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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

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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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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..........206

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). 245

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List of abbreviations

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

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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.

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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

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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).

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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.

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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

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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.

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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

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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.

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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.

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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).

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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.

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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

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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).

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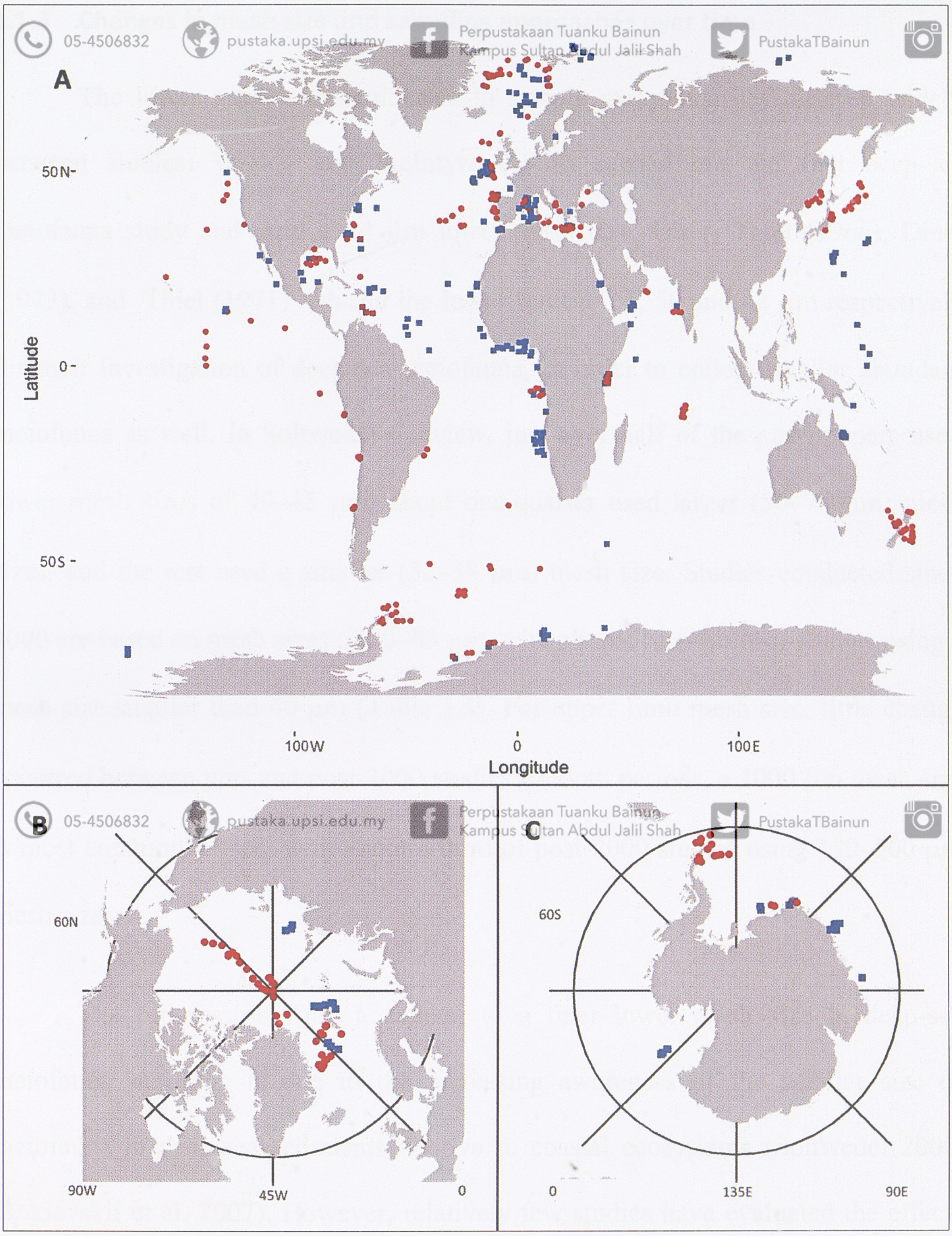

Figure 1.1. Map showing the distribution of ecological studies of deep-sea meiofauna before (blue squares) and after (red circles) the review by Soltwedel (2000) in (A) the world oceans, (B) Arctic region, and (C) Antarctic region. The circle in (B) and (C) shows the position of latitude 60°.

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