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Environmental and spatial constraints on Antarctic marine nematode distribution

Omgevings- en ruimtelijke beperkingen op de verspreiding van Antarctische mariene nematoden

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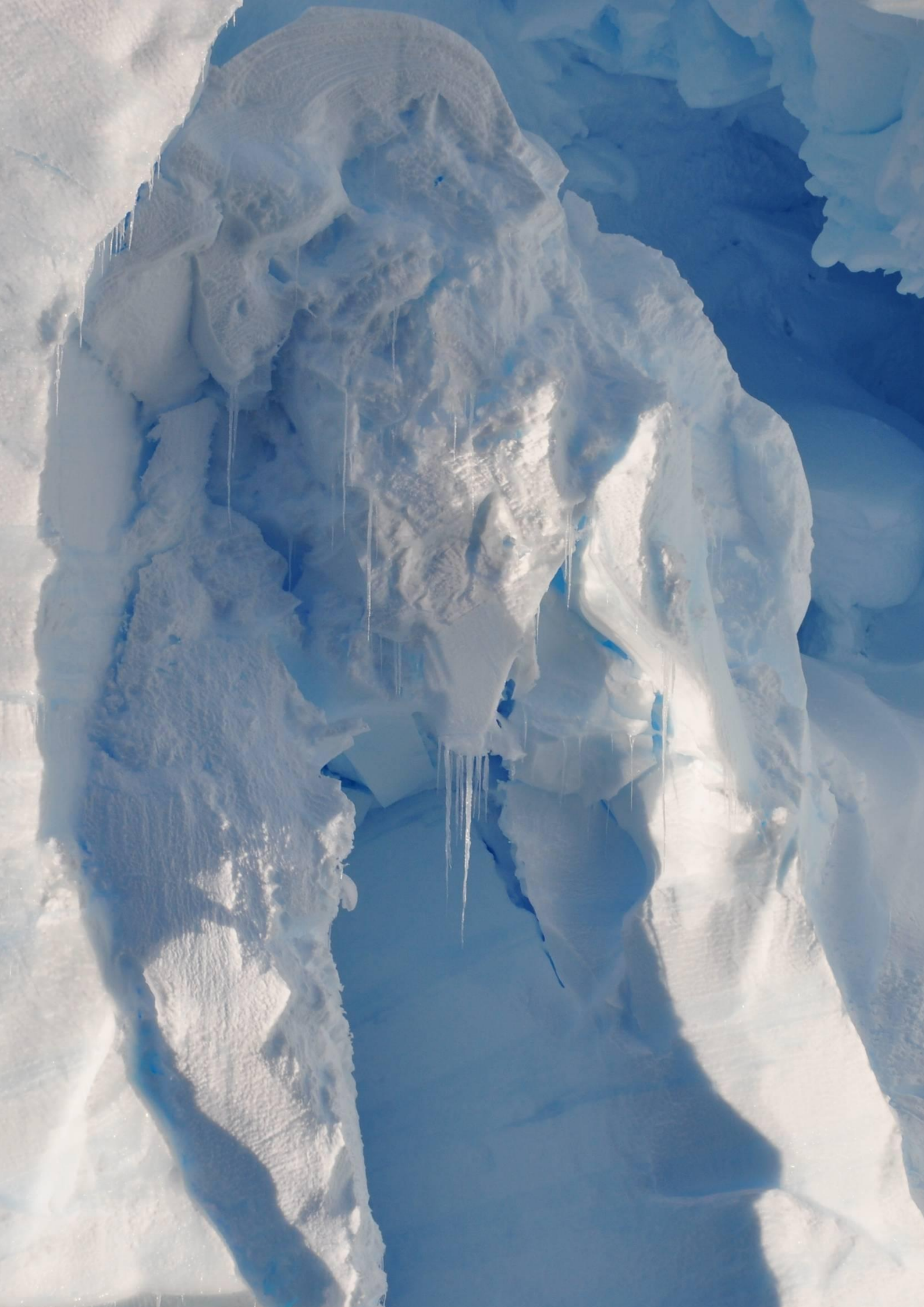

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SAMENVATTING

De verspreiding van soorten op deze wereldbol is verre van willekeurig. De zoektocht naar een verklaring voor de patronen in soortensamenstelling en diversiteit in verschillende habitats vormt één van de belangrijkste uitdagingen binnen de domeinen van ecologie en biogeografie. Onderzoek doorheen de jaren heeft uitgewezen dat de lokale soortensamenstelling binnen ecologische gemeenschappen kan verklaard worden door processen die plaatsvinden op verschillende ruimtelijke en temporele schalen. Zo kunnen soorten bijvoorbeeld gelinkt worden aan veranderingen in omgevingsfactoren op een relatief kleine schaal (voedsel, sedimentsamenstelling, zuurstof) of aan grootschalige gradiënten in klimaat. Het ontrafelen van de huidige verspreidingspatronen van organismen vereist dus de integratie van een (macro-) ecologische en biogeografische aanpak (Logue et al., 2011).

Het voorkomen van soorten op een bepaalde plaats hangt af van een complex samenspel van verschillende factoren. Dispersie en de uitwisseling van individuen tussen locaties spelen daarbij een belangrijke rol, en zowel habitat- als soortskenmerken kunnen dit proces beïnvloeden. In het mariene milieu wordt algemeen aangenomen dat de verspreiding van soorten minder beperkt is dan in meer geografisch afgebakende aquatische systemen zoals vijvers en meren. Het mariene ecosysteem bezit van nature een zekere continuïteit doordat de verschillende oceanen met elkaar in verbinding staan. In combinatie met de aanwezigheid van grootschalige zeestromingen vergemakkelijkt dit het transport van organismen over lange afstanden. Dit geldt zowel voor actieve zwemmers als voor soorten die passief worden meegevoerd met de stromingen als pelagische larven of andere dispersieve stadia. In principe zouden soorten op deze manier wereldwijde verspreidingspatronen kunnen ontwikkelen. Vaak wordt dit echter niet in praktijk omgezet doordat lokale omgevingsfactoren binnen het leefgebied ook een selectieve rol kunnen spelen in de samenstelling van de soortengemeenschap (niche concept[1]). De situatie is ook verschillend voor organismen die in de zeebodem leven (het benthos) en geen pelagische dispersieve stadia bezitten. Hun aanwezigheid in de waterkolom is eerder sporadisch waardoor dispersie in theorie meer gelimiteerd is, en afstand en grootschalige processen een grotere rol spelen in hun verspreiding. Toch strookt dit beeld niet altijd met de realiteit. Verschillende benthische organismen komen wereldwijd voor, ondanks hun verwachte dispersie limitatie. Het metagemeenschapsconcept (Leibold et al., 2004) is één van de vele theoriën binnen de ecologie die tracht om het relatieve belang van zulke niche- en dispersie-gerelateerde

[1] Niche concept = soorten zullen voorkomen op plaatsen waar zij de condities vinden die nodig zijn voor het uitbouwen en onderhouden van een stabiele en leefbare populatie

processen te ontrafelen. Doorheen dit doctoraatsproefschrift zal dit concept dienst doen als theoretische achtergrond om na te gaan in hoeverre lokale (bv. interacties tussen soorten, en tussen soorten en hun omgeving) en regionale (bv. geografische scheiding, dispersie limitatie) processen verantwoordelijk zijn voor de huidige gemeenschapsstructuur van mariene nematoden in de zeebodem van het continentaal plat[2] (200 – 500 m waterdiepte) in de Zuidelijke Oceaan. De regio en de biologische gemeenschappen die er voorkomen delen een opmerkelijke geschiedenis van isolement en afwisselend glaciale en interglaciale condities. Deze combinatie heeft geleid tot doorgaans subtiele evenwichten tussen organismen en hun omgeving, welke nu onder druk komen te staan door de huidige klimaatverandering. Het fylum Nematoda (rondwormen) is voornamelijk gekend onder de parasitaire vormen in zowel planten als dieren, maar dit onderzoek spitst zich toe op de vrijlevende vertegenwoordigers binnen deze groep die zich ophouden tussen de sedimentpartikels in de zeebodem. Ze zijn klein van gestalte (veelal < 1mm), vormen vaak de meest dominante groep binnen de meiofauna[3] (aantallen die oplopen tot meerdere 1000^{en} individuen per 10 cm² zijn niet ongewoon), en komen voor in een hoge diversiteit op zowel genus- als soortsniveau (Heip et al., 1985). Ondanks hun endobenthische[4] levenswijze en passieve dispersie via resuspensie en transport in de waterkolom, zijn nematoden veelal wijdverspreid (zeker op genus- en soms ook op soortsniveau). Deze meiofauna paradox (Giere, 2009) vormt het onderwerp van menig debat tussen meiofauna ecologen onderling, en werd recent meerdere malen op de proef gesteld door nieuwe moleculaire inzichten in de verspreiding van soorten. Doorheen de hoofdstukken van dit proefschrift worden meerdere aspecten van nematodengemeenschappen (abundantie, diversiteit, gemeenschapssamenstelling en verspreiding) belicht met behulp van verschillende technieken, en op een verschillende ruimtelijke schaal en taxonomische resolutie.

In de eerste twee hoofdstukken werd er een correlatieve aanpak gehanteerd om variatie in gemeenschappen te verklaren op een relatief geringe ruimtelijke schaal van enkele tientallen tot honderden kilometers, aangevuld met een temporeel aspect van enkele jaren in hoofdstuk

[2] Continentaal plat = het gebied van de zeebodem dat zich uitstrekt tussen de kustlijn en de continentale helling. Algemeen wordt aangenomen dat de maximale diepte van het continentaal plat op 100 – 200 m ligt. Rond Antarctica is deze echter dieper en stijler en kan ze oplopen tot wel 1000 m op sommige plaatsen.

[3] Meiofauna = groep organismen met een grootte tussen 44 en 1000 µm (Giere, 2009). In dit doctoraat wordt er echter een ondergrens van 32 µm gehanteerd om zelfs de kleinste en fijnste taxa te behouden.

[4] Endobenthisch = ingegraven in het sediment

2. Alle staalnamelocaties waren gesitueerd in de nabijheid van het Antarctisch Schiereiland maar verschilden in lokale omgevingscondities en dynamiek. In een eerste studie (hoofdstuk 2) werd er gekeken naar het effect van het afsmelten van de Larsen ijsplaat (Rack & Rott, 2004) aan de oostelijke zijde van het schiereiland en de bijgaande drastische veranderingen in lichtregime en primaire productie aan het zeeoppervlak op de benthische gemeenschappen. De respons van nematoden over een tijdspanne van vier jaar wees voornamelijk op het belang van lokale omgevingsfactoren (voedselbeschikbaarheid) en kolonisatiepatronen in het verklaren van distributie en plaatselijke dominantie van enkele opportunistische genera. Een vergelijkbare associatie tussen nematodengemeenschappen en omgevingscondities werd ook waargenomen in hoofdstuk 3, op een grotere schaal waarbij gebieden aan weerszijden van het schiereiland met elkaar werden vergeleken. Variatie in gemeenschappen werd in dit geval gekoppeld aan de contrasterende oceanografische invloeden, en de daarmee gepaard gaande verschillen in efficiëntie van bentho-pelagische koppeling[5] en de aanwezigheid van zee-ijs.

In tegenstelling tot deze twee studies die meer kaderen binnen de traditionele ecologische aanpak van het koppelen van gemeenschapssamenstelling aan omgevingsgradiënten (zogenaamde 'species sorting' binnen het metagemeenschapsconcept; Leibold et al., 2004), werd er in de volgende twee hoofdstukken meer de nadruk gelegd op processen en dynamiek van gemeenschappen op een grotere ruimtelijke schaal. De staalnamepunten lagen in dit geval zowel binnen als buiten eenzelfde biogeografische zone geassocieerd met zeestromingen. In hoofdstuk 4 werd heel de nematodengemeenschap onderworpen aan 'variation partitioning[6] analyse (metagemeenschapsniveau) terwijl hoofdstuk 5 zich toespitste op fylogeografische en populatiegenetische aspecten van twee genera en hun soorten (populatieniveau). De uitkomst van beide technieken leverde doorgaans dezelfde conclusies op waarin de rol van historische scheiding en dispersie limitatie op de verspreiding van nematoden op grotere schaal werd benadrukt. Immers, gemeenschappen op de verschillende locaties in hoofdstuk 4 verschilden meer in genus- en soortensamenstelling naarmate de afstand tussen hen groter werd. Op een vergelijkbare manier werd er in hoofdstuk 5 aangetoond dat populaties van soorten sterke genetische verschillen vertonen naargelang hun locatie. Hoewel beide patronen ook deels aan

[5] Bentho-pelagische koppeling = fenomeen waarbij processen die plaatsvinden aan het zee-oppervlak (bijvoorbeeld primaire productie door fytoplankton) worden vertaald naar de zeebodem

[6] Variation partitioning = statistische methode waarbij variatie in een afhankelijke dataset (bijvoorbeeld soortenmatrix met relatieve abundanties) wordt onderverdeeld in fracties die kunnen toegeschreven worden aan unieke en gezamenlijke invloeden van verschillende sets verklarende variabelen (bijvoorbeeld omgevingsfactoren of ruimtelijke parameters) (Borcard et al., 1992)

veranderingen in omgevingsvariabelen kunnen gelinkt worden, blijkt dat ruimtelijke patronen domineren. Een mogelijke conclusie hierbij is dat dispersie limitatie een belangrijke rol speelt en grootschalige zeestromingen in de regio niet efficiënt genoeg zijn om een nauwe connectie te onderhouden tussen nematodengemeenschappen op locaties die honderden km van elkaar verwijderd zijn.

Doorheen dit proefschrift werd aangetoond dat 1) nematodengemeenschappen in de Zuidelijke Oceaan variëren naargelang hun geografische locatie en positie in het sediment (aan het oppervlak of dieper), 2) genera wijdverspreid zijn maar verschillen in hun relatieve abundantie tussen locaties en dieptelagen in het sediment, 3) soorten zowel beperkte als grote verspreiding kunnen vertonen, 4) lokale invloeden op het voorkomen van genera en soorten voornamelijk een rol spelen op kleinere schaal en voor gemeenschappen aan het sedimentoppervlak, 5) regionale processen zoals dispersie limitatie aan belang winnen op grotere schaal, en ten slotte 6) dat cryptische[7] soorten aanwezig zijn voor ten minste één genus en het dus gevaarlijk is om enkel op morfologische soortsafbakening te vertrouwen bij het bestuderen van macro-ecologische patronen in deze groep kleine organismen. Deze inzichten brengen ons weer een stap dichter tot het begrijpen hoe het komt dat soorten voorkomen op een bepaalde plaats. Dit is van belang willen we kunnen voorspellen hoe gemeenschappen zullen veranderen in de toekomst, en dan zeker met het oog op nakende veranderingen onder de invloed van klimaatverandering.

[7] Cryptische soorten = organismen die wel genetisch verschillen (en dus soorten zijn), maar niet onderscheiden kunnen worden op basis van morfologische kenmerken

SUMMARY

The distribution of organisms across the globe is not random, an observation that has stimulated the search for rules and explanations for the processes behind it. In general, there is a consensus that local species composition, richness and abundance are the result of processes that operate at different spatial and temporal scales. For example, species diversity and composition might reflect both local changes in environmental characteristics (food, sediment grain size, oxygen) as well as large-scale gradients in climate. Resolving distribution patterns therefore requires the integration of approaches at the crossing of (macro-) ecology and biogeography (Logue et al., 2011).

Whether species occur at a certain place and time depends on a complex interplay of various factors. Dispersal and exchange of individuals between patches plays a crucial role in this process. Theoretically, the marine environment with its open continuous character and its presence of large-scale ocean currents forms a more connected system than geographically confined freshwater systems such as ponds and lakes. Long-distance travel of species in the ocean is thus more likely, both for active swimmers as well as for those species with passive pelagic dispersive stages (e.g., larvae). While this implies a possibility for developing cosmopolitan distributions, limits to such ubiquity[8] are imposed by niche dynamics, where characteristics of local habitat patches preclude the presence of some species while favouring others. The situation becomes somewhat different for organisms living in seafloor sediments (the benthos) that lack pelagic dispersive stages and whose presence in the water column is therefore a sporadic event. In this instance, distance and dispersal limitation probably play a more active role in structuring communities at large spatial scales. Metacommunity theory (Leibold et al., 2004) forms one example of a theoretical framework that tries to disentangle the role of such niche effects and dispersal effects on distribution patterns of organisms. This concept served as a background for this thesis, which aims at resolving the relative contribution of local (i.e. species-species interactions, species-environment relationships) and regional (i.e. geographic separation, dispersal limitation) processes on contemporary community structure of marine nematodes in continental shelf[9] locations (200 – 500 m water depth) of the Southern Ocean. The area and its biota share a remarkable history of isolation and glaciation events, and evolved subtle equilibria which are currently put to the test by

[8] Ubiquity = presence of organisms everywhere, or at least in many places simultaneously (Baas Becking, 1934)

[9] Continental shelf = the area of the seabed extending from the coastline to the continental slope. The lower depth limit of the shelf is typically placed at roughly 100 – 200 m. However, the Antarctic continental shelf is unusually steep and deep, and extends to 1000 m depth at some places

imminent changes related to global warming. Nematoda or roundworms are mainly known as parasites in both plants and animals, but this study will focus on the free-living representatives of this phylum, which occupy the interstitial spaces in seafloor sediments. They are small in size (generally < 1 mm), are often the numerically dominant taxon within the meiofauna[10] (densities of several thousands of individuals per 10 cm^2 are not uncommon), and occur in high genus and species numbers in almost all aquatic habitats (Heip et al., 1985). Despite their endobenthic[11] lifestyle and passive dispersal mode, hence presumed limited dispersal capacities, genera (and also some species) are widely spread. This meiofauna paradox (Giere, 2009) forms the topic of considerable debate among meiofauna ecologists, but has been challenged recently by insights gained through molecular advances. Throughout the chapters of this thesis, different aspects of nematode communities (i.e. abundance, diversity, community composition and distribution) were assessed in different ways, at different spatial scales, and with increasing taxonomic resolution.

The first two research chapters adopted a correlative approach to analyse variation between nematode communities at a modest spatial scale of tens to a few hundreds of km, complemented by a temporal scale of a few years in Chapter 2. Sampling locations were all situated in the premises of the Antarctic Peninsula, but differed in local conditions and dynamics. In the first study, climate-induced ice-shelf collapse in the Larsen area east of the peninsula (Rack & Rott, 2004) resulted in drastic changes in light regime and primary productivity, hence food input for benthic communities. These benthic communities were studied 7 and 11 years after the initial ice-shelf collapse to investigate their response to this change from an ice-covered oligotrophic to a more productive system. Nematodes' response to these changes over the course of four years pointed towards the importance of environmental filtering and colonisation rate in stimulating localised proliferation of one or a few opportunistic genera. Compared to other Antarctic continental shelf locations, the nematode communities in the Larsen area were very different in terms of genus composition, density and vertical distribution in the sediment. Differences in nematode assemblages between locations within the area itself could be related to a different timing of the loss of ice cover and related food input. A similar correlation between nematode communities and

[10] Meiofauna = animals retained between sieve mesh sizes of 44 and 1000 µm (Giere, 2009). For the purpose of this thesis, the lower size limit is set at 32 µm to include even the smallest and finest taxa

[11] Endobenthic = refers to organisms living (almost exclusively) within seafloor sediments, between the sediment particles

environmental conditions was demonstrated in the next study (Chapter 3), but at a bigger spatial scale involving areas under different oceanographic influence at both sides of the peninsula. In this case, variation in communities was mainly attributable to the efficiency of bentho-pelagic coupling[12] processes and sea-ice dynamics (or the lack thereof).

While these two studies were more in line with traditional ecological approaches of linking community composition at a local scale to environmental gradients (cf. species sorting within the metacommunity theory; Leibold et al., 2004), the next two chapters incorporated dynamics at a larger spatial extent. Sampling locations covered areas both within and beyond biogeographic zones and oceanographic current systems, and nematode assemblages were analysed using variation partitioning analysis[13] at the level of the entire community (Chapter 4) or phylogeographic and population genetic techniques at a more detailed level for two selected genera and their species (Chapter 5). Outcomes of both studies were largely congruent and highlighted the importance of historical separation and dispersal limitation for nematode community assembly at large spatial scales. More specifically, nematode genus and species communities in Chapter 4 were largely different between the different locations, and these differences increased with increasing distance between locations. In a similar fashion, populations for several species within the genera *Sabatieria* and *Desmodora* in Chapter 5 showed high levels of genetic differentiation depending on their location. Although both results could partially be linked to changes in environmental conditions, distance and spatial heterogeneity proved to be more important drivers for the observed differences. A possible explanation could be that the current systems operating in the area are not efficient enought to maintain high levels of connectivity between nematode communities separated by several hundreds of km.

The work performed during this thesis has revealed that 1) nematode communities in the Southern Ocean differ according to their geographical location as well as vertical position in the sediment, 2) genera are widely distributed but show different relative abundances between locations and sediment depth layers, 3) species have either restricted or wide distributions, 4) influence of local processes on genus and species occurrence is mainly limited to smaller

[12] Bentho-pelagic coupling = the interplay between processes happening at the sea surface (e.g., primary production by phytoplankton) and their translation towards the seabed

[13] Variation partitioning = statistical technique where the variation in a dependent dataset (e.g., species relative abundance) is partitioned into combined and unique fractions attributable to different sets of explanatory variables (e.g., abiotic variables, spatial predictors) (Borcard et al., 1992)

spatial scale and communities at the seafloor surface, 5) regional processes (historical events, dispersal limitation) gain importance at larger spatial scales, and finally 6) cryptic[14] species are present within one genus which demonstrates the potential bias in macroecological studies when relying on morphological species delineations alone. Together, these aspects provide information on why species are distributed in a certain way, and might help to understand and predict how community patterns of small organisms might change in the near future. Especially in light of current climate change, further assessment of species distribution patterns and structuring processes is vital.

[14] Cryptic species = species that are morphologically indistinguishable, but are genetically distinct

CHAPTER 1: GENERAL INTRODUCTION

This chapter will briefly introduce the theoretical framework, study locations and organisms of interest that were analysed throughout this thesis. I looked at endobenthic marine nematode communities in the Atlantic sector of the Southern Ocean, both from an ecological as well as from a more biogeographical point of view. While they might not seem a very appealing taxon at first sight, there is much to say in favour of nematodes, and being 'small' by no means should be synonymised with being 'boring'. The main link between the chapters presented in this thesis is the search for an explanation behind current nematode community composition and species distribution across different spatial scales. The first part of this introduction focuses on the more general theoretical considerations that served as an inspiration for the topics discussed here, and on the description of some characteristics of the Antarctic marine ecosystem and its biota to set the scene in which patterns and processes were assessed. This is followed by a few important notes on the phylum Nematoda, and finally an outline of recent advances in the field of molecular analyses which provide new tools in the study of species distributions.

BIOGEOGRAPHY AND (META-) COMMUNITY ECOLOGY – ON THE CROSSROAD OF TWO DOMAINS

Ever since the recognition that the occurrence of organisms around the globe is not random and certain patterns can be recognised in their distributions, a large body of scientific work has been dedicated to the description of underlying processes that may have caused these patterns. A common goal of these efforts has been to find an answer to the question "*What drives species' distribution and community organisation across space and time?*" Of central importance in this quest are concepts such as species 'niche', and frameworks that try to explain species richness and coexistence (e.g., MacArthur and Wilson's theory on 'island biogeography'; 'neutral theory'; Hubbell, 2001; Pielou, 1975). The unabated search for answers and patterns explaining species distribution has led to several additions and modifications of such recurring themes and forms the shared interest of the fields of ecology and biogeography. The study of local interactions between functionally distinct species and environments pertains mainly to the field of ecology ('diversity and interactions within discrete boundaries'), while processes operating at larger spatial and temporal scales are typically more associated with biogeography ('origin of species diversity and distribution') (Holt, 1993; Logue et al., 2011). The need for synthesis across scales has repeatedly been mentioned (Ricklefs, 1987) and has led to several initiatives in 'ecology at the mesoscale' – at the intercept between local and regional scales (Holt, 1993).

The suggestion that local communities are ephemeral ensembles drawn from a larger regional species pool which reflects (historical) processes operating at large spatial and temporal scales (Holt, 1993; Logue et al., 2011; Ricklefs, 2008) conceivably unites both views on species distribution. Local species richness (i.e. 'point diversity' or α-diversity) is therefore correlated with i) the large-scale processes (cf. macroecology, species formation, geographic dispersal) that determine regional species richness (γ-diversity), ii) sample area (cf. species-area curve), and iii) the outcome of processes that determine the ability of species or populations to spread and maintain over ecological or geographical gradients (i.e. local interactions as well as dispersal abilities; Ricklefs, 2008). For the purpose of this thesis, the processes considered in the previous sentence can either be 'stochastic' (e.g., ecological drift) or more 'deterministic' (e.g., environmental selection) in their nature.

Local (α) and regional (γ) species diversity are linked by compositional changes among communities (β-diversity; Anderson et al., 2011; Whittaker, 1972), which in itself might hold clues on the processes responsible for it (cf. nestedness or turnover; Baselga, 2010). For example, high turnover patterns between communities can suggest low levels of dispersal or local selective forces resulting in different assemblages. Alternatively, low turnover may indicate efficient exchange of species between habitat patches, yielding similar species assemblages. Obviously, many other processes might be of importance as well, and linking community dynamics at different spatial scales forms one way of dealing with the ecological puzzle of species distribution. The metacommunity concept is an example of how processes operating at different spatial scales can be incorporated into one theory, and will serve as a framework for some of the chapters in this thesis. The concept defines metacommunity as a set of local entities linked by the dispersal of multiple potentially interacting species (Holyoak et al., 2005; Leibold et al., 2004). Depending on how much emphasis is put on environmental heterogeneity, the degree of functional equivalence among species and dispersal rate, (meta-) community dynamics can roughly be divided into four categories: neutral models (NM), patch dynamics (PD), mass effects (ME) and species sorting (SS) (Cottenie, 2005; Leibold et al., 2005; Logue et al., 2011; see Fig. 1.1). Neutral models assume ecological equivalence among species, ignoring species-environment interactions, and suggest that a decrease in similarity between communities with distance relates to ecological drift (also referred to as 'stochastic' processes; Chase & Myers, 2011; Hubbell, 2001; Vellend, 2010; Vellend et al., 2014). Alternatively, the other paradigms in metacommunity ecology consider interactions between species' niches with the biotic and abiotic environment (referred to as 'species-sorting',

'environmental filtering', 'deterministic processes', 'ecological niche'; Chase & Myers, 2011; Cottenie, 2005; Leibold et al., 2004). Species sorting can occur when dispersal is efficient for the majority of species and stresses the importance of environmental heterogeneity between habitat patches (abiotic environment) which results in species tracking their preferred niche in space and time. Patch dynamics and mass effects can be considered special cases of species sorting, which differ in the degree of dispersal (see Winegardner et al., 2012 for an update on terminology). Mass effects invoke source-sink dynamics and high dispersal capacities for some species to explain their occurrence in patches that are normally not considered part of their environmental niche. In patch dynamics, the focus lies more on the interactions between species (biotic environment). Spatiotemporal niches with different species composition develop due to competition/colonisation trade-offs, priority effects, and dispersal limitation for some species (Cottenie, 2005; Winegardner et al., 2012). In all cases, dispersal thus plays an important role, for it allows species to track environmental gradients in space and time or escape competitional exclusion. While natural communities seldom form perfect examples of either one of the four paradigms described above (see Logue et al., 2011), metacommunity theory served as a useful starting point for many ecological studies over the past decades.

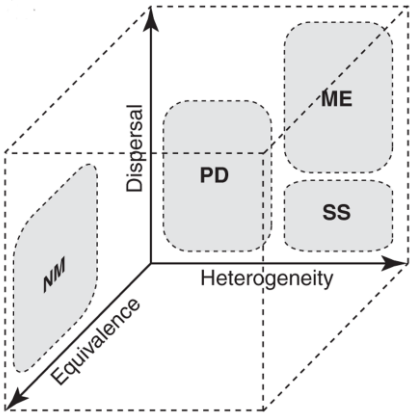

Figure 1.1. *Overview of the four paradigms recognised in metacommunity theory. They are ordered according to the degree of importance of environmental heterogeneity, species equivalence and dispersal. Abbreviations explained in main text. Scheme reproduced from Logue et al. (2011).*

A considerable amount of empirical studies have assessed and interpreted local community assembly within the theoretical framework of metacommunities, for different organisms and in different habitats (e.g., Beisner et al., 2006; Cottenie, 2005; Vanschoenwinkel et al., 2007; Verleyen et al., 2009; Vyverman et al., 2007). Most of these tested the different paradigms within permanent habitats with discrete boundaries (e.g., lakes, ponds; Logue et al., 2011), and stressed the importance of species-sorting dynamics in many cases. Yet many local communities in nature lack geographic boundaries, which is certainly true for open marine systems. To think of marine biota under a metacommunity umbrella seems rather intuitive,

since theoretically, ocean currents can promote dispersal between habitat patches (Srivastava & Kratina, 2013), hence link local assemblages across scales.

Throughout the years, it has become clear that the answer to the question of what drives species distributions and community assembly very much depends on the spatial scale considered (e.g., Soininen et al., 2007). Increasing the spatial extent of a study can imply a larger amount of environmental heterogeneity (e.g., sampling across productivity regimes, in different sediments or habitat types) that needs to be incorporated, an increased importance of regional dispersal-related dynamics (since larger distances need to be crossed), and a higher probability of uncovering patterns that bear a historical signature (e.g., due to differences in the tectonic or climatic history of areas). Conversely, studies conducted at small scales might expose patterns more indebted to local processes such as species' responses to environmental cues or biotic interactions. Yet it is the *interaction* of processes at *different scales* that ultimately affects local community composition and diversity (Logue et al., 2011). Spatial scale also relates to the organisms under study. For small organisms such as the nematodes in this thesis, even small distances may be difficult to cross, and variations in community composition or diversity can occur at a scale of only a few centimetres or metres (e.g., Van Gaever et al., 2010).

WHY STUDY SOUTHERN OCEAN BENTHIC COMMUNITIES?

Antarctic marine communities form interesting study objects in light of historical (e.g., origin of biota in terms of climatic and tectonic history) as well as contemporary events (e.g., vulnerability and adaptation of biota to changing environmental conditions). The relatively isolated character of Southern Ocean waters has resulted in biota that are well-adapted to the specific environmental conditions, some of which are now put to the test due to imminent climate-induced changes.

The evolutionary origin of Antarctic marine benthic communities

Antarctica is considered the most isolated, coldest, driest and windiest continent of our planet, yet its waters are teeming with life that has found a way to cope with the extreme environmental conditions (Arntz et al., 1994; Peck et al., 2006). On an evolutionary timescale, Antarctica formed part of the Gondwana supercontinent in Palaeozoic times, and climate was much warmer than observed today. The clearing of the South Tasman Rise (Australia – East-Antarctica) and the opening of the Drake Passage (South America – Antarctic Peninsula) in Cenozoic times was the onset for a drastic decrease in temperatures and increase in ice

coverage (Lawver & Gahagan, 2003). It was in the absence of these geological barriers that the west wind drift was established, resulting in the Antarctic Circumpolar Current (ACC) as an effective isolating barrier between the Southern Ocean and other oceanic basins (Barker et al., 2007). Whereas this is a mainly wind-driven current system, its effects extend to the seabed and the fronts associated with it (Polar Front, Sub-Antarctic Front; Fig. 1.2) form the actual delineation of the Antarctic region and Southern Ocean. These fronts are accompanied by steep gradients in temperature, phyto- and zooplankton distribution and climatic conditions which act as a biological barrier to most exchange across the Polar Front. The gradual cooling of Southern Ocean waters associated with the development of the ACC resulted in a shift in faunal communities that had been present until then, and the composition of modern Antarctic biota is believed to reflect this tectonic and climatic change. Groups such as decapod crabs and several representatives of cartilaginous and teleost fish were eradicated (or at least strongly reduced) from southern waters, while others such as certain echinoderms and peracarid crustaceans flourished (Aronson & Blake, 2001; Clarke et al., 2004; Thatje et al., 2005). With the exception of migratory seabirds and marine mammals, which are able to actively cross the Polar Front, Antarctic and Southern Ocean organisms have thus evolved in (semi-) isolation since the development of the ACC (Barnes et al., 2006; Griffiths et al., 2009; but see Clarke et al., 2005). Relatively high levels of endemism observed or expected for several benthic taxa are believed to have resulted from this isolating effect (Arntz et al., 1994; Brandt et al., 2007a; Griffiths et al., 2009). However, the observation of faunal links between the Antarctic and southernmost South America (Arntz et al., 2005; Figuerola et al., 2014) as well as a certain level of gene flow across the Polar Front (Damereau et al., 2012; Díaz et al., 2011), and even bipolar species (e.g., Havermans et al., 2013), indicate that isolation is far from complete. Island chains such as the Scotia Arc, which are surrounded by shallower shelves, might continue to serve as a "stepping-stone" route towards 'true' Antarctic waters (Arntz et al., 2005; Clarke, 2008; Ingels et al., 2006).

On a shorter evolutionary timescale, the Quaternary Milankovitch forcing and associated glacial-interglacial cycles in the Pliocene – Pleistocene are held responsible for the expansion and restriction of species' ranges along the Antarctic continental shelf and slope (Barnes et al., 2006). This pattern is still traceable in extended levels of eurybathy in various benthic taxa, resulting from their emigration to deeper areas when ice conditions prevented occupation of the upper shelf (Brandt et al., 2007a; Brey et al., 1996). The origin of modern Antarctic benthic communities is thus strongly coupled to the tectonic, climatic and oceanographic

history of the continent and surrounding Southern Ocean, and the study of their current distributions can reveal important insights from both historical and contemporary points of view.

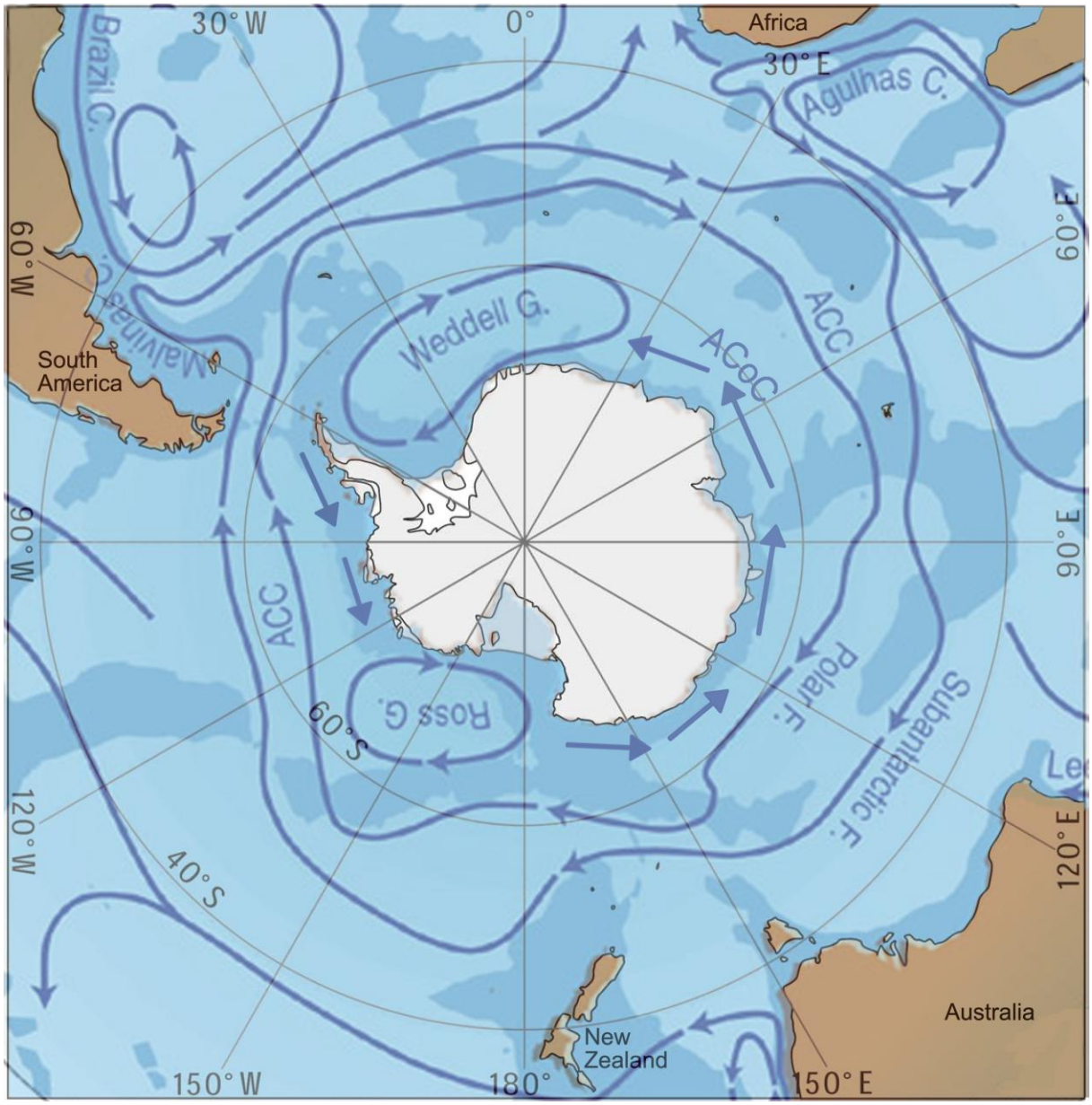

Figure 1.2. *Overview map of the Antarctic continent, the surrounding Southern Ocean and the most important current systems in the area. ACC = Antarctic Circumpolar Current (cf. West Wind Drift), which marks the Polar Front (Polar F.). Further north lies the Subantarctic Front (Subantarctic F.). The position of both fronts can shift with time and season. ACoC = Antarctic Coastal Current (cf. East Wind Drift). Next to these circumpolar current systems, there are two clockwise gyres that originate in the Weddell and Ross Seas (Weddell G., Ross G.). Figure modified from Rintoul (2011).*

Connectivity and biogeography in the Southern Ocean

Attempts to define and describe biogeographic subdivisions in the Southern Ocean date back to the work of Ekman (early 1950s) and more importantly Hedgpeth (1960-1970s) (reviewed in Griffiths et al., 2009), and recently culminated in the 'Biogeographic Atlas of the Southern Ocean', a joint effort to provide an overview of what is known on biogeography of the different Antarctic benthic and pelagic taxa (De Broyer et al., 2014). As a general outcome, the presence of several current systems in the Southern Ocean is pinpointed as an important driver for connectivity and biogeography of its biota (Fig. 1.2). On one hand, the opening of circum-Antarctic seaways and establishment of the ACC resulted in the isolation from other oceanic basins described previously, but at the same time it mediated free dispersal of organisms across the Antarctic. Together with the relatively homogeneous conditions (e.g., seabed temperatures) in Southern Ocean waters, this has enabled many organisms to establish a circumpolar distribution (Arntz et al., 1994; Clarke & Johnston, 2003; Griffiths et al., 2009; Riesgo et al., 2015). Other current systems such as the westward Antarctic Coastal Current (ACoC; Fahrbach et al., 1992) and clockwise gyres within the Weddell and Ross Seas (Deacon, 1979) further maintain a high level of connectivity between locations on a smaller scale. And also in the deep sea, formation of Antarctic Bottom Water in the Weddell and Ross Seas fuels ocean circulation and transportation of cold, nutrient-rich water on a global scale (i.e. thermohaline circulation; Barnes et al., 2006; Orsi et al., 1999). The extensive current systems surrounding the Antarctic continent, both at the surface and in the deep, potentially serve as dispersal highways and homogenising factors for the marine biota present. This has lead to the conclusion that "although there is clear regional and local variation in the Antarctic marine fauna [...] when compared with its Southern Hemisphere neighbours, the Southern Ocean seems to show very few regional patterns" (Griffiths et al., 2009). In terms of benthic biogeography, the transportation and resuspension potential of currents at shelf depths is important. While detailed acquisition of current speed at greater depth is logistically challenging, several authors report mean velocities in the range of 3 – 12 cm s^{-1} at depths around 200 – 700 m for different locations around the continent (ACC-controlled waters) and in Drake Passage (Barker & Thomas, 2004; Nowlin et al., 1977; Nowlin & Zenk, 1988; Pillsbury & Jacobs, 1985). Barker and Thomas (2004) noted that although current speed may be limited at some time intervals, the pattern can be disrupted by strong bottom currents associated with ACC transport in narrow jets. Similarly, research near the continental shelf in the eastern Weddell Sea (Kapp Norvegia; Fahrbach et al., 1992; Isla et al., 2006a) showed

annual mean current velocities of 10 – 20 cm s^{-1} flowing at depths of 400 – 480 m along the coast to the southwest (i.e. ACoC direction). Such current speeds are high enough to resuspend (mainly fine) material from the benthic boundary layer and transport it along the path of the Weddell gyre (Isla et al., 2006a, b). Also here, current speeds above the seabed varied with seasonal and tidal patterns (Isla et al., 2006b).

Life on the Antarctic continental shelf and the impact of climate change

The Antarctic continental shelf is unusually deep, extending to roughly 1000 m at some locations, due to i) increased iceberg scouring during glacial times, and ii) isostatic depression by the thick ice sheet covering the continent (Clarke et al., 2004). Contrary to early expectations regarding Antarctic biodiversity, benthic life on these shelves is not "poor" (although not all taxa are equally speciose; Clarke & Johnston, 2003; Clarke et al., 2004; Clarke, 2008; Gutt et al., 2004), yet faces some 'extreme' conditions, most notably the cold temperatures, strong seasonality in (fresh) food input, and ice conditions (Arntz et al., 1994). In terms of food input, benthic biota are mainly dependent upon the occasional pulses of phytodetritus from surface waters to the seafloor during blooming events (i.e., bentho-pelagic coupling; Lins et al., 2014, 2015); and on lateral advection and resuspension otherwise (Arntz et al., 1994; Isla et al., 2006b). Thanks to the cold temperatures and slow degradation rates in Southern Ocean waters, some of the freshly deposited phytodetritus accumulates as a 'food bank' on the seafloor (Smith et al., 2008). Bottom boundary layer dynamics (e.g., tidal forcing) may effectively resuspend fine material and organic deposits from the seabed, and explain year-round food supply (Isla et al., 2006b). Ice conditions, both in the form of 'permanent' ice shelves as well as seasonally varying sea ice, put another constraint on benthic life in the Southern Ocean, mainly through their indirect effects on food availability, but also as a possible element of physical disturbance (e.g., iceberg scouring; Lee et al., 2001).

Because of the particular character of the environment in which Antarctic communities have evolved through time, organisms might be especially vulnerable to even small changes in this setting (Barnes & Peck, 2008; Clarke et al., 2007a; Kaiser et al., 2013). Despite its remote and pristine character, the Antarctic continent is not entirely isolated from climate-induced changes, and current climate change thus forms a major threat to Antarctic ecosystems. In fact, certain parts of the Antarctic (most notably the peninsula and coastal areas) belong to the fastest warming regions on earth today (Smale & Barnes, 2008; Vaughan et al., 2003), and

consequences of this warming trend are already visible near the Antarctic Peninsula. Seasonal sea ice has decreased in time and extent, most glaciers in the region have retreated, surface waters in the seas west of the peninsula have warmed and a number of ice shelves have collapsed (Clarke et al., 2007b; Cook et al., 2005; Meredith & King, 2005; Rack & Rott, 2004; Smale & Barnes, 2008). This in turn has lead to significant changes and shifts in pelagic phytoplankton assemblages, with possible bottom-up effects on all levels of the food web (Bertolin & Schloss, 2009; Cape et al., 2014; Mendes et al., 2013; Moline et al., 2004; Montes-Hugo et al., 2006). Studies examining the response of benthic communities to these changes are increasing too (Aronson et al., 2007; Clarke et al., 2007b; Gutt et al., 2013, 2014; Ingels et al., 2012; Kaiser et al., 2013; Sañé et al., 2012; Smale & Barnes, 2008), yet primarily focus on macro- and megafaunal taxa (Kaiser et al., 2013), often ignoring the smaller-sized meiofauna (but see Raes et al., 2010). In order to be able to predict and partly mitigate the consequences of current climate change, insights on all levels of the food web are required.

WHY STUDY MARINE FREE-LIVING NEMATODES?

Nematodes as study organisms

Marine free-living nematodes constitute the most abundant metazoan meiofaunal taxon in many marine environments (Giere, 2009; Heip et al., 1985). For the purpose of this thesis, meiofauna is defined as the organisms that are retained between a mesh size of 32 µm and 1 mm (see Vincx et al., 1994). The level of success of nematodes in standing stocks, species diversity and survival in some of the most extreme environments found on this planet, is unmet by any other benthic metazoan taxon. Due to their high densities in most marine environments and occurrence in nearly every single habitat, sampling of nematodes is easy, but mainly limited by the accessibility of locations (e.g., deep sea and remote areas; see also Kaiser et al., 2013). Also in the Southern Ocean, nematodes are present in a variety of habitats, usually in rather high densities (De Mesel et al., 2006; Hauquier et al., 2011; Ingels et al., 2006; Vanhove et al., 2004; Vermeeren et al., 2004). No endemic genera have been recovered from the Southern Ocean so far, and communities mainly differ in the relative abundance of certain genera, rather than their presence or absence. Nematode community composition also tends to vary with depth in the sediment, a characteristic that is usually linked to species interactions (e.g., predation, competition; Steyaert et al., 1999) and/or changes in abiotic variables such as oxygen content or food availability (Heip et al., 1985; Moens et al., 2013).

Nematodes have a rather simple body plan, consisting of two concentric cylinders (digestive tract and body wall), but with a lot of variations as adaptations to their differential feeding mode or habitat (Decraemer et al., 2013; Heip et al., 1985; Fig. 1.3). In theory, their translucent body would make the study of internal morphology and species-specific body traits rather straightforward. However, most of these important morphological traits are difficult to discern with traditional light microscopy as a result of their small size (De Ley et al., 2005). This renders identification to lower taxonomic levels a time-consuming endeavour, particularly in juvenile individuals. Especially in the deep sea and Antarctic sediments, nematodes tend to be smaller compared to their shallow and intertidal counterparts (Moens et al., 2013). As a consequence, macroecological studies have mainly been limited to genus level, and a large part of species diversity remains unresolved. According to the latest reports on global marine diversity, roughly 6900 free-living nematode species have been described in the marine environment, which is only 14 % of the estimated ~50 000 that is expected based on historical rates of species descriptions and expert polls (Appeltans et al., 2012; previous estimates ranged from 10 000 – 1 000 000; Lambshead & Boucher, 2003). An update of these numbers is available through the NeMys database (World Database of Free-Living Marine Nematodes; Guilini et al., 2016) and reports total described species numbers of ~ 7900, but of which only approximately 6400 are accepted (i.e. not taking into account synonyms). However, based on recent molecular advances and observations of cryptic diversity (e.g., Derycke et al., 2005, 2008; see later), previous estimates on total nematode species diversity might be an underestimation of true diversity.

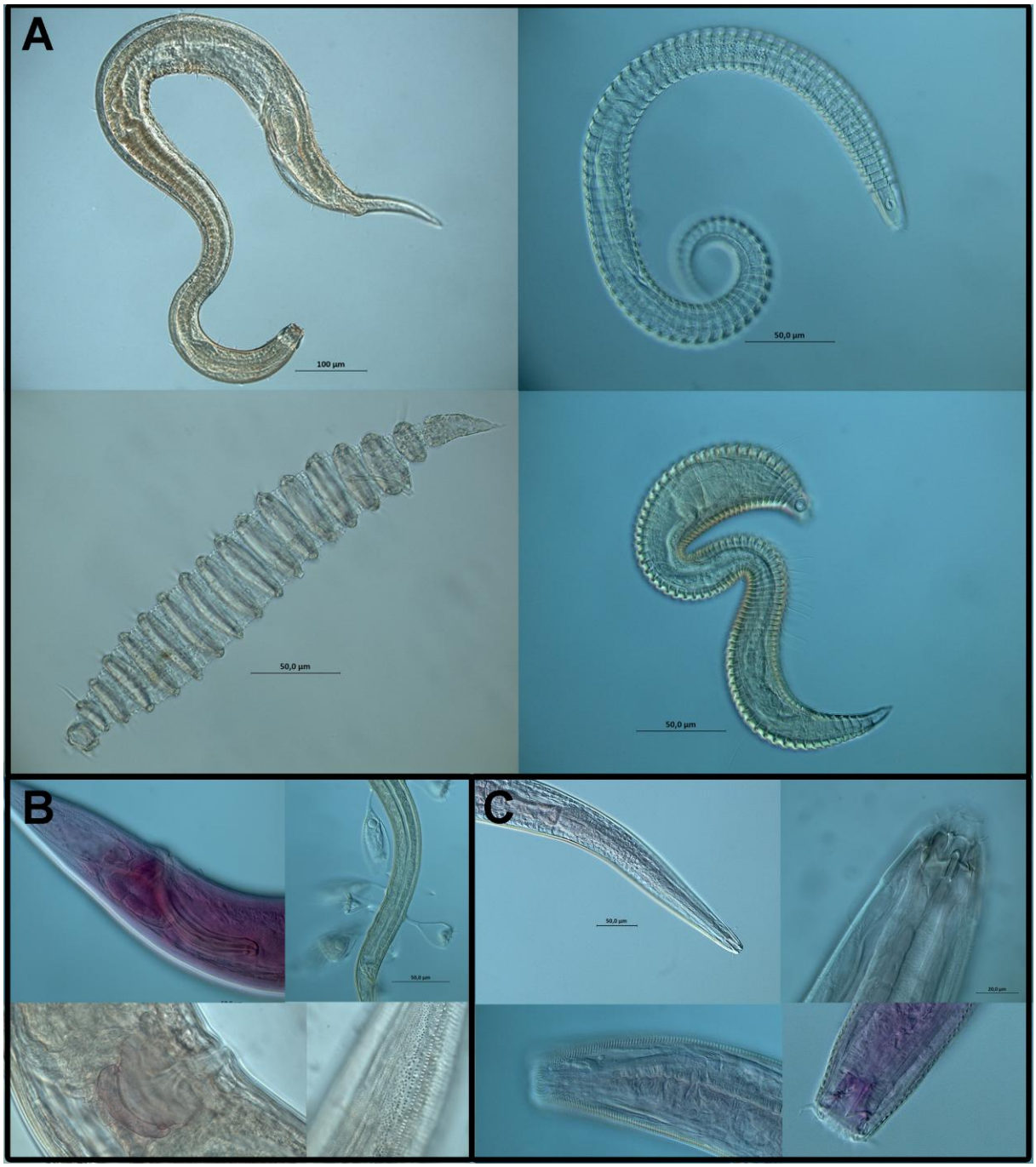

Figure 1.3. *Illustration of morphological characteristics and adaptations of marine free-living nematodes. Panel* ***A****: entire body morphology (i.e. habitus) – genera are (clockwise, starting from upper left corner) Desmodora, Metadasynemella, Metepsilonema and Desmoscolex. Panel* ***B*** *(clockwise): details of (1) a male spicule apparatus (Sabatieria), (2) a body section with ciliates attached to it, and the cuticle pattern (3) and vulva (4) of a Dorylaimopsis female. Panel* ***C*** *(clockwise): details of the head region of (1) Axonolaimus, (2) Paramesacanthion, (3) Pomponema and (4) Paracyatholaimoides.*

Nematode distribution and community composition in a larger context

Nematode genera have wide distribution ranges (see earlier), yet it is uncertain whether such generalisations also apply to the level of species. Nevertheless, diversity, abundance and community composition of nematode genera may vary considerably among habitats, between sediment depth strata, and at different spatial scales (see Heip et al., 1985; Moens et al., 2013). Depending on which sampling scale is adopted, patterns in nematode communities can be linked to different ecological processes since these too are scale dependent (i.e. processes structuring nematodes at small scales are not necessarily identical to those operating at larger scales – see earlier sections of this chapter; Danovaro et al., 2013; Fonseca et al., 2010). For instance, small-scale (mm – cm) variability in nematode communities can be as high as that observed at larger spatial scales and is attributed to local variations in microtopography, oxygen availability, food aggregation and interactions with other benthic organisms (Fonseca et al., 2010; Gallucci et al., 2009). On a larger scale, nematode distribution patterns have been associated with differences in physical parameters (e.g., oceanographic water mass characteristics, bottom currents), productivity regimes and increased environmental heterogeneity (e.g., Bianchelli et al., 2013; Lins et al., 2014; Moens et al., 2013; Vanreusel et al., 2010b).

Despite the fact that nematode density and diversity can show large variability at scales ranging from a few cm to several hundreds of km, some generalities do apply which allow nematode ecologists to formulate careful predictions on what to expect in certain areas. For example, certain habitat types host parallel nematode assemblages in very different parts of the world (e.g., increased relative abundance of *Sabatieria* and *Microlaimus* on continental shelves versus ‘deep-sea’ genera such as *Acantholaimus* and *Halalaimus* at slopes; Vanreusel et al., 2010b). Such habitat associations tend to be more important than trends related to latitude or geographical area and suggest a significant structuring role of environmental conditions (cf. species sorting; Moens et al., 2013). Similarly, certain nematode genera (or even families) show strong associations with sediment grain size and other parameters such as oxygen (Heip et al., 1985). From a metacommunity perspective, marine nematode communities might thus form interesting study objects to test whether environment truly explains the larger fraction of community variation across scales, and whether this also applies to the species level.

Dispersal of nematodes and the meiofauna paradox – being small in a large ocean

In order to explain some of the distribution patterns that were observed for the marine nematodes in this thesis, a few words have to be dedicated to dispersal capacities within this animal group. As already pointed out in the first section of this introduction, dispersal is the mechanism that connects populations and communities across locations and may allow species to track their preferred niche or food source. Species-specific dispersal capacity, together with distance, physical connection and the presence of transportation vectors (e.g., currents) between habitat patches will ultimately define the level of connectivity among populations. Cottenie (2005) showed that the relative importance of the four metacommunity paradigms described earlier can shift according to habitat (streams, lakes or marine) and dispersal-related features of the organisms under study (see also Soininen, 2015). Compared with other benthic invertebrate taxa, marine free-living nematodes do not possess planktotrophic larvae or resting stages, but instead develop through four different molting stages (Decraemer et al., 2013). In terms of dispersal capacity, this strictly endobenthic lifestyle has important consequences.

It is generally accepted that active dispersal over large distances is rather unlikely for marine nematodes. Although they can actively move through the sediment in response to certain environmental triggers or biotic stressors (cf. vertical segregation discussed earlier), their small size renders long-distance dispersal in this way highly inefficient (Derycke et al., 2013; Moens et al., 2013). In a similar fashion, while some nematodes show active swimming abilities, most of them are deemed poor swimmers (Moens et al., 2013; Palmer, 1988). Marine nematode dispersal is thus considered to be a passive rather than active process, where hydrodynamics play a key role. Other means of passive dispersal (ballast water of ships, rafting on macroalgae; Derycke et al., 2013) are of less importance in the context of this thesis and will not be further discussed here. Once nematodes are located within the water column, either as a result of active emergence or passive erosion (cf. Palmer, 1988), they are subject to transportation through bottom currents (Boeckner et al., 2009). Dispersal is therefore linked to the probability of resuspension, the intensity of prevailing hydrodynamic forces, and the retention time of nematodes in the water column (which is higher for small nematodes; cf. Ullberg & Olafsson, 2003). Not all nematodes are equally prone to resuspension, which is due to their vertical distribution and abundance in the sediment (Moens et al., 2013). Surface communities living closer to the sediment-water interface are more likely to become

suspended than deeper-dwelling individuals (Commito & Tita, 2002; Eskin & Palmer, 1985; Thomas & Lana, 2011) and thus more prone to long-distance dispersal.

Despite the consensus on the dominant dispersal mode for marine endobenthic nematodes, substantial uncertainty exists for its efficiency across scales and in different environments. Most knowledge on nematode dispersal stems from experimental work within a confined set-up (Boeckner et al., 2009; De Meester et al., 2012) and hence yields no information on the distances that could be covered. Recent advances in the molecular study of nematode distribution patterns indicated that dispersal may be substantial at geographical scales of a few tens of km, but more limited at scales of several hundreds of km (Derycke et al., 2013). Nevertheless, several marine nematode species have wide geographic distributions (Bik et al., 2010; Derycke et al., 2008), which does not seem to support the idea of dispersal limitation in this taxon. This meiofauna paradox (Boeckner et al., 2009; Giere, 2009) continues to fuel debates between nematode ecologists, as two scenarios exist concerning nematode distribution patterns. First, observations of cosmopolitanism (mainly genus level) suggest that nematodes might fall under the so-called 'ubiquity' hypothesis which is usually applied in a microorganism context (Baas Becking, 1934; Fenchel & Finlay, 2004). This concept considers local environment as the main determinant of species distribution and suggests that a combination of small body size and large population sizes enables microorganisms to rapidly erase imprints of historical and ecological events through long-distance dispersal and colonisation. Alternatively, one can think of nematodes as being rather limited in their dispersal abilities due to their lack of pelagic larvae and endobenthic lifestyle. Under this assumption, distribution is mainly the result of regional processes related to dispersal limitation and species will have restricted distribution ranges. Until now, the question has not fully been answered, and nematode ecologists have been swayed back and forth between both perspectives, depending in which direction their results guided them. For example, cosmopolitan species distributions point towards a prevalence of the first hypothesis (e.g., Bik et al., 2010), while high levels of endemism and occurrence of cryptic species with limited range size are more in favour of the second (e.g., Derycke et al., 2008, 2010a) (see also Moens et al., 2013 and Derycke et al., 2013 for an overview of both types of patterns).

Perhaps the truth about nematode – and by extension meiofauna in general – dispersal lies somewhere in the middle. A recent metagenetic study of marine meiobenthic eukaryotes near Europe demonstrated that community composition is partly niche-driven, but also shares some macroecological features of microorganisms ('everything is everywhere') by showing

high levels of cosmopolitanism (Fonseca et al., 2014). But even for other microorganisms, the concept of ubiquity is disputable, since it was revealed that many of them are actually capable of showing a biogeographic pattern, even in systems without barriers to long-distance dispersal (Cermeño & Falkowski, 2009; Martiny et al., 2006; Soininen, 2007; Verleyen et al., 2009). Yet the general belief remains that the smaller the taxon, the less constrained by dispersal hence the more homogenised its communities will be (Shurin et al., 2009; Soininen, 2015). The vastness of the marine realm, with only few obvious geographical barriers to dispersal and gene flow *in theory* presents the ultimate background for organisms to develop wide distribution ranges and low spatial structure. However, dispersal barriers need not be visible per se, and can also exist in the form of complex oceanic circulation patterns (Srivastava & Kratina, 2013), strong temperature gradients (cf. Polar Front as mentioned earlier) or extensive areas of possibly unsuitable habitat patches (Palumbi, 1994).

MOLECULAR ADVANCES SHIFT PHYLOGEOGRAPHIC AND POPULATION GENETIC PARADIGMS

Much of what we know today on species distribution and biogeography stems from conventional studies on the systematics and morphological diversity of taxa. However, morphological similarity does not necessarily reflect true evolutionary relationships between organisms (Rogers, 2012). The advent of molecular techniques has provided a different set of tools to extend our knowledge on species diversity, taxonomy and distributions. As mentioned before, the origin of modern Antarctic (benthic) communities shows strong affinities with the continent's climatological, tectonic and oceanographic history, which resulted in Southern Ocean 'particularities' such as high levels of endemism, circumpolar species distributions and extended eurybathy in certain organisms (Griffiths et al., 2009). Vicariance after the Gondwana break-up is thought to form one of the main drivers of speciation since Palaeozoic times, whereas dispersal mediated by large oceanic currents such as the ACC helped shaping current species distributions (Rogers, 2012). This shows that also from a molecular and evolutionary perspective, dispersal is crucial since it influences gene flow among populations and indirectly affects genetic diversity, phylogeography, adaptation of organisms to local selective pressures and ultimately, the probability of speciation. Referring once more to the open character of the marine environment and the presence of current systems as dispersal highways, high dispersal of marine species is often translated into relatively low genetic differentiation among populations and hence slow species diversification (cf. Palumbi, 1992, 1994). However, an increasing body of work incorporating molecular data for Antarctic organisms has indicated that (some) species distributions seem to be more restricted than

previously thought and that cryptic speciation is evident in a variety of taxa (e.g., Allcock & Strugnell, 2012; Hemery et al., 2012; Wilson et al., 2007). Insights gathered through molecular analyses, in combination with those from traditional morphological approaches, may thus provide a different angle on distribution patterns observed for marine organisms.

This also applies to free-living nematodes, where the scenario of cosmopolitan species distributions (see 'meiofauna paradox' earlier) has been challenged by molecular evidence of morphological species constituting complexes of several phylogenetically distinct (cryptic) species with restricted distributions (Derycke et al., 2013). This brings us back to the question of how efficient dispersal across large distances is for this taxon (see previous section). To date, molecular studies on free-living nematodes have mainly focused on shallow, intertidal species (e.g., De Oliveira et al., 2012; Derycke et al., 2005, 2008, 2010a) or deep-sea inhabitants (e.g., Bik et al., 2010). Assessment of cryptic speciation, phylogenetics and population genetics at intermediate shelf depths is considerably less studied. In his thesis, we will try to fill this knowledge gap.

RATIONALE AND OUTLINE OF THE THESIS

The topics introduced here will all be discussed to a certain extent throughout this thesis. The chapters constitute separate entities, each with their own focus on different aspects of nematode communities. Therefore, some overlap in introductions and discussions is inevitable. Chapters have been ordered according to their spatial extent, and the sampling locations are indicated as separate boxes on Figure 1.4. In **Chapter 2**, research questions are related to the change in nematode communities in the Larsen B area near the eastern Antarctic Peninsula (box 1, blue). In this area, climate change induced the disintegration of large parts of the permanent ice shelf over the course of only a few years, which marked a drastic change in the productivity regime in formerly ice-covered waters and the possibility for colonisation of newly opened patches on the seafloor. Samples collected in two different years and for two locations at approximately 70 km distance within the embayment were compared in terms of nematode abundance, composition and diversity. As such, both a 'time' and 'space' effect were of interest. Despite the lack of pre-collapse information on nematode communities under permanent ice shelves, obtained results provide insights on the colonisation abilities of nematodes and their response to enhanced primary productivity after ice-shelf collapse. **Chapter 3** further builds on the relationship between benthic nematodes and local environmental conditions, but with a focus on the comparison of locations at both sides of the Antarctic Peninsula (box 2, green). Areas were characterised by different oceanographic and

productivity regimes, which sets different environmental constraints on the structuring and composition of benthic nematodes. The location of sampling areas at the tip of the Antarctic Peninsula converges with a transition from more oceanic conditions in the Drake Passage to truly Antarctic water masses at the Weddell Sea side. The main topics in this chapter focus on bentho-pelagic coupling and local environmental effects on community dynamics. In **Chapters 4** and **5**, the aim is to extend the spatial scale from a local to a more regional view on nematode distributions, spanning locations at both sides of the Weddell Sea and along the Scotia Arc and Antarctic Peninsula. An overarching theme of both chapters is whether nematode species are as widely spread as their genera at the scale considered here (cf. meiofauna paradox) and how distribution can be linked to environmental heterogeneity or geographic distance (cf. metacommunity concept). Chapter 4 describes nematode genus and species diversity at different levels of spatial organisation to assess whether distribution patterns differ between both taxonomic levels (only for locations in box 3). These data are then included in an overarching analysis combining all sampling locations of the previous chapters (box 1, 2, 3 combined) to evaluate whether distribution patterns mainly result from environmental or from spatial heterogeneity across areas. Chapter 5 revolves around some of the sampling locations presented in Chapter 4 (box 3, red), but highlights phylogeographic and population genetic aspects of the distribution of two genera that were widespread and relatively abundant across the entire area. Outcomes there lead to a reflection on cryptic speciation, gene flow and connectivity between Antarctic benthic communities and link that knowledge to certain habitat preferences of both genera. Finally, **Chapter 6** forms a general discussion on the results of the four previous chapters, lists the main limitations of the current thesis and ends with some recommendations for future research on Southern Ocean nematode communities. This work is definitely one that has generated more questions than conclusive answers, and its main value therefore lies in forming a guideline for future research projects dealing with nematode distribution at various scales.

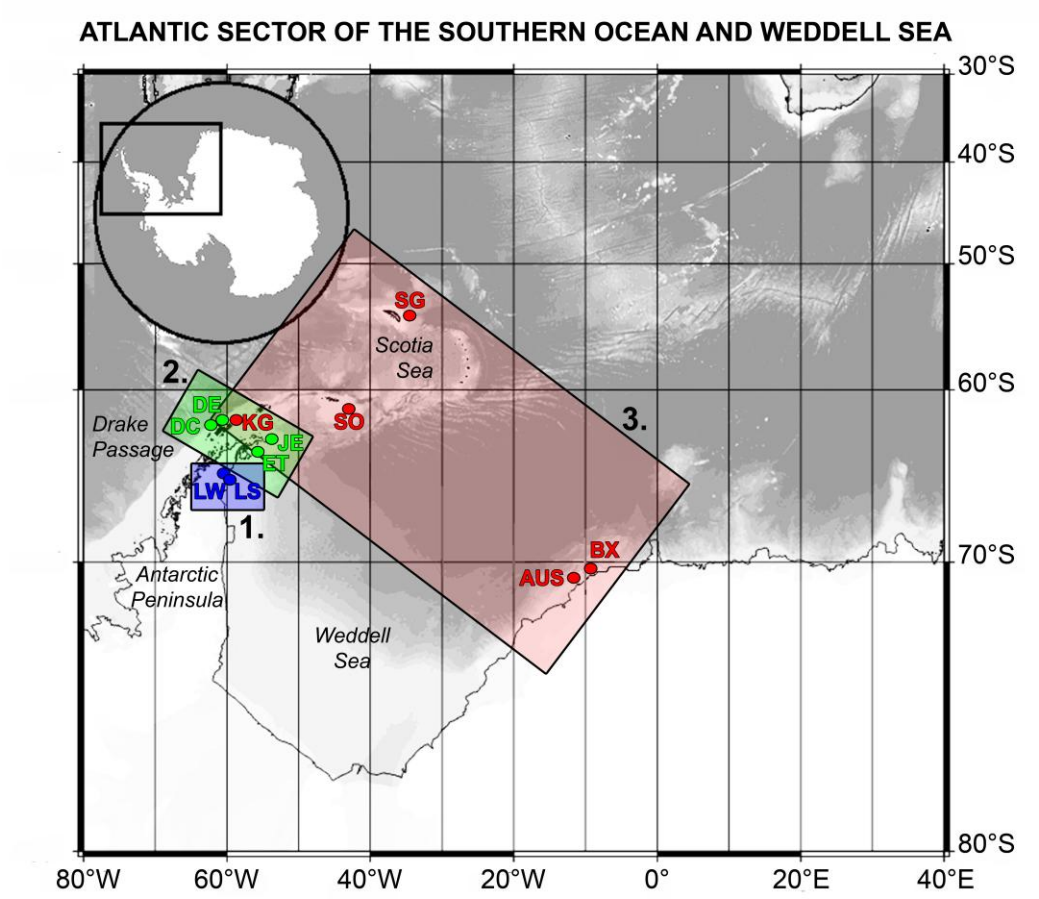

Figure 1.4. *Overview of the sampling locations of the different chapters in this thesis.* ***Box 1*** *(blue) includes two stations that were sampled at different time periods and will be discussed in Chapter 2. LS = Larsen B.South, LW = Larsen B.West. Stations in* ***box 2*** *(green) are the subject of Chapter 3. JE = Joinville Island East (referred to as W-120 in Chapter 3), ET = Erebus & Terror Gulf (W-163), DC = Drake Passage Central (DP-243), DE = Drake Passage East (DP-250). Chapter 5 considers the stations of* ***box 3*** *(red). SG = South Georgia, SO = South Orkneys, KG = King George, AUS = off Auståsen, BX = Bendex. Chapter 4 combines all three boxes.*

CHAPTER 2: COMMUNITY DYNAMICS OF NEMATODES AFTER LARSEN ICE-SHELF COLLAPSE IN THE EASTERN ANTARCTIC PENINSULA

Modified from: Hauquier F, Ballesteros-Redondo L, Gutt J & Vanreusel A (2016) Community dynamics of nematodes after Larsen ice-shelf collapse in the eastern Antarctic Peninsula. *Ecology and Evolution*, 6(1): 305 – 317. doi:10.1002/ece3.1869

ABSTRACT

Free-living marine nematode communities of the Larsen B embayment at the eastern Antarctic Peninsula were investigated to provide insights on their response and colonisation rate after large-scale ice-shelf collapse. This study compares published data on the post-collapse situation from 2007 with new material from 2011, focusing on two locations in the embayment that showed highly divergent communities in 2007 and that are characterised by a difference in timing of ice-shelf breakup. Data from 2007 exposed a more diverse community at outer station B.South, dominated by the genus *Microlaimus*. By contrast, station B.West in the inner part of Larsen B was poor in both numbers of individuals and genera, with dominance of a single *Halomonhystera* species. Re-assessment of the situation in 2011 showed that communities at both stations had diverged even more, due to a drastic increase in *Halomonhystera* at B.West compared to relatively little change at B.South. On a broader geographical scale, it seems that B.South gradually starts resembling other Antarctic shelf communities, although absence of the genus *Sabatieria* and high abundance of *Microlaimus* still set it apart nine years after the main Larsen B collapse. In contrast, thriving of *Halomonhystera* at B.West further separates its community from other Antarctic shelf areas.

INTRODUCTION

The Antarctic Peninsula is one of the most affected areas worldwide by rapid regional warming (Vaughan et al., 2003), and this has led, amongst other things, to large-scale ice-shelf destabilisation and disintegration. The Larsen area east of the Peninsula is one of the regions where ice-shelf collapse is evident: in 1995, the Larsen A ice shelf (LIS-A) disintegrated almost completely, and in February-March 2002 the Larsen B ice shelf (LIS-B) lost with roughly 3250 km² the largest proportion of its surface after a decade of several smaller disintegration events and millennia of stability (Rack & Rott, 2004; Domack et al., 2005; Rebesco et al., 2014). The sudden collapse of LIS-B was mainly attributable to surface processes, rather than basal melting in response to oceanic warming (Gilbert & Domack, 2003; Vaughan et al., 2003; Rack & Rott, 2004; Scambos et al., 2004; Rebesco et al., 2014). Prior to the actual breakup, there had been an exceptionally warm summer and the surface net mass balance of the ice shelf had been decreasing for several years (Rack & Rott, 2004). This eventually led to ice thinning and the formation of meltwater ponds and crevasses at the surface, further enhancing rapid disintegration (Gilbert & Domack, 2003; Rack & Rott, 2004). Currently, the remnant LIS-B (and its tributary glaciers; Rott et al., 2011; Berthier et al., 2012)

continues to decrease, evidenced by an additional loss of 50 % of the initial collapsed area over the period 2002 – 2009 (Shuman et al., 2011).

Sudden ice-shelf collapse results in profound changes for associated marine benthic ecosystems. In areas like Larsen (e.g., the western Antarctic Peninsula; e.g., Moline et al., 2004; Clarke et al., 2007b), loss of permanent shelf ice enables phytoplankton to bloom in areas previously ice-locked for several millennia (Bertolin & Schloss, 2009; Barnes & Clarke, 2011). Furthermore, ice algae released upon seasonal ice melt may provide a valuable additional food source, especially in seasonally opened polynyas nearby the continent (Cape et al., 2014). Together, both processes enhance direct fresh food supply to seafloor-dwelling organisms, triggering colonisation of previously ice-covered habitats from nearby sources. On the downside, sudden ice-shelf decay increases the risk of iceberg scouring as large icebergs break off and ground in areas further offshore (Gutt et al., 1996; Lee et al., 2001).

Despite all efforts in the study of benthic response to climate-induced events such as ice-shelf collapse and iceberg scouring, considerable uncertainty remains on how biodiversity is affected by, and what the resultant ecological responses are of these processes. To gain long-term information, several benthic faunal components of Larsen B were sampled during two expeditions onboard the German icebreaking RV *Polarstern* in austral summer of 2007 (ANT-XXIII/8; Gutt, 2008) and 2011 (ANT-XXVII/3; Knust et al., 2012). Meiobenthos (32 – 1000 µm) of the first expedition was assessed by Raes et al. (2010) and Hauquier et al. (2011), focusing on the numerically most important Nematoda. Already then, five years after the main LIS-B collapse, significant differences were observed between Larsen stations for all faunal groups, driven by different response rates to the change from an oligotrophic sub-ice-shelf to a more productive ecosystem (Gutt et al., 2011). Based on faunal abundance and diversity, stations B.South located at the original ice-shelf edge and B.West in the middle of the embayment contrasted most. For Nematoda, this observation was explained by a combination of the duration of the ice-free period and the connection with pre-collapse open Weddell Sea conditions (Raes et al., 2010). The main objective of expedition ANT-XXVII/3 in 2011 was to revisit 2007 locations and look at benthic ecosystem recovery and dynamics. This study re-analyses 2007 data for stations B.South and B.West and compares them with new (i.e. 2011) nematode community data to resolve nematode community response to ice-shelf collapse on a longer time scale. Given continued increase in vertical food supply and exchange with the open Weddell Sea, we hypothesise that:

i) Abundance and diversity at B.West will increase and nematode communities at both locations will converge in terms of numbers, diversity and generic composition,

ii) Communities within Larsen B will increasingly resemble other Antarctic shelf areas of similar water depth that do not necessarily share the same history of permanent ice shelter.

MATERIAL AND METHODS

Sampling area and strategy

Stations B.South and B.West of Polarstern expedition ANT-XXIII/8 (January 2007) were re-sampled during ANT-XXVII/3 (March 2011) using five random replicate multicorer deployments (MUC, inner diameter 57 mm, surface area 25.52 cm²; Barnett et al., 1984) per location, allowing for equivalent and comparable sample coverage (Table 2.1, Fig. 2.1). B.South was always located at the border of the original ice shelf in open connection to the Weddell Sea (hence referred to as 'outer' station), whereas B.West (inner station) experienced permanent ice cover until after the 2002 collapse (evolution of ice-shelf extent is depicted in Fig. 2.1; see also Raes et al., 2010).

Table 2.1. *Geographic position and depth of Larsen B.South and B.West replicates, both for ANT-XXIII/8 (2007) and ANT-XXVII/3 (2011).*

	2007				**2011**			
	replicate	latitude	longitude	depth (m)	replicate	latitude	Longitude	depth (m)
B.South	700-8	65° 54.98' S	60° 20.54' W	422	246-3	65° 54.95' S	60° 20.43' W	424
	700-9	65° 54.95' S	60° 20.88' W	417	246-4	65° 54.95' S	60° 21.49' W	395
	702-4	65° 55.12' S	60° 19.96' W	427	246-5	65° 54.99' S	60° 20.70' W	419
	702-7	65° 54.49' S	60° 21.37' W	405	247-3	65° 55.12' S	60° 19.83' W	428
	702-8	65° 54.95' S	60° 20.95' W	410	247-4	65° 55.15' S	60° 20.01' W	425
B.West	710-2	65° 33.03' S	61° 36.98' W	277	233-4	65° 32.99' S	61° 36.94' W	277
	710-3	65° 33.04' S	61° 37.18' W	281	233-5	65° 32.97' S	61° 36.94' W	278
	710-7	65° 33.03' S	61° 37.01' W	275	235-4	65° 32.96' S	61° 36.88' W	276
	710-8	65° 33.03' S	61° 37.00' W	283	235-5	65° 33.01' S	61° 36.96' W	280
	710-9	65° 33.07' S	61° 37.06' W	288	235-6	65° 33.01' S	61° 37.00' W	279

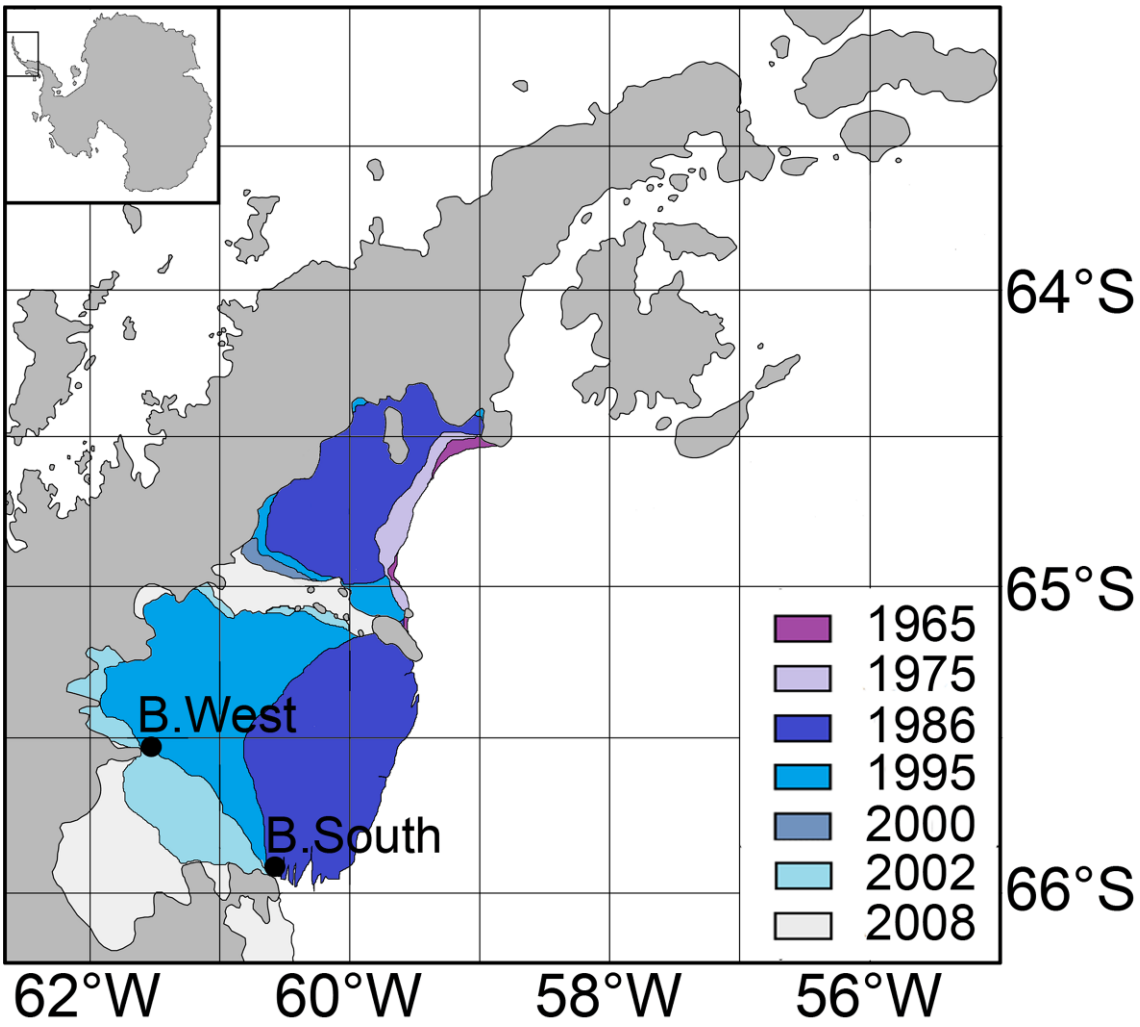

Figure 2.1. *Sampling locations B.West and B.South and the evolution of the ice-shelf extent over selected years.*

The top 0 – 5 cm of one core per replicate deployment were sliced at a 1 cm-resolution and preserved in 4 – 8 % formalin for meiofauna analysis. Table 2.1 gives the geographic position and depth of the 2011 and – for ease of comparison – the 2007 samples. Meiofauna was extracted from the sediment using 1 mm and 32 µm sieves and density gradient centrifugation with Ludox (specific density 1.18 g cm^{-3}; Heip et al., 1985; Vincx, 1996), fixed in 4 % formalin, and dyed with Rose Bengal (0.5 g l^{-1}). All meiofauna was counted and identified at higher taxon level using a stereomicroscope and the guide of Higgins and Thiel (1988).

From each layer, 150 nematodes were randomly picked (or all when the number of nematodes < 150), transferred to anhydrous glycerol (Seinhorst, 1959), and mounted on slides. Genus-level identification (using a Leica DMLS compound microscope, 1000 × magnification) was

based on the pictorial key of Warwick et al. (1998) and the NeMYS database (Guilini et al., 2016).

As for 2007, samples for faunal analysis were complemented with an additional sample set for the measurement of environmental variables. These were analysed at a coarser vertical resolution, 0 – 3 cm and 3 – 5 cm. Sediment grain size distribution was determined by laser diffraction (Malvern Mastersizer 2000, size range 0.02 – 2000 µm) and classified following Wentworth (1922). Granulometric variables considered in this study were median grain size, silt (< 63 µm) and sand (> 63 µm) percentage. Pigments were extracted from lyophilised sediments by adding 10 mL 90 % acetone, and chlorophyll *a* (chl*a*; µg g^{-1}) was measured with a fluorescence detector after HPLC (High Performance Liquid Chromatography) separation[15]. Additionally, total organic carbon (TOC) and nitrogen (TN) fractions were measured on 2011 freeze-dried samples using a Flash 2000 organic elemental analyser (protocol available through Interscience B.V., Breda, The Netherlands). Their ratio was calculated and multiplied by 14:12 to account for the difference in molar mass ($C:N_{molar}$). Finally, sediment total organic matter (TOM) was determined after combustion at 550 °C.

Statistical analyses

Nematode abundance and community composition in 2011 were analysed both separately and in conjunction with 2007 data. Analyses were executed in PRIMER v6 (Clarke & Gorley, 2006) with the PERMANOVA+ add-on (Anderson et al., 2008), unless mentioned otherwise. Nematode assembly data were standardised to individuals per 10 cm^2 (ind. 10 cm^{-2}) and square-root transformed to limit influence of dominant genera.

Differences in communities between areas and sediment depth layers in 2011 were assessed using a PERMANOVA (permutational ANOVA) design with two fixed factors (area, layer; Bray-Curtis similarity of genus ind. 10 cm^{-2}; 9999 permutations); and visualised using PCO (principal coordinates analysis). SIMPER (similarity of percentages) identified which genera were responsible for (dis)similarities between samples. Community data were then summed for 0 – 3 and 3 – 5 cm depth for each replicate preceding correlation with environmental

[15] Details on HPLC protocol: Samples were lyophilised, extracted in 90 % acetone, and filtered at 0.2 µm after a few hours. Depending on the concentration, 50 or 100 µl was injected into the HPLC system (Gilson, Inc.). Reverse phase chromatography used a C18 column (MACHEREY-NAGEL) with a particle size of 5 µm, inner diameter of 4.6 mm and length of 25 cm. Concentrations were measured by means of a spectrophotometer, diode array detector and fluorimeter.

variables (as these were measured at a rougher scale) and averaged for both areas. TOM was log-transformed to reduce right-skewness and sand content was omitted from the analysis owing to its high correlation ($r > 0.9$) with silt. All environmental variables were normalised. BEST analysis quantified the correlation between environmental setting and nematode assemblages.

Comparison of 2011 and 2007 data was done by PERMANOVA. Univariate analysis of nematode densities used a two-factor design (area, year = fixed; Euclidean distances of nematode ind. 10 cm^{-2}, 9999 permutations), multivariate nematode composition data a three-factor design (area, year, sediment depth = fixed; Bray-Curtis similarity of genus ind. 10 cm^{-2}, 9999 permutations). Pairwise tests were performed between all pairs of levels for significant factors. When the number of unique permutations exceeded 100, true permutational p-values were reliable. When this number was below 100, Monte Carlo p-values were interpreted. Results were accompanied by a PCO graph, combined with CLUSTER results, to gain visual insight in the data cloud.

Diversity indices (N_0 = number of genera; H' = Shannon index (log$e$); *EG(200)* = expected number of genera in a sample of 200 individuals; Hill's N_1[16]) and evenness (Hill's N_{inf}; J' = Pielou's evenness) were calculated in accordance with Raes et al. (2010). The rarefaction index *EG(n)* was based on 200 since the lowest number of identified specimens in one of the replicates was 215 (Clarke & Gorley, 2006). After assumption testing in R (R core team, 2013), several indices did not fulfil requirements for two-way ANOVA; hence, differences in diversity between areas and years were assessed using PERMANOVA (design identical to that for abundance data).

Finally, the 2007 and 2011 Larsen data were included in a larger dataset on (sub)-Antarctic nematode shelf assemblages (0 – 1000 m), to examine relationships within a broader geographical context (Table 2.7). Data were grouped over larger geographical scales to simplify analysis. Groupings were chosen arbitrarily, disregarding geographical coordinates, and should not be interpreted as true biogeographical provinces. One-way ANOSIM (analysis of similarity) assessed differences between areas, which were visualized with non-metric MDS (multi-dimensional scaling).

[16] Note that N_1 is the true number's equivalent of Shannon entropy H', calculated as exp(H') (Jost, 2006).

RESULTS

Nematode abundance and vertical distribution

In all 2011 samples, regardless of their location or sediment depth, nematodes formed the most abundant meiofaunal taxon (relative contribution 93 – 95 %). Whereas nematode total densities (i.e. summed over 0 – 5 cm) in both areas differed a lot in 2007, they were comparable in 2011 (and no longer significantly different; Table 2.2, 2.3: pairwise tests for factor area). This is the result of a clear increase in total nematode densities at B.West, and a slight (but insignificant) decrease at B.South (Table 2.2, 2.3: pairwise tests for factor year). Also nematode vertical distribution differed between stations and years (Fig. 2.2). Vertical profiles showed steep declines with depth in both years for B.South. Profiles were less steep at B.West, especially in 2011 when nematode density peaked at 1 – 2 cm and remained relatively high down to 4 cm depth.

Table 2.2. *Overview of total nematode density (ind.10cm^{-2}), diversity (N_0, EG(200), H', N_1) and evenness (N_{inf}, J'), averaged for five replicates per area × year combination. Values in brackets represent standard deviation.*

		Density (ind. 10 cm^{-2})	***N_0***	***EG(200)***	***H'***	***N_1***	***N_{inf}***	***J'***
2011	**B.South**	2547.81 (472.38)	35.60 (4.56)	24.13 (3.44)	2.29 (0.32)	10.23 (3.10)	2.38 (0.51)	0.64 (0.07)
	B.West	4832.24 (1038.26)	10.80 (2.39)	6.24 (1.35)	0.40 (0.16)	1.51 (0.26)	1.09 (0.06)	0.17 (0.05)
2007	**B.South**	3075.94 (235.34)	29.40 (1.52)	24.63 (0.82)	2.53 (0.08)	12.57 (1.01)	3.16 (0.41)	0.75 (0.02)
	B.West	604.71 (63.03)	20.80 (4.97)	16.90 (4.36)	1.57 (0.32)	4.99 (1.58)	1.89 (0.32)	0.52 (0.06)

Table 2.3. *Two-factor PERMANOVA main and pairwise test results for univariate parameters. Pseudo-F/t = effect size; P (perms) = permutational (perms > 100) or Monte Carlo (perms < 100) P-value. Numbers in brackets represent the number of unique permutations. Significance codes: *** P < 0.001; ** P < 0.01; * P < 0.05; • P < 0.1; ns = non-significant.*

		Density		**N_0**		**EG(200)**		**H'**		**N_1**		**N_{inf}**		**J'**	
	Main test	Pseudo-F/t	*P* (perms)	Pseudo-F/t	*P* (perms)	Pseudo-F/t	*P* (perms)	Pseudo-F/t	*P* (perms)	Pseudo-F/t	*P* (perms)	Pseudo-F/t	*P* (perms)	Pseudo-F/t	*P* (perms)
	Area	0.027	ns (>9000)	104.26	*** (>9000)	98.279	*** (>9000)	174.52	*** (>9000)	100.66	*** (>9000)	61.446	*** (>9000)	196.12	*** (>9000)
	Year	10.041	** (>9000)	1.3495	ns (>9000)	18.703	*** (>9000)	42.733	*** (>9000)	12.834	** (>9000)	23.622	*** (>9000)	83.039	*** (>9000)
	Area × Year	16.6	*** (>9000)	24.527	*** (>9000)	15.459	** (<9000)	18.331	** (>9000)	0.485	ns (>9000)	0.0025	ns (>9000)	22.775	*** (>9000)
	Pairwise test														
Area	2007	10.144	*** (126)	3.701	** (21)	3.895	** (126)	6.603	** (126)	–	–	–	–	7.444	** (126)
	2011	1.999	• (123)	10.772	*** (40)	10.826	** (126)	11.871	** (126)	–	–	–	–	11.967	** (126)
Year	B.South	1.001	ns (123)	2.885	* (13)	0.321	ns (126)	1.653	ns (126)	–	–	–	–	3.278	** (126)
	B.West	4.061	** (126)	4.056	** (26)	5.221	** (126)	7.398	** (126)	–	–	–	–	9.263	** (126)

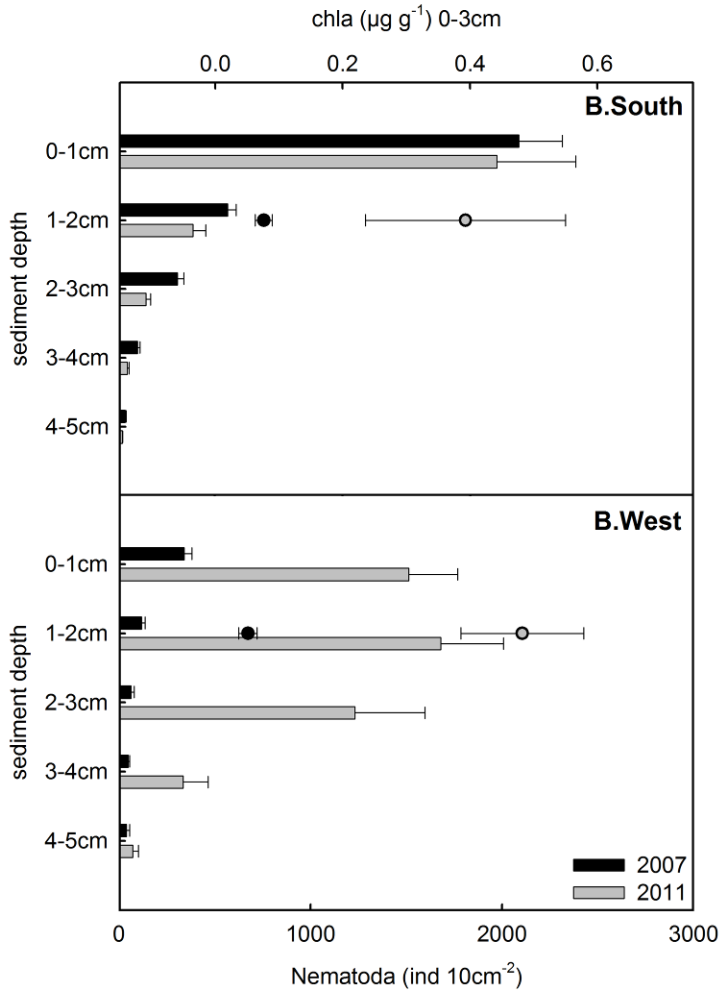

Figure 2.2. *Average vertical nematode abundance (bars) and surface (0-3cm) chlorophyll a values (dots) at stations B.West and B.South in 2007 (black) and 2011 (grey). Error bars indicate standard error (standard deviation/√number of replicates).*

Nematode community composition

Nematode community composition in 2011 differed significantly between stations and cm-layers (two-factor PERMANOVA, significant interaction 'area × layer'; results not shown) with largest differences between surface layers, gradually declining when moving deeper into the sediment (all pairwise $P < 0.05$). This is visible in the PCO plot for both stations in 2011 (Fig. 2.3). The first PCO axis (37.1 % variation) divides samples according to their location, while the second axis (20.2 % variation) is related to sediment depth. The dominant genera were *Microlaimus* at B.South and (a single species of) *Halomonhystera* at B.West (Table 2.4),

which together explained almost half of the dissimilarity between both stations (average dissimilarity = 85.58 %; contribution *Halomonhystera* + *Microlaimus* = 46.92 %; SIMPER).

Table 2.4. *Overview of the dominant genera at each station in 2007 and in 2011 (only genera with relative abundance > 1 % are included).*

B.South				**B.West**			
2007		**2011**		**2007**		**2011**	
Genus	%	Genus	%	Genus	%	Genus	%
Microlaimus	32.20	*Microlaimus*	23.65	*Halomonhystera*	57.88	*Halomonhystera*	94.02
Metadesmolaimus	10.98	*Monhystrella*	14.98	*Thalassomonhystera*	21.00		
Paracanthonchus	9.90	*Halomonhystera*	14.89	*Theristus*	3.83		
Halomonhystera	9.09	*Chromadorita*	10.36	*Acantholaimus*	3.17		
Monhystrella	4.23	*Leptolaimus*	6.65	*Daptonema*	2.28		
Neochromadora	3.11	*Dichromadora*	5.19	*Monhystrella*	1.97		
Prochromadorella	3.09	*Acantholaimus*	4.32	*Desmodorella*	1.83		
Araeolaimus	3.07	*Thalassomonhystera*	2.62	*Halalaimus*	1.19		
Acantholaimus	2.78	*Daptonema*	2.45				
Thalassomonhystera	2.35	*Halichoanolaimus*	1.83				
Theristus	2.00	*Syringolaimus*	1.36				
Leptolaimus	1.87	*Cervonema*	1.23				
Elzalia	1.42	*Amphimonhystrella*	1.15				
Daptonema	1.33						
Desmodorella	1.30						
Halichoanolaimus	1.27						
Dichromadora	1.18						
Desmodora	1.10						

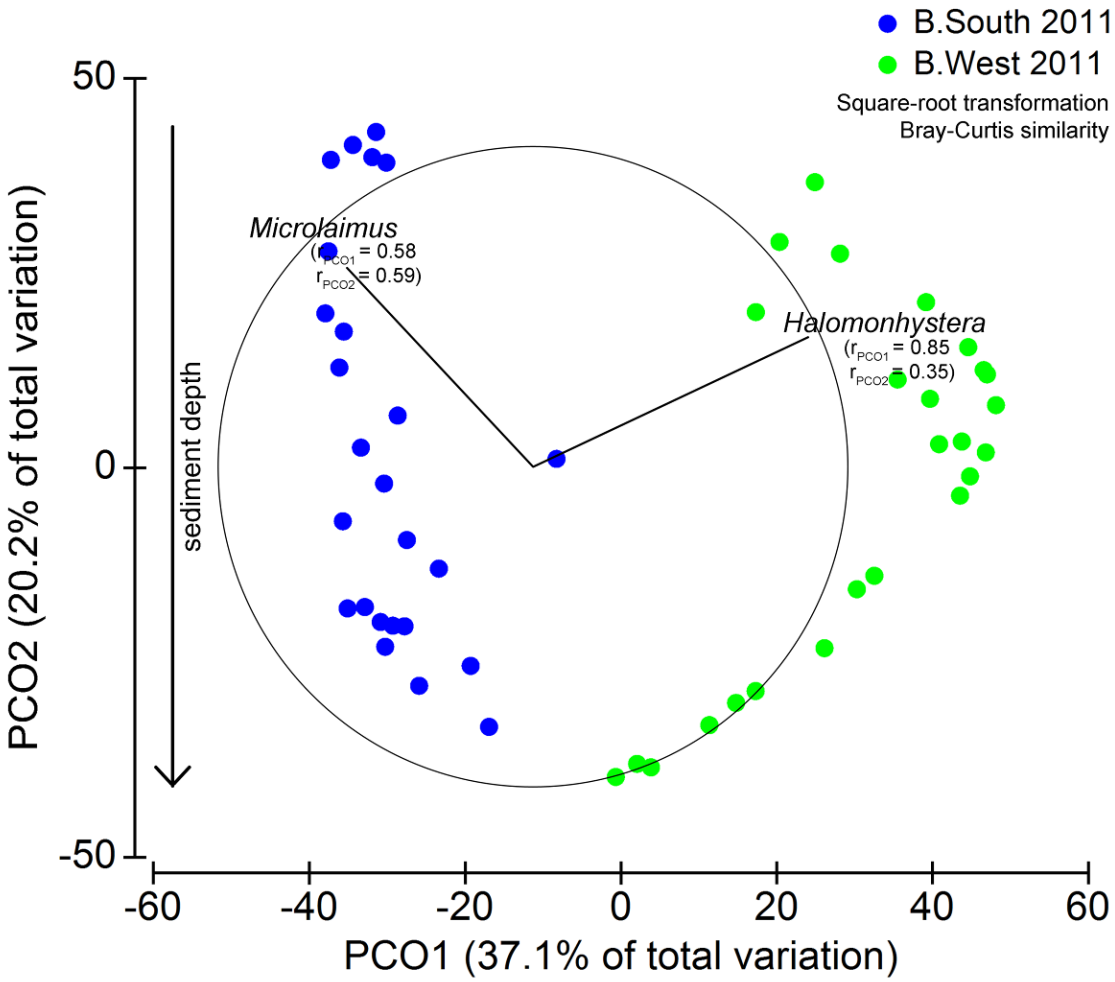

Figure 2.3. *PCO of square-root transformed nematode ind. 10 cm^{-2} in 2011. Vector overlays are genera with correlation > 0.77 with the resulting plot. For each genus, its correlation with both PCO axes is indicated.*

These two genera were also responsible for the clear separation between stations in terms of years (Fig. 2.4), since they remained most abundant at their respective area (Table 2.4). As a result, genus composition at B.South was relatively similar in 2007 and 2011, apart from some smaller differences (e.g., no *Metadesmolaimus* in 2011, Table 2.4). Also diversity and evenness remained fairly similar over the years (Table 2.2), with few significant differences (only N_1 and J'; Table 2.3: pairwise tests for factor year). On the contrary, diversity and evenness at B.West were even lower than in 2007 (and differences were always significant; Table 2.3), due to a profound increase in *Halomonhystera*, mainly in the upper two centimetres of sediment (Table 2.4; Fig. 2.2). Hence, as was the case in 2007, genus diversity and evenness remained highest at B.South.

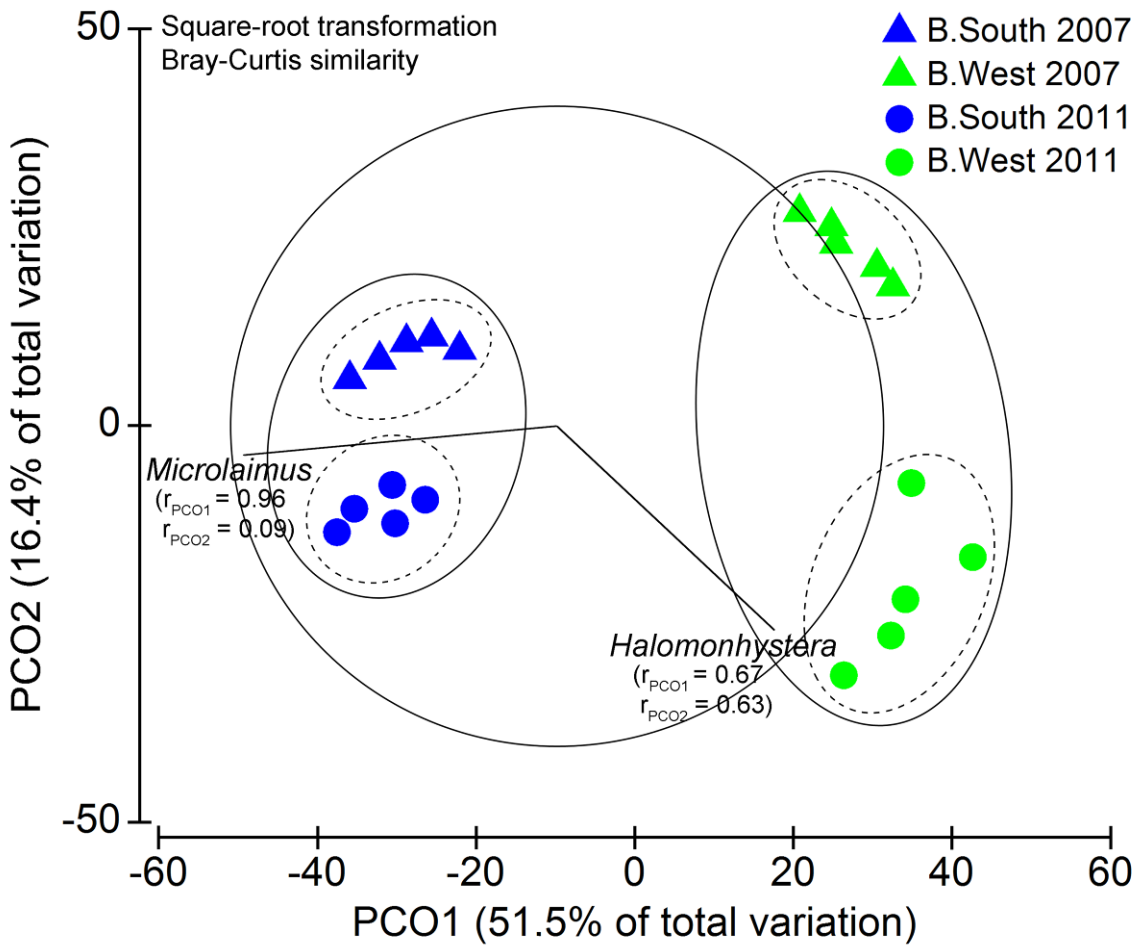

Figure 2.4. *PCO and CLUSTER analysis. Plot based on square-root transformed total ind. 10 cm^{-2} for each replicate of both stations and years (triangles = 2007, circles = 2011). Contours indicate 40 (full) and 60 % (dashed) similarity levels as calculated by CLUSTER. Vectors show overlays of Microlaimus and Halomonhystera, with their respective correlations with PCO axes.*

Three-factor PERMANOVA, including sediment depth, showed that the differences in nematode assemblages between areas and years further depended on depth in the sediment (significant three-way interaction, $P < 0.05$; Table 2.5). Communities of both areas differed mostly in surface layers and became more similar with depth (Fig. 2.5A: pairwise differences between stations for all levels of factors 'year' and 'layer'). This trend was more obvious in 2007 since communities in 2011 were more distinct in almost all depth layers. Alternatively, communities of both years became more similar at B.West with increasing depth, while the opposite occurred at B.South (Fig. 2.5B: pairwise dissimilarities across all levels of factors

'area' and 'layer'). This means that nematode assemblages in deeper layers of B.South diverged over the years, while they increasingly resembled each other at B.West (due to the large *Halomonhystera* contribution in all sediment layers in 2011).

Table 2.5. *Three-factor PERMANOVA main test results for nematode community data (ind. 10 cm^{-2}). Significance codes *** P < 0.001. df = degrees of freedom, Pseudo-F = effect size, P(perm) = permutational p-value, Perms = number of unique permutations*

Source	df	Pseudo-F	*P*(perm)	Perms
Area	1	57.055	***	9936
Year	1	15.321	***	9930
Layer	4	15.404	***	9877
Area × Year	1	13.625	***	9917
Area × Layer	4	6.594	***	9868
Year × Layer	4	2.543	***	9845
Area × Year × Layer	4	2.507	***	9855
Res	80			
Total	99			

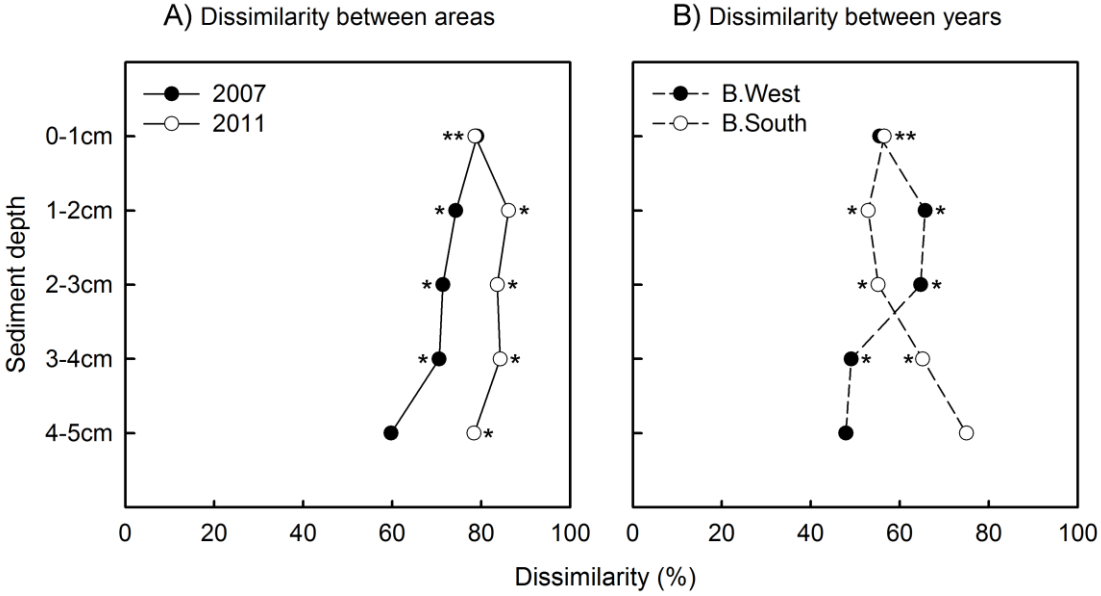

Figure 2.5. *Visualisation of PERMANOVA three-way interactions. A) Dissimilarities (%) between stations for each layer in 2007 (black) and 2011 (white). B) Dissimilarities (%) between years at B.West (black) and B.South (white). Asterisks indicate significant differences (pairwise P-values < 0.05).*

Environmental setting

Averaged environmental variables for each layer in both stations and years (where available) are given in Table 2.6 (data grouped over 0 – 3 and 3 – 5 cm for 2007; n(2007) = 5; n(2011) = 2). Silt was the dominant grain size for all layers at both locations. B.South had a slightly higher sand content in 2007, but only for the upper centimetres. The biggest difference was a significant increase in chl*a* from 2007 to 2011, for both B.South and B.West (Fig. 2.2). Chl*a* content was higher in surface layers (0 – 3 cm) than deeper down (3 – 5 cm). Chl*a* values in 2011 alone did not differ much between stations, only between sediment layers. B.South samples had about twice as much TOC and TOM than B.West, leading to a higher $C:N_{molar}$ as well (2011 only). BEST routine attributed 64 % of 2011 nematode community variation to a combination of chl*a* and TOC.

Table 2.6. *Average (standard deviation) values of environmental variables for 2007 and 2011 for each station, both divided in two layers, 0 – 3 cm and 3 – 5 cm. n = 5 for 2007 and n = 2 for 2011 samples. MGS = median grain size, silt% = percentage silt of total, sand% = percentage sand of total, chla = chlorophyll a concentration, TOM = wt% of total organic matter, TOC = wt% of total organic carbon, TN = wt% of total nitrogen,* $C:N_{molar}$ *= molar carbon:nitrogen ratio*

		MGS (µm)	silt% (<63 µm)	sand% (>63 µm)	chl*a* (µg g^{-1})	TOM (wt%)	TOC (wt%)	TN (wt%)	C:N molar
2011	**B.South**	19.50	96.09	3.91	0.39	0.08	0.58	0.06	11.57
	0 – 3 cm	(2.09)	(0.71)	(0.71)	(0.22)	(0.06)	(0.02)	(0.00)	(0.09)
	B.South	11.19	98.64	1.36	0.03	0.05	0.57	0.06	11.60
	3 – 5 cm	(6.52)	(1.92)	(1.92)	(0.00)	(0.01)	(0.01)	(0.00)	(0.17)
	B.West	18.15	99.70	0.30	0.48	0.03	0.25	0.05	7.05
	0 – 3 cm	(9.95)	(0.27)	(0.27)	(0.14)	(0.00)	(0.03)	(0.02)	(2.56)
	B.West	8.74	99.85	0.15	0.06	0.02	0.21	0.10	5.16
	3 – 5 cm	(0.40)	(0.03)	(0.03)	(0.04)	(0.01)	(0.03)	(0.04)	(2.84)
2007	**B.South**	34.34	90.56	9.44	0.08	–	–	–	–
	0 – 3 cm	(14.69)	(4.76)	(4.76)	(0.03)				
	B.South	14.85	97.77	2.23	0.01	–	–	–	–
	3 – 5 cm	(8.06)	(2.30)	(2.30)	(0.01)				
	B.West	10.14	99.28	0.72	0.05	–	–	–	–
	0 – 3 cm	(1.07)	(0.31)	(0.31)	(0.03)				
	B.West	9.87	99.43	0.57	0.00	–	–	–	–
	3 – 5 cm	(3.08)	(0.84)	(0.84)	(0.00)				

Broader geographic comparison

Plotting of Larsen communities within a larger geographical context showed that, despite large dissimilarities observed within the area, communities differed substantially from those in other Antarctic shelf regions (Table 2.7, Fig. 2.6). Significant differences were found between all regions (R = 0.633, $P < 0.05$; one-way ANOSIM), but they were largest between B.West and the other locations. Pairwise differences between the Larsen B stations and the other areas decreased from 2007 to 2011 for B.South, but increased for B.West (data not shown). Differences with other regions were (mostly) due to the low abundance of *Sabatieria* and high abundance of *Microlaimus* for B.South; while they were mainly attributable to high contributions of the Monhysteridae (including *Halomonhystera*) and the absence of *Sabatieria* in the case of B.West (SIMPER).

Table 2.7. *Location and depth range of references included in the (sub)-Antarctic database.*

reference	publication year	region	broader area	depth range (m)	collection year
Chen et al.	1999	Beagle Channel, Magellan Strait	Magellan	10 – 550 m	1994
Hauquier et al.	2011	Larsen B	Larsen 2007	~ 820 m	2007
Hauquier et al.	2015	Drake Passage, NE Weddell Sea	Peninsula	470 – 520 m	2013
Ingels et al.	2006	Signy Island, South Georgia	Peninsula	~ 300 m	2002
Lee et al.	2001	Kapp Norvegia	eastern Weddell	200 – 300 m	1998
Lee et al.	unpublished	Bransfield Strait, Drake Passage	Peninsula	200 – 430 m	1998
Lee et al.	unpublished	Kapp Norvegia, Vestkapp	eastern Weddell	~ 200 m	1996
Luyten	1999	Adelaide Island	Peninsula	5 – 30 m	1998
Manachini	1997	Kapp Norvegia, Ross Sea	eastern Weddell /Ross Sea	200 – 600 m	1994, 1996
Raes et al.	unpublished	Elephant Island	Peninsula	~ 430 m	2006
Raes et al.	2010	Larsen A, B	Larsen 2007	240 – 430 m	2007
Vanhove et al.	1997	Kapp Norvegia, Halley Bay	eastern Weddell	200 – 800 m	1989
Vanhove et al.	1998	Signy Island	Peninsula	~ 10 m	1994
Vanhove et al.	2004	South Sandwich Trench	Peninsula	~ 750 m	2002

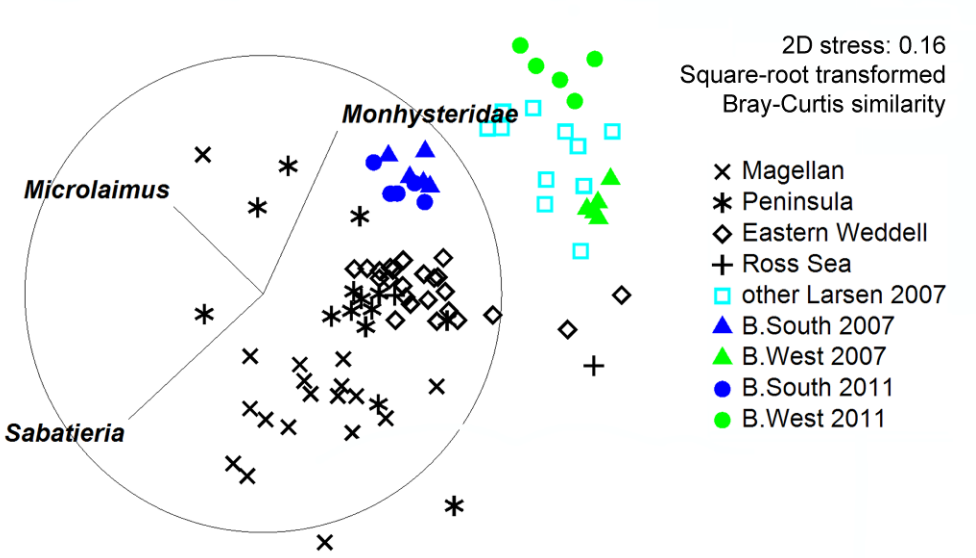

Figure 2.6. *Comparison of different Antarctic shelf areas. Vector overlays represent three main contributors to community differences. Only data of 0 – 1000 m depth range were included in the reference database. nMDS based on Bray-Curtis similarity of square-root transformed data.*

DISCUSSION

Large-scale ice-shelf disintegration is one of many consequences of the rapid warming trend observed along the Antarctic Peninsula. Although most of the LIS-A/B disintegration occurred over a rather short time period (1995 – 2002), its effects will persist over a longer time span. Therefore, the aim of both ANT-XXIII/8 and ANT-XXVII/3 was to collect information at different time intervals for several components of the marine food web to be able to anticipate to future responses, and relate changes and patterns to the situation observed before (Gutt et al., 2011).

Environmental setting and implications for benthic communities

Four years after the first sampling campaign, rapid regional warming in Antarctic Peninsula surroundings continues, evoking additional ice-mass loss in the Larsen area (Shuman et al., 2011; Berthier et al., 2012). Consequently, seasonal phytoplankton blooms emerge (Barnes & Clarke, 2011), further modifying benthic habitats at former ice-shelf locations from an oligotrophic to a more productive state. New organic matter production in the Larsen area was demonstrated by remote sensing of net primary productivity in 1997 – 2011 (Cape et al., 2014), and diatom siliceous frustules found in the upper two centimetres of the sediment (i.e.

the layer corresponding to post-ice-shelf deposition; Sañé et al., 2013). Productivity in Larsen A and B is now as high as that for other Antarctic shelf locations, and tightly linked to seasonal polynya dynamics (Cape et al., 2014). Average chl*a* values reported in 2011 surface sediments (Table 2.6) are indeed comparable to those found elsewhere on the Antarctic shelf (e.g., Fabiano & Danovaro, 1999: 0.25 – 0.38 µg g^{-1} at 430 – 590 m in the Ross Sea; Vanhove et al., 2004: 0.36 – 0.52 µg g^{-1} at 750 m in the Weddell Sea). The five to tenfold increase in sediment chl*a* compared to 2007 conceivably demonstrates higher productivity in the area as more time passed since ice-shelf collapse. However, considering a time lag between production in surface photic layers and transport of phytodetritus through the water column, summer-bloom chlorophyll could have already reached the seafloor and benthic communities in 2011 (late-summer sampling), but not in 2007 (early-summer sampling). Furthermore, primary production in the Larsen area depends heavily on the sporadic break-up of seasonal sea ice, which makes food supply to the benthos hardly predictable in space and time, especially in terms of the high interannual variability (Gutt et al., 2013).

Since meiofaunal assemblages are tightly linked to fresh food input (Lins et al., 2014, 2015), it is almost inevitable that the transition to a more productive (yet still highly seasonal) state will influence nematode communities (cf. TOC and chl*a* main explanatory variables in BEST results). Organic matter in surface marine sediments lies usually within the range of 0.1 – 5 wt%, of which the lower extreme (0.1 – 0.2 wt%) typically occurs in fine-grained sediments of well-oxygenated bathyal and abyssal depths, while average TOC values of 0.5 – 3 wt% dominate in deltas and on upper continental margins (Hedges & Oades, 1997). Surface TOC content at B.West was thus relatively low compared to global means, while values at B.South were clearly higher, situated within the intermediate range, and comparable to values reported in other Antarctic studies at similar depths (0.2 – 0.75 wt%; Domack & Ishman, 1993; Giordano et al., 1999).

Not only the quantity, but also the quality and source of food can influence benthic community composition. Due to the cold temperatures of Antarctic waters, phytodetritus degradation is slow, allowing its accumulation in sediment 'foodbanks' (Mincks et al., 2008; Smith et al., 2006, 2008). These foodbanks can sustain a rich benthic community throughout the year (especially in long winters), even when fresh input is lacking. In addition, phytoplankton supply to the seafloor in sub-ice zones is considerably lower than in open water owing to lower sedimentation rates (Post et al., 2007). Combining both phenomena (i.e. low degradation and sedimentation rates) and taking into account the closer connection of

B.South to open water and phytodetritus input, a substantial foodbank could have developed at this site; and nematode assemblages could be feeding on organic matter that accumulated over the course of many years (cf. higher TOC and TOM; Table 2.6). In contrast, longer persisting ice cover at B.West prevented the establishment of an extensive foodbank, rendering communities highly dependent upon short pulses of fresh material after ice-shelf collapse (demonstrated by higher chl*a* values).

2007 – 2011 Nematode community change

The original high dissimilarity in nematode community composition between B.South and B.West in 2007 (Raes et al., 2010) was still evident four years later, and temporal changes in nematode assemblages were quite different for both stations.

Density, diversity and generic composition at B.South remained fairly similar over the years (Fig. 2.2, 2.4; Table 2.2, 2.4), and changed with depth into the sediment. The community was still dominated by *Microlaimus*, an epistratum-feeder (Wieser, 1953) that is generally widespread in shallow and deep-sea habitats (Tita et al., 2002; Gambi et al., 2003; Vanhove et al., 2004; Sebastian et al., 2007; Van Gaever et al., 2009b; Portnova et al., 2010; Vanreusel et al., 2010b). This opportunistic genus often attains elevated abundance in deeper areas that are more organically enriched (Sebastian et al., 2007; Van Gaever et al., 2004, 2006, 2009b) or recently disturbed (e.g., after iceberg scouring; Lee et al., 2001), in which case it is considered a pioneering coloniser. Since there were no signs of disturbance related to iceberg scouring at the time of sampling, the first explanation seems more likely. To reach current numbers at B.South, *Microlaimus* could have benefited from lateral advective food input from the Weddell Sea during ice-shelf cover, complemented by increased levels of phytodetritus accretion after ice-shelf collapse. Even so, in spite of continued seasonal ice-free periods and enhanced food conditions, changes between 2007 and 2011 nematode assemblages at B.South were not very prominent, suggesting a relatively steady community, comparable to other Antarctic shelf areas in terms of abundance and biodiversity (Raes et al., 2010). Nevertheless, generic composition at B.South was not entirely comparable to that of other Antarctic shelf areas, mainly attributable to the genera *Sabatieria* and *Microlaimus* (SIMPER; Fig. 2.6). Only a few individuals of *Sabatieria* were observed at B.South whilst it is usually quite common in shelf samples, especially in muddy sediments (as was the case in the Larsen; Schratzberger et al., 2009; Van Gaever et al., 2009b). It tends to reside in deeper sediment layers (associated with the Redox Potential Discontinuity (RPD) layer; Vanreusel et al., 2010a; Guilini et al.,

2011), where a substantial fraction of organic material becomes incorporated below the oxic zone. Perhaps Larsen sediment conditions were not yet favourable for *Sabatieria*, since organic matter burial was rather limited in the millennia preceding ice-shelf collision; or, alternatively, *Sabatieria* could not reach the area or establish a stable population within the four years time. Either way, the nematode community at B.South did not converge with other Antarctic shelf fauna as we hypothesised, although differences with other areas did decline over the years (pairwise ANOSIM).

Nematode assemblages at B.West were even more distinct from other shelf communities than at B.South (Fig. 2.6), since > 90 % of total abundance consisted of *Halomonhystera* (and *Sabatieria* was virtually absent). *Halomonhystera* is classified as a non-selective deposit feeder *sensu* Wieser (1953) and a general opportunistic genus (Bongers et al., 1991). Compared to the 2007 situation, densities increased drastically while diversity decreased due to proliferation of *Halomonhystera*. According to Raes et al. (2010), low density and low genus richness in 2007 reflected pre-collapse oligotrophic conditions. At that time, *Halomonhystera* was mainly found in deeper sediment layers (upper cm dominated by *Thalassomonhystera*), which generally contain less food. The drastic increase in *Halomonhystera* densities at station B.West over the course of only a few years is thus at least remarkable. One possible explanation is that increased direct supply of fresh food to the seabed has triggered opportunistic feeding behaviour of *Halomonhystera*[17]. Earlier research on one species of *Halomonhystera*, *H. disjuncta*, has classified it as an efficient coloniser, capable of expressing priority effects (Derycke et al., 2007b; Van Gaever et al., 2009a), a situation where first colonising individuals have such a strong population development that they inhibit the settlement of other species. This could explain why community composition at B.West was still very different from B.South, even after a longer time period: *Microlaimus* and other genera potentially able to profit from open-water conditions do not get a chance to settle in the *Halomonhystera*-dominated sediments (provided that they did reach the area

[17] Elevated densities and relative abundance of *Halomonhystera* at B.West might also be related to a seasonality effect. Both in 2007 as well as in 2011 community composition at station B.West was dominated by members of the family Monhysteridae (Table 2.4), accounting for > 79 % of total communities. The increased dominance of *Halomonhystera* over *Thalassomonhystera* in 2011 can thus also be related to a difference in timing of sampling in both years. In 2007, sampling occurred in early summer at the peak of phytoplankton blooming (hence, probably before the input of fresh phytodetritus; Cape et al., 2014), while this was late summer in 2011 (after settlement of phytodetritus). *Halomonhystera* has a relatively short life cycle (Van Gaever et al., 2006), which can make it the most opportunistic genus within the monhysterid group. Nevertheless, differences between B.West and B.South remain large, even when accounting for the possibility of a seasonal enhancement of *Halomonhystera* numbers.

though; see further). Alternatively, it is possible that *Halomonhystera* is responding to sedimentary features other than fresh phytodetritus input. In fact, the subsurface (1 – 2 cm) maximum in *Halomonhystera* abundance strongly resembles the vertical profile observed at station Larsen B.Seep reported by Hauquier et al. (2011), where a low-active cold seep was found (~ 800 m; Niemann et al., 2009) within the same area. Also there, nematode assemblages were characterised by high densities, deeper density maxima and high dominance of one *Halomonhystera* species. This prompted the question whether *Halomonhystera* depended upon chemosynthetically-derived organic matter, as was the case with *Halomonhystera hermesi* (earlier identified as *H. disjuncta*) in sulphidic, microbial mat sediments at the Håkon Mosby Mud Volcano (~ 1300 m; Van Gaever et al., 2006). However, stable isotope data for B.Seep did not indicate such a relationship, leading to the conclusion that *Halomonhystera* thrives on phytoplanktonic rather than chemosynthetic resources (Hauquier et al., 2011). The fact that there were no signs of elevated sulphide levels, anoxia or seepage at the time of sampling at B.West further strengthens this conclusion.

Whatever the reason or mechanism behind it, the success of *Halomonhystera* at B.West in 2011 further isolated the community from B.South (and by extension any other Antarctic shelf region) compared to 2007. Instead of anticipated convergence of communities at both stations, they increasingly diverged from each other.

Nematode colonisation dynamics

Besides food availability as a local, environmental driver for differences between areas, also more regional processes such as colonisation ability of organisms can structure benthic communities. Marine nematode dispersal is dependent on body morphology, swimming ability and feeding strategies (Thomas & Lana, 2011), and since nematodes lack pelagic larvae or propagules, dispersal is in this case synonymous to gene flow (Derycke et al., 2013). It was already shown that nematode colonisation is a slow process (Post et al., 2007), predominantly driven by passive transport via bottom currents (Boeckner et al., 2009); and not necessarily related to higher food input (e.g., Guilini et al., 2011). Furthermore, colonisation dynamics depend on the distance (Derycke et al., 2007a), proximity of a source population, and the time needed for successful settlement and reproduction (Schratzberger et al., 2006; Raes et al., 2010). Closer connection of B.South to the open Weddell Sea as a source for new recruits may therefore partly explain observed differences with B.West. Raes et al. (2010) calculated a speed of recovery of 60.8 m yr^{-1} and hence, approximately 1000

years needed to cross the distance of 70.8 km between B.West and B.South[18]. So far, too little time has passed for the nematodes to travel between both Larsen stations on one hand, and between larger geographical areas on the other hand.

Comparison with other benthic groups

Nematodes are only one taxonomic player in the Antarctic marine benthic food web and it can be valuable to compare their response with other food-web compartments, as changes at one trophic level may impact other faunal components (either bottom-up or top-down) or remineralisation processes in the sediment (e.g., Moline et al., 2004; Montes-Hugo et al., 2009). As already shown in 2007 (Gutt et al., 2011), different benthic components react in different ways to the ice-shelf collapse, each at their own pace (some organisms are more sensitive to disturbance, especially long-lived taxa such as Porifera). Results on other trophic levels for the 2011 expedition remain scarce so far, but Gutt et al. (2013) found a drastic decrease in the aggregations of two ascidians between 2007 and 2011 but an increase in abundances of deposit-feeding ophiuroids. Although they could not relate their findings to particular environmental characteristics, it clearly shows the high dynamics of Antarctic benthos and the probability for both negative and positive effects to arise after large-scale alterations. Together with this study, their research highlights the difficulties to relate changes in faunal communities to environmental factors because benthic responses may take a long time and are highly variable.

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[18] Results from a current meter moored at 242 m depth in the southern Larsen A embayment (i.e. in close connection to the northern part of the Larsen B area) at the time of sampling indicated a net north-east current direction with a velocity of roughly 2.1 m s^{-1} (Gutt et al., 2013). In case this value is representative for the entire area, and if bottom currents are capable of resuspending and transporting nematodes, the distance between both stations might be crossed much more rapidly (~ 39 days for 71 km). However, detailed information across the entire area is not available.

CHAPTER 3: DIFFERENT OCEANOGRAPHIC REGIMES IN THE VICINITY OF THE ANTARCTIC PENINSULA REFLECTED IN BENTHIC NEMATODE COMMUNITIES

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ABSTRACT

Marine free-living nematode communities were studied at similar depths (~ 500 m) at two sides of the Antarctic Peninsula, characterised by different environmental and oceanographic conditions. At the Weddell Sea side, benthic communities are influenced by cold deep-water formation and seasonal sea-ice conditions, whereas the Drake Passage side experiences milder oceanic conditions and strong dynamics of the Antarctic Circumpolar Current. This resulted in different surface primary productivity, which contrasted with observed benthic pigment patterns and varied according to the area studied: chlorophyll *a* concentrations (as a proxy for primary production) were high in the Weddell Sea sediments, but low in the surface waters above; this pattern was reversed in the Drake Passage. Differences between areas were largely mirrored by the nematode communities: nematode densities peaked in Weddell stations and showed deeper vertical occurrence in the sediment, associated with deeper penetration of chlorophyll *a* and indicative of a strong bentho-pelagic coupling. Generic composition showed some similarities across both areas, though differences in the relative contribution of certain genera were noted, together with distinct community shifts with depth in the sediment at all locations.

INTRODUCTION

The Antarctic Peninsula and surrounding Southern Ocean have been studied extensively during past decades due to their relevance in a historical, climatological, ecological and biogeographical context. Ever since the opening of the Drake Passage in the Oligocene (32 – 23 Ma; (Lawver & Gahagan, 2003; Thomson, 2004; but see also Barker & Thomas, 2004) and the subsequent establishment of the Antarctic Circumpolar Current (ACC; Barker, 2001), the Antarctic Peninsula has lost its direct connection to southernmost South America. Faunal links and gene flow, however, are still recognisable for some taxonomic groups (Damereau et al., 2012; Díaz et al., 2011; Figuerola et al., 2014) and many authors argue that the Scotia Arc islands continue to serve as a "stepping-stone" route towards 'true' Antarctic waters (Arntz et al., 2005; Clarke, 2008; Ingels et al., 2006). Throughout history, the ACC has effectively isolated Antarctica from sub-Antarctic influences (although it cannot be seen as an impermeable barrier; Barnes et al., 2006; Brandt et al., 2007a, b; Clarke & Johnston, 2003; Clarke et al., 2005). The resulting gradual cooling of Southern Ocean waters (due to a decrease in atmospheric CO_2 and changes in ocean circulation; Barker & Thomas, 2004; DeConto & Pollard, 2003) inhibited successful settlement and survival of some animal taxa (e.g., decapod crabs and teleost fish), whereas others flourished (e.g., peracarid crustaceans

and echinoderms; Arntz et al., 2005; Aronson & Blake, 2001; Crame, 1999). Not surprisingly, it is mainly this difference in seabed temperatures between the cold Southern Ocean and warmer waters north of the polar front that defines the nature of Antarctic benthic assemblages (Clarke et al., 2009). Over the course of history, they have adapted to the prevailing conditions and are usually vulnerable to environmental change (Barnes & Peck, 2008; Peck et al., 2004).

Currently, the Antarctic Peninsula is classified as one of the regions worldwide that is experiencing rapid atmospheric and oceanic warming (Meredith & King, 2005; Vaughan et al., 2003), and as such is amongst the fastest warming and changing regions on Earth (Smale & Barnes, 2008). It should therefore come as no surprise that consequences (either direct or indirect) can already be observed in both physical and chemical properties of the marine environment (e.g., southward movement of ACC; Allan et al., 2013), ice-shelf and sea-ice dynamics (e.g., large-scale ice-shelf disintegration; Rack & Rott, 2004), and characteristics of the marine food web (e.g., shifts in phytoplankton communities; Mendes et al., 2013; Moline et al., 2004; Montes-Hugo et al., 2009). Seafloor-inhabiting communities near the Antarctic Peninsula are strongly dependent on bentho-pelagic coupling for their every-day life. Variable conditions in ice cover, temperatures, hydrographic dynamics and circulation patterns, and seasonality in primary productivity all interfere with each other and play a significant role in the functioning and structuring of the Antarctic ecosystem (Grebmeier & Barry, 1991; Jiang et al., 2013; Montes-Hugo et al., 2009). Even though food supply in Antarctic waters is highly seasonal, related transfer and input of organic matter to the sediment is able to sustain an abundant benthic community (Arntz et al., 1994; Dayton, 1990; Ingels et al., 2010; San Vicente et al., 1997; Smith et al., 2006; Veit-Köhler et al., 2011). In this regard, the quantity and quality of phytodetritus deposition to the marine sediment largely define the success of benthic fauna (Arrigo et al., 2008; Glover et al., 2008; Maar & Hansen, 2011; Webb & Montagna, 1993; Witbaard et al., 2001). At the same time, current dynamics and water-mass origin influence a variety of benthic processes, such as larval dispersion, transport of nutrients, oxygenation of the sediment (enhancing bacterial activity; Morán et al., 2001; Videau et al., 1994), and growth, recruitment and feeding strategy of local fauna (Jumars & Nowell, 1984). All these parameters have shaped benthic communities over time and will continue to do so in the near future. Climate change has added an extra dimension of complexity that cannot be ignored; imminent changes in physical parameters, productivity regimes and seasonality as a result of continued warming in the Antarctic Peninsula region will undoubtedly influence

benthic communities, but the consequences are barely understood (Gutt et al., 2014). Understanding the responses of the benthos to such climate-induced changes therefore requires as much information as possible on all levels of the food web.

To this end, the main goal of expedition ANT-XXIX/3 in 2013 (Gutt, 2013) was to assess a variety of taxonomic groups in the Antarctic Peninsula region, sampling from the high-Antarctic Weddell area through the Bransfield Strait towards ACC-controlled waters north of the South Shetland Islands. This region marks the transition from cold Weddell Sea waters to warmer waters of the ACC (Lockhart & Jones, 2008; Schröder et al., 2002). The associated shift in seabed temperatures is largely mirrored by megabenthic communities, with a change from suspension-feeding hexactinellid sponge-dominated communities at Weddell Sea continental shelves to more motile echinoderm-dominated assemblages north of the South Shetland Islands in the Drake Passage (Lockhart & Jones, 2008; Piepenburg et al., 2002). Apparently, the physical properties of the ACC and Weddell Sea water masses dictate these differences in megafaunal composition and feeding mode, hence, a similar pattern can be expected for other benthic components (Clarke et al., 2009). Within this broader framework, this study will look at the smaller meiobenthos (32 – 1000 µm) at both sides of the peninsula to relate patterns in distribution and diversity to pelagic and oceanographic processes and dynamics. More specifically, focus will be on the free-living nematodes, a phylum with high ecological relevance. Nematodes are widespread around the world, even in the most extreme habitats, and are normally present in high abundance (Heip et al., 1985). They show a strong correlation with biochemical conditions and characteristics of the sediment, which in turn are influenced by surface-water dynamics. Additionally, the link between surface primary productivity and nematode community structure has been verified on different occasions (Guilini et al., 2013; Lins et al., 2014, 2015), proving their dependence upon food input from photic layers.

In accordance with the findings for the megabenthos (Lockhart & Jones, 2008) in the area and with findings for other Southern Ocean nematode communities (Guilini et al., 2013; Lins et al., 2014, 2015), it is hypothesised that:

i. regions with high surface primary production will support high nematode densities due to strong bentho-pelagic coupling,
ii. nematode community structure will depend on the physical characteristics (mainly temperature, cf. Clarke et al., 2009) of the different water masses,

iii. nematode genus composition and feeding mode will differ between both sides (cf. pronounced shift in feeding mode, hence composition, of the surface-dwelling megafauna; Lockhart & Jones, 2008).

MATERIAL AND METHODS

Sampling area and strategy

Sampling was conducted near the Antarctic Peninsula during expedition ANT-XXIX/3 of the German icebreaking RV *Polarstern* in January – March 2013 (Gutt, 2013), under permission of German (German Federal Environment Agency - Umweltbundesamt) and Belgian (Federal Public Service Health, Food Chain Safety and Environment - DG Environment) authorities, in compliance with the Antarctic Treaty System for all locations. No endangered or protected species have been collected for this study. Samples were taken at deep shelf depths (approx. 500 m) at two main locations: (1) northeast of the AP under Weddell Sea influence and (2) west of the AP, on the shelf of the South Shetland Islands in Drake Passage waters (Table 3.1, Fig. 3.1a). Each location is represented by two stations with one CTD and three repeated multicorer (MUC) deployments (core diameter 57 mm, surface area 25.52 cm²; Barnett et al., 1984). For clarity and consistency throughout this manuscript, the four stations will be abbreviated by using their location initials (W for Weddell; DP for Drake Passage) combined with the station number (e.g., 120).

Table 3.1. *Details of the four sampling areas: each station was sampled once with a CTD, followed by three replicate MUC deployments.*

Station	Gear	Replicate	Date	Latitude	Longitude	Depth (m)
W-120	CTD	1	28/01/2013	63°4.62´S	54°33.11´W	530.4
	MUC	1	28/01/2013	63°4.58´S	54°31.00´W	503.6
	MUC	2	28/01/2013	63°4.10´S	54°30.86´W	484.8
	MUC	3	28/01/2013	63°3.72´S	54°30.87´W	436.8
W-163	CTD	1	10/02/2013	63°53.07´S	56°26.19´W	468
	MUC	1	11/02/2013	63°50.95´S	56°24.43´W	517.6
	MUC	2	11/02/2013	63°51.01´S	56°23.97´W	516.6
	MUC	3	11/02/2013	63°51.03´S	56°23.68´W	517.1
DP-243	CTD	1	10/03/2013	62°12.27´S	60°44.42´W	497.4
	MUC	1	10/03/2013	62°12.32´S	60°44.47´W	497.8
	MUC	2	10/03/2013	62°12.31´S	60°44.48´W	497.7
	MUC	3	10/03/2013	62°12.31´S	60°44.54´W	495.2
DP-250	CTD	1	12/03/2013	62°2.28´S	60°12.11´W	487
	MUC	1	12/03/2013	62°2.22´S	60°12.01´W	489
	MUC	2	12/03/2013	62°2.24´S	60°12.06´W	488
	MUC	3	12/03/2013	62°2.24´S	60°12.03´W	488

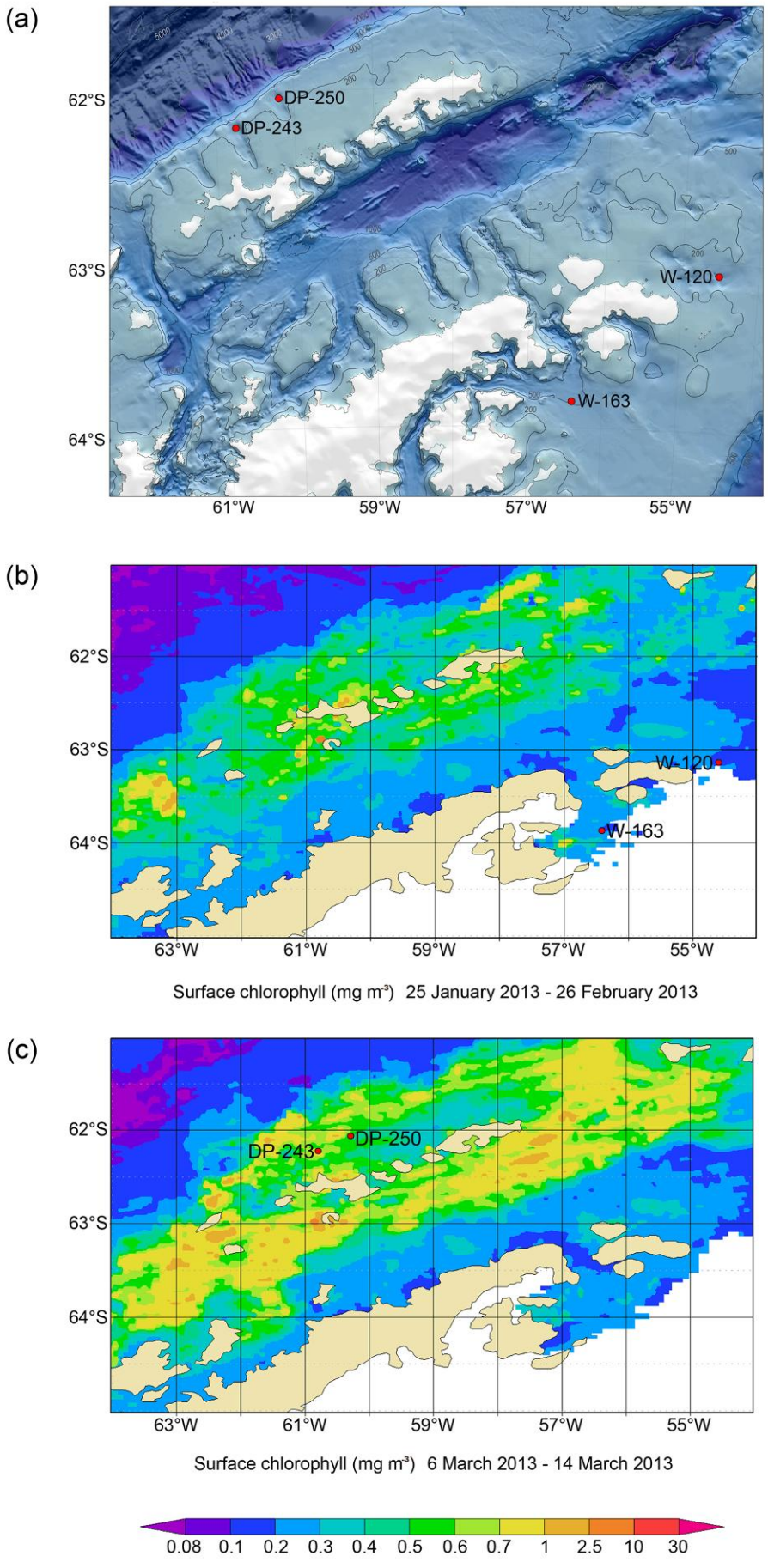
(a)
62°S
63°S
64°S
DP-250
DP-243
W-120
W-163
61°W
59°W
57°W
55°W
(b)
62°S
63°S
64°S
W-120
W-163
63°W
61°W
59°W
57°W
55°W
Surface chlorophyll (mg m-3) 25 January 2013 - 26 February 2013
(c)
62°S
63°S
64°S
DP-243
DP-250
63°W
61°W
59°W
57°W
55°W
Surface chlorophyll (mg m-3) 6 March 2013 - 14 March 2013
0.08 0.1 0.2 0.3 0.4 0.5 0.6 0.7 1 2.5 10 30

Figure 3.1. (previous page) *(a) Location of the four sampling stations (W-120 and W-163 east of the Antarctic Peninsula; DP-243 and DP-250 west in Drake Passage); map adapted from Alfred Wegener Institute bathymetry group; (b) + (c) Surface chl a concentrations (in mg* m^{-3}*) at the respective sampling times for both sites. Graphs are based on MODIS Aqua data (NASA) of the sea surface on 8 – day averages during the period of sampling and produced with the Giovanni online data system, developed and maintained by the NASA GES DISC.*

One core from each replicate deployment was sliced per centimetre down to 5 cm depth and stored in a 4 % formaldehyde-seawater solution for faunal analysis, while a second set of cores was collected for the analysis of environmental variables. These latter cores were sub-sampled with cut-off 10 ml syringes pushed into the sediment (0 – 5 cm) and stored at –20 °C (granulometry, total organic carbon TOC and nitrogen TN) or –80 °C (pigment content). In conjunction with sediment sampling, Niskin bottles mounted on a CTD rosette were deployed at chlorophyll-maximum (~ 20 – 50 m, defined by looking at in-situ chlorophyll profiles) and bottom depths (~ 450 – 510 m) of each station to assess water-mass properties (temperature and salinity) and chlorophyll content in the water column (see Figs 3.1b and 3.1c for surface chlorophyll *a* concentrations based on satellite data from NASA MODIS)[19]. Collected water was first poured over a 100 µm mesh to remove larger particles, after which 3 to 5 l was filtered at approximately 250 mbar over glass microfiber GF/C filters (1.2 µm pore size; Knefelkamp et al., 2007; no replication) until colouring of the filters became apparent. Filters were then stored at –80 °C.

Meiofauna and Nematoda

The upper 5 cm of the cores for faunal analysis were divided into cm-layers. Meiofauna was extracted from the sediment using two stacked sieves (upper limit 1 mm, lower limit 32 µm; Giere, 2009) and density gradient centrifugation (3 × 12 min at 3000 rpm) with Ludox HS-40 as a flotation medium (specific density of 1.18 g cm^{-3}; Heip et al., 1985; Vincx, 1996). All taxa were counted and identified under a stereomicroscope (magnification 50 ×) using the identification key of Higgins and Thiel (1988). From each layer, 150 nematodes (all if the layer contained less than 150 individuals) were randomly selected, stored in anhydrous

[19] A time-integrated overview of surface chlorophyll concentrations in the area based on satellite data has recently been published and can be consulted in the work of Dorschel et al. (2016).

glycerol and mounted on glycerine slides for identification (De Grisse, 1969). Genus-level identification (9000 specimens) was done with a Leica DMLS compound microscope (magnification 1000 ×), using the pictorial key to nematode genera of Platt & Warwick (1983, 1998), the Nematoda chapter in the Handbook of Zoology (Bain et al., 2013) and the NeMys database (Guilini et al., 2016). Supplementary data on nematode genus composition is available at http://doi.pangaea.de/10.1594/PANGAEA.846306.

Environmental characterisation

Chl *a* concentration in the water column (at both chlorophyll maximum and bottom depth) was determined with a fluorimeter from the GF/C filters. Concentrations are reported in µg l^{-1} (= equivalent to mg m^{-3}). Pigment content of the sediment was measured with a fluorescence detector after separation using HPLC (High Performance Liquid Chromatography)[20]. Prior to analysis, syringe cores were divided at the same vertical resolution as faunal samples. Pigments were extracted from the lyophilised sediments by adding 10 ml of 90 % acetone. For each slice, both chl *a* and phaeopigments (i.e. degradation products of chl *a*) were determined and results expressed in µg g^{-1}. Chloroplastic pigment equivalents (CPE) are then the sum of chlorophyll *a* and phaeopigments, whereas their ratio indicates the amount of fresh material. Grain size was determined with laser diffraction (Malvern Mastersizer 2000, size range: 0.02 – 2000 µm) and size fractions were classified according to Wentworth (1922). For simplicity reasons, fractions have been summed to restrict their number to three: silt+clay % (< 63 µm), sand % (63 – 500 µm) and coarse sand % (> 500 µm). Finally, weight percentages of total organic carbon (TOC) and nitrogen (TN) were determined by combustion of freeze-dried samples using a Flash 2000 organic elemental analyser (protocol available through Interscience B.V., Breda, The Netherlands; methodology similar to Verardo et al., 1990). The ratio of C:N was calculated, multiplying with a factor 14:12 to account for the difference in molar mass of both elements.

[20] Details on HPLC protocol: Samples were lyophilised, extracted in 90 % acetone, and filtered at 0.2 µm after a few hours. Depending on the concentration, 50 or 100 µl was injected into the HPLC system (Gilson, Inc.). Reverse phase chromatography used a C18 column (MACHEREY-NAGEL) with a particle size of 5 µm, inner diameter of 4.6 mm and length of 25 cm. Concentrations were measured by means of a spectrophotometer, diode array detector and fluorimeter.

Data analysis

Faunal data were analysed using PRIMER v6 software (Clarke & Gorley, 2006) with the PERMANOVA+ add-on package (Anderson et al., 2008). Nematode genus data were standardised to individuals per 10 cm² and square-root transformed to down-weight the importance of dominant genera prior to statistical analyses. Differences in community composition between stations and cm-layers were visualised using nMDS (non-metric multidimensional scaling) and CLUSTER based on a Bray-Curtis similarity matrix. Two-way crossed ANOSIM (Analysis of Similarities; factors 'area' = Weddell Sea or Drake Passage; and 'layer' = sediment depth; 9999 permutations) and SIMPER (Similarities of Percentages) quantified within- and between-station differences in community composition and contribution of genera to observed differences, respectively. PERMANOVA (permutational ANOVA) with four factors ('area' = fixed, 'station' = fixed, 'layer' = fixed, 'replicate' = random and nested within station; 9999 permutations) analysed differences in assemblages between stations and layers. Pairwise tests were performed between all pairs of levels for the different factors. True permutational p-values *P*(perm) were interpreted when the number of unique permutations exceeded 100, and Monte Carlo *P*-values P(MC) when this was not the case. PERMDISP tested for homogeneity of dispersions in the multivariate space of the different groups of significant factors (distances to centroids; *P*-value by permutation of least-squares residuals).

Draftsman plots were constructed for the environmental variables to check for skewness in the data and for multi-collinearity. This resulted in a log-transformation for 'median grain size', and omission of variables 'coarse sand %', 'chl *a*', 'phaeopigments' and 'TN' (correlation > 0.88 with others). A PCA plot was constructed based on the normalised values for all cm-layers and replicates of each station to look at variations in environmental setting between areas.

PRIMER software was also used to evaluate taxonomic diversity (N_0 = number of genera; H' = Shannon index (log*e*); EG(200) = expected number of genera in a sample of 200 individuals; Hill's N_1[21]) and evenness (Hill's N_{inf}; J' = Pielou's evenness; see Heip et al. (1998) and references therein). Functional diversity and trophic structure was approached by classifying nematode genera into feeding guilds according to the marine feeding type classification of

[21] Note that N_1 is the true number's equivalent of Shannon entropy H', calculated as exp(H') (Jost, 2006).

Wieser (1953). Four different feeding types are recognised: selective (1A) and non-selective (1B) deposit feeders, epigrowth-feeders (2A) and omnivores/predators (2B). Based on this classification, one can calculate the trophic diversity index for each station (ITD): ITD = $\Sigma\theta^2$ where θ is the contribution of each trophic group to total nematode density (Gambi et al., 2003; Heip et al., 1998). ITD ranges from 0.25 (highest trophic diversity, i.e. the four trophic guilds account for 25 % each) to 1.0 (lowest diversity, i.e. one trophic guild accounts for 100 % of total density). In this study, the inverse ITD^{-1} is used, ranging from 1 (low functional diversity) to 4 (high functional diversity). All biodiversity indices and feeding types were analysed and compared using one-way ANOVA as well as post-hoc pairwise comparisons between stations with R (R Core Team, 2013).

RESULTS

Oceanography and sedimentary environmental characterisation

Assessment of parameters in the water column confirmed that the stations in this study are influenced by different water masses. CTD measurements showed negligible variations in salinity between stations, yet lower temperatures in the Weddell Sea than in Drake Passage (Table 3.2).

Table 3.2. *Water column properties at chl a max and bottom depth. Temperature and salinity are derived from CTD recordings, chl a from laboratory measurements. na = below detection.*

		Temperature (°C)	**Salinity (psu)**	**Chl *a* (mg m^{-3})**
W-120	Chl *a* max	-1.81	34.31	0.088
	Bottom	-1.81	34.50	0.025
W-163	Chl *a* max	-1.48	34.30	0.070
	Bottom	-1.77	34.50	0.013
DP-243	Chl *a* max	1.19	34.20	0.589
	Bottom	0.99	34.60	na
DP-250	Chl *a* max	1.12	34.15	0.452
	Bottom	0.57	34.58	na

Deep cold Antarctic Bottom Water formation in the Weddell Sea is responsible for the observed surface and bottom temperature differences between W and DP stations (almost –2 °C vs. ~ 1 °C, respectively; Table 3.2). As this bottom water flows northward along the Weddell basin, it fuels thermohaline circulation and transports oxygen and nutrients on a global scale.

Cold water combined with cold atmospheric conditions in the Weddell Sea area results in sea-ice cover present throughout most of the year, rendering primary production highly seasonal. However, upon annual sea-ice melt in austral summer, the meltwater enhances water-column stability and seeds regional phytoplankton (predominantly diatom-based) blooms in the Marginal Ice Zones (MIZ; Kang et al., 2001; Lizotte, 2001; Smith & Comiso, 2008; Wing et al., 2012) and temporary polynyas near the continent (Grebmeier & Barry, 1991). This local and temporal enhancement of biogenic material (Lizotte, 2001; Smith & Nelson, 1986) is further complemented by sea-ice algae released upon ice melt, which can account for up to 25 % of total annual primary production in ice-covered waters (Arrigo & Thomas, 2004). Whereas sea-ice dynamics dictate food input in the eastern Antarctic Peninsula, continental shelves near the South Shetland Islands (region of DP-243 and DP-250) at the western side lie within the (usually) ice-free zones of the ACC (Grebmeier & Barry, 1991). The ACC abuts the continental shelves in this area, allowing Upper Circumpolar Deep Water (UCDW) to flood onto the shelf, principally through glacially carved canyons (as was observed from bathymetry onboard; Clarke et al., 2007b, 2009). This relatively warm UCDW (values of > 1.5 °C are not uncommon, but we encountered values around 1.2 °C; Table 3.2) is then mixed upward, introducing elevated concentrations of nutrients into the upper water column and allowing diatom-dominated phytoplankton assemblages to form subsurface chl *a* maxima above the pycnocline (Prézelin et al., 2004). The processes described above were only partly reflected in satellite data of the area averaged for the period of sampling (Figs 3.1b and 3.1c). Surface concentration of chl *a* was higher in Drake Passage (0.5 – 0.7 mg m^{-3}) than in the Weddell Sea (0.1 – 0.2 mg m^{-3}), which was confirmed by surface water measurements (Table 3.2).

Different oceanographic regimes east and west of the Antarctic Peninsula also partly result in differences concerning the fate of photosynthetically-derived organic matter. In general, produced phytodetritus in the Weddell Sea after ice melt is transported rapidly through the water column, e.g., in the form of faecal pellets of zooplanktonic grazers (e.g., copepods and krill; Lizotte, 2001; Suzuki et al., 2001), resulting in seasonally high POC flux to the seafloor. Conversely, deep vertical mixing of ACC surface waters facilitates substantial recycling and consumption of phytodetritus by zooplankton already in the water column, accompanied by in-situ microbial degradation (Grebmeier & Barry, 1991; Lochte et al., 1997). This typically results in a rather low carbon flux to the bottom (Watson et al., 2013; Zhou et al., 2010). Measurements near the seafloor resulted in bottom water chlorophyll concentrations that were

below detection limit in the Drake Passage and very low (< 0.03 µg l^{-1}) in the Weddell Sea (Table 3.2).

Once at the seafloor, cold bottom-water temperatures in the Weddell Sea lead to slow organic degradation rates and contribute to an accumulation of fresh organic matter or "foodbank" in the sediment (Bathmann et al., 1991; Glover et al., 2008) able to sustain a high meiobenthic standing stock throughout the year, even in deeper sediment layers (Fabiano & Danovaro, 1999; Vanhove et al., 1995). Temperature thus plays a paramount role in food availability at both the surface and seafloor level. Conversely, in the high-dynamic region of the Drake Passage, the fraction of freshly produced organic matter that does reach the seafloor is subject to lateral advection and resuspension by bottom currents, preventing sedimentation of finer fractions and fresh phytodetritus, and resulting in higher C:N values and lower pigment concentrations (Vanhove et al., 1999).

Sedimentary data collected for our sampling stations showed that mainly pigment values are largely different between the two regions. Chl *a* and phaeopigment content was up to more than 100 times higher in Weddell Sea stations (Table 3.3), resulting in higher CPE concentrations and a higher amount of fresh material compared to Drake Passage. Vertical distribution of CPE values was different, too: while CPE concentrations remained high throughout the sediment depth layers in the Weddell Sea, their values decreased with each centimetre in the Drake Passage (Fig 3.2). Also TOC content peaked in the Weddell Sea (mainly W-163). By contrast, DP-243 and DP-250 were characterised by coarser sediment than W-120 and W-163. Highest $C:N_{molar}$ values were obtained in Drake Passage station DP-243. A PCA plot of the different stations (Fig 3.3) indicated that the environmental setting at the two Drake Passage stations was quite similar (stations DP-250 and DP-243 placed closer together), while there was a higher discrepancy in the case of Weddell Sea stations (but they are also more geographically separated than Drake Passage stations).

Table 3.3. *Sedimentary environmental variables per station (± standard deviation), both for the upper centimetre separately and averaged over all replicates and layers. CPE = chloroplastic pigment equivalents; MGS = median grain size; silt+clay % = fraction < 63 µm; sand % = between 63 – 500 µm; coarse sand % = fraction > 500 µm; TN = % total nitrogen; TOC = % total organic carbon; C:N_{molar} = ratio of TOC:TN. *Values based on only one replicate measurement, due to large bias in data (i.e. stone present in 0 – 1 cm of replicate 243-3). na = not assessed*

	W-120		**W-163**		**DP-243**		**DP-250**	
	0–1 cm	**0–5 cm**	**0–1 cm**	**0–5 cm**	**0–1 cm**	**0–5 cm**	**0–1 cm**	**0–5 cm**
Chl *a* (µg g^{-1})	9.31 (7.57)	15.33 (10.23)	25.20 (4.81)	30.68 (11.11)	0.15 (0.13)	0.06 (0.06)	0.10 (0.03)	0.06 (0.03)
Phaeo (µg g^{-1})	8.96 (6.36)	7.89 (2.09)	12.92 (0.43)	11.27 (1.83)	0.69 (0.39)	0.52 (0.38)	1.05 (0.55)	0.49 (0.37)
CPE (µg g^{-1})	18.27 (13.78)	23.22 (11.76)	38.12 (5.15)	41.96 (12.07)	0.83 (0.52)	0.58 (0.42)	1.15 (0.57)	0.54 (0.39)
Chl *a*:phaeo	1.04 (0.44)	1.94 (0.84)	1.95 (0.33)	2.72 (0.84)	0.22 (0.08)	0.11 (0.06)	0.09 (0.06)	0.11 (0.06)
MGS (µm)	37.58 (5.85)	35.56 (2.66)	27.10 (0.54)	24.79 (1.58)	49.81* (na)	48.75 (3.18)	78.43 (2.24)	69.24 (6.93)
Silt+clay %	83.96 (3.83)	84.61 (1.11)	91.94 (0.63)	93.74 (1.17)	84.07* (na)	84.28 (1.56)	73.46 (2.50)	76.73 (3.32)
Sand %	15.75 (3.75)	15.22 (1.08)	8.06 (0.63)	6.26 (1.17)	15.38* (na)	15.12 (1.55)	24.93 (3.02)	22.01 (3.38)
Coarse sand %	0.29 (0.50)	0.17 (0.23)	0.00 (0.00)	0.00 (0.00)	0.55* (na)	0.60 (0.04)	1.61 (0.53)	1.25 (0.30)
TN %	0.22 (0.01)	0.21 (0.02)	0.25 (0.02)	0.24 (0.01)	0.08 (0.00)	0.07 (0.00)	0.09 (0.02)	0.08 (0.01)
TOC %	1.13 (0.11)	1.09 (0.06)	1.64 (0.13)	1.56 (0.05)	0.56 (0.00)	0.52 (0.04)	0.61 (0.14)	0.53 (0.06)
C:N_{molar}	6.00 (0.50)	6.18 (0.32)	7.54 (0.54)	7.51 (0.20)	8.29 (0.25)	8.18 (0.14)	7.76 (0.25)	7.97 (0.15)

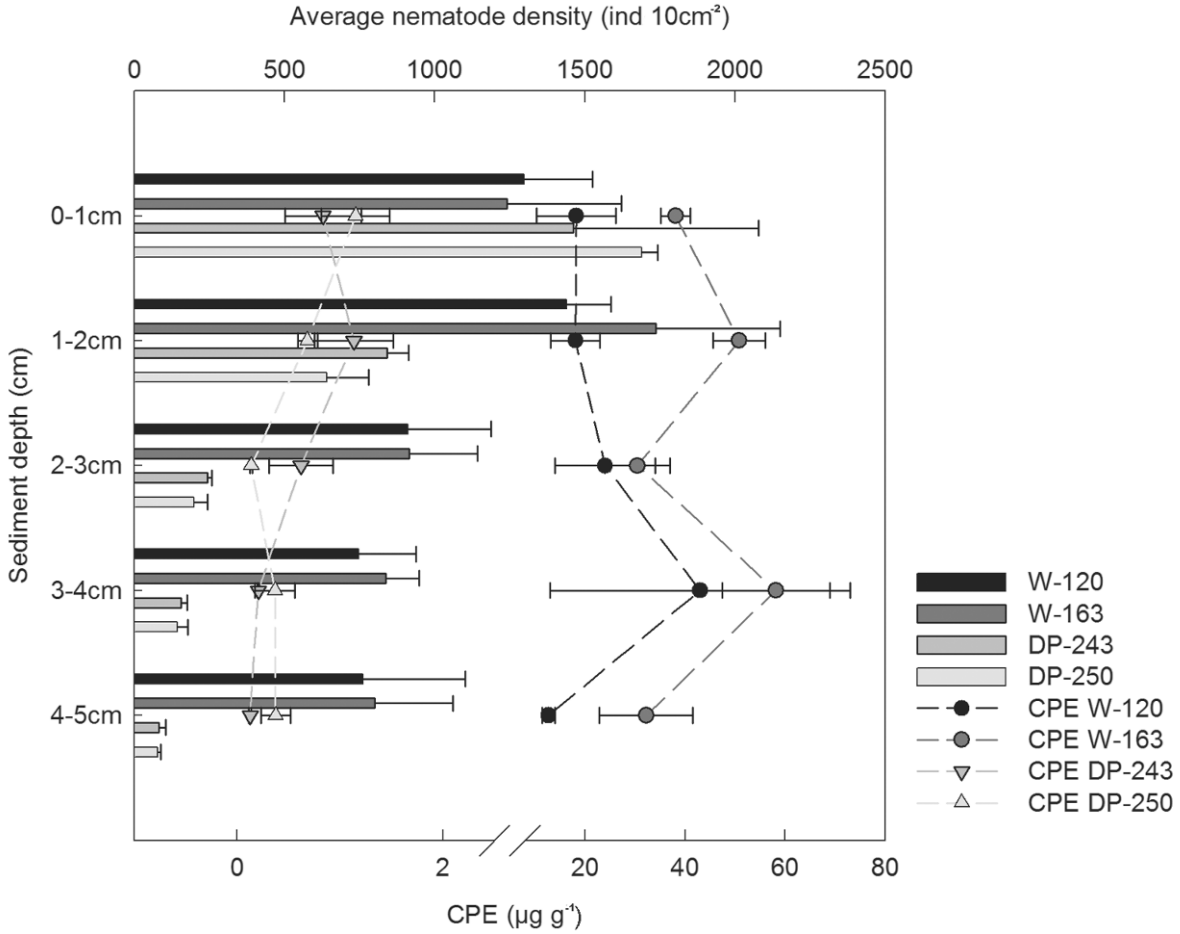

Figure 3.2. *Vertical distribution of pigments and nematodes. Average CPE values (µg g^{-1}; dots) and nematode densities (ind 10 cm^{-2}, bars) with their respective standard error in the sediment for all four stations (n = 3).*

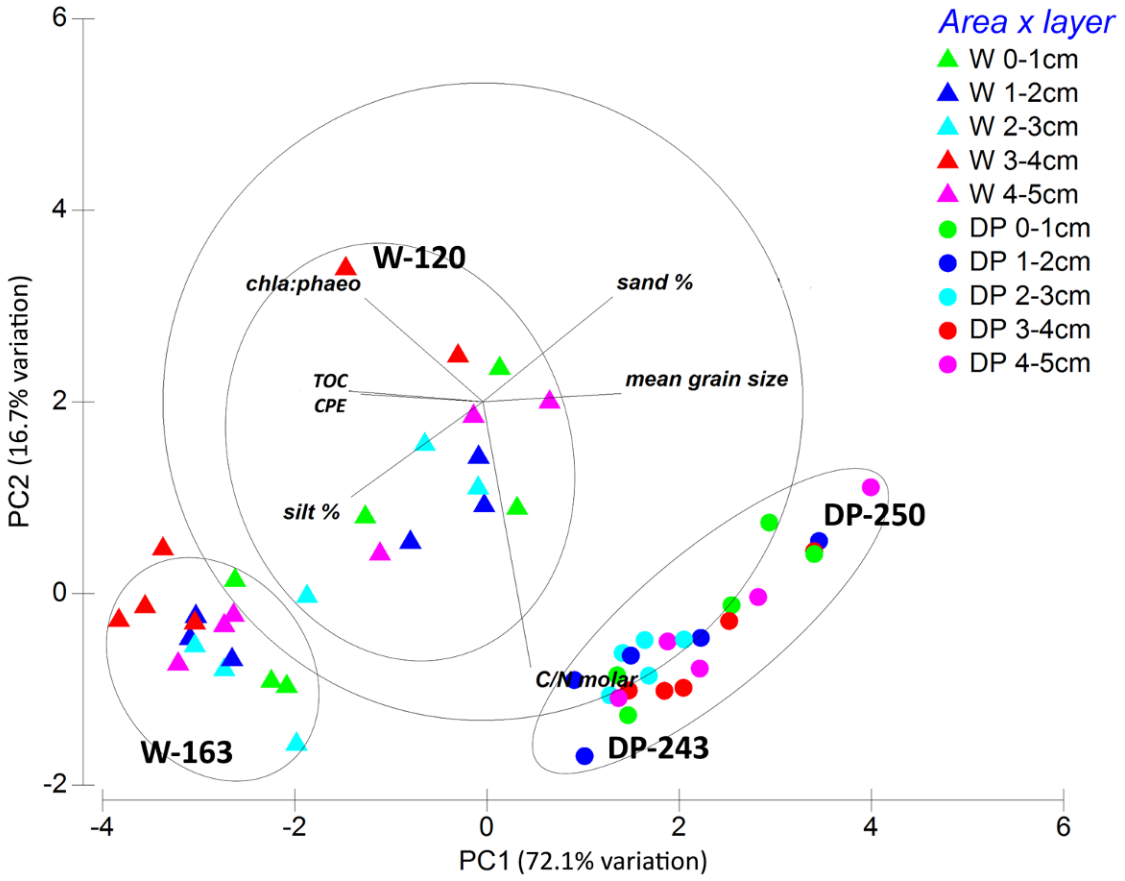

Figure 3.3. *PCA plot based on Euclidean distances between samples. Each symbol corresponds to a centimetre layer of a different replicate in Weddell Sea or Drake Passage and represents the environmental setting in the sediment.*

Meiofauna and nematode abundance

Total meiofauna densities (averaged for the three replicates of each station) were twice as high in W-120 and W-163 (6235 ± 704 and 7196 ± 1274 ind 10 cm^{-2}, respectively) than in DP-243 (3075 ± 1083 ind 10cm^{-2}) and DP-250 (3049 ± 41 ind 10 cm^{-2}). There was a significant difference in the number of individuals between Weddell Sea and Drake Passage (one-way ANOVA, $P < 0.05$) but not between stations of the same area (post-hoc pairwise comparisons). A total of 20 different taxa could be distinguished in the samples, with a clear dominance of nematodes in all samples of all four stations (average contribution 75 – 96 % of total abundance). Nematodes were followed by harpacticoid copepods (1 – 13 %), nauplius larvae (1 – 14 %) and polychaetes (0.3 – 1.6 %), after which a variety of other taxa was recognised in low numbers (e.g., Ostracoda, Kinorhyncha and Gastrotricha). Averaged

nematode densities ranged between 2751 ± 82 (station DP-250) and 5532 ± 878 ind 10 cm^{-2} (station W-163). As for meiofauna, densities were higher in Weddell Sea stations than in Drake Passage. However, nematode density was similar in the first sediment layers (0 – 1 cm) of stations at both sides (approx. 1200 – 1700 ind 10 cm^{-2}), and only started to vary from the second centimetre onwards. There was a steep decline in numbers with depth for Drake Passage stations, while Weddell Sea nematodes continued to be present in higher numbers even in the deeper layers (Fig 3.2).

Nematode assemblages and diversity

Nematode assemblages were significantly different between areas (R = 0.84, $P < 0.05$) and sediment layers (R = 0.62, $P < 0.05$; two-way crossed ANOSIM), with differences increasing with sediment depth (ANOSIM pairwise comparisons). This was also revealed by PERMANOVA analysis (significant interaction effect of factors 'station' and 'layer'; Table 3.4) and visualised in Figure 3.4. Analogously to the situation for the environmental setting (Fig 3.3), Drake Passage communities were more similar to each other for most sediment layers than those of the Weddell Sea. Within the same area, similarity between DP-243 and DP-250 remained relatively high throughout the sediment layers, while it varied with depth for stations W-120 and W-163 (Fig 3.4). When comparing similarities between stations across both sides, largest differences in communities were noted between station W-163 and both DP stations, while station W-120 was more similar to DP stations. For both W-163 and W-120, similarity with DP stations decreased when moving further down into the sediment, indicating that nematode assemblages were more divergent in deeper sediment layers. This was also revealed by ANOSIM pairwise tests. Pairwise comparisons for different sediment depths within the different stations rendered significant differences between both the first and the second centimetre with the deeper layers (mainly for stations W-120 and DP-250; detailed results not shown). PERMDISP of the interaction term 'station × layer' yielded a *P*-value of 0.654, meaning that dispersions are homogeneous in multivariate space. However, since within-group sample size is < 5 (each station × layer combination has three replicates), this should be interpreted with care (Anderson et al., 2008). Horizontal (i.e. between stations) and vertical (between sediment depths) differences in community composition were confirmed by MDS (Fig. S3.1) and CLUSTER analyses, which showed a segregation of upper cm-layers (0 – 1 cm and 1 – 2 cm) from the deeper layers for all stations.

Table 3.4. *PERMANOVA of nematode assemblages in Weddell Sea and Drake Passage (main test results). Asterisks represent significant results. Df = degrees of freedom; Pseudo-F = effect size; P(perm) = permutational P-value*

Source	df	Pseudo-F	*P*(perm)	Unique perms
Area	0	No test		
Station	2	2.9196	0.0273*	8917
Layer	4	12.823	0.0001*	9917
Replicate (Station)	8	No test		
Station × Layer	8	1.4319	0.0086*	9803

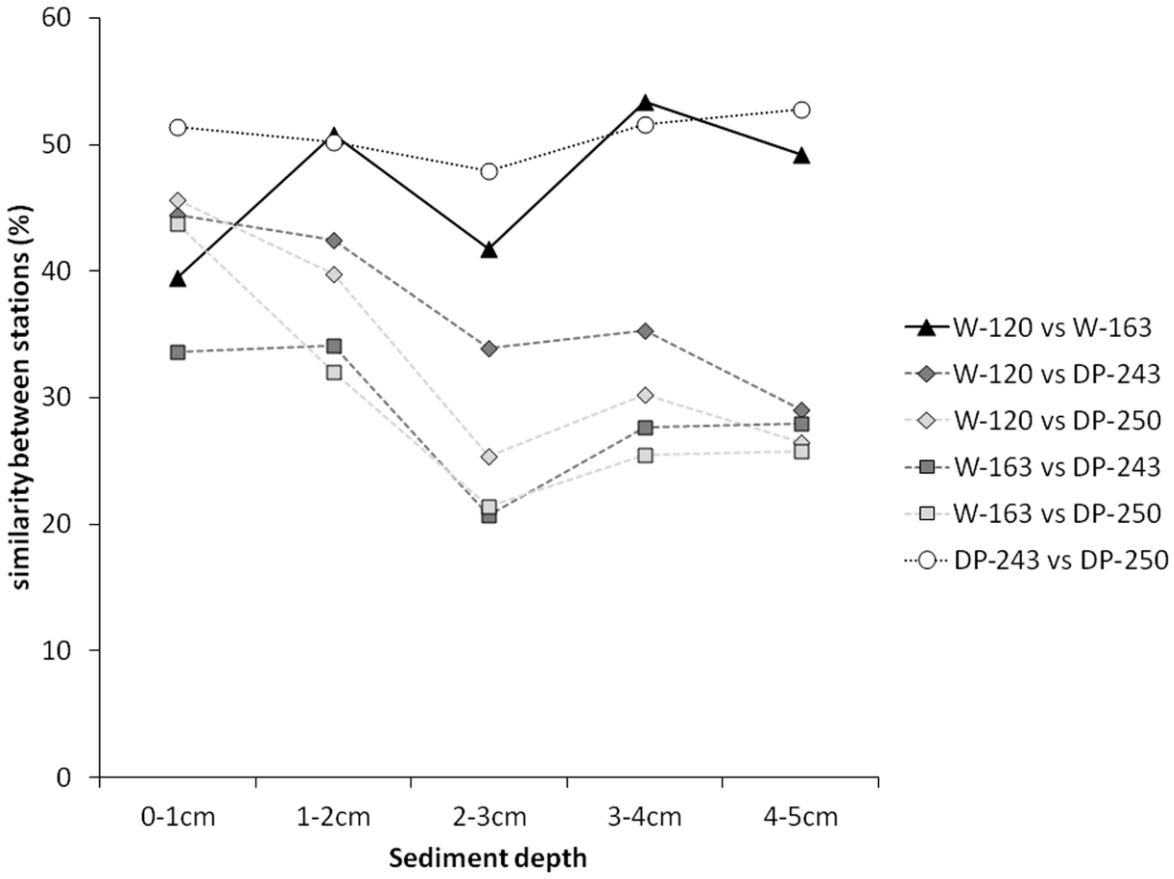

Figure 3.4. *Visualisation of pairwise comparisons of the PERMANOVA interaction 'station × layer'. Graph plots similarities of nematode assemblages between the different stations according to depth in the sediment.*

Nematode assemblages in the Weddell Sea consisted of 74 genera belonging to 28 different families (mainly Comesomatidae, Chromadoridae and Monhysteridae), while 88 genera belonging to 29 families (mainly Xyalidae and Comesomatidae) were found in Drake Passage. Of these total numbers of genera, 54 were shared between the two locations (albeit in different abundance; e.g., *Microlaimus*, *Daptonema*, *Linhomoeus*), 20 occurred only in the Weddell Sea and 34 only in Drake Passage (e.g., *Dorylaimopsis*), yielding a total of 108 genera recognised in the samples. Average dissimilarity within and between regions is given in Table 3.5, together with the genera that contributed most to these dissimilarities (SIMPER). In terms of dominance, there were no highly dominant (relative abundance > 25 %) genera present in any of the four stations (maximum of 11 – 22 %). Several genera occurred in relative abundance > 1 % (ranging from 15 genera in W-163 to 26 in DP-243), but there were many rare genera as well in all stations. A total of 43 genera were unique, meaning that they only occurred in one out of four stations, but none of them contributed a lot to total numbers.

Table 3.5. *Dissimilarity (%) of nematode assemblages within and between areas (averaged over replicates and sediment depths) and first five genera contributing most to observed differences (SIMPER).*

	Weddell Sea	**Drake Passage**
Weddell Sea	50.35 %	
	Microlaimus	
	Linhomoeus	
	Daptonema	
	Sabatieria	
	Halalaimus	
Drake Passage	67.75 %	46.85 %
	Microlaimus	*Sabatieria*
	Linhomoeus	*Daptonema*
	Sabatieria	*Dorylaimopsis*
	Terschellingia	*Comesa*
	Daptonema	*Leptolaimus*

Vertical profiles of nematode generic composition per station (Fig 3.5) showed that some genera were present throughout the samples (indicated in blue colours), while others occurred more specifically in one area (brown colours in W-120, green for W-163, and red for DP-243 and DP-250) or depth layer, or were shared between two locations. Community composition clearly changed with depth: genera *Daptonema* and *Halalaimus* were abundant in the first

layers of both areas, but were replaced in the deeper layers by *Linhomoeus* and/or *Sabatieria*. As for the PCA and PERMANOVA results, W-120 and W-163 showed more variation in community composition among them than did DP-243 and DP-250.

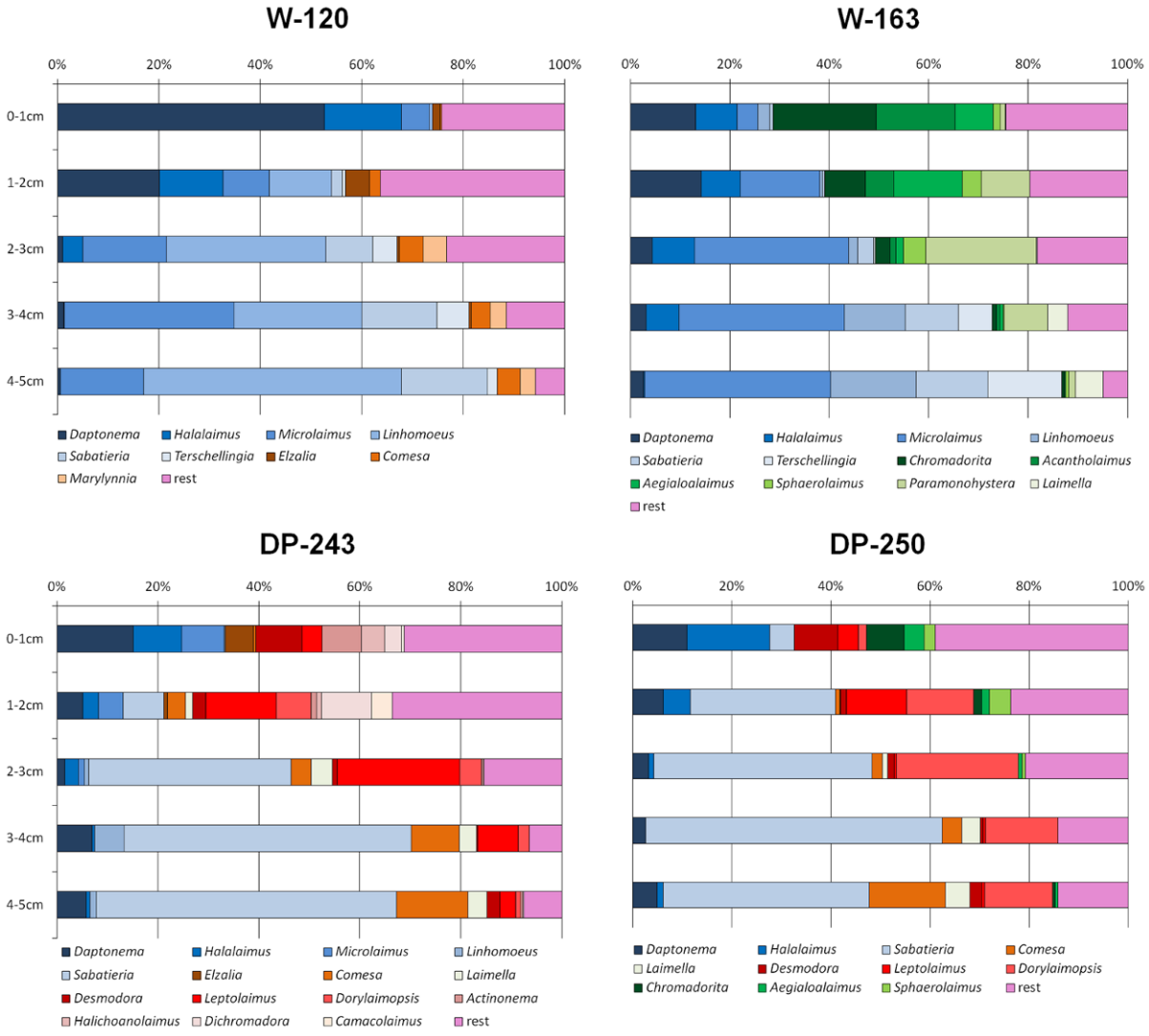

Figure 3.5. *Vertical profiles of relative genus abundances for each station. Only genera with an abundance > 4 % in one of the layers were included, all others were grouped as "rest". Where possible, we used the same colours for the same genera in all different plots.*

In terms of diversity, both sides of the Antarctic Peninsula showed differences, too. Average values of structural (diversity indices and evenness) and functional (ITD^{-1}) diversity measures per station are listed in Table S3.1. Drake Passage stations exhibited highest values in general, for all diversity measures. One-way ANOVA for each index combined with post-hoc pairwise

comparisons indicated that for most indices there were no significant differences between stations of the same area, but there were between stations of different areas (N_{inf} was never significantly different; Table 3.6, Fig 3.6).

Table 3.6. *One-way ANOVA results for each index with their P-values. Significance codes: *** P < 0.001, ** P < 0.01, * P < 0.05, ns = not significant.*

	Df	**Sum Sq**	**Mean Sq**	**F-value**	***P*-value (>F)**
N_0					
Station	3	432.250	144.080	13.722	**
Residuals	8	84.000	10.500		
N_1					
Station	3	246.155	82.052	12.744	**
Residuals	8	51.508	6.439		
EG(200)					
Station	3	206.518	68.839	16.198	***
Residuals	8	33.999	4.250		
N_{inf}					
Station	3	25.909	8.636	3.522	ns
Residuals	8	19.615	2.452		
J'					
Station	3	0.031	0.010	6.968	*
Residuals	8	0.012	0.001		
ITD^{-1}					
Station	3	2.510	0.837	11.718	**
Residuals	8	0.571	0.071		

Both the observed number of genera N_0 and the expected number of genera in a sample of 200 individuals, EG(200), were highest at stations DP-243 and DP-250; and lowest at W-163. For the other parameters (H', N_1) and evenness (N_{inf}, J'), station W-120 had lowest values, while DP-243 remained highest. This means that communities at DP-243 were most diverse and had similar relative contributions of the various genera, whilst stations W-120, and to a lesser extent W-163, had lowest diversity with more variation in genus contributions to total abundance. Also trophic diversity (ITD^{-1}) was higher at DP-243 and DP-250, and differed significantly from Weddell Sea stations (except for DP-250 and W-163). The Weddell Sea stations had high relative contributions of feeding type 2A (epistratum feeders), represented by 44 % in W-120 and 50 % in W-163. Type 1B (non-selective deposit feeders) was second most abundant with percentages of 37 and 26 %, respectively. In stations DP-243 and DP-250,

there was a more even distribution among feeding types (except for type 2B), with relative contributions around 20 – 35 % (1B had highest percentages in both stations).

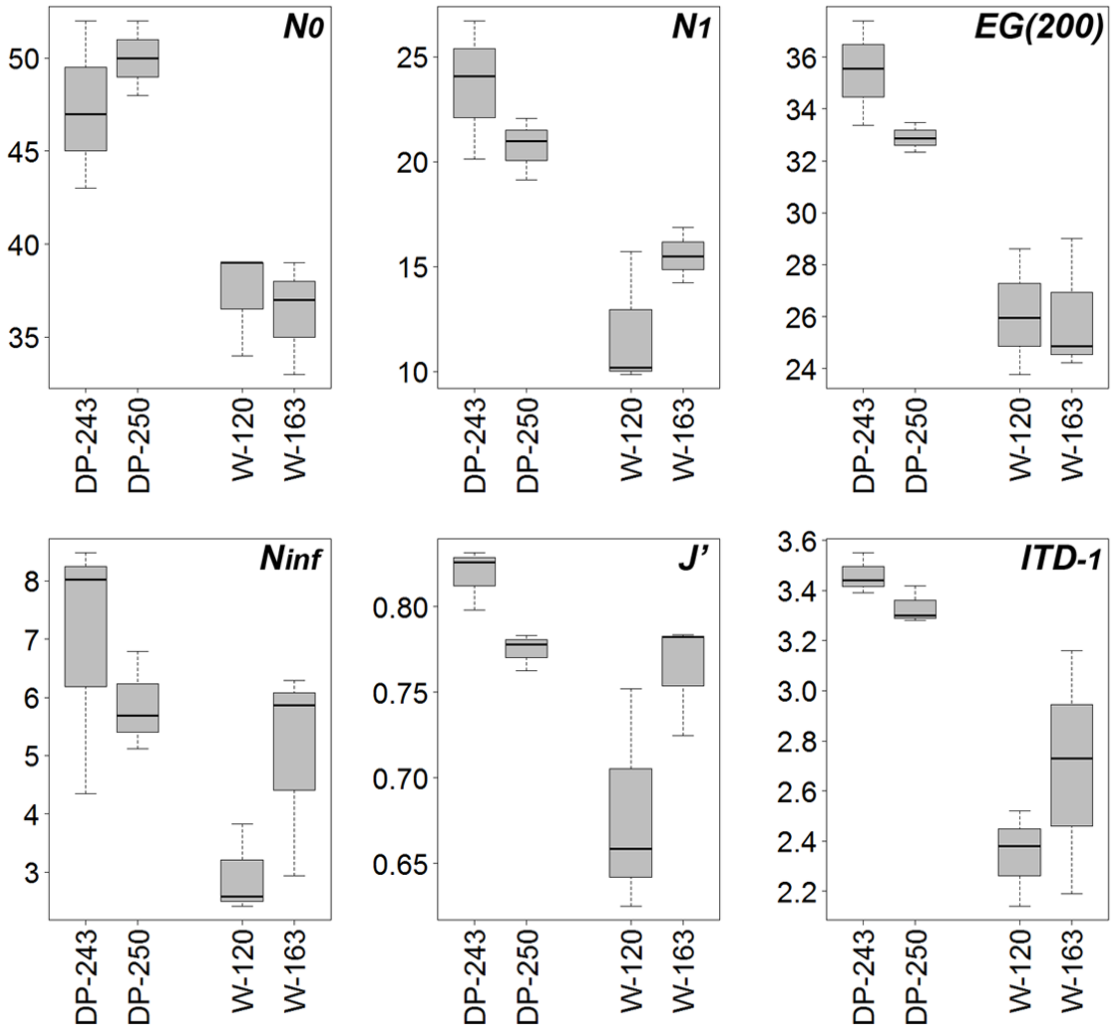

Figure 3.6. *Box plots of the different diversity indices for the different stations. Boxes display median, first and third quartiles, minimum and maximum.*

DISCUSSION

Our study area coincides with the collision of true Antarctic (i.e. Weddell gyre; Deacon, 1979) and oceanic (i.e. ACC) water masses, resulting in clear differences in temperature and surface primary production at a relatively small geographical distance (see Results section). Bentho-pelagic coupling is responsible for the translation of these differences in surface-water processes to the seabed, leading to a distinct environmental setting for the benthos (cf.

pigment and organic matter content). Larger (mega-) benthic communities are known to track these differences as cold Weddell water turns around the peninsula tip and meets and mixes with ACC warm water (Lockhart & Jones, 2008; Piepenburg et al., 2002). Therefore, a similar change in nematode community structure was anticipated. In terms of abundance, results of this study are comparable to previous Antarctic observations (e.g., Hauquier et al., 2011; Ingels et al., 2010; Raes et al., 2010), yet exceed those of other areas worldwide (de Skowronski & Corbisier, 2002; Herman & Dahms, 1992). Higher nematode densities in the northwestern Weddell Sea compared to Drake Passage are mainly the result of high subsurface, rather than surface abundances (see Fig 3.2). Conversely, nematode genus richness is highest in Drake Passage stations. As hypothesised, nematode community composition varies depending on the region and is related to prevailing oceanographic and environmental conditions. Seasonal sea-ice retreat and subsequent enhanced food availability in the Weddell Sea at the time of sampling result in a community dominated by opportunistic genera (e.g., *Daptonema*, *Microlaimus*) able to benefit from deeper oxygen and food penetration (judging from their high numbers in subsurface layers; Fig 3.2). Conversely, open oceanic conditions and presumed low organic matter flux in Drake Passage triggers dominance of long motile nematodes such as *Sabatieria*, *Dorylaimopsis* and *Comesa*. These findings confirm the hypotheses that oceanic differences (i.e. temperature and water-column processes) between both east and west Antarctic Peninsula result in different nematode communities, mainly through indirect controls on food availability.

Weddell Sea dynamics and nematode abundance

High productivity and POC flux in Weddell Sea stations are confirmed by observed sediment pigment values but not reflected in surface water measurements and ocean colour data. Measured values for chl *a* in surface waters at the northwestern Weddell Sea tip (Table 3.2) are low compared to longer timescale averages (Arrigo et al., 2008) and reported values of > 1.0 mg m^{-3} during phytoplankton blooms in areas similarly influenced by seasonal sea-ice retreat (Moore & Abbott, 2000). This observation presumably relates to timing of sampling, since the contribution of ice algae to primary production in the Southern Ocean generally peaks in December, a few weeks before maximum production rates are noted in open shelf waters (Arrigo et al., 1998; Lizotte, 2001). Therefore, our snap-shot measurements most likely missed the actual blooming event while the satellite-based averages in Fig 3.1b failed to depict ephemeral sea-ice algal contribution. However, longer-term chlorophyll averages for surface waters in the area (Dorschel et al., 2016) clearly show enhanced concentrations at the

eastern side of the Antarctic Peninsula, related to seasonal sea-ice retreat and higher rates of primary production. Although this is not reflected by water-column chlorophyll values for this study, sedimentary measurements are in line with expectations of high POC flux and food bank formation in cold waters (see Results section). Pigment values, the amount of fresh material and TOC content in Weddell Sea sediments are highest and remain high throughout the upper five centimetres. Encountered CPE values between 20 and 40 µg g^{-1} exceed those found in other areas worldwide (~ 1.4 – 6 µg g^{-1} at 200 – 800 m in the Central Mediterranean Sea; Danovaro et al., 2013) and in the Antarctic at similar times of the year (0.25 – 0.45 µg g^{-1} at a depth of ~ 400 – 550 m in the Ross Sea; Fabiano & Danovaro, 1999; ~ 0.5 – 1.6 µg g^{-1} at 750 m in the South Sandwich Trench; Vanhove et al., 2004). Pigment values indicate that the influence of a foodbank is more pronounced at station W-163, located deeper into the Weddell Sea, than at W-120 positioned at the tip of the peninsula, at the edge of the cold-water influence.

The combination of high fluxes of phytodetritus and cold bottom temperatures has resulted in higher meiofauna and nematode densities in Weddell Sea stations compared to Drake Passage, mainly in the subsurface. Congruence between sedimentary pigment values and nematode vertical profiles points to a drawdown of organic matter, either by biological activity and/or sedimentary processes in the form of increased mixing. In this respect, bioturbation by other benthic groups (mainly macro- and megafaunal burrowers) might play a key role in the oxygenation of deeper sediment layers and can lead to a transfer of organic matter to deeper horizons (Brandt, 1993, 1995; Mermillod-Blondin & Rosenberg, 2006). Although macrofauna organisms such as polychaetes and ophiuroids with the potential to rework upper sediment layers have been observed in the cores during sampling, no data on higher trophic level have been published so far for our stations. Therefore, the degree to which they might affect nematode communities and vertical distribution cannot be quantified. Alternatively, higher nematode abundance and deeper occurrence within seafloor sediments at W-120 and especially W-163 may (partly) arise from higher oxygen availability in this area compared to Drake Passage (due to oxygen-rich bottom water in the Weddell Sea; Gordon et al., 2001).

In accordance with other findings (e.g., Guilini et al., 2013; Lins et al., 2014), also here, high primary production and food availability lead to high numbers of benthic nematodes, which is indicative of strong bentho-pelagic coupling (Lins et al., 2015) and confirms the first hypothesis.

Drake Passage dynamics and nematode abundance

As opposed to Weddell Sea observations, high primary production in the water column (see also Dorschel et al., 2016), noticeable through intense coloration of filters, contrasts with lowest sediment pigment values and highest C:N ratios in Drake Passage stations. Chl *a* concentrations at the surface are within the range of satellite estimates at the time of sampling (see Fig 3.1c, Table 3.2), and at a broader temporal and geographical scope including the sampled area (1997 – 2006 averages of approximately 0.34 – 0.62 mg m^{-3} for the Southern Ocean, West Antarctic Peninsula and Weddell/Scotia Sea; Arrigo et al., 2008). In contrast, CPE content in Drake Passage sediments is much lower and mainly composed of phaeopigments, resulting in extremely low chl *a* concentrations (< 0.1 µg g^{-1}); even compared to other nearby shelf regions at the South Shetland Islands and Elephant Island (~ 0.6 – 0.8 µg g^{-1}; Sañé et al., 2010). Lower quantity and quality of phytodetritus in Drake Passage sediments probably result from water-column consumption and/or stronger bottom dynamics compared to the Weddell Sea, as discussed earlier. Contrary to Weddell sediments, where pigment values remain relatively high throughout the different depth horizons, their values rapidly decline in Drake Passage stations. Consequently, meiofauna and nematode density profiles follow a similar pattern of decrease with depth. This preference for surface sediment layers has been demonstrated in many studies (e.g., Boeckner et al., 2009), although occasionally also subsurface maxima have been observed (Galéron et al., 2001; Guilini et al., 2013; Hauquier et al., 2011).

Nematode genus composition

Variation in oceanography and primary productivity at both sides of the peninsula has clearly resulted in differences in nematode abundance and vertical occurrence. Next to that, also nematode community composition and feeding mode differ depending on the area and depth in the sediment (see PERMANOVA results; Fig 3.5). Although most genera are not restricted to either Weddell or Drake Passage stations, their relative contributions vary for both areas and can be linked again to differences in environmental conditions.

In Weddell Sea sediments, surface layers (0 – 3 cm) contain high numbers of the genera *Daptonema* and *Halalaimus*, while *Linhomoeus*, *Sabatieria* and *Terschellingia* reside in deeper layers (3 – 5 cm). *Microlaimus* is present in considerable numbers throughout all layers. Similar depth ranges for these genera have been observed on different occasions (e.g., Lins et al., 2015; Portnova et al., 2010). *Daptonema* and *Microlaimus* are comparably

widespread in different oceans worldwide (e.g., Ingels et al., 2006; Shirayama & Ohta, 1990; Vanhove et al., 1999) and also *Halalaimus* is described as a eurytopic, cosmopolitan genus occurring in various types of sediments (Portnova et al., 2010; Sharma et al., 2011; Vanreusel et al., 2010b). Because of its long thin shape, this latter genus can move easily through finer sediments (mainly associated with deep-sea habitats; Sharma et al., 2011; Van Gaever et al., 2004), such as the ones we observe in both Weddell Sea stations (Table 3.3). *Microlaimus* is found in various habitats, including the deep sea, and can respond opportunistically to organic enrichment (Portnova et al., 2010; Sebastian et al., 2007; Van Gaever et al., 2004). Therefore, the seasonally high flux of organic matter and freshness of deposited material in Weddell stations has lead to considerable numbers of this genus throughout all sediment depths, and explains why it is much less abundant in Drake Passage. Also *Terschellingia* is often present in organically enriched (mainly fine-grained) sediments (Portnova et al., 2010; Vitiello, 1974).

In the Drake Passage stations, surface layers (0 – 1 cm) contain some of the abundant genera encountered in the Weddell Sea (*Daptonema*, *Halalaimus* and *Microlaimus*), but these are complemented by a variety of other genera, such as *Desmodora* (epistratum-feeder occurring mainly in surficial sediments; Ingels et al., 2006) and *Leptolaimus*. Although *Desmodora* has previously been described as an opportunistic genus usually encountered in highly productive areas (Vanreusel et al., 2010b), here it is most likely associated with the coarser sediment in Drake Passage stations (Lins et al., 2015). More strikingly, compared to Weddell stations, the genus *Sabatieria* becomes increasingly dominant in Drake Passage sediments, where it also occurs closer to the seafloor surface (already dominant from second centimetre onwards). Deeper down, it thrives in the company of *Leptolaimus*, *Dorylaimopsis* and *Comesa*. *Sabatieria* is known for its presence in sub- or anoxic conditions (Portnova et al., 2010; Schratzberger et al., 2006). It tends to inhabit deeper sediment layers, mainly in association with the Redox Potential Discontinuity (RPD) layer (Guilini et al., 2011; Vanreusel et al., 2010a), where its large body size and higher mobility allow it to move upward in the sediment to access oxygen and food in the upper layers (Guilini et al., 2011). Also *Leptolaimus* has been found in reduced deep-sea conditions (e.g., Vanreusel et al., 1997). The presence of these genera might therefore indicate hypoxic conditions in Drake Passage stations although there were no clear visual signs (i.e. dark coloration of sediments, pronounced smell) of oxygen depletion observed deeper down in the sediment cores (unfortunately, precise oxygen profiles are lacking for all stations). Similarly as for *Sabatieria*, also *Dorylaimopsis* and *Comesa* have a long, slender body, which facilitates movement in the sediment. Well-

oxygenated sediments at the Weddell side of the peninsula (see earlier) may explain why these genera are less abundant there.

In terms of dominant feeding mode, Drake Passage stations have more deposit-feeders (i.e. guilds 1A and 1B, together accounting for approximately 60 % of total community) compared to dominance of epistratum-feeders (2A; approx. 50 %) in the Weddell stations. Both epistratum- and deposit-feeders may use the same food sources, which are essentially limited to small particles (e.g., fungi, bacteria and unicellular microalgae; Jensen, 1987, 1988; Wieser, 1953). In this case, higher relative contributions of deposit-feeding genera such as *Sabatieria* in Drake Passage may result from the lower quality of deposited material, since they ingest particles as a whole (Jensen, 1987). Next to the obvious relationship between feeding mode and the nature and size of food particles, also temperature is known to affect feeding characteristics within benthic nematodes (Ingels et al., 2012; Moens et al., 2006). Details at the genus level are, however, too scarce to draw specific conclusions for this study.

Coming back to the hypotheses at the beginning of this study, above-described results on nematode genus composition confirm that not only megabenthic, but also smaller-sized meiobenthic communities respond to the different oceanographic regimes around the Antarctic Peninsula, although shifts are less pronounced and mainly directed vertically. Predicted further warming of surface waters and atmospheric temperatures in the Antarctic Peninsula region will inevitably affect associated biota (Ingels et al., 2012), judging from the tight link between oceanic features, primary production and nematode assemblages.

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SUPPLEMENTARY INFORMATION

Table S3.1. *Overview of structural diversity (N_0, EG(200), H' and N_1) and evenness (N_{inf} and J'), as well as a functional diversity measure (ITD^{-1}) with their respective standard deviation for the nematode assemblages of the different stations calculated in PRIMER and averaged over three replicates.*

	N_0	EG(200)	H'	N_1	N_{inf}	J'	ITD^{-1}
W-120	37.33	26.12	2.46	11.94	2.94	0.68	2.35
	(2.89)	(2.42)	(0.26)	(3.29)	(0.77)	(0.07)	(0.19)
W-163	36.33	26.02	2.74	15.52	5.03	0.76	2.69
	(3.06)	(2.60)	(0.08)	(1.32)	(1.83)	(0.03)	(0.49)
DP-243	47.33	35.44	3.16	23.63	6.95	0.82	3.46
	(4.51)	(2.01)	(0.14)	(3.32)	(2.27)	(0.02)	(0.08)
DP-250	50.00	32.89	3.03	20.73	5.86	0.77	3.33
	(2.00)	(0.58)	(0.07)	(1.48)	(0.85)	(0.01)	(0.07)

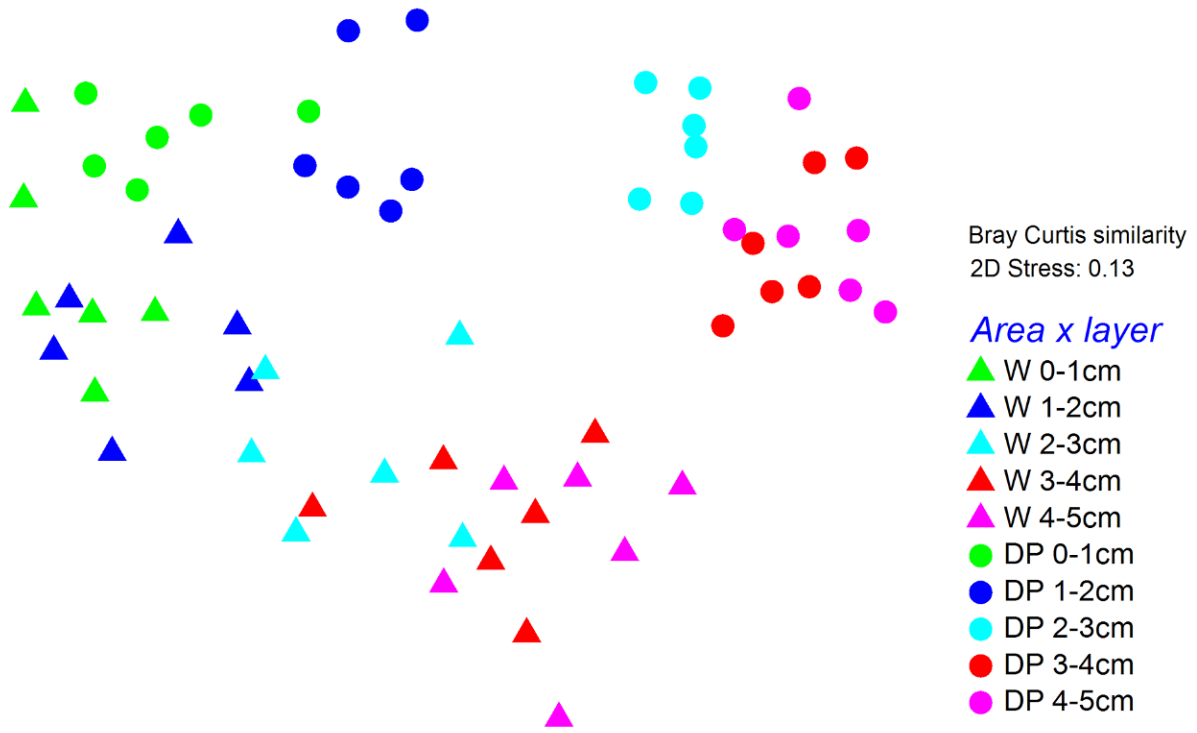

Figure S3.1. *Non-metric multidimensional scaling plot based on Bray-Curtis similarity of square-root transformed nematode abundance data. Symbols indicate the sampling location (triangles = Weddell Sea, circles = Drake Passage), and colours represent the different sediment depth layers.*

CHAPTER 4: ENVIRONMENTAL FILTERING AND DISPERSAL LIMITATION IN SURFACE AND SUBSURFACE FREE-LIVING NEMATODES OF THE SOUTHERN OCEAN CONTINENTAL SHELF

To be submitted as: Hauquier F, Verleyen E, Tytgat B & Vanreusel A (xxxx) Environmental filtering and dispersal limitation in surface and subsurface free-living nematodes of the Southern Ocean continental shelf

ABSTRACT

Aim Many marine meiofauna taxa are believed to possess ubiquitous distribution patterns, despite their endobenthic lifestyle and presumed restricted dispersal capacities. Here we aim to i) test this meiofauna paradox for free-living nematodes by using the metacommunity concept as a theoretical framework to study turnover patterns in their spatial distribution, and ii) assess the importance of local environmental conditions in explaining differences between communities in surface and subsurface sediments.

Location The continental shelf zone of the Atlantic sector of the Southern Ocean, along the Scotia Arc, near the Antarctic Peninsula, and in the eastern Weddell Sea.

Methods We analysed the community structure of free-living nematodes in two different sediment layers (0 – 3 cm and 3 – 5 cm) of different Antarctic shelf locations maximum 2400 km apart. A first part focused on a subset of locations to evaluate whether the genus level is sufficiently taxonomically fine-grained to enable the study of large-scale patterns in community ecology. In a second part, redundancy and variation partitioning analyses were used to quantify the unique and combined effects on generic community composition of local environmental conditions and spatial descriptors approximated by principal coordinates of neighbour matrices.

Results Macroecological patterns in community structure were highly congruent between the genus and species level. The nematode community composition appeared to be highly divergent between both depth strata, which is probably related to local abiotic conditions. Variation in community structure (beta diversity) between the different regions largely stemmed from turnover (i.e. replacement by new taxa) rather than nestedness (i.e. genus/species loss). The level of turnover among communities increased with geographic distance and was more pronounced in subsurface layers compared to surface sediments. Variation partitioning analysis revealed that both environmental and spatial predictors significantly explained variation in community structure. Moreover, the shared fraction of both sets of variables was high which suggested a substantial amount of spatially structured environmental variation.

Main conclusions A large-scale assessment of free-living nematode diversity and abundance in the Atlantic sector of the Southern Ocean shelf zone revealed strong horizontal and vertical spatial structuring in response to local environmental conditions, in combination with (most likely) dispersal limitation. The latter refutes wide species distributions as observed under the

meiofauna paradox and stresses the importance of including regional-scale information when studying marine nematode communities.

INTRODUCTION

Many marine meiofauna species were generally believed to possess ubiquitous geographic distributions (Boeckner et al., 2009; Giere, 2009), which is attributed to their small body size and large populations, in combination with ocean currents facilitating long-distance dispersal. However, multi-marker gene sequencing of focal taxa (e.g., Mollusca, Gastrotricha; Jörger et al., 2012; Kieneke et al., 2012) recently revealed the presence of a substantial amount of cryptic diversity and the existence of multiple genetic lineages within morphological species boundaries (Jörger et al., 2012; Chapter 5: Hauquier, unpublished). Hence, species previously believed to possess global or ubiquitous distributions based on morphological taxon delineation might in fact constitute several lineages with more restricted range sizes (Derycke et al., 2013). This revived the discussion on endobenthic meiofaunal invertebrates being effectively dispersal-limited at larger geographic scales, despite the relatively homogeneous nature of the marine ecosystem, the presence of homogenising ocean currents, and the absence of geographic barriers to exchange of organisms (Srivastava & Kratina, 2013). Large-scale taxonomic inventories of meiofauna groups are therefore needed to evaluate the validity of this so-called meiofauna paradox and to assess the structuring roles of more regional (e.g., dispersal from a regional species pool) and local (e.g., environmental habitat, biotic interactions) processes on community assembly (cf. Fonseca et al., 2014).

In this respect, the metacommunity concept (Holyoak et al., 2005; Leibold et al., 2004) provides a useful theoretical starting point to test this. As species diversity is governed by a balance between processes operating at different spatial (local versus regional) and temporal scales (Cornell & Harrison, 2013; Holyoak et al., 2005; Ricklefs, 1987), several attempts have been made to disentangle the interplay between local and regional processes (Holyoak et al., 2005; Leibold et al., 2004). In the metacommunity theory, communities are defined as sets of local assemblages that reflect regional-scale as well as local-scale dynamics, and that are linked by the dispersal of multiple, potentially interacting species. Depending on how much emphasis is put on environmental heterogeneity, the degree of functional equivalence among species, and dispersal rate, (meta-) community dynamics were traditionally divided into four main paradigms, namely neutral models, patch dynamics, mass effects and species sorting (see Cottenie, 2005; Leibold et al., 2005; Logue et al., 2011 for a detailed assessment of these paradigms). Several studies characterised metacommunities based on how well they conform

to these four paradigms, or alternatively and more recently, at what point and for which spatial scale deterministic and stochastic processes become more important (e.g., Chase & Myers, 2011; Cottenie, 2005; Declerck et al., 2011; Vellend et al., 2014; Viana et al., 2016). A substantial amount of these studies focused on habitat patches with relatively discrete geographical boundaries such as lake and pond ecosystems (Beisner et al., 2006; Vanschoenwinkel et al., 2007), and highlighted the importance of local species-sorting dynamics in explaining community turnover (i.e. β-diversity). In these cases, compositional variation between communities largely stemmed from associations between species and local environmental conditions (ecological niche). At the same time, historical processes and dispersal limitation were shown to explain patterns of restricted distributions in some lacustrine groups that were previously believed to possess unlimited dispersal capacities, such as diatoms (Soininen, 2007; Verleyen et al., 2009). While the application and validation of the metacommunity theory are ever-increasing, empirical studies in marine metacommunities are rare compared to terrestrial and lacustrine habitats, and mostly focus on taxa with a larval development or a pelagic propagule stage (e.g., Moritz et al., 2013: benthic polychaetes; Okuda et al., 2010: macroalgae, benthic invertebrates and molluscs). In the few studies available for the marine realm, local environmental conditions appeared to explain the vast majority of the β-diversity patterns through the process of species sorting, while dispersal limitation was of secondary importance as a result of the strong connectivity between ocean basins (Heino et al., 2015 and references therein; but see McClain et al., 2012).

This study focuses on free-living nematode communities on the continental shelf of the Atlantic sector of the Southern Ocean (Fig. 4.1), at a regional spatial scale spanning the Scotia Arc, Antarctic Peninsula and eastern Weddell Sea. Free-living nematodes are the most abundant and speciose marine metazoan taxon in various seafloor sediments, at different depths, and in different regions, including the Antarctic continental shelf (De Mesel et al., 2006; Hauquier et al., 2015, 2016; Heip et al., 1985; Lambshead & Boucher, 2003). At the same time, they do not possess pelagic larval stages and are therefore dependent on passive dispersal through hydrodynamics in the water column (Boeckner et al., 2009; Moens et al., 2013; Thomas & Lana, 2011). This has obviously important implications regarding their dispersal capacities making nematodes interesting study objects to test the meiofauna paradox. The traditional view in nematode macroecology assumes that most nematodes are cosmopolitan, and community variation is largely correlated with the sedimentary properties of the different habitat patches (parallel to the “everything is everywhere” hypothesis for

micro-organisms; Moens et al., 2013). However, these assumptions rely almost entirely on assessments at the genus level, because studying patterns at the species level is often hampered by their taxonomically challenging identification, inconsistency in species descriptions, the presence of cryptic diversity, and poor sampling coverage (Derycke et al., 2013).

The aims of this study are twofold. First, we tested to what extent (macro-) ecological patterns differ between the genus- and species-level and whether nematode species are as widely distributed as genera. This was done for five stations across the Scotia Arc and Weddell Sea where a hierarchical sampling strategy was adopted. Second, these data were combined with existing datasets on nematode genus composition in the South Atlantic sector of the Southern Ocean to i) investigate community variation at a scale ranging from a few 100 m to as much as 2400 km, and link the patterns observed to local environmental conditions while considering the underlying spatial configuration, and ii) test whether nematodes residing deeper in the sediments express different distribution patterns than surface-dwelling taxa that are less protected from bottom dynamics and passive transportation by ocean currents in the area (e.g., the Weddell gyre; Deacon, 1979).

MATERIAL AND METHODS

Sampling area

Nematode community samples were collected during scientific expeditions ANT-XXVII/3 and ANT-XXIX/3 of the German icebreaker RV *Polarstern* in austral summer 2011 and 2013, respectively (Gutt, 2013; Knust et al., 2012). A multicorer (MUC, 12 cores mounted, each with an inner diameter 57 mm and a surface area of 25.52 cm²; Barnett et al., 1984) was used to gather undisturbed sediment-water interface samples at continental shelf depths (~ 240 – 520 m) at locations along the Scotia Arc and the Antarctic Peninsula, and in the eastern Weddell Sea. Eleven locations are included in this study (see Table 4.1, Fig 4.1), of which five were used to investigate macroecological patterns at both genus and species level. These latter ones were South Georgia (SG), King George Island (KG), South Orkneys (SO), off Auståsen (AUS) and Bendex (BX). The first three are located in the vicinity of Scotia Arc and South Shetland islands and are named after their geographical reference, while the latter two are situated at the eastern Weddell Sea continental shelf (AUS = off Auståsen ice rise, BX = arbitrary name assigned upon time of sampling) (Knust et al., 2012). Detailed information on the other stations can be found in Hauquier et al. (2015, 2016). Two of these (LW & LS) were

situated in an area east of the Antarctic Peninsula where the ice shelf collapsed prior to 2002 (Hauquier et al., 2016). The other stations were distributed near the Antarctic Peninsula tip (JE & ET) and the South Shetland Islands (DC & DE) (Hauquier et al., 2015). Despite the lack of obvious geographical barriers between most of the locations covered in this study and the presence of large-scale oceanic currents (Fig. 4.1), both sides of the Weddell Sea are separated by a vast area of deep-sea habitat, while locations near the Peninsula are influenced by different oceanographic regimes (Hauquier et al., 2015, 2016).

Table 4.1. *Sampling locations and codes with the number of cores collected, geographic coordinates and water column depth. LW = Larsen B.West, LS = Larsen B.South, JE = Joinville Island east, ET = Erebus and Terror Gulf, DC = Drake Passage central, DE = Drake Passage east, SG = South Georgia, SO = South Orkneys, KG = King George, AUS = off Auståsen, BX = Bendex. All locations were sampled during expedition ANT-XXVII/3 in 2011(Knust et al., 2012), except for JE, ET, DC and DE which were sampled in 2013 during ANT-XXIX/3 (Gutt, 2013). Locations indicated with an asterisk are used in the genus-species level comparison.*

Location	Station	Cores	Latitude	Longitude	Depth (m)
Larsen B.West	LW1	1	65° 32.99' S	61° 36.94' W	277
	LW2	1	65° 32.97' S	61° 36.94' W	278
	LW3	1	65° 32.96' S	61° 36.88' W	276
	LW4	1	65° 33.01' S	61° 36.96' W	280
	LW5	1	65° 33.01' S	61° 37.00' W	279
Larsen B.South	LS1	1	65° 54.95' S	60° 20.43' W	424
	LS2	1	65° 54.95' S	60° 21.49' W	395
	LS3	1	65° 54.99' S	60° 20.70' W	419
	LS4	1	65° 55.12' S	60° 19.83' W	428
	LS5	1	65° 55.15' S	60° 20.01' W	425
Joinville East	JE1	1	63°4.58´S	54°31.00´W	503.6
	JE2	1	63°4.10´S	54°30.86´W	484.8
	JE3	1	63°3.72´S	54°30.87´W	436.8
Erebus and Terror Gulf	ET1	1	63°50.95´S	56°24.43´W	517.6
	ET2	1	63°51.01´S	56°23.97´W	516.6
	ET3	1	63°51.03´S	56°23.68´W	517.1

Table 4.1. *Continued.*

Location	Station	Cores	Latitude	Longitude	Depth (m)
Drake Passage Central	DC1	1	62°12.32´S	60°44.47´W	497.8
	DC2	1	62°12.31´S	60°44.48´W	497.7
	DC3	1	62°12.31´S	60°44.54´W	495.2
Drake Passage East	DE1	1	62°2.22´S	60°12.01´W	489
	DE2	1	62°2.24´S	60°12.06´W	488
	DE3	1	62°2.24´S	60°12.03´W	488
South Georgia *	SG	6	54°25.612'S	35°41.799'W	257
South Orkneys *	SO	3	61°08.658'S	43°58.002'W	382
King George *	KG	3	62°13.283'S	58°50.948'W	242
off Auståsen *	AUS	2	70°48.385'S	10°39.718'W	436
Bendex *	BX	3	70°56.348'S	10°33.998'W	313

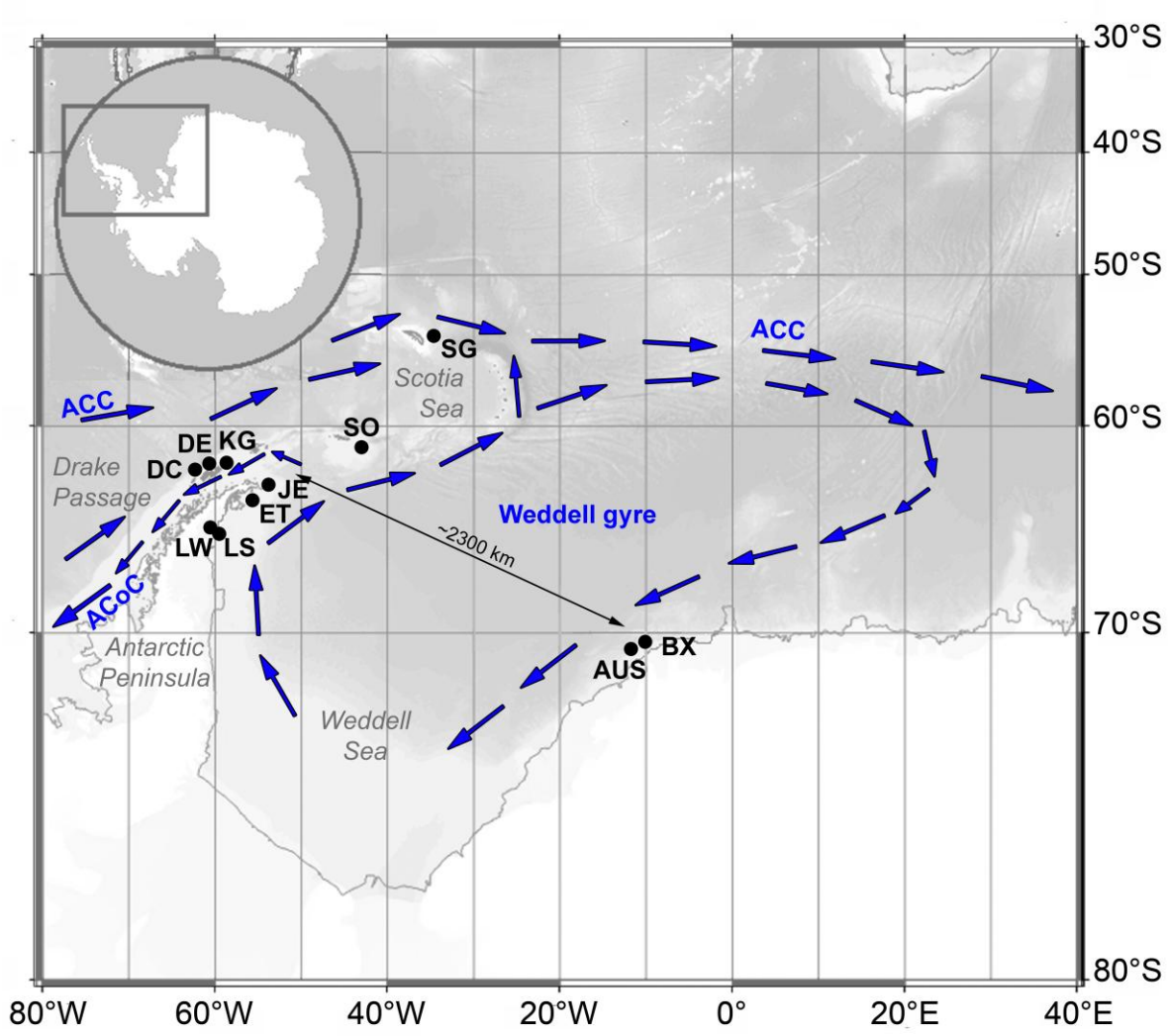

Figure 4.1. (previous page) *Overview of the Atlantic Sector of the Southern Ocean with the different sampling localities and main current systems indicated (see main text for abbreviations). ACC = Antarctic Circumpolar Current, ACoC = Antarctic Coastal Current. In reality, the ACC constitutes a zone of eastward jets between 48 and 61 °S, of which the position can shift with both time and location. For simplicity, only the main direction of the flow is considered here. Modified from cruise plot ANT-XXVII/3 (Knust et al., 2012).*

Sampling strategy

Part I – comparison taxonomic levels: Within the five locations used for genus and species assessment (Table 4.1, asterisks), a hierarchical sampling design was adopted to collect specimens at three spatial levels. Between-location distances range from approximately 15 km (AUS & BX) to almost 2300 km (BX & KG) as the crow flies, which constitutes the largest scale. From each MUC deployment, three individual cores were selected (two in the case of AUS). The distances between these cores in the MUC frame were measured and ranged from a few tens of centimetres to 1 m. This is considered the second spatial scale, namely between cores within locations. This intra-site comparison is warranted given that earlier research has indicated that local heterogeneity in nematode communities (cm to m scale) can be as high, or even higher, than regional patchiness (m to km scale) (Gallucci et al., 2009; Levin et al., 2001; Moens et al., 2013). However, restrictions at the time of sampling prevented the collection of cores from multiple MUC deployments for most of the sites. Finally, for each core, samples were subdivided into 6 equally-sized sections by means of a pie-shaped aid piece, which corresponds to the smallest scale of this study (i.e. within cores; cm-scale). The above-described sampling protocol was adopted for two sediment layers, 0 – 3 cm and 3 – 5 cm, yielding two different depth strata (i.e. slices) per subdivision. The choice for these strata was based on observations of changes in nematode community composition with sediment depth (e.g., Hauquier et al., 2015; Vanhove et al., 1998), but is still arbitrary. From the smallest-scale subdivisions per depth, three were immediately stored on a 4 % formalin – seawater solution (pre-filtered at 32 µm and borax-buffered) for nematode community analysis (referred to as subdivision A, B and C); and two were frozen at –20 or –80 °C for the measurement of environmental variables (A and B). This allowed measurement of environmental heterogeneity at the same spatial levels as community variation.

Part II – regional community structure: At the other locations not contained in part I of the analyses, replicate multicorer deployments yielded several samples at distances ranging from a few 10s of m to several hundreds of km. While samples were originally collected at a vertical resolution of 1 cm (see Hauquier et al., 2015, 2016), they were pooled for this study in two layers (0 – 3 cm and 3 – 5 cm) to be able to merge them with the genus data of the five locations described above. As for the locations in the first part, several environmental variables were recorded for each sample to complement the faunal communities.

Environmental setting

For each sampling location and replicate, hydrological and sedimentary variables were measured (see Table S4.1). Hydrological values (near-bottom temperature and salinity) were obtained from CTD measurements onboard. Sedimentary variables were measured at the same resolution as the nematode communities and averaged over replicates for two separate depth strata (surface 0 – 3 cm, subsurface 3 – 5 cm). Chlorophyll *a* content of the different sections (in µg g^{-1}) was measured by means of fluorescence detection following extraction from lyophilised sediments with 10 ml 90 % acetone and separation by reverse-phase HPLC (High Performance Liquid Chromatography; C18 column with a particle size of 5 µm, inner diameter of 4.6 mm and length of 25 cm). Median grain size (MGS), silt (< 63 µm) and sand (> 63 µm) percentages were determined by laser diffraction (Malvern Mastersizer 2000, size range 0.02 – 2000 µm) and classified according to Wentworth (1922). Weight percentages of total organic carbon (TOC) and nitrogen (TN) were measured on freeze-dried samples using a Flash 2000 organic elemental analyser, and their ratio (C:N) was calculated. Skewness in the different variables was assessed using draftsman plots in PRIMER v6 (Clarke & Gorley, 2006). As a result, most environmental variables were log-transformed (except temperature) and all data were normalised prior to analysis. Environmental setting of the different sampling locations was visualised by means of Principal Component Analysis (PCA) based on Euclidean distances. For a subset of locations (SG, SO, KG, AUS & BX), samples for environmental assessment were collected at a finer resolution. Environmental heterogeneity at these locations was calculated for each level of spatial information and later on averaged for the second part of this study.

Nematode community analyses

Nematodes were separated from the sediment by means of 1 mm and 32 µm sieves and density gradient centrifugation using Ludox (specific density 1.18 g cm^{-3}, centrifugation 3 ×

12 min at 3000 rpm; Heip et al., 1985; Vincx, 1996), and dyed with Rose Bengal (0.5 g l^{-1}). All specimens of each sample were counted at 50 × magnification under a stereoscopic microscope and standardised to individuals per 10 cm² (to account for differences in densities across samples). Thereafter, 10 % of their total density (ranging between approx. 30 and 400 individuals per sample) was randomly picked, transferred to anhydrous glycerol (Seinhorst, 1959), and mounted on glass slides. Identification at genus level (Leica DMLS compound microscope, 1000 × magnification) was based on the pictorial key of Warwick et al. (1998) as well as relevant literature and the NeMYS database (Guilini et al., 2016). Identification at species level (i.e. for a subset of locations) was done by comparing specimens with information and descriptions contained in literature and NeMYS. To facilitate classification into putative morphospecies, certain morphological characteristics (e.g., body length, width, spicule length) were measured using Leica LAS 3.3 imaging software after which relevant ratios (e.g., de Man ratios) were calculated. Since only little information is available for Southern Ocean nematodes at species level, specimens were given arbitrary working names (sp.1, sp.2, etc.). While this approach precludes comparison with approved species in WoRMS (WoRMS editorial board, 2015) and other sources, it ensures taxonomic consistency of the identifications between the different locations.

Statistical analyses

Part I – comparison taxonomic levels: The genus and species counts (standardised as individuals per 10cm²) for the five locations and two depth strata were transformed into relative abundances and presence-absence depending on the analysis. To compare community patterns at genus and species level, beta diversity for the different spatial levels was assessed in two ways. First, the Bray-Curtis dissimilarity of square-root transformed abundance data was calculated at both taxonomic levels in PRIMER v6. The transformation served to limit the influence of rare genera/species, while Bray-Curtis was chosen due to its insensitivity to joint absences (Clarke & Gorley, 2006). Compositional variation among the locations was evaluated against the spatial organisation of the samples. Second, Sørensen's index of β-diversity was calculated based on presence-absence data to quantify the contribution of 'nestedness' and 'turnover' patterns to community variation (Baselga, 2010) at the different spatial levels (within-core, between-core, among-location). This was done by partitioning beta diversity in the 'betapart' package (Baselga et al., 2013) for R (R Core Team, 2013). The partitioning between those components is important since it can give clues on the underlying processes governing species distribution patterns. For example, nestedness has been linked to

non-random processes (e.g., historical events, dispersal limitation) that result in species loss and differences in species richness between sites. Turnover, on the other hand, might relate to species replacement as a consequence of niche processes or historical and spatial constraints (Baselga, 2010; Chase et al., 2011; Viana et al., 2016).

Part II – regional community structure: The main part of this study focused on evaluating whether local environmental conditions or presumed dispersal limitation for nematodes are the main factors influencing their distribution. We therefore applied variation partitioning analysis (Borcard et al., 1992) for both surface and subsurface communities using the Vegan package (Oksanen et al., 2013) in R. This method requires three datasets, namely i) a biotic matrix containing the relative abundances of taxa (genera in this case) in individual samples, ii) a matrix with local environmental variables, and iii) a matrix consisting of spatial predictors. The biotic dataset consisted of the genus counts as individuals per 10 cm^2 per sediment layer. Data contained in the hierarchical samples of Part I were summed per core (A + B + C) and averaged over the different cores within each of the five locations before inclusion. To account for differences in nematode abundance at the different locations, genus counts were first rarefied to the lowest abundance before proceeding. Then, relative abundances were calculated and Hellinger transformed because this has been shown to be a valid data transformation when analysing variation between communities at individual sites (Legendre et al., 2005; Peres-Neto et al., 2006). The matrix with the environmental factors contained the sedimentary and hydrological variables for each location described earlier. These were log-transformed and normalised. Finally, the matrix with the spatial variables contained Principal Coordinates of Neighbour Matrices (PCNMs) of the geographic coordinates of the samples (Borcard & Legendre, 2002; Dray et al., 2006). These are eigenvectors with positive eigenvalues obtained by principal coordinate analysis (PCoA) of a truncated matrix of Euclidian distances between the sampling sites. Distances were calculated in R, based on geographic coordinates of the samples. To account for the spatial clustering in the dataset (i.e. replicate MUC stations closer to each other than to other locations in the dataset), PCNMs were calculated within blocks of samples (local scale), as well as between all locations together (regional scale). The different PCNMs were then combined in one set of spatial predictors to capture as much spatial information as possible. For the within-location PCNMs, blocks considered were the Larsen stations (LW + LS; PCNM 1 – 6), the stations near the Antarctic Peninsula tip (JE + ET; PCNM 7 – 10) and those in the Drake Passage (DC + DE; PCNM 11 – 14). PCNM values for the other stations within these blocks were set to

zero. For the large-scale PCNM calculation, three 'ghostpoints' were included to increase their discriminating power at smaller spatial scales. Points were located at intermediate geographic positions within the Weddell Sea, as this is the largest distance to cross and possibly 'blurs' the outcome of smaller-scale patterns. After PCNM calculation, these ghostpoints were removed from further analyses. Eight additional PCNMs (PCNM 15 – 22) were included, bringing the total set of spatial predictors at 22 variables. Redundancy analysis (RDA) was applied to assess the relationships between the biotic datasets and both the environmental and spatial variables using the Vegan package in R. A stepwise selection procedure (Monte Carlo permutation tests, n = 999) was applied to retain only those variables in the environmental and spatial matrix separately that significantly contributed to the variation in community composition. Variation inflation factors (VIF) were used to detect collinearity between variables. A VIF-value > 10 for a certain variable led to its removal from the final model and repetition of all previous steps until all VIFs < 10. The significant environmental (E) and spatial (S) variables were subsequently used in partial RDAs. This procedure divides the variation in the dependent dataset (i.e. community composition at genus level) in relative contributions of the different components: total explained variation [E+S], variation explained by environmental factors [E], variation explained by spatial factors [S], variation explained by environmental factors irrespective of spatial structure [E|S] and variation explained by spatial structure irrespective of environment [S|E]. The function "varpart" in the Vegan package in R was used to calculate adjusted R^2 for each fraction (i.e. taking into account sample size and number of constraining variables in the E and S model; Peres-Neto et al., 2006), while Monte Carlo permutation tests (n = 999) computed the significance (5 % level) for the different fractions. Two additional fractions were derived as well (no significance testing possible): the unexplained variation [U] = 1 – [E+S], and the spatially structured environmental variation [E∩S].

RESULTS

Part I – spatial turnover patterns for genera and species

Environmental heterogeneity, approximated by the average pairwise Euclidean distance between samples at the three levels of spatial organisation, increased with spatial scale (Fig. 4.2A). The stations in the eastern Weddell Sea (AUS and BX) were situated at higher latitude than the others (approx. 70 °S versus 54 – 60 °S) and characterised by lower (below-zero) temperatures at the seafloor and more oligotrophic conditions (lower chl*a* and organic carbon

content) (Fig. 4.4; Table S4.1). Also, sediments at this side were coarser than near the Antarctic Peninsula.

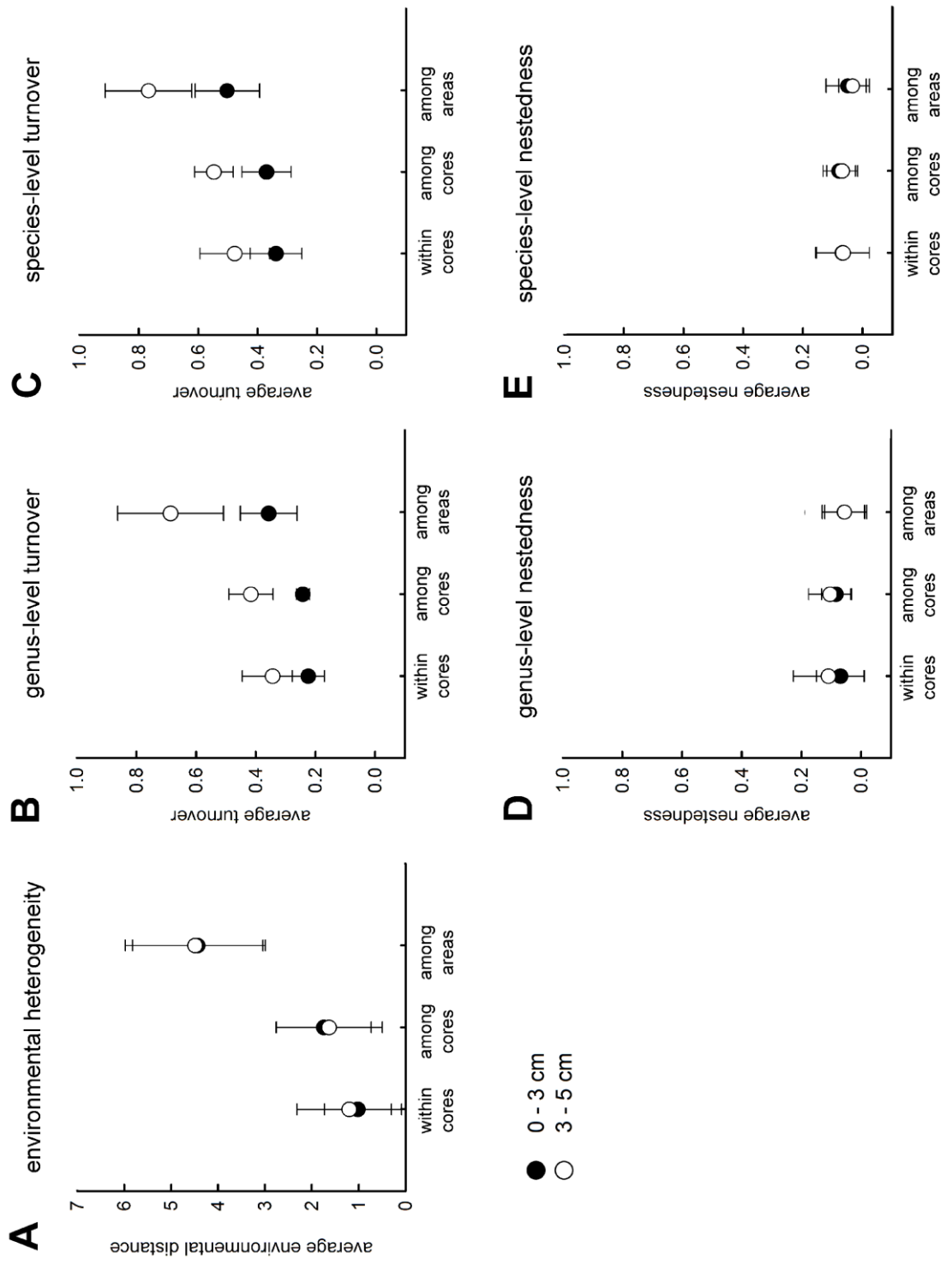

Figure 4.2. (previous page) *Average environmental heterogeneity (A), turnover (B + C) and nestedness (D + E) components of beta diversity – both for genus and species level – across the three levels of spatial scale. Full circles represent values for surface layers (0 – 3 cm), while open circles are subsurface values (3 – 5 cm). Environmental heterogeneity is the average Euclidean distance between pairs of samples. Turnover and nestedness are the respective components of Sørensen dissimilarity between samples, based on presence-absence data. Error bars denote standard deviation.*

The increase in environmental heterogeneity was mirrored by nematode genus and species community variation. A total of 142 genera and 274 species were identified across all samples, and their numbers were higher in surface than in subsurface layers (one-way ANOVA $P << 0.001$). In terms of beta-diversity, partitioning of the Sørensen index into its turnover and nestedness components revealed that variation in community composition largely stems from species/genus replacement (turnover) rather than loss (nestedness; Fig. 4.2B-E; Table S4.2). This was true at all three spatial levels and for both taxonomic levels considered. Turnover was similar at both within- and between-core levels and peaked at the largest spatial scale (Fig. 4.2B, C). Nestedness did not show any obvious trend with spatial scale (Fig. 4.2D, E). When relative abundances of genera and species were taken into account, pairwise comparison between samples based on Bray-Curtis (dis)similarity showed that similarity was lower for species than for genera (~ 10 % difference) and decreased with distance between samples at both taxonomic levels. This pattern was more pronounced for the subsurface layers than at the surface (Fig. 4.3A, B left panel). Overall, turnover patterns between communities were similar for both taxonomic levels.

Large differences between both sides of the Weddell Sea and lower similarity of subsurface communities compared with surface ones was evident from the number of species shared between locations for both layers. Deeper layers at both sides of the Weddell Sea shared only 31 % of their species (and only 14 % occurred at all five locations), whereas this was 51 % in surface samples (31 % at all locations). Conversely, 49 % of the species was restricted to either the eastern or western side of the Weddell Sea in the surface layers (of which 36 % were present at a single location) compared to almost 70 % in the deeper layers (49 % singletons). Again, patterns were largely congruent at genus level. This suggests that dispersal might be more limited in deeper layers than at the surface; an observation which is also supported by plots summarising the averaged relative abundance of a genus or species in the 0 – 3 cm or 3 – 5 cm dataset in relation to its occurrence across the samples (Fig. 4.3 right

panel). In both surface and deeper sediments, genera and species with the highest relative abundance (rank 1) were most widely spread. Next to these large differences between communities across the Weddell Sea, also within one location significant differences between sediment depths could be observed. The average amount of shared species between surface and deeper layers within locations was 41.4 ± 9.1 %, while this was slightly higher (47.8 ± 7.6 %) for genera.

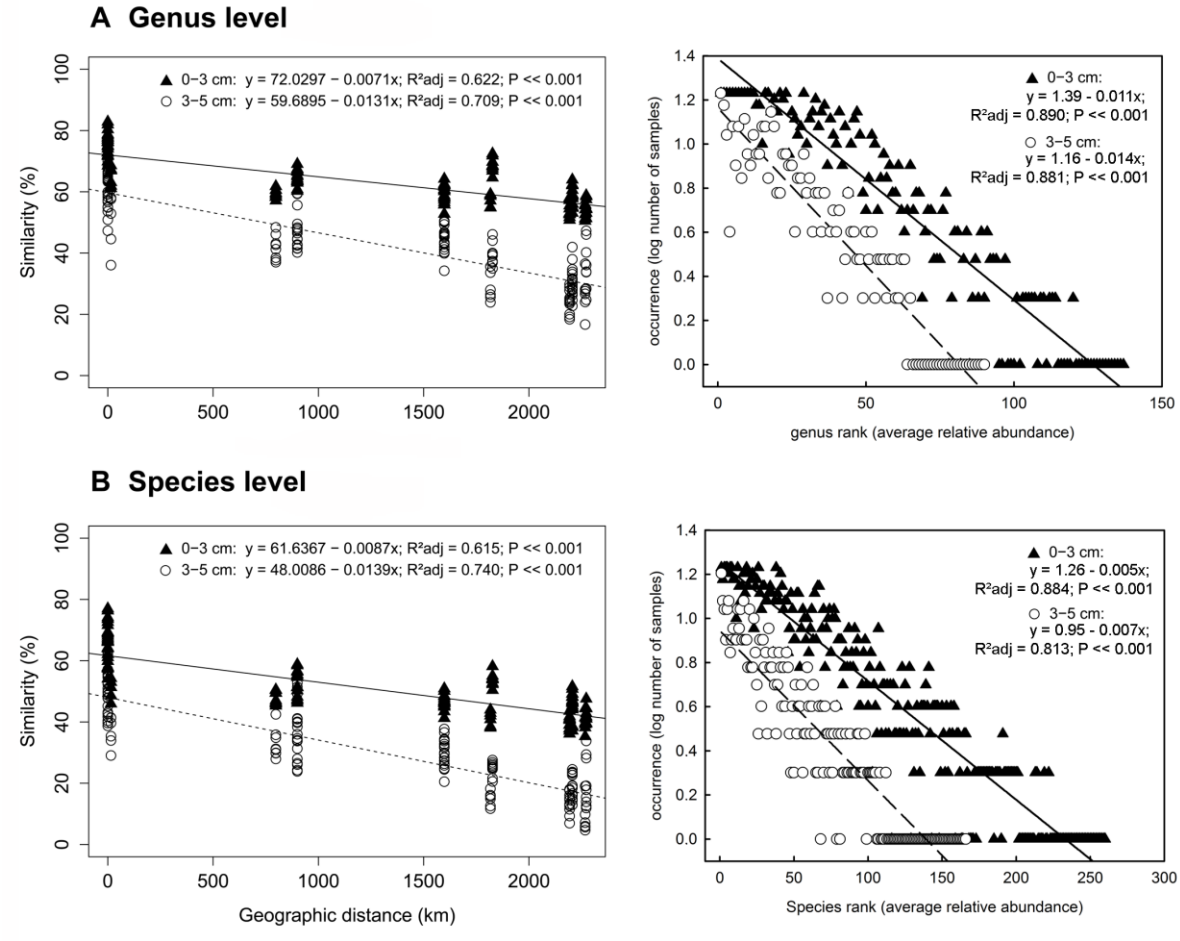

Figure 4.3. *Overview of community similarity at genus (A) and species (B) level.* ***A. Left panel*** *Distance decay in Bray-Curtis similarity for nematode genus composition against geographical distance (as the crow flies), both for 0 – 3 cm (triangles) and 3 – 5 cm (circles). Lines indicate the linear regression fit (0 – 3 cm = solid, 3 – 5 cm = dashed).* ***Right panel*** *Scatterplot showing the relation between the rank of the different genera according to their averaged relative abundance and the occurrence in the samples (expressed as log number of samples). Lines indicate the linear regression fit (0 – 3 cm = solid, 3 – 5 cm = dashed).* ***B.*** *Same for species. In all cases, linear regression equations, as well as the adjusted R² and P-value are given.*

Part II – regional distribution patterns and drivers

Nematode communities at the genus level significantly differed between locations and sediment depths (see Fig S4.1). The different depth strata were therefore analysed separately (although strictly speaking, they are not independent of each other), since we wanted to test whether different patterns emerge for surface and subsurface communities. Also environmental variables showed variation among the different sampling locations and depth layers (see Hauquier et al., 2015, 2016 for a detailed assessment) (Fig. 4.4, Table S4.1).

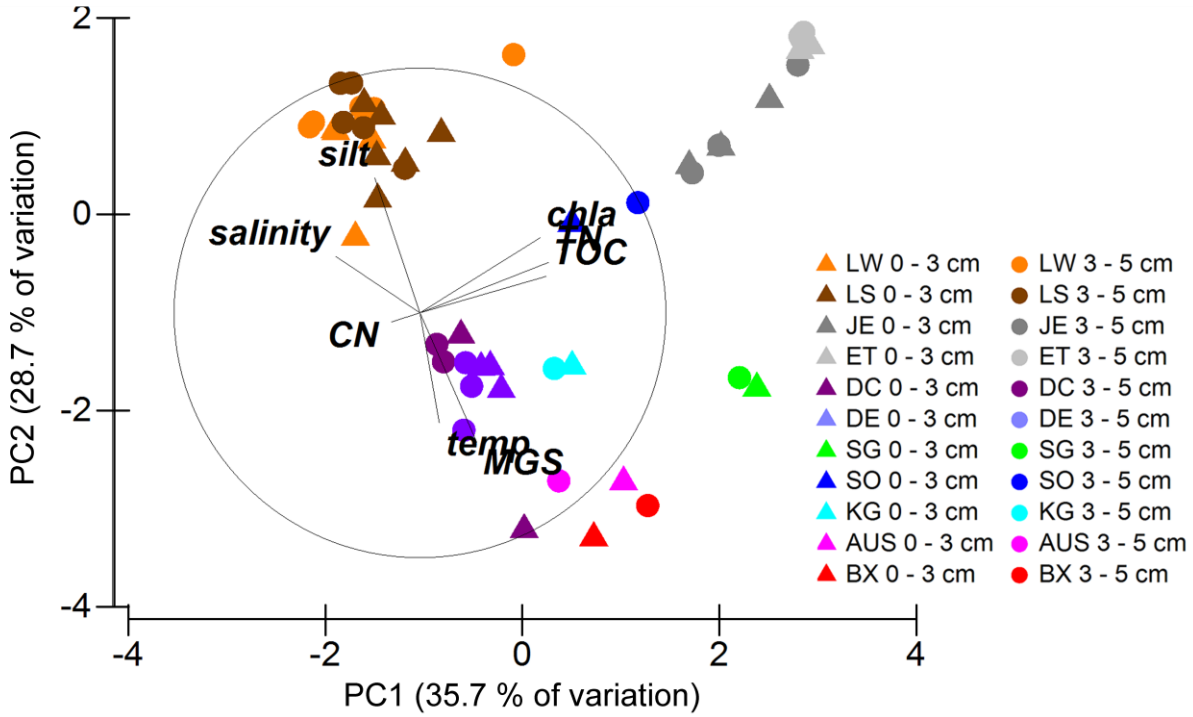

Figure 4.4. *PCA of the sampling locations according to their environmental setting based on Euclidean distances between samples. Triangles are surface layers (0 – 3 cm), while circles depict subsurface layers (3 – 5 cm). Variables were log-transformed and normalised prior to analysis. TOC = total organic carbon, TN = total nitrogen, CN = ratio of TOC:TN, chla = chlorophyll a, temp = bottom temperature, MGS = median grain size, silt = silt fraction (< 63 µm).*

Stepwise selection of environmental and spatial variables by RDA revealed that the differences in genus community structure at the surface could be significantly ($P < 0.05$)

explained by a combination of sedimentary and hydrological variables (total organic carbon content, temperature, silt fraction and salinity; Table 4.2 [E]). In deeper layers some of the same variables were selected (median grain size, TOC, temperature, chlorophyll and silt). Analysing relationships between community composition and the spatial predictors yielded a combination of both small-scale PCNMs for the blocks (PCNM 1, 10 and 11) and large-scale PCNMs for the entire area (PCNM 15, 19, 20, 21 and 22) (Table 4.2 [S]).

Table 4.2. *Partition of variation in nematode communities using partial RDA analyses on Hellinger-transformed relative abundance data. Abbreviations of different fractions explained in main text.* R^2_{adj} *= variation explained (%),* Df_{model} *= degrees of freedom of model,* Df_{res} *= residual degrees of freedom, F = F-statistic, P = Monte Carlo P-value (n = 999; 5 % significance). * note that the 3 – 5 cm dataset had 1 datapoint less than the 0 – 3 cm.*

	0 – 3 cm					**3 – 5 cm***				
	R^2_{adj} (%)	Df_{model}	Df_{res}	*F*	*P*	R^2_{adj} (%)	Df_{model}	Df_{res}	*F*	*P*
[E]	33.6 [a]	4	22	4.2925	0.001	59.3 [c]	5	20	8.2825	0.001
[S]	62.0 [b]	8	18	6.299	0.001	68.1 [d]	7	18	8.6143	0.001
[E|S]	7.7	4	14	2.1404	0.004	5.7	5	13	1.7882	0.006
[S|E]	36.0	8	14	4.2684	0.001	14.5	7	13	2.5833	0.001
[E∩S]	25.9	no test				53.6	no test			
[E+S]	69.7	12	14	5.977	0.001	73.8	12	13	6.8703	0.001
[U]	30.3	no test				26.2	no test			

[a] environmental model constructed with variables TOC, temperature, silt and salinity
[b] spatial model constructed with variables PCNM 20, 1, 21, 15, 19, 11, 10 and 22
[c] environmental model constructed with variables MGS, TOC, temperature, chla and silt
[d] spatial model constructed with variables PCNM 20, 21, 1, 15, 19, 16 and 22

Variation partitioning resulted in highly significant contributions of both the significant set of environmental and spatial variables (Table 4.2). Together, both components explained almost 70 – 74 % of community variation in the dataset. Further partitioning into unique ([E|S], [S|E]) and shared ([E∩S]) contributions indicated that relatively more variation could be unambiguously assigned to either environment or space when considering the surface ($[E|S]_{up}$ = ~ 8 %; $[S|E]_{up}$ = 36 %) rather than deeper layers ($[E|S]_{low}$ = ~ 6 %; $[S|E]_{low}$ = ~ 15 %). It follows that the amount of variation explained by spatially structured environmental factors was higher in the 3 – 5 cm layer ($[E\cap S]_{low}$ = ~ 54 %) compared with the 0 – 3 cm layer (~ 26 %).

DISCUSSION

The first part of this study showed that ecological patterns of community variation are similar at both the genus and species level. Community dissimilarity was almost entirely attributed to turnover, and increased with spatial scale and environmental heterogeneity between locations. Both genus and species communities consisted of a combination of taxa that were widely spread and taxa that showed restricted ranges. Nevertheless, our region-scale analysis of free-living marine nematode metacommunities in this part of the Southern Ocean revealed a strong spatial structure and distance decay in community similarity which supports the hypothesis that dispersal over large distances might be limited in this important meiobenthic group (Derycke et al., 2013). Especially in subsurface layers, genera and species seemed more limited in their distribution than at the surface. Hubbell (2001), in his neutral theory, already postulated that communities further apart will increasingly differ from one another, even under homogeneous environmental conditions, due to dispersal limitation. The question therefore remains to what extent nematodes communities are structured by such dispersal limitation or by niche processes (as traditionally accounted for).

Nematode genus and species turnover at different levels of spatial clustering

Analysis of beta diversity at three levels of spatial organisation within a subset of locations showed that almost all variation between nematode genus and species communities was due to turnover patterns. At the two lowest levels of spatial scale, within cores (cm) and between cores (m), the amount of turnover was comparable (Fig. 4.2). Such small-scale variation in communities has been described before and can be related to complex interactions between species, and between species and their environment (Fonseca et al., 2010; Gallucci et al., 2009). Given the low level of environmental heterogeneity at these small scales (Fig. 4.2A), biotic interactions seem a more plausible explanation for the observed turnover. However, a more detailed analysis on the genera and species present would be warranted in this case and falls outside the scope of this study. When turning to the largest spatial scale (i.e. among locations), environmental heterogeneity and nematode turnover increased substantially (Fig. 4.2). There were thus large differences between communities of the five locations studied, both in surface as well as in subsurface sediments. This was also evident from pairwise Bray-Curtis similarities, which additionally showed that communities further apart were more distinct than those in nearby regions, resulting in distance decay in similarity (Fig. 4.3 left panels). Particularly when comparing both sides of the Weddell Sea, variation in composition and relative abundance of nematodes was substantial, and a rather low amount of species was

shared between both regions. This distance decay was more pronounced for subsurface communities and could relate to their position in the sediment. Nematode dispersal is a predominantly passive process at scales that surpass within-site distances (Derycke et al., 2013; Giere, 2009; Moens et al., 2013) and requires resuspension and transportation in the water column. Nematodes themselves are usually poor swimmers, but bottom currents and boundary layer dynamics are able to mediate their dispersal across longer distances (Palmer, 1988). Surface communities are believed to be more prone to such passive dispersal dynamics (Commito & Tita, 2002; Eskin & Palmer, 1985; Thomas & Lana, 2011), which could partly contribute to the observed differences in similarity between surface and subsurface layers. A higher dispersal probability for surface communities combined with the high number of individuals might homogenise their composition across a larger geographic distance compared to deeper assemblages. Based on the observation that highly abundant species (and genera) showed a wide distribution range (Fig. 4.3 right panels), such a scenario might be plausible. Nevertheless, at very large spatial distances (across the Weddell Sea) this passive dispersal mode might become rather inefficient and distance decay in similarity also appears in surface layers. Alternatively, large differences between both sides of the Weddell Sea might also reflect a strong association between nematode genus and species communities and prevailing environmental gradients in the area. In such a scenario, nematodes would not be dispersal-limited per definition, but instead efficiently dispersed through the current systems operating in the area (Weddell gyre, Antarctic Coastal Current; Fig. 4.1). Variation in community composition and abundance between locations would then result from species tracking their preferred niche (cf. species sorting). Indeed, environmental conditions were largely different at both sides of the Weddell Sea (Table S4.1), rendering also this hypothesis theoretically possible.

The limited amount of samples in this subset of locations prevented unambiguous testing of both possibilities. The high levels of turnover at the regional spatial scale considered here might therefore indicate a low connectivity between locations or a high degree of environmental filtering. Therefore, variation partitioning was applied on a larger regional dataset and results are discussed in the next section. From the results discussed above it is clear that we observed relatively small differences in turnover patterns in community structure between the genus and species level. This is not entirely surprising given that habitat preference of nematodes can already be expressed at a higher taxonomic level (see reviews

Heip et al., 1985; Moens et al., 2013). This observation justifies the use of genera in subsequent variation partitioning analyses.

Spatial structuring and environmental filtering as drivers for nematode community turnover

Variation partitioning was carried out on surface and subsurface genus community data from a total of 11 locations (27 independent samples) in the Southern Ocean. The choice to perform such separate analyses was based on the higher probability of nematode resuspension and passive transportation through bottom dynamics in surface layers compared to deeper ones (see earlier) and the observation of significantly different communities with vertical sediment depth in Hauquier et al. (2015) for some of the locations included here. This approach revealed that both environmental and spatial variables were important in explaining regional turnover patterns in surface as well as subsurface communities. Overall, a large fraction of community variation could be explained by the combination of environmental and spatial models ([E + S] in Table 4.2). In both sediment depth strata, spatial models explained the larger fraction of community variation among locations ([S] > [E]). These models included mainly those spatial descriptors for the entire dataset (i.e. between the 11 locations), combined with one (subsurface) or a few (surface) PCNMs discriminating between the stations within the blocks (so at a smaller scale) (Table 4.2). In addition to spatial variables, environmental conditions partially and significantly accounted for the observed differences in nematode community structure. Both for surface and subsurface communities, sedimentary median grain size and/or silt percentage and total organic carbon significantly contributed to the environmental models (Table 4.2). Grain size and organic carbon content were also observed to structure nematode communities in Antarctic shallow sediments (Vanhove et al., 1998) as well as Arctic deep seas (Fonseca et al., 2010), so the fact that they show up in the models is not surprising. Grain size indirectly influences other physical and chemical (e.g., biochemistry and oxygen penetration) properties of the sediment (Giere, 2009) which can further affect nematode community composition (Heip et al., 1985). In addition to sedimentary characteristics, hydrological near-bottom features such as temperature and salinity also significantly explained part of the observed variation in nematode community composition. This influence of water-mass characteristics was reported before for the Antarctic Peninsula and Drake Passage stations included in this study (JE, ET, DC and DE; Hauquier et al., 2015).

The presence of significant spatial clustering in the nematode genus dataset might suggest an important role of dispersal limitation at the scale considered in this study (see previous section). Yet variation partitioning revealed that the importance of spatial variables was partly due to an overlap between the spatial and environmental sets of predictors ([E∩S] = 26 and 54 % for surface and subsurface, respectively). This was particularly true for the subsurface variation. Similar observations have been made in metacommunities of both freshwater (Shurin et al., 2009) as well as marine (Moritz et al., 2013) invertebrates, where such 'spatial noise' formed a confounding factor in trying to disentangle the roles of local and regional processes. Part of this overlap may be due to the co-variation of environmental variables such as temperature, salinity, but also grain size and total organic carbon content with geographic distance between the locations (Table S4.1). In this case, observed geographic distribution patterns in the nematode communities might reflect exogenous autocorrelation (i.e. spatial autocorrelation in the underlying environmental variables) rather than endogenous autocorrelation (i.e. due to spatial activities of the nematodes – such as dispersal) (Bahn & McGill, 2007; Buschke et al., 2014; Currie, 2007; Moritz et al., 2013; Soininen et al., 2007; Tuomisto et al., 2012). Also, unmeasured environmental variables as well as biotic interactions are potentially contributing to this exogenous autocorrelation fraction and can have an impact on nematode genus composition at the different locations. Especially for subsurface communities, it seems that we might have missed some important structuring agent, which could influence our conclusions. For example, oxygen is known to have a profound influence on nematode diversity and abundance, and some genera are more tolerant to situations where oxygen is limited (e.g., *Sabatieria*; Portnova et al., 2010; Schratzberger et al., 2006). In this respect, also bottom boundary layer dynamics (current strength, resuspension potential, etc.) and related vertical mixing of the sediment may influence availability of oxygen and food (cf. Isla et al., 2006b) and therefore indirectly affect nematode community composition. Since detailed information on such dynamics for our sampling locations is lacking, it is uncertain whether their inclusion might shift the balance towards higher levels of.species sorting. Based on the set of available variables at this point, it has to be concluded that the pure environmental niche effect is limited, though significant, at the larger scale for this study ([E|S] only 6 – 8 %). By contrast, the large amount of unique spatial variation (endogenous autocorrelation [S|E] in Table 4.2) for the surface layers does point towards a high probability of dispersal limitation (although the high values do not necessarily reflect the strength of this process and interpretation must be cautious; Gilbert & Bennett, 2010; Smith & Lundholm, 2010). Even in light of the limited amount of samples available in

this study, the variation partitioning method demonstrates that large-scale inventories of nematode community composition and their relation with the abiotic environment should ideally be combined with assessment of spatial structure within both datasets. Whether similar patterns appear for nematode communities in other marine areas that are better known, remains to be tested. However, such information could shed more light on the spatial scale at which nematode communities might shift from being niche-structured to dispersal-structured.

Conclusions

Here we have shown that spatial processes and environmental conditions are important in explaining differences in community structure in endobenthic nematodes at shelf depths in the Antarctic. The importance of environmental filtering varies with spatial scale and vertical segregation in the sediment. Surface communities might be partly aided in their dispersal through the presence of hydrodynamic features such as the Weddell gyre and circumpolar current. Yet, large-scale dispersal across the entire Weddell Sea is probably not very effective, resulting in large differences between communities from both sides. Subsurface communities show higher levels of dissimilarity, probably related to the fact that they are more sheltered from resuspension and passive transportation. Further research might benefit from a) larger sample coverage to fully investigate effective dispersal limitation across the Southern Ocean, b) combined morphological and phylogenetic assessment of species diversity and community structure, and c) detailed assessments of differences in dispersal capacities of species between the surface layers and the subsurface sediments.

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SUPPLEMENTARY INFORMATION

Table S4.1. *Environmental matrix with sedimentary and hydrological parameters used in variation partitioning analyses for the different locations and sediment depths. Explanation of abbreviations in main text. na = not available (below detection limit).*

		SEDIMENT							WATER	
station	**layer**	**MGS (µm)**	**silt (%)**	**sand (%)**	**TN (wt%)**	**TOC (wt%)**	**C:N**	**chla (µg g^{-1})**	**salinity (PSU)**	**temp (°C)**
LW1	0 - 3 cm	10.59	99.87	0.13	0.04	0.23	7.76	0.50	34.55	-1.97
	3 - 5 cm	8.20	99.76	0.24	0.03	0.20	7.22	0.02	34.55	-1.97
LW2	0 - 3 cm	11.67	99.93	0.07	0.03	0.22	9.61	1.17	34.55	-1.97
	3 - 5 cm	8.07	99.82	0.18	0.03	0.23	8.79	0.26	34.55	-1.97
LW3	0 - 3 cm	53.27	99.89	0.12	0.03	0.24	9.20	0.07	34.55	-1.97
	3 - 5 cm	9.10	99.94	0.06	0.31	0.25	5.50	na	34.55	-1.97
LW4	0 - 3 cm	9.05	99.90	0.10	0.07	0.26	4.56	0.16	34.55	-1.97
	3 - 5 cm	8.11	99.97	0.03	0.07	0.21	3.64	0.02	34.55	-1.97
LW5	0 - 3 cm	13.33	98.97	1.03	0.06	0.33	5.97	na	34.55	-1.97
	3 - 5 cm	9.98	99.83	0.17	0.07	0.16	2.77	na	34.55	-1.97
LS1	0 - 3 cm	19.57	96.38	3.62	0.09	0.67	8.41	0.33	34.59	-2.01
	3 - 5 cm	12.54	98.26	1.74	0.06	0.54	10.99	0.01	34.59	-2.01
LS2	0 - 3 cm	30.52	92.12	7.88	0.04	0.48	13.53	0.38	34.59	-2.01
	3 - 5 cm	10.61	98.78	1.22	0.05	0.53	13.11	na	34.59	-2.01
LS3	0 - 3 cm	12.83	98.25	1.75	0.05	0.55	12.57	0.93	34.59	-2.01
	3 - 5 cm	24.25	94.81	5.19	0.07	0.62	11.06	0.09	34.59	-2.01
LS4	0 - 3 cm	24.32	94.69	5.31	0.07	0.63	11.43	0.29	34.61	-1.89
	3 - 5 cm	6.80	100.00	0.00	0.06	0.59	11.29	0.07	34.61	-1.89
LS5	0 - 3 cm	10.00	98.93	1.07	0.06	0.57	11.87	0.39	34.61	-1.89
	3 - 5 cm	6.36	100.00	0.00	0.06	0.57	11.67	na	34.61	-1.89
JE1	0 - 3 cm	34.28	88.36	11.64	0.22	1.26	6.65	20.73	34.49	-1.81
	3 - 5 cm	28.65	89.77	10.23	0.23	1.31	6.77	42.18	34.49	-1.81
JE2	0 - 3 cm	38.52	83.56	16.45	0.19	1.06	6.45	5.00	34.49	-1.81
	3 - 5 cm	38.05	80.66	19.34	0.20	0.94	5.56	5.53	34.49	-1.81
JE3	0 - 3 cm	36.10	82.54	17.46	0.20	1.02	5.84	9.94	34.49	-1.81
	3 - 5 cm	36.65	82.49	17.51	0.20	0.92	5.50	13.75	34.49	-1.81
ET1	0 - 3 cm	25.53	93.24	6.76	0.24	1.63	7.80	23.27	34.50	-1.77
	3 - 5 cm	23.95	94.33	5.67	0.23	1.51	7.70	42.06	34.50	-1.77
ET2	0 - 3 cm	25.60	92.99	7.01	0.25	1.62	7.67	29.14	34.50	-1.77
	3 - 5 cm	23.54	94.41	5.59	0.25	1.53	7.07	26.41	34.50	-1.77
ET3	0 - 3 cm	25.60	93.26	6.74	0.24	1.54	7.39	30.92	34.50	-1.77
	3 - 5 cm	23.31	95.06	4.94	0.24	1.51	7.30	36.67	34.50	-1.77

Table S4.1. *Continued*

DC1	0 - 3 cm	346.94	65.81	34.19	0.07	0.54	8.45	0.04	34.61	0.99
	3 - 5 cm	54.22	81.51	18.49	0.07	0.49	8.18	0.02	34.61	0.99
DC2	0 - 3 cm	198.16	75.42	24.58	0.08	0.55	8.18	0.09	34.61	0.99
	3 - 5 cm	50.94	82.99	17.01	0.07	0.49	8.20	0.01	34.61	0.99
DC3	0 - 3 cm	49.38	85.03	14.97	0.08	0.55	7.90	0.14	34.61	0.99
	3 - 5 cm	47.66	84.47	15.54	0.07	0.49	8.21	0.01	34.61	0.99
DE1	0 - 3 cm	66.96	79.45	20.56	0.09	0.59	8.05	0.04	34.57	0.57
	3 - 5 cm	69.63	76.46	23.54	0.07	0.49	8.08	0.11	34.57	0.57
DE2	0 - 3 cm	75.48	74.61	25.39	0.09	0.58	7.72	0.07	34.57	0.57
	3 - 5 cm	83.18	69.58	30.42	0.06	0.40	7.71	0.03	34.57	0.57
DE3	0 - 3 cm	63.47	78.92	21.08	0.08	0.55	7.92	0.06	34.57	0.57
	3 - 5 cm	57.66	79.99	20.01	0.07	0.53	8.48	0.01	34.57	0.57
SG	0 - 3 cm	34.00	79.59	20.41	0.19	1.08	7.16	0.87	34.23	1.68
	3 - 5 cm	28.85	81.50	18.50	0.18	1.08	7.34	0.60	34.23	1.68
SO	0 - 3 cm	31.23	83.33	16.67	0.14	1.27	10.63	1.06	34.63	0.02
	3 - 5 cm	33.56	80.90	19.10	0.17	1.21	9.01	4.57	34.63	0.02
KG	0 - 3 cm	31.71	76.57	23.43	0.08	0.66	9.94	1.47	34.39	0.87
	3 - 5 cm	29.84	76.73	23.27	0.07	0.60	9.84	1.24	34.39	0.87
AUS	0 - 3 cm	140.82	49.33	50.67	0.11	0.61	6.64	0.53	34.45	-1.36
	3 - 5 cm	110.46	51.13	48.87	0.08	0.52	7.75	0.02	34.45	-1.36
BX	0 - 3 cm	94.38	42.93	57.07	0.06	0.31	6.64	0.56	34.31	-1.89
	3 - 5 cm	87.74	44.71	55.29	0.11	0.49	5.98	0.07	34.31	-1.89

Table S4.2. *Overview of turnover and nestedness components (± standard deviation) of genus and species β-diversity for the different spatial scales, depth strata and taxonomic levels.*

Genera		**turnover**	**nestedness**	**Sørensen**
within cores	**0 - 3 cm**	0.224 ± 0.054	0.069 ± 0.081	0.293 ± 0.054
	3 - 5 cm	0.343 ± 0.103	0.109 ± 0.118	0.453 ± 0.108
among cores	**0 - 3 cm**	0.242 ± 0.022	0.084 ± 0.049	0.326 ± 0.036
	3 - 5 cm	0.416 ± 0.074	0.104 ± 0.072	0.521 ± 0.087
among areas	**0 - 3 cm**	0.377 ± 0.083	0.062 ± 0.075	0.438 ± 0.061
	3 - 5 cm	0.665 ± 0.155	0.061 ± 0.068	0.725 ± 0.134
Species		**turnover**	**nestedness**	**Sørensen**
within cores	**0 - 3 cm**	0.338 ± 0.087	0.067 ± 0.090	0.405 ± 0.082
	3 - 5 cm	0.477 ± 0.117	0.065 ± 0.088	0.542 ± 0.102
among cores	**0 - 3 cm**	0.370 ± 0.083	0.078 ± 0.054	0.446 ± 0.050
	3 - 5 cm	0.547 ± 0.065	0.068 ± 0.052	0.615 ± 0.048
among areas	**0 - 3 cm**	0.525 ± 0.099	0.057 ± 0.074	0.583 ± 0.078
	3 - 5 cm	0.767 ± 0.133	0.041 ± 0.047	0.808 ± 0.101

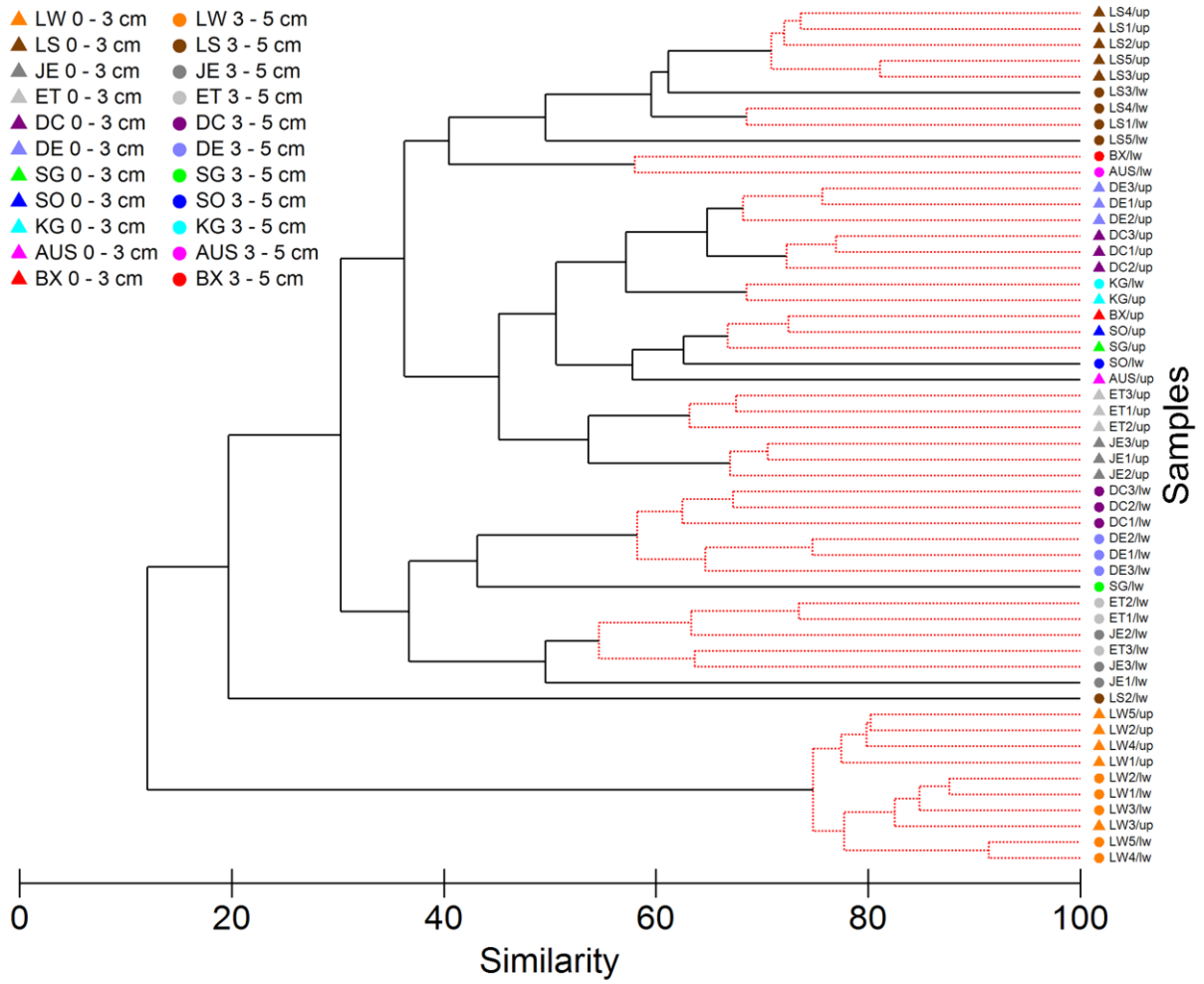

Figure S4.1. *Results of Cluster analysis with SIMPROF test in PRIMER v6 (Bray-Curtis similarity). Colour code according to sampling location, triangles = surface layers, circles = deeper layers. Red branches indicate non-significant differences at the 5 % significance level.*

CHAPTER 5: HABITAT-LINKED POPULATION GENETIC DIFFERENTIATION AND SPECIES DIVERSIFICATION IN TWO ANTARCTIC NEMATODES

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ABSTRACT

Dispersal abilities, population genetic structure and species divergence in marine nematodes are still poorly understood, especially in remote areas such as the Southern Ocean. We investigated genetic differentiation of species and populations of the free-living endobenthic nematode genera *Sabatieria* and *Desmodora* at intermediate Antarctic shelf depths (200 – 500 m) using nuclear 18S rDNA, internal transcribed spacer (ITS) rDNA, and mitochondrial cytochrome oxidase I (COI) gene sequences. The two nematode genera co-occurred at all sampled locations near the Antarctic Peninsula and at the eastern Weddell Sea, but with different vertical distribution in the sediment. Specimens of *Sabatieria* occurred mainly in deeper layers of seafloor sediments (3 – 5 cm), while individuals of *Desmodora* were typically surface-dwelling, with highest occurrence in the upper sediment layers (> 3 cm). Sequence analyses resulted in four divergent species lineages in *Sabatieria* – two of which could not be discriminated morphologically and most likely constitute cryptic species – and two in *Desmodora*, one of which showed large intraspecific morphological variation. Both genera comprised species that were either restricted to one side of the Weddell Sea, or that were widely spread across it. Population genetic structuring was highly significant, indicating that contemporary gene flow is probably restricted at large geographic distance. This casts doubt on the efficiency of the Antarctic Circumpolar Current as a homogenising factor in the Southern Ocean. Finally, population genetic structure was more pronounced in the deeper-dwelling *Sabatieria* species, which are generally less prone to resuspension and passive dispersal in the water column than surface *Desmodora* species. These results show that genetic structuring of and cryptic speciation in nematode species isolated from the same geographic area, but with different habitat preferences (surface versus deeper sediment layers) may be very distinct.

INTRODUCTION

Marine nematodes are the most abundant metazoan inhabitants of seafloor sediments and estimates of total species numbers (including parasites) are believed to exceed 50 000 (Appeltans et al., 2012). Yet most of this diversity remains undescribed due to the difficult and time-consuming taxonomy, and logistically challenging recovery from several (mainly deep-sea) habitats and remote areas (Bik et al., 2010; De Ley et al., 2005). To date, the number of described nematode species in the marine environment is ca. 12 000 (of which 6900 are free-living; Appeltans et al., 2012), which obviously covers only a limited fraction of total estimates (Bouchet, 2006; Bucklin et al., 2011). As a consequence, accurate

characterisation of species diversity and biogeographic distributions for this highly abundant phylum is currently lacking and the study of macroecological patterns is inevitably limited to genus-level data. Additionally, the observation of extensive cryptic species diversity in species with different life history traits (De Oliveira et al., 2012; Derycke et al., 2005, 2007b, 2008, 2010a, 2013) further hampers correct estimation of global and local species diversity. Globally distributed nematode species may in fact constitute geographically structured populations of cryptic species for which morphological characteristics are not readily observable (Derycke et al., 2005). Coexistence of such cryptic nematode species at local scales may then partly be driven by differential ecological tolerances, preferences for abiotic factors and/or resource differentiation (De Meester et al., 2011, 2015; Derycke et al., 2016). A profound understanding of species-specific life history traits (e.g., habitat preference, dispersal ability), in combination with knowledge on physical drivers of connectivity among marine populations (e.g., hydrodynamic forces, habitat characteristics) is thus imperative in the study of nematode species distribution patterns across various spatial scales and habitats. Reconstruction of speciation patterns further requires the combination of multiple, unlinked genetic markers, and thorough morphological assessment of nematode species with different ecological characteristics. Only then will we be able to evaluate the applicability of widely used concepts in ecology and biogeography for free-living marine nematodes, such as endemism, cosmopolitanism and connectivity.

In terms of connectivity, the intrinsic nature of the marine environment presenting few obvious barriers to gene flow has led to predictions of little genetic structure of marine species over large spatial scales (Palumbi, 1992) and speciation being mainly driven by broad-scale allopatric processes (e.g., Taylor & Hellberg, 2005; Wilke & Pfenninger, 2002). In the Southern Ocean, genetic exchange between locations around the continent may be facilitated by the eastward Antarctic Circumpolar Current (ACC) and westward Antarctic Coastal Current (ACoC) systems, as well as the Weddell gyre (Deacon, 1979) (Arntz et al., 1994; Riesgo et al., 2015). As a result, many studies on Antarctic marine benthic invertebrates have reported circum-Antarctic and eurybathic distributions, together with high predicted levels of endemism (e.g., Brandt et al., 2007a; Brey et al., 1996). However, compelling evidence from DNA markers showed that populations of marine organisms present substantial genetic differentiation and may be isolated over smaller spatial scales and depth ranges than previously thought (Allcock & Strugnell, 2012; Cowen et al., 2007).

The effective population size and dispersal rate between populations determine phylogeographic patterns in marine species (Hellberg et al., 2002). In cases where dispersal is limited and effective population size large, historical constraints probably play a major role as well (Derycke et al., 2008; Hellberg et al., 2002), and also spatial scale can influence the type of genetic differentiation pattern that is observed. One of the most commonly tested patterns is the stepping stone gene flow model (i.e. isolation-by-distance principle (IBD); Slatkin, 1993; Wright, 1943), which predicts a decrease in population connectivity with increasing geographical distance. Yet many populations in the marine environment show a seemingly random organisation without geographical trends – referred to as chaotic patchiness (Selkoe et al., 2010). Other mechanisms underlying species distributions may range from closed populations, over progressive geographic clines or abrupt phylogeographic breaks, to panmixia (i.e. open populations) (Hellberg et al., 2002).

In this study, we investigate the phylogeographic and population genetic structure of species belonging to two marine nematode genera (*Sabatieria* and *Desmodora*) in the Antarctic using mitochondrial (cytochrome oxidase c subunit 1, COI) and nuclear (internal transcribed spacer (ITS) rDNA and small subunit (18S) rDNA) markers. Both types of molecular markers have been successfully applied in phylogenetic and population genetic studies of free-living nematodes (e.g., Bik et al., 2010; Blouin, 2002; Derycke et al., 2005, 2007b, 2010a; De Ley et al., 2005; Meldal et al., 2007), but mtDNA accumulates substitutions more quickly than nuclear loci, making it more suitable for investigation of contemporary gene flow at small geographic scales, and for discriminating between closely related species (Blouin, 2002; Derycke et al., 2010b, 2013). Spatial scale ranged from a few kilometres to > 2000 km, comprising five locations spread along the Scotia Arc, Antarctic Peninsula and Weddell Sea. The focus was on shelf communities between 240 and 440 m depth. The two genera are abundant and cosmopolitan in marine environments and have more than 100 described species each (Guilini et al., 2016). However, only four accepted species of *Desmodora* and 15 of *Sabatieria* have been reported in the Antarctic (including Scotia Arc islands; Ingels et al., 2006, 2014; Guilini et al., 2016). *Desmodora* is a genus of epistratum-feeders (sensu Wieser, 1953) that is often present in surface sediments, whereas *Sabatieria* species are deposit-feeders that typically reside in deeper sediment layers but are able to migrate upwards to access food and oxygen (Hauquier et al., 2015; Ingels et al., 2006). Also in our study area, *Desmodora* and *Sabatieria* predominantly (but not exclusively) occurred at different sediment depths. This vertical segregation has important consequences, since nematodes are dispersal-

limited (cf. lack of pelagic larvae, small body size, endobenthic lifestyle; Derycke et al., 2013) and therefore dependent upon passive transportation through hydrodynamics for their long-distance dispersal (Boeckner et al., 2009). Thus, differential vertical distribution and abundance in the sediment will influence their presence in the water column and the level to which they are prone to resuspension and passive dispersal via bottom currents (Eskin & Palmer, 1985; Thomas & Lana, 2011).

In light of current knowledge on cryptic speciation, cosmopolitan distribution and genetic structure in nematodes, we expected to find 1/ cryptic nematode species and strong genetic structuring in view of the large geographic distances between locations; 2/ increased population genetic structure with increasing geographic distance (cf. IBD), given the presumed limited dispersal capacity for nematodes (see also Derycke et al., 2013); 3/ stronger population genetic structuring in *Sabatieria* than in *Desmodora* based on its preference for different sediment depths, assuming that surface dwellers have higher dispersal probability than species that occur deeper in the sediment.

MATERIAL AND METHODS

Nematode collection, isolation and vouchering

Nematode specimens were collected onboard the German RV *Polarstern* in February-March 2011 (expedition ANT-XXVII/3, Knust et al., 2012) using a multicorer (MUC) device for undisturbed seafloor sampling. Five locations were sampled along the Scotia Arc (South Georgia SG, South Orkneys SO), Antarctic Peninsula (King George Island KG) and eastern Weddell Sea (Austasen AUS, Bendex BX; Fig. 5.1; Table 5.1), at shelf depths ranging between 240 and 440 m. Minimum distance between sampling locations was 15 km (AUS & BX), whereas the largest distance (as the crow flies) was almost 2300 km (KG & BX). MUC cores were divided into an upper (0 – 3 cm) and lower (3 – 5 cm) sediment slice. Samples were stored on DESS (Yoder et al., 2006) until further analysis in the lab. Nematodes were extracted from the sediments using 32 and 1000 µm sieves and density gradient centrifugation (Ludox specific density 1.18 g cm^{-3}, centrifugation 3 × 12 min at 3000 rpm; Heip et al., 1985; Vincx, 1996).

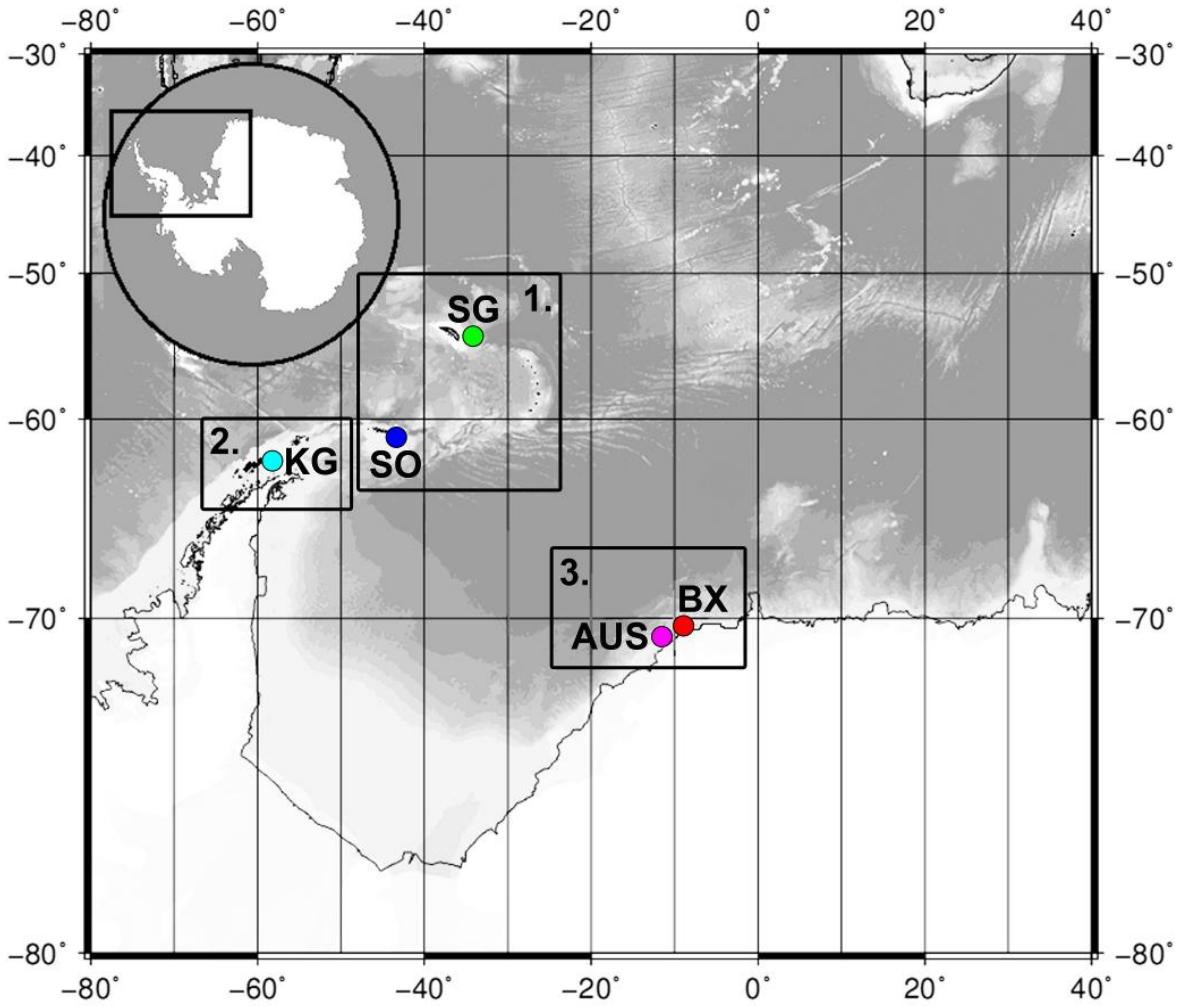

Figure 5.1. *Map of Antarctica highlighting the geographic location of the five sampling stations. Box 1: Scotia Sea: SG = South Georgia, SO = South Orkneys; Box 2: Antarctic Peninsula: KG = King George; Box 3: eastern Weddell Sea: AUS = off Auståsen, BX = Bendex. The same colour code is maintained in figures and graphs throughout the manuscript. Adapted from cruise plot ANT-XXVII/3 (Knust et al., 2012) © Alfred Wegener Institute.*

Table 5.1. *Overview of the five sampling locations with their geographic position and depth. The amount of sequences for each genetic marker per genus and species are given as well. First values = ITS; second = 18S; third = COI. Total specimen = total number of specimens available for PCR reactions. Species numbers represent numbers of sequences available (after successful amplification) for each genetic marker.*

– indicates that no information is available. Sequence numbers have been summed per species ('total'), and per population ('total per location').

				SABATIERIA						***DESMODORA***			
Location acronym	**Latitude (Dm)**	**Longitude (Dm)**	**Depth (m)**	**total specimens**	**species I**	**species II**	**species III**	**species IV**	**total per location**	**total specimens**	**species I**	**species II**	**total per location**
SG	54°25.612'S	35°41.799'W	257	155 | 35 | 28	114 | 10 | 2	25 | 4 | -	8 | 5 | -	- | - | -	147 | 19 | 2	30 | - | 34	17 | - | 9	- | - | -	17 | - | 9
SO	61°08.658'S	43°58.002'W	382	53 | 22 | 6	8 | - | -	25 | 3 | -	19 | 4 | -	- | - | -	52 | 7 | -	37 | - | 30	5 | - | 8	- | - | 12	5 | - | 20
KG	62°13.283'S	58°50.948'W	242	44 | 15 | 41	27 | 4 | -	1 | - | -	8 | 1 | -	- | - | -	36 | 5 | -	- | - | -	- | - | -	- | - | -	- | - | -
AUS	70°48.385'S	10°39.718'W	436	11 | 6 | 11	4 | 1 | -	1 | - | 1	- | - | -	2 | - | -	7 | 1 | 1	6 | - | 1	1 | - | 1	- | - | -	1 | - | 1
BX	70°56.348'S	10°33.998'W	313	89 | 24 | 90	46 | 5 | -	16 | 2 | 11	- | - | -	22 | 3 | 2	84 | 10 | 13	11 | - | 11	2 | - | 7	- | - | -	2 | - | 7
total				352 | 102 | 176	199 | 20 | 2	68 | 9 | 12	35 | 10 | -	24 | 3 | 2	326 | 42 | 16	79 | - | 76	25 | - | 25	- | - | 12	25 | - | 37

DESS samples were carefully screened under a stereomicroscope (50 × magnification) and individuals from both targeted genera were handpicked with a fine needle and washed in three separate dishes with sterile distilled water to remove all remaining DESS compounds. Individuals were mounted on a temporary microscopic slide in a drop of distilled water and identified under a Leica DLMS compound microscope (1000 × magnification). During this 'vouchering' process, each specimen was assigned to a certain morphological group based on conspicuous body features, which were photographed at different magnifications. For *Sabatieria*, we distinguished three morphological groups, with differences in tail shape, number of amphid turns and male copulatory organs (see Table S5.1). For *Desmodora* at least three distinct morphological groups (cf. *D. campbelli*, *D.* sp.A/B and *D.* sp.D of Ingels et al., 2006; Table S5.1) were recognised based on body length, position and length of somatic setae, male precloacal supplements and spicule apparatus, and presence of lateral body lines. After the vouchering process (5 – 10 min per specimen), each nematode was transferred into a microcentrifuge tube containing 20 µl Worm Lysis Buffer (WLB: 50 mM KCl, 10 mM Tris–HCl pH 8.3, 2.5 mM $MgCl_2$, 0.45 % NP40, 0.45 % Tween 20; Williams et al., 1992), and stored at –20 °C.

DNA extraction, amplification and sequencing

Proteinase K (1 µl; 10 mg ml^{-1}) was added to the WLB-stored specimens for digestion after which samples were incubated at 65 °C for 1 h, followed by 10 min at 95 °C. They were centrifuged for 1 min at 14 000 rpm prior to usage of the DNA. Three markers were amplified by polymerase chain reaction (PCR): the nuclear ribosomal DNA (rDNA) Internal Transcribed Spacer (ITS) region, part of the mitochondrial cytochrome oxidase c subunit 1 (COI) gene, and for a subset of *Sabatieria* specimens, part of the nuclear small subunit (18S) rDNA. Final reaction volumes for PCR were 25 µl, containing 14.875 µl nuclease-free water, 0.125 µl TOPTAQ Polymerase (Qiagen®), 2.5 µl 10 × PCR buffer with 15 mM $MgCl_2$, 2.5 µl coral load PCR buffer 10 ×, 2 µl $MgCl_2$ 25 mM, 0.5 µl dNTP (deoxynucleotide triphosphate, 10 mM), 0.250 µl primer (at 25 µM; both forward and reverse) and 2 µl DNA template. Used primers were JB3 (5'-TTTTTTGGGCATCCTGAGGTTTAT-3') and JB5GED (5'-AGCACCTAAACTTAAAACATARTGRAARTG-3') for COI of *Sabatieria* (Derycke et al., 2005), and universal primers CO1490F (5'-GGTCAACAAATCATAAAGATATTGG-3') and CO2211R (5'-AATGAGAATATAAACTTCWGGRTG-3') for COI of *Desmodora*. The first primer combination yields a DNA fragment of approximately 320 bp, while the latter one gives an amplicon of roughly 720 bp. Both fragments do not overlap. For amplification of the

ITS region of both genera, a new set of primers was developed (forward 18S-1F: 5'-GTCGTAACAAGGTTTYCGTAGGTGAACC-3'; reverse 28S-R: 5'-CCTTGTTAGTTTCTTTTCCTCCGCC-3'), resulting in a fragment of ~ 700 bp, including ITS-1, 5.8S and ITS-2 regions. Finally, primer combination G18S4 (F: 5'-GCTTGTCTCAAAGATTAAGCC-3') and 4R (R: 5'-GTATCTGATCGCCKTCGAWC-3') was used for amplification of approximately 860 bp of the 18S region of a subset of *Sabatieria* specimens (ITS haplotypes). PCR conditions for COI were initial denaturation for 5 min at 94 °C, followed by denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s and extension at 72 °C for 45 s repeated in 40 cycles, followed by a final extension for 10 min at 72 °C. For ITS, conditions were: 3 min at 94 °C, followed by 40 cycles of 1 min 94 °C, 1 min 55 °C and 1 min 30 s 72 °C, and finally 5 min of extension at 72 °C. PCR of the 18S region of *Sabatieria* started with an initial step of 5 min at 94 °C, then 40 cycles of 30 s at 94 °C, 30 s at 56 °C and 1 min at 72 °C, again followed by a final extension step at 72 °C for 10 min.

Quality of PCR products was checked on 1 % agarose gels (stain = 0.0003 % ethidium bromide; size marker = 2 kbp DNA Easy Ladder (Bioline®)). Sanger sequencing was performed by Macrogen sequencing service (Macrogen Inc, Europe) with forward primers (JB3, CO1490F and 18S-1F; 10 µM) for all PCR products, and with both forward and reverse primers for the individual haplotypes. Sequences were verified with a BLASTn 2.3.1 search against the GenBank non-redundant nucleotide collection (nr/nt) (Altschul et al., 1997; Table S5.2). Dubious sequences (i.e. no hit with nematodes or low similarity (< 70 %) and/or coverage in the case of COI and 18S (< 85 %)) and short fragments were removed. Sequences can be found in GenBank under accession numbers xxxxx – xxxxx.

DNA sequence alignments

Electropherograms of the COI, ITS and 18S sequences were analysed and assembled with LASERGENE v7.1.0 and trimmed to remove primer ends. Sequences were aligned for the two genera and each gene separately using CLUSTALW v2 with default gap opening/extension costs of 15/6.66 in MEGA v6.0 (Larkin et al., 2007; Tamura et al., 2013). For each alignment, the best fit substitution model was selected in jModelTest (Darriba et al., 2012; Guindon & Gascuel, 2003), using the Bayesian Information Criterion (BIC) (Table S5.3). Selected substitution models differed in the number of substitution rate parameters and base frequencies. The Kimura-2-parameter model (K2P; Kimura, 1980) and Hasegawa-Kishino-Yano model (HKY; Hasegawa et al., 1985) each consider two substitution classes

(one transition and one transversion rate), but base frequencies are equal in K2P and variable in HKY. Under the generalised time reversible model (GTR; Tavaré, 1986), there are six substitution rates and variable base frequencies.

Phylogeny

The different alignments were analysed using different tree construction algorithms. First, gene trees were constructed using the neighbor-joining (NJ; Saitou & Nei, 1987) algorithm in MEGA (1000 bootstrap replicates) as an initial visual inspection for the presence of concordant terminal clades among different markers. Mean inter- and intraclade differences (pairwise deletion of gaps; K2P (+ G) correction; Table S5.3) were calculated in MEGA v6.0. Secondly, maximum likelihood (ML) trees (bootstrap replication = 1000) were generated with RAxML v8.2.4 (Stamatakis, 2014). Finally, ultrametric trees were produced using BEAUti v1.8.2 and BEAST v1.8.2 (Bayesian Evolutionary Analysis Sampling Trees; Drummond et al., 2012) under different substitution models (Table S5.3), lognormal relaxed clock model, and coalescent tree prior. A Markov Chain Monte Carlo analysis was run for 10 million generations, of which every 1000^{th} generation was sampled, resulting in 10 000 Bayesian trees. Convergence of runs was checked in Tracer v1.6 (Rambaut et al., 2014), after which the first 5000 trees were discarded as burn-in, while the last 5000 trees were used to construct a consensus tree in TreeAnnotator v1.8.2 (BEAST package) and define posterior probabilities. Resulting consensus trees for all markers were visualised in FigTree (http://tree.bio.ed.ac.uk/software/figtree/) and used in further analysis. ML and BEAST analyses were run on the XSEDE server of the CIPRES Science Gateway v3.3 (https://www.phylo.org; Miller et al., 2010).

DNA-based species delimitation

To test whether sequence datasets constituted a single or multiple species, a General Mixed Yule Coalescent (GMYC) model approach was applied (Pons et al. 2006). Using the ultrametric gene tree as input, the GMYC algorithm compares two alternative models: i) a single coalescence model that assumes a single species, and ii) a model that combines a coalescent model of intraspecific branching with a Yule model for interspecific branching, thus assuming multiple species. The location of the switch (threshold T) from speciation to coalescence nodes is then fitted on the tree, resulting in an estimation of species diversity. Rejection of a single coalescence model indicates several species. Alternatively, if the GMYC model does not provide a significantly better fit than the null model, sequences belong to one

species, or the dataset consists of too few individuals, weakening the power of the test to actually detect the transition time T (Pons et al., 2006). Species delimitation under a single-threshold GMYC model was assessed in R (R core team, 2013) using packages APE (Paradis et al., 2004) and SPLITS (Ezard et al., 2013). Lineages-Through-Time (LTT) plots marking the position of threshold T on a relative timescale were constructed in R.

The presence of species-level lineages in sequence variation was also assessed by means of statistical parsimony (Templeton et al., 1992). TCS v1.21 software (Clement et al., 2000) partitioned the data into independent haplotype networks (gaps = missing data), connected by changes that are non-homoplastic with a probability of 95 %. Final TCS haplotype networks (Clement et al., 2002; Templeton et al., 1992) were built using the PopART software (http://popart.otago.ac.nz), which only takes unambiguous sites into account.

We relied on a conservative consensus approach towards reconciling the results of the different species delimitation methods to maximize the reliability of species boundaries. More specifically, we recognised species clades that 1/ received high nodal support (at least 70 %) in NJ, ML and Bayesian tree topologies, 2/ showed compatible patterns based on statistical parsimony and GMYC analyses, 3/ formed separate entities in tree topologies of unlinked nuclear and mitochondrial markers and/or expressed different morphological characteristics.

Population genetics

Population genetic analyses were performed on ITS for *Sabatieria* and COI for *Desmodora* species as these were the most complete datasets (see later). Single-level Analysis of Molecular Variance (AMOVA; 1000 permutations, 0.05 significance level) was carried out in Arlequin v3.5.1.2 (Excoffier & Lischer, 2010) to calculate fixation index Φ_{st} (Holsinger & Weir, 2009) The fixation index calculates the expected genetic diversity within and between populations and compares it to the total genetic diversity. In the case of selectively neutral markers (such as the ones in this study), Φ_{st} can be linked to dispersal and gene flow. Low values indicate substantial genetic exchange between populations, while high values are related to low levels of dispersal between populations hence strong genetic differentiation (Moens et al., 2013). Only species clades (cf. previous section) consisting of more than two populations with more than 5 individuals each were included in population genetic analyses. Standard measures of genetic variation within populations, such as nucleotide diversity (π; Nei, 1987) and gene diversity (h; Tajima, 1983; Nei, 1987) were also assessed in Arlequin. Intra-population and pairwise inter-population divergences were calculated where appropriate,

using pairwise deletion of gaps and K2P-corrected distances (based on jModelTest results, Table S5.3). Finally, isolation by distance (IBD) was assessed through Mantel testing in IBDWS v3.23 (Jensen et al., 2005) based on DNA sequences (ignoring gaps; between-population distance Φ_{st}; between-sequence distance K2P) and 30 000 randomisations.

RESULTS

Sabatieria

Phylogeny. The alignment of 326 ITS rDNA sequences of *Sabatieria* was 679 sites long, containing 276 variable sites (196 parsimony informative) and 18 indel sites. Tree topologies from both Bayesian inference (BEAST) and maximum likelihood (RAxML) procedures for ITS haplotypes (see further) separated the sequences into four highly differentiated and relatively well-supported clades according to morphotype and/or geographic location (I – IV; Fig. 5.2). Individuals in clades I and II had the same physical appearance (morphological group 1; Table S5.1), and were further divided into several well-supported sub-clades corresponding to different geographical locations (Ia – Ic, and IIa – IIc in clades I and II respectively). Specimens belonging to clades III and IV were morphologically distinguishable (morphological group 2 and 3, respectively; Table S5.1). Individuals in clade III had a different amphid and spicule shape, while individuals in clade IV had a blunt tail end (as opposed to the clavate tail tip typically observed in *Sabatieria*).

Phylogenetic results based on ITS haplotype sequence data were compared with those based on a subset of the slower-evolving 18S rDNA (n = 42, alignment length 864 bp, 47 variable sites, 30 parsimony informative; Fig. 5.3A), and an unlinked similarly variable mitochondrial marker (COI; n = 16, alignment length 313 bp, 120 variable sites, 113 parsimony informative; Fig. 5.3B). In both cases, the phylogenies were generally congruent with the ITS tree, although not all ITS clades had COI sequence representatives due to amplification difficulties. The 18S tree did include individuals of all ITS clades, and showed high nodal support for clades IIa, III and IV (posterior probabilities > .95; ML bootstrap values 100; Fig. 5.3A). The rest of the sequences were lumped into two clades with low support (Ia + IIb + IIc and Ic), indicating that the slower evolving 18S was unable to differentiate the recently diverged species I and II. COI sequence data showed high support for clades I and IV with posterior probabilities and ML bootstrap values of (almost) 100, and also clade IIa specimens formed a (less well-supported) clade (Fig. 5.3B). Hence, despite less successful amplification of COI and 18S data for *Sabatieria*, some of the same clades were recovered in tree topologies.

DNA-based species delimitation. Statistical parsimony analysis collapsed the 326 ITS sequences into 95 haplotypes (sequence divergence based on K2P distances = 0.2 – 26 %) and 7 separate haplotype networks (Ia/b, Ic, IIa, IIb, IIc, III and IV; connection limit = 95 % or 11 mutations), all corresponding to clades or sub-clades of the Bayesian tree (Fig. 5.2). The GMYC model gave a significantly better fit for the ITS data (likelihood ratio = 20.6; $P < 0.001$) than did the null model assuming uniform branching rates. The position of the threshold time T, marking the transition from between- to within-species rate of lineage branching, was estimated at –0.004 on a relative timescale (Fig. 5.2 upper left). The confidence interval for the estimated number of species ranged from 8 to 26. As opposed to ITS, the GMYC model was insignificant when applied to 18S and COI data ($P > 0.1$), possibly as a consequence of the low number of sequences available.

Table 5.2. *Mean Sabatieria intra- and interspecific genetic divergence based on K2P distances (gamma = 4 for ITS and COI; uniform rates for 18S). Values are given in percentages with their standard error. Diagonal values are intraspecific divergences, while values below diagonal represent interspecific divergences. n = number of individuals analysed. – no data available.*

ITS Sabatieria (n=326; 679bp)	species I	species II	species III	species IV
species I	1.40 ± 0.28			
species II	11.09 ± 1.24	3.73 ± 0.50		
species III	15.16 ± 1.59	20.71 ± 1.93	1.26 ± 0.15	
species IV	14.92 ± 1.60	18.56 ± 1.73	19.86 ± 1.90	0.22 ± 0.08
18S Sabatieria (n=42; 864bp)				
species I	0.15 ± 0.05			
species II	0.24 ± 0.08	0.24 ± 0.11		
species III	1.57 ± 0.41	1.70 ± 0.41	0.22 ± 0.09	
species IV	1.48 ± 0.33	1.58 ± 0.34	2.87 ± 0.52	1.13 ± 0.28
COI Sabatieria (n=16; 313bp)				
species I	0.00 ± 0.00			
species II	25.20 ± 3.24	1.49 ± 0.38		
species III	–	–	–	
species IV	37.78 ± 4.37	37.09 ± 4.14	–	0.64 ± 0.45

Based on the three pre-defined criteria for species delimitation, the *Sabatieria* ITS dataset was divided into 4 putative species (clades in Figs. 5.2, 5.3): 1/ statistical parsimony and GMYC outcome pointed towards the presence of several species; 2/ nodal support in Bayesian and ML tree topology for the four clades was substantial; 3/ unlinked loci (ITS & COI) consistently recovered species I, II and IV, while species III was considered a valid species based on its morphological differences with the other three species. The level of sequence divergence between the four species (average K2P distances between 11 and 21 %) was considerably higher than within-species distances (~ 0.2 to 4 %) (Table 5.2), giving further indication for species-level divergence. Also for 18S and COI, sequence divergence within putative species was lower than between species (especially for COI; Table 5.2).

Population genetics. Of the four *Sabatieria* species recognised in this study, three were used in population genetic analyses (I – III). Species I and II were clearly the most abundant (n = 200 and 66, respectively), genetically diverse (42 and 21 haplotypes, respectively) and widespread, comprising populations from both sides of the Weddell Sea (Fig. 5.2; Table S5.4). Single-level AMOVA (Table 5.3) yielded large and significant among-population differences for both species (Φ_{st} = 0.886 and 0.765; $P < 0.001$), as could already be suspected from tree topologies (cf. sub-clades Ia – Ic; IIa – IIc) and haplotype networks (Fig. 5.2). Pairwise Φ_{st} values (Table 5.4) between populations of species I were significant in all cases except between AUS and BX (clade Ic), and between KG and SG (clade Ia). Most haplotypes were limited to one location, but in case they were shared (7 haplotypes), it was always between neighbouring locations at one side of the Weddell Sea (Table S5.4). Average K2P divergence ranged between 0.23 and 3.28 % (Table S5.5), and was higher between populations on both sides of the Weddell Sea (e.g. BX and SG) than between populations on either side. Pairwise comparisons for species II were always significant, and again larger for populations divided by the Weddell Sea (SG vs. BX, SO vs. BX) than at the same side of it (SG vs. SO). As for species I, almost all haplotypes were restricted to a particular location, except for two that were shared among locations at both sides of the Weddell Sea (Table S5.4).

Next to these species that were found across the Weddell Sea, the other two species (III and IV) were restricted to one side. Species III solely occurred at the western side of the Weddell Sea and consisted of three populations (SG, SO & KG) for which genetic structuring was significant, but considerably lower than for species I and II for the same populations on this side of the Weddell Sea (AMOVA $\Phi_{st\ species\ III}$ = 0.178, $P < 0.001$; Table 5.3; $\Phi_{st\ species\ I\ \&\ II}$ = 0.589 – 0.599, $P < 0.001$; results not shown). Within-population variation for species III (~82

%) exceeded that between populations (17.8 %). Genetic differences were non-significant between locations SG and SO (Table 5.4), which also shared one haplotype (Table S5.4). Average K2P distances between these populations were also clearly lower than for the other two species (Table S5.5). Species IV was restricted to the two locations at the eastern Weddell Sea, and comprised 11 haplotypes. Within-population divergence was comparable or even larger than between-population differences, which were non-significant (Table S5.5).

Despite the observation that main differences between populations of species were situated between different sides of the Weddell Sea (hence, at a large spatial scale), genetic divergence did not consistently decrease with increasing geographic distance (IBD r-values for species I, II and III were non-significant; $P > 0.05$; results not shown).

Table 5.3. *Single-level AMOVA results for each Sabatieria ITS species (based on a K2P model, as indicated by jModelTest). df = degrees of freedom, var = percentage of variation, Φ_{st} = fixation index, P = permutational P-value, based on 1000 permutations. Significant Φ_{st} values are indicated in bold. Significance codes: ns = non-significant, *** P < 0.001.*

Source of variation	df	var (%)	Φ_{st}	P
Species I				
Among populations	4	88.59	**0.886**	***
Within populations	195	11.41		
Species II				
Among populations	2	76.48	**0.765**	***
Within populations	63	23.52		
Species III				
Among populations	2	17.84	**0.178**	***
Within populations	32	82.16		

Table 5.4. *Pairwise Φ_{st} values between populations of the different Sabatieria species. Numbers between brackets indicate the amount of individuals for each population. Species with only two populations (i.e. species IV) were not included and populations consisting of a single individual have not been taken into account. Significance codes: NS = non-significant, *** P < 0.001.*

Species I (n = 200)	**SG** (114)	**SO**	**KG**	**AUS**
SO (8)	0.857 ***			
KG (27)	0.028 ^{NS}	0.778 ***		
AUS (5)	0.938 ***	0.898 ***	0.896 ***	
BX (46)	0.927 ***	0.878 ***	0.898 ***	–0.098 ^{NS}
Species II (n = 66)	**SG** (25)	**SO**		
SO (25)	0.597 ***			
KG	–	–		
AUS	–	–	–	
BX (16)	0.955 ***	0.743 ***	–	–
Species III (n = 35)	**SG** (8)	**SO**		
SO (19)	0.002 ^{NS}			
KG (8)	0.380 ***	0.235 ***		
AUS	–	–	–	
BX	–	–	–	–

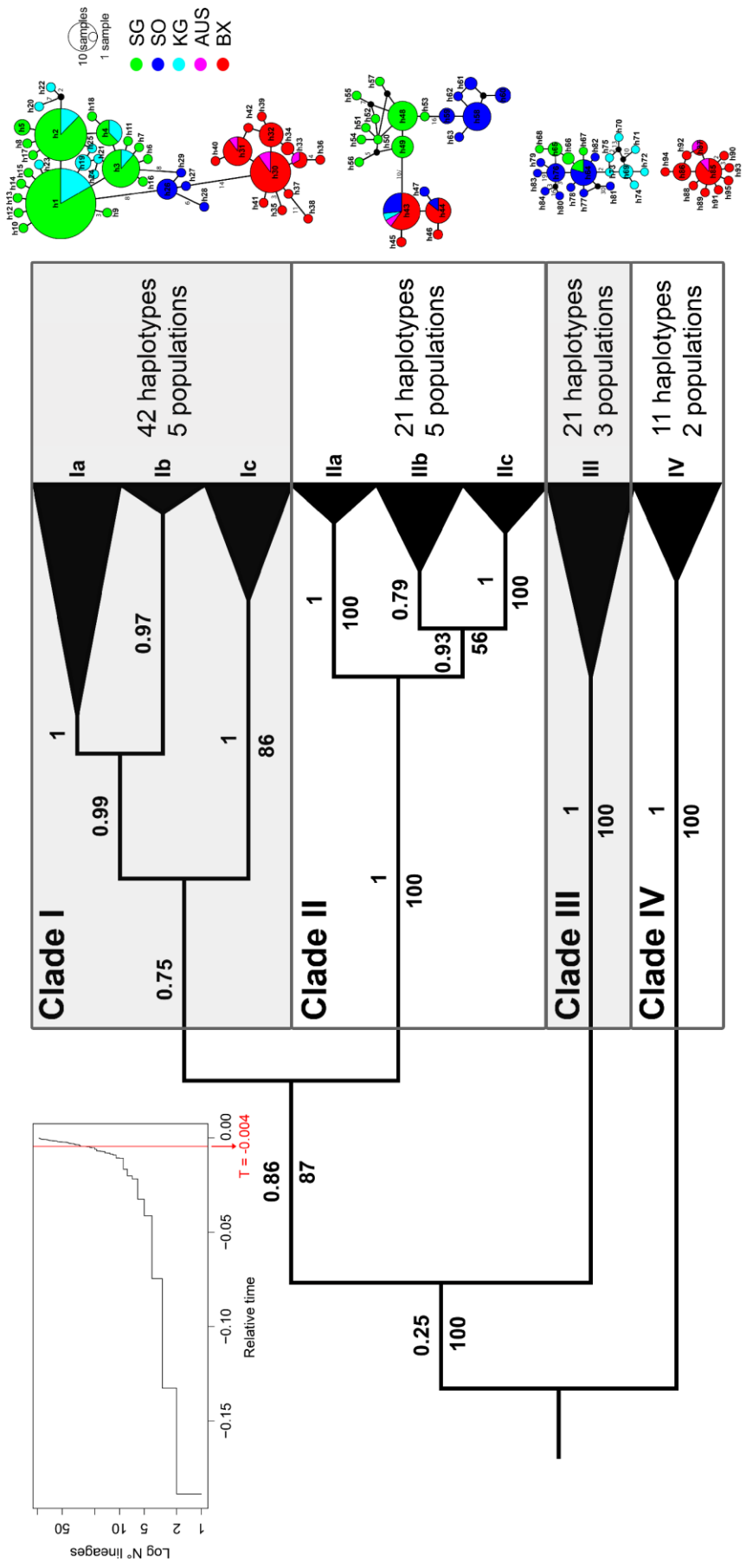
10 samples
1 sample
SG
SO
KG
AUS
BX
Clade I
Clade II
Clade III
Clade IV
Ia
Ib
Ic
IIa
IIb
IIc
III
IV
42 haplotypes
5 populations
21 haplotypes
5 populations
21 haplotypes
3 populations
11 haplotypes
2 populations
1
0.97
0.99
1
86
0.75
1
100
0.79
0.93
56
1
100
1
100
1
100
0.86
87
0.25
100
T = −0.004
0.00
−0.05
−0.10
−0.15
Relative time
50
10
5
2
1
Log N° lineages

Figure 5.2. (previous page) *Upper left corner: Log-lineages through time plot (LTT) indicating position of threshold time T (red line). Middle: Bayesian tree output for ITS haplotypes of Sabatieria; numbers above branches indicate posterior probabilities as calculated in BEAST, numbers below (where indicated) are ML bootstrap percentages (only when values > 50; RAxML output). Number of populations (i.e. geographical locations) and haplotypes are indicated next to each clade. Right: corresponding TCS haplotype networks of all four ITS clades for Sabatieria. Haplotype networks were constructed using PopART (http://popart.otago.ac.nz). Numbers along branches indicate the amount of mutations/base pair differences between the two connecting haplotypes. When this number is not indicated, there was only 1 mutation. Black dots represent missing haplotypes. Size of circles is proportional to the amount of individuals belonging to that specific haplotype. Colour code based on the different locations.*

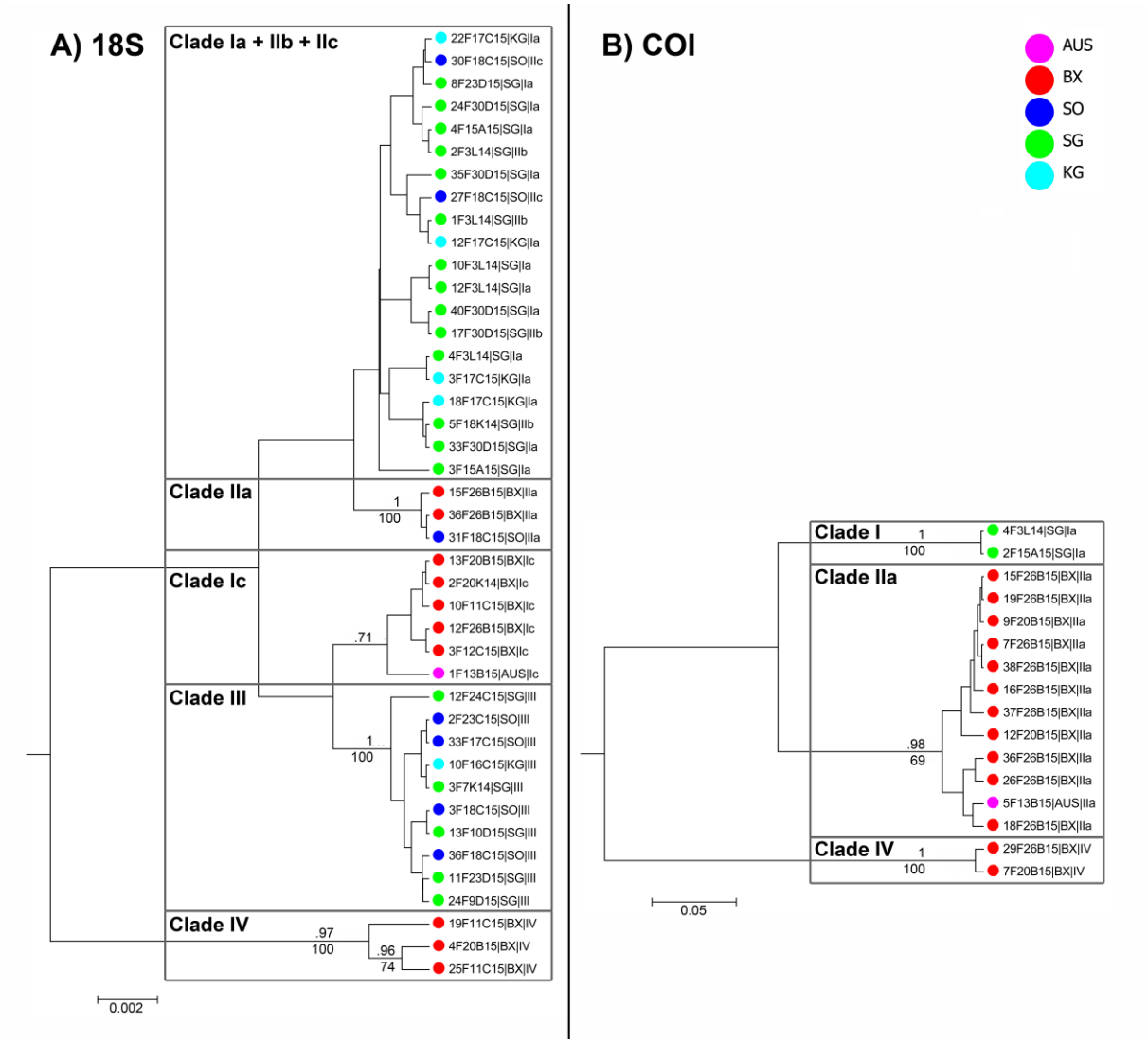

Figure 5.3. *Bayesian trees for A) 18S and B) COI of Sabatieria. Numbers above branches indicate posterior probabilities as calculated by BEAST procedure, while numbers below branches depict ML bootstrap percentages from RAxML files. Only values above 50 are included in the graphs. Scale length represents number of substitutions per site. Colours represent location.*

Desmodora

Phylogeny. The ITS alignment for *Desmodora* comprised 25 sequences and 599 sites of which 88 were variable (41 parsimony informative). For COI, the alignment included 37 sequences and 662 sites of which 196 variable (151 parsimony informative). *Desmodora* specimens showed distinct discontinuities in variation of several morphological features, including body size, amphid shape, male copulatory organs, and cuticle ornamentation (Table S5.1). In contrast to *Sabatieria*, these morphological groups did not correspond to distinct clades in ITS tree topology (Fig. 5.4A). Most specimens were clustered irrespective of morphology, and both posterior probabilities and bootstrap values were low. In case posterior probabilities were above 0.95, bootstrap values were either very low (< 50), or specimens were not put into the same clade in the ML tree. As a result, it is highly unlikely that separate species lineages can be detected based on ITS data, and morphological differences between specimens are not diagnostic. In contrast to ITS, both Bayesian and ML tree topologies based on COI data hinted towards a clear differentiation between two species-level lineages (high posterior probabilities and bootstrap values), of which one corresponded to a different morphological group for which no ITS sequences were available (Fig. 5.4B; Table S5.1). Further differentiation into sub-clades according to location as seen in the tree topology was never supported by high posterior probabilities and bootstrap values.

DNA-based species delimitation. The COI tree output indicated two species lineages for this genus (clades I, II on Fig. 5.4B), which was verified by the GMYC model (significant divergence: LR = 12.81, $P < 0.01$). The confidence interval for the number of species was 2 – 7, but posterior probabilities and ML bootstrap values clearly pointed towards the lower end of this range. Also statistical parsimony divided the COI data into two separate networks at the 95 % probability level. Unfortunately, unsuccessful amplification of the ITS region of specimens belonging to clade II (= morphological group 3; Table S5.1) prevented additional verification of this conclusion based on another unlinked genetic marker. However, co-occurrence of both species at the same location (SO), their high interspecific genetic divergence (Table 5.5) and morphological differences (Table S5.1) strongly hint towards a separation into true species. They will therefore be considered as such in further analyses.

Population genetics. Population genetic structure within *Desmodora* was based on COI data (most complete dataset). The five sampling locations are considered as the separate populations. Whereas species I occurred at both sides of the Weddell Sea, species II solely

appeared in the South Orkneys samples (no population genetic structure to be tested). This means that two species occur sympatrically at this latter location. Genetic structuring between populations of *Desmodora* species I was significant, but lower than for *Sabatieria* species I and II (Table 5.6). Genetic variation within populations of *Desmodora* species I was comparable or sometimes even higher than between populations (Table S5.5). Mantel tests for IBD within species I with three populations (SG, SO & BX) resulted also here in non-significant r-values (P = 0.66), which is expected since similarity is higher between populations SG and SO than between both of them and BX across the Weddell Sea (see Table 5.6).

Table 5.5. *Mean intra- and interspecific genetic divergence for COI of Desmodora (based on K2P distance; gamma = 4). Diagonal values are intraspecific divergences with their standard error; values below diagonal are interspecific divergences. n = number of individuals analysed.*

COI Desmodora (n = 37; 662 bp)	Species I	Species II
Species I	1.76 ± 0.25	
Species II	23.44 ± 2.08	1.59 ± 0.25

Table 5.6. *Single-level AMOVA main and pairwise results for Desmodora species I. Values in brackets indicate the number of individuals per populations. Populations of only one individual have not been taken into account. df = degrees of freedom, var = percentage of variation, Φ_{st} = fixation index, P = permutational P-value, based on 1000 permutations. Significant Φ_{st} values indicated in bold. Significance codes ** P < 0.01, *** P < 0.001. n = number of specimens.*

Source of variation	**df**	**var (%)**	**Φ_{st}**	***P***
Species I				
Among populations	2	26.55	**0.266**	***
Within populations	21	73.45		

Pairwise Φ_{st} *(n = 24)*	**SG** (9)	**SO**	**KG**	**AUS**
SO (8)	0.307 ***			
KG	–	–		
AUS	–	–	–	
BX (7)	0.286 ***	0.153 **	–	–

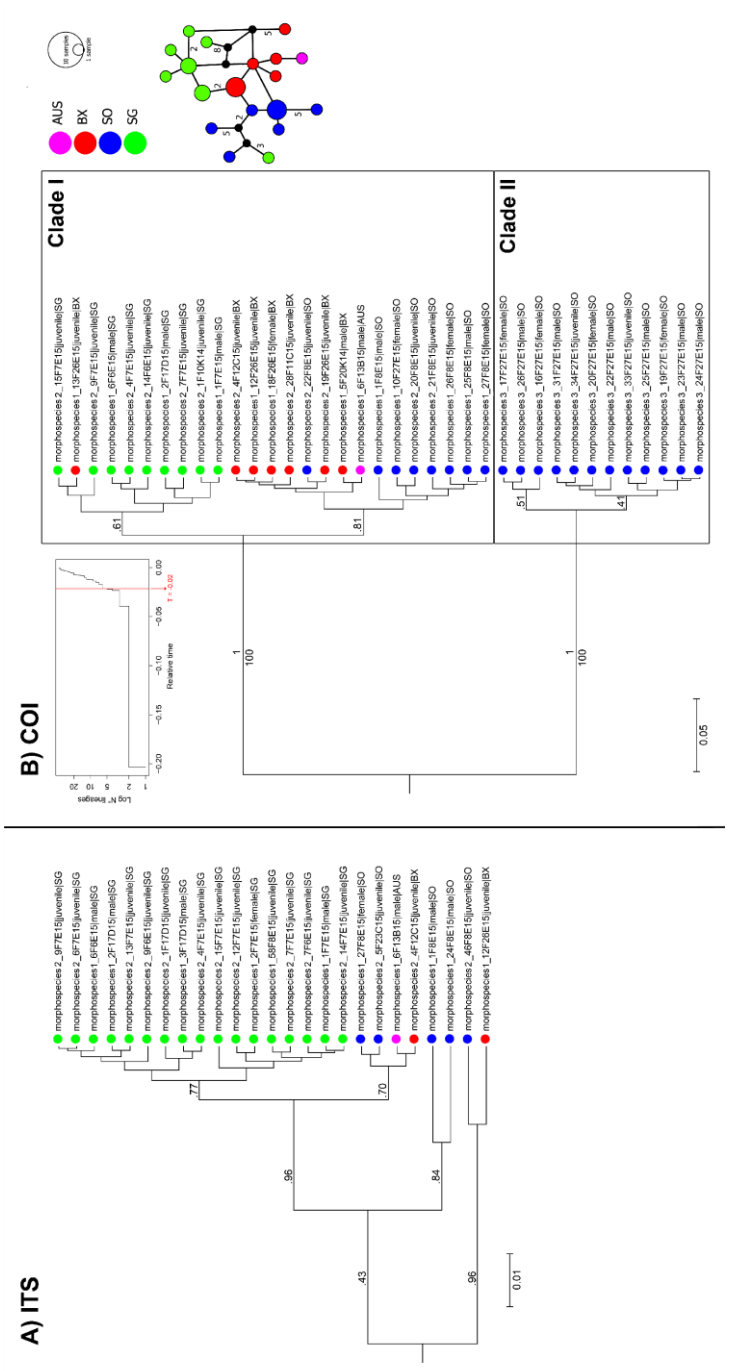

Figure 5.4. *Bayesian trees of A) ITS, and B) COI haplotypes for Desmodora. Names of specimens are linked to morphological groups (here indicated as 'morphospecies'). Numbers above branches are posterior probabilities as calculated in BEAST. In case there are two numbers indicated, the percentage below the branch gives the maximum likelihood bootstrap value from RAxML output (only when this value was > 90). Colours represent locations. Scale length represents number of substitutions per site. The COI plot includes also the log-lineages through time plot with threshold time T indicated in red, and the haplotype network for Desmodora species I. Numbers along branches indicate the amount of mutations/base pair differences between the two connecting haplotypes. When this number is not indicated, there was only 1 mutation. Black dots represent missing haplotypes. Size of circles is proportional to the amount of individuals belonging to that specific haplotype. Colour code based on the different locations.*

DISCUSSION

In the different sections of this discussion, results on species diversification and population genetic structure within the endobenthic nematode genera *Sabatieria* and *Desmodora* will be related to the three hypotheses formulated in the introduction. In the first sections, phylogeographic patterns for species and populations of both genera are discussed and evaluated in terms of isolation-by-distance. We speculate on the factors that might lead to biogeographic patterns in marine free-living nematodes. Second, population genetic results for both *Sabatieria* and *Desmodora* species are partly linked to their habitat preferences, suggesting that this might influence the level of genetic heterogeneity for small endobenthic taxa. Finally, we discuss the presence of cryptic species diversity for both genera and the discrepancy between classic taxonomy and molecular techniques in the delimitation of marine nematode species in the Southern Ocean.

Combination of wide and narrow species distributions within *Sabatieria* and *Desmodora*

Results of this study have revealed a combination of species within both genera that either have a wide distribution range across the Weddel Sea, or a more limited range without crossing the Weddell Sea. In the case of *Desmodora*, given the lower amount of sequence data available, this might be due to an undersampling and calls for careful interpretation. The combination of wide and narrow species ranges has been noted in several other Antarctic benthic taxa (Havermans et al., 2013; Jörger et al., 2013) and shows the complexity of unravelling species distribution patterns at larger spatial scales. *Sabatieria* species I and II (and also *Desmodora* species I) were distributed sympatrically across locations separated by the deep Weddell Sea, indicating a connection at some point in time. Wide species ranges and even apparent cosmopolitanism have been reported before in marine nematodes (e.g., Bik et al., 2010; Derycke et al., 2008) and can reflect ongoing dispersal as well as historical connections (Hellberg et al., 2002). Given the fact that nematodes are passive dispersers and that locations in this study are separated by several hundreds of km, historical events might be very important in this case (cf. Hellberg et al., 2002; Pelc et al., 2009). On an evolutionary timescale, the origin of modern Antarctic biota is put shortly after the Gondwana break-up, which marked the onset of vicariance, allopatric speciation and diversification (Rogers, 2012; Thatje et al., 2005). Yet the resulting Antarctic Circumpolar Current (ACC) maintained a certain level of horizontal connectivity between species and populations along the continent, reflected in circum-Antarctic distributions observed in several benthic invertebrate species (Riesgo et al., 2015). Large-scale distribution of both *Sabatieria* and *Desmodora* species in

this study might have a similar early origin of allopatric speciation followed by long-distance dispersal mediated by the presence of large current systems (ACC, ACoC, Weddell gyre) and relatively homogeneous environmental conditions (e.g., seabed temperatures) in the area (Arntz et al., 1994; Griffiths et al., 2009). High levels of genetic divergence between species (Table 5.2, 5.5) and long branches in tree topologies (Fig. 5.3, 5.4) seem to support speciation in the distant past. The question to what extent currents are able to maintain connectivity along the Weddell Sea and Scotia Arc was investigated by means of population genetics and is discussed in the next sections.

Large population genetic differences suggest low levels of gene flow in the Southern Ocean

The physical setting of the Southern Ocean – without obvious barriers to gene flow and with the presence of large-scale currents capable of mediating long-distance dispersal – did not change much over the course of history. Combined with the large population sizes of nematodes and the possibility of passive dispersal, this should result in mild genetic differentiation over large distances (Palumbi, 1994). Nevertheless, population genetic structuring within *Sabatieria* and *Desmodora* species was substantial. Haplotypes were generally confined to a single geographic location or shared between neighbouring sites (only two *Sabatieria* haplotypes had representatives at both sides of the Weddell Sea; Fig. 5.2; Table S5.4), a characteristic of closed populations and not uncommon in taxa that lack pelagic development (Allcock & Strugnell, 2012; Hellberg et al., 2002). Pairwise Φ_{st} values for *Sabatieria* species I and II were significant in most cases and largest between locations at different sides of the Weddell Sea (Table 5.4). Similarly large genetic differences between eastern and western Weddell Sea were also revealed by COI and ITS sequences of benthic ostracods in the area (Brandt et al., 2007a). *Desmodora* species I also showed highly significant pairwise Φ_{st} values (Table 5.6) but largest differences were situated between populations SG and SO, rather than between eastern and western Weddell Sea locations (Table S5.5). The high levels of population genetic differentiation described above can have multiple origins. First of all, they might reflect poor dispersal capacity (Allcock & Strugnell, 2012) and suggest that contemporary gene flow between populations might be strongly limited at the spatial scale considered here. Similar studies for coastal and estuarine nematodes have demonstrated that population genetic structure can be significant at scales of 100 km and less (Derycke et al., 2005, 2007, 2013), which is well below distances between the different locations for this study. If gene flow is indeed limited due to dispersal limitation,

the large observed population genetic differences might point towards a limited efficiency of the ACC and Weddell gyre in homogenising nematode communities at large distances. Second, barriers to genetic exchange between populations in a marine setting can exist in many forms, such as temperature gradients, depth differences and large areas of unsuitable habitat conditions (Derycke et al., 2013; Palumbi, 1994). The large pairwise differences between populations at both sides of the Weddell Sea and along the Scotia Arc might therefore result from such 'invisible' barriers to gene flow rather than true dispersal limitation (see Chapter 4: Hauquier, unpublished). However, based on the few locations in this study, such a hypothesis would be difficult to test. Finally, even in the presence of extensive dispersal between habitat patches, populations can show large genetic differences due to differences in the succesful establishment and reproduction of dispersers after settling in a new environment (Marshall et al., 2010). Local habitat conditions and species-specific niche preferences, followed by rapid adaptation and population growth, may result in situations where priority effects, founder effects and genetic bottlenecks result in certain haplotypes being favoured over others (Derycke et al., 2007b). Such a paradox between high (in this case, passive) dispersal rates and low gene flow has been shown for other aquatic ecosystems (De Meester et al., 2002), but is difficult to assess based on the data at hand for this study. More specifically for marine nematodes, such local colonisation dynamics have been shown to result in strong population genetic differentation between nearby patches (< 1 km) for shallow-water nematodes (Derycke et al., 2013), but are generally assumed to be of less importance at large spatial scales.

Phylogeographic patterns across the Weddell Sea do not support isolation by distance

Strong genetic structure at large spatial scales (> 300 km) has been observed in many marine populations (Derycke et al., 2013; Pelc et al., 2009; Selkoe et al., 2010), and has often been attributed to an isolation-by-distance mode of genetic differentiation. Yet for all species of *Sabatieria* and *Desmodora* with sufficient sample size, no IBD was observed. The reason for this is probably related to large variability in genetic divergence between Antarctic Peninsula and Scotia Arc populations. For example, in *Sabatieria* species I, gene flow was not restricted between populations SG and KG, located approximately 1600 km apart (non-significant small genetic distance; Table 5.4, S5) but was very much so between SG and SO, which are separated by 900 km distance. This pattern was reversed in species III, where pairwise genetic differences between SG and SO were non-significant (Table 5.4, S5). Within *Desmodora* species I, genetic differences were larger between SG and SO than between either of them and

location BX at the other side of the Weddell Sea. Although it has been argued that the tip of the Antarctic Peninsula and Scotia Arc are highly connected due to the Antarctic Circumpolar Current system (e.g., Hemery et al., 2012), our population genetic results do not support this. Instead, there seems to be a rather random pattern of genetic structuring between populations at the western Weddell Sea. Hellberg et al. (2002) noticed that 'a history of isolation and secondary contact might result in highly complex patterns which are surprisingly resistant to gene flow'. Thus, rather than isolation by distance, chaotic patchiness or geographic clines might be invoked as an explanation for genetic structure along the Antarctic Peninsula. Derycke et al. (2013) already noticed that in many cases, genetic structuring in marine nematodes does not seem to correlate with geographic distance, but rather shows a chaotic pattern. In some cases, this can be linked to oceanographic currents or other environmental variables (White et al., 2010), which proves that these can be equally important drivers for marine nematode population genetic structure than geographic distance alone (as assumed under IBD). Further sampling in the area at a higher spatial resolution might reveal more details on the applicability of such genetic differentiation patterns.

Gene flow in the Weddell Sea is strongly reduced in both genera, but more so in the deeper dwelling *Sabatieria* species

The two genera in this study are endobenthic and long-distance dispersal is dependent upon suspension and transportation through the water column (Derycke et al., 2013). Given the great deal of stochasticity involved (e.g., suspension might only occur occasionally), nematode dispersal capacity is considered limited at larger geographic distances. Not surprisingly, observed Φ_{st} values (0.25 – 0.9) were higher than those observed for nematode genera rafting on macroalgae (see results in Derycke et al., 2013) and indicate the importance of species-specific life history traits on genetic structure. But although both genera share a similar endobenthic lifestyle, population genetic structuring was more pronounced within the *Sabatieria* species than within *Desmodora* species I (cf. AMOVA results). This may be the result of their differential vertical distribution and feeding habits. Nematode dispersal is predominantly passive and mediated through hydrodynamic forces, but individuals living in sediment surface layers are more susceptible to resuspension and transportation in the water column, while deeper dwellers are rarely resuspended (Boeckner et al., 2009; Commito & Tita, 2002; Thomas & Lana, 2011). *Desmodora* prefers surface sediments where it can feed on algal particles scraped off the sediment grains, which potentially facilitated contemporary and historical gene flow over larger areas. Dispersal capacity of organisms plays an important

role in connectivity between populations, and previous studies have indicated differences in structuring processes between active and passive dispersers (e.g., Bradbury et al., 2008; Pelc et al., 2009). Results of this study thus extend this knowledge and prove that vertical distribution in the sediment can be an important proxy for dispersal probability in marine nematodes. Because of its important implications for connectivity between populations at Antarctic – and possibly other – shelf depths, future genetic studies on small endobenthic taxa without active dispersal stages should take this into account.

Conflict between morphological and phylogenetic species definitions in *Sabatieria* and *Desmodora*

Objective species delimitation is challenging in animal groups where taxonomic information is incomplete and scattered, yet remains fundamental in biodiversity research (Bucklin et al., 2011). For this reason, a combination of several techniques and a conservative method were adopted to delineate species in this study. Congruence in the outcomes of various species delimitation approaches led to the recognition of four species-level lineages for *Sabatieria* and two for *Desmodora*. Not all of these coincided with the initial morphologically defined groups, and vice versa (Table S5.1). In fact, rates of phenotypic and molecular divergence do not always converge (Fujita et al., 2012), which makes species delimitation all the more tricky. Especially for relatively young species there might be an offset between the process of speciation and the acquisition of secondary properties such as distinct morphology. However, sequence divergence for COI in both genera was substantial (*Sabatieria*: 25 – 38 %; *Desmodora*: 23 %; Table 5.2, 5.5; Figs 5.3B, 5.4B), making the possibility of dealing with recent divergence less likely in this case.

Within the genus *Sabatieria*, two out of four species differed from the others in morphological appearance (species III and IV), while the other two (species I and II) were not readily distinguishable and might constitute cryptic species. Cryptic speciation is not uncommon in marine free-living nematode genera (Derycke et al., 2013 and references therein). Also in other Southern Ocean benthic inhabitants, recent molecular findings have indicated that species which were previously considered eurybathic and/or circum-Antarctic can in fact be partitioned into cryptic species according to depth or geography (Allcock & Strugnell, 2012; Hemery et al., 2012; Riesgo et al., 2015). Local coexistence of cryptic species such as observed in this study may be enabled by differential ecological preferences or tolerances (De Meester et al., 2015; Derycke et al., 2006, 2016).

In contrast to *Sabatieria*, *Desmodora* specimens showed no evidence of cryptic speciation. Instead, the opposite phenomenom was observed where (conspicuous) morphological characteristics were not diagnostic in the delimitation of species. This observation of high intraspecific morphological variation for *Desmodora* casts doubt on previous reports of six different species within the genus based on morphological data for the same locations (Ingels et al., 2006). Recently, similar high levels of intraspecific variation in morphology were reported in the deep-sea nematode genus *Acantholaimus* from the Pacific (Miljutin & Miljutina, 2016), demonstrating again the potential bias in relying on morphology alone when discriminating between species. This is even more true considering that some nematodes might be capable of resource polyphenism, a situation in which different phenotypes are induced by different thresholds of an environmental cue during their development (Fonderie et al., 2013; Kiontke & Fitch, 2011). For this study however, the different morphogroups of *Desmodora* occurred in similar environmental conditions, so it is not sure to what extent intraspecific morphological differences could be triggered by a single environmental stressor. This would require a more extensive study design, including many more specimens for this genus.

CONCLUSION

Our results demonstrate the occurrence of cryptic speciation in Antarctic continental shelf nematodes, and provide evidence for different mechanisms underlying spatial genetic structure within surface- and deeper-dwelling nematode taxa. Historically, current systems such as the ACC and Weddell gyre in the area may have served as a transportation route for species across the Weddell Sea, mainly for taxa occurring in surface sediments such as *Desmodora*, which showed less geographic structure in its distribution than the *Sabatieria* species. Currently, dispersal limitation in marine nematodes effectively hampers large-scale connectivity between populations across the Weddell Sea. Nematode distributions at present thus most likely reflect a long history of disrupted gene flow due to the large geographic distance between locations across the Weddell Sea. The genetically divergent populations at both sides of the Weddell Sea might evolve into separate species as more time passes. At a smaller spatial scale, population genetic structuring on the western side of the Weddell Sea is rather random and might relate to geographic clines or chaotic patchiness.

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SUPPLEMENTARY INFORMATION

See next page.

Table S5.1. *Overview of the morphological groups per genus, used in first identification (i.e. prior to DNA extraction). For Desmodora, the three morphological groups correspond to the species described by Ingels et al. (2006). For Sabatieria, species have been assigned arbitrarily, based on the characteristics provided here. na = not assessed*

SABATIERIA	**amphid**	**tail shape**	**precloacal supplements**	**spicule shape**	**max body length**	**cephalic setae**	
morphospecies 1	1.5 turns	clavate/ short	> 15	clear S-shape	> 2.5 mm	2 rows of stout setae	
morphospecies 2	2.5 turns / large	clavate/elongate	11-13	short, broader towards end	2.5 mm	1 row of long setae	
morphospecies 3	2 turns	blunt/stout	na	na	< 1.5 mm	2 rows of stout setae	
DESMODORA	**amphid**	**tail shape**	**precloacal supplements**	**spicule shape**	**max body length**	**somatic setae**	**lateral line**
morphospecies 1 (*campbelli*)	1 turn / large	conical/short	present	short, broader towards end	1.5 - 2 mm	long, all over body	very obvious
morphospecies 2 (*sp.D*)	1 - 1.5 turns / small	conical/short	na	na	< 1.5 mm	short, all over body	obvious
morphospecies 3 (*sp.A/B*)	1.5 turns / small	slender/elongate	absent	longer, slender	~ 1 mm	inconspicuous/absent	absent

Table S5.2. *Summary of BLASTn results, showing GENBANK comparison for both Sabatieria (18S) and Desmodora (COI) species.*

GENBANK		***SABATIERIA* % coverage**				***SABATIERIA* % similarity**			
species	accession	sp. I	sp. II	sp. III	sp. IV	sp. I	sp. II	sp. III	sp. IV
Sabatieria sp.	AY854238	99 - 100	99 – 100	100	97 - 98	98 - 99	99	98 – 99	97 - 98
Sabatieria punctata	AY854235	99 - 100	99 – 100	100	97 - 98	98 - 99	99	98 – 99	97 - 98
GENBANK		***DESMODORA* % coverage**				***DESMODORA* % similarity**			
species	accession	sp. I	sp. II			sp. I	sp. II		
Metachromadora sp.	KC014987	91 - 93	91 – 92			81 - 82	82 -83		

Table S5.3. *Overview of jModelTest output (Darriba et al., 2012; Guindon & Gascuel, 2003) for the different genetic markers of both genera. The latter two columns indicate the used substitution model in BEAST analysis, and when calculating genetic distances. Not all models are incorporated in the different software programs, so second choices were also used. K2P = Kimura 2 parameter model; HKY = Hasegawa, Kishino & Yano model; SYM = symmetrical model; GTR = generalised time reversible model; G = gamma rate variation between sites; I = invariable sites; BIC = Bayesian Information Criterion.*

genus	**marker**	**1st**	**BIC**	**reference**	**2nd**	**BIC**	**reference**	**BEAST**	**distances**
Sabatieria	18S	K2P	3714.8	Kimura, 1980	HKY	3730.1	Hasegawa et al., 1985	HKY	K2P
	ITS	K2P + G	9301.3	Kimura, 1980	HKY + G	9312.4	Hasegawa et al., 1985	HKY + G	K2P + G
	COI	HKY + I	2297.3	Hasegawa et al., 1985	K2P + I	2309.9	Kimura, 1980	HKY + I	K2P + I
Desmodora	ITS	SYM + G	3991.6	Zharkikh, 1994	GTR + G	3997.0	Tavaré, 1986	GTR + G	K2P + G
	COI	HKY + G	5312.7	Hasegawa et al., 1985	K2P + G	5461.0	Kimura, 1980	HKY + G	K2P + G

Table S5.4. *Overview of the number of unique and shared haplotypes per population and species of Sabatieria (ITS) and Desmodora (COI). Also gene diversity and nucleotide diversity are given for each population, as well as the number of individuals per location. Populations consisting of only one individual were never included in further analyses.*

SABATIERIA

Species I	unique haplotypes	shared haplotypes	number of individuals	gene diversity (h)	nucleotide diversity (π)
SG	14	4	114	0.731	0.002
SO	4	0	8	0.643	0.003
KG	7	4	27	0.860	0.004
AUS	0	3	5	0.833	0.002
BX	10	3	46	0.795	0.003
Species II					
SG	10	0	25	0.767	0.003
SO	7	1	25	0.807	0.030
KG	0	1	1	–	–
AUS	0	1	1	–	–
BX	3	1	16	0.617	0.001
Species III					
SG	4	1	8	0.893	0.004
SO	9	1	19	0.842	0.016
KG	7	0	8	0.964	0.012
AUS	–	–	–	–	–
BX	–	–	–	–	–
Species IV					
SG	–	–	–	–	–
SO	–	–	–	–	–
KG	–	–	–	–	–
AUS	0	2	2	1.000	0.002
BX	9	2	22	0.849	0.002

DESMODORA

Species I					
SG	9	0	9	1.000	0.015
SO	8	0	8	1.000	0.015
KG	–	–	–	–	–
AUS	1	0	1	–	–
BX	7	0	7	1.000	0.009

Table S5.5. *Mean intra- and interpopulation genetic divergences for the four Sabatieria ITS species and Desmodora COI species I, based on K2P distances (gamma = 4). Populations of only one individual were not taken into account. Values are given in percentages with their standard error. Diagonal values are intra-population divergences, while values below diagonal represent interpopulation divergences. n = number of individuals analysed.*

SABATIERIA

Species I (n = 200)	**SG**	**SO**	**KG**	**AUS**	**BX**
SG	0.17 ± 0.08				
SO	1.49 ± 0.44	0.31 ± 0.10			
KG	0.24 ± 0.09	1.57 ±0.45	0.31 ± 0.11		
AUS	3.16 ± 0.68	2.53 ± 0.60	3.25 ± 0.68	0.15 ± 0.10	
BX	3.19 ± 0.67	2.57 ± 0.59	3.28 ± 0.67	0.23 ± 0.08	0.32 ± 0.09
Species II (n = 66)					
SG	0.34 ± 0.10				
SO	6.20 ± 0.72	6.62 ± 0.65			
KG	–	–	–		
AUS	–	–	–	–	
BX	18.84 ± 1.92	15.63 ± 1.56	–	–	0.16 ± 0.08
Species III (n = 35)					
SG	0.21 ± 0.11				
SO	0.88 ± 0.14	1.42 ± 0.18			
KG	1.15 ± 0.28	1.71 ± 0.28	1.18 ± 0.22		
AUS	–	–	–	–	
BX	–	–	–	–	–
Species IV (n = 24)					
SG	–				
SO	–	–			
KG	–	–	–		
AUS	–	–	–	0.15 ± 0.15	
BX	–	–	–	0.18 ± 0.09	0.23 ± 0.08

DESMODORA

Species I (n = 24)					
SG	1.60 ± 0.26				
SO	2.22 ± 0.37	1.49 ± 0.25			
KG	–	–	–		
AUS	–	–	–	–	
BX	1.80 ± 0.33	1.45 ± 0.27	–	–	0.95 ± 0.21

CHAPTER 6: GENERAL DISCUSSION AND CONCLUSION

The present thesis has focused on the unravelling and understanding of patterns observed in nematode distribution in the Southern Ocean across different spatial scales, and at different taxonomic resolutions. We mainly analysed the spatial and environmental processes underlying these distribution patterns, using different approaches: correlative analyses in Chapters 2 and 3, variation partitioning in Chapter 4, and molecular analyses in Chapter 5. The answer to the question *'What drives species distribution in marine free-living nematodes in the Southern Ocean?'* is not straightforward and seems to depend on a combination of factors. Especially spatial extent of the study can have an impact on the conclusions drawn. Furthermore, historical aspects of environment and connectivity between locations are intrinsically linked to current species distributions but difficult to account for based on the few data available for this work. This last chapter will highlight some of the findings of this thesis, combine that knowledge in a synthetic overview, and end with some perspectives for the future. First, I will summarise the environmental and faunal data gathered in this thesis and relate that to what is known for other areas in the world. Second, local and regional drivers for community variation are discussed for the different scales. This is followed by an update on the molecular results. The final part of this thesis lists the main findings of the work presented, together with the main limitations and, perhaps most importantly, suggestions for further research.

THE SPATIAL AND ENVIRONMENTAL CONTEXT

In the attempt to provide a synoptic overview of the main conclusions of the previous chapters, a first step is to set the scene for the different studies (Fig. 6.1). We sampled 11 locations, distributed along different areas of the Southern Ocean shelf. In the Larsen area (**Chapter 2**), the focus mainly involved temporal response of communities after drastic changes in environmental conditions following ice-shelf collapse (blue box Fig. 6.1A). Locations in **Chapter 3** differed in the oceanographic conditions of the prevailing water masses and associated productivity regimes (green box). Finally, **Chapters 4 and 5** looked at genus and species distribution in a wider geographical context, while speculating about the influence of environmental (local) and spatial (regional) processes on nematode community assembly. For Chapter 4, this involved all sampling locations in this thesis (combination of blue, green and red box), while Chapter 5 dealt with a subset of locations (red box).

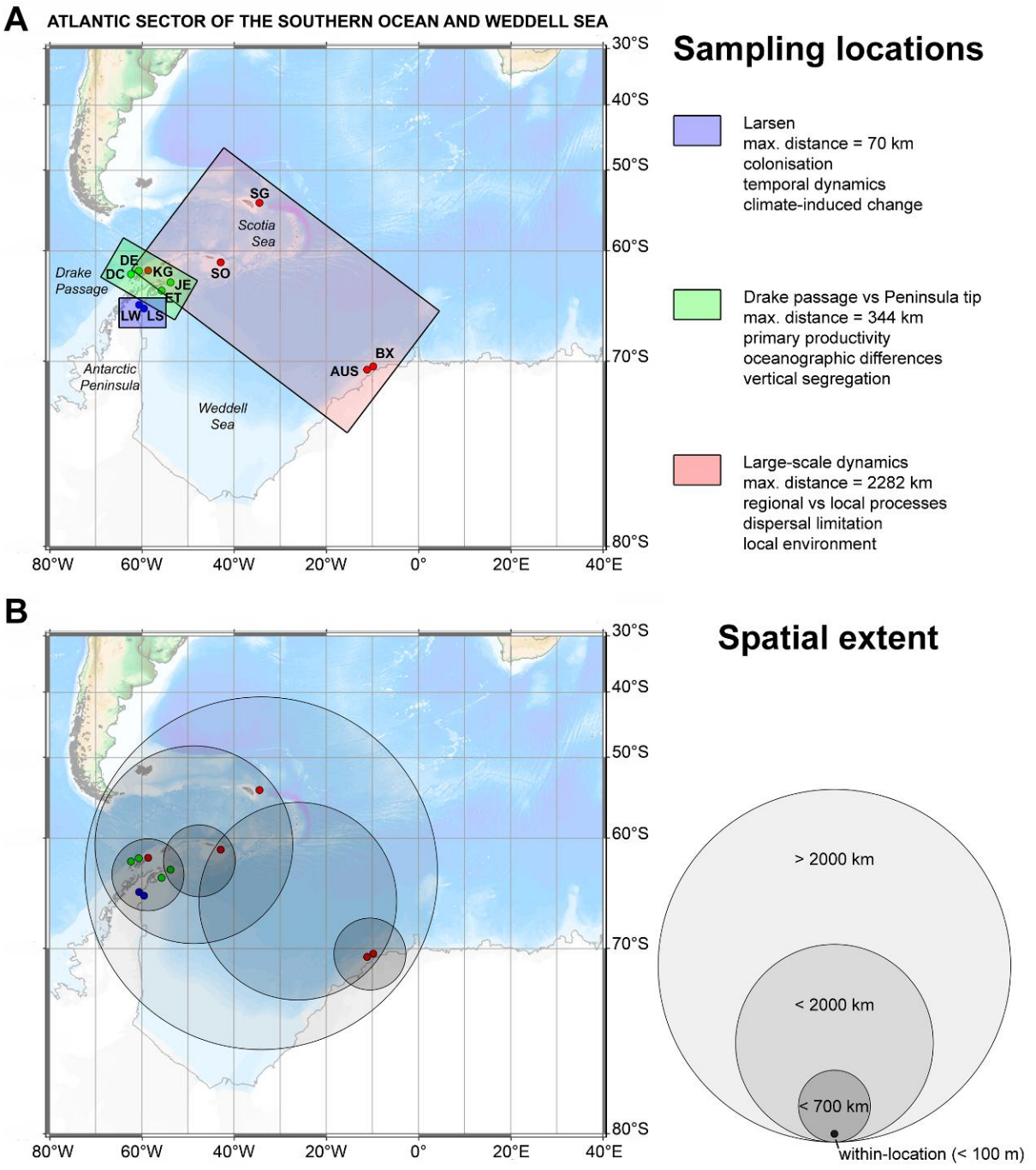


Figure 6.1. A. *Overview of the sampling locations of the different chapters. Blue box = Chapter 2, Larsen area. Green box = Chapter 3, Drake Passage versus Antarctic Peninsula tip. Red box = Chapter 4 and 5, locations along the Scotia Arc, at the western Antarctic Peninsula, and eastern Weddell Sea. The legend gives a short update on the main topics covered in the different chapters. Stations LW, LS, JE, ET, DC and DE are labelled differently in Chapters 2 and 3; LW = B.West, LS = B.South, JE = W-120, ET = W-163, DC = DP-243 and DE = DP-250.* ***B.*** *Visualisation of the spatial extent of the different locations. Diameter of each circle represents the largest geographic distance between any two locations within that circle.*

Geographic distances between locations ranged from 15 to more than 2300 km (measured as the shortest seaborne path without crossing land masses), and can be arbitrarily divided into categories as visualised in Figure 6.1B. The smallest scale is that within locations, between replicates typically only a few m apart; or even within replicates, between different sediment depth layers (vertical profiles) or subsamples of a core. On the next level, divisions are roughly based on biogeographic information for the Southern Ocean (see De Broyer & Koubbi, 2014 for an overview). Although Griffiths et al. (2009) pointed to the lack of a clear biogeographic zonation within the Southern Ocean (see **Chapter 1**) past classifications did make distinctions based on oceanography and faunal occurrence. These classifications all have their subtle variations, but a recurrent theme is the consideration of South Georgia (SG in Fig. 6.1A) as a separate (sub-) province or district (De Broyer & Koubbi, 2014). The rest of the Southern Ocean (i.e. the area within the Polar Front) is either considered a single province or region, or is further differentiated in a Scotia subregion (including the South Orkneys (SO), South Shetland islands (KG, DC, DE), and Antarctic Peninsula (JE, ET, LW, LS); Fig. 6.1A) and a High Antarctic subregion (AUS, BX). For our study locations, considering a scale below 700 km places all locations within that range in the same province, whereas they belong to different provinces when above 700 km distance (Fig. 6.1B). At the largest scale (> 2000 km), locations span the vast Weddell Sea.

As the biogeographical classifications mentioned above are partially based on oceanographic parameters, it is not surprising that we found distinct local conditions for the different study sites of this thesis. Although some environmental variables largely depend on the timing of sampling (e.g., pigment concentrations, TOC and TN content; see also **Chapter 2 – 4**), there are some generalisations to make (Fig. 6.2). The Southern Ocean is characterised by a series of pronounced surface current systems that are primarily wind-driven (Fig. 6.2; see also Fig. 1.2 in **Chapter 1**), but of which the influence reaches down to different vertical strata in the water column and on the upper shelf (Orsi et al., 1995). Current speeds gradually decrease when moving deeper in the water column due to shear stress between different water layers, yet still attain average values of 3 – 20 cm s^{-1} near the seafloor at shelf depths (Barker & Thomas, 2004; Isla et al., 2006a, b). Also, the location of the oceanic fronts associated with these current systems can change over time and bottom current dynamics can show seasonal or tidal variation in strength (Isla et al., 2006b).

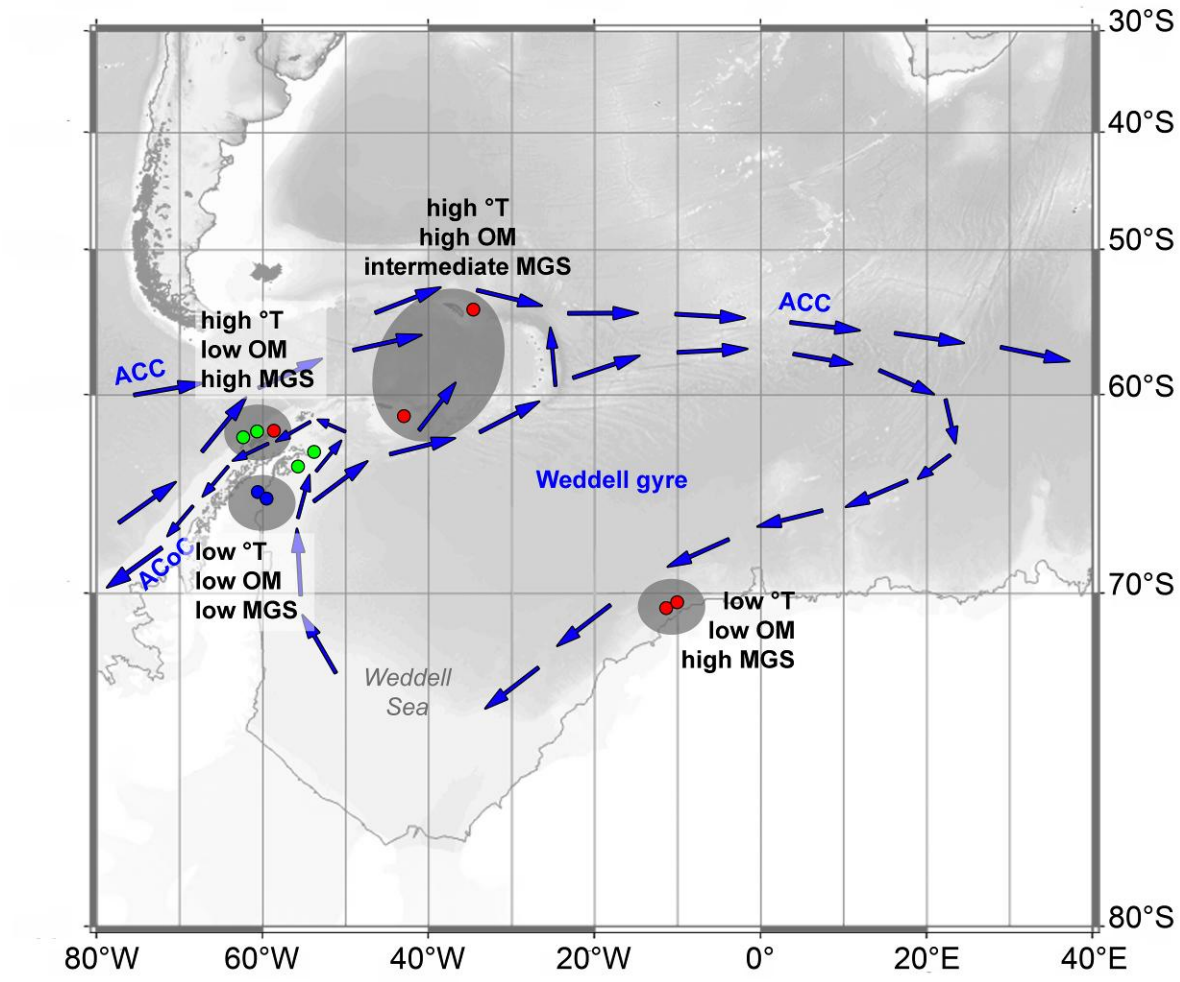


Figure 6.2. *Overview of the main surface current systems in the Weddell Sea and Atlantic sector of the Southern Ocean, based on literature data and observations during time of sampling. ACC = Antarctic Circumpolar Current, ACoC = Antarctic Coastal Current. In reality, the ACC constitutes a zone of eastward jets between 48 and 61°S, of which the position can shift with both time and location. For simplicity, I only considered the main direction of the flow. Next to current systems, I indicated a generalisation of the sedimentary environmental conditions at the different locations. Underlying data stems from analyses of variables of both ANT-XXVII/3 (2011) and ANT-XXIX/3 (2013). Naturally, since both expeditions took place at different times, this is only a momentarily snapshot and merely serves as a general setting for the results discussed here. OM = organic matter, MGS = median grain size, °T = bottom temperature.*

For our stations, the largest differences are situated between locations where Antarctic Circumpolar Current (ACC) conditions prevail (South Georgia, South Orkneys, Drake Passage and South Shetland Islands), and locations under Weddell gyre influence (eastern Antarctic Peninsula and eastern Weddell Sea). Such a differential influence is mainly obvious

from oceanographic parameters (e.g., bottom temperature; Fig. 6.2), but also affects other processes that are possibly important for benthic communities (e.g., seasonal sea-ice extent; primary productivity, sediment sorting; see also **Chapter 2 and 3**). This was reflected by variation in sediment grain size, organic matter and pigment content (Fig. 6.2), all of which have been proven important features of benthic habitats. Since nematodes are bound by the sedimentary properties of their habitat, correlations with community assembly, density, diversity and morphology have repeatedly been demonstrated (Heip et al., 1985; Moens et al., 2013 and references therein). Within each location, environmental conditions – most notably food-related parameters – also varied with sediment depth (see results **Chapter 2 – 4**). In most cases, organic matter and pigment content decreased with sediment depth, although stations W-120 and W-163 in **Chapter 3** formed an exception to this trend.

THE FAUNAL CONTEXT: (MACRO-) ECOLOGICAL AND BIOGEOGRAPHICAL PATTERNS IN SOUTHERN OCEAN NEMATODES

Density and diversity

Throughout all four chapters, hence for different spatial scales and environmental conditions, nematodes consistently formed the most abundant metazoan meiofaunal taxon in sediment samples, with percentages ranging between 75 and 100 % of total numbers. Average densities in the study locations ranged from roughly 300 to 6000 individuals per 10 cm², which is high (e.g., values of ~ 100 – 230 ind 10 cm^{-2} at similar depths in Vanhove et al., 1999) but not uncommon in Antarctic shelf zones (Ingels et al., 2006), and largely exceeds reported macrofauna numbers in the area (0.17 – 20 ind 10 cm^{-2} at depths between 100 and 800 m; Glover et al., 2008; Sañé et al., 2012). The upper range of nematode abundance encountered in this thesis is comparable to values found in some fine sediments of beach ecosystems and shallow marine subtidal zones (see Heip et al., 1985 for an overview), yet exceeds that of most deep-sea sediments as well as those at comparable depths in the Northeast Atlantic (~ 600 – 900 ind 10 cm^{-2} at 200 – 700 m; Vanaverbeke et al., 1997; 2000 ind 10 cm^{-2} at 500 m; Vincx et al., 1994). Also genus diversity was substantial in most cases, with a maximum of 65 genera co-occurring in the upper sediment layer (depth 3 cm, surface area 25 cm²) at South Georgia, and 36 genera in the subsurface layers near South Orkneys and King George (depth 2 cm, surface area 25 cm²). Recalculated to sample volume, maximum genus numbers are thus ~ 9 (surface) and 7 (subsurface) genera per 10 cm³, which is slightly above other reported values for the Antarctic (Vanhove et al., 1999: maximum of 7 genera per 10 cm³). Station B.West in **Chapter 2** formed the only exception, with total genus numbers that were very low

(only 3 – 6 genera in one core sample). In accordance with previous findings, genus abundance and diversity generally decreased with increasing sediment depth (see Fig. 6.3), a pattern considered to be the result of the depletion in food supply and changes in oxygen and other biochemical compounds (Heip et al., 1985). Presence of macrofauna is also known to impact vertical nematode distribution, both directly (e.g., predation) and indirectly (e.g., alteration of biochemical gradients through burrowing activities) (Moens et al., 2013 and references therein). Exceptions to the decreasing trend were (again) station B.West in **Chapter 2**, and stations W-120 and W-163 in **Chapter 3** which noted subsurface peaks in abundance (1 – 3 cm).

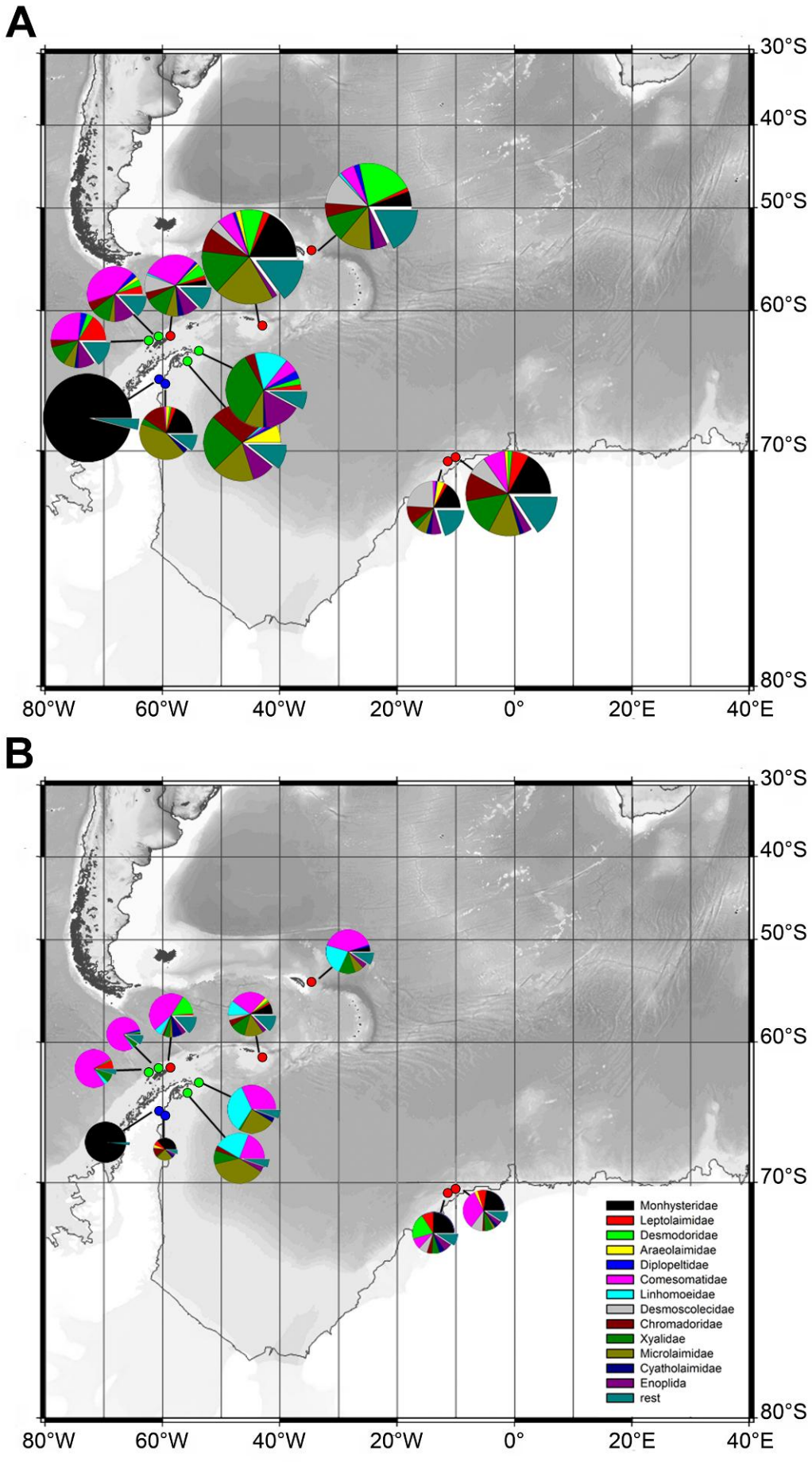
While it has repeatedly been established that nematodes are the numerically dominant taxon in marine sediments (particularly also in the Southern Ocean; see general introduction), and results presented here merely confirm these previous findings, it is still puzzling why small organisms would occur in such high densities and diversity. Unlike phytoplankton, protists or bacteria, for which the function in the food web is generally well understood and appreciated (cf. their role as producers and/or nutrient remineralizers; Azam et al., 1983), the role and trophic position of nematodes are often much less obvious (e.g., Guilini et al., 2010; Heip et al., 1985; but see Yeates et al., 2009). Furthermore, they are less important in terms of biomass compared to the – usually more patchily distributed – macrofauna (Heip et al., 1985; Moens et al., 2013).

Community composition at genus and species level

Nematode community composition varied across the different locations of this thesis, both at genus and at species level, and also showed different vertical distribution in the sediment (results **Chapter 2 – 4**). An integrative assessment of the genus pool across all chapters yields a total of 180 genera (see Appendix 1 for a taxonomic list) and indicates that nematode genera in the Southern Ocean are – to a large extent – widely spread, in line with ubiquity assumptions for small organisms. The majority of genera are present at more than one location, and differences that were observed in genus assemblages stem from distinct relative abundances rather than true absences (see Appendix 2 – 5). Additionally, all genera encountered have previously been reported in other areas. Together, these observations are in agreement with results from other studies worldwide, and corroborate earlier statements of cosmopolitan genus distributions and lack of endemism in marine nematodes (e.g., Giere, 2009; Vanhove et al., 1999). As a side effect of the large diversity observed, many genera (>

50 % of totals) are only present in relative abundances < 1 % (i.e. 'rare' genera). Figure 6.3 shows how nematode assemblages vary both horizontally and with depth in the sediment across the Scotia Arc, Peninsula and Weddell Sea. The plots are based on average genus relative abundances for the different locations (only when > 1 %) which have been summed according to the family they belong to. While this naturally is an oversimplification, the main trends are obvious nonetheless: nematode community composition, diversity and density differ between locations and between sediment depths (with a shift around 2 – 3 cm; see results **Chapter 3**). Genera belonging to the families Xyalidae, Monhysteridae and Desmoscolecidae are more common in surface layers, while genera of the Comesomatidae and Linhomoeidae prefer deeper sediments. The locations near the South Shetland Islands (KG, DC and DE) formed an exception to this latter statement, since genera such as *Sabatieria*, *Dorylaimopsis* and *Comesa* constituted a large fraction of totals at the surface as well (although their numbers in deeper layers of the same locations were even higher; Appendix 4 – 5). These latter genera generally consist of more elongated specimens with a higher body surface to volume ratio. This is believed to facilitate the uptake of oxygen and the movement between anoxic and oxic layers of the sediment (Moens et al., 2013). Therefore, although communities occurring in surface and subsurface depth layers are analysed independently from each other in some of the previous chapters, they do not form isolated assemblages and vertical migration within the sediment should be taken into account.

One very clear deviation from 'normal' genus composition (i.e. applicable to the majority of locations) in both surface and subsurface sediments was present at Larsen B.West (and to a lesser extent B.South; **Chapter 2**). Communities there showed much lower diversity and very different composition than other stations in the neighbourhood (Fig. 6.3). Only the family Monhysteridae was well represented at B.West, attributable to the proliferation of one *Halomonhystera* species after ice-shelf collapse. Apparently, this drastic change in environment resulted in a community that is largely different from any other shelf assemblage covered in this thesis (or in other Antarctic sediments – see Fig. 2.6).


A
B
30°S
40°S
50°S
60°S
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80°S
80°W
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40°W
20°W
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40°E
Monhysteridae
Leptolaimidae
Desmodoridae
Araeolaimidae
Diplopeltidae
Comesomatidae
Linhomoeidae
Desmoscolecidae
Chromadoridae
Xyalidae
Microlaimidae
Cyatholaimidae
Enoplida
rest

Figure 6.3. (previous page) *Average density and family-level diversity for surface* ***(A)*** *and subsurface* ***(B)*** *sediment layers of the different locations in this thesis. Diagrams are based on average relative abundance of genera per location. Only genera with a relative abundance > 1 % were included, the others have been summed and incorporated as 'rest'. The genera were assigned and grouped according to their respective families to limit the amount of different colours in the diagrams and to make comparison across areas easier. The size of the diagrams is proportionate to the average nematode density (standardised to individuals per 10 cm²) at each location, and represents their rank order (as absolute numbers are highly divergent). The legend at the lower plot accounts for both graphs, and diagram colours are ordered in counter clockwise direction, starting at 0° (horizontal). For each separate diagram, the part sticking out indicates the rest fraction.*

Besides the demonstration that community composition and genus relative abundance differed significantly among locations, there also were indications of a certain directionality of these variations. Results in **Chapter 4** showed a decrease in genus similarity with increasing geographic distance between locations (Fig. 4.2, 4.3), a pattern referred to as distance decay (Soininen et al., 2007). Especially when crossing the Weddell Sea, communities became highly dissimilar as a result of high turnover patterns (beta diversity partitioning results **Chapter 4**). When the same exercise is repeated with the combined genus data of all sampling locations, this trend is absent (Fig. 6.4A; $P > 0.05$ for both regressions) which is due to (again) the atypical assemblages within the Larsen embayment and their high dissimilarities with any other shelf location incorporated in this thesis (cf. 'Larsen effect', Fig. 6.4A). When the Larsen locations were removed from the analyses, similarity did significantly decrease with increasing geographic distance, although the effect was rather weak in surface layers ($R^2 = 0.13$; $P = 0.031$; Fig. 6.4B). It shows that surface communities across the Atlantic sector of the Southern Ocean are more similar in composition than deeper-dwelling assemblages, a conclusion also made in **Chapter 4**. Besides the (weak) correlation between similarity and distance, no further trends in density or diversity were discovered with latitude (cf. Thorson's rule; Gray, 2001; Thorson, 1957) or water depth. In both cases this might be related to the fact that latitudinal (54 – 71 °S) and depth (240 – 520 m) ranges were too limited in this study to cause significant differences in nematode communities. Previous studies on nematode communities in various parts of the world already showed that nematode genus and species composition is largely driven by habitat type and local environmental conditions rather than geographic area or latitude (see Moens et al., 2013 and references therein).

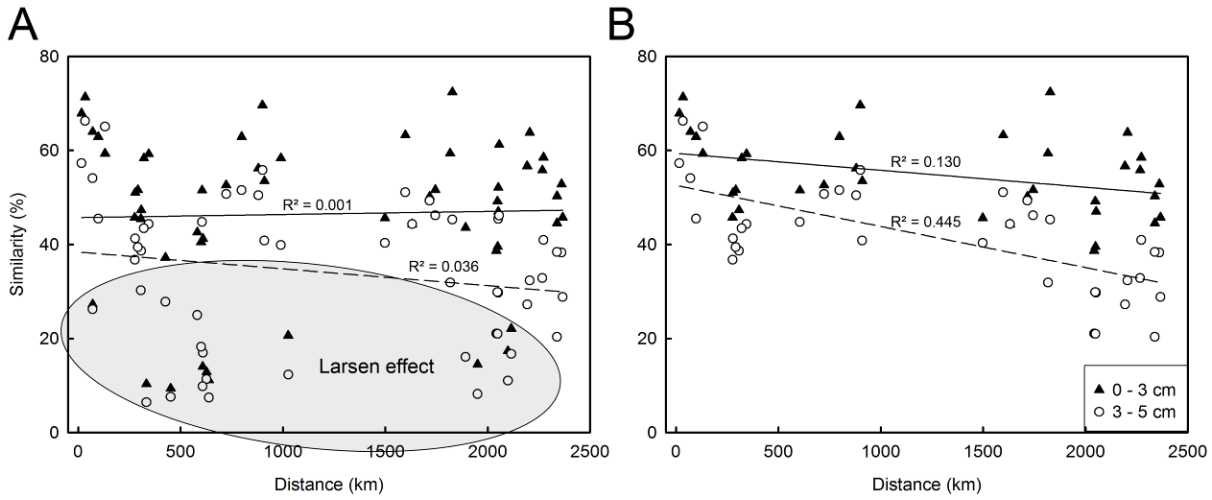

Figure 6.4. *Average similarity (Bray-Curtis) in genus composition plotted against geographic distance (measured as the shortest seaborne distance between each pair of locations) for surface (triangles) and subsurface layers (circles) of all combined datasets. In plot **A** all pairs of sampling locations were included, while the Larsen locations (LS and LW) were removed from the dataset for plot **B**. Trendlines indicate linear regression fit (solid = surface; dashed = deeper). For plot A, P-values for the regression were never significant at the 5 % level, while in plot B they were (surface: P = 0.031, deeper: P < 0.0001).*

Chapters 4 and 5 of this thesis incorporated species-level information for nematodes, first for the entire community (**Chapter 4**) and later on for two selected genera (**Chapter 5**). Results there showed that also at this finer taxonomic resolution, communities differed both horizontally and vertically (**Chapter 4**). Not surprisingly, rare genera are represented by only one species in most cases, while the more abundant ones often have several congeneric species (Appendix 6). The regional species pool of **Chapter 4** had a total of 274 species, of which 260 were present in surface (0 – 3 cm) and 166 in subsurface (3 – 5 cm) sediments (see Appendix 6 for a species list). More species were shared between surface layers of the different locations (51 %) than between deeper layers (31 %), again indicating a higher level of large-scale connectivity at the surface. Additionally, both sediment strata had a high percentage of singletons (i.e. species occurring at only one sampling location; 36 and 49 %, respectively), pointing to the fact that nematode distribution at the species level is more restricted than for widespread genera (**Chapter 4 and 5**). In accordance with suggestions in microbial macroecology that the most abundant and dominant species have higher levels of ubiquity, species with highest relative abundance were also more widely spread (see results **Chapter 4**; Fig 4.3), especially at the surface. Therefore, lower similarity in subsurface layers might also be related to the fact that those species occur in lower numbers and are hence less

widely distributed. Yet some of the species preferring deeper sediment layers were also present at all sampled locations across the Weddell Sea (see *Sabatieria* sp. I and II in **Chapter 5**).

ENVIRONMENTAL AND SPATIAL CONSTRAINTS ON NEMATODE DISTRIBUTION

It is one thing to describe patterns in nematode genus and species distribution for an area where sample recovery is logistically challenging. Of equal importance is trying to link these patterns to their underlying processes. In the large body of literature concerning (meta-) community dynamics, environmental selection (cf. species sorting paradigm) is often put forward as highly important in structuring communities in both freshwater as well as marine systems (e.g., Cottenie, 2005; Heino et al., 2015; Moritz et al., 2013). Also for nematodes, traditional approaches yield strong associations between communities and their environment, which has suggested that nematodes might indeed be globally distributed but that compositional variation is structured by niche effects (cf. ubiquity hypothesis). Results from the different studies in this thesis provide further evidence for this habitat filtering by showing significant correlations between nematode community structure and environmental variables. Most notably, productivity-related characteristics (**Chapter 2, 3 and 4**) and sediment grain size (**Chapter 3 and 4**) were important in structuring communities. However, when a larger spatial scale is considered, these relationships are not always as clear as on a small scale, which leaves room for speculation on other potential drivers (e.g., large-scale differences in oceanography, biological and physical barriers, dispersal limitation). I will elaborate on the importance of these processes for scales ranging from within cores to between locations in the same biogeographic zone and ultimately between different biogeographic zones (Fig. 6.1B). It is important to note here that any division based on spatial scale in this study is arbitrary, and does not suggest that the same cut-off level should be used in other studies.

A recurrent theme throughout almost all chapters is the **vertical within-location** segregation of nematodes, hence variation at a very small spatial scale (see also Fig. 6.3; Appendix 2 – 5). On average only 45 % of genera are shared between surface and deeper layers (all locations included), while this number is even lower for species (41 %; only locations of part I in **Chapter 4**). The fact that it consistently are the same genera (even families; Fig. 6.3) that occur in either surface or deeper sediments means that this pattern is not random and probably results from associations with environmental variables that vary with depth (see discussion **Chapter 4**; Steyaert et al., 2003). Earlier in this chapter we have shown that food levels tend to decrease when digging deeper in the sediment (cf. results of **Chapter 2 – 4**), and also

oxygen can drop after a few mm or cm (although this was never explicitly tested for the locations in this study; Moens et al., 2013). However, since we are dealing with an area where well-oxygenated water masses originate (Gordon et al., 2001; Orsi et al., 1999), oxygen limitation might not be the most important driver for differences in composition. Nevertheless, such a statement should ideally be backed by in-situ measurements, which are unfortunately lacking (a factor that has also been mentioned in the discussion of **Chapter 4**). By contrast, the impact of food availability on nematodes' vertical distribution was demonstrated by subsurface peaks in genus abundance coinciding with deeper penetration of fresh food (W-120 and W-163 in **Chapter 3**). Preference of nematodes for a certain depth layer is also related to their different feeding strategies (Wieser, 1953). Epistratum feeders will generally prefer upper layers, while deposit feeders can occur throughout and migrate up and down if needed. In this sense, segregation of *Desmodora* and *Sabatieria* species in **Chapter 5** correlates well with this theory. Finally, vertical segregation of nematode species can be related to interactions with other nematodes or other taxonomic groups (e.g., macrofauna organisms) (Steyaert et al., 2003; see earlier). Macrofauna organisms observed in the samples mainly included polychaete worms, small crustaceans (e.g., amphipods) and ophiuroids (personal observations). However, their distribution is patchier compared with the smaller meiofauna taxa, and densities are much lower (they were only sporadically observed in the small multicorer tubes). A consistent effect of their assemblages on nematode vertical distribution is therefore unlikely. To conclude, if environmental filtering is truly important in explaining vertical nematode distributions, results of this thesis indicate that analysing nematode communities in bulk (e.g., Fonseca et al., 2014) can mask a rather large source of variation (see also Steyaert et al., 2003).

When increasing the spatial scale to **distances between replicates** (ranging from cm to a few m) earlier research demonstrated that heterogeneity of local conditions can generate a highly patchy environment, leading to a mosaic of nematode assemblages in different successional stages and enhancing the coexistence of multiple species (Heip et al., 1985; Moens et al., 2013; Vanreusel et al., 2010b). Similar processes might possibly explain the high diversity observed in many of our sampled locations (see earlier in this chapter). Within-core variation (cm) was comparably large as that between cores for the same location (**Chapter 4**; Fig. 4.2), which further confirms the presence of microscale variation in nematode communities (Fonseca et al., 2010; Gallucci et al., 2009). Nevertheless, contrary to earlier observations of small-scale (< 1 km) variation in benthic communities (including nematodes) exceeding that

across areas (Chapman et al., 2010), variation in Southern Ocean nematode communities did increase with the spatial scale considered (**Chapter 4**).

At the next level, at a scale ranging from tens to a few hundreds of km (**within biogeographic zones**; Fig. 6.1), results of **Chapters 2** and **3** showed that short-term environmental changes or differences in conditions related to the geographic position of sampling locations can directly cause localised variation in communities. Especially shifts in primary productivity regime, which is highly correlated with seasonal phytoplankton blooms and sea-ice dynamics (cf. **Chapter 3**), can provoke compositional and abundance-related responses in benthic nematodes. The relatively short generation time of most marine free-living nematodes (ranging from a few days to several months; Bongers et al., 1991; Heip et al., 1985) might allow them to rapidly establish a viable population, especially after disturbance (e.g., Gallucci et al., 2008; Lee et al., 2001). However, generation times of several marine nematode genera can show significant variation with temperatures (see Heip et al., 1985 for an overview) and this might be of importance in an Antarctic context. Results from experiments on (mainly) temperate and tropical specimens showed increased generation times at colder temperatures (5 – 7 °C), ranging from 71 days (*Theristus*; Gerlach & Schrage, 1971) to 570 days (*Oncholaimus*, Heip et al., 1978). At the same time, it was also shown that the species *Monhystera disjuncta* (now *Halomonhystera disjuncta*), which has also been recovered from the Antarctic, expresses shorter generation times and increased longevity at 3 °C, compared to 17 °C (Heip et al., 1985). It can therefore be suspected that generation time is highly dependent upon the species and the habitat under consideration. Nevertheless, it remains to be tested to what extent the colder temperatures in the Antarctic might impact generation times of Southern Ocean nematodes.

From a metacommunity point of view, the wide distribution ranges and large population sizes observed for nematode genera provide local communities with a large (almost unlimited) regional pool of potential colonisers. The presence of food is known to trigger colonisation and proliferation of nematodes (e.g, experiments by Gallucci et al., 2008) and can similarly be invoked in the case of the Larsen area, where enhanced water-column productivity and related fresh phytodetritus input after ice-shelf collapse triggered a drastic increase in the abundance of one *Halomonhystera* species (**Chapter 2**). Clearly, this species benefits from some selective agent that allows its proliferation at a relatively small spatial scale, possibly by mediating a priority effect and monopolisation of resources (cf. De Meester et al., 2002). Similar dynamics were observed for other species of the same genus in different areas

(Derycke et al., 2007b; Van Gaever et al., 2009a). Also in **Chapter 3**, differences in nematode community composition between areas east and west of the Antarctic Peninsula were predominantly linked to local differences in primary productivity at the time of sampling and subsequent efficiency of the bentho-pelagic coupling process (e.g., Lins et al., 2014). In this chapter, we demonstrated the importance of ice margins and related processes as drivers of benthic diversity and abundance. It is not surprising that mainly productivity-related variables play an important role in a system where there is a large seasonality in such variables. Hence, the variation in the genus matrix of **Chapter 4** could also be linked to chlorophyll and organic carbon content (Table 4.2). This was complemented by sediment grain size and hydrological variables (bottom temperature and salinity).

At the largest spatial scale in this thesis (> 700 km; between **different biogeographic zones**; Fig. 6.1), niche differences visualised in Figure 6.2 lead to a pattern where similarity in environmental conditions declines with distance between patches (cf. Fig. 4.2A). This higher probability of locations close to each other of expressing a similar environment (Soininen et al., 2007) might give rise to the general distance decay in nematode community similarity described in **Chapter 4** and Figure 6.4 of this chapter. Yet combined analysis and variation partitioning of all stations in Chapter 4 indicated that large-scale differences in local environment contributed less to community variation than did spatial processes (Table 4.2). The unique fraction of environmentally explained variation was therefore rather low, both for surface (~ 8 %) and subsurface communities (~ 6 %; Table 4.2) and a large amount of variation in nematode community structure remained 'undecided' (i.e. spatial nuisance [E∩S]; Bahn & McGill, 2007; Logue et al., 2011; Peres-Neto & Legendre, 2010). The association between nematode assemblages and environmental variables is probably to a large extent attributable to environmental predictors that are themselves spatially structured. In this respect, environmental models included variables that hold an intrinsic spatial signal as well (e.g., salinity and temperature; Table 4.2) because they depend on the oceanography of the area. The same remark can be made for observations in **Chapter 3**, where differences in nematode assemblages were partly linked to variables related to water-mass origin. However, it is very likely that several other variables with a potential influence on nematode distribution were missed in our analyses. Such variables might include (amongst others) oxygen concentration (see earlier), bacterial biomass (as a potential food source; Wieser, 1953), bottom shear stress and vertical mixing, as well as bioturbation by other animal groups. Ideally, these should be incorporated in the variation partitioning analyses, since they might increase the fraction of

variation that can be explained by environment. At this point, based on the results from **Chapter 4**, the conclusion would be that spatial processes, rather than species-sorting dynamics, are responsible for the large-scale variation and turnover in nematode communities. In this instance, any small-scale associations between nematode communities and their environment might be overruled by dispersal limitation which would contradict earlier assumptions of nematode genus and species distribution being mainly driven by habitat type and local environmental conditions (Moens et al., 2013; Vanreusel et al., 2010b). Especially when considering communities separated by the vast deep Weddell Sea, differences between nematode communities were substantial and variation partitioning indicated a large amount of spatial structuring – irrespective of environmental gradients (**Chapter 4**). Similarly, although some species occurred throughout the entire area, most populations of *Sabatieria* and *Desmodora* species were restricted to their geographic location and showed significant genetic differences among them (AMOVA results **Chapter 5**). Therefore, contrary to observations of circum-Antarctic distributions for other invertebrate taxa (Riesgo et al., 2015), large-scale current systems in the Southern Ocean might not be efficient enough to allow regular exchange between nematode communities further apart. Nevertheless, based on the observation that some nematodes are occurring in different locations separated by large distances, long-distance dispersal did occur at a certain point in time.

CONGRUENCE BETWEEN COMMUNITY ECOLOGY AND POPULATION GENETICS

There are quite some parallels to be drawn between the fields of community ecology and population genetics, and together they can form an integrative way of looking at species distribution patterns (cf. Leibold et al., 2010; Vellend, 2010). Variation partitioning and molecular approaches used in **Chapters 4** and **5** therefore complement each other, but focus on either the communities as a whole (**Chapter 4**) or species and populations of the genera *Sabatieria* and *Desmodora* (**Chapter 5**). Results of phylogeography and population genetics in **Chapter 5** were largely congruent to those of previous metacommunity analyses, and reinforce the conclusion of a potential role of dispersal limitation described in the previous section. There was a mixture of species being restricted to one side of the Weddell Sea and others that were not (see Appendix 7 for *Sabatieria*). Similar observations have been made based on taxonomic species descriptions in another nematode genus (*Dichromadora*) recovered in the same area but at deeper locations (1000 – 2000 m) (Vermeeren et al., 2004). Yet even for those species that were widely spread across the study area of this thesis, populations showed limited (probably even no) signs of contemporary gene flow in all cases.

So analogously to the possibility of dispersal limitation at the community level, gene flow was restricted at the population level. Also, as a counterpart for the larger variation in subsurface communities of **Chapter 4**, the level of pairwise genetic differences between populations of the deeper-dwelling *Sabatieria* species was higher than for surface populations of *Desmodora* (cf. larger pairwise Φ_{st} for *Sabatieria*; **Chapter 5**). However, strong population genetic structure is not necessarily related to dispersal limitation, and might also indicate high levels of biotic filtering (e.g., priority effects, competition; De Meester et al., 2002; Derycke et al., 2007) or habitat filtering upon settlement of dispersed individuals (Marshall et al., 2010). This again relates to the fact that, with inclusion of more environmental variables, environmental filtering might become more important in explaining community variation across locations. Isolation-by-distance testing was indeed not significant for any of the *Sabatieria* or *Desmodora* species with wide distribution ranges. Populations closer to each other were sometimes equally different than those further apart, a pattern that mainly originated from substantial genetic differentiation between the three locations along the Scotia Arc (SO, SG) and South Shetland Islands (KG). Together with the large level of spatial autocorrelation in variation partitioning analyses of **Chapter 4**, this leaves room for debate on the respective roles of dispersal limitation versus environmental filtering. Finally, the large genetic differences between species and populations across the Weddell Sea might also be related to the historical context of the region. Throughout glacial-interglacial cycles, varying connectivity of suitable habitats on the continental shelf probably promoted allopatric speciation of organisms (Kaiser et al., 2013). The assumption that marine speciation is rather quick and occurs at small spatial scales (Rocha-Olivares et al., 2001) may have helped taxa such as the nematodes in this study to rapidly establish sexually isolated populations. The question whether marine nematodes in the Southern Ocean show extended levels of eurybathy and/or endemism as proposed for other invertebrate taxa (Brey et al., 1996; Griffiths et al., 2009; but see Riesgo et al., 2015) is very difficult to evaluate based on the data from this thesis. Previous work by De Mesel et al. (2006) and Vermeeren et al. (2004) on two nematode genera (*Acantholaimus* and *Dichromadora*, respectively; morphological species delimitation only) in shelf and slope sediments in roughly the same area showed that some (or even most) species occurred throughout the depth range studied (180 – 2000 m and 1000 – 2000 m). More recently, also phylogeographic studies using 18S and 28S data provided evidence for regular species interchanges across depths in marine nematode genera from intertidal and deep-sea sediments (Bik et al., 2010; Lins et al., 2016). Eurybathymetric species distributions are therefore theoretically plausible, but the depth range considered in this thesis is too narrow

to verify such conclusions. Bik et al. (2010) additionally pointed towards low levels of endemism within the order Enoplida on a global scale. Based on our dataset, such a conclusion cannot be made due to its limited scope and the scarcity of reference material in public data repositories such as GenBank.

NEMATODE DISTRIBUTION – A SYNTHESIS ACROSS SCALES

From the results gathered in this thesis and discussed in the previous sections of this chapter it is clear that the relative role of local environment and regional dispersal in structuring marine nematode communities remains elusive. In what follows, I will try to provide a general synthesis of the different findings, referring to the frameworks and concepts that served as a basis for this thesis. I propose that there are two scenarios that might relate to the patterns in community variation that were observed across scales in the Southern Ocean (Fig. 6.5). Since these are based on the results specifically for the animals and locations contained within this thesis, extrapolation to other systems should be cautious. Both scenarios differ in the underlying assumptions regarding nematode dispersal, and should be interpreted as hypotheses requiring further investigation rather than evidence of what is really going on.

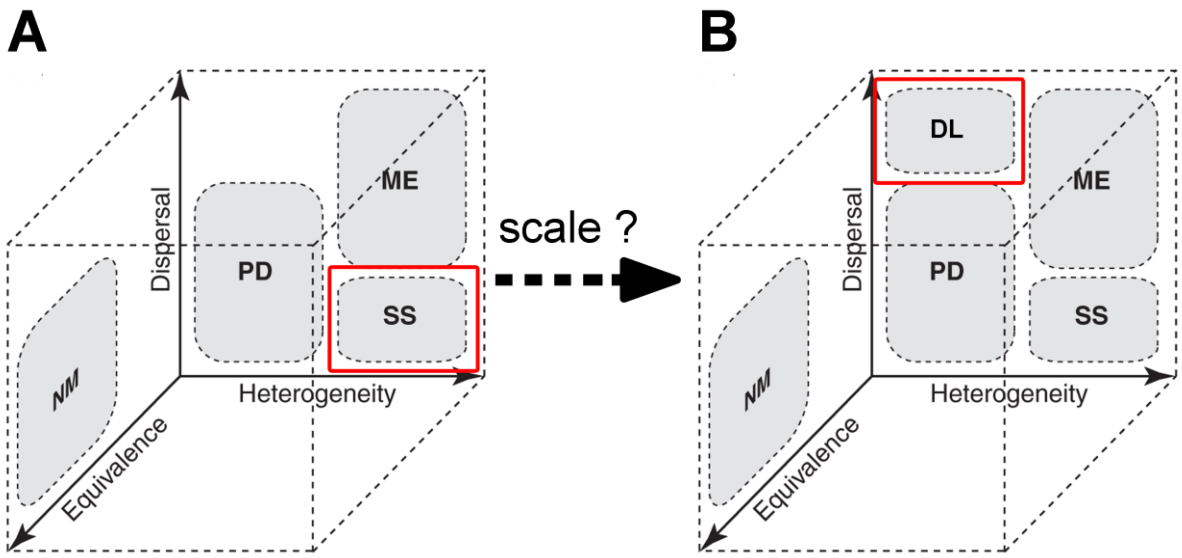

Figure 6.5. *Schematic diagram of Logue et al. (2011), adapted to represent two possible scenarios for factors influencing marine nematode distribution in part of the Southern Ocean. NM = neutral model, PD = patch dynamics, ME = mass effects, SS = species sorting, DL = dispersal limitation. Explanation in main text.*

The first scenario (Fig. 6.5A), much like the "everything is everywhere" concept for microorganisms (Fenchel & Finlay, 2004) assumes that nematodes are efficient in their dispersal owing to their small body size and large population sizes. Results in this thesis have repeatedly demonstrated that nematode abundance at Southern Ocean shelf depths is considerable, presenting communities with a large number of potential dispersers. Dispersal is further mediated by large-scale current systems present in the area. Local niche effects – i.e. species sorting in the metacommunity theory – are thus the main constraining factor responsible for compositional variation among communities (cf. **Chapter 2, 3**). Observations of small-scale variation in nematode communities, wide distributional ranges for several species (**Chapter 4, 5**) and occurrence of genera that are globally distributed in all chapters seem to comply with such a scenario. Alternatively, dispersal of nematodes is considered a limited or sporadic event based on their endobenthic lifestyle and bottom currents that might be too weak to maintain regular exchange of individuals (Fig. 6.5B). Such a scenario differs from neutral models in that species are not necessarily ecologically equivalent, but they are equally limited in their dispersal (hence different box in Fig. 6.5). In this case, any effect of environmental heterogeneity is overruled by the influence of oceanographic barriers and distance. High levels of unique spatial structure ([S|E]) in variation partitioning (**Chapter 4**), distance decay in similarity and large genetic differences between species populations in *Sabatieria* and *Desmodora* (**Chapter 5**) all provide some evidence that such a scenario may exist. Specifically for nematode communities in the Southern Ocean continental shelf zone, I would argue that species sorting prevails at a small within-location scale, while dispersal limitation becomes more likely when studying communities from different locations separated by hundreds of km. Both scenarios presented here are not mutually exclusive and their importance might shift depending on the system and spatial scale that is studied. For example, nematode communities in high-dynamic coastal environments with stronger environmental gradients might correspond more to scenario A, while increasing spatial extent of a study might lead to results that are more indicative of scenario B. To complicate things even more, historical aspects on the location and organisms under study can interfere with both scenarios.

LIMITATIONS OF THE CURRENT STUDY

Like so many other studies dealing with faunal assemblages occurring in less accessible habitats such as the deep sea or remote Southern Ocean, the present thesis work has generated far more questions than conclusive answers. Inevitably, there are some drawbacks that need to be considered when trying to extrapolate the conclusions of the different chapters to other

nematode communities or marine ecosystems worldwide. However, this also provides us with important lessons for future research, and helps formulating suggestions to improve our knowledge (the subject of the next section). In this section, I want to elaborate on some of the difficulties that were encountered during this thesis, to serve as a guideline for the future.

A first important remark is related to the sampling itself. It is not always logistically possible to obtain a set of highly representative, well-replicated seafloor samples, and this obviously leads to problems during further statistical analyses. Especially for some of methods in **Chapter 4** (most notably the PCNM analysis), high spatial interdependence and nestedness of samples (e.g., samples within cores, within MUC deployments, within locations) can yield unreliable outcomes in case the number of samples is limited. More regular sampling designs yield better results in PCNM analyses as this technique was originally developed for such high-resolution sampling schemes (see earlier; Borcard & Legendre, 2002). Next, there is the question of scale, both at the level of the organism considered and that of the sampling locations. Nematodes are relatively small in size (set aside bacterial and viral communities), and therefore possibly influenced by small-scale variation in their surroundings (see also Gallucci et al., 2009; Vanreusel et al., 2010b). It is therefore not easy to determine the appropriate scale at which (meta-) community dynamics should be studied. When extending the spatial scale to a very large region compared to the individual habitat patches of the nematodes, the probability of unveiling processes operating at historical timescales becomes larger, potentially masking the role of local metacommunity dynamics (see Logue et al., 2011). While we did our best to sample at different spatial scales and to adopt a hierarchical sampling design, future assessments of nematode distribution at the mesoscale would benefit from a more comprehensive sampling, with a higher resolution at intermediate spatial scales. Here the step from within-location variation (maximum 1.5 km) to the next level of spatial information (between locations at the same side of the Antarctic Peninsula for example) was rather large. This might also help to establish a more precise transition point at which communities become mainly governed by local or regional processes (cf. shift between scenario A and B in Fig. 6.5).

Second, although variation partitioning provides a useful tool for the assessment of environmental and spatial determinants of community variation, it is not without limitations. For example, only the unique environmental fraction [E|S] can be realistically estimated under current models. This is due to the spatial autocorrelation that was mentioned in the previous sections and chapters (Peres-Neto & Legendre, 2010), and for which there currently exists no

solution. Next to spatial autocorrelation in community data and environmental variables, also temporal autocorrelation exists. The fact that we only rely on snapshot measurements of environmental variables and assessment of communities naturally entails some risks. Seasonal dynamics might be important as well in the interpretation of certain distribution patterns (see footnote in **Chapter 2**). Ideally, such a temporal aspect should be taken into account while setting up the sampling design.

In terms of environmental variables that were assessed during the different sampling campaigns, it is important to notice that we certainly did not measure all relevant ones. Previous studies on marine nematodes have repeatedly demonstrated the link between variables such as sediment grain size, pigments and organic matter content (Heip et al., 1985; Lins et al., 2014; Moens et al., 2013; Vanhove et al., 1998), yet other variables can play a role. The fact that these were not measured may limit the reliability of some of the conclusions in **Chapter 4**. Another type of information that is lacking in most of the chapters of this thesis, but which is probably very important in structuring nematode distribution patterns, is information on biotic interactions. Together with unmeasured environmental variables, these might shift the outcome of variation partitioning analyses to a larger fraction of variation explained by local niche effects.

In a similar way that it is sometimes hard to get many samples while being at sea, it can also be difficult to obtain satisfactory results while performing lab analyses. This manifested itself mainly during the molecular analyses of **Chapter 5**. To come to the results presented here, quite a high number of PCR protocols were tested and refined, and most of those did not provide good results (or not for all species/genera). Related to the molecular work included in this thesis, there is also a lack of reference material. When searching public databases such as GenBank for marine free-living nematodes, one will rapidly notice that for some genetic markers, the information is scant. Or that some genera are underrepresented in terms of genetic sequence information. For example, for the *Desmodora* specimens in **Chapter 5**, hardly any sequences were found which increases the risk of finding a match that has low similarity or coverage percentages. And even when there is reference material available, it might not be identified correctly to start with, making comparison all the more difficult.

This brings us to the next issue when working with nematodes: their challenging taxonomy. Mainly due to their small size, identification to species level is difficult, as evidenced by several descriptions and re-descriptions of genera and species. Presence of cryptic species

forms another challenge for modern taxonomy (Decraemer & Backeljau, 2015). The occurrence of cryptic species diversity in *Sabatieria* suggests that morphological species delineations as applied in **Chapter 4** may not suffice for decisive answers concerning biogeographic patterns in nematode species distribution.

Finally, as already mentioned several times throughout this thesis, studying nematode distribution patterns in different sediment depth layers may be biased. Since nematodes are able to move through the sediments, sediment layers are therefore not independent. Ideally, some of the analyses contained in this thesis should be repeated with the 0 – 5 cm combined. Alternatively, a clearer divide between surface and subsurface (e.g., 0 – 1 cm vs 4 – 5 cm) might also be interesting to explore.

WHAT ELSE IS THERE TO LEARN ON SOUTHERN OCEAN NEMATODES – AND WHY SHOULD WE CARE?

The results of this thesis provide new insights and thoughts on the distribution patterns within a taxon that is widely distributed yet often ignored, in an isolated yet rapidly changing environment. Most ecological studies involving nematodes follow more traditional approaches of ascribing variation in community composition to environmental gradients via the process of species sorting, but our results have shown that spatial processes should be taken into consideration as well. Apart from this general conclusion, there remains a considerable amount of doubt and questions related to nematode distribution in the Southern Ocean. Some of these stem from inherent limitations of the present study and its sampling design, while others were stumbled upon at the time of analysing datasets and interpreting results. The work performed during this thesis is far from exhaustive and there is room for improvement.

Logue and co-authors (2011) reviewed both observational and empirical approaches to metacommunity study and formulated suggestions for further research. They highlighted the need for information on not only spatial and environmental distance, but also aspects that differ among species and their actual dispersal rates. Indeed, several studies have indicated that differences in species-specific traits and dispersal capacities are very important in the outcome of metacommunity dynamics (e.g., Leibold et al., 2010; Pandit et al., 2009; Székely & Langenheder, 2013). Also for nematodes, Derycke and co-authors (2013) stressed the need for a better understanding of the role of life history and dispersal capacity in population genetics (e.g., are endobenthic nematode species more dispersal-limited than those rafting on

macroalgae?). While we partly differentiated between communities that are more prone to passive transportation (surface layers) versus those that have lower probability for dispersal (subsurface), this is a rather arbitrary division and nematodes are able to move between sediment layers. Further study would benefit greatly from extending this knowledge on connectivity between populations and dispersal rates to other genera and species. Population genetic analyses might help, but more variable markers would provide additional details in this respect (e.g., microsatellites – although their amplification has been proven difficult in marine nematodes; Derycke et al., 2013). Experiments might be of use in this case (cf. De Meester et al., 2012), but in their own suffer from manipulative bias compared to in-situ studies.

In terms of genetic analyses, we adopted a multi-locus approach for two endobenthic genera that share the same habitat but with different ecological preferences. The need for such analyses has been pointed out by Derycke et al. (2013), together with the call for an inclusion of information at wide spatial scales. Earlier studies of shallow- and deep-sea nematodes have shown that genetic structuring very much depends on spatial scale, dispersal capacities (e.g., rafting on macro-algae versus passive) and lifestyle (e.g., endobenthic versus epiphytic) (Derycke et al., 2013). Detailed assessment of the phylogeography of true endobenthic nematode species was largely lacking, so this thesis provides some insights on the matter. Nevertheless, it would be advisable to extend this approach to other genera as well, and assess whether similar patterns occur throughout different nematode taxa.

We have shown that nematodes are capable of rapidly changing their relative abundance and numbers in response to a temporal change in their environment (**Chapter 2**). Such temporal dynamics are important to assess into more detail as they can give us an idea on the resilience of small, dispersal-limited organisms. Especially in light of current climate-induced changes, such insights on colonisation ability and rate may prove useful.

In terms of colonisation dynamics, the question remains that – assuming nematodes are dispersal-limited, as was partly evidenced by this study – it is difficult to understand where species come from exactly, and to what extent stochastic events are important. We are often so focused on resolving deterministic interactions between species and their environment, that we ignore the impact of drift. Experiments where identical (as far as that is possible) nematode communities are subjected to and cultivated under different replicated treatments (e.g., different food conditions, temperature or oxygen regimes) could shed light on the

impact of selection versus drift. In case communities from different treatments but from replicates within the same treatment consistently include the same genera and in comparable relative abundances, environment selects for the same taxa. If not, and different genera become abundant in different replicates (i.e. more random patterns), this would provide evidence for drift. Alternatively, as was done for bacterial communities in Langenheder et al. (2006), the experiment could be repeated with nematode communities collected from different environments and placed under identical environmental conditions. If communities remain different after cultivation (i.e. not significantly different from their original source control; cf. results Langenheder et al., 2006), this would indicate that historical effects and regional species pool dynamics are more important in community assembly than environmental selection.

A combination of ecological and molecular techniques and an integration of approaches at different spatial scales remains the way forward in species distribution studies. Not only for nematodes, but also for other taxa in the Southern Ocean (e.g., Allcock & Strugnell, 2012; Hémery et al., 2013; Riesgo et al., 2015), detailed assessment of genetic links between species and populations raises awareness on how they were distributed across the Antarctic throughout evolutionary history. For nematodes, this information should be extended by including other areas (also across the Polar Front; cf. endemism question) and depth ranges (eurybathy question). From what was observed in this study concerning differences in patterns at the sediment surface versus deeper down, it is probably advisable to include such information for other small endobenthic organisms as well. In case of nematodes, inclusion of detailed results for different genera and species might further unravel the distinct assembly processes in sediment depth layers and strengthen the conclusion that communities at the surface are more homogenised. Also in other systems, with different current dynamics and environmental conditions, such analyses would be useful.

Metacommunity phylogenetics might also provide a useful approach to combine population genetic and community ecological insights (Leibold et al., 2010; Peres-Neto et al., 2012). Unfortunately, the limited amount of sequence data, combined with the fact that they were pooled per location for the five locations contained in **Chapter 5** prevented us from adopting such an approach in the current thesis.

Finally, although molecular advances continue to yield interesting new viewpoints on animal distribution patterns (also for nematodes), the field of traditional taxonomy should not be

neglected. As the amount of reference material for marine nematodes is still rather scant, and cryptic species can show very subtle variations in morphological parameters, the tedious work related to α-taxonomy (Decraemer & Backeljau, 2015) is essential to fill some of the gaps. Basically, both approaches should be viewed as complementary in answering the question *"What drives marine nematode distribution?"*

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APPENDICES

APPENDIX 1: TAXONOMIC GENUS LIST

PHYLUM NEMATODA Potts, 1932
Class ENOPLEA Inglis, 1983
Subclass ENOPLIA Pearse, 1942
Order Enoplida Filipjev, 1929
Suborder Enoplina Chitwood & Chitwood, 1937
Family Thoracostomopsidae Filipjev, 1927
Enoploides Ssaweljev, 1912
Mesacanthion Filipjev, 1927
Paramesacanthion Wieser, 1953
Thoracostomopsis Ditlevsen, 1918
Trileptium Cobb, 1933
Family Anoplostomatidae Gerlach & Riemann, 1974
Anoplostoma Bütschli, 1874
Family Phanodermatidae Filipjev, 1927
Crenopharynx Filipjev, 1934
Micoletzkyia Ditlevsen, 1926
Phanoderma Bastian, 1865
Phanodermopsis Ditlevsen, 1926
Family Anticomidae Filipjev, 1918
Anticoma Bastian, 1865
Odontanticoma Platonova, 1976
Paranticoma Micoletzky, 1930

Suborder Oncholaimina De Ley & Blaxter, 2002
Family Oncholaimidae Filipjev, 1916
Metoncholaimus Filipjev, 1918
Viscosia de Man, 1890
Family Enchelidiidae Filipjev, 1918
Bathyeurystomina Lambshead & Platt, 1979
Ledovitia Filipjev, 1927

Suborder Ironina Siddiqi, 1983
Family Ironidae de Man, 1876
Syringolaimus de Man, 1888
Thalassironus de Man, 1889
Family Leptosomatidae Filipjev, 1916
Platycomopsis Ditlevsen, 1926
Pseudocella Filipjev, 1927
Synonchus Cobb, 1894
Thoracostoma Marion, 1870

Family Oxystominidae Chitwood, 1935
Cricohalalaimus Bussau, 1993
Halalaimus de Man, 1888
Oxystomina Filipjev, 1921
Thalassoalaimus de Man, 1893
Wieseria Gerlach, 1956

Order Triplonchida Cobb, 1919
Suborder Tobrilina Tsalolikhin, 1976
Family Rhabdodemaniidae Filipjev, 1934
Rhabdodemania Baylis & Daubney, 1926
Family Pandolaimidae Belogurov, 1980
Pandolaimus Allgén, 1929

Class CHROMADOREA
Subclass CHROMADORIA
Order Chromadorida Chitwood, 1933
Suborder Chromadorina Filipjev, 1929
Family Chromadoridae Filipjev, 1917
Acantholaimus Allgén, 1933
Actinonema Cobb, 1920
Chromadora Bastian, 1865
Chromadorella Filipjev, 1918
Chromadorita Filipjev, 1922
Dichromadora Kreis, 1929
Endeolophos Boucher, 1976
Euchromadora de Man, 1886
Innocuonema Inglis, 1969
Karkinochromadora Blome, 1982
Neochromadora Micoletzky, 1924
Parachromadorita Blome, 1974
Prochromadorella Micoletzky, 1924
Rhips Cobb, 1920
Spilophorella Filipjev, 1917
Steineridora Inglis, 1969
Trochamus Boucher & de Bovée, 1971
Family Neotonchidae Wieser & Hopper, 1966
Comesa Gerlach, 1956
Dystomanema Bezerra, 2013
Filitonchus Platt, 1982
Gomphionchus Platt, 1982
Nannolaimus Cobb, 1933
Neotonchus Cobb, 1933

Family Cyatholaimidae Filipjev, 1918
Cyatholaimus Bastian, 1865
Longicyatholaimus Micoletzky, 1924
Marylynnia Hopper, 1977
Metacyatholaimus Stekhoven, 1942
Minolaimus Vitiello, 1970
Paracanthonchus Micoletzky, 1924
Paracyatholaimoides Gerlach, 1953
Paracyatholaimus Micoletzky, 1922
Paralongicyatholaimus Stekhoven, 1950
Pomponema Cobb, 1917
Family Selachnematidae Cobb, 1915
Choanolaimus de Man, 1880
Gammanema Cobb, 1920
Halichoanolaimus de Man, 1886
Synonchiella Cobb, 1933

Order Desmodorida De Coninck, 1965
Suborder Desmodorina De Coninck, 1965
Family Desmodoridae Filipjev, 1922
Desmodora de Man, 1889
Desmodorella Cobb, 1933
Metachromadora Filipjev, 1918
Molgolaimus Ditlevsen, 1921
Perspiria Wieser & Hopper, 1967
Pseudochromadora Daday 1899
Family Epsilonematidae Steiner, 1927
Epsilonema Steiner, 1927
Metepsilonema Steiner, 1927
Family Draconematidae Filipjev, 1918
Draconema Cobb, 1913
Paradraconema Allen & Noffsinger, 1978
Prochaetosoma Micoletzky, 1922
Family Microlaimidae Micoletzky, 1922
Bolbolaimus Cobb, 1920
Calomicrolaimus Lorenzen, 1976
Microlaimus de Man, 1880
Spirobolbolaimus Soetaert & Vincx, 1988
Family Monoposthiidae Filipjev, 1934
Monoposthia de Man, 1889
Nudora Cobb, 1920

Order Desmoscolecida Filipjev, 1929
- Family Desmoscolecidae Shipley, 1896
  - *Desmoscolex* Claparède, 1863
  - *Desmolorenzenia* Decraemer, 1984
  - *Greeffiella* Cobb, 1922
  - *Prototricoma* Timm, 1970
  - *Tricoma* Cobb, 1894

Order Monhysterida Filipjev, 1929

Suborder Monhysterina De Coninck & Schuurmans Stekhoven, 1933
- Family Monhysteridae de Man, 1876
  - *Diplolaimella* Allgén, 1929
  - *Diplolaimelloides* Meyl, 1954
  - *Halomonhystera* Andrássy, 2006
  - *Monhystrella* Cobb, 1918
  - *Thalassomonhystera* Jacobs, 1987
- Family Sphaerolaimidae Filipjev, 1918
  - *Doliolaimus* Lorenzen, 1966
  - *Metasphaerolaimus* Gourbault & Boucher, 1982
  - *Sphaerolaimus* Bastian, 1865
  - *Subsphaerolaimus* Lorenzen, 1978
- Family Xyalidae Chitwood, 1951
  - *Amphimonhystera* Allgén, 1929
  - *Amphimonhystrella* Timm, 1961
  - *Cobbia* de Man, 1907
  - *Daptonema* Cobb, 1920
  - *Echonema* Bussau, 1993
  - *Elzalia* Gerlach, 1957
  - *Gnomoxyala* Lorenzen, 1977
  - *Linhystera* Juario, 1974
  - *Marisalbinema* Tchesunov, 1990
  - *Metadesmolaimus* Schuurmans Stekhoven, 1935
  - *Paramonhystera* Steiner, 1916
  - *Parelzalia* Tchesunov, 1990
  - *Promonhystera* Wieser, 1956
  - *Rhynchonema* Cobb, 1920
  - *Theristus* Bastian, 1865

Suborder Linhomoeina Andrássy, 1974
- Family Siphonolaimidae Filipjev, 1918
  - *Siphonolaimus* de Man, 1893
- Family Linhomoeidae Filipjev, 1922
  - *Desmolaimus* de Man, 1880
  - *Eleutherolaimus* Filipjev, 1922

Linhomoeus Bastian, 1865
Megadesmolaimus Wieser, 1954
Metalinhomoeus de Man, 1907
Monhysteroides Timm, 1961
Paralinhomoeus de Man, 1907
Sarsonia Gerlach, 1967
Terschellingia de Man, 1888

Order Araeolaimida De Coninck & Schuurmans Stekhoven, 1933
Family Axonolaimidae Filipjev, 1918
Ascolaimus Ditlevsen, 1919
Axonolaimus de Man, 1889
Odontophora Bütschli, 1874
Parodontophora Timm, 1963
Family Comesomatidae Filipjev, 1918
Actarjania Hopper, 1967
Cervonema Wieser, 1954
Comesoma Bastian, 1865
Dorylaimopsis Ditlevsen, 1918
Laimella Cobb, 1920
Paracomesoma Hope & Murphy, 1972
Pierrickia Vitiello, 1970
Sabatieria Rouville, 1903
Setosabatieria Platt, 1985
Vasostoma Wieser, 1954
Family Diplopeltidae Filipjev, 1918
Araeolaimus de Man, 1888
Campylaimus Cobb, 1920
Cylindrolaimus de Man, 1880
Diplopeltula Gerlach, 1950
Intasia Tchesunov & Miljutina, 2008
Pararaeolaimus Timm, 1961
Southerniella Allgén, 1932

Order Plectida Malakhov, 1982
Family Leptolaimidae Örley, 1880
Antomicron Cobb, 1920
Leptolaimoides Vitiello, 1971
Leptolaimus de Man, 1876
Family Camacolaimidae Micoletzky, 1924
Alaimella Cobb, 1920
Camacolaimus de Man, 1889
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APPENDIX 2: GENUS – STATION INCIDENCE SURFACE LAYERS (0 – 3 CM)

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Acantholaimus	X	X	X	X	X	X	X	X	X	X	X
Actarjania	–	–	–	–	–	–	–	X	–	–	–
Actinonema	X	–	X	X	X	X	X	X	X	X	X
Aegialoalaimus	X	X	X	X	X	X	X	X	X	X	X
Alaimella	–	–	X	–	–	X	–	–	X	–	–
Amphimonhystera	–	–	X	–	–	–	X	X	–	X	X
Amphimonhystrella	X	X	X	X	X	X	X	X	X	X	X
Anoplostoma	–	–	–	X	–	–	–	X	–	X	–
Anticoma	–	X	–	X	–	X	X	X	X	X	X
Antomicron	–	–	–	–	–	X	–	X	X	–	X
Araeolaimus	X	X	–	–	–	–	X	X	–	X	X
Ascolaimus	–	–	–	–	–	–	X	–	–	–	–
Axonolaimus	–	X	X	X	–	X	X	X	X	–	–
Bathyeurystomina	–	–	–	–	–	–	X	–	–	–	X
Bolbolaimus	–	–	–	–	–	–	–	–	–	–	–
Calomicrolaimus	–	–	–	–	X	–	X	X	X	X	X
Camacolaimus	X	X	X	X	X	X	–	X	X	X	X
Campylaimus	–	X	X	X	X	X	X	X	X	X	X
Ceramonema	–	–	–	–	–	–	X	X	X	–	–
Cervonema	X	X	–	X	X	X	X	X	X	X	X
cf. Amphimonhystera	X	–	–	–	–	–	–	–	–	–	–
cf. Amphimonhystrella	–	X	–	–	–	–	–	–	–	–	–
cf. Daptonema	–	–	–	–	–	–	–	–	–	–	X
cf. Echonema	–	–	–	–	–	–	–	–	–	–	X
cf. Intasia	–	–	–	–	–	–	–	X	–	–	–
cf. Oxystomina	–	X	–	–	–	–	–	–	–	–	–
cf. Pandolaimus	–	–	–	–	–	–	–	X	–	–	–
cf. Paracanthonchus	–	–	–	–	–	–	–	–	–	–	–
cf. Phanodermopsis	–	X	–	–	–	–	–	–	–	–	–
cf. Siphonolaimus	–	–	–	–	–	–	–	–	–	–	X
cf. Terschellingia	–	–	–	–	–	–	–	–	–	–	X
cf. Wieseria	–	–	–	–	–	–	–	–	–	–	–
Choanolaimus	–	X	–	–	–	–	–	–	–	–	–
Chromadora	–	–	–	X	–	–	X	–	–	–	–
Chromadorella	–	–	–	–	–	–	X	–	X	–	X
Chromadoridae indet.	–	X	–	–	X	–	X	X	–	–	X
Chromadorita	–	X	X	X	X	X	X	X	X	X	X
Cobbia	–	–	–	–	–	X	–	–	–	–	–
Comesa	–	–	X	X	X	X	X	X	X	X	–
Comesoma	–	X	–	–	X	X	–	–	–	–	–
Comesomatidae indet.	–	–	–	–	X	–	–	–	–	–	–
Crenopharynx	–	–	–	–	–	–	–	–	–	–	–

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Cricohalalaimus	–	–	–	–	–	–	X	–	–	X	X
Cyartonema	–	–	X	–	–	X	X	–	–	X	–
Cyatholaimidae indet.	–	–	–	X	–	–	–	X	–	X	–
Cyatholaimus	–	–	–	–	–	–	X	–	X	–	X
Cylindrolaimus	–	–	–	–	X	–	–	–	–	–	–
Daptonema	X	X	X	X	X	X	X	X	X	X	X
Desmodora	–	X	X	X	X	X	X	X	X	X	X
Desmodorella	X	X	–	–	–	–	X	X	X	X	X
Desmolaimus	–	–	X	X	–	–	–	–	–	–	–
Desmolorenzenia	–	–	–	–	–	X	–	–	–	–	–
Desmoscolecidae indet.	–	–	–	–	–	–	–	–	–	X	X
Desmoscolex	X	X	X	X	X	–	X	X	X	X	X
Dichromadora	–	X	X	X	X	X	X	X	X	X	X
Diplolaimella	–	–	–	–	–	–	X	–	–	–	–
Diplolaimelloides	–	–	X	–	–	–	–	–	–	–	–
Diplopeltoides	–	–	X	–	X	X	–	–	–	X	–
Diplopeltula	X	–	–	–	–	–	X	X	X	X	X
Doliolaimus	–	–	–	–	–	X	–	–	–	–	–
Dorylaimopsis	–	–	–	–	X	X	X	X	X	–	–
Draconema	–	–	–	–	X	–	X	–	X	–	X
Dystomanema	–	–	–	–	X	–	–	–	–	–	–
Eleutherolaimus	X	–	X	–	–	–	–	–	–	–	–
Elzalia	–	–	X	X	X	X	X	X	X	–	X
Endeolophos	–	–	X	–	–	–	X	X	X	X	X
Enoploides	–	–	–	X	–	–	–	–	–	–	–
Epsilonema	–	–	–	–	–	–	–	–	–	X	–
Euchromadora	–	–	–	–	X	–	X	X	–	–	–
Filitonchus	–	–	–	–	X	X	X	X	X	–	–
Gammanema	–	–	–	–	–	X	–	–	–	–	–
Gnomoxyala	–	–	–	–	–	–	X	–	–	–	–
Gomphionchus	–	–	–	–	–	–	–	–	–	–	–
Greeffiella	–	X	–	–	–	–	X	X	–	X	X
Halalaimus	X	X	X	X	X	X	X	X	X	X	X
Halichoanolaimus	–	X	X	X	X	X	–	X	X	X	X
Haliplectus	–	X	–	–	–	–	–	–	–	X	–
Halomonhystera	X	X	–	–	X	X	X	X	X	X	X
Innocuonema	–	–	–	–	–	–	X	–	X	–	–
Karkinochromadora	–	–	–	–	–	–	–	–	–	–	–
Laimella	–	–	X	X	X	X	X	X	–	–	X
Ledovitia	X	X	X	X	X	X	X	–	X	X	X
Leptolaimidae indet.	–	–	–	–	–	–	–	–	–	–	–
Leptolaimoides	–	X	–	X	X	X	X	–	X	X	X
Leptolaimus	X	X	X	X	X	X	X	X	X	X	X
Linhomoeidae indet.	–	–	–	–	–	X	–	–	–	–	–

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Linhomoeus	–	–	X	X	X	X	X	–	X	–	X
Linhystera	–	X	–	–	–	–	X	–	–	–	–
Longicyatholaimus	–	–	–	X	–	–	X	–	X	X	X
Marisalbinema	–	X	–	–	X	X	–	X	X	X	X
Marylynnia	–	X	X	–	X	–	X	X	X	X	X
Megadesmolaimus	–	–	–	–	–	–	–	–	X	X	–
Mesacanthion	–	–	–	–	–	–	–	–	X	–	–
Metachromadora	–	–	–	–	–	–	–	–	–	X	–
Metacyatholaimus	–	–	–	X	–	–	X	–	–	–	–
Metadasynemella	–	–	–	–	–	–	X	X	–	X	–
Metadesmolaimus	–	–	–	–	–	–	X	X	X	–	–
Metalinhomoeus	–	–	X	X	–	–	–	X	X	–	X
Metasphaerolaimus	–	–	–	–	X	X	X	X	X	–	–
Metepsilonema	–	–	–	–	–	–	–	–	–	X	–
Metoncholaimus	–	–	–	–	–	X	–	–	–	–	–
Micoletzkyia	–	–	–	–	X	–	X	–	X	–	–
Microlaimus	X	X	X	X	X	X	X	X	X	X	X
Minolaimus	–	–	–	–	X	–	–	–	–	–	–
Molgolaimus	–	–	–	–	X	X	X	X	X	X	X
Monhysteridae indet.	–	–	X	–	–	–	X	–	–	X	–
Monhysteroides	–	–	–	–	–	–	X	–	–	–	–
Monhystrella	X	X	–	–	X	X	X	X	X	X	X
Monoposthia	–	X	–	–	–	–	–	–	–	–	–
Nannolaimus	–	X	–	–	–	–	–	–	–	–	–
Neochromadora	–	X	–	–	–	–	X	–	–	X	–
Neotonchus	–	–	–	–	–	X	–	–	–	–	–
Nudora	–	–	X	–	–	–	–	–	–	–	X
Odontanticoma	–	X	–	X	X	X	X	X	X	–	X
Odontophora	–	–	X	X	X	X	–	–	–	–	–
Oxystomina	X	X	X	X	X	X	X	X	X	X	X
Pandolaimus	–	–	–	X	–	–	–	–	–	–	–
Paracanthonchus	–	X	X	X	X	X	X	X	X	X	X
Parachromadorita	–	X	–	–	–	–	X	–	–	X	X
Paracomesoma	–	–	–	–	–	–	–	–	–	–	–
Paracyatholaimoides	–	–	–	–	X	–	–	–	–	X	–
Paracyatholaimus	–	X	X	X	–	X	X	X	–	X	X
Paradraconema	–	–	–	–	–	–	–	–	–	X	X
Paraelzalia	–	–	–	–	–	–	–	–	–	–	–
Paralinhomoeus	–	–	–	–	–	–	–	–	–	–	X
Paralongicyatholaimus	–	X	–	–	–	X	X	X	X	X	X
Paramesacanthion	–	X	X	X	X	X	X	X	X	X	X
Paramicrolaimus	–	–	–	–	–	X	–	–	–	–	–
Paramonohystera	–	–	X	X	X	X	X	–	–	–	–
Paranticoma	–	X	–	–	–	–	X	X	–	X	X

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Pararaeolaimus	–	X	–	–	–	–	–	–	–	X	–
Paraterschellingia	–	–	–	–	–	–	–	–	–	–	X
Parodontophora	–	–	–	X	–	–	–	–	–	–	–
Perspiria	–	–	–	–	–	–	X	–	X	X	–
Phanoderma	–	–	–	–	–	–	X	–	–	–	X
Phanodermatidae indet.	–	–	–	–	X	–	–	–	–	–	–
Phanodermopsis	X	–	–	X	X	X	X	–	–	–	–
Pierrickia	–	–	X	X	X	X	X	X	X	–	X
Platycomopsis	–	–	–	–	–	X	–	–	–	–	–
Pomponema	–	X	–	–	X	X	X	X	X	X	X
Procamacolaimus	–	–	–	–	–	–	–	–	–	–	X
Prochaetosoma	–	–	–	–	–	–	X	–	–	X	–
Prochromadorella	–	–	–	–	–	–	X	–	–	–	–
Promonhystera	–	–	–	X	–	–	X	–	–	–	X
Prototricoma	X	X	–	X	–	–	X	X	X	X	X
Pselionema	X	–	X	X	X	–	X	X	X	X	X
Pseudocella	–	–	–	–	–	–	–	–	–	X	–
Pseudochromadora	–	–	–	X	–	X	–	–	–	–	–
Rhabdocoma	–	–	–	–	–	–	–	X	–	X	X
Rhabdodemania	–	–	–	–	–	–	–	–	–	X	X
Rhips	–	–	–	–	–	–	X	–	–	–	–
Rhynchonema	–	–	–	–	–	–	X	–	X	–	X
Sabatieria	–	X	X	X	X	X	X	X	X	X	X
Sarsonia	–	–	–	X	–	–	–	–	–	–	–
Setosabatieria	–	–	–	–	–	–	–	–	X	–	–
Southerniella	–	X	–	–	X	X	X	X	X	X	X
Sphaerolaimus	–	X	X	X	X	X	X	X	X	X	–
Spilophorella	–	X	X	X	X	X	X	X	X	X	X
Spirobolbolaimus	–	–	–	–	–	–	–	X	–	–	–
Steineridora	–	–	–	–	–	X	–	–	–	–	–
Stephanolaimus	–	–	–	–	–	–	–	–	X	X	–
Subsphaerolaimus	–	–	–	–	–	–	–	–	X	–	–
Synonchiella	–	–	–	–	–	–	X	–	–	–	–
Synonchus	–	–	–	–	–	–	–	–	–	–	–
Syringolaimus	–	X	–	–	–	–	–	–	–	X	X
Terschellingia	–	–	X	X	–	X	X	X	X	–	X
Thalassironus	–	–	–	–	–	–	X	X	–	–	–
Thalassoalaimus	–	X	–	–	X	X	X	X	X	X	X
Thalassomonhystera	X	X	X	X	X	X	X	X	X	X	X
Theristus	–	–	X	–	–	X	X	X	X	X	X
Thoracostoma	–	–	X	–	–	–	–	–	–	–	–
Thoracostomopsidae indet.	–	–	–	–	–	–	X	–	–	–	–
Thoracostomopsis	–	–	–	–	–	X	–	–	–	–	–
Tricoma	–	X	–	–	X	X	X	X	X	X	X

	LW	**LS**	**W-120**	**W-163**	**DP-243**	**DP-250**	**SG**	**SO**	**KG**	**AUS**	**BX**
Trileptium	–	–	–	–	–	–	X	–	X	–	–
Trochamus	–	–	–	–	–	–	–	–	–	X	–
Vasostoma	–	–	–	–	–	–	X	–	X	–	–
Viscosia	–	X	X	X	X	–	–	–	X	X	X
Wieseria	–	X	–	X	–	X	X	–	–	X	X
Xyalidae indet.	–	X	X	–	X	X	X	X	X	X	X
Total genera	24	59	50	55	62	69	96	72	75	79	82

APPENDIX 3: GENUS – STATION INCIDENCE SUBSURFACE LAYERS (3 – 5 CM)

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Acantholaimus	X	X	X	X	–	–	X	X	X	X	X
Actarjania	–	–	–	X	–	–	–	–	–	–	–
Actinonema	–	–	–	–	X	–	X	–	X	–	X
Aegialoalaimus	X	X	X	X	–	X	X	X	X	X	X
Alaimella	–	–	–	–	–	–	–	–	–	–	–
Amphimonhystera	–	–	–	–	–	–	X	X	X	–	–
Amphimonhystrella	–	X	X	X	–	–	X	X	X	X	X
Anoplostoma	–	–	–	–	–	–	X	–	–	X	–
Anticoma	–	X	–	–	–	X	–	–	–	–	–
Antomicron	–	–	–	–	–	–	–	X	X	–	–
Araeolaimus	–	X	–	–	–	–	–	–	–	X	–
Ascolaimus	–	–	–	–	–	–	–	–	X	–	–
Axonolaimus	–	–	–	X	–	–	–	X	–	–	–
Bathyeurystomina	–	–	–	–	–	–	–	–	–	–	–
Bolbolaimus	–	–	–	–	–	X	–	–	–	–	–
Calomicrolaimus	–	–	–	–	–	–	–	–	–	–	–
Camacolaimus	–	X	X	–	–	–	–	–	–	X	X
Campylaimus	–	–	X	X	X	–	–	X	–	–	–
Ceramonema	–	–	–	–	–	–	–	–	–	–	–
Cervonema	–	X	X	–	–	X	–	X	X	–	X
cf. Amphimonhystera	X	–	–	–	–	–	–	–	–	–	–
cf. Amphimonhystrella	–	–	–	–	–	–	–	–	–	–	–
cf. Daptonema	–	–	–	–	–	–	–	–	–	–	X
cf. Echonema	–	–	–	–	–	–	–	–	–	–	–
cf. Intasia	–	–	–	–	–	–	–	–	–	–	–
cf. Oxystomina	–	–	–	–	–	–	–	–	–	–	–
cf. Pandolaimus	–	–	–	–	–	–	–	–	–	–	–
cf. Paracanthonchus	–	–	–	–	–	–	–	X	–	–	–
cf. Phanodermopsis	–	–	–	–	–	–	–	–	–	–	–
cf. Siphonolaimus	–	–	–	–	–	–	–	–	–	–	–
cf. Terschellingia	–	–	–	–	–	–	–	–	–	–	–
cf. Wieseria	–	X	–	–	–	–	–	–	–	–	–
Choanolaimus	–	X	–	–	–	–	–	–	–	–	–
Chromadora	–	–	–	–	–	–	–	–	–	–	–
Chromadorella	–	–	–	–	–	–	–	–	X	–	–
Chromadoridae indet.	–	–	–	–	–	–	–	X	–	–	–
Chromadorita	X	X	X	X	–	X	X	X	X	–	X
Cobbia	–	–	–	–	–	–	–	–	–	–	–
Comesa	–	–	X	X	X	X	X	X	X	–	–
Comesoma	–	–	X	–	–	X	–	–	–	–	–
Comesomatidae indet.	–	–	–	–	–	–	–	–	–	–	–
Crenopharynx	–	–	–	–	–	X	–	–	–	–	–

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Cricohalalaimus	–	–	–	–	–	–	–	–	–	–	–
Cyartonema	–	–	–	–	–	–	X	–	–	–	–
Cyatholaimidae indet.	–	–	–	–	–	–	–	–	–	–	–
Cyatholaimus	–	–	–	–	–	–	–	–	–	–	–
Cylindrolaimus	–	–	–	–	–	–	–	–	–	–	–
Daptonema	X	X	X	X	X	X	X	X	X	X	X
Desmodora	–	X	–	X	X	X	X	X	X	–	X
Desmodorella	–	–	–	–	–	–	X	X	–	–	–
Desmolaimus	–	–	X	–	–	X	–	–	–	–	–
Desmolorenzenia	–	–	–	–	–	–	–	–	–	–	–
Desmoscolecidae indet.	–	–	–	–	–	–	–	–	–	–	–
Desmoscolex	X	X	X	–	–	–	–	–	X	X	X
Dichromadora	–	X	X	X	X	X	X	X	X	–	–
Diplolaimella	–	–	–	–	–	–	–	–	–	–	–
Diplolaimelloides	–	–	X	–	–	–	–	–	–	–	–
Diplopeltoides	–	–	X	–	X	X	–	–	–	–	–
Diplopeltula	–	–	–	–	–	–	X	X	–	–	–
Doliolaimus	–	–	–	–	–	–	–	–	–	–	–
Dorylaimopsis	–	–	–	–	X	X	X	X	X	–	–
Draconema	–	–	–	–	–	–	–	–	–	–	X
Dystomanema	–	–	–	–	X	X	–	–	–	–	–
Eleutherolaimus	–	–	X	–	–	–	–	–	–	–	–
Elzalia	–	X	X	X	–	–	X	X	–	X	–
Endeolophos	–	–	–	–	–	–	–	–	–	X	–
Enoploides	–	–	–	–	–	–	–	–	–	–	–
Epsilonema	–	–	–	–	–	–	–	–	–	–	–
Euchromadora	–	–	–	–	–	–	X	–	–	–	–
Filitonchus	–	–	–	–	–	X	X	X	X	–	–
Gammanema	–	–	–	–	–	–	–	–	–	–	–
Gnomoxyala	–	–	–	–	–	–	–	X	–	–	–
Gomphionchus	–	–	–	–	–	–	X	–	–	–	–
Greeffiella	–	–	–	–	–	–	X	–	–	X	X
Halalaimus	–	X	X	X	X	X	X	X	X	X	X
Halichoanolaimus	–	X	–	–	–	–	X	–	X	X	X
Haliplectus	–	–	–	–	–	–	–	–	–	–	–
Halomonhystera	X	X	X	–	–	X	–	X	X	–	X
Innocuonema	–	–	–	–	–	–	–	–	–	–	–
Karkinochromadora	–	X	–	–	–	–	–	–	–	–	–
Laimella	–	–	X	X	X	X	X	X	–	–	–
Ledovitia	–	X	–	–	–	X	–	–	–	X	–
Leptolaimidae indet.	–	X	–	–	–	–	–	–	–	–	–
Leptolaimoides	–	–	–	–	–	–	–	–	X	X	–
Leptolaimus	X	X	–	X	X	X	–	X	X	X	X
Linhomoeidae indet.	–	–	–	–	–	–	X	–	–	–	–

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Linhomoeus	–	–	X	X	X	X	X	X	X	–	–
Linhystera	–	–	–	–	–	X	–	X	–	–	–
Longicyatholaimus	–	–	–	–	–	–	–	–	X	–	–
Marisalbinema	–	–	–	–	–	–	–	–	X	–	–
Marylynnia	–	–	X	X	X	–	X	–	X	X	–
Megadesmolaimus	–	–	–	–	–	–	–	–	–	–	–
Mesacanthion	–	–	–	–	–	–	–	–	–	–	–
Metachromadora	–	–	–	–	–	–	–	–	–	–	–
Metacyatholaimus	–	–	–	–	–	–	X	–	X	–	–
Metadasynemella	–	–	–	–	–	–	–	X	–	–	–
Metadesmolaimus	–	–	–	–	–	–	–	–	–	–	–
Metalinhomoeus	–	–	–	X	–	–	X	X	X	–	–
Metasphaerolaimus	–	–	–	–	–	X	X	X	X	–	–
Metepsilonema	–	–	–	–	–	–	–	–	–	–	–
Metoncholaimus	–	–	–	–	–	–	–	–	–	–	–
Micoletzkyia	–	–	–	–	–	–	–	–	–	–	–
Microlaimus	–	X	X	X	–	X	X	X	X	–	X
Minolaimus	–	–	–	–	–	–	–	–	–	–	–
Molgolaimus	–	–	–	X	–	X	X	X	X	X	X
Monhysteridae indet.	–	X	–	–	–	–	–	–	–	X	–
Monhysteroides	–	–	–	–	–	–	X	X	–	–	–
Monhystrella	X	X	X	–	X	X	X	X	X	X	X
Monoposthia	–	–	–	–	–	–	–	–	–	–	–
Nannolaimus	–	–	–	–	–	–	–	–	–	–	–
Neochromadora	–	X	–	–	–	–	–	–	–	–	–
Neotonchus	–	–	–	X	–	X	–	–	–	–	–
Nudora	–	–	–	–	–	–	–	–	–	–	X
Odontanticoma	–	X	–	–	–	–	X	X	X	–	–
Odontophora	–	–	–	X	–	–	–	–	–	–	–
Oxystomina	–	–	–	–	X	X	X	–	X	–	X
Pandolaimus	–	–	–	–	–	–	–	–	–	–	–
Paracanthonchus	–	–	X	–	–	–	X	X	–	–	X
Parachromadorita	–	–	–	–	–	–	–	–	–	–	X
Paracomesoma	–	–	–	–	–	–	–	–	X	–	–
Paracyatholaimoides	–	–	–	–	–	–	–	–	–	–	–
Paracyatholaimus	–	–	–	X	–	X	X	–	–	–	–
Paradraconema	–	–	–	–	–	–	–	–	–	–	–
Paraelzalia	–	–	–	–	–	–	–	–	–	–	X
Paralinhomoeus	–	–	–	–	–	–	–	–	–	–	–
Paralongicyatholaimus	–	–	–	–	–	–	–	X	X	–	X
Paramesacanthion	–	–	–	–	–	–	–	X	X	X	–
Paramicrolaimus	–	–	–	–	–	X	–	–	–	–	–
Paramonohystera	–	–	X	X	–	–	–	–	–	–	–
Paranticoma	–	–	–	–	–	–	X	–	–	–	–

	LW	LS	W-120	W-163	DP-243	DP-250	SG	SO	KG	AUS	BX
Pararaeolaimus	–	–	–	–	–	–	–	–	–	–	–
Paraterschellingia	–	–	–	–	–	–	–	–	–	–	–
Parodontophora	–	–	–	–	–	–	–	–	–	–	–
Perspiria	–	–	–	–	–	–	–	–	X	X	X
Phanoderma	–	–	–	–	–	–	–	–	–	–	–
Phanodermatidae indet.	–	–	–	–	–	–	–	–	–	–	–
Phanodermopsis	–	–	–	–	–	–	–	–	–	–	–
Pierrickia	–	–	X	X	X	X	X	X	X	–	X
Platycomopsis	–	–	–	–	–	–	–	–	–	–	–
Pomponema	–	–	–	–	–	–	–	X	–	–	–
Procamacolaimus	–	–	–	–	–	–	–	–	–	–	–
Prochaetosoma	–	–	–	–	–	–	–	–	–	–	–
Prochromadorella	–	–	–	–	–	–	–	–	–	–	–
Promonhystera	–	–	X	–	–	–	X	–	–	–	–
Prototricoma	–	X	–	–	–	–	X	–	X	X	X
Pselionema	–	X	–	X	–	–	–	X	–	–	–
Pseudocella	–	–	–	–	–	–	–	–	–	–	–
Pseudochromadora	–	–	–	–	–	–	–	–	–	–	–
Rhabdocoma	–	–	–	–	–	–	–	–	–	X	X
Rhabdodemania	–	–	–	–	–	–	–	–	–	–	–
Rhips	–	–	–	–	–	–	–	–	–	–	–
Rhynchonema	–	–	–	–	–	–	–	–	–	–	–
Sabatieria	–	X	X	X	X	X	X	X	X	X	X
Sarsonia	–	–	–	–	–	–	–	–	–	–	–
Setosabatieria	–	–	–	–	–	–	–	–	–	–	–
Southerniella	–	X	–	–	X	–	–	X	–	–	X
Sphaerolaimus	–	–	X	X	–	–	–	X	X	X	X
Spilophorella	–	–	X	X	X	X	X	X	X	X	X
Spirobolbolaimus	–	–	–	–	–	–	–	–	–	–	–
Steineridora	–	–	–	–	–	–	–	–	–	–	–
Stephanolaimus	–	–	–	–	–	–	–	–	–	–	–
Subsphaerolaimus	–	–	–	–	–	–	–	–	–	–	–
Synonchiella	–	–	–	–	–	–	–	–	–	–	–
Synonchus	–	X	–	–	–	–	–	–	–	–	–
Syringolaimus	–	X	–	–	–	–	–	–	–	X	–
Terschellingia	–	–	X	X	–	X	X	X	X	–	–
Thalassironus	–	–	–	–	–	–	–	–	–	–	–
Thalassoalaimus	–	X	–	–	X	X	–	–	X	–	X
Thalassomonhystera	X	X	–	–	X	X	X	X	X	X	X
Theristus	X	–	–	–	X	–	X	X	–	X	X
Thoracostoma	–	–	–	–	–	–	–	–	–	–	–
Thoracostomopsidae indet.	–	–	–	–	–	–	–	–	X	–	–
Thoracostomopsis	–	–	–	–	–	–	–	–	–	–	–
Tricoma	–	X	–	–	–	–	X	X	X	X	X

	LW	**LS**	**W-120**	**W-163**	**DP-243**	**DP-250**	**SG**	**SO**	**KG**	**AUS**	**BX**
Trileptium	–	–	–	–	–	–	–	–	–	–	–
Trochamus	–	–	–	–	–	–	–	–	–	–	–
Vasostoma	–	–	–	–	–	–	X	–	–	–	–
Viscosia	–	X	X	X	X	–	X	X	X	–	–
Wieseria	–	–	–	–	–	–	–	–	–	X	X
Xyalidae indet.	–	–	–	–	X	X	X	–	–	X	X
Total genera	11	37	33	31	25	38	50	50	49	33	40

APPENDIX 4: AVERAGE RELATIVE GENUS ABUNDANCE – SURFACE LAYERS (0 – 3 CM)

LW		LS		W-120		W-163		DP-243		DP-250	
Halomonhystera	92.39	*Microlaimus*	42.21	*Daptonema*	26.83	*Microlaimus*	17.68	*Sabatieria*	16.76	*Sabatieria*	24.76
Thalassomonhystera	3.58	*Halomonhystera*	9.16	*Linhomoeus*	12.68	*Chromadorita*	11.19	*Leptolaimus*	14.28	*Dorylaimopsis*	13.36
Rest (22)	4.03	*Monhystrella*	8.84	*Halalaimus*	12.54	*Daptonema*	10.30	*Daptonema*	6.41	*Halalaimus*	7.98
		Chromadorita	7.59	*Microlaimus*	8.30	*Paramonhystera*	8.93	*Halalaimus*	5.16	*Daptonema*	7.26
		Daptonema	3.64	*Sabatieria*	3.54	*Halalaimus*	8.08	*Microlaimus*	5.02	*Leptolaimus*	4.89
		Dichromadora	3.50	*Desmodora*	2.76	*Acantholaimus*	8.03	*Dichromadora*	4.48	*Desmodora*	3.65
		Acantholaimus	3.29	*Comesa*	2.36	*Aegialoalaimus*	7.37	*Desmodora*	3.93	*Chromadorita*	3.07
		Leptolaimus	2.77	*Leptolaimus*	2.29	*Dichromadora*	3.94	*Actinonema*	3.59	*Sphaerolaimus*	2.60
		Araeolaimus	2.26	*Dichromadora*	2.26	*Sphaerolaimus*	3.06	*Dorylaimopsis*	3.50	*Aegialoalaimus*	2.20
		Halichoanolaimus	1.58	*Elzalia*	2.18	*Spilophorella*	2.55	*Comesa*	2.72	*Diplopeltoides*	1.91
		Paracanthonchus	1.46	*Odontophora*	2.16	*Linhomoeus*	1.74	*Sphaerolaimus*	2.48	*Cervonema*	1.83
		Cervonema	1.24	*Chromadorita*	2.06	*Campylaimus*	1.43	*Halichoanolaimus*	2.06	*Molgolaimus*	1.72
		Desmodora	1.10	*Paramonhystera*	1.97	*Oxystomina*	1.38	*Laimella*	1.86	*Microlaimus*	1.64
		Thalassomonhystera	1.05	*Actinonema*	1.80	*Elzalia*	1.33	*Molgolaimus*	1.85	*Elzalia*	1.60
		Rest (45)	10.25	*Terschellingia*	1.77	*Chromadora*	1.17	*Elzalia*	1.79	*Paramesacanthion*	1.49
				Campylaimus	1.58	*Sabatieria*	1.16	*Camacolaimus*	1.71	*Dichromadora*	1.30
				Sphaerolaimus	1.56	Rest (39)	10.67	*Cervonema*	1.45	*Ledovitia*	1.20
				Marylynnia	1.20			*Thalassoalaimus*	1.35	*Comesa*	1.14
				Ledovitia	1.18			*Oxystomina*	1.25	*Campylaimus*	1.13
				Amphimonhystrella	1.10			Xyalidae indet.	1.06	*Oxystomina*	1.11
				Rest (30)	7.89			*Odontophora*	1.05	*Acantholaimus*	1.06
								Viscosia	1.05	Rest (48)	13.10
								Rest (40)	15.23		

SG		SO		KG		AUS		BX	
Desmodora	17.61	*Microlaimus*	17.06	*Sabatieria*	9.23	*Monhystrella*	12.35	*Daptonema*	11.51
Microlaimus	8.05	*Daptonema*	13.71	*Dorylaimopsis*	8.08	*Greeffiella*	7.40	*Microlaimus*	10.95
Monhystrella	5.56	*Monhystrella*	12.35	*Comesa*	6.75	*Prototricoma*	7.20	*Halomonhystera*	7.83
Daptonema	5.16	*Desmodora*	4.65	*Halalaimus*	6.40	*Tricoma*	5.78	*Monhystrella*	7.40
Prototricoma	4.53	*Sabatieria*	4.30	*Desmodora*	5.14	*Halalaimus*	4.59	*Leptolaimus*	4.71
Desmoscolex	4.21	*Chromadorita*	3.68	*Amphimonhystrella*	4.69	*Acantholaimus*	3.57	*Sabatieria*	4.42
Molgolaimus	4.01	*Tricoma*	3.41	*Pierrickia*	4.22	*Desmoscolex*	3.31	*Acantholaimus*	4.42
Desmodorella	3.74	*Desmodorella*	3.23	*Desmoscolex*	3.78	*Microlaimus*	3.10	*Tricoma*	4.21
Spilophorella	3.35	*Molgolaimus*	3.18	*Daptonema*	3.61	*Chromadorita*	2.22	*Cervonema*	4.05
Xyalidae indet.	3.07	*Thalassomonhystera*	2.89	*Molgolaimus*	3.47	*Daptonema*	2.22	*Chromadorita*	3.41
Tricoma	3.07	*Halomonhystera*	2.58	*Tricoma*	2.98	*Thalassomonhystera*	2.21	*Halalaimus*	2.10
Halalaimus	2.54	*Acantholaimus*	2.45	*Microlaimus*	2.95	*Leptolaimus*	2.07	*Prototricoma*	1.87
Paranticoma	2.49	*Leptolaimus*	2.28	*Prototricoma*	2.60	*Spilophorella*	2.05	*Thalassomonhystera*	1.85
Sabatieria	2.49	*Dichromadora*	2.11	*Dichromadora*	2.46	*Parachromadorita*	1.92	*Camacolaimus*	1.69
Actinonema	2.09	*Aegialoalaimus*	1.74	*Leptolaimus*	2.22	*Theristus*	1.92	*Theristus*	1.67
Chromadorita	1.84	*Halalaimus*	1.73	*Sphaerolaimus*	1.98	*Aegialoalaimus*	1.91	*Spilophorella*	1.58
Amphimonhystera	1.61	*Cervonema*	1.41	*Marylynnia*	1.98	*Molgolaimus*	1.87	*Desmodora*	1.53
Dorylaimopsis	1.52	*Amphimonhystrella*	1.27	*Metasphaerolaimus*	1.76	*Halomonhystera*	1.74	*Halichoanolaimus*	1.50
Thalassomonhystera	1.51	*Campylaimus*	1.00	*Chromadorita*	1.67	*Sabatieria*	1.73	Xyalidae indet.	1.36
Leptolaimus	1.48	Rest (53)	14.98	*Monhystrella*	1.64	*Paracanthonchus*	1.71	*Aegialoalaimus*	1.34
Metacyatholaimus	1.27			*Oxystomina*	1.64	*Wieseria*	1.55	*Dichromadora*	1.33
Terschellingia	1.06			*Actinonema*	1.41	*Calomicrolaimus*	1.39	*Desmoscolex*	1.22
Rest (74)	17.71			*Thalassomonhystera*	1.36	*Araeolaimus*	1.22	*Molgolaimus*	1.12
				Aegialoalaimus	1.21	*Dichromadora*	1.22	*Paranticoma*	1.06
				Metalinhomoeus	1.06	*Halichoanolaimus*	1.20	Rest (58)	15.86
				Halichoanolaimus	1.05	*Southerniella*	1.19		
				Cervonema	1.03	*Actinonema*	1.00		
				Perspiria	1.03	Rest (52)	20.34		
				Rest (47)	12.61				

* numbers between brackets indicate how many genera contributed to the rest fraction for each station

APPENDIX 5: AVERAGE RELATIVE GENUS ABUNDANCE – SUBSURFACE LAYERS (3 – 5 CM)

LW		LS		W-120		W-163		DP-243		DP-250	
Halomonhystera	96.60	*Microlaimus*	23.30	*Linhomoeus*	28.15	*Microlaimus*	37.50	*Sabatieria*	57.83	*Sabatieria*	51.31
Monhystrella	1.24	*Monhystrella*	17.08	*Microlaimus*	23.92	*Linhomoeus*	13.31	*Comesa*	11.65	*Dorylaimopsis*	13.79
Rest (9)	2.16	*Halomonhystera*	13.22	*Sabatieria*	22.52	*Sabatieria*	13.11	*Leptolaimus*	7.34	*Comesa*	9.21
		Chromadorita	6.98	*Terschellingia*	5.91	*Terschellingia*	9.15	*Daptonema*	5.48	*Daptonema*	3.95
		Leptolaimus	5.84	*Comesa*	5.61	*Laimella*	4.71	*Laimella*	4.05	*Laimella*	3.87
		Thalassomonhystera	4.61	*Marylynnia*	3.19	*Paramonhystera*	4.67	*Linhomoeus*	3.20	*Diplopeltoides*	2.06
		Acantholaimus	3.93	*Pierrickia*	2.06	*Halalaimus*	3.48	Xyalidae indet.	2.10	*Filitonchus*	1.44
		Syringolaimus	2.43	*Laimella*	1.68	*Daptonema*	2.61	*Dorylaimopsis*	1.46	*Pierrickia*	1.40
		Dichromadora	1.91	*Daptonema*	1.14	*Dichromadora*	2.32	*Desmodora*	1.05	*Desmodora*	1.34
		Aegialoalaimus	1.67	Rest (24)	5.81	*Amphimonhystrella*	1.49	*Pierrickia*	1.01	*Halomonhystera*	1.10
		Elzalia	1.67			*Pierrickia*	1.31	Rest (15)	4.83	*Metasphaerolaimus*	1.06
		Monhystrieidae indet.	1.67			*Spilophorella*	1.05			Rest (27)	9.46
		Southerniella	1.67			Rest (19)	5.31				
		Synonchus	1.67								
		Halichoanolaimus	1.63								
		Camacolaimus	1.36								
		Desmoscolex	1.35								
		Thalassoalaimus	1.15								
		Rest (19)	6.89								

SG		SO		KG		AUS		BX	
Sabatieria	25.17	*Sabatieria*	20.96	*Sabatieria*	29.07	*Monhystrella*	23.03	*Sabatieria*	31.05
Terschellingia	15.31	*Microlaimus*	12.75	*Comesa*	10.58	*Perspiria*	20.37	*Monhystrella*	18.37
Molgolaimus	6.65	*Daptonema*	8.16	*Desmodora*	9.28	*Sabatieria*	8.82	*Desmoscolex*	5.00
Xyalidae indet.	6.35	*Monhystrella*	6.61	*Perspiria*	5.64	*Leptolaimus*	7.53	*Leptolaimus*	3.96
Laimella	5.61	*Terschellingia*	4.56	*Dorylaimopsis*	4.41	*Halichoanolaimus*	4.21	*Daptonema*	3.50
Dorylaimopsis	4.80	*Tricoma*	3.70	*Marylynnia*	4.41	*Acantholaimus*	3.99	*Camacolaimus*	3.02
Filitonchus	4.47	*Filitonchus*	3.46	*Metalinhomoeus*	4.39	*Theristus*	3.65	*Aegialoalaimus*	2.58
Monhystrella	3.52	*Metasphaerolaimus*	3.20	*Halalaimus*	3.49	*Greeffiella*	3.48	*Halichoanolaimus*	2.35
Metasphaerolaimus	3.45	*Metalinhomoeus*	2.92	*Longicyatholaimus*	2.65	*Syringolaimus*	3.48	*Prototricoma*	2.31
Linhomoeus	3.12	*Laimella*	2.31	*Molgolaimus*	2.21	*Leptolaimoides*	1.80	*Microlaimus*	2.26
Pierrickia	2.88	*Chromadorita*	2.06	*Amphimonhystrella*	2.06	*Thalassomonhystera*	1.74	*Halomonhystera*	2.22
Amphimonhystrella	2.16	*Dorylaimopsis*	2.04	*Pierrickia*	1.63	*Desmoscolex*	1.69	*Thalassomonhystera*	2.13
Comesa	1.95	*Leptolaimus*	1.80	*Daptonema*	1.26	*Prototricoma*	1.69	*Acantholaimus*	1.99
Diplopeltula	1.45	*Paramesacanthion*	1.52	*Dichromadora*	1.16	*Wieseria*	1.69	*Greeffiella*	1.95
Halalaimus	1.35	*Dichromadora*	1.50	*Terschellingia*	1.13	*Rhabdocoma*	1.23	*cf. Daptonema*	1.59
Paranticoma	1.22	*Molgolaimus*	1.42	*Leptolaimus*	1.11	Xyalidae indet.	1.18	*Rhabdocoma*	1.55
Odontanticoma	1.22	*Odontanticoma*	1.35	*Metasphaerolaimus*	1.08	*Daptonema*	1.12	*Cervonema*	1.55
Rest (33)	9.32	*Pierrickia*	1.32	*Desmoscolex*	1.06	Rest (16)	9.32	*Theristus*	1.20
		Desmodora	1.31	Rest (31)	13.40			*Wieseria*	1.15
		Axonolaimus	1.29					*Halalaimus*	1.11
		Southerniella	1.28					Rest (20)	9.17
		Acantholaimus	1.03						
		Thalassomonhystera	1.03						
		Rest (27)	12.44						

* numbers between brackets indicate how many genera contributed to the rest fraction for each locations

APPENDIX 6: NEMATODE SPECIES – STATION INCIDENCE (CHAPTERS 4 & 5)

	0 – 3 cm					3 – 5 cm				
	SG	**SO**	**KG**	**AUS**	**BX**	**SG**	**SO**	**KG**	**AUS**	**BX**
Acantholaimus sp.indet.	X	–	–	X	X	X	–	–	X	–
Acantholaimus sp.1	X	X	X	X	X	–	X	X	X	X
Acantholaimus sp.2	–	X	–	X	X	–	–	–	X	–
Acantholaimus sp.3	X	–	–	X	X	–	–	–	–	–
Acantholaimus sp.4	–	X	–	–	X	–	–	–	–	–
Acantholaimus sp.5	–	X	–	–	X	–	–	–	–	X
Acantholaimus sp.6	X	–	–	–	X	–	–	–	–	X
Acantholaimus sp.7	–	–	–	X	–	–	–	–	X	–
Actarjania sp.	–	X	–	–	–	–	–	–	–	–
Actinonema sp.	X	X	X	X	X	X	–	X	–	X
Aegialoalaimus sp.indet.	X	–	–	X	–	–	–	–	–	X
Aegialoalaimus sp.1	X	X	X	–	X	X	X	–	–	X
Aegialoalaimus sp.2	X	X	X	X	X	–	–	X	–	–
Aegialoalaimus sp.3	–	–	–	X	X	–	–	–	X	X
Aegialoalaimus sp.4	–	–	–	–	–	–	–	–	–	X
Aegialoalaimus sp.5	–	–	–	X	–	–	–	–	–	–
Alaimella sp.	–	–	X	–	–	–	–	–	–	–
Amphimonhystera sp.1	X	X	–	X	X	X	X	X	–	–
Amphimonhystrella sp.1	X	X	X	X	X	X	X	X	–	X
Amphimonhystrella sp.2	–	–	X	–	–	–	–	–	X	–
Amphimonhystrella sp.3	X	–	–	–	–	–	–	–	–	–
Anoplostoma sp.indet.	–	X	–	X	–	X	–	–	X	–
Anticoma sp.1	X	X	X	X	X	–	–	–	–	–
Antomicron sp.1	–	X	X	–	X	–	X	X	–	–
Araeolaimus sp.1	X	X	–	X	X	–	–	–	X	–
Ascolaimus sp.1	X	–	–	–	–	–	–	X	–	–
Axonolaimus sp.indet.	–	–	X	–	–	–	–	–	–	–
Axonolaimus sp.1	X	X	–	–	–	–	X	–	–	–
Axonolaimus sp.2	X	X	–	–	–	–	X	–	–	–
Bathyeurystomina sp.1	X	–	–	–	X	–	–	–	–	–
Calomicrolaimus sp.1	X	X	X	X	X	–	–	–	–	–
Camacolaimus sp.1	–	X	X	X	X	–	–	–	X	X
Campylaimus sp.1	X	X	X	X	X	–	X	–	–	–
Ceramonema sp.indet.	X	X	X	–	–	–	–	–	–	–
Cervonema sp.1	X	X	X	X	X	–	X	X	–	X
cfr. Daptonema	–	–	–	–	X	–	–	–	–	X
cfr. Echonema	–	–	–	–	X	–	–	–	–	–
cfr. Intasia	–	X	–	–	–	–	–	–	–	–
cfr. Pandolaimus	–	X	–	–	–	–	–	–	–	–
cfr. Paracanthonchus	–	–	–	–	–	–	X	–	–	–

	0 – 3 cm					3 – 5 cm				
	SG	**SO**	**KG**	**AUS**	**BX**	**SG**	**SO**	**KG**	**AUS**	**BX**
cfr. Siphonolaimus	–	–	–	–	X	–	–	–	–	–
cfr. Terschellingia	–	–	–	–	X	–	–	–	–	–
Chromadora sp.indet.	X	–	–	–	–	–	–	–	–	–
Chromadorella sp.indet.	X	–	X	–	X	–	–	X	–	–
Chromadoridae *sp.indet.*	X	X	–	–	X	–	X	–	–	–
Chromadorita sp.indet.	X	–	X	X	X	–	–	X	–	–
Chromadorita sp.1	X	X	X	X	X	–	X	–	–	–
Chromadorita sp.2	X	X	X	X	X	X	X	X	–	X
Chromadorita sp.3	–	–	–	–	X	–	–	–	–	–
Comesa sp.	X	X	X	X	–	X	X	X	–	–
Cricohalalaimus sp.	X	–	–	X	X	–	–	–	–	–
Cyartonema sp.1	X	–	–	X	–	–	–	–	–	–
Cyartonema sp.2	X	–	–	–	–	X	–	–	–	–
Cyatholaimus sp.	X	–	X	–	X	–	–	–	–	–
Cyatholaimidae *sp.indet.*	–	X	–	X	–	–	–	–	–	–
Daptonema sp.indet.	X	–	X	X	X	–	–	X	–	X
Daptonema sp.1	X	–	–	–	X	–	–	–	–	–
Daptonema sp.2	X	X	X	X	X	X	X	–	X	–
Daptonema sp.3	–	–	–	–	–	X	–	–	–	–
Daptonema sp.4	X	X	–	–	–	X	–	–	–	–
Daptonema sp.5	X	–	–	–	X	–	–	–	–	–
Daptonema sp.6	–	X	–	–	X	–	–	–	–	–
Daptonema sp.7	–	–	X	–	–	–	–	–	–	–
Daptonema sp.8	X	X	X	X	X	X	X	X	–	X
Daptonema sp.9	X	X	X	–	X	–	X	–	–	–
Daptonema sp.10	–	X	–	–	–	–	X	–	–	–
Desmodora sp.1	X	–	X	X	–	–	–	X	–	X
Desmodora sp.2	X	–	–	–	–	–	–	–	–	–
Desmodora sp.A	–	X	–	–	–	–	X	–	–	–
Desmodora sp.B	–	X	–	–	–	–	–	–	–	–
Desmodora sp.C	X	X	–	–	–	–	–	–	–	–
Desmodora sp.D	X	X	X	–	X	X	X	X	–	–
Desmodora campbelli	X	X	X	–	X	X	X	X	–	–
Desmodora sp.3	X	–	–	–	–	–	–	–	–	–
Desmodorella sp.1	X	X	–	–	X	–	–	–	–	–
Desmodorella aff.balteata	X	X	–	X	X	X	X	–	–	–
Desmodorella sp.A	X	X	–	–	–	–	–	–	–	–
Desmodorella sp.B	X	X	X	X	–	–	X	–	–	–
Desmoscolecidae *sp.indet.*	–	–	–	X	X	–	–	–	–	–
Desmoscolex sp.	X	X	X	X	X	–	–	X	X	X
Dichromadora sp.	X	X	X	X	X	X	X	X	–	–
Diplolaimella sp.1	X	–	–	–	–	–	–	–	–	–

	0 – 3 cm					3 – 5 cm				
	SG	SO	KG	AUS	BX	SG	SO	KG	AUS	BX
Diplolaimella sp.2	X	–	–	–	–	–	–	–	–	–
Diplopeltoides sp.	–	–	–	X	–	–	–	–	–	–
Diplopeltula sp.1	X	X	X	X	–	X	–	–	–	–
Diplopeltula sp.2	X	X	–	–	–	X	X	–	–	–
Diplopeltula sp.3	X	X	–	–	–	X	X	–	–	–
Diplopeltula sp.4	–	–	–	X	–	–	–	–	–	–
Diplopeltula sp.5	X	–	–	–	–	–	–	–	–	–
Diplopeltula sp.6	–	X	–	–	X	–	–	–	–	–
Dorylaimopsis sp.	X	X	X	–	–	X	X	X	–	–
Draconema sp.	X	–	X	–	X	–	–	–	–	X
Elzalia sp.	X	X	X	–	X	X	X	–	X	–
Endeolophos sp.	X	X	X	X	X	–	–	–	X	–
Epsilonema sp.	–	–	–	X	–	–	–	–	–	–
Euchromadora sp.	X	X	–	–	–	X	–	–	–	–
Filitonchus sp.	X	X	X	–	–	X	X	X	–	–
Gnomoxyala sp.	X	–	–	–	–	–	X	–	–	–
Gomphionchus sp.	–	–	–	–	–	X	–	–	–	–
Greeffiella sp.	X	X	–	X	X	X	–	–	X	X
Halalaimus sp.1	X	–	X	X	X	X	–	–	X	–
Halalaimus sp.2	X	X	X	X	X	X	X	X	–	X
Halalaimus sp.3	X	X	X	X	X	X	X	X	–	–
Halalaimus sp.4	–	–	X	–	–	–	–	–	–	–
Halalaimus sp.5	X	–	–	–	–	–	–	–	–	–
Halalaimus sp.6	X	–	–	–	–	X	–	–	–	–
Halalaimus sp.7	–	–	–	–	–	X	–	–	–	–
Halichoanolaimus sp.1	–	–	–	–	X	–	–	–	X	–
Halichoanolaimus sp.2	–	X	X	X	X	–	–	X	–	X
Halichoanolaimus sp.3	–	–	–	X	X	–	–	–	–	X
Halichoanolaimus sp.4	–	–	–	–	–	X	–	–	–	–
Halichoanolaimus sp.5	–	–	–	X	–	–	–	–	X	–
Haliplectus sp.	–	–	–	X	–	–	–	–	–	–
Halomonhystera sp.	X	X	X	X	X	–	X	X	–	X
Innocuonema sp.	X	–	X	–	–	–	–	–	–	–
Laimella sp.1	X	X	–	–	X	X	X	–	–	–
Laimella sp.2	–	X	–	–	–	–	–	–	–	–
Ledovitia sp.	X	–	X	X	X	–	–	–	X	–
Leptolaimoides sp.1	X	–	X	–	X	–	–	X	–	–
Leptolaimoides sp.2	X	–	–	X	X	–	–	–	X	–
Leptolaimus sp.1	X	–	X	–	–	–	–	X	X	–
Leptolaimus sp.2	X	X	X	X	X	–	–	X	X	–
Leptolaimus sp.3	–	X	X	X	–	–	–	–	X	–
Leptolaimus sp.4	X	X	X	X	X	–	X	X	–	–

	0 – 3 cm					3 – 5 cm				
	SG	**SO**	**KG**	**AUS**	**BX**	**SG**	**SO**	**KG**	**AUS**	**BX**
Leptolaimus sp.5	X	X	X	X	X	–	X	X	X	X
Leptolaimus sp.6	–	X	–	X	X	–	–	–	–	–
Leptolaimus sp.7	–	–	–	–	X	–	–	–	–	–
Leptolaimus sp.8	–	–	–	X	–	–	–	–	X	–
Linhomoeus sp.	X	–	X	–	X	X	X	X	–	–
Linhomoeidae *sp.indet.*	–	–	–	–	–	X	–	–	–	–
Linhystera sp.	X	–	–	–	–	–	X	–	–	–
Longicyatholaimus sp.	X	–	X	X	X	–	–	X	–	–
Marisalbinema sp.1	–	X	X	–	X	–	–	X	–	–
Marisalbinema sp.2	–	–	–	X	–	–	–	–	–	–
Marylynnia sp.indet.	X	–	X	X	–	–	–	–	–	–
Marylynnia sp.1	X	X	X	–	X	X	–	X	–	–
Marylynnia sp.2	–	–	–	X	X	–	–	X	X	–
Marylynnia sp.3	–	–	–	–	X	–	–	–	–	–
Megadesmolaimus sp.	–	–	X	X	–	–	–	–	–	–
Mesacanthion sp.	–	–	X	–	–	–	–	–	–	–
Metachromadora sp.	–	–	–	X	–	–	–	–	–	–
Metacyatholaimus sp.1	X	–	–	–	–	–	–	–	–	–
Metacyatholaimus sp.2	X	–	–	–	–	X	–	X	–	–
Metadasynemella sp.	X	X	–	X	–	–	X	–	–	–
Metadesmolaimus sp.indet.	–	X	X	–	–	–	–	–	–	–
Metadesmolaimus sp.1	X	–	–	–	–	–	–	–	–	–
Metalinhomoeus sp.indet.	–	–	–	–	–	X	–	–	–	–
Metalinhomoeus sp.1	–	X	X	–	X	X	X	X	–	–
Metalinhomoeus sp.2	–	–	–	–	–	X	–	–	–	–
Metasphaerolaimus sp.indet.	X	–	–	–	–	–	–	–	–	–
Metasphaerolaimus sp.1	X	X	X	–	–	X	X	–	–	–
Metasphaerolaimus sp.2	X	X	–	–	–	X	X	X	–	–
Metepsilonema sp.	–	–	–	X	–	–	–	–	–	–
Micoletzkyia sp.	X	–	X	–	–	–	–	–	–	–
Microlaimus sp.indet.	X	X	X	X	X	–	X	X	–	–
Microlaimus sp.1	X	X	X	X	X	–	X	–	–	X
Microlaimus sp.2	X	X	X	X	X	X	X	X	–	X
Microlaimus sp.3	–	X	–	–	–	–	–	–	–	–
Microlaimus sp.4	X	X	X	–	–	–	X	–	–	–
Microlaimus sp.5	X	X	X	X	X	–	–	X	–	–
Molgolaimus sp.indet.	X	X	X	X	–	X	–	X	–	–
Molgolaimus sp.1	X	X	X	X	–	X	X	X	X	–
Molgolaimus sp.2	X	X	X	X	X	X	–	X	–	X
Molgolaimus sp.3	–	X	–	–	–	–	–	–	–	–
Monhysteridae *sp.indet.*	X	–	–	X	–	–	–	–	X	–
Monhysteroides sp.1	X	–	–	–	–	–	X	–	–	–

	0 – 3 cm					3 – 5 cm				
	SG	SO	KG	AUS	BX	SG	SO	KG	AUS	BX
Monhysteroides sp.2	–	–	–	–	–	X	–	–	–	–
Monhystrella sp.indet.	X	X	X	X	X	X	X	X	X	X
Monhystrella sp.1	X	X	X	X	X	X	X	X	–	X
Monhystrella sp.2	X	X	–	X	X	X	X	–	X	X
Monhystrella sp.3	–	X	–	–	–	X	–	–	–	–
Monhystrella sp.4	X	–	–	–	–	X	–	–	–	–
Monhystrella sp.5	–	–	–	X	X	–	–	–	X	X
Monhystrella sp.6	X	X	X	X	X	X	–	X	X	X
Monhystrella sp.7	X	–	–	–	–	–	–	–	–	–
Monhystrella sp.8	X	–	–	–	X	–	–	–	–	–
Monhystrella sp.9	X	X	–	X	X	X	X	–	X	X
Neochromadora sp.	X	–	–	X	–	–	–	–	–	–
Nudora sp.	–	–	–	–	X	–	–	–	–	X
Odontanticoma sp.1	X	X	X	–	X	X	X	X	–	–
Odontanticoma sp.2	–	–	–	–	X	–	–	–	–	–
Oncholaimus sp.	X	–	–	–	–	–	–	–	–	–
Oxystomina sp.1	X	X	X	X	X	X	–	X	–	X
Oxystomina sp.2	X	X	X	–	–	–	–	–	–	–
Oxystomina sp.3	–	–	–	X	–	–	–	–	–	–
Paracanthonchus sp.1	X	–	X	X	X	X	–	–	–	–
Paracanthonchus sp.2	X	X	X	X	X	–	X	–	–	X
Parachromadorita sp.	X	–	–	X	X	–	–	–	–	X
Paracomesoma sp.	–	–	–	–	–	–	–	X	–	–
Paracyatholaimoides sp.	–	–	–	X	–	–	–	–	–	–
Paracyatholaimus sp.	X	X	–	X	X	X	–	–	–	–
Paradraconema sp.	–	–	–	X	X	–	–	–	–	–
Paraelzalia sp.	–	–	–	–	–	–	–	–	–	X
Paralinhomoeus sp.	–	–	–	–	X	–	–	–	–	–
Paralongicyatholaimus sp.1	X	X	X	–	X	–	X	X	–	X
Paralongicyatholaimus sp.2	X	–	–	X	–	–	–	–	–	–
Paramesacanthion sp.	X	X	X	X	X	–	X	X	X	–
Paramonohystera sp.	X	–	–	–	–	–	–	–	–	–
Paranticoma sp.	X	X	–	X	X	X	–	–	–	–
Pararaeolaimus sp.	–	–	–	X	–	–	–	–	–	–
Paraterschellingia sp.	–	–	–	–	X	–	–	–	–	–
Perspiria sp.indet.	X	–	–	X	–	–	–	X	–	X
Perspiria sp.1	X	–	X	–	–	–	–	–	X	–
Phanoderma sp.	X	–	–	–	X	–	–	–	–	–
Phanodermopsis sp.	X	–	–	–	–	–	–	–	–	–
Pierrickia sp.indet.	X	–	–	–	–	–	–	–	–	–
Pierrickia sp.1	X	X	X	–	X	X	X	X	–	X
Pierrickia sp.2	–	–	X	–	–	–	–	–	–	–

	0 – 3 cm					3 – 5 cm				
	SG	**SO**	**KG**	**AUS**	**BX**	**SG**	**SO**	**KG**	**AUS**	**BX**
Pomponema sp.	X	X	X	X	X	–	X	–	–	–
Procamacolaimus sp.	–	–	–	–	X	–	–	–	–	–
Prochaetosoma sp.	X	–	–	X	–	–	–	–	–	–
Prochromadorella sp.	X	–	–	–	–	–	–	–	–	–
Promonhystera sp.	X	–	–	–	X	X	–	–	–	–
Prototricoma sp.1	X	X	X	X	X	X	–	X	X	X
Prototricoma sp.2	–	–	–	–	X	–	–	–	–	–
Pselionema sp.1	X	X	X	–	X	–	X	–	–	–
Pselionema sp.2	–	–	–	X	–	–	–	–	–	–
Pseudocella sp.	–	–	–	X	–	–	–	–	–	–
Rhabdocoma sp.	–	X	–	X	X	–	–	–	X	X
Rhabdodemania sp.	–	–	–	X	X	–	–	–	–	–
Rhips sp.	X	–	–	–	–	–	–	–	–	–
Rhynchonema sp.	X	–	X	–	X	–	–	–	–	–
Sabatieria sp.indet.	X	X	X	–	–	X	X	X	X	–
Sabatieria sp.1	X	–	–	–	–	X	–	–	–	–
Sabatieria sp.2	X	–	–	–	–	–	–	–	–	–
Sabatieria sp.3	–	–	–	X	–	–	–	–	–	–
Sabatieria sp.4	–	X	X	X	X	X	X	X	X	X
Sabatieria sp.5	–	–	–	–	–	X	–	–	–	–
Sabatieria sp.6	X	X	X	–	X	X	X	X	X	X
Sabatieria sp.7	X	X	X	–	–	X	X	X	–	–
Sabatieria sp.8	X	X	–	X	X	X	X	–	X	X
Setosabatieria sp.	–	–	X	–	–	–	–	–	–	–
Southerniella sp.indet.	X	X	X	–	X	–	X	–	–	–
Southerniella sp.1	X	–	–	–	X	–	–	–	–	–
Southerniella sp.2	X	X	–	X	X	–	X	–	–	X
Southerniella sp.3	–	X	–	–	–	–	–	–	–	–
Southerniella sp.4	X	–	–	–	–	–	–	–	–	–
Sphaerolaimus sp.1	X	X	X	X	–	–	X	X	X	X
Sphaerolaimus sp.2	X	–	–	–	–	–	–	–	–	–
Spilophorella sp.	X	X	X	X	X	X	X	X	X	X
Spirobolbolaimus sp.	–	X	–	–	–	–	–	–	–	–
Stephanolaimus sp.	–	–	X	X	–	–	–	–	–	–
Subsphaerolaimus sp.	–	–	X	–	–	–	–	–	–	–
Synonchiella sp.	X	–	–	–	–	–	–	–	–	–
Syringolaimus sp.	–	–	–	X	X	–	–	–	X	–
Terschellingia sp.1	–	X	–	–	X	X	X	–	–	–
Terschellingia sp.2	X	X	X	–	–	X	X	X	–	–
Terschellingia sp.3	X	–	–	–	–	X	–	–	–	–
Thalassironus sp.	X	X	–	–	–	–	–	–	–	–
Thalassoalaimus sp.1	–	–	–	X	–	–	–	–	–	–

	0 – 3 cm					3 – 5 cm				
	SG	**SO**	**KG**	**AUS**	**BX**	**SG**	**SO**	**KG**	**AUS**	**BX**
Thalassoalaimus sp.2	X	X	X	X	X	–	–	–	–	X
Thalassoalaimus sp.3	–	–	–	–	–	–	–	X	–	–
Thalassomonhystera sp.indet.	X	X	X	X	X	X	X	–	X	X
Thalassomonhystera sp.1	X	X	X	X	–	–	X	X	X	–
Thalassomonhystera sp.2	–	–	–	X	–	–	–	–	–	–
Thalassomonhystera sp.3	X	–	–	–	X	–	–	–	–	–
Theristus sp.indet.	–	–	X	–	–	X	–	–	–	–
Theristus sp.1	X	X	X	X	X	–	X	–	–	–
Theristus sp.2	X	X	X	X	X	X	–	–	X	X
Theristus sp.3	–	X	–	–	–	–	X	–	–	–
Theristus sp.4	–	–	–	–	X	–	–	–	–	–
Thoracostomopsidae *sp.indet.*	X	–	–	–	–	–	–	X	–	–
Tricoma sp.indet.	X	X	X	–	X	–	–	–	–	–
Tricoma sp.1	X	X	X	–	–	X	–	X	–	–
Tricoma sp.2	X	X	X	X	X	X	X	–	X	X
Tricoma sp.3	X	X	–	–	X	–	X	–	–	–
Trileptium sp.	X	–	X	–	–	–	–	–	–	–
Trochamus sp.	–	–	–	X	–	–	–	–	–	–
Vasostoma sp.1	X	–	–	–	–	X	–	–	–	–
Vasostoma sp.2	X	–	X	–	–	X	–	–	–	–
Viscosia sp.1	–	–	X	–	X	X	X	X	–	–
Viscosia sp.2	–	–	–	X	–	–	–	–	–	–
Wieseria sp.	X	–	–	X	X	–	–	–	X	X
Xyalidae *sp.indet.*	X	X	X	X	X	X	–	–	X	X

APPENDIX 7: *SABATIERIA* PHYLOGENETIC SPECIES LINEAGES OCCURRENCE (CHAPTER 5)

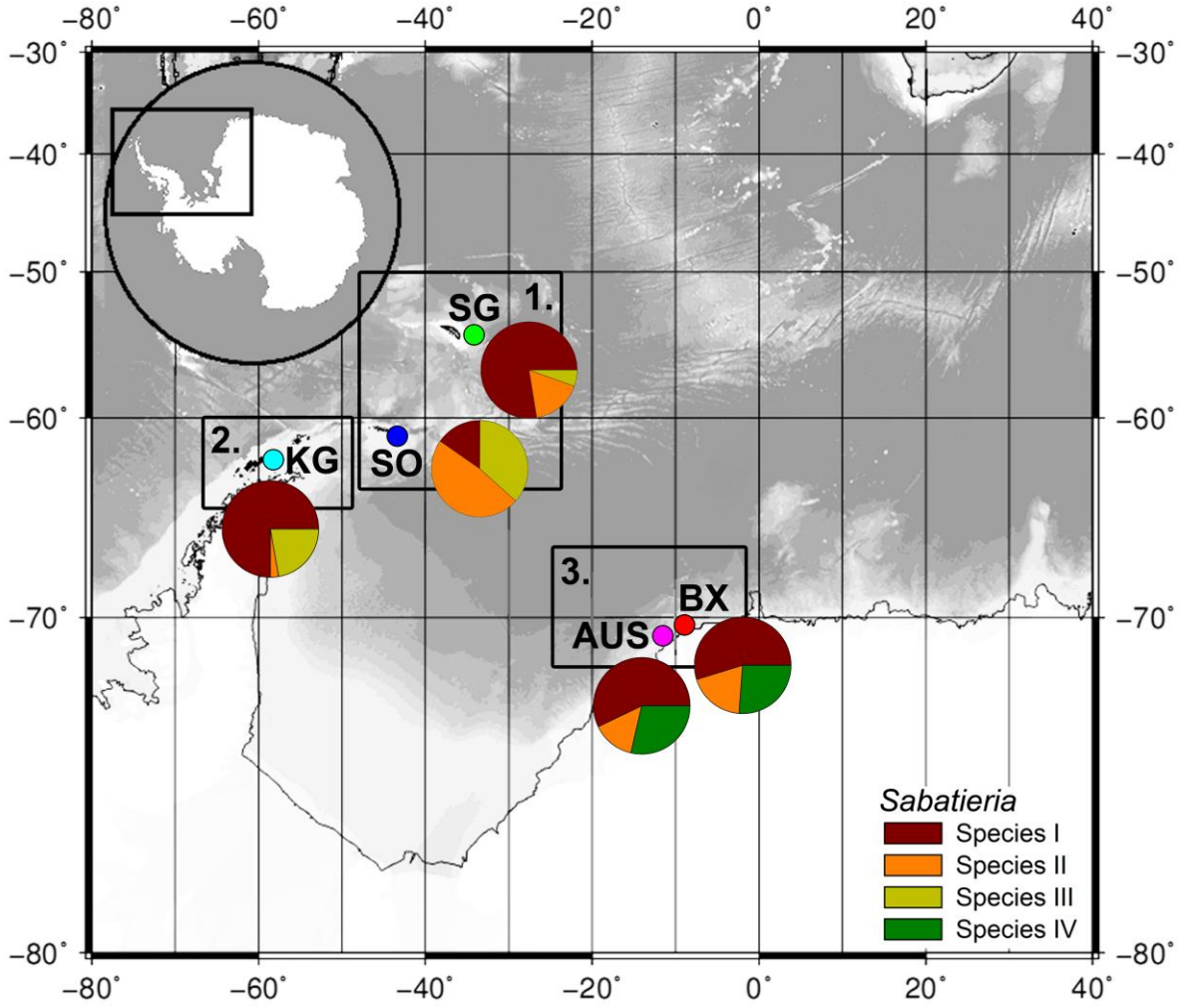

Figure showing the incidence of the four species lineages at the five different locations of the study in Chapter 5. Note that only sequence information has been taken into account, so relative abundance of the different species is only based on that information and might not reflect true composition.