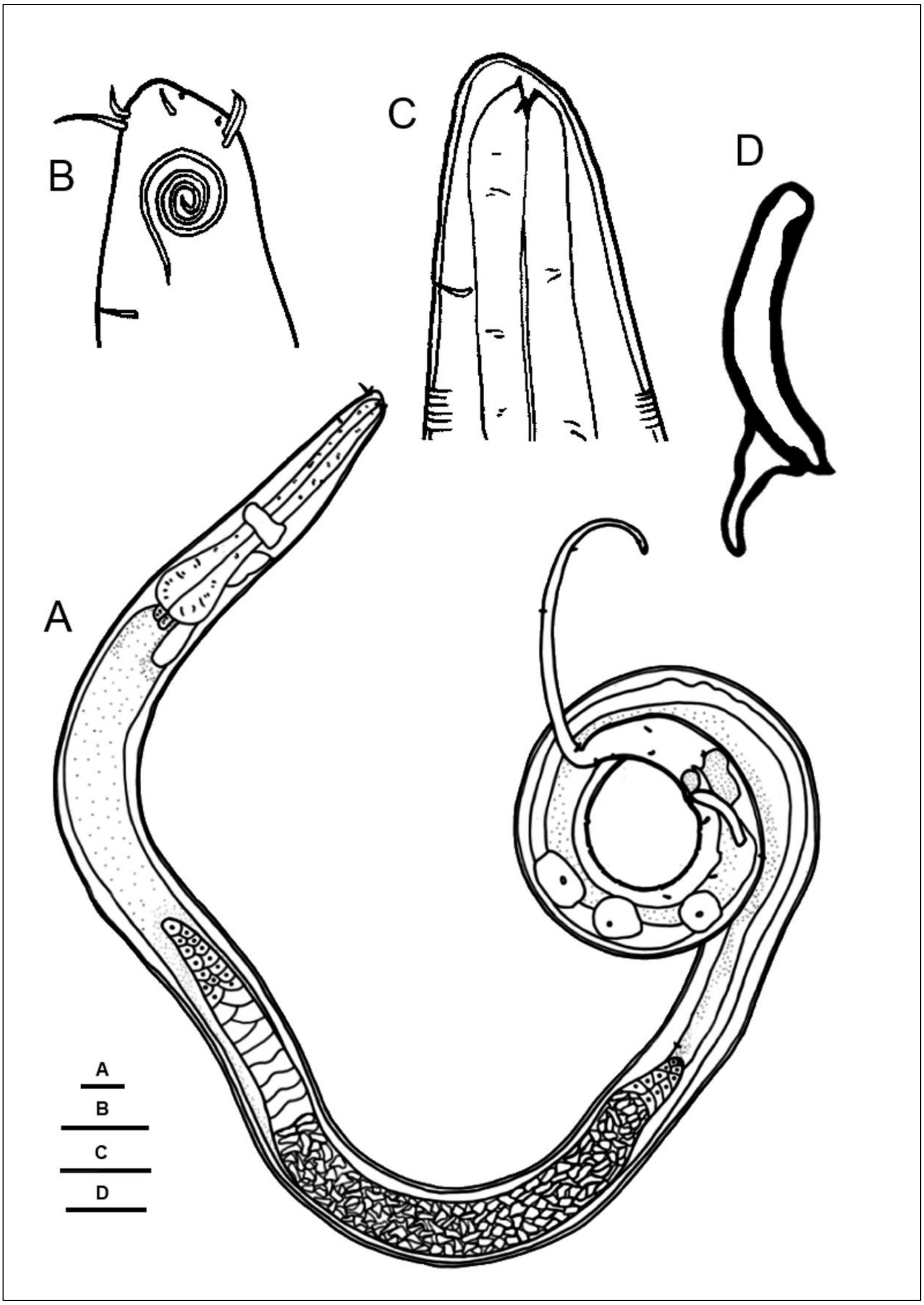

Figure 4.8. *Laimella subterminata* Chen & Vincx, 2000. Male. A. Entire body; B. Lateral surface view of anterior end showing amphid and setae; C. Anterior head showing buccal cavity and teeth; D. Spicule with gubernaculum. Scale bars: A: 20 µm; B–D: 10 µm.

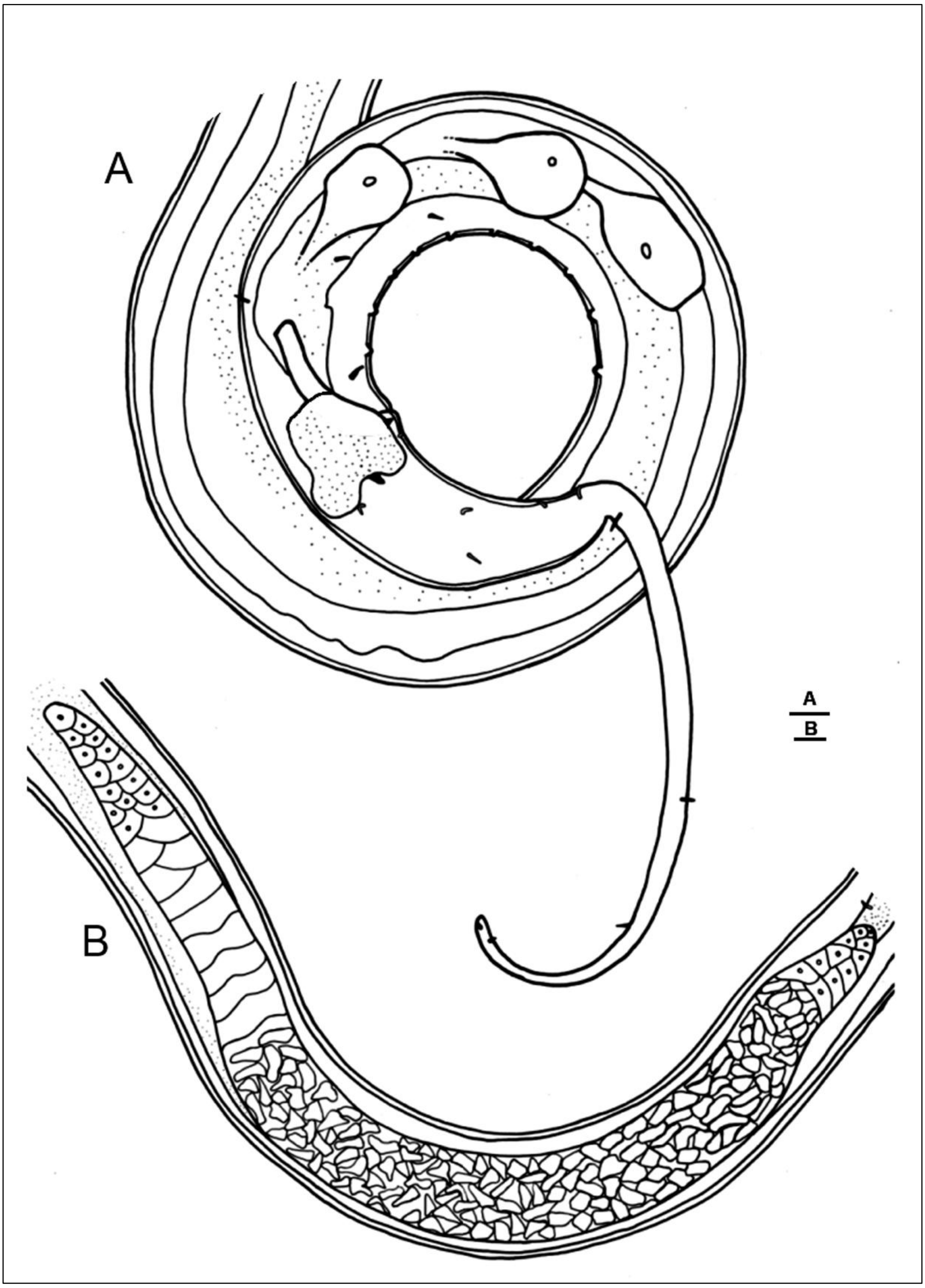

Figure 4.9. *Laimella subterminata* Chen & Vincx, 2000. Male. A. Cloacal region showing cloacal supplements, ejaculatory glands, and cloacal gland cells; B. Testes with sperm cells. Scale bars: A–B: 10 µm.

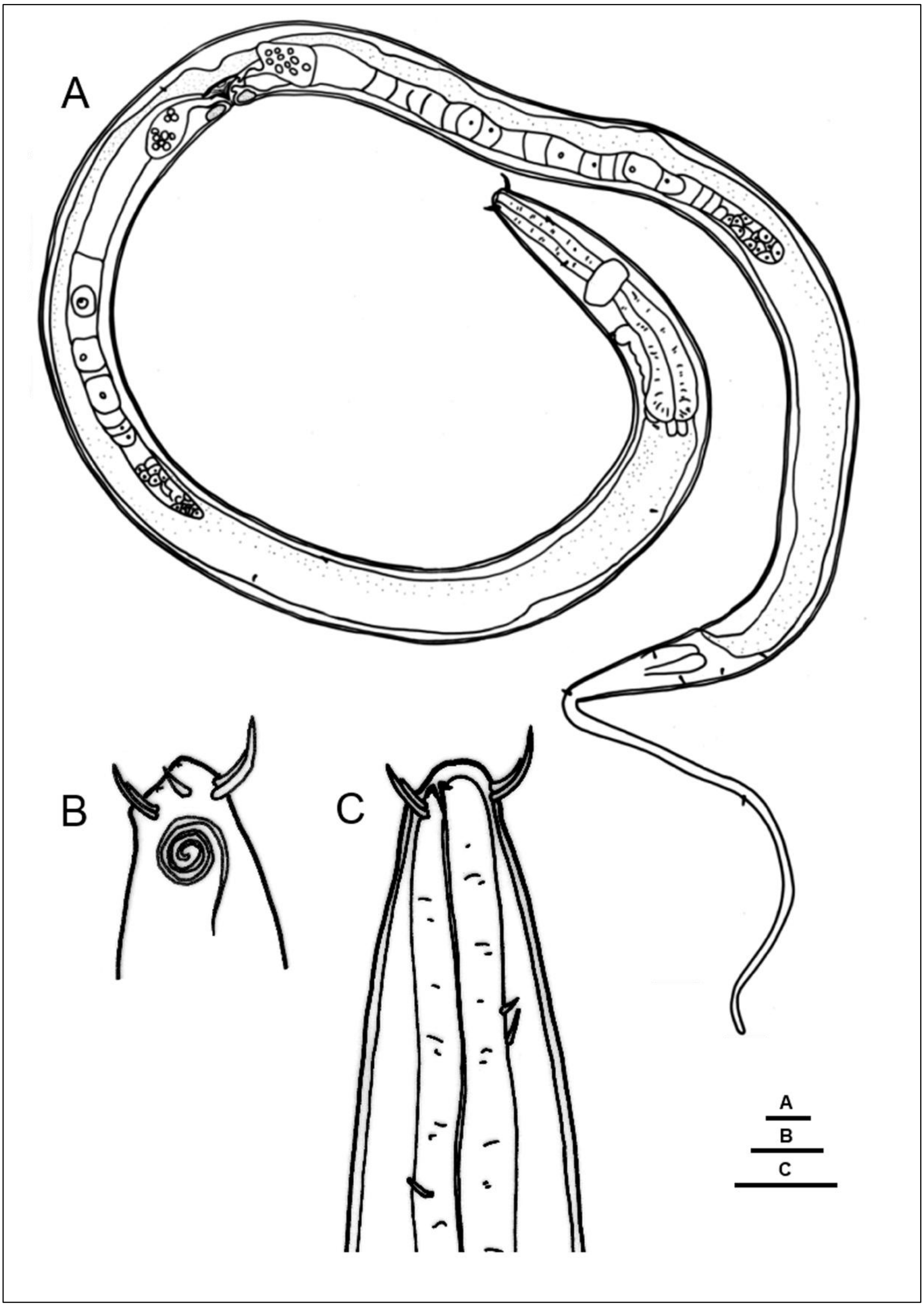

Figure 4.10. *Laimella subterminata* Chen & Vincx, 2000. Female. A. Entire body; B. Lateral surface view of anterior end showing amphid and setae; C. Anterior head showing buccal cavity and teeth. Scale bars: A: 20 µm; B: 8 µm; C: 12 µm.

### 4.3.2 Checklist of free-living marine nematodes of New Zealand

Since the checklist of marine nematode species was compiled by Leduc and Gwyther (2008), a total of sixty-six species have been described/recorded and were included in the updated checklist, together with seven species that had been omitted from the previous checklist. Four species of Rhabditidae have been assigned to a new genus according to the latest systematic review by Sudhaus (2011), and one species of *Sabatieria*, *Sabatieria annulata*, has been synonymised to *S. mortenseni* (Leduc 2013d). The updated checklist for marine nematodes in the New Zealand region and Southern Hemisphere now includes a total of 168 species belonging to 102 genera and thirty families that have been recorded from intertidal to hadal trench habitats (0–9000 m) (Table 4.2). Of the 168 species listed, 159 are considered valid, two are *incertae sedis* (i.e. of uncertain affinities) and seven are considered species *inquirendae* (i.e. doubtful due to inadequate descriptions). Of these 159 valid species, 47% are exclusively found in the New Zealand region, 34% are cosmopolitan (i.e. recorded in both Northern and Southern Hemispheres), 18% are found only in the Southern Hemisphere, and 1% are found only in the New Zealand and Australian regions.

A total of twenty-five comesomatid species belonging to nine genera have been described/recorded from New Zealand waters, making this the most diverse family recorded from New Zealand waters to date. Of these, 17 species (68%) have not been recorded elsewhere (Leduc and Gwyther 2008, Leduc 2012, Leduc et al. 2012a, Leduc 2013d, Leduc et al. 2014). Prior to this study, eight *Sabatieria*, three *Cervonema*, two *Setosabatieria*, and one *Dorylaimopsis*, *Hopperia* and *Vasostoma* species had been described from the region.

Table 4.2. List of New Zealand and Southern Hemisphere localities with their abbreviations used in the checklist.

| **Localities** | **Abbreviation** |
|---|---|
| **New Zealand** | |
| North Island | **NI** |
| South Island | **SI** |
| Stewart Island | **StI** |
| Auckland Island | **AI** |
| Campbell Island | **CI** |
| Three Kings Island | **TKI** |
| Kermadec Arc/Trench | **KA** |
| Unspecific locality under New Zealand | **NZ** |
| **Southern Hemisphere** | |
| Antarctica | Ant |
| Argentina | Arg |
| Australia | Aus |
| Brazil | Bra |
| Chile | Chi |
| Falkland Islands (United Kingdom) | FaI |
| Heard Island (Australia) | HeI |
| Kenya | Ken |
| Kerguelen Archipelago (France) | KeA |
| Macquarie Island (Australia) | MaI |
| New Caledonia (France) | NeC |
| Peru | Per |
| South Georgia (United Kingdom) | SoG |
| South Africa | SoA |
| Tonga Trench (Tonga) | Ton |
| Uruguay | Uru |
| **Northern Hemisphere** | *NH* |

### 4.3.3 Checklist of valid species

## Order ENOPLIDA

### Family Enoplidae Dujardin, 1985

Genus *Enoplus* Dujardin, 1985

*Enoplus benhami* Ditlevsen, 1930
Distribution: **NI**, Chi
Depth: Shallow

### Family Thoracostomopsidae Filipjev, 1927

Genus *Mesacanthion* Filipjev, 1927

*Mesacanthion infantile* (Ditlevsen, 1930) De Conink & Stekhoven, 1933
Distribution: **StI**, Aus, Ant, Chi
Depth: Shallow

*Mesacanthion virile* (Ditlevsen, 1930) De Conink & Stekhoven, 1933
Distribution: **StI**, Ant, FaI, SoG
Depth: Shallow

Genus *Oxyonchus* Filipjev, 1927

*Oxyonchus australis* (de Man, 1940) Filipjev, 1927
Distribution: **CI**, Ant, Chi, FaI, KeA
Depth: Shallow

*Oxyonchus dentatus* (Ditlevsen, 1918) Filipjev, 1927
Distribution: **StI**, Ant, Bra, Chi, FaI, SoG, *NH*
Depth: Shallow

Genus *Paramesacanthion* Wieser, 1953

*Paramesacanthion microsetosum* (Allgén, 1932) Wieser, 1953
Distribution: **CI**, Ant, SoG
Depth: Shallow

### Family Anoplostomatidae Gerlach & Riemann, 1974

Genus *Anoplostoma* Bütschli, 1874

*Anoplostoma campbelli* Allgén, 1932
Distribution: **CI**, KeA, MaI, *NH*
Depth: Shallow

### Family Phanodermatidae Filipjev, 1927

Genus *Phanoderma* Bastian, 1865

*Phanoderma campbelli* Allgén, 1927
Distribution: **CI**, Ant, Aus, FaI, Kea, MaI, SoG, *NH*
Depth: Shallow

*Phanoderma cocksi* Bastian, 1865
Distribution: **CI**, FaI, KeA, MaI, SoG, *NH*
Depth: Shallow

*Phanoderma serratum* Ditlevsen, 1930
Distribution: **NI**
Depth: Shallow

Genus *Crenopharynx* Filipjev, 1934

*Crenopharynx crassa* (Ditlevsen, 1934) Filipjev, 1934
Distribution: **StI**
Depth: Shallow

### Family Anticomidae Filipjev, 1918

Genus *Anticoma* Bastian, 1865

*Anticoma acuminata* (Eberth, 1863) Bastian, 1865
Distribution: **CI**, Ant, Aus, Chi, FaI, SoG, *NH*
Depth: Shallow

*Anticoma campbelli* Allgén, 1932
Distribution: **CI**, Ch, KI, MI, *NH*
Depth: Shallow

*Anticoma pellucida* Bastian, 1865
Distribution: **CI**, *NH*
Depth: Shallow

**Family Ironidae De Man, 1876**

Genus *Dolicholaimus marioni* de Man, 1888

*Dolicholaimus marioni* de Man, 1888
Distribution: **CI**, Chi, FaI, SoG, *NH*
Depth: Shallow

Genus *Syringolaimus* de Man, 1888

*Syringolaimus striatocaudatus* de Man, 1888
Distribution: **CI**, Bra, Chi, *NH*
Depth: Shallow

**Family Leptosomatidae Filipjev, 1916**

Genus *Deontostoma* Filipjev, 1916

*Deontostoma aucklandiae* (Ditlevsen, 1921) Platonova, 1962
Distribution: **AI**, Aus, Chi, FaI, SoG
Depth: Shallow

*Deontostoma tridentum* Leduc, 2013 Leduc (2013c)
Distribution: **SI**
Depth: Deep

Genus *Thoracostoma* Marion, 1870

*Thoracostoma bruuni* Wieser, 1956
Distribution: **SI**
Depth: Deep

*Thoracostoma campbelli* Ditlevsen, 1921

Distribution: **CI**, Chi, HeI, KeA, MaI

Depth: Shallow

*Thoracostoma papillosum* Ditlevsen 1921

Distribution: **CI**

Depth: Shallow

*Thoracostoma vallini* Allgén, 1927

Distribution: **AI**, Ant Chi, FaI, SoG

Depth: Shallow

Genus *Synonchoides* Wieser, 1956

*Synonchoides galatheae* (Wieser, 1956) Platonova, 1970

Distribution: **SI, KA**

Depth: Deep

**Family Oxystominidae Chitwood, 1935**

Genus *Halalaimus* de Man, 1888

*Halalaimus ciliocaudatus* Allgén, 1932

Distribution: **CI**, Bra

Depth: Shallow

Genus *Nemanema* Cobb, 1920

*Nemanema campbelli* (Allgén, 1932) Wieser, 1953

Distribution: **CI**, KeA

Depth: Shallow

Genus *Thalassoalaimus* de Man, 1893

*Thalassoalaimus septentrionalis* Filipjev, 1927

Distribution: **CI**, *NH*

Depth: Shallow

## Family Oncholaimidae Filipjev, 1916

Genus *Viscosia* de Man, 1890

*Viscosia carnleyensis* (Ditlevsen, 1921) Kreis, 1932
Distribution: **AI, CI**, Chi, *NH*
Depth: Shallow

Genus *Oncholaimus* Dujardin, 1845

*Oncholaimus aegypticus* Steiner, 1921
Distribution: **CI**, *NH*
Depth: Shallow

*Oncholaimus brachycercus* de Man, 1889
Distribution: **StI**, **CI**, *NH*
Depth: Shallow

*Oncholaimus chiltoni* Ditlevsen, 1930
Distribution: **NI**
Depth: Shallow

*Oncholaimus dujardini* de Man, 1876
Distribution: **NI, CI**, Aus, Chi, FaI, KeA, *NH*
Depth: Shallow

*Oncholaimus moanae* Leduc, 2009
Distribution: **SI**
Depth: Shallow

*Oncholaimus viridis* Bastian, 1865
Distribution: **AI, CI,** Aus, Cih, FaI, SoG, *NH*
Depth: Shallow

Genus *Pelagonema* Cobb, 1894

*Pelagonema obtusicauda* Filipjev, 1894
Distribution: **CI**, Ant, Aus, Chi, FaI, SoG, *NH*
Depth: Shallow

Genus *Phaenoncholaimus* Kreis, 1934

*Phaenoncholaimus monodon* (Ditlevsen, 1930) Kreis, 1934
Distribution: **NI**
Depth: Shallow

**Family Enchelidiidae Filipjev, 1918**

Genus *Eurystomina* Filipjev, 1921

*Eurystomina eurylaima* (Ditlevsen, 1930)
Distribution: **NI**, Aus
Depth: Shallow

*Eurystomina stenolaima* (Ditlevsen, 1930)
Distribution: **NI**, Chi, FaI
Depth: Shallow

*Eurystomina tenuicaudata* Allgén, 1932
Distribution: **CI**, Ant, Chi, FaI, SoG, Uru
Depth: Shallow

Genus *Polygastrophora* de Man, 1922

*Polygastrophora hexabulba* (Filipjev, 1918) Kreis 1926
Distribution: **TKI**, Aus, Chi, FaI, *NH*
Depth: Shallow

**Family Tripyloididae Filipjev, 1918**

Genus *Bathylaimus* Cobb, 1894

*Bathylaimus australis* Cobb, 1894
Distribution: **SI**, Aus, Bra, Chi, *NH*
Depth: Shallow

**Family Trefusiidae Lorenzen, 1981**

Genus *Trefusia* de Man, 1893

*Trefusia piperata* Leduc 2013
Distribution: **SI**
Depth: Deep

Genus *Trefusialaimus* Riemann, 1974

*Trefusialaimus idrisi* Leduc 2013
Distribution: **SI**
Depth: Deep

**Order CHROMADORIDA**

**Family Chromadoridae Filipjev, 1917**

Genus *Atrochromadora* Wieser, 1959

*Atrochromadora parva* (de Man, 1893) Wieser, 1954
Distribution: **CI**, Ant, Chi, *NH*
Depth: Shallow

Genus *Chromadora* Wieser, 1959

*Chromadora nudicapitata* Bastian, 1865
Distribution: **SI**, **CI**, Aus, Chi, FaI, SoG, *NH*
Depth: Shallow

Genus *Prochromadorella* Micoletzky, 1924

*Prochromadorella paramuchrodonta* (Allgén, 1929) Wieser, 1951
Distribution: **CI**, Aus, Chi, FaI, *NH*
Depth: Shallow

Genus *Graphonema* Kreis, 1929

*Graphonema amokurae* (Ditlevsen, 1921) Inglis, 1969
Distribution: **NI**, **CI**, **AI**, Ant, Aud, Chi, FaI, SoG
Depth: Shallow

Genus *Rhips* Cobb, 1920

*Rhips ornata* Cobb, 1920
Distribution: **CI**, Bra, *NH*
Depth: Shallow

Genus *Chromadorita* Filipjev, 1922

*Chromadorita brachypharynx* (Allgén, 1932) Wieser, 1954
Distribution: **CI**, *NH*
Depth: Shallow

*Chromadorita heterophya* (Steiner, 1916) Filipjev, 1922
Distribution: **CI**, *NH*
Depth: Shallow

*Chromadorita minor* (Allgén, 1927) Wieser, 1954
Distribution: **CI**, Aus, Chi
Depth: Shallow

Genus *Dichromadora* Kreis, 1929

*Dichromadora cephalata* (Steiner, 1916) Kreis, 1929
Distribution: **CI**, *NH*
Depth: Shallow

Genus *Neochromadora* Micoletzky, 1924

*Neochromadora craspedota* (Steiner, 1916) Micoletzky, 1924
Distribution: **CI**, Ant, FaI, SoG, Uru, *NH*
Depth: Shallow

Genus *Spilophorella* Filipjev, 1917

*Spilophorella campbelli* Allgén, 1927
Distribution: **StI**, **CI**, Aus, FaI, *NH*
Depth: Shallow

*Spilophorella paradoxa* (de Man, 1888) Filipjev, 1917
Distribution: **CI**, Aus, Chi, FaI, SoA, *NH*
Depth: Shallow

Genus *Spiliphera* Bastian, 1865

*Spiliphera dolichura* de Man, 1893
Distribution: **CI**, Aus, Chi, *NH*
Depth: Shallow

**Family Selachinematidae Cobb, 1915**

Genus *Halichoanolaimus* de Man, 1886

*Halichoanolaimus ovalis* Ditlevsen, 1921
Distribution: **AI**, **CI**, Aus, FaI, SoG
Depth: Shallow

*Halichoanolaimus robustus* (Bastian, 1865) de Man, 1886
Distribution: **NI**, Aus, *NH*
Depth: Shallow

*Halichoanolaimus anisospermus* Leduc & Zhao, 2016
Distribution: **NI**
Depth: Deep

Genus *Cobbionema* Filipjev, 1922

*Cobbionema trigamma* Leduc, 2013
Distribution: **SI**
Depth: Deep

Genus *Gammanema* Cobb, 1920

*Gammanema agglutinans* Leduc, 2013
Distribution: **SI**
Depth: Deep

Genus *Bendiella* Leduc, 2013

*Bendiella thalassa* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Bendiella longicauda* Leduc & Zhao, 2016
Distribution: **NI**
Depth: Shallow

Genus *Synonchiella* Cobb, 1933

*Synonchiella rotundicauda* Leduc, 2013
Distribution: **NI**, **SI**
Depth: Shallow & deep

Genus *Pseudocheironchus* Leduc, 2013

*Pseudocheironchus ingluviosus* Leduc, 2013
Distribution: **NI**, **SI**
Depth: Shallow & deep

Genus *Cheironchus* Leduc, in press

*Cheironchus haurakiensis* Leduc & Zhao, 2016
Distribution: **NI**
Depth: Shallow & deep

Genus *Latronema* Wieser, 1954

*Latronema whataitai* Leduc & Zhao, 2015
Distribution: **NI**
Depth: Shallow

**Order MONHYSTERIDA**

**Family Linhomoeidae Filipjev, 1922**

Genus *Desmolaimus* de Man, 1880

*Desmolaimus courti* Leduc & Gwyther, 2008
Distribution: **SI**
Depth: Shallow

Genus *Terschellingia* de Man, 1888

*Terschellingia longicaudata* de Man, 1907
Distribution: **NI**, Aus, Chi, Bra, *NH*
Depth: Shallow

Genus *Linhomoeus* Bastian, 1865

*Linhomoeus elongatus* Bastian, 1865
Distribution: **CI**, FaI, *NH*
Depth: Shallow

Genus *Thelonema* Bussau, 1993

*Thelonema clarki* Leduc, 2015
Distribution: **KA**
Depth: Deep

**Family Sphaerolaimidae Filipjev, 1918**

Genus *Sphaerolaimus* Bastian, 1865

*Sphaerolaimus campbelli* Allgén, 1927

Distribution: **CI**, Chi

Depth: Shallow

Genus *Metasphaerolaimus* Gourbault & Boucher, 1981

*Metasphaerolaimus constrictus* Leduc, 2015

Distribution: **KA**

Depth: Deep

**Family Xyalidae Chitwood, 1951**

Genus *Theristus* Bastian, 1865

*Theristus acer* Bastian, 1865

Distribution: **CI**, FaI, *NH*

Depth: Shallow

*Theristus velox* Bastian, 1865

Distribution: **CI**, *NH*

Depth: Shallow

*Theristus problematica* (Allgén, 1927) Wieser, 1956

Distribution: **CI**, *NH*

Depth: Shallow

*Theristus heterospiculum* (Allgén, 1932) Gerlach, 1953

Distribution: **CI**, *NH*

Depth: Shallow

*Theristus oistospiculum* (Allgén, 1932)

Distribution: **CI**, *NH*

Depth: Shallow

Genus *Paramphimonhystrella* Huang & Zhang, 2006

*Paramphimonhystrella glossalga* Leduc, 2014

Distribution: **NI**, **SI**

Depth: Deep

*Paramphimonhystrella barbula* Leduc, 2014

Distribution: **NI**, **SI**

Depth: Deep

*Paramphimonhystrella scutula* Leduc, 2014

Distribution: **NI**

Depth: Deep

*Paramphimonhystrella echinocauda* Leduc, 2014

Distribution: **NI**

Depth: Deep

Genus *Manganonema* Bussau, 1993

*Manganonema rowdeni* Leduc, 2015

Distribution: **KA**

Depth: Deep

*Manganonema majusculum* Leduc, 2015

Distribution: **KA,** Ton

Depth: Deep

### Family Monhysteridae de Man, 1876

Genus *Halomonhystera* Andrássy, 2006

*Halomonhystera disjuncta* (Bastian, 1865)

Distribution: **SI**, **CI**, Chi, FsI, SoG, *NH*

Depth: Shallow & deep

*Halomonhystera tangaroa* Leduc, 2014

Distribution: **KA**

Depth: Deep

Genus *Monhystrella* Cobb, 1918

*Monhystrella kermadecensis* Leduc, 2015
Distribution: **KA**
Depth: Deep

**Order ARAEOLAIMIDA**

**Family Comesomatidae Filipjev, 1918**

Genus *Comesoma* Bastian, 1865

*Comesoma tenuispiculum* (Ditlevsen, 1921) Wieser, 1954
Distribution: **AI**, Chi, FaI
Depth: Shallow

Genus *Cervonema* Wieser, 1954

*Cervonema shiae* Chen & Vincx, 2000
Distribution: **SI**, Chi
Depth: Deep

*Cervonema kaikouraensis* Leduc, 2012
Distribution: **SI**
Depth: Deep

*Cervonema multispira* Leduc, 2012
Distribution: **SI**
Depth: Deep

*Cervonema proberti* Leduc, 2012
Distribution: **SI**
Depth: Deep

Genus *Laimella* Cobb, 1920

*Laimella subterminata* Chen & Vincx, 2000
Distribution: **NI**, Chi
Depth: Deep

Genus *Sabatieria* Rouville, 1903

*Sabatieria mortenseni* (Ditlevsen, 1921)
Distribution: **AI, SI,** Arg, Chi, Bra
Depth: Shallow

*Sabatieria punctata* (Kreis, 1924)
Distribution: **AI**, Ant, Arg, Bra, Chi, FaI, SoG, *NH*
Depth: Shallow

*Sabatieria bitumen* Botelho et al., 2007
Distribution: **SI,** Bra, *NH*
Depth: Deep

*Sabatieria challengerensis* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Sabatieria parapraedatrix* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Sabatieria bubulba* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Sabatieria exculta* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Sabatieria balbutiens* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Sabatieria pumila* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Sabatieria bathycopia* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Sabatieria dispunctata* Rosli et al., 2014
Distribution: **NI**
Depth: Deep

Genus *Setosabatieria* Platt, 1985

*Setosabatieria australis* Leduc & Gwyther, 2008
Distribution: **SI**
Depth: Shallow

*Setosabatieria conicauda* Leduc et al. 2012
Distribution: **SI**
Depth: Deep

Genus *Dorylaimopsis* Ditlevsen, 1918

*Dorylaimopsis nodderi* Leduc, 2012
Distribution: **SI**
Depth: Deep

Genus *Hopperia* Vitiello, 1969

*Hopperia ancora* Leduc, 2012
Distribution: **SI**
Depth: Deep

*Hopperia beaglense* Chen & Vincx, 1998

Distribution: **SI**, Chi

Depth: Deep

Genus *Kenyanema* Muthumbi et al., 1997

*Kenyanema monorchis* Muthumbi et al., 1997

Distribution: **SI,** Ken

Depth: Deep

Genus *Vasostoma* Wieser, 1954

*Vasostoma auratum* Leduc et al., 2012

Distribution: **SI**

Depth: Deep

*Vasostoma hexodontium* Rosli et al., 2014

Distribution: **NI**

Depth: Deep

**Family Diplopeltidae Filipjev, 1918**

Genus *Araeolaimus* de Man, 1888

*Araeolaimus elegans* de Man, 1888

Distribution: **AI, CI**, Ant, Cht, SoG, FaI, *NH*

Depth: Shallow

Genus *Diplopeltis* Cobb in Stiles & Hassal, 1903

*Diplopeltis cirrhatus* (Eberth, 1863) Cobb, 1891

Distribution: **CI**, Bra, Chi, FaI, *NH*

Depth: Shallow

Genus *Diplopeltula* Gerlach, 1950

*Diplopeltula cylindricauda* (Allgén, 1932) Gerlach, 1950

Distribution: **CI**

Depth: Shallow

Genus *Mudwigglus* Leduc, 2013

*Mudwigglus patumuka* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Mudwigglus macramphidum* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Mudwigglus plebeius* Leduc, 2013
Distribution: **SI**
Depth: Deep

*Mudwigglus nellyae* (Vincx & Gourbault, 1992) Leduc 2013
Distribution: **SI,** NeC
Depth: Deep

Genus *Southerniella* Allgén, 1932

*Southerniella simplex* Allgén, 1932
Distribution: **CI**, Chi, *NH*
Depth: Shallow

## Order DESMODORIDA

### Family Desmodoridae Filipjev, 1922

Genus *Croconema* Cobb, 1920

*Croconema stateni* (Allgén, 1927) Wieser, 1954
Distribution: **CI**, **TKI**, Ant, Chi, FaI, SoG
Depth: Shallow

Genus *Desmodora* de Man, 1889

*Desmodora bilacinia* Leduc & Zhao, 2016

Distribution: **NI**

Depth: Shallow

Genus *Pseudochromadora* Daday, 1899

*Pseudochromadora reathae* Leduc & Wharton, 2010

Distribution: **SI**

Depth: Shallow

Genus *Pseudodesmodora* Boucher, 1975

*Pseudodesmodora lacrima* Leduc & Wharton, 2010

Distribution: **NI**

Depth: Shallow

Genus *Desmodorella* Cobb, 1933

*Desmodorella tenuispiculum* (Allgén, 1927) Verschelde et al. 1998

Distribution: **CI**, Ant, FaI, SoG, *NH*

Depth: Shallow

*Desmodorella verscheldei* Leduc & Zhao, 2016

Distribution: **NI**

Depth: Shallow

Genus *Paradesmodora* Shuurmans Stekhoven, 1950

*Paradesmodora campbelli* (Allgén, 1932) Gerlach, 1963

Distribution: **CI**, Bra, *NH*

Depth: Shallow

Genus *Molgolaimus* Ditlevsen, 1921

*Molgolaimus tenuispiculum* Ditlevsen, 1921
Distribution: **AI**, Chi
Depth: Shallow

Genus *Onepunema* Leduc & Verschelde, 2013

*Onepunema enigmaticum* Leduc & Verschelde, 2013
Distribution: **SI**
Depth: Deep

Genus *Pseudonchus* Cobb, 1920

*Pseudonchus virginiae* Leduc & Verschelde, 2013
Distribution: **SI**
Depth: Deep

Genus *Centonema* Leduc, 2013

*Centonema renamphidum* Leduc, 2013
Distribution: **SI**
Depth: Deep

Genus *Eubostrichus* Greef, 1869

*Eubostrichus hortulanus* Leduc, 2013
Distribution: **SI**
Depth: Deep

Genus *Spirinia* Gerlach, 1963

*Spirinia verecunda* Leduc & Verschelde, 2015
Distribution: **SI**
Depth: Deep

Genus *Stygodesmodora* Blome, 1982

*Stygodesmodora confusa* Leduc & Verschelde, 2015
Distribution: **NI, SI**
Depth: Deep

Genus *Acanthopharynx* Marion, 1870

*Acanthopharynx dormitata* Leduc & Zhao, 2016
Distribution: **NI**
Depth: Shallow

**Family Draconematidae Filipjev, 1918**

Genus *Draconema* Cobb, 1913

*Draconema cephalatum* Cobb, 1913
Distribution: **CI**, Ant, Chi, FaI, SoG, KeA, *NH*
Depth: Shallow

Genus *Prochaetosoma* Micoletzky, 1922

*Prochaetosoma campbelli* (Allgén, 1932) Allen & Noffsinger, 1978
Distribution: **CI**, *NH*
Depth: Shallow

*Prochaetosoma longicapitatum* (Allgén, 1932) Allen & Noffsinger, 1978
Distribution: **CI**
Depth: Shallow

Genus *Draconactus* Allen & Noffsinger, 1978

*Draconactus suillus* (Allgén, 1932) Allen & Noffsinger, 1978
Distribution: **CI**
Depth: Shallow

Genus *Dracograllus* Allen & Noffsinger, 1978

*Dracograllus ngakei* Leduc & Zhao, 2016

Distribution: **NI**

Depth: Shallow

**Family Epsilonematidae Steiner, 1927**

Genus *Epsilonema* Steiner, 1927

*Epsilonema rugatum* Lorenzen, 1973

Distribution: **NI**, **SI**, Chi

Depth: Shallow

Genus *Metepsilonema* Steiner, 1927

*Metepsilonema laterale* Lorenzen, 1973

Distribution: **SI**

Depth: Shallow

*Metepsilonema limbatum* Lorenzen, 1973

Distribution: **NI**, **SI**

Depth: Shallow

**Family Microlaimidae Micoletzky, 1922**

Genus *Aponema* Jensen, 1978

*Aponema subtile* Leduc & Wharton, 2008

Distribution: **SI**

Depth: Shallow

Genus *Microlaimus* de Man, 1880

*Microlaimus falciferus* Leduc & Wharton, 2008

Distribution: **SI**

Depth: Shallow

*Microlaimus korari* Leduc, 2016
Distribution: **SI,** Ant
Depth: Deep

Genus *Maragnopsia* Leduc, 2016

*Maragnopsia hadalis* Leduc, 2016
Distribution: **KA**
Depth: Deep

**Family Monoposthiidae Filipjev, 1934**

Genus *Nudora* Cobb, 1920

*Nudora campbelli* (Schulz, 1935) Wieser, 1954
Distribution: **CI**
Depth: Shallow

**Order PLECTIDA**

**Family Leptolaimidae Örley, 1880**

Genus *Camacolaimus* de Man, 1889

*Camacolaimus tardus* de Man, 1889
Distribution: **CI**, Chi, FaI, SoG, *NH*
Depth: Shallow

Genus *Ionema* Southern, 1916

*Ionema cobbi* (Steiner, 1916)
Distribution: **CI**, Bra, FaI, SoG, *NH*
Depth: Shallow

Genus *Cricolaimus* Southern, 1916

*Cricolaimus coronatus* Ditlevsen, 1930
Distribution: **NI**
Depth: Shallow

**Family Ceramonematidae Cobb, 1933**

Genus *Pselionema* Cobb, 1933

*Pselionema annulatum* (Filipjev, 1922)
Distribution: **CI**, *NH*
Depth: Shallow

**Order RHABDITIDA**

**Family Rhabditidae Oerley, 1880**

Genus *Prodontorhabditis* Timm, 1961

*Prodontorhabditis wirthi* Sudhaus, 1974
Distribution: **SI**, *NH*
Depth: Shallow

Genus *Buetschlinema* Sudhaus, 2011

*Buetschlinema validum* Sudhaus, 1974
Distribution: **SI**
Depth: Shallow

Genus *Litoditis* Sudhaus, 2011
*Litoditis allgeni* (Johnston, 1938)
Distribution: **CI**
Depth: Shallow

*Litoditis marina* (Bastian, 1865) Andrássy, 1983
Distribution: **NZ**, Aus, Bra, FaI, *NH*
Depth: Shallow

*Litoditis meditteranea* (Sudhaus, 1974) Andrássy, 1983
Distribution: **CI, SI**, *NH*
Depth: Shallow

Genus *Rhabditoides* Goodey, 1929

*Rhabditoides intermiformis* Sudhaus, 1974
Distribution: **NZ**
Depth: Shallow

**Order RHAPTOTHYREIDA**

**Family Rhaptothyreidae Hope & Murphy, 1969**

Genus *Rhaptothyreus* Hope & Murphy, 1969

*Rhaptothyreus typicus* Hope & Murphy, 1969
Distribution: **NI**, Chi, SoA, *NH*
Depth: Deep

**Order BENTHIMERMITHIDA**

**Family Benthimermithidae Petter, 1980**

Genus *Trophomera* Rubtsov & Platonova, 1974

*Trophomera* cf. *marionensis* (Petter, 1983)
Distribution: **KA,** Per, Bra, *NH*
Depth: Deep

### 4.3.4 Checklist of *species inquirendae*

**Order CHROMADORIDA**

**Family Chromadoridae Filipjev, 1917**

Genus *Prochromadorella* Micoletzky, 1924

*Prochromadorella ungulidentata* (Allgén, 1932) Wieser, 1954

Distribution: **CI**

Depth: Shallow

*Prochromadorella affinis* (Allgén, 1932) Wieser, 1954

Distribution: **CI,** Chi

Depth: Shallow

Genus *Spiliphera* Bastian, 1865

*Spiliphera amokuroides* (Allgén, 1927) Inglis, 1969

Distribution: **CI**

Depth: Shallow

## Order MONHYSTERIDA

### Family Monhysteridae de Man, 1876

Genus *Monhystera* Bastian, 1865

*Monhystera elegans* Allgén, 1927

Distribution: **CI**

Depth: Shallow

*Monhystera paraambiguoides* Allgén, 1932

Distribution: **CI**

Depth: Shallow

*Monhystera praevulvata* Allgén, 1932

Distribution: **CI**

Depth: Shallow

*Monhystera tasmaniensis* Allgén, 1927

Distribution: **CI,** Aus, Chi

Depth: Shallow

### 4.3.5 Checklist of *species incertae sedis*

**Order CHROMADORIDA**

**Family Desmodoridae Filipjev, 1922**

Genus *Desmodora* Filipjev, 1922

*Desmodora campbelli* (Allgén, 1932)
Distribution: **CI,** Ant, Arg, Chi, FaI, SoG
Depth: Shallow

**Family Siphonolaimidae Filipjev, 1918**

Genus *Siphonolaimus* de Man, 1893

*Siphonolaimus pellucidus* Allgén, 1932
Distribution: **CI**
Depth: Shallow

## 4.4 Discussion

Nematode diversity on the New Zealand continental margin is estimated to exceed 1000 species (Leduc et al. 2012b), and a similar number may exist in coastal and shelf areas of the region. To date, only 159 valid species have been described/recorded from the New Zealand Exclusive Zone, with eight species being described per year on average since the last checklist (Leduc and Gwyther 2008). At this rate, it will take about two centuries to describe the remaining free-living marine nematode diversity of the region. This timeframe is clearly too long given the increased pressure from human activities which may result in species loss in the short to medium term. Since nematodes are highly diverse, it is suggested that taxonomic research could be concentrated on certain family, such as Comesomatidae family, so that a partial assessment of diversity can be completed to inform management practices. Comesomatidae species are widespread, as they are common in coastal, shelf and upper continental slope environments (Vanreusel 1990, Schratzberger et al. 2009, Muthumbi et al. 2011). Comesomatids are also diverse and comprise of variety functional (trophic) groups (Fonseca and Bezerra 2014), making them suitable for assessements of both structural and functional diversity. In deeper environments, *Acantholaimus* is one of the most species-rich deep-sea genera and has been relatively well studied (Miljutina and Miljutin 2012, Miljutina et al. 2012), and may therefore be suitable for deep-sea community investigation. This genus is abundant in deep habitats of the New Zealand region, but no species records are yet available. This genus should therefore be the focus of future taxonomic studies so that meaningful ecological information can be made available to inform management of lower continental slope and abyssal environments.

The genus *Sabatieria* is very diverse, and the species groups devised by Platt (1985) have been useful in helping species identification. However, *S. dispunctata* sp. n. cannot be satisfactorily grouped with any of these groups. This new species is characterised by a minute buccal cavity, as opposed to a larger and cup-shaped cavity in all other *Sabatieria* species. It is suggested that perhaps another new group should be created in the future for *Sabatieria* species with a minute buccal cavity. However, the formation of this new proposed group should wait until more new species with small buccal cavities are described in the future. Currently all *Sabatieria* species except *S. dispunctata* sp. n. are classified as deposit feeders, whereas the new species should be classified as a microvore due to the small size of its buccal cavity (Moens and Vincx 1997). This finding shows that there may be considerable intra-generic variability in the functional characteristics of nematodes, which can only be grasped through detailed investigation of the morphology of accurately identified species.

The new record of *Laimella subterminata* from the New Zealand Exclusive Zone suggests a relationship between the New Zealand and South American nematode fauna. Other comesomatid species also show similar distribution, namely *Cervonema shiae* and *Hopperia beaglense*, which were originally described from the South American continent but are also found in the New Zealand region. Another comesomatid species, *Kenyanema monorchis*, is found in Indian Ocean off Kenya in addition to New Zealand, while *Sabatieria mortenseni*, *S. punctata*, *S. bitumen*, and *Comesoma tenuispiculum* appear to have a cosmopolitan distribution. Whilst molecular data will be required to verify the identity of these species across distant locations, it is possible that these species disperse throughout the Southern Hemisphere through passive dispersal from currents flow. Such transport is likely to be slow, but nematodes generally show low level of environment specificity (Vanreusel et al. 2010b), and can be transported by currents over long distances through passive dispersal (Boeckner et al. 2009). Nematode dispersal also can occur through the ballast water of ships (Radziejewska et al. 2006). Alternatively, they may have drifted with the continents during breakup of Pangea over geological timescales. Further taxonomic research is needed to investigate this hypothesis, not only using morphological approach but also molecular works to examine levels of genetic connectivity and evolutionary relationships.

# Chapter 5

# Synthesis of results and suggestions for further study

The research presented here shows that deep-sea meiofaunal and nematode community attributes vary across a range of spatial scales on New Zealand's continental margin: at regional, bathymetric, habitat and centimetre scales, with most of the variation occurring at regional and centimetre scales. Environmental drivers linked with variability in meiofaunal communities also operated at different spatial scales, and several influenced meiofaunal communities at each of these scales. Disturbance from fishing and bioturbation also influenced meiofaunal communities at both regional and small scales. Detailed analyses of nematode specimens led to the discovery and description of two new species from the Hikurangi Margin and one new species record for the New Zealand Exclusive Economic Zone. These findings are discussed below in relation to the implications of the results for research on nematode biodiversity, meiofaunal community patterns among different spatial scales, and the role of disturbance in structuring these patterns. Suggestions for future study are also made on these topics. Finally, this chapter concludes with a brief discussion about what the study has revealed about the relative vulnerability of meiofaunal communities to anthropogenic activities, and the consequences of these findings.

## 5.1 Nematode biodiversity and taxonomy

It has been estimated that about 1200 nematode species are present on Chatham Rise and Challenger Plateau based on the Chao2 method (incidence-based estimator; Leduc et al. (2012b)), with the majority of this diversity likely to be new to science. Therefore, several hundreds, perhaps thousands of species, remain to be described from deep-sea habitats in New Zealand. The present study described only two species new to science, but I estimate that perhaps more than two hundred species remain undescribed from the samples that I examined. Thus it is clear that more extensive sampling and taxonomic research are required to determine the true extent of the region's marine nematode biodiversity. New molecular techniques will most likely help to quantify biodiversity in the future (Powers et al. 2011, Bik et al. 2012, Thomsen and Willerslev 2015). Environmental DNA (eDNA) metabarcoding offers a powerful tool to complement morpho-taxonomic studies and accelerate the assessment of deep-sea biodiversity for pure and applied deep-sea environmental research (Sinniger et al. 2016). By using *en masse* sequencing of environmentally derived DNA, or metabarcoding as it is commonly termed, biodiversity can be assessed in less time and not just restricted to single taxa as the method can be used to explore the biodiversity of all taxa in parallel (Bik et al. 2012). However, despite its high potential for assessing biodiversity, lack of taxonomic knowledge and appropriate reference databases of molecular sequences make it difficult to exploit metabarcoding as a tool (Dell'Anno et al. 2015, Sinniger et al. 2016). Therefore, further studies combining taxonomic and molecular methods are still needed, particularly for deep-sea fauna, in order to integrate biodiversity assessment approaches and develop a more complete sequence database.

Of the 159 valid nematode species currently recorded from New Zealand waters, 47% are exclusively found in the region. This level of endemism is relatively high compared to other taxa in the New Zealand marine environment; such as crustaceans (31%; Yaldwyn and Webber (2011)), molluscs and fishes, (19 and 5.5%, respectively;  Duffy and Ahyong (2015)). Nematode taxonomy is not well studied in

New Zealand, and therefore it is difficult to predict whether the level of endemism for nematode species in this region will increase or decrease when more species are found and described here and in other parts of the world. Nematodes generally display a low level of environmental specificity (Vanreusel et al. 2010b), and can be easily transported by currents through passive dispersal (Boeckner et al. 2009). Cosmopolitan species have been recorded in the present and previous meiofaunal studies in New Zealand waters (Leduc and Gwyther 2008), and molecular studies also support the existence of cosmopolitan nematode species in the deep-sea (Bik et al. 2010). However, the existence of cryptic species suggests that nematode endemism could be high in the New Zealand region (Derycke et al. 2016).

Recent efforts to integrate molecular methods and digital 3D image-capturing technology in nematode taxonomy, to enhance the identification accuracy of such a taxonomically challenging group, are promising (De Ley et al. 2005, Abebe et al. 2011). The 3D image allows nematode specimens to be identified to genus level, and can be used to match specimens with subsequent species identifications and descriptions of preserved specimens, when molecular sequence data do not match with any sequences in public databases (De Ley et al. 2005). The molecular approach is essential for identifying marine cryptic species (Derycke et al. 2013, Derycke et al. 2016), because taxonomic identification solely based on morphological evidence is now insufficient for species identification and to confirm the endemicity of the species. However, molecular information alone cannot be used to predict the ecological functionality of a species. A recent study showed that morphologically similar cryptic species can have different functional traits and show different feeding behaviour (Derycke et al. 2016). Therefore, a combination of morphological and molecular methods is the best way forward for nematode identification. Furthermore, this combination of a good species description with molecular sequences data can be applied for biodiversity assessment using eDNA metabarcoding approaches. In the present study, the nematode taxonomy and identification was based on morphological data alone, since the samples were preserved in formalin and it was not possible to do any molecular work. It is recommended that for future taxonomic studies, and to obtain a better ecological understanding, it will be necessary to integrate the molecular approach in order to gain a more complete understanding of nematode species.

From updating the checklist of marine nematode fauna in New Zealand, it is apparent that nematode study is still uneven, with most of the studies concentrated at shallow water and certain deep-sea sites. Most of the described species were recorded from Chatham Rise and Challenger Plateau (200–3000 m water depth), and Kermadec Trench (6000–10 800 m) (Leduc 2013d, Leduc 2014, 2015), while the rest have been recorded from shallow subtidal and intertidal habitats (Ditlevsen 1921, Allgén 1927, Ditlevsen 1930, Leduc and Gwyther 2008). More than half of shallow water species were recorded from Campbell Island, mostly from subtidal habitats, and only four species have been recorded from shelf depths. Most marine nematode families have not been well studied. The Comesomatidae family, which is so far represented by 25 species records in New Zealand, is the most studied family in the region. This family has probably received the most attention because of its high abundance and wide distribution in coastal and continental slope environments (Vanreusel 1990, Muthumbi et al. 2011), as well as relatively large body size, and thus it remains a useful family on which to concentrate taxonomic effort. However, some common families such as the Desmoscolecidae and Chromadoridae have been poorly studied, and this may cause a problem in developing further ecological understanding. For example, *Desmoscolex* (Desmoscolecidae) and *Acantholaimus* (Chromadoridae) were responsible for the community dissimilarity between seamount and the other habitats in the present study, but no species have yet been described/recorded for these genera in this region. Further study at seamounts and other habitats are needed in order to better explore the potential of nematode biodiversity elsewhere in the deep-sea. Only a few studies have so far been conducted at seamounts, and the present study showed that diversity at seamount habitat was higher compared to canyon and slope habitats. Studies at cold seep and hydrothermal vent habitats are also scarce, although nematode diversity at these habitats can be very high and comprise nematode taxa not found elsewhere (Van Gaever et al. 2004, Van Gaever et al. 2006, Zeppilli et al. 2011). Further study of nematode taxa that can tolerate the extreme environmental conditions of seep and vent habitats will not only provide new biodiversity information, but will also promote understanding of how certain species can function in extreme environments. However, in the present study, there were no samples available for nematode analysis from vent habitats, and future study should therefore include this and other habitats that have not been sampled (e.g., abyssal plain) or are difficult to sample without remotely operated vehicles (e.g. vent habitats).

## 5.2 Meiofaunal community patterns

Previous studies have shown that the greatest difference in nematode community attributes occur either between regions, habitats, or sediment depths (Fonseca et al. 2010, Bianchelli et al. 2013, Danovaro et al. 2013, Ingels and Vanreusel 2013, Gambi et al. 2014). In the present multi-scale study – one of only a few that have been carried out to date – habitat effects on meiofaunal communities are relatively small compared with regional and sediment depth effects, at least for meiofauna found in soft sediments of seamount, canyon and slope habitats. Different biotic and environmental processes are likely to be operating at different spatial scales (Levin et al. 2001, Rex and Etter 2010, Bianchelli et al. 2013, Ingels and Vanreusel 2013), and the present study showed this to be the case (see Figure 5.1). At the regional scale, the difference in meiofaunal communities between the Hikurangi Margin and the Bay of Plenty was related to differences in surface productivity and food proxies, suggesting that food availability is an important driver of regional differences in meiofaunal and nematode communities. This was clearly observed in the analysis of meiofauna in Chapter 2, where meiofaunal abundance, diversity, and community structure showed differences between these two regions and were significantly correlated with food proxies. Similar patterns were observed for nematode analysis in Chapter 3, where nematode diversity, community structure and trophic structure also significantly correlated with food proxies. Fonseca et al. (2010) showed a similar result where at larger scale, food proxy of organic matter positively correlated with nematode abundance and diversity. Disturbance from fishing and bioturbation activities can also influence meiofaunal communities at the regional scale. Differences in meiofaunal diversity were significantly correlated with trawling activity. Regional differences in nematode diversity, community structure and trophic structure also were significantly correlated with bioturbation proxies, whereas nematode diversity and community structure were significantly correlated with trawling disturbance.

At the habitat scale, meiofaunal community patterns were shown to be influenced by seafloor topography variables, proxies for food availability, water depth sediment characteristics and and bioturbation (see Figure 5.1). Only meiofaunal abundance differed significantly at habitat scale, whereas seafloor topography variables, food proxies, and water depth were significantly correlated with meiofaunal abundance. For nematode analysis, all nematode community attributes were significantly different at habitat scale. Nematode diversity was significantly correlated with sediment characteristics and bioturbation proxies, whilst nematode community structure was significantly correlated with food proxies, water depth and bioturbation proxies. Nematode trophic structure, on the other hand, was significantly correlated with seafloor topography variables and water depth.

At the small scale, surface and subsurface sediment meiofaunal communities were influenced by similar environmental variables of seafloor topography, food proxies, sediment characteristics, water depth and the disturbance proxies of fishing activity and bioturbation by larger fauna. Meiofauna abundance, diversity and community structure were significantly correlated with seafloor topography, food proxies, and sediment characteristics at small scale, whereas only meiofauna diversity was significantly correlated with water depth and trawling disturbance. For nematode community attributes however, only trophic structure was significantly correlated with seafloor topography and water depth, whilst nematode diversity and trophic structure were significantly correlated with sediment characteristics. All nematode community attributes, however, were significantly correlated with food proxies, whereas only nematode diversity and community structure were significantly correlated with disturbance proxies. Correlation analysis between nematode community attributes and food proxies at small scales by Fonseca et al. (2010) suggest that other unmeasured environmental factors are responsible.

These findings reveal the complexity of the interactions between meiofaunal communities and their environment, as more than one environmental variable plays a role in influencing meiofaunal communities at each of these scales. Thus, change in one or more environmental variables would likely disrupt the multi-scale interactions between meiofaunal communities and their environment, potentially making meiofaunal communities vulnerable to anthropogenic disturbance. The findings revealed by the present multi-scale study indicate how important it is to understand the complex interplay between meiofaunal community attributes and environmental controls, and that community patterns should ideally not be interpreted by single-scale studies only.

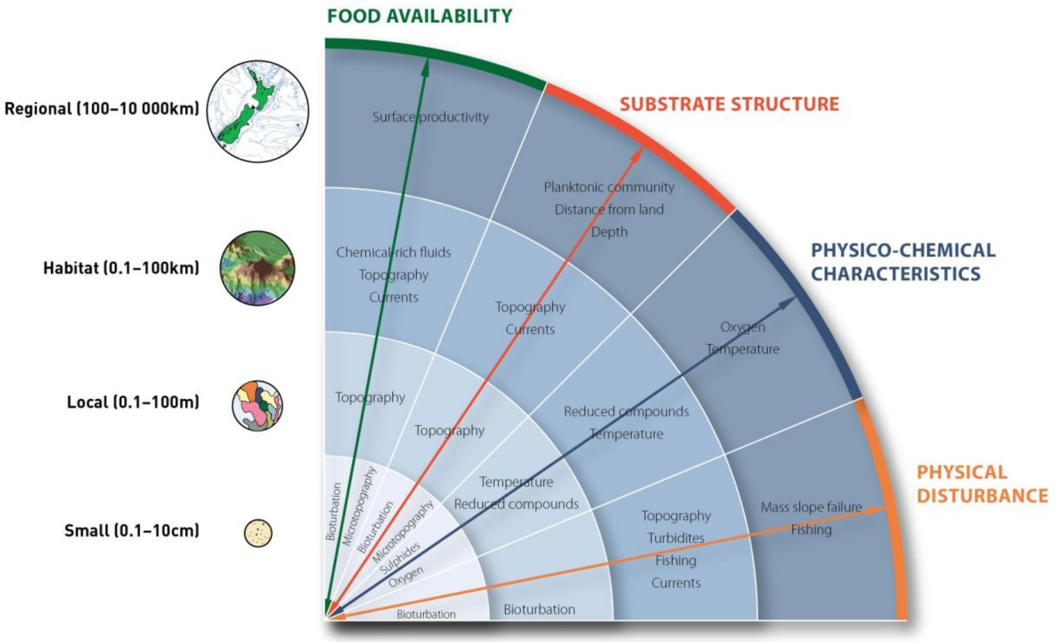

Figure 5.1. Schematic of factors that are responsible for meiofauna community differences at regional, habitat and sediment depth scales. Big arrows show that environmental variables change from regional, habitat to sediment depth scale through different processes (in italic).

The influence of spatial scale on meiofaunal communities showed slight variation when different taxonomic resolution was used in the analysis (meiofauna, Chapter 2; nematode, Chapter 3). However, this slight difference was noticeable only at habitat scale, whereas at regional and small scale significant differences between meiofauna and nematode were not evident (see Table 5.1). At habitat scale, the difference was more obvious in Hikurangi Margin than Bay of Plenty, where at genus level, nematode diversity and community structure showed significant difference between habitats. At the higher level of identification, meiofaunal community showed the opposite pattern of no significant difference between habitat. This suggests that data at finer taxonomic resolution (genus) is more likely to show a response to habitat affects that data on coarse taxonomic resolution (meiofaunal groups). Correlation with environmental variables also varies slightly with taxonomic resolution, but more noticeable at small scale. At small scale, meiofauna communities were significantly influenced by seafloor topography proxies, sediment characteristics and food proxies, whereas nematode communities were significantly influenced by sediment characteristics and food proxies. This difference may be due to lower taxonomic resolution used, as it may respond differently to the environmental variables tested compared to coarse taxonomic resolution. Therefore, it is suggested that for ecological studies concerning different spatial scales and assessing vulnerability, lower taxonomic resolution such as nematode genus level is required for investigation to prevent any loss of information.

Table 5.1. Meiofaunal and nematode community attributes and environmental relationship differences at different spatial scales. R = regional scale, H = habitat scale, S = small scale, D = diversity, CS = community structure, HIK = Hikurangi Margin, BoP = Bay of Plenty. √ = significant difference based on PERMANOVA, $P < 0.05$, x = not significant. Significant correlation of environmental results based on DistLM analysis, $P < 0.05$.

| | | Community attributes | | | | Correlated environmental variables | |
|---|---|---|---|---|---|---|---|
| | | Meiofauna | | Nematode | | Meiofauna | Nematode |
| **R** | D | √ | | √ | | Surface productivity, food proxies, disturbance | Surface productivity, food proxies, disturbance |
| | CS | √ | | √ | | Surface productivity, food proxies, | |
| | | HIK | BoP | HIK | BoP | | |
| **H** | D | x | x | √ | x | x | Sediment characteristic, bioturbation |
| | CS | x | x | √ | √ | x | Food proxies, water depth, bioturbation |
| **S** | D | √ | √ | √ | √ | Food proxies, sediment characteristic, water depth, seafloor topography, disturbance | Food proxies, sediment characteristic, disturbances |
| | CS | √ | √ | √ | √ | Food proxies, sediment characteristic, seafloor topography | Food proxies, disturbances |

It is worth remembering that the results of the nematode community study are based on genus level identifications. This level of taxonomic identification could have implications for the interpretations that can be made from the present study, and comparability with other studies, some of which are based on species level identifications. A previous multi-scale study that used genus level identifications showed a similar result with the greatest difference in nematode community structure occurring between sediment depth layers and between margins (Ingels and Vanreusel 2013). A study based on species community data showed a similar result, with the greatest difference in nematode community composition observed between margins (Fonseca et al. 2010). Greater variability in diversity also implies a difference in nematode community composition, and results of a study by Fonseca et al. (2010) showed a slight difference when using species and genus data. At species level, greatest variability was observed between cores (ca. 20 cm), while at genus level, greatest variability was observed between sediment depth layers (1–5 cm). Nematode species are more restricted in their distribution compared to genera, and therefore may be more sensitive in discriminating changes in communities. However, this difference in the pattern exhibited between taxonomic levels is only small, since the aforementioned studies both identified the smallest scale (within cm range) as the most important, and suggests that multivariate analyses show similar patterns at genus and species levels. Other studies have also shown that genus data can be used in ecological studies without noticeable loss of information (Miljutin et al. 2010, Leduc et al. 2012b). Therefore, nematode genus data could be used for most ecological studies instead of species data, since the identification process requires less effort and unidentified new species should be able to be identified to genus level. However, for certain ecological studies, such as investigating the role of nematode biodiversity in ecosystem function, nematode species level data are required in order to fully understand the processes involved (Danovaro et al. 2008a).

## 5.3 Disturbance

Only one previous study of the effects of trawling disturbance on deep-sea meiofauna has been conducted (Pusceddu et al. 2014a), and the present study is one of the few studies that have looked at the effects of physical disturbance on deep-sea meiofauna (Radziejewska 2002, Ingole et al. 2005, Miljutin et al. 2011, Leduc and

Pilditch 2013). Bioturbation marks were used in the present study as a measure of biotic disturbance, a method which had not been used previously. Bioturbation marks are considered a useful proxy to measure biotic disturbance as most benthic fauna leave traces during their feeding and burrowing activity which disturbs the sediment. Bioturbation marks can be divided into different categories (e.g. surface versus subsurface disturbance), as the marks can be distinguished according to their feeding type. However, this method has a drawback as bioturbation marks may either persist for long periods or disappear rapidly depending on local current conditions and the nature of the sediments (Jumars and Ekman 1983). However, relationships between meiofaunal communities and bioturbation have been previously investigated in shallow water habitats (Olafsson et al. 1993, Olafsson 2003). These shallow water studies, based on experimental manipulations, showed that bioturbation plays an important role in structuring meiofaunal communities in the sediment. Here, bioturbation marks were used instead for studying remote deep-sea communities. The present study is one of the few deep-sea studies that incorporates an investigation of bioturbation effects together with the influence of other environmental variables in a single comparable analysis, instead of focusing solely on bioturbation effects (Gallucci et al. 2008a). The findings of the present study showed that bioturbation may play an important role in influencing differences in meiofaunal community attributes by altering the distribution of food, oxygen, as well as partition the sediment particle size. Therefore, bioturbation effects on meiofaunal communities can be suggested to have similar importance like other environmental variables. However, when effect size is taken into account, the amount of variation explained by bioturbation proxies on meiofaunal communities was smaller (> 4% but less than 20%) compared to the total amount explained by the physical environment (> 30%), or the total amount of food proxies (> 10%) or sediment characteristics (> 10%) alone. Thus, I conclude that bioturbation had significant effects on meiofauna communities, but bioturbation proxies alone did not greatly contribute to meiofaunal community differences as much as other environmental variables such as food availability. Based on these results, effect size explained by amount variation can plays an important role in interpreting the ecological significance, and should be considered when interpreting the significance of correlations involving complex interactions between environment variables and deep-sea meiofauna community attributes. Trawling intensity was shown to be related to meiofaunal community patterns at regional scales on the Hikurangi Margin. The results of the analysis of nematode data suggest that the communities in this region may be in an altered state from the effects of past disturbance by fishing activity. Analysis of mega-epifaunal communities from the same sites also showed a similar response to trawling effects in the Hikurangi Margin region (Bowden et al. 2016), but no relationship was found for macro-infauna (Leduc et al. 2016b). Therefore, further impact on physical disturbance in this region may force benthic community structure to an alternative state and will likely affect ecosystem function.

Disturbance affects meiofaunal communities by reducing diversity and causing a shift in community and trophic structure. It has been shown that different trophic groups respond to environmental factors differently; disturbance often causes a decline in the abundance of susceptible taxa such as epigrowth feeders, as well as increased dominance of opportunistic deposit-feeding taxa (Schratzberger et al. 2009). However, the presence of a trophically diverse community may be necessary for the persistence of the ecosystem function following disturbance (Walker 1995, Naeem 1998, De Mesel et al. 2006a). Therefore, lower diversity and changes in community and trophic structure following disturbance will likely affect the contribution of meiofauna to benthic ecosystem function. Megafaunal community also showed a clear shift in community and trophic structure on the intensively trawled Hikurangi Margin, with a greater density of predator-scavenger taxa relative to the Bay of Plenty region (Bowden et al. 2016). Meiofauna showed a similar effect of disturbance with megafauna in the present study, where they showed a shift in abundance of trophic groups after disturbance, which suggests that meiofauna may be a useful proxy for the wider benthic community. Meiofauna play an important role in the ecosystem, and their study with respect to disturbance, should be equally valued with those of mega- and macro-fauna (Rogers et al. 2008, Schratzberger 2012, Zeppilli et al. 2015a). Furthermore, meiofauna may be particularly useful for investigating disturbance impacts in the deep-sea because they are likely to be more responsive to disturbance than larger fauna because of their inability to actively avoid disturbed areas (Vranken et al. 1986, Palmer 1988). Moreover, their feeding types are easily recognizable, making it possible to identify functional diversity traits that can be used to explore relationships between disturbance and ecosystem function.

Information on the role of disturbance by anthropogenic activities and bioturbation in shaping deep-sea meiofaunal communities is still limited, and the present findings give relatively limited insights into disturbance processes in the deep-sea relating to meiofauna. Future investigations are needed to test and confirm the findings of the present study, ideally through experiments both *in situ* and in the laboratory. A disturbance experiment was originally planned for this study, with the aim of investigating the effects of a physical disturbance event (resuspension of surface sediments) on sediment characteristics (sediment grain size, pigment content), nematode community attributes and ecosystem function (sediment community oxygen consumption (SCOC)). However, due to the time constraints imposed by finishing the observational studies, this experimental part had to been excluded from the present study. Future disturbance experiments should test the effects of physical disturbance not just at surface level but also through subsurface sediment to see whether meiofaunal recovery level between surface and subsurface sediment is equal or not, and investigate the effects of disturbance on nematode functional groups and their link to ecosystem function.

## 5.4 Conclusion

Meiofaunal communities have been shown to vary at different spatial scales from regional, habitat, to cm scale, and this pattern was influenced by environmental variability of food availability and sediment characteristics. Disturbance (fishing activity and bioturbation) also accounts for some of the variability of meiofaunal communities. This variability shows the relative importance of processes that occur at each spatial scale in influencing meiofaunal communities, and the potential for their vulnerability to anthropogenic activities. The potential impact of disturbance on meiofaunal community has been shown in this study, especially at the most important scale, regional and sediment depth scale, where disturbance has been linked to changes in meiofaunal community structure. Changes in meiofaunal community structure, often reflect decreases in abundance of susceptible taxa and increased dominance of opportunistic taxa, which may not be able to sustain normal ecosystem function following disturbance.

An effective management scheme should be established in order to manage the effects of anthropogenic activities such as bottom trawling on continental margin fauna. Meiofaunal communities showed a clear regional difference, between the lower productivity region of Bay of Plenty and the high productivity region of Hikurangi Margin. Higher food availability has been shown to help with meiofaunal resilience to disturbance (Gallucci et al. 2008b), which would imply lower vulnerability of meiofaunal communities in the high productivity region of Hikurangi Margin. The Bay of Plenty region also has higher abundance of *Acantholaimus,* a nematode genus with limited colonisation abilities, than Hikurangi Margin. The vulnerability differences between these two regions suggests that they should be subject to distinct management strategies. More studies are also needed since information on deep-sea benthic vulnerability based on differences in regional productivity is limited, which prevents robust management strategies based on regional differences in community structure.

Differences in meiofaunal communities at different habitats also imply different relative vulnerability. Meiofaunal communities of canyon and seep habitats on the Hikurangi Margin differed from each other, and from seamount and slope communities due to differences in the abundance of the number of shared taxa, and the presence of a higher number of rare taxa. Both canyon and seep habitats are also characteristically more vulnerable to physical disturbance than the other habitats, as disturbance may modify the habitat characteristics permanently, such as fluid flow patterns in seep habitats. The dissimilarity of these two habitats and their communities, suggests that that they should be considered as distinct habitats in ecological risk assessments and area protection planning and management for the Hikurangi Margin region. However, the vulnerability differences among different habitats can vary by region, and therefore, each region should be subject to separate habitat evaluation for environmental planning and management. For example, habitats in regions that have been less impacted than the Hikurangi Margin, such as the Bay of Plenty where less trawling activity occurred.

Clear differences in meiofaunal communities between surface and subsurface sediments may also imply different relative vulnerability, but surface and subsurface meiofaunal communities are likely to be equally vulnerable to direct physical disturbance from bottom trawling or seabed mining, as these two activities can cause disruption and compaction to the seafloor sediment to depths of > 5 cm. Meiofaunal communities in surface sediment, however, may be less vulnerable than subsurface communities, since meiofaunal communities can quickly recolonise surface sediment through suspended sediment transport. Even though there is a potential difference in vulnerability between the sediment layers, they cannot be considered separately at this small scale for environmental risk assessment due to practical reasons. But the information on the vulnerability of this small scale is still important, as it may help identify the impact of physical disturbance on the smallest but most abundant component of the benthic fauna, with likely implications for ecosystem function in the deep-sea.

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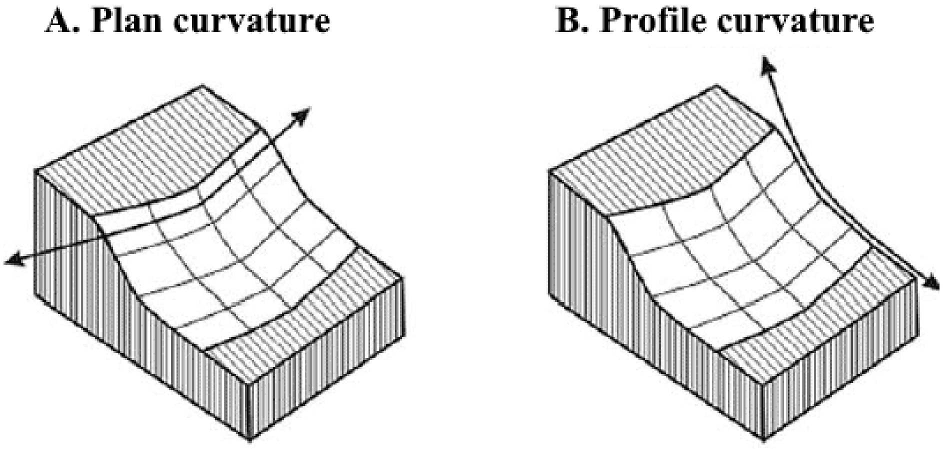
# Appendices

## Appendix A

Appendix A. Visual representation of plan curvature and profile curvature (Harrison et al. 2008).



# Appendix B

Appendix B. List of final environmental variables that were used in the DistLM analysis and the correlated variables that were removed prior to analysis of nematode for Hikurangi Margin and Bay of Plenty study region. [STD = Standard deviation of depth based on 3, 5, 7, 15 grid cell focal mean, Slope STD = Standard deviation of slope, Vrm = terrain rugosity, range = depth range, curvature = change of the slope, profile curvature = curvature of the surface in the direction of the slope, plan curvature = curvature of the surface perpendicular to the slope direction].

| **Hikurangi Margin** | | **Bay of Plenty** | |
|---|---|---|---|
| Final variables | Correlated variables removed | Final variables | Correlated variables removed |
| Latitude | Longitude | %OC | %N |
| Surface water chlorophyll concentration | Longitude | Phaeopigment | Sediment Chl *a* |
| %OC | %N | Sorting | Mean particle size |
| Phaeopigment | Sediment Chl *a* | %silt/clay | Particle size diversity |
| Mean particle size | Sorting | Vrm05 | Vrm03 |
| Particle size diversity | %silt/clay | STD07 | STD15 and STD05 |
| Vrm05 | Vrm03 | STD05 | STD03 |
| STD15 | STD07 | Slope STD07 | Slope STD15 |
| STD07 | STD05 | Slope STD05 | Slope STD07 and slope STD03 |
| STD05 | STD03 | Range 07 | Range 15 and Range 05 |
| Slope STD15 | Slope STD07 | Range 05 | Range 03 |
| Slope STD03 | Slope STD05 | Plan curvature | Curvature |
| Range 07 | Range 15 | Depth | Pit (bioturbation) |
| Range 05 | Range 07 and Range 03 | Fishing intensity | |
| Curvature | Plan curvature | Slope | |
| Depth | | Profile curvature | |
| %$CaCO_3$ | | Longitude | |
| %OM | | Latitude | |
| Skewness | | Surface chlorophyll concentration | |
| Kurtosis | | %$CaCO_3$ | |
| Fishing intensity | | %OM | |
| Slope | | Skewness | |
| Profile curvature | | Kurtosis | |
| Macrofauna deposit feeder | | Macrofauna deposit feeder | |
| Macrofauna grazer | | Macrofauna grazer | |
| Macrofauna total abundance | | Macrofauna total abundance | |
| Track (bioturbation) | | Track (bioturbation) | |
| Faecal coil (bioturbation) | | Faecal coil (bioturbation) | |
| Burrow (bioturbation) | | Hemichordate spiral (bioturbation) | |

| | |
|---|---|
| Mound (bioturbation) | Burrow (bioturbation) |
| Ring of burrows (bioturbation) | Mound (bioturbation) |
| Pit (bioturbation) | Ring of burrows (bioturbation) |
| Total bioturbation | Pepperpots (bioturbation) |
| | Total bioturbation |

# Appendix C

Appendix C. SIMPER analysis results showing environmental variables accounting for regional dissimilarity between the Hikurangi Margin and Bay of Plenty study regions (cut-off applied at 70% contribution). [Av.Value = average environmental variable value, Av.Sq.Dist = average dissimilarity, Sq.Dist/SD = Dissimilarity/Standard Deviation, Contrib% = % contribution to overall dissimilarity, Cum.% = % cumulative dissimilarity]. Higher average value are shown in bold.

| Variable | Av.Value | Av.Value | Av.Sq.Dist | Sq.Dist/SD | Contrib% | Cum.% |
|---|---|---|---|---|---|---|
| | Hikurangi Margin | Bay of Plenty | | | | |
| Surface water chlorophyll concentration | **0.96** | -0.80 | 3.56 | 1.43 | 12.4 | 12.4 |
| Phaeopigment | **0.87** | -0.73 | 3.34 | 1.02 | 11.65 | 24.05 |
| %OM | **0.76** | -0.63 | 2.94 | 1.09 | 10.26 | 34.31 |
| %OC | **0.74** | -0.62 | 2.91 | 0.98 | 10.12 | 44.43 |
| Particle size diversity | -0.69 | **0.57** | 2.78 | 1.12 | 9.67 | 54.1 |
| Mean particle size | -0.52 | **0.43** | 2.32 | 0.49 | 8.08 | 62.18 |
| Fishing intensity | **0.29** | -0.24 | 2.31 | 0.25 | 8.05 | 70.24 |

# Appendix D

Appendix D. Results of PERMANOVA analysis test for the effects of habitat, water depths, sediment depth and their interaction on meiofaunal abundance at the Hikurangi Margin and Bay of Plenty study region. Significant factors at the 5% level are shown in bold. [df = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistic, P = Probability, Unique perms = number of unique permutations, √ECV = square root of estimates of components of variation].

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | √ECV |
|---|---|---|---|---|---|---|---|
| ***Hikurangi Margin*** | | | | | | | |
| **Habitat** | 2 | 395440 | 197720 | 11.761 | **0.0009** | 9959 | 86.8 |
| **Water depth** | 3 | 256260 | 85421 | 5.621 | **0.0060** | 9965 | 57.4 |
| **Sediment depth** | 1 | 485630 | 485630 | 16.608 | **0.0013** | 9844 | 89.0 |
| Habitat x Water depth | 5 | 183590 | 36717 | 2.4977 | 0.0766 | 9954 | 49.2 |
| **Habitat x Sediment depth** | 2 | 267030 | 133510 | 5.3691 | **0.0151** | 9953 | 78.9 |
| **Water depth x Sediment depth** | 3 | 1068600 | 356200 | 13.63 | **0.0004** | 9944 | 154.9 |
| **Habitat x Water depth x Sediment depth** | 5 | 427750 | 85550 | 3.5745 | **0.0225** | 9949 | 113.2 |
| Residuals | 56 | 2004600 | 35797 | | | | |
| Total | 117 | 6076700 | | | | | |
| | | | | | | | |
| ***Bay of Plenty*** | | | | | | | |
| **Habitat** | 1 | 117540 | 117540 | 10.275 | **0.0059** | 9858 | 46.4 |
| **Water depth** | 3 | 136240 | 45413 | 3.8586 | **0.0283** | 9963 | 33.2 |
| **Sediment depth** | 1 | 103300 | 103300 | 9.9835 | **0.0046** | 9831 | 36.6 |
| **Habitat x Water depth** | 3 | 129350 | 43118 | 3.3632 | **0.0383** | 9956 | 42.5 |
| Habitat x Sediment depth | 1 | 29028 | 29028 | 2.9675 | 0.1080 | 9818 | 24.2 |
| Water depth x Sediment depth | 3 | 970.06 | 323.35 | 0.24741 | 0.8632 | 9957 | -21.2 |
| Habitat x Water depth x Sediment depth | 3 | 41288 | 13763 | 1.5202 | 0.2432 | 9950 | 24.9 |
| Residuals | 92 | 1133500 | 12321 | | | | |
| Total | 141 | 2087800 | | | | | |

# Appendix E

Appendix E. Results of PERMANOVA analysis test for the effects of habitat, water depths, sediment depth and their interaction on meiofaunal diversity at the Hikurangi Margin and Bay of Plenty study region. Significant factors at the 5% level are shown in bold. [df = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistic, P = Probability, Unique perms = number of unique permutations, √ECV = square root of estimates of components of variation].

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | √ECV |
|---|---|---|---|---|---|---|---|
| ***Hikurangi Margin*** | | | | | | | |
| Habitat | 2 | 12.405 | 6.2026 | 2.4885 | 0.1092 | 9953 | 0.4 |
| Water depth | 3 | 1.7434 | 0.58114 | 0.22955 | 0.8682 | 9961 | -0.3 |
| **Sediment depth** | 1 | 19.525 | 19.525 | 5.9379 | **0.0230** | 9816 | 0.5 |
| Habitat x Water depth | 5 | 13.764 | 2.7527 | 1.0685 | 0.4121 | 9950 | 0.1 |
| Habitat x Sediment depth | 2 | 1.5687 | 0.78437 | 0.35846 | 0.6945 | 9955 | -0.3 |
| Water depth x Sediment depth | 3 | 8.1917 | 2.7306 | 1.0174 | 0.4056 | 9960 | 0.1 |
| Habitat x Water depth x Sediment depth | 5 | 0.6599 | 0.13199 | 0.11159 | 0.988 | 9960 | -0.7 |
| Residuals | 56 | 113.83 | 2.0326 | | | | |
| Total | 117 | 277.83 | | | | | |
| ***Bay of Plenty*** | | | | | | | |
| Habitat | 1 | 0.2016 | 0.20164 | 8.99E-02 | 0.7677 | 9842 | -0.2 |
| Water depth | 3 | 14.765 | 4.9216 | 2.1041 | 0.1390 | 9962 | 0.3 |
| **Sediment depth** | 1 | 70.423 | 70.423 | 65.788 | **0.0001** | 9805 | 1.0 |
| Habitat x Water depth | 3 | 2.3767 | 0.79222 | 0.42299 | 0.7460 | 9947 | -0.3 |
| Habitat x Sediment depth | 1 | 0.9167 | 0.91675 | 1.174 | 0.2935 | 9827 | 0.1 |
| Water depth x Sediment depth | 3 | 5.3266 | 1.7755 | 1.9749 | 0.1577 | 9960 | 0.2 |
| Habitat x Water depth x Sediment depth | 3 | 2.4522 | 0.81741 | 1.0809 | 0.3921 | 9948 | 0.1 |
| Residuals | 92 | 170.97 | 1.8584 | | | | |
| Total | 141 | 325.55 | | | | | |

## Appendix F

Appendix F. Results of PERMANOVA analysis test for the effects of habitat, water depths, sediment depth and their interaction on meiofaunal community structure at the Hikurangi Margin and Bay of Plenty study region. The effect of spatial covariates were taken into account for community analysis (result not shown). Significant factors at the 5% level are shown in bold. [df = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistic, P = Probability, Unique perms = number of unique permutations, √ECV = square root of estimates of components of variation].

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | √ECV |
|---|---|---|---|---|---|---|---|
| ***Hikurangi Margin*** | | | | | | | |
| Habitat | 2 | 1057.1 | 528.54 | 2.0555 | 0.0871 | 9940 | 3.4 |
| Water depth | 3 | 1459.7 | 486.56 | 1.887 | 0.0593 | 9939 | 3.3 |
| **Sediment depth** | 1 | 4212.1 | 4212.1 | 14.351 | **0.0001** | 9959 | 8.2 |
| Habitat x Water depth | 5 | 1177.1 | 235.43 | 0.91475 | 0.5403 | 9928 | -1.6 |
| Habitat x Sediment depth | 2 | 681.65 | 340.82 | 1.4507 | 0.219 | 9958 | 2.5 |
| Water depth x Sediment depth | 3 | 1440.7 | 480.24 | 1.9645 | 0.0793 | 9942 | 4.3 |
| Habitat x Water depth x Sediment depth | 5 | 693.6 | 138.72 | 0.64912 | 0.772 | 9947 | -4.2 |
| Residuals | 56 | 13935 | 248.84 | | | | |
| Total | 117 | 35644 | | | | | |
| | | | | | | | |
| ***Bay of Plenty*** | | | | | | | |
| Habitat | 1 | 320.16 | 320.16 | 1.3191 | 0.2718 | 9950 | 1.3 |
| **Water depth** | 3 | 1687.1 | 562.38 | 2.2748 | **0.0499** | 9948 | 3.2 |
| **Sediment depth** | 1 | 9383.5 | 9383.5 | 46.915 | **0.0001** | 9950 | 11.4 |
| Habitat x Water depth | 3 | 803.97 | 267.99 | 1.1084 | 0.3732 | 9945 | 1.3 |
| Habitat x Sediment depth | 1 | 171.3 | 171.3 | 1.0966 | 0.3920 | 9965 | 0.7 |
| Water depth x Sediment depth | 3 | 836.3 | 278.77 | 1.6326 | 0.1323 | 9941 | 2.7 |
| Habitat x Water depth x Sediment depth | 3 | 290.08 | 96.694 | 0.72397 | 0.6677 | 9937 | -2.5 |
| Residuals | 92 | 24228 | 263.35 | | | | |
| Total | 141 | 45542 | | | | | |

# Appendix G

Appendix G. Results of second-stage analysis for stations from 700, 1000 and 1200 m water depth strata showing meiofaunal abundance and diversity between habitats and sediment depths for Hikurangi Margin. [Abundance shown in total meiofauna individuals per 10 $cm^2$; diversity as meiofaunal taxon richness].

| Stations | Abundance | Diversity | Abundance | Diversity | Strata (m) |
|---|---|---|---|---|---|
| **Surface sediment (0–1 cm)** | | | **Subsurface sediment (1–5 cm)** | | |
| ***Canyon*** | | | | | |
| 31_1 | 514 | 7 | 1236 | 5 | 700 |
| 31_2 | 400 | 6 | 2231 | 6 | 700 |
| 31_3 | 236 | 6 | 2467 | 7 | 700 |
| 58_3 | 418 | 7 | 2207 | 8 | 700 |
| 58_6 | 518 | 6 | 2116 | 8 | 700 |
| 58_7 | 241 | 5 | 2101 | 8 | 700 |
| 92_2 | 712 | 6 | 780 | 5 | 700 |
| 92_4 | 418 | 6 | 1089 | 4 | 700 |
| 27_4 | 571 | 7 | 1653 | 9 | 1000 |
| 27_6 | 1040 | 8 | 905 | 7 | 1000 |
| 27_8 | 1364 | 9 | 1312 | 6 | 1000 |
| 53_3 | 416 | 6 | 249 | 4 | 1000 |
| 62_6 | 416 | 5 | 771 | 5 | 1200 |
| 62_7 | 656 | 7 | 980 | 6 | 1200 |
| 62_8 | 403 | 6 | 441 | 4 | 1200 |
| 97_1 | 799 | 4 | 748 | 6 | 1000 |
| 98_1 | 648 | 5 | 641 | 3 | 1000 |
| 98_2 | 341 | 5 | 528 | 4 | 1000 |
| 22_1 | 752 | 6 | 908 | 7 | 1200 |
| 22_2 | 641 | 6 | 667 | 4 | 1200 |
| 22_5 | 654 | 6 | 1025 | 7 | 1200 |
| 127_3 | 516 | 5 | 827 | 3 | 1200 |
| **Average** | 576 | 6.1 | 1176 | 5.7 | |
| ***Seamount*** | | | | | |
| 69_1 | 369 | 6 | 812 | 8 | 700 |
| 69_2 | 379 | 4 | 443 | 2 | 700 |
| 69_5 | 430 | 5 | 852 | 4 | 700 |
| 72_1 | 286 | 6 | 639 | 5 | 1000 |
| 72_4 | 601 | 5 | 313 | 8 | 1000 |
| 72_8 | 160 | 6 | 415 | 4 | 1000 |
| 130_4 | 456 | 8 | 381 | 4 | 1000 |
| **Average** | 383 | 5.7 | 551 | 5.0 | |
| ***Seep*** | | | | | |
| 84_8_R1 | 290 | 7 | 1276 | 6 | 1000 |
| 84_8_R2 | 388 | 8 | 273 | 4 | 1000 |

| | | | | | |
|---|---|---|---|---|---|
| 86_9_R1 | 317 | 8 | 528 | 5 | 1000 |
| 86_9_R2 | 782 | 8 | 309 | 5 | 1000 |
| 112_10_R1 | 392 | 8 | 592 | 6 | 1000 |
| 112_10_R2 | 1136 | 9 | 669 | 7 | 1000 |
| 116_15_R1 | 1261 | 10 | 680 | 8 | 1000 |
| 116_15_R2 | 535 | 8 | 465 | 9 | 1000 |
| 118_16_R1 | 972 | 9 | 528 | 6 | 1000 |
| 118_16_R2 | 814 | 9 | 797 | 7 | 1000 |
| 123_17_R1 | 1195 | 9 | 546 | 7 | 1000 |
| 123_17_R2 | 840 | 6 | 514 | 4 | 1000 |
| **Average** | 744 | 8.3 | 598 | 6.2 | |
| ***Slope*** | | | | | |
| 44_4 | 580 | 6 | 933 | 4 | 700 |
| 44_5 | 269 | 5 | 814 | 7 | 700 |
| 44_7 | 575 | 6 | 989 | 6 | 700 |
| 124_4 | 699 | 5 | 773 | 5 | 700 |
| 124_7 | 861 | 6 | 901 | 5 | 700 |
| 4_4 | 710 | 7 | 997 | 5 | 1000 |
| 4_5 | 714 | 8 | 1095 | 6 | 1000 |
| 4_7 | 938 | 7 | 999 | 6 | 1000 |
| 41_1 | 328 | 5 | 354 | 2 | 1000 |
| 41_3 | 145 | 5 | 933 | 5 | 1000 |
| 41_8 | 675 | 7 | 548 | 7 | 1000 |
| 76_4 | 1214 | 7 | 671 | 6 | 1200 |
| 76_5 | 816 | 9 | 379 | 7 | 1200 |
| 38_2 | 1125 | 10 | 959 | 5 | 1200 |
| 38_3 | 599 | 6 | 961 | 7 | 1200 |
| 38_4 | 492 | 4 | 158 | 5 | 1200 |
| **Average** | 671 | 6.4 | 779 | 5.5 | |

## Appendix H

Appendix H. Results of PERMANOVA analysis tests on second stage analysis. Results showed the effects of habitat (slope, canyon, seamount and seep), water depths (700 m, 1000 m, 1200 m), sediment depth and their interaction on meiofaunal community structure at the Hikurangi Margin region, after accounting for the effect of spatial covariates (result not shown). Significant factors at the 5% level are shown in bold. [df = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistic, P = Probability, Unique perms = number of unique permutations, √ECV = square root of estimates of components of variation].

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | √ECV |
|---|---|---|---|---|---|---|---|
| **Habitat** | 3 | 4031.7 | 1343.9 | 5.1547 | **0.0001** | 9919 | 6.6 |
| **Sediment depth** | 1 | 4532.6 | 4532.6 | 17.385 | **0.0001** | 9955 | 8.7 |
| Habitat x Sediment depth | 3 | 1170.5 | 390.16 | 1.4965 | 0.1354 | 9916 | 3.1 |
| Residuals | 104 | 27114 | 260.71 | | | | |
| Total | 113 | 38625 | | | | | |

# Appendix I

Appendix I. List of nematode genera with their corresponding groups according to Moens & Vincx (1997). (M = microvores, CF = ciliate feeders, DF = deposit feeders, EF = epigrowth feeders, FP = facultative predators, P = predators).

| Genera | Feeding group | Genera | Feeding group |
|---|---|---|---|
| *Anoplostoma* | CF | *Quadricoma* | M |
| *Ascolaimus* | CF | *Rhabdocoma* | M |
| *Axonolaimus* | CF | *Southernia* | M |
| *Bathylaimus* | CF | *Southerniella* | M |
| *Chaetonema* | CF | *Stephanolaimus* | M |
| *Elzalia* | CF | *Tarvaia* | M |
| *Eumorpholaimus* | CF | *Terschellingia* | M |
| *Odontophora* | CF | *Thalassoalaimus* | M |
| *Amphimonhystera* | DF | *Trefusia* | M |
| *Amphimonhystrella* | DF | *Tricoma* | M |
| *Anticoma* | DF | *Wieseria* | M |
| *Cervonema* | DF | *Acantholaimus* | EF |
| *Comesoma* | DF | *Acanthopharynx* | EF |
| *Daptonema* | DF | *Aponema* | EF |
| *Desmolaimus* | DF | *Calomicrolaimus* | EF |
| *Diplolaimella* | DF | *Camacolaimus* | EF |
| *Diplolaimelloides* | DF | *Cephalanticoma* | EF |
| *Eleutherolaimus* | DF | *Chromadora* | EF |
| *Halomonhystera* | DF | *Chromadorina* | EF |
| *Kenyanema* | DF | *Chromadorita* | EF |
| *Megadesmolaimus* | DF | *Chromaspirinia* | EF |
| *Metacomesoma* | DF | *Cobbia* | EF |
| *Metadesmolaimus* | DF | *Croconema* | EF |
| *Minolaimus* | DF | *Cyatholaimus* | EF |
| *Monhystrella* | DF | *Deontolaimus* | EF |
| *Parampimonhystrella* | DF | *Desmodora* | EF |
| *Paranticoma* | DF | *Desmodorella* | EF |
| *Pararaeolaimus* | DF | *Dichromadora* | EF |
| *Phanoderma* | DF | *Diodontolaimus* | EF |
| *Pierrickia* | DF | *Dolicholaimus* | EF |
| *Promonhystera* | DF | *Dorylaimopsis* | EF |
| *Retrotheristus* | DF | *Echinodesmodora* | EF |
| *Rhynchonema* | DF | *Endeolophos* | EF |
| *Sabatieria* | DF | *Euchromadora* | EF |
| *Setosabatieria* | DF | *Filitonnchus* | EF |
| *Thalassomonhystera* | DF | *Graphonema* | EF |
| *Tricotheristus* | DF | *Hopperia* | EF |
| *Aegialoalaimus* | M | *Innocuonema* | EF |
| *Alaimella* | M | *Kraspedonema* | EF |

| Genera | Feeding group | Genera | Feeding group |
|---|---|---|---|
| *Antomicron* | M | *Laimella* | EF |
| *Araeolaimus* | M | *Longicyatholaimus* | EF |
| *Campylaimus* | M | *Metacyatholaimus* | EF |
| *Catanema* | M | *Microlaimus* | EF |
| *Ceramonema* | M | *Molgolaimus* | EF |
| *Coninckia* | M | *Monoposthia* | EF |
| *Crenopharynx* | M | *Nannolaimoides* | EF |
| *Cricohalalaimus* | M | *Neochromadora* | EF |
| *Cyartonema* | M | *Neotonchus* | EF |
| *Cytolaimium* | M | *Odontanticoma* | EF |
| *Dasynemoides* | M | *Paracanthonchus* | EF |
| *Desmoscolex* | M | *Paracomesoma* | EF |
| *Desmoscolex* | M | *Paracyatholaimus* | EF |
| *Diplopeltoides* | M | *Paradesmodora* | EF |
| *Diplopeltula* | M | *Paralongicyatholaimus* | EF |
| *Disconema* | M | *Paramesonchium* | EF |
| *Draconema* | M | *Paramicrolaimus* | EF |
| *Eubostrichus* | M | *Parironus* | EF |
| *Greeffiella* | M | *Parodontophora* | EF |
| *Halalaimus* | M | *Perspiria* | EF |
| *Hapalomus* | M | *Procamacolaimus* | EF |
| *Intasia* | M | *Spirinia* | EF |
| *Leptolaimoides* | M | *Stygodesmodora* | EF |
| *Leptolaimus* | M | *Syringolaimus* | EF |
| *Leptosomatum* | M | *Thalassironus* | EF |
| *Linhomoeus* | M | *Thoracostomopsis* | EF |
| *Linhystera* | M | *Trochamus* | EF |
| *Litinium* | M | *Vasostoma* | EF |
| *Manganonema* | M | *Zalonema* | EF |
| *Metadasynemella* | M | *Choniolaimus* | FP |
| *Metadasynemoides* | M | *Eurystomina* | FP |
| *Metalinhomoes* | M | *Filoncholaimus* | FP |
| *Micoletzkyia* | M | *Gammanema* | FP |
| *Morlaixia* | M | *Marylynnia* | FP |
| *Mudwigglus* | M | *Oncholaimus* | FP |
| *Nemanema* | M | *Pomponema* | FP |
| *Notochaetonema* | M | *Rhabdodemania* | FP |
| *Onepunema* | M | *Siphonolaimus* | FP |
| *Oxystomina* | M | *Trophonema* | FP |
| *Paradraconema* | M | *Viscosia* | FP |
| *Paralinhomoeus* | M | *Belbolla* | P |
| *Paramonohystera* | M | *Calyptronema* | P |
| *Paratricoma* | M | *Enoplus* | P |
| *Pareudesmoscolex* | M | *Enoplolaimus* | P |
| *Phanodermella* | M | *Halichoanolaimus* | P |

| Genera | Feeding group | Genera | Feeding group |
|---|---|---|---|
| *Phanodermopsis* | M | *Mesacanthion* | P |
| *Prochaetosoma* | M | *Paramesacanthion* | P |
| *Prototricoma* | M | *Parasphaerolaimus* | P |
| *Prototricomoides* | M | *Pseudocheironchus* | P |
| *Pselionema* | M | *Sphaerolaimus* | P |

## Appendix J

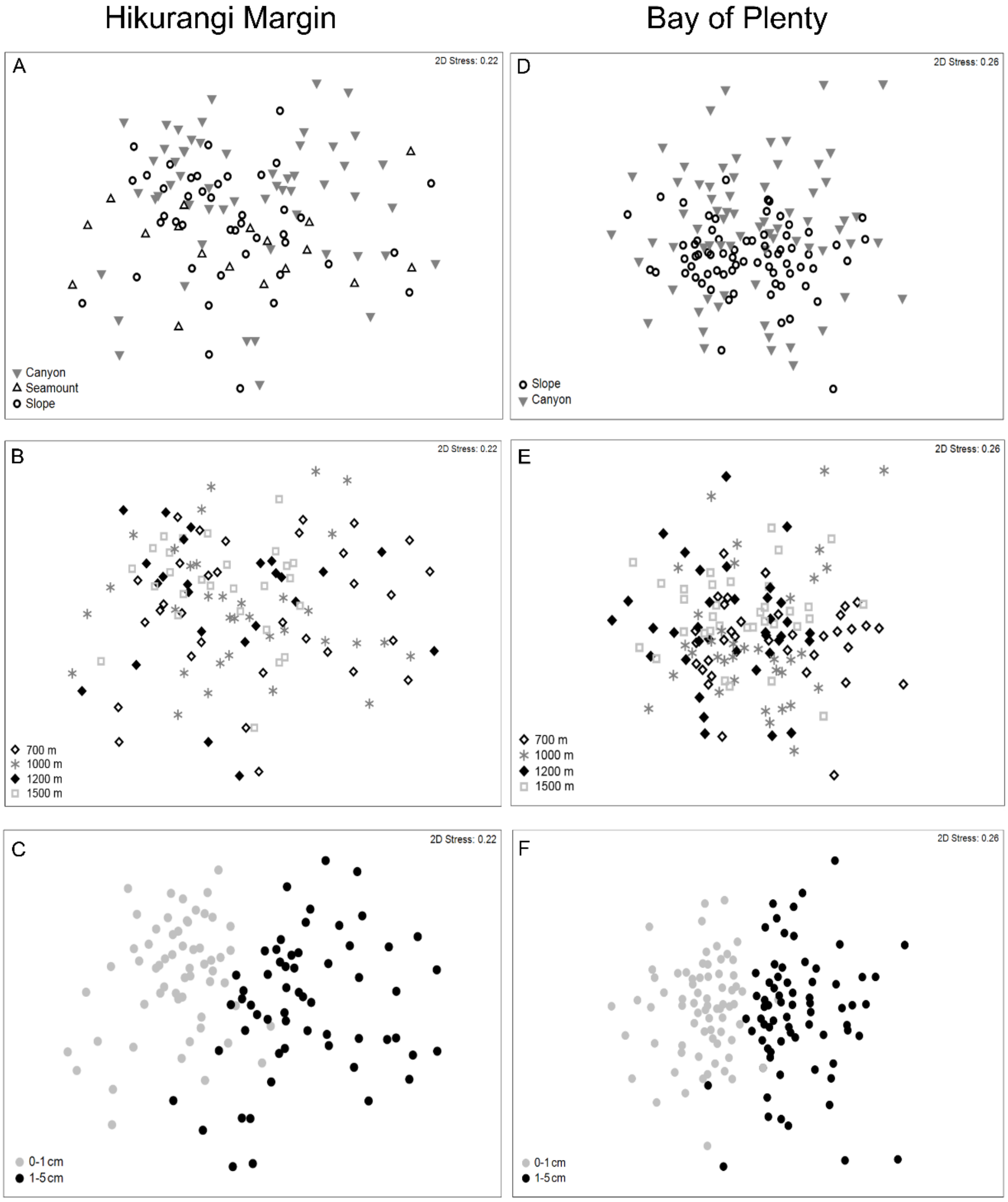
Appendix J. Results of PERMANOVA analysis test for the effects of habitat, water depths, sediment depth and their interaction on nematodes community attributes at the Hikurangi Margin and Bay of Plenty study region. Significant factors at the 5% level are shown in bold. [Reg. = region, df = degrees of freedom, SS = sum of squares, MS = mean square, Pseudo-F = Pseudo-F statistic, P = Probability, Uniq. perms = number of unique permutations, ECV = square root of estimates of components of variation, Ha = habitat, Wd = water depth, Sd = sediment depth].

| Reg. | Source | df | SS | MS | Pseudo-F | P | Uniq. perms | ECV | ECV (%) |
|---|---|---|---|---|---|---|---|---|---|
| | *Diversity* | | | | | | | | |
| HIK | **Ha** | 2 | 99.3 | 49.7 | 10.437 | **0.0015** | 9950 | 1.2 | 12.8 |
| | **Wd** | 3 | 51.1 | 17.0 | 3.576 | **0.0374** | 9963 | 0.7 | 7.5 |
| | **Sd** | 1 | 52.5 | 52.5 | 24.402 | **0.0002** | 9832 | 1.1 | 11.8 |
| | **Ha x Wd** | 5 | 88.9 | 17.8 | 3.746 | **0.0180** | 9958 | 1.2 | 12.8 |
| | **Ha x Sd** | 2 | 16.3 | 8.1 | 4.121 | **0.0307** | 9948 | 0.6 | 6.4 |
| | **Wd x Sd** | 3 | 59.6 | 19.9 | 10.056 | **0.0006** | 9963 | 1.2 | 12.8 |
| | **Ha x Wd x Sd** | 5 | 29.7 | 5.9 | 3.071 | **0.0365** | 9948 | 0.9 | 9.6 |
| | Residuals | 57 | 342.5 | 6.0 | | | | 2.5 | 26.2 |
| | Total | 116 | 834.1 | | | | | | 100 |
| BoP | Ha | 1 | 13.4 | 13.4 | 2.001 | 0.1788 | 9840 | 0.3 | 6.5 |
| | Wd | 3 | 52.5 | 17.5 | 2.618 | 0.0844 | 9953 | 0.6 | 12.9 |
| | **Sd** | 1 | 43.2 | 43.2 | 9.219 | **0.0078** | 9833 | 0.8 | 17.2 |
| | Ha x Wd | 3 | 19.1 | 6.4 | 0.952 | 0.4368 | 9954 | -0.1 | -2.2 |
| | Ha x Sd | 1 | 0.4 | 0.4 | 0.076 | 0.7820 | 9843 | -0.4 | -8.6 |
| | Wd x Sd | 3 | 36.6 | 12.2 | 2.613 | 0.0962 | 9942 | 0.7 | 15.1 |
| | Ha x Wd x Sd | 3 | 16.1 | 5.4 | 1.151 | 0.3642 | 9951 | 0.3 | 6.5 |
| | Residuals | 94 | 564.6 | 6.0 | | | | 2.5 | 52.7 |
| | Total | 141 | 919.1 | | | | | | 100 |
| | *Community structure* | | | | | | | | |
| HIK | **Ha** | 2 | 8651.3 | 4325.6 | 3.627 | **0.0001** | 9916 | 11.4 | 10.8 |
| | **Wd** | 3 | 5304.5 | 1768.2 | 1.466 | **0.0471** | 9877 | 5.2 | 4.9 |
| | **Sd** | 1 | 25305 | 25305 | 26.881 | **0.0001** | 9949 | 20.5 | 19.4 |
| | **Ha x Wd** | 5 | 11399 | 2279.9 | 1.843 | **0.0015** | 9871 | 10.7 | 10.2 |
| | **Ha x Sd** | 2 | 2754.6 | 1377.3 | 1.785 | **0.0176** | 9911 | 6.0 | 5.7 |
| | **Wd x Sd** | 3 | 5050 | 1683.3 | 2.072 | **0.0017** | 9901 | 8.5 | 8.1 |
| | **Ha x Wd x Sd** | 5 | 5484.6 | 1096.9 | 1.454 | **0.0338** | 9839 | 8.9 | 8.4 |
| | Residuals | 55 | 64245 | 1168.1 | | | | 34.2 | 32.4 |
| | Total | 116 | 175150 | | | | | | 100 |
| BoP | **Ha** | 1 | 2157.6 | 2157.6 | 1.792 | **0.0243** | 9926 | 4.4 | 4.5 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Wd** | 3 | 12201 | 4067 | 3.297 | **0.0001** | 9885 | 9.7 | 10.0 |
| | **Sd** | 1 | 24056 | 24056 | 23.582 | **0.0001** | 9943 | 18.1 | 18.7 |
| | **Ha x Wd** | 3 | 6745 | 2248.3 | 1.758 | **0.0047** | 9866 | 7.8 | 8.0 |
| | **Ha x Sd** | 1 | 1890.1 | 1890.1 | 2.076 | **0.0252** | 9932 | 5.6 | 5.8 |
| | **Wd x Sd** | 3 | 5728.9 | 1909.6 | 2.094 | **0.0004** | 9886 | 8.0 | 8.3 |
| | Ha x Wd x Sd | 3 | 3649 | 1216.3 | 1.420 | 0.0814 | 9888 | 7.0 | 7.2 |
| | Residuals | 92 | 121310 | 1318.6 | | | | 36.3 | 37.5 |
| | Total | 141 | 218680 | | | | | | 100 |
| | | | | | | | | | |
| | *Trophic structure* | | | | | | | | |
| HIK | **Ha** | 2 | 428.7 | 214.3 | 2.417 | **0.0385** | 9954 | 2.3 | 7.1 |
| | **Wd** | 3 | 587.4 | 195.8 | 2.191 | **0.0293** | 9944 | 2.3 | 7.0 |
| | **Sd** | 1 | 5601.5 | 5601.5 | 66.736 | **0.0001** | 9950 | 9.7 | 30.1 |
| | **Ha x Wd** | 5 | 1315.7 | 263.1 | 2.856 | **0.0008** | 9923 | 4.3 | 13.4 |
| | Ha x Sd | 2 | 140.8 | 70.4 | 1.078 | 0.4088 | 9947 | 0.6 | 1.8 |
| | Wd x Sd | 3 | 261.7 | 87.2 | 1.323 | 0.2631 | 9947 | 1.4 | 4.3 |
| | Ha x Wd x Sd | 5 | 413.1 | 82.6 | 1.253 | 0.2668 | 9931 | 2.0 | 6.1 |
| | Residuals | 55 | 5317.2 | 96.7 | | | | 9.8 | 30.4 |
| | Total | 116 | 17693 | | | | | | 100 |
| | | | | | | | | | |
| BoP | Ha | 1 | 27.3 | 27.3 | 0.319 | 0.7622 | 9970 | -1.0 | -4.5 |
| | **Wd** | 3 | 824.2 | 274.7 | 3.216 | **0.0067** | 9950 | 2.5 | 11.5 |
| | **Sd** | 1 | 3177.5 | 3177.5 | 27.484 | **0.0001** | 9948 | 7.1 | 32.9 |
| | Ha x Wd | 3 | 207.5 | 69.2 | 0.810 | 0.6032 | 9945 | -1.0 | -4.8 |
| | Ha x Sd | 1 | 82.6 | 82.6 | 0.714 | 0.5994 | 9966 | -1.0 | -4.8 |
| | Wd x Sd | 3 | 488.7 | 162.9 | 1.410 | 0.1852 | 9933 | 1.8 | 8.2 |
| | Ha x Wd x Sd | 3 | 417.3 | 139.1 | 1.205 | 0.3109 | 9923 | 1.8 | 8.1 |
| | Residuals | 94 | 12456 | 132.5 | | | | 11.5 | 53.4 |
| | Total | 141 | 21229 | | | | | | 100 |

# Appendix K

Appendix K. Two-dimensional MDS ordination of nematode community structure at the study regions. Hikurangi Margin: A. Habitat; B. Water depth; C. Sediment depth; Bay of Plenty: D. Habitat. E. Water depth; F. Sediment depth.



# Appendix L

Appendix L. DistLM analysis results showing correlation between environmental variables and nematode attributes in the Hikurangi Margin. [P = probablity, $R^2$ = proportion of explained variation attributable to each variable, $R^2$ (cum) = cumulative proportion of variation, rs.df = residual degrees of freedom, Slope STD = Standard deviation of slope based on 3, 5, 7, 15 grid cell focal mean, STD = Standard deviation of depth, Vrm = terrain rugosity, Range = depth range, (+/-) = positive/negative relationship, non-significant value is shown in italic].

| Variable | P | $R^2$ | Variable | P | $R^2$ | $R^2$ cum | rs. df |
|---|---|---|---|---|---|---|---|
| **MARGINAL TESTS** | | | **SEQUENTIAL TESTS** | | | | |
| **Diversity 0-1 cm** | | | **Diversity 0-1 cm** | | | | |
| (-) Kurtosis | 0.0032 | 0.14 | (-) Kurtosis | 0.0035 | 0.14 | 0.14 | 57 |
| (-) Phaeopigment | 0.0044 | 0.13 | (+) Profile curvature | 0.0063 | 0.11 | 0.25 | 56 |
| (+) Profile curvature | 0.0090 | 0.11 | | | | | |
| (+) Macrofauna deposit feeder | 0.0106 | 0.11 | | | | | |
| (+) Fishing intensity | 0.0142 | 0.10 | | | | | |
| (+) Curvature | 0.0231 | 0.09 | | | | | |
| (-) %OM | 0.0244 | 0.09 | | | | | |
| (-) %OC | 0.0299 | 0.08 | | | | | |
| (-) Depth | 0.0318 | 0.08 | | | | | |
| (+) Macrofauna total abundance | 0.0403 | 0.07 | | | | | |
| (+) Mean particle size | 0.0430 | 0.07 | | | | | |
| **Diversity 1-5 cm** | | | **Diversity 1-5 cm** | | | | |
| (-) Particle size diversity | 0.0087 | 0.11 | (-) Particle size diversity | 0.0084 | 0.11 | 0.11 | 56 |
| (-) Vrm05 | 0.0218 | 0.09 | (-) Phaeopigment | 0.0067 | 0.11 | 0.22 | 55 |
| (-) Skewness | 0.0341 | 0.08 | (-) %OC | 0.0121 | 0.08 | 0.37 | 52 |
| (-) Slope STD15 | 0.0406 | 0.07 | (-) STD05 | 0.0304 | 0.04 | 0.64 | 41 |
| (+) Burrow (bioturbation) | 0.0456 | 0.07 | | | | | |
| **Community structure 0-1 cm** | | | **Community structure 0-1 cm** | | | | |
| Phaeopigment | 0.0001 | 0.07 | Phaeopigment | 0.0001 | 0.07 | 0.07 | 55 |
| Profile curvature | 0.0001 | 0.05 | Mean particle size | 0.0025 | 0.03 | 0.10 | 54 |
| %OC | 0.0001 | 0.05 | Faecal coil (bioturbation) | 0.0035 | 0.03 | 0.13 | 53 |
| Kurtosis | 0.0001 | 0.05 | %OC | 0.0315 | 0.02 | 0.15 | 52 |
| Mean particle size | 0.0002 | 0.05 | Surface chlorophyll concentration | 0.0423 | 0.02 | 0.17 | 51 |
| Fishing intensity | 0.0011 | 0.04 | Slope STD15 | 0.0482 | 0.02 | 0.19 | 50 |
| Particle size diversity | 0.0002 | 0.04 | Particle size diversity | 0.0025 | 0.03 | 0.22 | 49 |
| Curvature | 0.0003 | 0.04 | Fishing intensity | 0.0471 | 0.02 | 0.24 | 48 |
| Depth | 0.0018 | 0.04 | | | | | |
| STD15 | 0.0088 | 0.03 | | | | | |
| Vrm05 | 0.0151 | 0.03 | | | | | |

| Variable | P | $R^2$ | Variable | P | $R^2$ | $R^2$ cum | rs. df |
|---|---|---|---|---|---|---|---|
| **MARGINAL TESTS** | | | **SEQUENTIAL TESTS** | | | | |
| Slope STD15 | 0.0163 | 0.03 | | | | | |
| Total surface bioturbation | 0.0176 | 0.03 | | | | | |
| %OM | 0.0182 | 0.03 | | | | | |
| Surface chlorophyll concentration | 0.0297 | 0.03 | | | | | |
| Faecal coil (bioturbation) | 0.0476 | 0.03 | | | | | |
| **Community structure 1-5 cm** | | | **Community structure 1-5 cm** | | | | |
| %OC | 0.0001 | 0.06 | %OC | 0.0001 | 0.06 | 0.06 | 54 |
| Kurtosis | 0.0001 | 0.06 | Depth | 0.0010 | 0.04 | 0.10 | 53 |
| Phaeopigment | 0.0001 | 0.06 | Particle size diversity | 0.0010 | 0.03 | 0.13 | 52 |
| Particle size diversity | 0.0001 | 0.06 | Surface chlorophyll concentration | 0.0028 | 0.03 | 0.16 | 51 |
| Depth | 0.0001 | 0.06 | Profile curvature | 0.0132 | 0.03 | 0.19 | 50 |
| Mean particle size | 0.0002 | 0.05 | Kurtosis | 0.0099 | 0.03 | 0.22 | 49 |
| Surface chlorophyll concentration | 0.0002 | 0.04 | %$CaCO_3$ | 0.0285 | 0.02 | 0.24 | 48 |
| Fishing intensity | 0.0009 | 0.04 | Macrofauna grazer | 0.0175 | 0.02 | 0.26 | 47 |
| Slope STD15 | 0.0014 | 0.04 | Skewness | 0.0330 | 0.02 | 0.28 | 46 |
| Mound (bioturbation) | 0.0034 | 0.04 | Curvature | 0.0329 | 0.02 | 0.30 | 45 |
| Total subsurface bioturbation | 0.0058 | 0.03 | STD15 | 0.0321 | 0.02 | 0.32 | 44 |
| Pit (bioturbation) | 0.0051 | 0.03 | Slope STD03 | 0.0394 | 0.02 | 0.34 | 43 |
| Burrow (bioturbation) | 0.0078 | 0.03 | Pit (bioturbation) | 0.0466 | 0.02 | 0.36 | 42 |
| Profile curvature | 0.0069 | 0.03 | | | | | |
| %OM | 0.0090 | 0.03 | | | | | |
| Skewness | 0.0106 | 0.03 | | | | | |
| Macrofauna grazer | 0.0228 | 0.03 | | | | | |
| Slope STD03 | 0.0290 | 0.03 | | | | | |
| Vrm05 | 0.0329 | 0.03 | | | | | |
| STD15 | 0.0341 | 0.03 | | | | | |
| Ring of burrows (bioturbation) | 0.0426 | 0.03 | | | | | |
| %$CaCO_3$ | 0.0446 | 0.03 | | | | | |
| **Trophic structure 0-1 cm** | | | **Trophic structure 0-1 cm** | | | | |
| Vrm05 | 0.0083 | 0.07 | Vrm05 | 0.0090 | 0.07 | 0.07 | 57 |
| Slope STD03 | 0.0103 | 0.07 | Curvature | 0.0244 | 0.06 | 0.12 | 56 |
| Curvature | 0.0195 | 0.06 | Total surface bioturbation | *0.0611* | 0.04 | 0.16 | 55 |
| Track (bioturbation) | 0.0295 | 0.05 | Track (bioturbation) | *0.1569* | 0.03 | 0.19 | 54 |
| Total surface bioturbation | 0.0312 | 0.05 | %OC | *0.0738* | 0.04 | 0.22 | 53 |
| | | | Particle size diversity | *0.1422* | 0.03 | 0.25 | 52 |
| | | | Slope STD15 | *0.0504* | 0.04 | 0.29 | 51 |

| Variable | P | $R^2$ | Variable | P | $R^2$ | $R^2$ cum | rs. df |
|---|---|---|---|---|---|---|---|
| **MARGINAL TESTS** | | | **SEQUENTIAL TESTS** | | | | |
| | | | Range07 | 0.0272 | 0.04 | 0.33 | 50 |
| **Trophic structure 1-5 cm** | | | **Trophic structure 1-5 cm** | | | | |
| Depth | 0.0267 | 0.05 | Depth | 0.0252 | 0.05 | 0.05 | 56 |
| %$CaCO_3$ | 0.0301 | 0.05 | | | | | |
| Vrm05 | 0.0415 | 0.05 | | | | | |

## Appendix M

Appendix M. DistLM analysis results showing correlation between environmental variables and nematode community attributes in the Bay of Plenty. [P = probablity, R2 = proportion of explained variation attributable to each variable, R2 (cum) = cumulative proportion of variation, rs.df = residual degrees of freedom, Slope STD = Standard deviation of slope based on 3, 5, 7, 15 grid cell focal mean, STD = Standard deviation of depth, Vrm = terrain rugosity, Range = depth range, (+/-) = positive/negative relationship, non-significant value are shown in italic].

| Variable | P | R$^2$ | Variable | P | R$^2$ | R$^2$ cum | rs. df |
|---|---|---|---|---|---|---|---|
| **MARGINAL TESTS** | | | **SEQUENTIAL TESTS** | | | | |
| **Diversity 0-1 cm** | | | **Diversity 0-1 cm** | | | | |
| (+) Profile curvature | *0.0569* | 0.05 | (+) Profile curvature | *0.0563* | 0.05 | 0.05 | 69 |
| | | | (-) Vrm05 | *0.0653* | 0.05 | 0.10 | 68 |
| | | | (-) STD07 | 0.0240 | 0.06 | 0.16 | 67 |
| | | | (+) Faecal coil (bioturbation) | 0.0449 | 0.05 | 0.31 | 63 |
| | | | (-) %OM | 0.0327 | 0.05 | 0.36 | 62 |
| **Diversity 1-5 cm** | | | **Diversity 1-5 cm** | | | | |
| (-) Surface chlorophyll concentration | 0.0097 | 0.09 | (-) Surface chlorophyll concentration | 0.009 | 0.09 | 0.09 | 69 |
| (-) Macrofauna total abundance | 0.0317 | 0.06 | | | | | |
| **Community structure 0-1 cm** | | | **Community structure 0-1 cm** | | | | |
| Depth | 0.0001 | 0.04 | Depth | 0.0001 | 0.04 | 0.04 | 67 |
| %CaCO$_3$ | 0.0001 | 0.04 | %CaCO$_3$ | 0.0001 | 0.03 | 0.07 | 66 |
| Slope STD05 | 0.0004 | 0.03 | Slope STD07 | 0.0012 | 0.03 | 0.10 | 65 |
| Vrm05 | 0.0008 | 0.03 | Plan curvature | 0.0013 | 0.03 | 0.13 | 64 |
| Slope STD07 | 0.0002 | 0.03 | Macrofauna total abundance | 0.0027 | 0.02 | 0.15 | 63 |
| Surface chlorophyll concentration | 0.0010 | 0.03 | Surface chlorophyll concentration | 0.0015 | 0.03 | 0.18 | 62 |
| Track (bioturbation) | 0.0008 | 0.03 | Profile curvature | 0.0014 | 0.02 | 0.20 | 61 |
| %OC | 0.0012 | 0.03 | STD07 | 0.0066 | 0.02 | 0.22 | 60 |
| %OM | 0.0015 | 0.03 | Macrofauna deposit feeder | 0.0154 | 0.02 | 0.24 | 59 |
| Faecal coil (bioturbation) | 0.0020 | 0.03 | Vrm05 | 0.0115 | 0.02 | 0.26 | 58 |
| Profile curvature | 0.0022 | 0.03 | Slope | 0.0191 | 0.02 | 0.28 | 57 |
| STD07 | 0.0033 | 0.03 | %OM | 0.0127 | 0.02 | 0.30 | 56 |
| Range05 | 0.0031 | 0.03 | | | | | |
| STD05 | 0.0023 | 0.03 | | | | | |
| Plan curvature | 0.0049 | 0.03 | | | | | |
| Range07 | 0.0038 | 0.03 | | | | | |
| Slope | 0.0059 | 0.03 | | | | | |
| %Silt/clay | 0.0119 | 0.02 | | | | | |
| Macrofauna total abundance | 0.0162 | 0.02 | | | | | |

| Variable | P | $R^2$ | Variable | P | $R^2$ | $R^2$ cum | rs. df |
|---|---|---|---|---|---|---|---|
| **MARGINAL TESTS** | | | **SEQUENTIAL TESTS** | | | | |
| Sorting | 0.0176 | 0.02 | | | | | |
| Kurtosis | 0.0172 | 0.02 | | | | | |
| Macrofauna deposit feeder | 0.0236 | 0.02 | | | | | |
| Skewness | 0.0232 | 0.02 | | | | | |
| Hemichordate spiral (bioturbation) | 0.0397 | 0.02 | | | | | |
| **Community structure 1-5 cm** | | | **Community structure 1-5 cm** | | | | |
| %OM | 0.0001 | 0.06 | %OM | 0.0001 | 0.06 | 0.06 | 67 |
| %Silt/clay | 0.0001 | 0.06 | Depth | 0.0001 | 0.05 | 0.11 | 66 |
| Kurtosis | 0.0001 | 0.06 | Kurtosis | 0.0010 | 0.03 | 0.14 | 65 |
| Sorting | 0.0001 | 0.05 | Surface chlorophyll concentration | 0.0007 | 0.03 | 0.17 | 64 |
| Depth | 0.0001 | 0.05 | %$CaCO_3$ | 0.0009 | 0.03 | 0.20 | 63 |
| Skewness | 0.0001 | 0.05 | Mound (bioturbation) | 0.0127 | 0.02 | 0.22 | 62 |
| Phaeopigment | 0.0001 | 0.04 | Macrofauna deposit feeder | 0.0160 | 0.02 | 0.24 | 61 |
| Mound (bioturbation) | 0.0001 | 0.04 | Macrofauna total abundance | 0.0062 | 0.02 | 0.26 | 60 |
| %$CaCO_3$ | 0.0003 | 0.04 | Fishing intensity | 0.0278 | 0.02 | 0.28 | 59 |
| Total subsurface bioturbation | 0.0003 | 0.04 | Burrow (bioturbation) | 0.0149 | 0.02 | 0.30 | 58 |
| Burrow (bioturbation) | 0.0015 | 0.03 | %Silt/clay | 0.0412 | 0.02 | 0.32 | 56 |
| Macrofauna total abundance | 0.0070 | 0.03 | Macrofauna grazer | 0.0424 | 0.02 | 0.34 | 55 |
| Macrofauna deposit feeder | 0.0079 | 0.03 | Profile curvature | 0.0080 | 0.02 | 0.36 | 50 |
| Surface chlorophyll concentration | 0.0103 | 0.03 | Total subsurface bioturbation | 0.0398 | 0.02 | 0.38 | 48 |
| Profile curvature | 0.0127 | 0.03 | STD05 | 0.0072 | 0.02 | 0.40 | 45 |
| Fishing intensity | 0.0337 | 0.02 | | | | | |
| Plan curvature | 0.0479 | 0.02 | | | | | |
| **Trophic structure 0-1 cm** | | | **Trophic structure 0-1 cm** | | | | |
| %OM | 0.0008 | 0.09 | %OM | 0.0002 | 0.09 | 0.09 | 69 |
| Skewness | 0.0004 | 0.09 | Depth | *0.0671* | 0.03 | 0.13 | 68 |
| %Silt/clay | 0.0024 | 0.08 | Macrofauna total abundance | *0.0527* | 0.03 | 0.16 | 67 |
| Sorting | 0.0039 | 0.07 | Skewness | 0.0086 | 0.05 | 0.21 | 66 |
| %$CaCO_3$ | 0.0214 | 0.05 | Plan curvature | 0.0493 | 0.03 | 0.24 | 65 |
| Phaeopigment | 0.0410 | 0.04 | | | | | |
| **Trophic structure 1-5 cm** | | | **Trophic structure 1-5 cm** | | | | |
| Skewness | 0.0011 | 0.09 | Skewness | 0.0005 | 0.09 | 0.09 | 69 |
| Sorting | 0.0012 | 0.08 | Vrm05 | 0.0077 | 0.06 | 0.14 | 68 |
| Kurtosis | 0.0026 | 0.08 | %OC | 0.0242 | 0.04 | 0.19 | 67 |
| %OC | 0.0017 | 0.07 | Burrow (bioturbation) | 0.0294 | 0.04 | 0.22 | 66 |
| %Silt/clay | 0.0025 | 0.07 | Depth | 0.0147 | 0.05 | 0.27 | 65 |
| Vrm05 | 0.0116 | 0.06 | Slope STD07 | 0.0309 | 0.03 | 0.30 | 64 |

| Variable | P | $R^2$ | Variable | P | $R^2$ | $R^2$ cum | rs. df |
|---|---|---|---|---|---|---|---|
| **MARGINAL TESTS** | | | **SEQUENTIAL TESTS** | | | | |
| Phaeopigment | 0.0099 | 0.06 | Sorting | *0.1363* | 0.02 | 0.32 | 63 |
| %OM | 0.0116 | 0.06 | %Silt/clay | *0.1369* | 0.02 | 0.34 | 62 |
| Range05 | 0.0137 | 0.05 | Surface chlorophyll concentration | *0.2820* | 0.01 | 0.36 | 61 |
| Burrow (bioturbation) | 0.0147 | 0.05 | Phaeopigment | *0.1141* | 0.02 | 0.38 | 60 |
| Profile curvature | 0.0184 | 0.05 | Fishing intensity | 0.0334 | 0.03 | 0.41 | 59 |
| Total subsurface bioturbation | 0.0177 | 0.05 | | | | | |
| Range07 | 0.0264 | 0.05 | | | | | |
| STD05 | 0.0223 | 0.05 | | | | | |
| Depth | 0.0238 | 0.05 | | | | | |
| STD07 | 0.0311 | 0.04 | | | | | |
| Slope STD05 | 0.0423 | 0.04 | | | | | |