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**Lidia Lins Pereira**

# Entendendo as causas e consequências provenientes do aumento da biodiversidade. Um estudo de caso baseado em nematódeos de ambientes dinâmicos e estáveis de margens continentais e sobre regimes contrastantes de produtividade

# Understanding causes and consequences of increases in biodiversity. A case study based on nematodes from stable and dynamic continental margins and contrasting productivity regimes

**Recife, 2016**

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal da Universidade Federal de Pernambuco (UFPE), como requisito parcial para obtenção do título de Doutor em Biologia Animal.

Orientador: Prof. Dr. André Morgado Esteves

Co-Orientadora: Prof. Dra. Ann Vanreusel

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# Resumo

Esta tese teve como objetivo estudar os principais fatores responsáveis por padrões ecológicos, em diferentes escalas, da meiofauna e, em especial, dos nematódeos de mar profundo. Neste estudo foi investigado o acoplamento bento-pelágico, sendo medidas variáveis ambientais (produtividade primária, fluxo de matéria orgânica, granulometria, clorofila, pigmentos, ácidos graxos, concentração de carbono e nitrogênio), além de fatores responsáveis por dispersão e conectividade genética em mar profundo. As áreas estudadas compreendem quatro estações localizadas na planície abissal do Oceano Austral e dez estações situadas na plataforma continental e talude da Margem Ibérica. O acoplamento bento-pelágico foi investigado através de como a produtividade primária na superfície e o fluxo de exportação de matéria orgânica, assim como outros fatores ambientais, são responsáveis por diferenças em diversidade, densidade, abundância e biomassa de meiofauna em pequena e grande escala. Além disso, a variação espacial e a conectividade entre as áreas de estudo com diferentes profundidades foram analisadas. Nas estações localizadas no Oceano Austral, a produtividade primária e o fluxo de matéria orgânica foram estimados. Para as duas áreas de estudo, as variáveis ambientais do sedimento analisadas incluíram clorofila a e seus derivados, granulometria, e carbono e nitrogênio totais. Adicionalmente, no Oceano Austral, ácidos graxos do sedimento e dos nematódeos foram medidos. Aspectos da comunidade de meiofauna e dos nematódeos estudados incluíram abundância, densidade e diversidade destes grupos para as duas áreas estudadas, assim como taxas de respiração e biomassa para o Oceano Austral. Além disso, aspectos de conectividade na Margem Ibérica foram analisados através do uso de técnicas moleculares usando 18S rDNA.

Os resultados mostraram que a produtividade primária na superfície do Oceano Austral possuiu uma correlação positiva com diversidade, abundância e ácidos graxos totais da meiofauna e dos nematódeos. Estes resultados sugerem que a produtividade primária representa a principal fonte de energia para a meiofauna. Por outro lado, a concentração de matéria orgânica proveniente da superfície que chega ao fundo mostrou ser dependente da profundidade. Isto foi mostrado através da diminuição de matéria orgânica com o aumento da profundidade na Margem Ibérica. Estas diferenças mostraram variações em densidade e diversidade dos nematódeos associados com a diminuição em agregamento de matéria orgânica em relação ao aumento da profundidade. Além da quantidade de matéria orgânica, outros fatores, como hidrodinamismo, inferido através da variação na composição do sedimento, regularam diversidade beta nas duas áreas estudadas através do aumento da heterogeneidade de hábitat. Desta forma, o hidrodinamismo foi identificado como um fator potencialmente promovedor de dispersão em algumas espécies de nematódeos. A ausência de diferenças genéticas entre áreas com diferentes batimetrias e também geograficamente distintas indicou ausência de endemismo para os grupos abordados entre as áreas estudadas. Portanto, podemos concluir neste estudo que as comunidades de nematódeos para as áreas estudadas se mostraram principalmente dependentes da matéria orgânica proveniente da superfície, seja ela em forma lábil ou não, e da heterogeneidade de hábitat criada por fatores ambientais que afetam a distribuição do sedimento.

**Palavras-chave:** fluxo de matéria orgânica, produtividade primária, dispersão, Frente Polar

# Abstract

This thesis aimed to unravel processes driving meiofaunal community patterns in the deep sea. Benthic-pelagic coupling and various physical parameters, such as surface primary productivity, organic matter flux, sediment composition, chlorophyll and other pigments, fatty acids, and carbon and nitrogen, were measured as well as connectivity between studied areas. The study areas comprised four stations located at the abyssal plain of the Southern Ocean (SO) and ten stations situated at the lower continental shelf and mid-slope of the Western Iberian Margin (WIM). Benthic-pelagic coupling was investigated by testing how surface primary productivity and export fluxes, as well as other environmental factors, relate to differences in meiofaunal diversity, density, and standing stocks, but also meiofauna distribution over local and regional scales. Moreover, spatial turnover and connectivity between bathymetrically different stations were analysed. In order to test our hypotheses, surface and benthic environmental parameters were calculated. At the SO, surface primary productivity values and particulate organic carbon fluxes were estimated. For both study areas, benthic environmental variables analysed included chlorophyll a and its derivatives, sediment composition, and total carbon and nitrogen. In addition, in the SO, sediment and nematode fatty acid concentrations were measured. Meiofauna and nematode community aspects included standing stock (biomass only for the SO), density and diversity for both areas, as well as nematode respiration for the SO. The potential role of connectivity was studied at the WIM through the use of 18S rDNA.

Results showed that net surface primary productivity at the SO was positively associated with the diversity, abundance, and total fatty acid content of meiofauna and nematodes. This shows that primary production represents the fundamental energy source for the meiobenthos. The export of organic matter to the benthos is depth dependent though. This could be shown by a decrease with depth in organic matter arriving at the sea bottom exhibited at the WIM. These differences accounted for disparity of density and diversity of nematodes associated with a decrease in patchiness with increasing depth. Besides organic matter content, other factors, such as hydrodynamics, inferred through variation in sediment composition, shaped alpha and beta diversity in both studied environments by increasing habitat heterogeneity. Hydrodynamics were also identified as potential promoter of dispersal of selected nematodes. The lack of genetic differentiation between bathymetrically and geographically different areas indicated connectivity between the study areas.

**Keywords:** POC flux, surface primary productivity, dispersal, Polar Front

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# General Introduction

## Benthic-pelagic coupling

Surface primary productivity and the subsequent sedimentation of phytoplankton is considered to be the main source of carbon input in the deep sea (Billett et al., 1983). Although most of the new organic matter (OM) production be consumed in the water column and commonly only 1–3 % reaches the sea bottom, 70–95 % of the particulate OM arriving there is composed of labile compounds (Boon and Duineveld, 1996; Sachs et al., 2009). Up to 90 % of the overall new OM production is concentrated at the continental margins (Levin and Dayton, 2009). Following the production of OM in the upper water layers, sea surface processes (e.g. upwelling events, gyres), water depth, and distance from land, determine its flux to the seabed (Fischer et al., 2000; Middelburg et al., 1997; Wei et el., 2010). As phytodetritus, this OM serves as a food source for organisms dwelling at the seafloor (Serpetti et al., 2013; Wei et al., 2010). Depth-related declines in standing stocks (abundance and biomass) are mainly observed along continental margins, where deeper regions will undergo a decrease in benthos-mediated mineralization processes (Danovaro et al., 2010; Glud, 2008; Middelburg et al., 1997). Exhibiting distinct bathymetric gradients, as well as water masses with strong hydrographic characteristics that are responsible for significant variations in pressure, oxygen, temperature, and food supply (Levin and Dayton, 2009; Levin et al., 2001), continental margins possess the largest habitat diversity in the oceans (Ramirez-Llodra et al., 2010). As a consequence of these factors, decreases in standing stocks, concomitant to an increase in diversity with increasing water depth, have been observed at continental margins for all benthic size classes (Flach et al., 2002; Muthumbi et al., 2011; Rowe et al., 2008; Thiel, 1978).

Furthermore, benthic-pelagic coupling in the deep sea seems to be heavily affected

by seasonality, which results in low resource availability in particular regions during most parts of the year (Gooday, 2002; Peck et al., 2006). Such a pronounced pattern resulting from seasonal differences can be observed near the poles, where seasonality is strongest (Griffiths, 2010). In these regions, the amount of OM arriving at the seafloor not only depends on water depth and distance from land, but is also determined by current regimes and ice coverage, leading to intricate effects on the benthos (Gutzmann et al., 2014; Peck et al., 2006). In the Southern Ocean (SO), the presence of the strong Antarctic Circumpolar Current is linked to lateral advection and consequently to east-west differences in primary productivity (Demidov et al., 2012). These differences have an impact on the benthic community dwelling beneath the Antartic Circumpolar Current and adjacent areas (Brandão et al., 2014).

Following its settlement at the bottom, phytodetritus undergoes mineralization processes mediated by the benthic biota (Jamieson et al., 2013, Serpetti et al., 2013). The responses of the sea-floor communities to variations in particle fluxes are commonly initiated by bacteria, which show high increases in abundance and biomass as a reaction to OM input, followed by foraminifera, and subsequently metazoans (Gooday, 2002; Moodley et al., 2008). Microbial degradation seems to be the major regulator of mineralization processes in the deep sea (Jamieson et al., 2013). In addition, mega- and macrofauna enhance mineralization processes through feeding (i.e. mechanic fragmentation and digestion) as well as burrowing activities (Levin et al., 1997; Serpetti et al., 2013). The role of meiofauna in OM mineralization was indirectly shown through an increase in respiration during an enrichment experiment (Nascimento et al., 2012), increases in body mass, as well as by assimilation of specific fatty acids derived from diatoms and/or dinoflagellates (Fabiano et al., 1999; Guilini et al., 2013; Vanreusel et al., 1995). Concurrently, fatty acid assimilation from surface-derived diatom deposits were also observed in macrofauna in the SO (Würzberg et al., 2011), thus confirming the idea of a food web dependent on surface production. In conclusion, all benthic size classes seem to contribute to OM mineralization and consequently to the functioning of the deep-sea ecosystem (Smith et al., 2008).

# Applied techniques in the study of nematode feeding ecology

Biochemical techniques, such as fatty acid analyses, represent an important tool to track the energy flow in deep-sea meiofauna (Duros et al., 2011; Ginger et al, 2001; Ingels et al., 2011). Similarly, they can also be an important instrument to study trophic interactions in marine habitats (Kelly and Scheibling, 2012). Most components of mega-, macro- and meiofauna have been shown to be dependent on 'labile' organic matter as a food source (Ginger et al., 2001; Würzberg et al., 2011). This can be seen by the high relative abundance of polyunsaturated fatty acids in many organisms, which are indicators of either a diatom-based or a dinoflagellate diet as most metazoans are not able to synthesize these macromolecules themselves (Daalsgard et al., 2003). However, the seasonality of the food input in the deep sea requires benthic organisms to change their feeding habits when fresh food is scarce. Thus, when food is limited, refractory detritus provides an important and regulating food component for the benthos (Ginger et al., 2001).

The recently use of fatty acids of nematodes (Guilini et al., 2013; Leduc, 2009; Leduc et al., 2015) have shown that nematodes can selectively feed on specific fatty acid groups. Fatty acids can be firstly grouped in phytoplankton-derived or bacterial-derived fatty acids. Secondly, the higher the unsaturation, the more food-rich the fatty acid is considered (Daalsgard et al., 2003). Thus, feeding on polyunsaturated fatty acids would mean feeding on a richer food source, while feeding on saturated fatty acids would represent a diet based mostly on refractory organic matter (Daalsgard et al., 2003). Specific fatty acid groups or ratios can also be used as biomarkers, such as the ratio $\frac{\sum 16{:}1\omega7}{\sum 16{:}0} > 1$, which indicates a diatom-based diet or $\frac{22{:}6\omega3(\mathrm{DHA})}{20{:}5\omega3(\mathrm{EPA})} \geq 1$, related to a dinoflagellate diet (Daalsgard et al., 2003). However, fatty acid results should still be interpreted with caution, since bioconversion pathways in nematodes are not yet unravelled.

## Factors shaping deep-sea benthic communities

Deep-sea communities in general seem to be driven by the same basic mechanisms of energy availability, biological interactions, disturbance, and heterogeneity as those found in other major marine ecosystems (Levin et al., 2001). Primarily, functioning in the deep sea seems to be regulated by the rate and quality of food flux to the seafloor (Company et al., 2008; Danovaro et al., 2008; Fabiano et al., 1999; Gooday, 2002; Levin et al., 2001; Rex, 1981; Sachs et al., 2009; Smith et al., 2008). Ecosystem functioning involves several aspects of production, consumption and transfer of OM to higher trophic levels (Danovaro et al., 2008). It can be measured through biomass production, organic matter decomposition, respiration, and stable isotope and fatty acid composition, etc. (Danovaro et al., 2008). In this regard, the input of phytodetritus shapes benthic communities by creating patchiness and increasing habitat heterogeneity, and therefore enabling species coexistence through niche differentiation and facilitation (Cardinale et al., 2000). In habitats with strong seasonality, such as the SO, particulate OM will reach the abyss seafloor within days or weeks after production at the surface (Brandt, 2014).

Besides food input, other mechanisms are also responsible for shaping the diversity of deep-sea communities. These include physical factors, such as disturbance, boundary constraints, and hydrodynamics (McClain and Schlacher, 2015), as well as biological factors, for instance bioturbation, population dynamics, and dispersal (Derycke et al., 2013; Gage, 1997). Some patterns are still not understood and unimodal trends of diversity can hence not be generalized for the deep sea (Danovaro et al., 2008; Duros et al., 2011). In theoretical ecology, moderate disturbance of the seafloor is viewed as one factor promoting peaks of biodiversity. Known as the intermediate disturbance hypothesis (Connell, 1978; Yachi and Loreau, 1999), this theory is strongly refuted nowadays because of the lack of empirical evidence (Fox, 2013). Nevertheless, the ecological impact of disturbance depends primarily on the strength of the impact and the susceptibility of organisms (McClain and Schlacher, 2015). Disturbance, for instance caused by relatively strong hydrodynamics, can shape biodiversity by the redistribution of resources, favouring an increase in biodiversity (Stachowicz et al., 2007). Interactions between water masses,

bottom currents, tides, and sediment diagenesis thus create ecological settings which support distinct communities (Levin and Sibuet, 2012). Besides habitat heterogeneity, disturbance events might also promote organism dispersal through the water column (Etter and Bower, 2015; Gallucci et al., 2008).

## Dispersal and connectivity in the deep sea

Food availability and biological interactions are seen as the main factors driving small-scale patterns of biodiversity (Levin et al., 2001). Small-scale differences modulate alpha diversity and are considered to be especially important in the deep sea due to the extraordinary patchiness characterizing this environment (Danovaro et al., 2013; Kaiser et al., 2007). However, near-bottom currents, sediment structure changes, habitat heterogeneity, besides other abiotic factors driven by hydrodynamics are considered responsible for large-scale differences in diversity (100–1000 m) in the deep sea (Gage, 1997). Accordingly, these factors determine beta diversity along bathymetrical gradients and across geographical distances (Havermans et al., 2013). Beta diversity patterns are furthermore affected by dispersal of organisms and population connectivity between areas (Derycke et al., 2013; Etter and Bower, 2015; Gallucci et al., 2008).

The dispersal of organisms is generally defined as the movement of individuals from one place to another with potential consequences for gene flow (Ronce, 2007). While some organisms possess larval stages, which commonly have relatively high dispersal capabilities (Etter and Bower, 2015), others disperse by passive/active transport through the water column (Gallucci et al., 2008). In the meiofauna, copepods have demonstrated to be the first meiofaunal organism to colonize a habitat after a disturbance event, due to their good swimming capabilities (Boeckner et al., 2009; da Fônseca-Genevois et al., 2006; Thistle et al., 1991). Nematodes, lacking a larval stage, were shown to be transported passively through the water column, arriving later than copepods in a disturbed site, but demonstrating strong resistance to disturbance and increasing gradually in abundance until they become the dominant group (Boeckner et al., 2009). Nematodes can disperse

over large distances throughout their whole life either passively in the water column or actively, using a variety of cues to choose preferential spots (Palmer, 1988; Ullberg and Ólaffson, 2003). This may explain the success of this group in colonizing different environments and in exhibiting trans-oceanic dispersal (Decraemer et al., 2001; Zeppili et al., 2011).

Dispersal leads to connectivity between areas or genetic structuring at small spatial scales (Derycke et al., 2013; Van Campenhout et al., 2014). Consequently, connectivity 'links dynamics at different scales and integrates local heterogeneity, affecting regional-scale dynamics and long-term persistence' (Etter and Bower, 2015). Shallow-water studies showed that connectivity can exist across large geographic scales (Derycke et al., 2013) but data are still scarce for deep-sea nematodes in general and especially across-depth connectivity in this taxon. The physical uniformity of the deep sea may provoke the assumption of the lack of barriers to dispersal, especially in abyssal plains, but bathymetric stratification was revealed for genotypes and phenotypes of several molluscs and crustaceans on small bathymetrical scales (Etter and Bower, 2015; France and Kocher, 1996; Havermans et al., 2013; Wilson, 1983). The genetic divergence across small bathymetrical gradients was more prominent than differences across large geographical distances, for instance in the cosmopolitan amphipod *Eurythenes gryllus* (Havermans et al. 2013). Contrastingly, nematode and isopod studies indicate exchange between deep sea and shallow water habitats (Bik et al., 2010; Hessler and Thistle, 1975; Riehl and Kaiser, 2012). These findings suggest that dispersal across depth or geographic distance may be taxon and/ or species specific.

## International Framework

Flemish and Brazilian funding provided the necessary support which allowed the performance of this doctoral study in a multidisciplinary way, were collaborations with other laboratories and sampling partnerships were possible.

In the framework of the projects ANDEEP-SYSTCO (ANtartic DEEP-sea benthic diversity – SYSTem Coupling in the deep Southern Ocean) and SYSTCO II (SYSTem Coupling in the deep Southern Ocean II), starting in summer 2007/08 and 2012, respectively, processes shaping communities in the Southern Ocean were studied. The ANDEEP-SYSTCO project focused on the understanding of the role of the Southern Ocean in global energy budgets, climate change and the functioning of atmospheric, pelagic and benthic systems of the Southern Ocean. Considering the benthic environment, ANDEEP-SYSTCO aimed to investigate the biology of abyssal key species, the role of the bottom-nepheloid layer for recruitment of benthic animals, as well as the influence on abyssal life of the quality and quantity of food sinking through the water column, feeding ecology, and trophic relationships of abyssal animals (Bathmann and Hermann, 2010). This doctoral research addressed the last aim of this project, using nematode communities and their link to the net primary productivity at the surface and to the flux of organic matter to the seafloor.

The SYSTCO II project targeted coupling processes, such as changes in the phytoplankton bloom through the water column and its impact on benthic communities. It comprised investigations of diversity, distribution of abundance of deep-sea benthic organisms and their impact on the biological productivity, as well as the ecology of deep-sea fauna (Wolf-Gladrow, 2012). This doctoral research addressed both objectives of this project, where meiofauna and specifically nematodes community characteristics were linked to surface primary productivity and other environmental variables potentially affecting community distribution. Moreover, the used of carbon flow techniques, such as fatty acids, was also incorporated to test benthic-pelagic coupling and functional diversity in the deep Southern Ocean.

The Flemish fund for scientific research promoted international collaborations through the project: **the enigma of the success of nematodes in the deep sea** (Project number: G083512N). The aim of this project was to investigate why nematodes are so successful in the deep sea. This project comprised diverse deep-sea regions and involved innovative tools, such as molecular barcoding and metagenomics, as well as traditional

techniques, to try to investigate the role of nematode communities in the deep sea. This thesis comprised investigations of connectivity in the deep sea, as well as benthic-pelagic coupling.

## Aims of the thesis

Considering the main aspects of benthic-pelagic coupling, particulate OM flux to the sea floor and OM mineralization, the aim of this thesis was to gain new understanding about the potential factors shaping deep-sea meiobenthic communities. Moreover, new insights in spatial turnover, patchiness and habitat heterogeneity, as well as hydrodynamic effects based on sediment heterogeneity were studied in different deep-sea habitats, such as continental margins and abyssal plains. Finally, connectivity patterns in nematodes were analysed across different spatial scales and linked to environmental factors potentially responsible for their dispersal.

The following hypotheses were thus studied:

(1). Meiofauna and nematode standing-stock patterns are related to differences in surface primary productivity (**Chapters 1 and 2);**

(2). Estimated particulate organic carbon flux and seafloor labile organic matter determine small-scale patterns of meiofauna standing stocks (**Chapter 1**), enhancing niche differentiation and alpha diversity (**Chapter 3**);

(3). Nematode community composition responses to changes in primary productivity can be visualized by the increase of specific genera that are adapted to feed on fresh labile organic material as well as by the high nutritional quality of fatty acids found in these organisms (**Chapter 2)**;

(4). Selectivity in feeding activities in nematodes is reflected in their differential fatty acid composition (**Chapter 2**);

(5). High hydrodynamics, observed through a high variability in sediment composition, will result in a higher beta diversity (**Chapter 3**);

(6). High Nematode beta diversity observed across stations within the same bathymetric transect will be lower than across depth transects (**Chapter 3**);

(7). Connectivity of specific nematode taxa occurs between different depths located at the same continental slope (**Chapter 3**).

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# Chapter 1

# The link between meiofauna and surface productivity in the Southern Ocean

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## 1.1 Introduction

Surface-water productivity in the Southern Ocean (SO) is largely determined by the unique environmental features of this region. The SO consists of water masses south of the Polar Front (PF), which marks the northern extent of low salinity and cold water (Knox, 1994). Due to its vastness, the SO plays an important role in the global ocean circulation system and possesses the fastest surface ocean current in the world, the Antarctic Circumpolar Current (Griffiths, 2010). The SO receives low terrestrial input and its prevailing flow of energy is defined by phytoplankton surface productivity, followed by sinking and breakdown in the pelagic and benthic microbial loop (Griffiths, 2010; Rowe et al., 2008 and references therein). Nevertheless, benthic–pelagic coupling is strongly influenced by the high seasonality of primary production resulting in rather low resource availability during most parts of the year (Gooday, 2002; Peck et al., 2006). Surface primary production, together with varying water depth, current regimes and seasonal ice coverage over large parts of the SO, lead to complex interactions with the benthos, the richest element of the food web in terms of number of species (Griffiths, 2010; Gutzmann et al., 2004; Peck et al.,2006).

Export fluxes of particulate organic matter (POM) through the vertical water column frequently reflect general patterns of primary production (Lutz et al., 2002) and are considered an important process for the benthic–pelagic coupling, as most of the POM consists of labile carbon compounds (Sachs et al., 2009). However, the transport of POM to the deep sea is considered relatively inefficient, with only about 1 % to 3 % of the primary production reaching the deep seabed and the rest being broken down on its way to the bottom (Lutz et al., 2002).

Numerous variables determine the intensity of these export fluxes, including photosynthetic production, zooplankton grazing, oxidative depth- dependent remineralisation rates and water depth (Lutz et al., 2002). In addition, sea-ice formation and lateral advection linked mainly to the Antarctic Circumpolar Current may regulate primary production and affect the fate of surface-produced organic matter in the SO (Griffiths, 2010). Seasonal sea ice has been suggested to be an important environment for sea-ice algal photosynthesis, providing suitable light and nutrient levels, as well as contributing to organic carbon export to the deep sea, favouring benthic organisms‘ establishment (Brandt and Ebbe, 2009; Brandt et al., 2011; Guilini et al., 2013; Sachs et al., 2009;

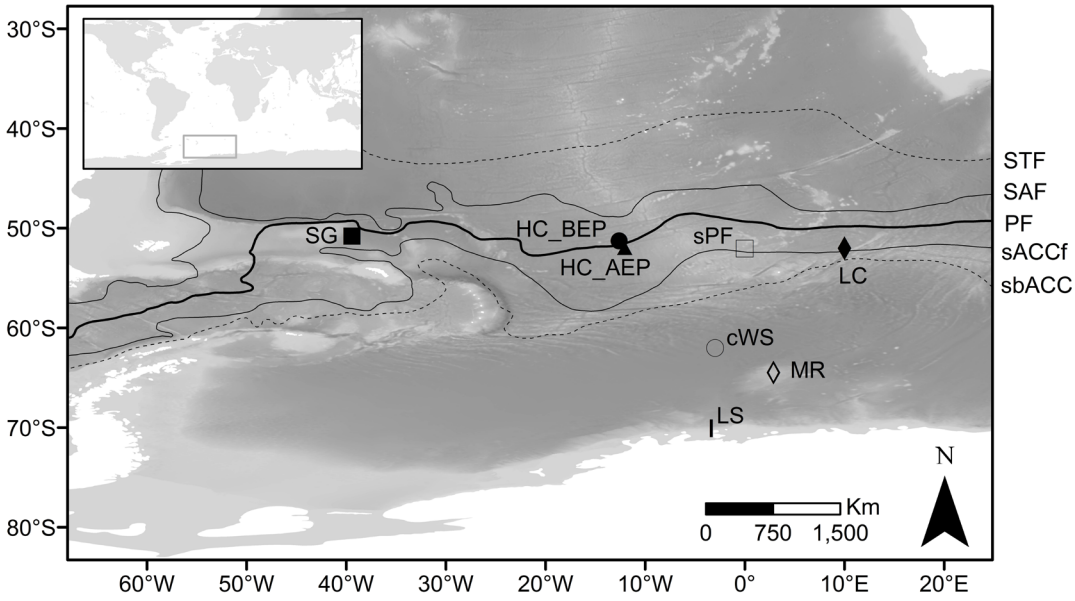


**Figure 1.1** Location of ANT-XXIV/2 and ANT-XXVIII/3 stations. Exact coordinates are given in Table 1. The map displays features of the Antarctic Circumpolar Current (Orsi et al., 2001): Subtropical Front (STF), Subantarctic Front (SAF), Polar Front (PF), southern Antarctic Circumpolar Current Front (sACCf) and southern boundary of the Antarctic Circumpolar Current (sbACC). Bathymetry data provided by ETOPO1 and world boundaries by ESRI (Amante and Eakins, 2009). Sampling stations are represented by symbols: SG (South Georgia), HC_BEP (High Chlorophyll before Eddy Pump), HC_AEP (High Clorophyll after Eddy Pump), sPF (South Polar Front), LC (Low Clorophyll), cWS (central Wedell Sea), MR (Maud Rise) and LS (Lazarev Sea). Source: the author (2016).

Vancoppenolle et al., 2013; Veit-Kohler et al., 2013).

Observed worldwide declines in standing stocks with depth are generally attributed to a decrease in food availability (e.g. POC flux, Rex et al., 2006), although other factors such as predation, competition and/or life history traits may also play a role (Ramirez-Llodra et al., 2010; Soetaert et al., 2002). A few studies report on the link between surface primary production and benthic communities in the SO. Some of them have highlighted the relationship between surface primary producers and standing stocks (i.e. abundance and biomass) of meiofauna and nematodes, but these studies are mainly restricted to shallow waters (Hauquier et al., 2011; Vanhove et al., 2000). Wei et al. (2010) used models to predict which factor contributed most to benthic–pelagic coupling worldwide. Shallow-water as well as deep-sea communities were found to be positively linked to surface primary productivity and particulate organic carbon (POC) flux.

Two recent papers compared the fatty acid composition of deep-sea nematodes to that of the sediment (Guilini et al., 2013) and studied the short-term response of nematode community structure to a natural phytodetritus pulse (Veit-Kohler et al., 2011). Both studies suggested a fresh phytodetritus diet based on (1) the relatively high proportion

of fatty acids indicative of phytodetritus in nematodes and (2) a vertical movement in the sediment towards surface layers as a response to food input. No studies in the SO, however, integrated seasonally-based surface primary production or estimated POC flux data with meiofauna standing stocks and seafloor labile organic matter in order to link those variables. Estimated POC fluxes reflect primary productivity processes and might be a better predictor of labile organic matter which arrives at the sea bottom than net primary productivity (NPP). Together with sediment Chlorophyll a (Chl*a*), estimated POC fluxes can reflect how much labile organic matter reaches the deep seabed, since the algorithm takes into account both NPP and water depth.

Metazoan meiofauna provide a good tool for studying standing stock patterns in the SO deep sea relative to surface productivity mainly due to their omnipresence and low mobility. Among the meiofaunal groups, nematodes usually dominate both in abundance and biomass, occurring frequently in percentages higher than 90 % (Giere, 2009).

In order to assess differences in meiofauna standing stocks (i.e. density and biomass) according to different surface-water productivity regimes in the SO, we integrated data from two sampling campaigns along a north–south (N–S) and an east–west (E–W) transect in the Atlantic part of the Southern ocean covering different water depths to test the following hypotheses:

(1). Meiofauna standing stocks in the SO are related to surface primary productivity.

(2). Estimated POC fluxes and sea-floor labile organic matter (depth-related variables) determine small-scale patterns of meiofauna standing stocks.

## 1.2 Material and methods

### 1.2.1 Study area and sampling procedure

During the RV Polarstern ANT-XXIV/2 (28.11.2007–04.02.2008) and ANT-XXVIII/3 (07.01.2012–07.03.2012) cruises (Bathmann and Herrmann, 2010; Wolf-Gladrow, 2013) to the SO, deep-sea sediment samples were collected in the

framework of ANDEEP- SYSTCO and SYSTCO II projects, respectively. The study area comprises of nine stations distributed along a N–S (Prime Meridian between 49°S and 70°S) and an E–W (between 10°E and 39°W) transect, covering depths ranging from 1935 m to 5323 m (Fig. 1.1 and Table 1.1). Samples from the ANT-XXVIII/3 campaign comprised both spatially different stations as well as one station which was sampled before and after an eddy (Eddy Pump project) event (Table 1.1).

Eddy Pump was a parallel project which intended to identify eddy structures between 50° and 60°S, where the upwelled deep-water masses interact with the atmosphere, in order to study the effect of circulation and carbon pumps. Sampling was conducted using a Multicorer (MUC) equipped with twelve Plexiglass cores to retrieve virtually undisturbed sediment cores. During the ANT- XXIV/2 campaign (henceforth referred to as NS-2007/8) the inner core diameter was 9.4 cm (equivalent to 69.4 $cm^2$ cross-sectional surface area) while for the ANT-XXVIII/3 (EW-2012) campaign it was 6 cm (25.5 $cm^2$ cross-sectional surface area).

**Table 1.1** Sampling details. PF = Polar Front. Source: research data (2016).

| Station | Deployment (core code) | Date | Depth (m) | Latitude | Longitude | Remarks |
|---|---|---|---|---|---|---|
| SG | 175-5 (**7**-8) | 04/03/2012 | 4154.2 | 50°46.69'S | 39°25.35'W | South Georgia |
| SG | 175-6 (**5**-6) | 04/03/2012 | 4155.2 | 50°46.59'S | 39°25.33'W | South Georgia |
| SG | 175-7 (**2**-3) | 04/03/2012 | 4154.2 | 50°46.60'S | 39°25.38'W | South Georgia |
| SG | 175-8 (1-**10**) | 04/03/2012 | 4154 | 50°46.60'S | 39°25.39'W | South Georgia |
| SG | 175-9 (**3**-6) | 04/03/2012 | 4152.1 | 50°46.57'S | 39°25.33'W | South Georgia |
| HC_AEP | 141-6 (3-**4**) | 18/02/2012 | 4113 | 51°15.98'S | 12°37.04'W | PF (After Eddy Pump) |
| HC_AEP | 141-9 (6-**8**) | 18/02/2012 | 4114 | 51°16.03'S | 12°37.06'W | PF (After Eddy Pump) |
| HC_AEP | 141-10 (3-**6**) | 19/02/2012 | 4113 | 51°15.97'S | 12°36.94'W | PF (After Eddy Pump) |
| HC_AEP | 141-11 (3-**5**) | 19/02/2012 | 4113.2 | 51°16.02'S | 12°37.12'W | PF (After Eddy Pump) |
| HC_BEP | 086-26 (4-**8**) | 01/02/2012 | 3966.2 | 51°58.87'S | 12°3.76'W | PF (Before Eddy Pump) |
| HC_BEP | 086-28 (6-**8**) | 01/02/2012 | 3968 | 51°58.74'S | 12°2.11'W | PF (Before Eddy Pump) |
| HC_BEP | 086-29 (**3**-5) | 01/02/2012 | 3970.8 | 51°58.78'S | 12°1.95'W | PF (Before Eddy Pump) |
| HC_BEP | 086-30 (**1**-3) | 02/02/2012 | 3965.4 | 51°58.91'S | 12°2.16'W | PF (Before Eddy Pump) |
| LC | 081-8 (**3**-4-6) | 19/01/2012 | 3760.5 | 51°59.99'S | 9°59.99'E | PF (Low Chlorophyll) |
| LC | 081-9 (8-**10**) | 19/01/2012 | 3760.7 | 52°0.01'S | 10°0.05'E | PF (Low Chlorophyll) |
| LC | 081-12 (**6**-8) | 19/01/2012 | 3757.5 | 51°59.93'S | 10°0.06'E | PF (Low Chlorophyll) |
| LC | 081-13 (**6**-7) | 19/01/2012 | 3760.5 | 52°0.042'S | 9°59.90'E | PF (Low Chlorophyll) |
| sPF | 013-12 (2-**6**-12) | 06/12/2007 | 2963 | 52° 2.22' S | 0° 1.04' W | South PF |
| sPF | 013-14 (**1**-**4**-9) | 06/12/2007 | 2970 | 52° 2.25' S | 0° 1.11' W | South PF |
| sPF(2nd) | 085-5 (2-**3**-11) | 26/01/2008 | 2965 | 52° 1.20' S | 0° 0.20' E | South PF (second visit) |
| sPF(2nd) | 085-7 (**1**-**4**-8) | 27/01/2008 | 2964 | 52° 1.53' S | 0° 0.16' E | South PF (second visit) |
| cWS | 033-10 (3-**4**) | 30/12/2007 | 5323 | 62° 0.80' S | 2° 59.05' W | Wedell Sea |
| MR | 039-10 (**5**) | 03/01/2008 | 2116 | 64° 28.83' S | 2° 52.48' E | Maud Rise |
| MR | 039-12 (**8**) | 03/01/2008 | 2123 | 64° 28.83' S | 2° 52.53' E | Maud Rise |
| MR | 039-14 (**11**) | 03/01/2008 | 2119 | 64° 28.84' S | 2° 52.49' E | Maud Rise |
| LS | 017-12 (**6**-8-11) | 22/12/2007 | 1935 | 70° 4.86' S | 3° 22.59' W | Lazarev Sea |
| LS | 017-14 (**1**-11-**12**) | 22/12/2007 | 1951 | 70° 4.80' S | 3° 22.71' W | Lazarev Sea |

### 1.2.2 Meiofauna sample processing

At every station, cores for community analysis were sliced into 1-cm layers down to 5 cm and together with the supernatant water (added to the first layer) preserved in a 4–7 % borax-buffered formaldehyde solution. Samples were washed over stacked sieves with a 1000 µm mesh and a 32 µm mesh to retain the meiofauna fraction and remove smaller particles. The 32 µm fraction was then elutriated and centrifuged three times (G-force=6056.12 g, RPM=4000, NS-2007/8, and RPM=5421, EW-2012) with colloidal silicagel Levasil (specific gravity 1.17), for the NS-2007/8 stations, and LUDOX HS40 Dupont (specific gravity 1.19), for the EW-2012 stations, as a flotation medium (Heip et al., 1985). After being stained with Rose Bengal, all metazoan organisms were classified at higher taxon level following Higgins and Thiel (1988) and counted under a stereo-microscope (50x magnification).

Nematodes were hand-picked and mounted in glass slides. The length (excluding filiform tail tips) and maximum body width of nematodes (100 specimens per layer if possible) were measured using the compound microscope Leica DMR and Leica LAS 3.3 imaging software. Nematode biomass was then calculated according to Andrassy's formula $G=a^2 \times b/1.6 \times 106$, where G= wet weight in µg, a= maximum body diameter (µm) and b= total length (µm) (Andrássy, 1956). A dry-to-wet ratio of 0.25 was assumed (Heip et al., 1985).

### 1.2.3 Environmental parameters

Cores for environmental analyses were obtained from the same MUC deployment as cores for meiofauna analysis. Previously frozen at -80 °C, each 1 cm-thick slice was subsampled and subsequently analysed for biochemical parameters down to 5 cm sediment depth. For total sedimentary organic carbon (TOC) and nitrogen (TN), samples were lyophilized, homogenized and acidified with 1 % HCl and the TOC and TN contents were measured using a Flash EA 1112 + Mas 200 elemental analyser. Samples for sediment Chl*a* were lyophilized, homogenized and the pigments extracted in 90 % acetone, after which they were separated using reverse-phase HPLC, and measured with a Gibson fluorescence detector (Wright and Jeffrey, 1997). NPP values were extracted from the Vertically Generalized Production Model (VGPM, resolution: 1°) described by Behrenfeld and Falkowski (1997). The VGPM model is a chlorophyll-based algorithm that estimates NPP values using satellite measurements of sea surface temperature,

surface Chl*a* and photosynthetically active radiation.

The available HDF format data were extracted using the Marine Geospatial Ecology Tools for ArcGIS and converted to raster using the software ArcGIS. Due to the long ice-coverage period in the Southern Ocean some NPP values could not be obtained from the satellite VGPM data. The values for Seasonal Variation Index (SVI) measurements and consequently for NPP and POC were then restricted to the ice-free months. The POC flux to the ocean floor was estimated based on the water depth ($z_e$) and seasonal variation in NPP calculated as the standard deviation divided by the mean of monthly NPP values (Lutz et al., 2002; Lutz et al., 2007):

$$\mathrm{SVI} = \frac{\sigma(\mathrm{NPP})}{\overline{\mathrm{NPP}}}, \text{ and } \mathrm{POC} = \mathrm{pr_d} \exp\left(\frac{-z_e}{\mathrm{rl_d}}\right) + \mathrm{pr_r}$$

$Pr_d$, $rl_d$ and $pr_r$ are functional forms of coefficient algorithms and are calculated as follows:

$pr_d = (31*SVI^2 + 49*SVI + 7.8)\ 10^{-3}$;

$rl_d = 1400 \exp(-0.54*SVI)$;

$pr_r = (2.6*SVI^2 - 4.2*SVI + 4.8)\ 10^{-3}$.

### 1.2.4 Data analysis

The multivariate assemblage data on higher taxon level was analysed by means of non-parametric permutational ANOVA based on Bray–Curtis similarities (Anderson et al., 2007) to assess N–S and E–W differences. N–S and E–W groupings were used to facilitate comprehension. The dataset was investigated using either a fully crossed three-factor model design (Station [ST]:fixed; Slice [SL]: fixed, Replicates [Rep]: random, nested within [ST]), to investigate differences between sediment layers, or a one-factor model design ([ST]: fixed) using the software PERMANOVA+ for PRIMER (Anderson et al., 2007). The one-factor design ([ST]: fixed) was used to compare only differences between stations.

A PERMDISP analysis was conducted to test for homogeneity of multivariate dispersions using distances among centroids. Pair-wise t-tests were performed between all pairs of levels to determine where the differences between each combination were located. This was followed by a SIMPER analysis to identify which meiofauna taxa were responsible for the dissimilarities between stations. A three-way non-parametric

permutational ANOVA was also performed on the biomass data, following the same procedure as for the multivariate assemblage data. Meiofauna taxon richness was used as a diversity index (S).

The set of seafloor and surface environmental data (TOC, TN, Chl*a*/TOC, Chl*a*, POC, NPP, SVI and Depth) was tested for collinearity with Draftsman plots and partial Spearman correlations (given depth) using R (Kim, 2013). Benthic variable analyses (TOC, TN, Chl*a*/TOC and Ch*la*) were only conducted for the EW-2012 samples due to the lack of a complete environmental dataset for the NS2007/8 campaign. DISTLM (distance-based linear model) routines were performed to analyse the relationship between meiofaunal assemblages and biomass, and the environmental variables. The DISTLM was built on 'step-wise' selection procedure and adjusted $R^2$ was chosen as the selection criterion (Anderson et al., 2007).

## 1.3 Results

### 1.3.1 Trends in NPP and estimated POC flux

NPP monthly average values ranged from 84.7 g C $m^{-2}$ $month^{-1}$ to 574.2 g C $m^{-2}$ $month^{-1}$ (Fig. 1.2). A significant increase in monthly NPP was observed along the E–W transect for all stations (EW-2012) from the LC to the SG station (one-way PERMANOVA, $p < 0.001$; pair-wise t-test, $p < 0.001$, Table S1). This longitudinal gradient was particularly more pronounced at the end of Antarctic summer (January/ February) (Fig. 1.2). In addition, the monthly NPP values at the LC station fell within the range of the south PF stations values of the NS-2007/8 campaign, while NPP values at the MR station grouped together with SG station values. Throughout most of the Antarctic summer, SG exhibited the most elevated NPP values when compared to the other stations, with monthly NPP values up to 972.3 g C $m^{-2}$ $month^{-1}$. Additionally, seasonal variability was greatest at MR (0.9), followed by HC_AEP (0.74) and SG (0.69). The longest ice-coverage period was observed for the southernmost station LS (11 months) followed by MR (9 months) and cWS (8 months). Average NPP was positively correlated with POC ($r = 0.81$, partial Spearman correlation) for the NS-2007/8 sites and with depth for the EW-2012 stations ($r = 0.80$, Spearman correlation).

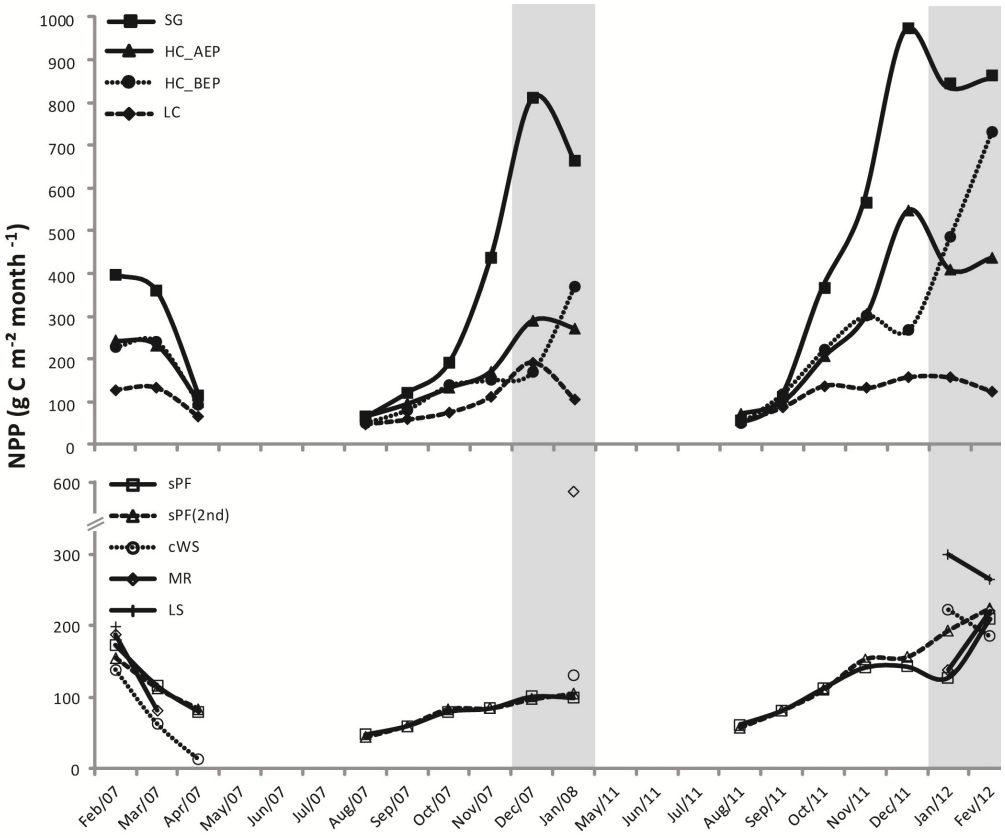


**Figure 1.2** Satellite-based estimates of Net Primary Productivity (NPP) monthly variation in the Southern Ocean for the ANT-XXIV/2 (bottom) and ANT- XXVIII/3 (top) stations. Grey zones represent the sampling period. Source: research data (2016).

Average estimated POC fluxes to the seafloor varied from 3.4 mg $m^{-2}$ $month^{-1}$ up to 13.6 mg $m^{-2}$ $month^{-1}$ (Fig. 1.3). They slightly increased eastwards (one-way PERMANOVA, $p < 0.001$; pair-wise t-test, $p < 0.001$, Table S1; Fig. 1.3) and overall declined with depth ($r = -0.76$, NS-2007/8, and $r = -0.99$, EW-2012, partial Spearman rank correlation). Fluxes at station MR were at least two times higher than at all other stations whilst cWS displayed the lowest values (Fig. 1.3).

### 1.3.2 Benthic environment and metazoan meiofauna

Sediment Chl*a* concentrations (only measured for EW-2012 stations) significantly differed between stations along the E–W transect (one-way PERMANOVA, $p < 0.0003$, pair-wise t-test, $p < 0.001$, Table S1). There was a westward increase towards SG, where Chl*a* concentrations reached 18.8 µg $g^{-1}$ sediment (Fig. 1.3).

A total of 23 higher metazoan meiofauna groups were identified. Taxon richness (S) varied from five to sixteen taxa and differed significantly between stations (one-way PERMANOVA, $p < 0.001$, Table 1.2). Nevertheless, pair-wise comparisons revealed only

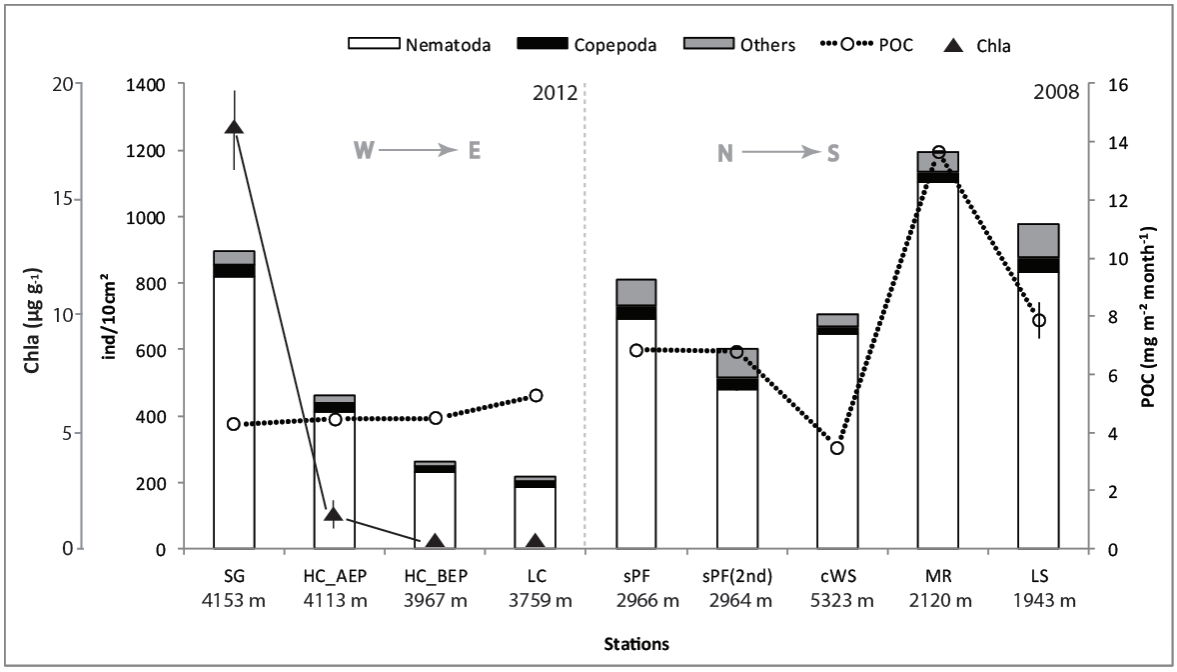


**Figure 1.3** Meiofauna densities (ind/10cm²) and seafloor Particulate Organic Carbon (POC) fluxes (mg $g^{-2}$ $month^{-1}$) for the ANT-XXIV/2 and ANT- XXVIII/3 stations, and Chlorophyll a (Chla, µg $g^{-1}$) for the ANT-2012 stations. Source: research data (2016).

significant differences between MR and EW-2012 stations (SG, HC_AEP, HC_BEP and LC), and between SG and the stations LS and sPF (2nd). The taxa Crinoidea and Gastropoda (macrofauna), and Loricifera and Tantulocarida were restricted to NS-2007/8 stations. The highest meiofauna densities were detected in MR and LS, while at LC and HC-BEP lowest densities were found (Table 1.2). At all stations, nematodes were consistently the dominant taxon (84.4–92.4 %), followed by copepods (2.6–8.2 %) and nauplius larvae (2.1–10.1 %). Densities of all three taxa followed the same pattern, with higher abundance found at MR and LS and lower abundance at LC (Table 1.2). Meiofauna densities significantly

**Table 1.2** Overview per station of taxon richness (number of groups), meiofauna density (ind/10cm²), nematode density (ind/10cm²) and biomass (µg dwt) and nematode relative abundance (%) for ANT-XXIV/2 and ANT-XXVIII/3 stations. Source: research data (2016).

| Station | Taxon richness | Meiofauna density | Nematode density | Nematode biomass | Nematode relative abundance |
|---|---|---|---|---|---|
| SG | 8.5 ± 1.8 | 893.3 ± 218.0 | 819.6 ± 197.4 | 8.15 ± 1.7 | 85.88 ± 3 |
| HC_AEP | 8.0 ± 1.1 | 461.5 ± 103.9 | 410.1 ± 99.8 | 3.48 ± 2.3 | 85.39 ± 4.4 |
| HC_BEP | 6.0 ± 0.8 | 263.6 ± 87.9 | 230.3 ± 76.2 | 0.80 ± 0.5 | 63.70 ± 3.4 |
| LC | 6.75 ± 1.3 | 219.2 ± 86.1 | 185.1 ± 78.4 | 3.07 ± 0.7 | 71.55 ± 8.6 |
| sPF | 16.0 | 807.4 ± 184.3 | 693.8 ± 173.5 | 6.70 ± 0.2 | 77.11 ± 2.4 |
| sPF(2nd) | 16.5 ± 0.7 | 599.8 ± 40.4 | 480.1 ± 17.2 | 7.35 ± 2.3 | 75.09 ± 1.2 |
| cWS | 11.0 | 704.2 | 648.4 | 11.75 | 92.77 |
| MR | 14.3 ± 1.1 | 1192.5 ± 248.1 | 1102.4 ± 232.5 | 4.99 ± 1.5 | 78.39 ± 3.1 |
| LS | 18.0 ± 1.4 | 978.1 ± 110.4 | 833.1 ± 101.6 | 12.45 ± 3.0 | 79.38 ± 3.2 |

**Table 1.3** Results from multivariate PERMANOVA analyses for differences in meiofauna, nematode and nematode biomass. Source: research data (2016).

| Source | df | SS | MS | Pseudo-F | *P*(perm) | Perms |
|---|---|---|---|---|---|---|
| **Meiofauna** | | | | | | |
| Station | 8 | 19238 | 2404.7 | 10.111 | **0.0001** | 9915 |
| Res | 18 | 4280.8 | 237.82 | | | |
| Total | 26 | 23518 | | | | |
| **Nematode** | | | | | | |
| Station | 8 | 18564 | 2320.5 | 9.376 | **0.0001** | 9932 |
| Res | 18 | 4454.8 | 247.49 | | | |
| Total | 26 | 23019 | | | | |
| **Nematode biomass** | | | | | | |
| Station | 8 | 25604 | 3200.5 | 98.058 | **0.0001** | 9934 |
| Res | 141 | 46020 | 326.38 | | | |
| Total | 149 | 71624 | | | | |

differed between stations (one-way PERMANOVA, $p < 0.001$, Table 1.3) and pair-wise comparisons can be found in Table S2. Nematode densities between stations were significantly different as shown by PERMANOVA tests ($p < 0.001$, Table 1.3) and pair-wise comparisons revealed significant dissimilarities between most EW-2012 stations (except for HC_BEP and LC). Nematode densities for stations HC_AEP, HC_BEP and LC were also significantly distinct from MR and LS stations, and HC_BEP and LC from sPF station. SIMPER analyses revealed that the dissimilarities between stations were mainly a result of differences in the relative abundance of nematodes, copepods and nauplii. When only the first sediment layer (0–1 cm) was considered (one-way PERMANOVA, $p < 0.001$) pairwise comparisons for EW-2012 revealed significant differences for meiofauna and nematode densities between all stations except for SG and HC_AEP, and HC_BEP and LC. Although nematode relative abundance diminished on average eastwards, this trend could not be tested due to a significant PERMDISP before the PERMANOVA analysis ($p < 0.0174$).

PERMANOVA analysis of individual nematode biomass indicated significant differences between stations ($p < 0.001$, Table 1.3). Pair-wise t-tests revealed significantly higher nematode biomass for SG, compared to the other EW-2012 stations. Nematode biomass at the NS-2007/8 stations did not diverge significantly as shown by the pairwise tests. Nevertheless, higher biomass values for all stations were present in cWS and LS (Table 1.2).

The results for the three-way PERMANOVA ([ST] and [SL] fixed and [Rep] random, nested in [ST]) were not considered for analysis due to significant p values found during PERMDISP routines ($p < 0.001$), indicating unequal dispersion within groups, making it difficult to distinguish real differences between sediment layers. Although a significant PERMDISP might mean that just part of the effect is due to multivariate

dispersion the data was not considered to avoid biases in the results and possible wrong statements.

### 1.3.3 Relation between environmental data and meiofaunal densities

Partial Spearman correlations between seafloor environmental variables and meiofauna densities (0–5 cm) for the EW-2012 samples revealed significant ($p < 0.05$) positive relationships for Chl*a* ($r = 0.79$) and Chl*a*/TOC ($r = 0.94$). In addition, densities of surface-dwelling nematodes (0–1 cm) had strong correlations with Chl*a* ($r = 0.96$). The DISTLM analysis for the EW-2012 stations indicated a significant effect of sediment Chl*a*/TOC on the meiofauna and nematode community composition, which was responsible for 60 % and 90 % of the entire assemblage variation, respectively (Table S2). Estimated POC fluxes were negatively correlated with meiofauna densities ($r = -0.67$) for the E–W sites and with nematode biomass ($r = -0.71$) for the N–S sites, and positively correlated with nematode densities ($r = 0.92$) for the NS-2007/8 stations.

Significant correlations occurred between depth and densities of meiofauna ($r = 0.82$) for the E–W sites, and between depth and nematode densities for both E–W and N–S stations ($r = 0.71$ and $r = -0.73$, respectively). No taxa richness-depth trend was observed. Correlations between NPP and SVI on one hand and meiofauna and nematode densities on the other hand were not significant. DISTLM analyses exhibited a significant effect of the estimated POC fluxes ($p < 0.0016$, Tables S3 and S4) on the meiofauna and nematode densities when just the first-centimetre layer was analysed (both adjusted $R^2 = 0.228$). These tests revealed that estimated POC fluxes are responsible for 18 % of the total meiofauna density variation. For the nematode total density over 5 cm sediment depth, POC and average NPP accounted for 43 % of total variation (Table S3).

## 1.4 Discussion

### 1.4.1 Trends in NPP and estimated POC flux

The east–west increase in NPP in the Atlantic part of the Southern Ocean is in agreement with previous *in situ* and satellite-based measurements for the SO (Atkinson et al., 2001; Demidov et al., 2012), whilst NPP values were higher than those reported previ-

ously for the SO (Lutz et al., 2007). An elevated NPP at SG was expected, as this region is characterized by local nutrient resupply due to upwelling processes which supports high phytoplankton productivity (Brandon et al., 2000; Orsi et al., 1995; Whitehouse et al., 1996). The low NPP values found for cWS and LS stations were possibly underestimated as a result of the long ice coverage period during which Chl*a* satellite measurements were not available. As such, sea-ice algal productivity is not taken into account although it can be considered an important food source in sea-ice ecosystems, accounting for 25 % of total primary production (Arrigo and Thomas, 2004).

A high NPP peak at the MR site was reported by other studies (Beckmann et al., 2001; Brandt et al., 2011) and surface-water sampling at this station indicated a vigorous pelagic food web associated with a rich ice-edge bloom (Brandt et al., 2011). These ice-covered areas are also favoured during sea-ice decay in summer, which creates a shallow mixed layer that significantly enhances primary production (Flores et al., 2011). Therefore, the high NPP peak observed for the MR station in January 2008 could be a response to ice melting and subsequent ice-algae sedimentation in the form of dissolved or particulate organic carbon, living cells or aggregations of dead and living cells (Arrigo and Thomas, 2004).

A slight increase in estimated POC deposition was associated with strong decreasing benthic Chl*a* concentrations and surface NPP values for the EW-2012 stations. Particularly for station SG, higher estimated POC estimations were expected since NPP values are higher than for other stations. So far, however, the processes influencing actual POC fluxes are not quantitatively understood (De La Rocha and Passow, 2007). POC flux estimates are water-depth dependent but they do not take into account small-scale patterns nor do they include biological-pump interrelated processes, such as (dis)aggregation of organic-rich particles (De La Rocha and Passow, 2007; Lutz et al., 2007). Its values are highly dependent on depth differences, which play a crucial role in the transfer efficiency of POC (De La Rocha and Passow, 2007; Lutz et al., 2007), illustrated by the negative correlation between estimated POC flux and water depth. This is possibly the reason why POC values do not vary as greatly for the EW-2012 stations (3760.5–4155.5 m) as they do for the NS-2007/8 stations (1935–5323 m).

### 1.4.2 Benthic-pelagic coupling

At the highly productive SG site, highest sediment Chl*a* values were in accor-

dance with the E–W NPP increase. Meiofauna and nematode densities and nematode relative abundance also increased westwards. The nematode densities observed for SG were higher than those reported in other abyssal plain studies (Sebastian et al., 2007; Vanreusel et al., 1995). Based on the observed patterns for NPP and Chl*a* in this study, we can conclude that the meiofauna and nematode communities are partially reliant on the surface primary productivity as their primary food source, despite the great water depth. The same outcome was already reported in other studies for other areas (Danovaro et al., 1999; Gooday, 2002; Pape et al., 2013b; Smith et al., 2008; Vanreusel et al., 1995). This hypothesis is corroborated by recent fatty acid and stable isotope studies (Guilini et al., 2013; Veit-Köhler et al., 2013), which clearly show the dependency of meiofauna on fresh phytodetritus at the NS-2007/8 stations. Sediment Chl*a* concentrations measured at the NS-2007/8 stations by Veit-Köhler et al. (2011, 2013) revealed higher Chl*a* values at the sPF stations, followed by LS and cWS. Nevertheless, these values may reflect local blooming and settlement events. The high meiofauna densities observed at the MR and LS stations could be then explained by seasonal ice coverage and elevated primary production at the seasonal ice edge (Froneman et al., 2004; Hunt et al., 2011; Flores et al., 2011; Soreide et al., 2010). Increases in benthic densities in areas covered by sea ice were not considered in previous studies. However, heavy carbon isotope signatures found for nematodes (-21.5–19.3 ‰) from the Weddell Sea might indicate that rapidly sinking ice algae may be a significant food source for metazoan meiobenthos (Moens et al., 2007). Likewise, enriched carbon isotope values for the meiofauna from the LS station (-25.4–-24.9 ‰), influenced by ice most of the year, were observed by Veit-Köhler et al. (2013), indicating the possible inclusion of isotopically enriched ice-algae in the meiofauna diet.

Although POC fluxes estimated from satellite images by means of the VGPM algorithm must be interpreted with caution, large-scale patterns can be inferred from this algorithm. There is a clear separation between stations south of the PF, which yielded higher meiofauna abundances and estimated POC fluxes (except for the cWS site), and stations at the PF, with lower meiofauna densities and POC fluxes. The lower densities observed for SG in comparison with the MR and LS sites (located closer to the continent and with much lower, though underestimated, NPP values) were not expected. This divergent pattern emphasizes the potential contribution of ice algae to POC fluxes. Conversely, great interannual variability of nutrients in the PF region could also play a role (Demidov et al., 2012). This high instability might be caused by the magnitude of phytoplankton nutrient utilization and the extent to which nutrients are recycled in

the mixed layer. In addition, S-shaped meanders formed in this area by the influence of two water masses, the South Georgia Shelf Water and the Antarctic Zone Water, create a turbulent environment (Brandon et al., 2000; Peterson and Stramma, 1991). These meanders have different surface temperatures and, together with strong currents, create a very complex area that is difficult to model by the algorithm used in this research (Lutz et al., 2002, 2007).

Taxon richness significantly differed between the NS-2007/8 and EW-2012 stations, with the former yielding higher diversity indices. The considerable variation in NPP observed at the PF stations and pulse nutrient loading can restrict resource exploitation to part of the annual cycle of production and consequently suppress diversity (Pape et al., 2013a). Moreover, the great variation in depth between the NS and the EW transects might also be responsible for the higher density and diversity found at the south PF stations. Conversely, constant NPP levels observed at stations south of the PF potentially favour feeding over a longer time period and can thus support more taxa (Rex and Etter, 2010). The southern sites are likely to be more stable due to less influence of strong currents, proximity to the continent and ice coverage in the winter, potentially favouring more diverse and steady communities, as well as higher standing stocks.

The lack of differences in nematode biomass linked to primary production between sites contrasts with studies conducted elsewhere in deep-sea environments (Billett et al., 2013; Gooday, 2002; Gontikaki et al., 2011; Pape et al., 2013b; Thistle, 2003; Wolff et al., 2011). Although the link between productivity and standing stock is well established for shallow water and deep-sea environments (Rex et al., 2006; Wei et al., 2010), it is less clear how standing stock is partitioned among species. Food supply can be foraged by a single species so that differences are masked when higher-group comparisons are made (Rex and Etter, 2010). Nevertheless, although no nematode biomass gradient was observed in this study, SG displayed the highest biomass for the PF-located stations, being positively associated with the highest PF-NPP and sediment Chl*a* values. Importantly, south of the PF, cWS and LS displayed the highest nematode biomass values as well as the highest observed taxon richness thereby supporting the biomass-diversity stability hypothesis of Cardinale et al. (2013), who suggests that more diverse communities are generally more efficient in capturing resources and thus able to produce more biomass than less diverse communities.

Although marine benthos reflect patterns in surface net primary production and

POC fluxes on a worldwide scale, meiobenthic communities in the SO display strong density heterogeneity or patchiness along a broad scale range. This high patchiness is the main factor causing high alpha and beta diversity at small spatial scale in the deep sea and thus enhancing deep-sea biodiversity (Danovaro et al., 2013). No significant link was found between meiofauna standing stocks and NPP. In addition, POC was negatively correlated with the meiofauna for the EW-2012 sites and positively correlated with nematodes for the NS-2007/8 sites. This implies that the use of estimated POC fluxes might not reflect the actual benthic food influx and consumption, as was also observed by Wei et al. (2010).

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## 1.6 Supplementary data

**Table S1.** Results of univariate PERMANOVA analyses for differences in abiotic variables. Source: research data (2016).

**NPP**

| Source | df | SS | MS | Pseudo-F | P(perm) | perms |
|---|---|---|---|---|---|---|
| Station | 8 | 1.03E+10 | 1.29E+09 | 5.20E+09 | 0.0001 | 9954 |
| Res | 18 | 44.569 | 0.24761 | | | |
| Total | 26 | 1.03E+10 | | | | |

**POC**

| Source | df | SS | MS | Pseudo-F | P(perm) | perms |
|---|---|---|---|---|---|---|
| Station | 8 | 2.27E+00 | 2.84E-01 | 1238.3 | 0.0001 | 9933 |
| Res | 18 | 4.12E-03 | 2.29E-04 | | | |
| Total | 26 | 2.27E+00 | | | | |

**Chla**

| Source | df | SS | MS | Pseudo-F | P(MC) | perms |
|---|---|---|---|---|---|---|
| Station | 3 | 418.01 | 139.34 | 87.199 | 0.0003 | 10 |
| Res | 4 | 63.917 | 15.979 | | | |
| Total | 7 | 424.4 | | | | |

**Table S2.** Results from pair-wise multivariate PERMANOVA analysis for differences in meiofauna community structure. Source: research data (2016).

| Groups | t | P(perm) | perms | P(MC) |
|---|---|---|---|---|
| SG, HC_AEP | 35.082 | 0.0238 | 126 | 0.0059 |
| SG, HC_BEP | 46.774 | 0.008 | 126 | 0.0008 |
| SG, LC | 4.672 | 0.0106 | 126 | 0.0005 |
| SG, sPF | 10.253 | 0.3839 | 21 | 0.3535 |
| SG, sPF(2nd) | 24.414 | 0.0497 | 21 | 0.05 |
| SG, cWS | 20.425 | 0.1654 | 6 | 0.0577 |
| SG, MR | 1.557 | 0.1404 | 56 | 0.1424 |
| SG, LS | 0.86279 | 0.5197 | 21 | 0.4659 |
| HC_AEP, HC_BEP | 23.523 | 0.0291 | 35 | 0.0359 |
| HC_AEP, LC | 26.901 | 0.0267 | 35 | 0.0189 |
| HC_AEP, sPF | 26.004 | 0.0632 | 15 | 0.0438 |
| HC_AEP, sPF(2nd) | 15.986 | 0.2708 | 15 | 0.1513 |
| HC_AEP, cWS | 3.135 | 0.2018 | 5 | 0.027 |
| HC_AEP, MR | 50.228 | 0.0271 | 35 | 0.0016 |
| HC_AEP, LS | 37.977 | 0.068 | 15 | 0.012 |
| HC_BEP, LC | 0.70897 | 0.4845 | 35 | 0.5363 |
| HC_BEP, sPF | 3.205 | 0.0695 | 15 | 0.0142 |
| HC_BEP, sPF(2nd) | 26.592 | 0.0642 | 15 | 0.0368 |
| HC_BEP, cWS | 28.209 | 0.2001 | 5 | 0.034 |
| HC_BEP, MR | 49.663 | 0.0284 | 35 | 0.0012 |
| HC_BEP, LS | 38.368 | 0.0671 | 15 | 0.008 |
| LC, sPF | 30.985 | 0.0642 | 15 | 0.0152 |
| LC, sPF(2nd) | 26.716 | 0.0658 | 15 | 0.0285 |
| LC, cWS | 25.725 | 0.2029 | 5 | 0.0404 |
| LC, MR | 46.277 | 0.0272 | 35 | 0.0017 |
| LC, LS | 35.739 | 0.0663 | 15 | 0.0078 |
| sPF, sPF(2nd) | 18.413 | 0.3381 | 3 | 0.1867 |
| sPF, cWS | 18.499 | 0.3275 | 3 | 0.2479 |
| sPF, MR | 22.123 | 0.1014 | 10 | 0.0853 |
| sPF, LS | 11.447 | 0.6643 | 3 | 0.3703 |
| sPF(2nd), cWS | 82.544 | 0.3225 | 3 | 0.0507 |
| sPF(2nd), MR | 46.293 | 0.0998 | 10 | 0.009 |
| sPF(2nd), LS | 53.091 | 0.3353 | 3 | 0.0259 |
| cWS, MR | 31.617 | 0.247 | 4 | 0.0505 |
| cWS, LS | 39.331 | 0.3267 | 3 | 0.1119 |
| MR, LS | 17.177 | 0.1994 | 10 | 0.1539 |

**Table S3.** Distance-based linear model (DistLM) marginal tests for higher taxonomical groups and Nematoda, and selected environmental variables. AV= Average net primary productivity, SVI= Seasonal variation, POC= Particulate organic carbon. Source: research data (2016).

**Meiofauna**

| Variable | SS(trace) | Pseudo-F | P | Prop. |
|---|---|---|---|---|
| AV | 2556 | 30.483 | 0.0627 | 0.10868 |
| SVI | 672.33 | 0.73571 | 0.45 | 2.86E+02 |
| POC | 4199.3 | 54.342 | 0.0102 | 0.17855 |

**Nematoda**

| Variable | SS(trace) | Pseudo-F | P | Prop. |
|---|---|---|---|---|
| AV | 6.43E+09 | 71.845 | 0.0129 | 0.22323 |
| SVI | 2.14E+09 | 20.092 | 0.163 | 7.44E+01 |
| POC | 1.02E+09 | 13.645 | 0.0006 | 0.35308 |

**Meiofauna (0-1cm)**

| Variable | SS(trace) | Pseudo-F | P | Prop. |
|---|---|---|---|---|
| AV | 1835.5 | 15.042 | 0.2109 | 5.68E+02 |
| SVI | 450.31 | 0.35299 | 0.7251 | 1.39E+02 |
| POC | 8335.9 | 86.806 | 0.0015 | 0.25773 |

**Nematoda (0-1cm)**

| Variable | SS(trace) | Pseudo-F | P | Prop. |
|---|---|---|---|---|
| AV | 1835.5 | 15.042 | 0.2187 | 5.68E+02 |
| SVI | 450.31 | 0.35299 | 0.7258 | 1.39E+02 |
| POC | 8335.9 | 86.806 | 0.0022 | 0.25773 |

**Meiofauna E-W 2012**

| Variable | SS(trace) | Pseudo-F | P | Prop. |
|---|---|---|---|---|
| Chl a | 2697.8 | 30.154 | 0.1015 | 0.33447 |
| Chla/TOC | 4866.2 | 9.125 | 0.0007 | 0.60331 |
| % TN | 392.64 | 0.30702 | 0.6905 | 4.87E+02 |
| % TOC | 532.6 | 0.4242 | 0.6299 | 6.60E+02 |

**Nematoda E-W 2012**

| Variable | SS(trace) | Pseudo-F | P | Prop. |
|---|---|---|---|---|
| Chl a | 4.62E+09 | 98.029 | 0.025 | 0.62032 |
| Chla/TOC | 6.73E+09 | 56.522 | 0.0009 | 0.90403 |
| % TN | 33185 | 0.27983 | 0.6157 | 4.46E+01 |
| % TOC | 46016 | 0.39515 | 0.5436 | 6.18E+02 |

**Table S4.** Distance-based linear model (DistLM) sequential tests for higher taxonomical groups and Nematoda, and selected environmental variables. Source: research data (2016).

**Meiofauna**

| Variable | Adj $R^2$ | SS(trace) | Pseudo-F | P | Prop. | Cumul. | res.df |
|---|---|---|---|---|---|---|---|
| +POC | 0.1457 | 4199.3 | 54.342 | 0.0116 | 0.17855 | 0.17855 | 25 |
| +AV | 0.17859 | 1486.9 | 20.012 | 0.1385 | 6.32E+02 | 0.24178 | 24 |
| +SVI | 0.21218 | 1441.8 | 20.232 | 0.1443 | 6.13E+02 | 0.30308 | 23 |

**Nematoda**

| Variable | Adj $R^2$ | SS(trace) | Pseudo-F | P | Prop. | Cumul. | res.df |
|---|---|---|---|---|---|---|---|
| +POC | 0.32721 | 1.02E+09 | 13.645 | 0.0016 | 0.35308 | 0.35308 | 25 |
| +AV | 0.43166 | 3.52E+09 | 55.949 | 0.0268 | 0.1223 | 0.47538 | 24 |
| +SVI | 0.48506 | 1.99E+09 | 34.888 | 0.0787 | 6.91E+02 | 0.54448 | 23 |

**Meiofauna (0-1cm)**

| Variable | Adj $R^2$ | SS(trace) | Pseudo-F | P | Prop. | Cumul. | res.df |
|---|---|---|---|---|---|---|---|
| +POC | 0.22804 | 8335.9 | 86.806 | 0.0018 | 0.25773 | 0.25773 | 25 |

**Nematoda (0-1cm)**

| Variable | Adj $R^2$ | SS(trace) | Pseudo-F | P | Prop. | Cumul. | res.df |
|---|---|---|---|---|---|---|---|
| +POC | 0.22804 | 8335.9 | 86.806 | 0.0026 | 0.25773 | 0.25773 | 25 |

**Meiofauna E-W 2012**

| Variable | Adj $R^2$ | SS(trace) | Pseudo-F | P | Prop. | Cumul. | res.df |
|---|---|---|---|---|---|---|---|
| +Chla/TOC | 0.53719 | 4866.2 | 9.125 | 0.0007 | 0.60331 | 0.60331 | 6 |
| +% TOC | 0.54618 | 585.08 | 11.189 | 0.3273 | 7.25E+02 | 0.67584 | 5 |
| +Chla | 0.57055 | 635.21 | 12.837 | 0.3153 | 7.88E+02 | 0.7546 | 4 |

**Nematoda E-W 2012**

| Variable | Adj $R^2$ | SS(trace) | Pseudo-F | P | Prop. | Cumul. | res.df |
|---|---|---|---|---|---|---|---|
| +Chla/TOC | 0.88804 | 6.73E+09 | 56.522 | 0.0006 | 0.90403 | 0.90403 | 6 |
| +% TOC | 0.90151 | 19080 | 18.209 | 0.2319 | 2.56E+01 | 0.92965 | 5 |

# Chapter 2

# Nematode community composition and feeding shaped by contrasting productivity regimes in the Southern Ocean

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## 2.1 Introduction

Marine sediments are considered major carbon reservoirs in the global carbon cycle (Jamieson et al., 2013; Killops and Killops, 2005; Serpetti et al., 2013). In general, surface primary productivity by phytoplankton, together with water depth and distance from land, is one of the main determinants of the flux of organic matter (OM) to the seabed, which in turn regulates rates of carbon mineralization and/or burial of organic matter in deeper sediment layers (Fischer et al., 2000; Middelburg et al., 1997). Although most of the OM (> 90 %) produced by the phytoplankton is directly consumed in the water column, 70–95 % of the particulate OM arriving at the seafloor is still composed of labile carbon compounds (Boon and Duineveld, 1996; Sachs et al., 2009). Part of the phytoplanktonic remains, together with zooplanktonic faecal pellets, form fluffy aggregates of marine snow, rapidly sinking to the sea bottom (Killops and Killops, 2005). After reaching the bottom, OM mineralization occurs mainly at the sediment surface (Killops and Killops, 2005; Nascimento et al., 2012).

When arriving at the seabed, microbial degradation becomes the dominant process directly or indirectly regulating different OM mineralization pathways (Jamieson et al., 2013; Thullner et al., 2009). The degree of remineralisation by benthic biota is a factor affecting the quantity and quality of particulate OM available to the bacteria dwelling in the sediment (Jamieson et al., 2013). Additionally, mega- and macrofauna may act as ecosystem engineers, altering habitat structure via their feeding and burrowing activities, which allows freshly-deposited OM to penetrate deep into the sediment (Levin et al., 1997; Serpetti et al., 2013). The role of macrofauna for the microbiology and biogeochemistry of aquatic sediments and their response to OM input are relatively well established (Hughes and Gage, 2004; Jeffreys et al., 2013; Levin et al., 1997; Rex et al., 2006; Ruhl et al., 2008). In contrast, few studies report on the function of meiofauna in OM recycling, although they become numerically dominant (in terms of densities and biomass) with increasing water depth (Danovaro et al., 2008; Thiel, 1975). Nascimento et al. (2012) clearly show that the presence of meiofauna enhances OM mineralization in marine sediments through a significant increase in respiration rates observed in an enrichment experiment with and without the meiofauna present. Nevertheless, the interaction between nematodes and microbes and their roles in enhancing remineralization processes and, moreover, their interaction in the food web remains unclear so far, especially in the deep sea (Ingels et al., 2010). On the other hand, fatty acid and stable

isotope analyses have shown that deep-sea meiofauna, especially nematodes, are mainly dependent on freshly-derived organic material from the surface, which constitutes a high quality food source (Leduc et al., in press; Veit-Köhler et al., 2011; Guilini et al., 2013).

A decrease in benthos-mediated mineralization occurs with an increase in water depth (Glud, 2008; Middelburg et al., 1997). In the abyss, many aspects of ecosystem function and structure are chiefly modulated by the rate and nature of food (in the form of aggregates) flux to the seabed (Sachs et al., 2009; Smith et al., 2008). Naturally occurring diatom blooms generally lead to very high benthic fluxes (Sachs et al., 2009). In addition, sinking velocities of organic aggregates are predominantly determined by aggregate size, although other factors such as stickiness and porosity, may also play a role in determining particle settlement (Iversen and Ploug, 2013; Karakas et al., 2009). When settled, these aggregates will potentially act as food source for the fauna dwelling at the deep-sea bottom. This benthic-pelagic coupling between food supply from the photic zone and its settlement to the seafloor was demonstrated in many bathyal and abyssal studies (Billett et al., 1983; Lampadariou et al., 2006; Lins et al., 2014; Pape et al., 2013b; Rex et al., 2006; Smith et al., 2006; Smith et al., 2008; Wei et al., 2010). On the contrary, differences in benthic community structure, diversity and biomass in conjunction with differences in surface primary productivity were poorly studied (Guilini et al., 2013 cf. revisited station at Polar Front; Jeffreys et al., 2013; Pape et al., 2013b; Ruhl et al., 2008; Sebastian et al., 2007).

The Southern Ocean, characterized by extreme seasonality in sea-ice cover and primary production, is considered a major driver in ocean circulation, connecting deep waters from the Pacific, Atlantic and Indian oceans (Griffiths, 2010). In the Atlantic sector of the Southern Ocean, east-west differences in primary productivity are observed (Demidov et al., 2012). In spring, western areas are characterized by a higher production than the eastern ones, while the opposite pattern is observed in summer due to the lateral eastwards displacement of waters with high chlorophyll a concentration (Demidov et al., 2012). These differences in primary productivity could affect patterns of community composition and biomass at the sea bottom (Brandão et al., 2014; Würzberg et al., 2014). For many benthic taxa including both meio- and macrobenthic groups, there is evidence that maximum body size significantly decreases with increasing depth, possibly due to diminishing food supply (Smith et al. 2008; Thiel, 1975; Ramirez-Llodra et al., 2010). Nevertheless, aspects of energy flow concerning the meiofauna are still not well-understood and remain mainly focused on standing stock quantification (Duros et al., 2011;

Ingels et al., 2011; Vanreusel et al., 1995). Recently used techniques, such as fatty acid (FA) analyses, could potentially provide more insights in meiofauna ecosystem functioning through the study of dietary intakes and food constituents to sequestering of lipid reserves (Dalsgaard et al., 2003; Leduc, 2009; Leduc et al., in press). This technique was already used for nematodes ("bulk") from the Southern Ocean (Guilini et al., 2013) as a trophic marker and indicated a selective feeding behaviour within this group. The presence of polyunsaturated fatty acids (PUFAs) in the analysed organisms indicates a rich phytoplankton-based diet (as these FA are not produced by bacteria) (Dalsgaard et al., 2003), which might be originated from direct grazing or indirect consumption of certain microorganisms (e.g. foraminiferans) or even small metazoans. This rich-based diet emphasizes the potential role of nematodes as high-quality food for higher trophic levels (Leduc, 2009; Leduc et al., in press).

Based on analyses of nematode assemblages from four stations in the Southern Ocean characterized by strong differences in surface primary productivity the following hypotheses are tested:

(1). Differences in surface primary productivity regulate nematode standing stocks (i.e. abundance and biomass) in the Southern Ocean;

(2). Nematode community composition mirrors increases in surface primary productivity through the increase in density of specific genera adapted to feed on fresh material, as well as alterations in high quality fatty acids (PUFAs) in nematodes;

(3). Different nematode taxa feed selectively on specific food sources as reflected by their different FA composition.

## 2.2 Material and methods

### 2.2.1 Sampling and study area

During the RV Polarstern ANT-XXVIII/3 (07.01.2012–11.03.2012) cruise (Wolf-Gladrow, 2012) to the Southern Ocean, sediment samples for nematode analyses were taken in the framework of the SYSTCO II project. The study area comprised four

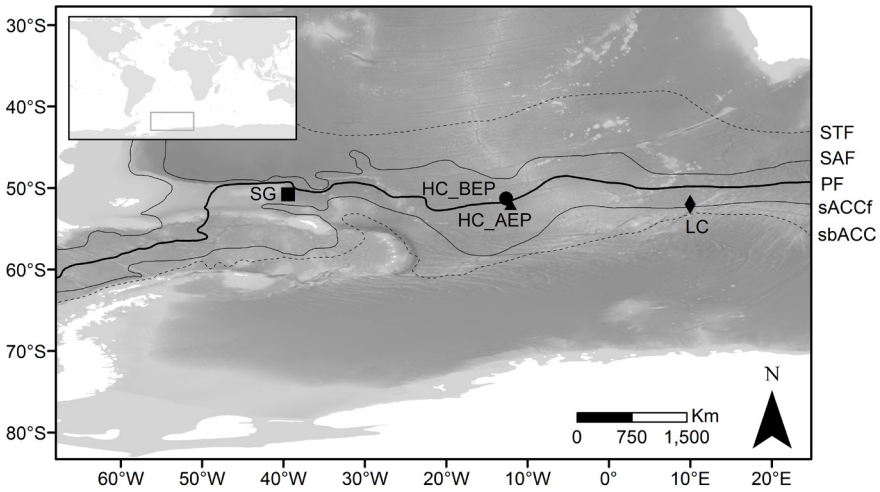


**Figure 2.1** Location of ANT-XXVIII/3 stations. The map displays features of the Antarctic Circumpolar Current (Orsi and Harris, 2001): Subtropical Front (STF), Subantarctic Front (SAF), Polar Front (PF), southern Antarctic Circumpolar Current Front (sACCf) and southern boundary of the Antarctic Circumpolar Current (sbACC). Bathymetry data provided by ETOPO1 and world boundaries by ESRI (Amante and Eakins, 2009). Sampling stations are represented by symbols: SG (South Georgia), HC_BEP (High Chlorophyll_before Eddy Pump), HC_AEP (High Chlorophyll_after Eddy Pump) and LC (Low Chlorophyll). Source: the author (2016).

stations at the Polar Front situated along an E-W (between 10° E and 39° W) gradient, and covering depths from 3760.5 m to 4155.2 m (Fig. 2.1; Table 2.1). Sampling was performed using a Multicorer (MUC) equipped with twelve Plexiglass tubes yielding samples with a virtually undisturbed sediment-surface (inner core diameter 6 cm, cross-sectional area

**Table 2.1** Sampling details from west to east. Core codes in bold were used for community analyses while non-bold core codes were used for nematode fatty acids and environmental analyses. PF = Polar Front. Source: research data (2016).

| Station | Deployment (core code) | Date | Depth (m) | Latitude | Longitude | Remarks |
|---|---|---|---|---|---|---|
| SG | 175-5 (**7**-8) | 04/03/2012 | 4154.2 | 50°46.69'S | 39°25.35'W | South Georgia |
| SG | 175-6 (**5**-6) | 04/03/2012 | 4155.2 | 50°46.59'S | 39°25.33'W | South Georgia |
| SG | 175-7 (**2**-3) | 04/03/2012 | 4154.2 | 50°46.60'S | 39°25.38'W | South Georgia |
| SG | 175-8 (1-**10**) | 04/03/2012 | 4154 | 50°46.60'S | 39°25.39'W | South Georgia |
| SG | 175-9 (**3**-6) | 04/03/2012 | 4152.1 | 50°46.57'S | 39°25.33'W | South Georgia |
| HC_AEP | 141-6 (3-**4**) | 18/02/2012 | 4113 | 51°15.98'S | 12°37.04'W | PF (After Eddy Pump) |
| HC_AEP | 141-9 (6-**8**) | 18/02/2012 | 4114 | 51°16.03'S | 12°37.06'W | PF (After Eddy Pump) |
| HC_AEP | 141-10 (3-**6**) | 19/02/2012 | 4113 | 51°15.97'S | 12°36.94'W | PF (After Eddy Pump) |
| HC_AEP | 141-11 (3-**5**) | 19/02/2012 | 4113.2 | 51°16.02'S | 12°37.12'W | PF (After Eddy Pump) |
| HC_BEP | 086-26 (4-**8**) | 01/02/2012 | 3966.2 | 51°58.87'S | 12°3.76'W | PF (Before Eddy Pump) |
| HC_BEP | 086-28 (6-**8**) | 01/02/2012 | 3968 | 51°58.74'S | 12°2.11'W | PF (Before Eddy Pump) |
| HC_BEP | 086-29 (**3**-5) | 01/02/2012 | 3970.8 | 51°58.78'S | 12°1.95'W | PF (Before Eddy Pump) |
| HC_BEP | 086-30 (**1**-3) | 02/02/2012 | 3965.4 | 51°58.91'S | 12°2.16'W | PF (Before Eddy Pump) |
| LC | 081-8 (**3**-4-6) | 19/01/2012 | 3760.5 | 51°59.99'S | 9°59.99'E | PF (Low Chlorophyll) |
| LC | 081-9 (8-**10**) | 19/01/2012 | 3760.7 | 52°0.01'S | 10°0.05'E | PF (Low Chlorophyll) |
| LC | 081-12 (**6**-8) | 19/01/2012 | 3757.5 | 51°59.93'S | 10°0.06'E | PF (Low Chlorophyll) |
| LC | 081-13 (**6**-7) | 19/01/2012 | 3760.5 | 52°0.042'S | 9°59.90'E | PF (Low Chlorophyll) |

25.5 cm²).

The Polar Front marks the northern extent of low salinity and cold water (Knox, 1994). Sampling locations were chosen based on previously available surface chlorophyll a (Chl*a*) concentrations data provided by the University of Bremen. South Georgia station (SG), located northwest of South Georgia Island, is considered a highly productive region during austral summer, supporting high phytoplankton biomass (Atkinson et al., 2001). The second region comprised two different stations located at the same transition zone and characterized by high annual primary production: HC_BEP (High Chlorophyll_ Before Eddy Pump) and HC_AEP (High Clorophyll_After Eddy Pump), which is the same position re-sampled after 13 days of a phytoplankton bloom in the area. Although a higher Chl*a* concentration was expected after the bloom, this was not visualized in the surface Chl*a* maps. This area was also supposed to exhibit eddies between sampling periods, which were tracked before and during the cruise using satellite remote sensing of sea surface high anomalies and ocean colour. Therefore, these stations received the name before and after Eddy Pump due to collaboration with the Eddy Pump project during the same campaign. The most eastern station (LC; Low Chlorophyll) exhibited low surface chlorophyll values throughout the year (Fig. 2.1).

### 2.2.2 Sediment analyses

Samples for granulometric and geochemical analyses (1 g of sediment) were divided per 1 cm-layer down to 5 cm and frozen at -80°C. Grain size distribution was measured with a Malvern Mastersizer 2000 (0.02 – 2000 μm size range) and divided from silt-clay to coarse sand fractions. Total sedimentary organic carbon (% TOC) and nitrogen (% TN) were determined with a Carlo Erba elemental analyser on freeze-dried and homogenised samples after acidification with 1% HCl to eliminate carbonates. Total organic matter (% TOM) content was determined after combustion of the sediment samples at 550°C.

Chl*a*, chlorophyll degradation products and carotenoids in the sediment were measured with a Gibson fluorescence detector (Wright and Jeffrey, 1997) after lyophilisation, homogenization and extraction in 90 % acetone, and separation of the samples via reverse-phase HPLC (High-Performance Liquid Chromatography). Chloroplastic Pigment Equivalents (CPE: sum of Chl*a* and its degradation products) was used to estimate surface-produced OM. The ratio Chla: phaeopigments served to estimate the

freshness of photosynthetically derived OM (Thiel, 1978).

Hydrolysis of total lipids and methylation to fatty acid methyl esters for FA analysis on the sediment was performed on 3 g sediment based on a modified one-step derivatisation method in which lipid extraction and esterification were combined (Abdulkadir and Tsuchiya, 2008). Sediment was lyophilised for 24h and the extraction performed with 2.5% sulfuric acid in methanol, which replaced boron trifluoride-methanol since BF3-methanol can create loss of PUFAs.

The FA methylnonadecanoeate C19:0 (0.1 mg/ml, Fluka 74208) was used as internal standard. Each vial was mixed for 30 seconds and heated (using a warming bath) up to 80°C for 1h30 after which they were treated with hexane and centrifuged for 10 minutes at 1000 RPM (Eppendorf centrifuge 5810R). Replicate extracts were analysed using a gas chromatograph (Hewlett Packard 6890N) coupled to a mass spectrometer (HP 5973). Samples were run in splitless mode, with a 5 µL injection per run at 250°C, using a HP88 column (60 m x 25 mm internal diameter, Df = 0.20; Agilent J&W; Agilent Co., USA). Fatty acid methyl esters were identified based on retention times and mass spectra's comparisons with authentic standards and available ion spectra in different libraries (WILEY, Niest and a self-made mass spectral library from 37 FA), and determined with the software MSD ChemStation (Agilent Technologies).

### 2.2.3 Surface environmental parameters

Annual average Net Primary Production (avNPP) values were extracted from the Vertically Generalised Production Model (resolution: 1°) (Behrenfeld and Falkowski, 1997). The Vertically Generalised Production Model is a chlorophyll-based algorithm that estimates avNPP values based on sea surface temperature, surface Chl*a* and photosynthetically active radiation via satellite measurements. The available HDF format data were extracted using the Marine Geospatial Ecology Tools for ArcGIS and converted to raster using the software ArcGIS (Lutz et al., 2002; Lutz et al., 2007).

### 2.2.4 Nematodes

At each station, four replicate samples (SG possessed five replicates) used for community analysis were sliced per cm down to 5 cm sediment depth and fixed in seawater buffered 4 % formalin. Samples were washed over a 1000 µm sieve and the meiofauna

was retained on a 32 µm sieve. The meiofauna was centrifuged three times using LUDOX HS40 Dupont (specific gravity 1.19) as flotation medium and then stained with Rose Bengal. Nematodes were counted under a stereomicroscope (50x magnification) and 140 individuals (whenever enough present) were picked out. The individuals were gradually transferred to glycerine (De Grisse, 1969), mounted on glass slides and identified to genus level using pictorial keys (Warwick et al., 1998). The most abundant genera were identified to species level.

Functional diversity of nematode assemblages was assessed using individual trophic levels based on buccal morphology according to Wieser (1953): selective deposit feeders (1A), non-selective deposit feeders (1B), epistratum feeders (2A) and predators (2B), complementing the 2B group (predators) with the notion of 'scavengers' (Jensen, 1987). Taxonomic diversity was calculated using Shannon-Wiener diversity (H'), Pielou's evenness (J') and total number of genera (S).

The length (excluding filiform tails) and the maximum body width were measured for all identified nematodes (32–100 % of the total nematodes per 10 $cm^2$) with the compound microscope Leica DMR and Leica LAS 3.3 imaging software. Biomass was then calculated per genus through the volumetric method according to Andrassy's formula $G = a^2 \times b / 1.6 \times 10^6$, with $G$ = wet weight in µg, $a$ = maximum body diameter (µm) and $b$ = total length (µm) (Andrássy, 1956).

Fatty acid methyl esters for FA of nematodes were measured on previously frozen samples (-80°C) at cm resolution to 5 cm sediment depth. Samples were centrifuged one time using LUDOX HS40 Dupont (specific gravity 1.19) and all individuals were picked out while kept on ice and immediately frozen at -20°C. The effect of thawing was, thus, regarded as negligible. From 2–4 replicate extracts from "bulk" nematodes (240–903 individuals, excluding desmoscolecids and *Desmodora*), the nematode family Desmoscolecidae (163–258 individuals) and the genus *Desmodora* (175–302 individuals) were performed following the same method as for the sediment FA. The last two groups were chosen because they were highly dominant in SG and easy to recognize in the samples under a stereomicroscope. A few FA served as biomarkers in order to unravel the relative contributions of possible food sources (phyto- and/or zooplankton) to the animals' diets.

Firstly, the planktonic-derived FA were divided in microalgae-derived planktonic (16:1ω7, 18:1ω9, 18:2ω6, 20:PUFA, 22:PUFA) and bacterial (15:0, 17:0, 17:1 and iso and

anteiso saturated FA [SFA] and monosaturated FA [MUFA]) markers. *Iso* + *anteiso* 15:0/ 15:0, *iso* + *anteiso* 15:0/ 16:0 and Σ*iso* + *anteiso* 15:0 +17:0 were also used to infer a bacterial-derived diet (Dalsgaard et al., 2003 and references therein). Then, specific biomarker ratios were used to verify diatom (if $\frac{\sum 16:1\omega7}{\sum 16:0} > 1$ and $\frac{\sum 16:0}{\sum 18:0}$ positively correlated with diatom biomass) or dinoflagellate-based (if $\frac{22:6\omega3(\mathrm{DHA})}{20:5\omega3(\mathrm{EPA})} \geq 1$) diet. ∑SFAs, ∑MUFAs and ∑PUFAs contents were compared between stations.

### 2.2.5 Nematode respiration

Nematode respiration rates (Resp) based on individual dry weight (DWT) were estimated according to de Bovée and Labat (1993), where $Q10 = 2$ and $T$ = Temperature at the seabed (°C):

Resp ($T$) = 0.0449 $DWT^{0.8544}$ $\exp^{(\ln Q10/10)^* (T-20)}$ (de Bovée and Labat, 1993).

This respiration formula was preferred instead of Shirayama (1992) respiration values measured for deep-sea nematodes at 2–4°C because the second suggests no temperature dependence of respiration rates in the deep sea, while de Bovée and Labat (1993) incorporate temperature in their formula. Moreover, considering that the temperatures of the seabed measured in this study remained below 2–4°C, we have considered the Bovée and Labat (1993) formula as the most appropriate method.

### 2.2.6 Data analysis

Trends in environmental (Chl*a*, Chl*a*: phaeopigments, Chl*a*: % TOC, CPE, % TN, % TOC, median grain size, total FA, avNPP, SFAs, MUFAs and PUFAs) and univariate nematode variables (total biomass, total respiration, H', J', S and total FA) were investigated by means of Spearman rank correlations in R (R Core Team, 2013) and Draftsman plots (Anderson et al., 2007).

The % TOM and its vertical profile in the sediment was used according to Soetaert et al. (1997) to estimate how food is drawn into the sediment. The % TOM can be used as a measure of bioturbation, where subsurface peaks are expected when OM from the superficial layers is brought to deeper layers by organisms' activity.

The community data on genus level (and on species level for the most dominant

genera) based on Bray-Curtis similarity was analysed by means of non-parametric permutational ANOVA (PERMANOVA; Anderson et al., 2007) to assess differences between stations (1-factor design) and whenever possible between sediment layers (3-factor nested design). The one-factor model design comprised station (ST) as a fixed factor. The three-factor model design included as factors station (ST: fixed), slice (SL: fixed) and replicate (REP: random, nested in station). The interaction STxSL informs about the difference in depth profiles of uni- or multivariate nematode measures or environmental variables among stations. Non-metrical multi-dimensional scaling (MDS) was used to visualize the results. Subsequent pairwise t-tests were performed between all pairs of levels to determine where the differences between each combination were located.

In addition, PERMDISP routines were executed in order to test for homogeneity of multivariate dispersions. The PERMDISP results were never significant, indicating location differences through equally dispersed distances to centroids. SIMPER routines were performed based on Bray-Curtis similarity, with a cut-off of 90 % for low contributions. The same PERMANOVA design used for the multivariate community data was applied to nematode relative abundance and all other multivariate data, such as nematode biomass, respiration, c-p matrix (coloniser-persister matrix calculated based on nematode trophic group), trophic groups, gender and life stage, as well as nematode FA profiles.

The multivariate environmental data was first normalized (subtracted mean divided by the standard deviation) and resemblance matrices calculated based on Euclidean distances. Then, PERMANOVA tests were performed using the same design as described for the multivariate community data. RELATE and DISTLM (distance-based linear model) routines were performed to analyse and model the relationship between nematode genus assemblage, biomass and FA profile on one hand, and the environmental variables with correlations lower than 0.9 (Chl*a*, Chl*a*:phaeopigments, Chl*a*: % TOC, CPE, % TN, % TOC, total FA and avNPP) on the other hand. Highly correlated variables (i.e. $r > 0.9$) were first transformed to cosine (Chl*a*: % TOC, CPE, medium grain size and total FA) and if high correlations persisted were excluded from the DISTLM analysis (medium grain size). The DISTLM assemblage was built using a step-wise selection procedure and adjusted $R^2$ as selection criterion. Euclidean distance was used as resemblance measure for DISTLM procedures and the results were visualized using dbRDA (distance-based redundancy analysis) plots.

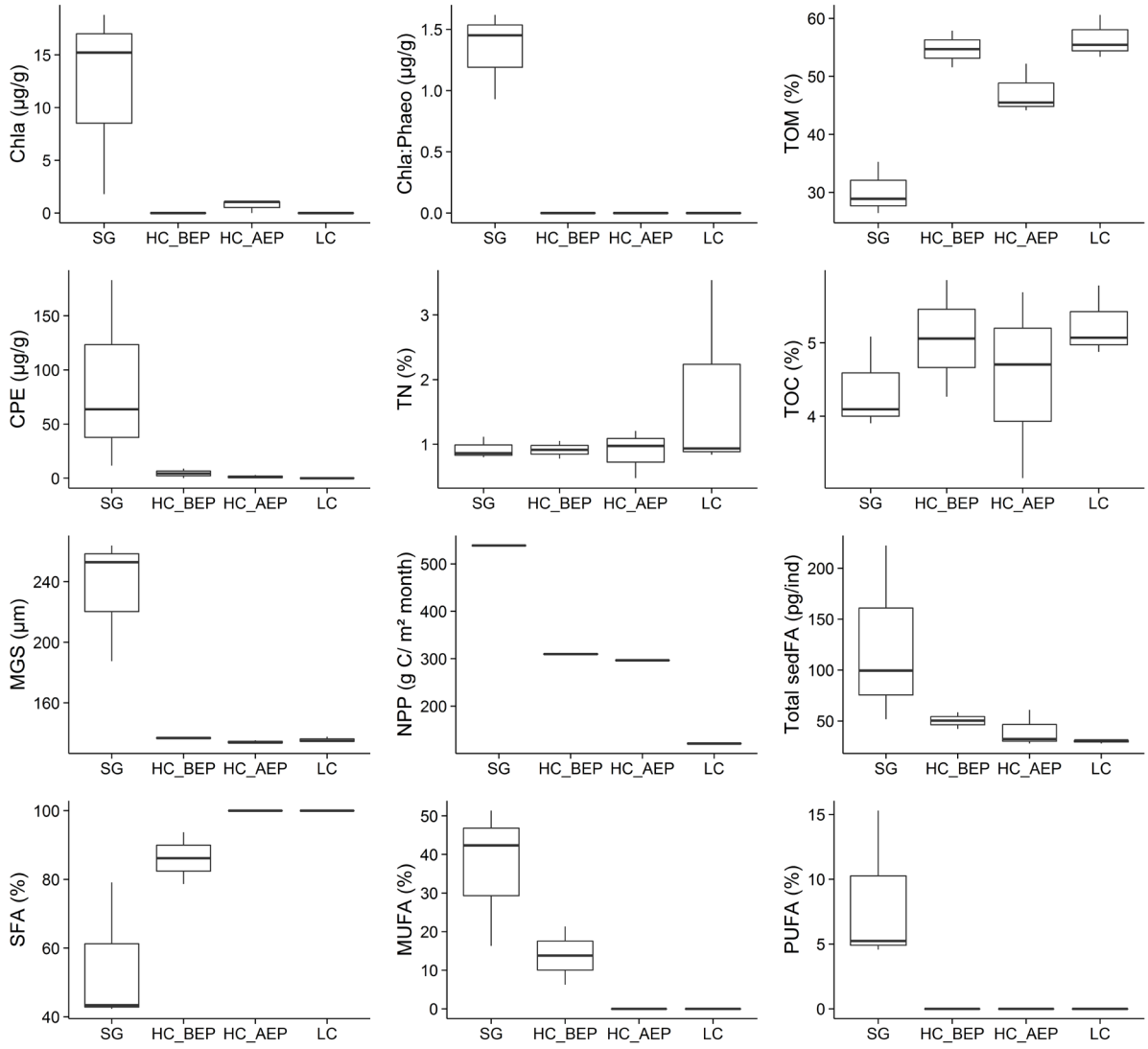


**Figure 2.2** Environmental variables used in this study for SG (South Georgia), HC_BEP (High Clorophyll before Eddy Pump), HC_AEP (High Chlorophyll before Eddy Pump), and LC (Low Clorophyll) stations: Chla (Chlorophyll a), Chla:Phaeo (Chlorophyll a: phaeopigments), Chla: % TOC (Chlorophyll a: % Total Organic Carbon), CPE (Chloroplastic Pigment Equivalent), TN (Total Nitrogen), TOC (Total Organic Carbon), MGS (Mean Grain Size), NPP (Net Primary Productivity), Total sedFA (Total Fatty Acid of the sediment) and relative abundance (% of total fatty acid) for SFA (Saturated Fatty Acid) in the sediment, MUFA (Monounsaturated Fatty Acid) in the sediment and PUFA (Polyunsaturated Fatty Acid) in the sediment. Black lines represent the median, lower box indicates the first quartile and upper box the third quartile. Upper line shows the maximum value and lower line the minimum value. Source: research data (2016).

## 2.3 Results

### 2.3.1 Environmental parameters

Biogeochemical properties of the sediment are shown in Fig. 2.2. The sediment at all stations was mainly composed of silt-clay fractions (82–92 %), followed by very fine sand. However, mean grain size was significantly higher at SG ($p$ = 0.02), with higher

**Table 2.2** Mean relative abundance of dominant genera (≥ 2 %) and feeding type (FT) per station over 5 cm depth. Source: research data (2016).

| SG | % | FT | HC_AEP | % | FT | HC_BEP | % | FT | LC | % | FT |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Thalassomonhystera* | 14.6 | 1A | *Microlaimus* | 19.5 | 2A | *Microlaimus* | 26.5 | 2A | *Thalassomonhystera* | 21.3 | 1A |
| *Acantholaimus* | 12.6 | 2A | *Thalassomonhystera* | 17.3 | 1A | *Thalassomonhystera* | 19.2 | 1A | *Acantholaimus* | 19.8 | 2A |
| *Desmodora* | 9.8 | 2A | *Acantholaimus* | 11.8 | 2A | *Daptonema* | 6 | 1B | *Microlaimus* | 7.2 | 2A |
| *Tricoma* | 7.6 | 1A | *Southerniella* | 5.3 | 1A | *Acantholaimus* | 5.9 | 2A | *Desmoscolex* | 4.8 | 1A |
| *Cervonema* | 5.1 | 1B | *Tricoma* | 5.1 | 1A | *Diplopeltula* | 4.8 | 1A | *Tricoma* | 4.7 | 1A |
| *Microlaimus* | 4.8 | 2A | *Diplopeltula* | 4.4 | 1A | *Theristus* | 3.2 | 2A | *Molgolaimus* | 3.7 | 1A |
| *Enchonema* | 4 | 1A | *Molgolaimus* | 2.8 | 1A | *Leptolaimus* | 3 | 1A | *Halalaimus* | 3.6 | 1A |
| *Southerniella* | 3.9 | 1A | *Halalaimus* | 2.8 | 1A | *Desmoscolex* | 2.8 | 1A | *Diplopeltula* | 3.4 | 1A |
| *Daptonema* | 2.8 | 1B | *Daptonema* | 2.7 | 1B | *Pareudesmoscolex* | 2.5 | 1A | *Daptonema* | 3.4 | 1B |
| *Diplopeltula* | 2.6 | 1A | *Leptolaimus* | 2.2 | 1A | *Tricoma* | 2.1 | 1A | | | |
| *Dichromadora* | 2.5 | 2A | XYALIDAE sp2 | 2.2 | 1B | | | | | | |
| *Halalaimus* | 2.4 | 1A | | | | | | | | | |
| *Actinonema* | 2.2 | 2A | | | | | | | | | |
| *Desmoscolex* | 2 | 1A | | | | | | | | | |

relative contribution of fine (0.2–3.2 %) and medium (2.2–4.7 % ) sand. Sedimentary % TOC and % TN did not differ between stations ($p > 0.05$) (Fig. 2.2). A significant eastwards increase in % TOM was observed, as well as a decrease towards deeper sediment layers ($p = 0.003$) but only for HC_AEP, HC_BEP and LC sites. Sediment Chl*a* ($p = 0.005$), as well as Chl*a*: phaeopigments ($p < 0.0002$) and CPE ($p = 0.02$) decreased eastwards, with SG displaying significantly higher values in comparison with the other stations (Fig. 2.2). Chl*a*: % TOC concentrations, although decreasing eastwards, did not exhibit significant differences between stations ($p >0.05$). Total sediment FA was lower at the eastern stations, but due to the high variation between samples (Fig. 2.2) these differences were not significant ($p > 0.05$, Table S1). Neither sediment FA profiles ($p > 0.05$) nor ∑SFAs ($p > 0.05$) or ∑MUFAs ($p > 0.05$) significantly differed between stations. On the other hand, ∑PUFAs were significantly more abundant at SG ($p = 0.003$) than at other stations (Fig. 2.2). Accordingly, when bacterial FA and planktonic FA were considered, SG clearly exhibited significantly higher values for both categories than the other stations ($p = 0.001$), except for HC_BEP. Surface average NPP followed the same eastward decrease as observed for the other environmental variables, with higher concentrations displayed at SG ($p < 0.0001$) (Fig 2.2).

### 2.3.2 Nematode community and biomass

Nematodes were the dominant meiofaunal group at all stations (78–94 %) and their mean abundance varied from 185 to 819 ind/10 cm². A total of 130 nematode genera

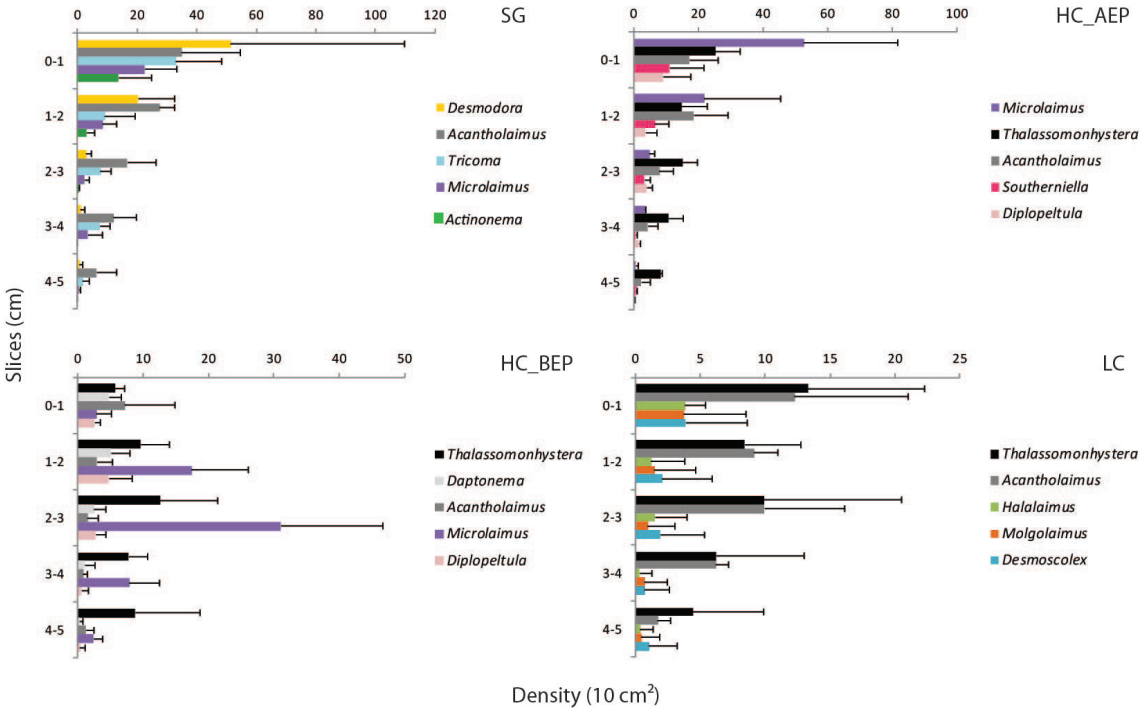


**Figure 2.3** Total nematode density (ind/10 cm²) of the five most abundant genera expressed per sediment layer and per station. Source: research data (2016).

were found over all stations. The most abundant genera per station (≥ 2 %) are represented in Table 2.2 and the vertical profile of the five most abundant genera per station is visualized in Fig. 2.3. Nematode total densities (Fig. 2.4) and total number of genera (S) were significantly higher at SG ($p < 0.0001$ and $p = 0.005$, respectively; Table S2) and

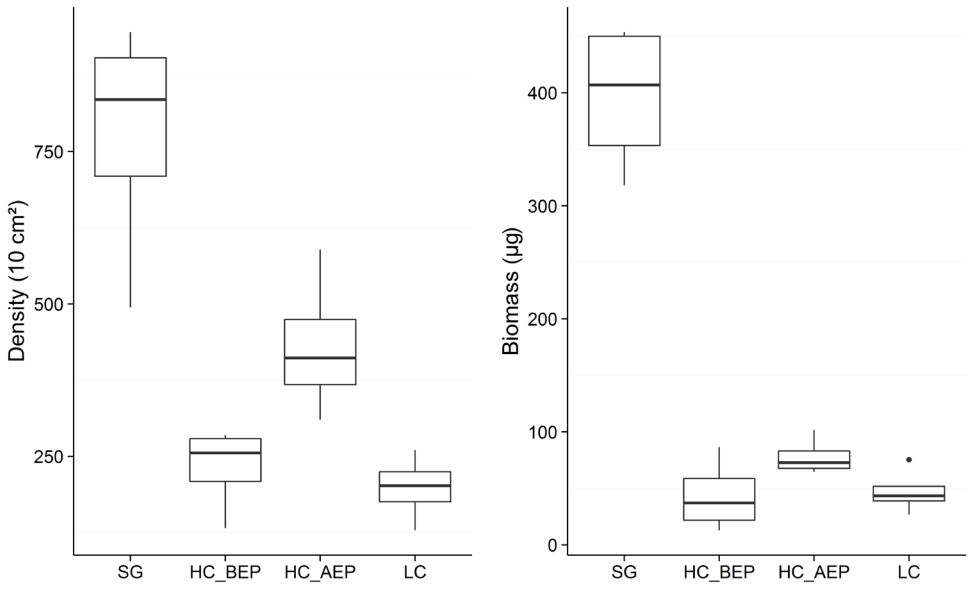


**Figure 2.4** Density (10 cm²) and Total Biomass (µg) per station of the total nematode community structure. Black lines represent the median, lower box indicates the first quartile and upper box the third quartile. Upper line shows the maximum value and lower line the minimum value. Source: research data (2016).

decreased eastwards. All stations differed in genus composition based on the relative abundances ($p < 0.0001$), whereas SIMPER test revealed that SG was more dissimilar compared to other stations. The genera *Desmodora* De Man, 1989, *Cervonema* Wieser, 1954, and *Tricoma* Cobb, 1893, with higher abundances in SG, together with *Acantholaimus* Allgén, 1933 and *Thalassomonhystera* Jacobs, 1987, being more abundant at the three other stations, were the major genera responsible for up to 31 % of the dissimilarity.

Total nematode biomass was significantly greater at SG ($p < 0.0001$) than at the other stations (Fig. 2.4) and decreased towards deeper sediment layers. Lack of differences in biomass between deeper layers ($p > 0.05$) among all pairs of stations indicated that differences between stations were mainly due to differences observed in the first centimetres.

### 2.3.3 Nematode species

Four genera were the most dominant at all stations and therefore identified up to species or morphotype level: *Acantholaimus, Desmodora, Microlaimus* De Man, 1880 and *Thalassomonhystera*. *Thalassomonhystera* showed the highest number of species (33), followed by *Acantholaimus* (20) and *Microlaimus* (12). The genus *Desmodora* was represented by only one species, *Desmodora profundum* Moura et al., 2014.

*Acantholaimus* species composition based on densities significantly differed between stations ($p = 0.02$) and between sediment layers ($p < 0.0001$). HC_AEP showed the highest number of *Acantholaimus* species (13) and also the highest number of unique *Acantholaimus* species (3), followed by HC_BEP (11), with two unique *Acantholaimus* species. SIMPER routines revealed *Acantholaimus elegans* Jensen, 1988 as responsible for dissimilarities between LC (where it possessed higher abundances) and the other stations. Two species contributed most to dissimilarities between sediment layers: *Acantholaimus invaginatum* Muthumbi & Vincx, 1997, which was present in higher abundances in the deeper layers, and *Acantholaimus maks* Gerlach, Schrage & Riemann, 1979, mainly present in superficial layers. *A. invaginatum* was also present in higher abundances in SG than at the other stations. PERMANOVA based on presence-absence of *Acantholaimus* did not reveal significant differences between stations ($p = 0.1222$).

*Desmodora profundum* was present at all stations, but showed highest densities (more than six times compared to other stations) at SG ($p < 0.0001$). This species was

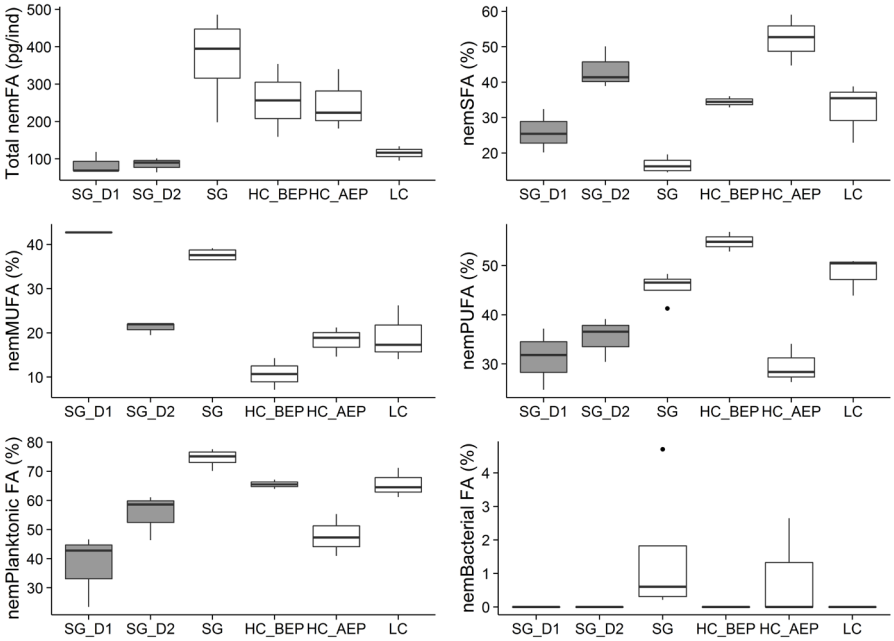


**Figure 2.5** Total *Desmodora* (SG_D1), Desmoscolecidae (SG_D2) and "bulk" nematode fatty acid represented per station in pg/g (Total nemFA) and relative concentrations (% of total fatty acid) of nemSFA (nematode Saturated Fatty Acid), nemMUFA (nematode Monounsaturated Fatty Acid), nemPUFA (nematode Polyunsaturated Fatty Acid), nemPlanktonic FA (nematode Planktonic Fatty Acid) and nemBacterial FA (nematode Bacterial Fatty Acid). Black lines represent the median, lower box indicates the first quartile and upper box the third quartile. Upper line shows the maximum value and lower line the minimum value. Source: research data (2016).

mainly found in superficial sediment layers (Fig. 2.3). Concerning the *Microlaimus* species, significant differences were observed between stations ($p = 0.01$) but not between slices ($p > 0.05$). HC_AEP exhibited the highest number of *Microlaimus* species (11) and was the only station which possessed a unique *Microlaimus* species (morphotype XII). SIMPER routines revealed differences in abundance of morphotype VI as the most important factor responsible for dissimilarities between HC_AEP/HC_BEP and the other stations. *Thalassomonhystera* species significantly differed between stations ($p = 0.01$) but not between slices ($p = 0.27$). SG possessed higher species diversity (25) in comparison with other stations, but only one species was unique for this station (morphotype XXIX). LC exhibited four unique species: morphotypes VI and XIII, and T*halassomonhystera mortalis* Bussau, 1993 and *Thalassomonhystera subtilis* Bussau, 1993, while morphotype XVIII was exclusive at HC_BEP.

### 2.3.4 Nematode fatty acids

Total "bulk" nematode FA, as well as ∑MUFAs, exhibited significantly greater concentrations in nematodes from SG compared with other stations ($p = 0.001$; Fig.

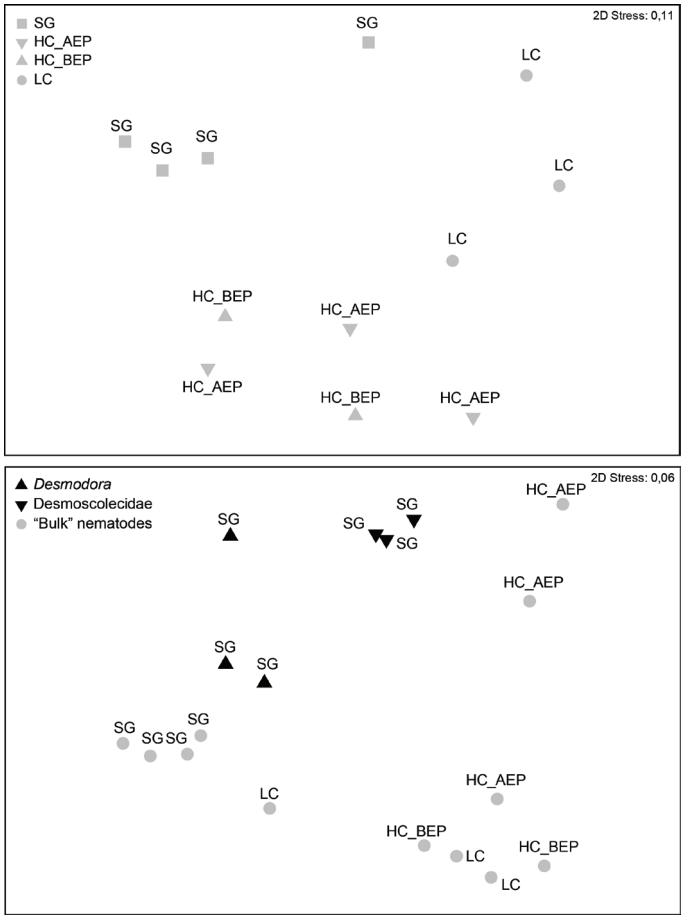


**Figure 2.6** Non-metric MDS plot (Bray-Curtis similarity) based on nematode fatty acid profiles. Upper figure represent total nematode fatty acid for the "bulk" nematodes. Lower figure include both total nematode "bulk" fatty acid as well as total fatty acid for *Desmodora* and Desmoscolecidae. Source: research data (2016).

2.5). MDS profiles based on the total FA concentrations on "bulk" nematodes showed SG as a separate cluster apart from the other stations (Fig. 2.6). Comparisons between "bulk" nematode FA content in species of the family Desmoscolecidae, and the genus *Desmodora* (for SG only) exhibited significantly lower amounts of FA for the two last groups in comparison with "bulk" nematode FA, which was composed by all other nematodes except desmoscolecids and *Desmodora* ($p$ = 0.0002; Table S2). MDS based on the FA relative abundances for the three groups showed separate clusters for *Desmodora* and desmoscolecids in comparison with nematode "bulk" FA profiles (Fig. 2.6). SIMPER routines revealed the ratio $\frac{\sum 16{:}0}{\sum 18{:}0}$ as the main responsible for dissimilarities between "bulk" nematode FA, *Desmodora* and desmoscolecids (Table S4).

When nematode FA were assigned to potential food sources, planktonic-derived FA were dominant in nematodes (including desmoscolecids and *Desmodora*) at all stations (Table S3). The ratio $\frac{\sum 16{:}1\omega7}{\sum 16{:}0}$, considered as a diatom biomarker, was higher than 1 in nematodes (except for the desmoscolecids) from SG (Table S3). The fatty acid 20:4ω6, shown to be an important component in foraminiferans (Würzberg et al., 2014), was found in relatively high abundances (12.7 % ± 2.0 % to 23 % ± 5.4 %) in all nematodes (except *Desmodora*). Bacterial FA were rarely present in nematodes, reaching maximum relative amounts of 6.1 % ± 1.5 %. PERMANOVA based on the nematode "bulk" FA revealed significant differences between stations ($p$ = 0.0003) and between all pairs of stations except for HC_AEP x HC_BEP and HC_BEP x LC. RELATE analyses revealed

weak correlations between the nematode FA profile and nematode density (Rho = 0.44, $p$ = 0.02), and nematode biomass (Rho = 0.42, $p$ = 0.04).

### 2.3.5 Structural and functional nematode diversity

Univariate significant correlations revealed that biomass was positively correlated with both Shannon-Wiener H' diversity (r = 0.76, $p$ = 0.009, n = 12) and Pielou's evenness J' (r = 0.75, $p$ = 0.01, n = 12), as well as total sediment FA (r = 0.92, $p$ < 0.0001, n = 12) (Fig. S1). Moreover, Shannon-Wiener was positively correlated to Pielou's evenness J' (r = 0.8, $p$ = 0.005, n = 12) and total sediment FA (r = 0.63, $p$ = 0.04, n = 12) (Fig. S1). PERMANOVA analyses based on trophic groups displayed significant differences between stations and slices ($p$ < 0.0001). SIMPER analysis revealed that dissimilarities were mainly due to the average abundance of feeding type 1A, which decreased in abundance with increasing sediment depth at HC_AEP and LC stations. Feeding type 2A was mainly concentrated in the superficial layers at SG and HC_AEP. Total nematode respiration estimates exhibited significantly higher values for SG in comparison with other sites ($p$ < 0.0001).

### 2.3.6 Correlation between environmental variables and nematode community structure, biomass and total FA

The DISTLM analysis based on nine environmental variables explained 49 % of the total nematode composition based on genus densities observed. Net surface primary productivity accounted for 36 % of the total variation and Chl*a*: phaeopigments for 13 % (Fig. 2.7A, Tables S5, S6). The other variables did not contribute significantly to the model and/or added < 5 % in explaining assemblage variation. For the DISTLM based on the biomass, freshness of photosynthetically derived OM (Chl*a*: phaeopigments) was the only significant variable explaining biomass variability (21 %) (Fig 2.7B, Tables S5, S6).

DISTLM based on total nematode FA showed similar results as for nematode community variation, with average productivity (avNPP) being responsible for 38 % of the total FA variability and Chla:phaeopigments for 23 %. The other variables did not contribute significantly to the model (Tables S5, S6).

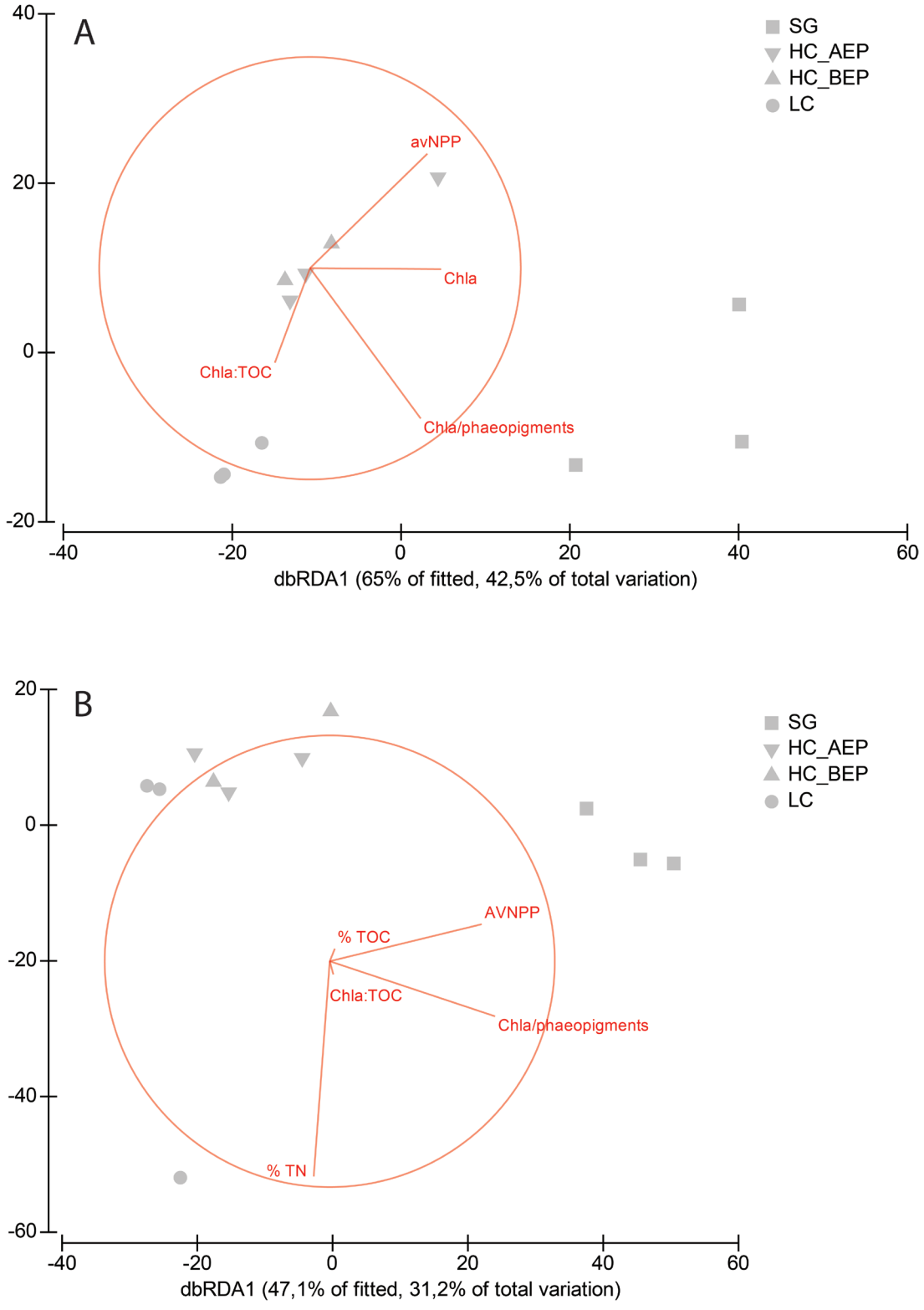


**Figure 2.7** Distance-based redundancy (dbRDA) illustrating the DISTLM model based on genera assemblage data (A) and genus individual biomass (B), and fitted environmental variables with their vector (strength and direction of effect of the variable on the ordination plot). AVPP = Average Net Primary Productivity, Chla= Chlorophyll a, Chla:TOC = Chlorophyll a: Total Organic Carbon, % TOC = Total Organic Carbon, % TN = Total Nitrogen. Source: research data (2016).

## 2.4 Discussion

### 2.4.1 Surface primary productivity, pigments and nematode standing stocks

Higher surface productivity at SG compared to the other stations, and its positive correlations with higher sediment Chl*a*, CPE and total sediment FA values point to a significant sedimentation of labile OM to the sea bottom. Next to that, highest nematode standing stocks (i.e. density and biomass) observed at SG suggests a strong benthic-pelagic coupling in the studied Atlantic part of the Southern Ocean, as was expected and already documented in previous studies (Lins et al., 2014; Veit-Köhler et al., 2011). The same link was also reported for the microbial communities (Ruff et al., 2014), megafauna (mainly echinoderms) (Würzberg et al., 2014) and ostracods (Brandão et al., 2014) studied at the same locations, where SG showed elevated abundances and biomass of these organisms compared to the more eastern located stations at the same latitude. Although other factors may play a role in the high standing stocks found at SG (e.g. grain size, bottom currents and bottom topography), nematode densities at SG were up to ten times higher than those previously reported for the Polar Front (Guilini et al., 2013) and other regions in the deep Southern Ocean (Sebastian et al., 2007), while the other stations (HC_AEP, HC_BEP and LC) exhibited a lower OM input and showed densities similar to adjacent abyssal areas (Guilini et al., 2013; Sebastian et al., 2007). The benthic-pelagic coupling effect was not very pronounced at HC_AEP and HC_BEP, which exhibited surface primary productivity values higher than LC, but this difference was barely reflected in the nematode biomass.

According to Sachs et al. (2009), the stations studied here (situated at the Polar Front) are located in the circumpolar "diatom ooze belt", which constitutes one of the most important areas of biogenic silica accumulation due to naturally occurring diatom blooms and very high benthic fluxes. This ooze belt can be divided in diatom provinces and SG region is situated within the *Chaetoceros* spp. province, while the other stations are dominated by *Fragilariopsis kergulensis*. *Chaetoceros* spp. are considered of major importance for carbon export and the highest benthic fluxes of the Southern Ocean were observed within this province (Abelmann et al., 2006). Thus, the high labile carbon values (Chl*a*: phaeopigments) displayed at SG are strongly linked to a nutrient-rich and extensive export as observed at the *Chaetoceros* spp. province. On the contrary, *F. kergu-*

*lensis* is responsible for low labile carbon fluxes (Abelmann et al., 2006), which might explain the weaker coupling observed between HC_AEP and HC_BEP relatively high surface primary productivity and nematode standing stocks. Hence, lower fresh and lower quality OM export to HC_AEP, HC_BEP and LC sediments were perhaps responsible for the lower nematode densities and biomass found at these sites when compared to SG.

Next to being located in the *Chaetoceros* spp. province, benthic fluxes might also be augmented at SG by the presence of year-round nutrient availability, with amounts twice that of the open water (Whitehouse et al., 1996), enhancing not only quality but also quantity of OM flux to the seabed. The reason for this high productivity at SG might occur by a combination of different factors: the occurrence of island-mass effects, the proximity of the Polar Front, the Weddell-Scotia Confluence, and the island's subantarctic location (Whitehouse et al., 1996). Additionally, nutrient resupply, such as upwelling at the adjacent shelf break, is also suggested to enhance annual primary production in SG (Ruff et al., 2014). This constantly high nutrient availability is most likely also responsible for the higher meiobenthic standing stocks displayed in the region (Lins et al., 2014).

The occurrence of fine, medium and coarse sand fractions (present at > 4000 m) at SG in association with lower and equally distributed % TOM until 5 cm sediment depth provides a strong indication of the high hydrodynamics in the area, with sediment being flushed down from the slope. The homogeneous distribution of % TOM in the sediment may in addition reflect bioturbation profiles. As opposed to the other stations where there is a decrease with depth, % TOM at SG expresses a homogeneous vertical distribution up to at least 5 cm depth in the sediment, which may suggest that OM is drawn into the sediment via bioturbation activities (Soetaert et al., 1997). Therefore, high nematode biomass and high density of large nematode genera found at SG, represented mainly by the genera *Acantholaimus*, *Desmodora* and *Cervonema*, could be an indication of sediment reworking at this station through the mixing of OM between sediment layers. At the other stations, the lower nematode biomass and their smaller size, together with the rapid decline of % TOM with depth into the sediment, might indicate low sediment reworking. Nevertheless, nematode bioturbation is generally overruled by macrobenthic bioturbation, following the organic matter reworked by the macrofauna. Unfortunately, the effect of the macrofauna in bioturbation processes in SG could not be inferred since no data are available (Brandt et al., 2014).

### 2.4.2 Nematode community structure

*Thalassomonhystera* (except in SG), *Acantholaimus* and *Microlaimus* (except in LC), commonly known as soft bottom deep-sea genera (Vanreusel et al., 2010), were dominant at all stations and, although possessing a high species diversity, displayed the same dominant species at all locations. The genus *Thalassomonhystera*, here dominated by one morphotype at all stations, is already known to exhibit a wide distribution, dominating many deep-sea environments including abyssal plains (Vanreusel et al., 2010; Sebastian et al., 2007). Thus, although stations were distant up to 3000 km from each other, the same morphospecies was responsible for the greater abundances of this genus overall, suggesting potentially high dispersal capability of this morphospecies. In respect to *Acantholaimus* species, *Acantholaimus invaginatum* dominated at all stations, decreasing in abundance with increasing sediment depth, while deeper sediment layers were dominated by *Acantholaimus maks*. The latter is approximately three times longer than *A. invaginatum*. The success of slender nematodes in deeper layers of the sediment was already observed in several studies both from shallow water and the deep sea (Jensen, 1986; Lins et al., 2013; Soetaert et al., 2002). Their slender body is supposed to enhance mobility, enabling them to migrate between anoxic patches of food and parts of the sediment where oxygen is available (Jensen, 1986; Soetaert et al., 2002), what might explain niche segregation observed between these two *Acantholaimus* species.

*Microlaimus*, dominated by one morphotype at all locations, displayed a typical opportunistic behaviour, suggesting a migration from deeper to superficial layers whenever fresh food supply was provided, as indicated by the high abundances observed in the superficial sediment layers at SG and HC_AEP and in deeper layers at LC. The same behaviour was also observed by Guilini et al. (2013) for the total nematode community and by Jeffreys et al. (2013) for deep dwelling Foraminifera. Unexpectedly, high densities of *Desmodora* and *Tricoma* were found in SG. These two genera are normally not encountered in such high numbers at abyssal depths (Vanreusel et al., 2010). Correspondingly, high densities of *Desmodora* in the Southern Ocean were previously described in a study conducted southeast of SG, along the Scotia Arc (Ingels et al., 2006).

Although dominated by other species (*Desmodora campbelli*), the presence of *Desmodora* in high abundances was also unexpected and its omnipresence at other distant sampled stations was attributed to passive transport in the bedload and water column (Ingels et al., 2006). In this study, *Desmodora* dominated at SG both in density

and biomass by a single species, *D. profundum*, previously described by Moura et al. (2014) for the deep south-east Atlantic, but it was also present at the other Polar Front stations. Its presence both in the south-east Atlantic deep sea, as well as at all stations from this study suggests that this species can be susceptible to erosion and passive transport in the water column. The genus *Desmodora* is considered as opportunistic, usually found in highly productive environments, such as seamounts, seeps and vents, but it also prefers coarser substrates unlike most nematodes (Vanreusel et al. 2010). Thus the high productivity at SG, together with a slightly coarser sediment fraction, may therefore have induced its dominance. Moreover, Gerlach and Schrage (1972) observed that this genus is able to have a life cycle of approximately 600 days, being able to persist throughout the year even if productivity is seasonal.

The genus *Tricoma* belongs to the family Desmoscolecidae and its presence is typical, although in lower numbers than observed here, for the abyssal deep sea (Soetaert and Heip, 1989 and references therein). This genus is mainly found in high abundances in environments dominated by coarser sediments, such as corals and seamounts. The high abundances of *Tricoma* at SG, then, could be due to the coarser sediment present there, as the nematodes from this family have a very typical way of locomotion favoured by a coarse sediment type (Giere, 1993).

### 2.4.3 Nematode fatty acids

Despite their importance, little is known on nematode FA composition in general (Leduc, 2009; Leduc et al., in press; Leduc and Probert, 2009) and in the abyssal Southern Ocean in particular (Guilini et al., 2013). This is mainly due to difficulties in assembling enough material for the analyses, as nematodes are very small organisms and even smaller in deep-sea sediments (Ramirez-Llodra et al., 2010). Thus, research is mainly concentrated on "bulk" analyses, diluting the signal from individual genera or species and muting the potential high degree of interspecific variability. In this study we could perform individual analyses on *Desmodora* and desmocolecids due to their high abundance at SG.

When total "bulk" FA content was analysed, nematodes exhibited higher total individual FA concentrations at SG compared to the other stations, as well as higher total sediment FA content. However, within sediment FA, ∑SFA and ∑MUFA were the most abundant groups, while ∑PUFA dominated in nematodes, indicating a selective uptake

behaviour of this group for high quality FA. Hence, this study corroborates with the low sediment ∑PUFA concentrations also found by Würzberg et al. (2011) and the high nematode ∑PUFAs revealed by Guilini et al. (2013) in the Southern Ocean. However, the potential of nematodes as high quality food source for higher trophic levels is still under debate (Leduc, 2009), as they generally possess very low FA concentrations when compared to other meiofaunal groups, such as copepods (De Troch et al., 2012). When FA from *Desmodora* and desmoscolecids (for SG) were compared to the "bulk" FA, ∑MUFAs and ∑SFAs dominated in each group, respectively. MUFAs are commonly found in faecal pellets, especially in environments subjected to a high food supply, where residence time of food in the guts of zooplankton is shortened (Reemtsma et al., 1990). The presence of intact faecal pellets in the sediment was observed at SG by Ruff et al. (2014). They observed that the presence of intact faecal pellets and chloroplast rRNA at the seafloor "provided evidence for a short transport time of few weeks and suggested a strong benthic-pelagic coupling". The higher amount of MUFAs in *Desmodora*, characterized as a sediment-surface dwelling epistratum feeder (according to Wieser, 1953), was clearly associated with elevated water and sediment pigment concentrations, as expressed by a diatom-bio-markers $\frac{\sum 16{:}1\omega7}{\sum 16{:}0}$ with ratio greater than 1, $\frac{\mathrm{DHA}}{\mathrm{EPA}}$ smaller than 1 and by elevated EPA content. In this study, FA content indicates they may probably feed on partially degraded diatoms present in intact faecal pellets, as suggested by their high MUFA concentrations. The lack of 20:4ω6 in *Desmodora* (and its presence in all other nematodes) was possibly the reason for the lower PUFA concentration found in this genus. This FA is normally found in high abundances in foraminiferans (Gooday et al., 2002; Suhr et al., 2003) and the lack of it only in *Desmodora* indicates the selective feeding behaviour of this group.

Plankton-based FA contributed most to the diet of nematodes. Bacterial FA were scarcely present in nematodes, indicating that their primary food source was fresh phyto-plankton detritus derived from the surface waters. The ratio $\frac{\sum 16{:}1\omega7}{\sum 16{:}0} > 1$, together with high EPA content, indicated a diatom-based diet for nematodes (including *Desmodora*) from SG, while the other sites had $\frac{\sum 16{:}1\omega7}{\sum 16{:}0}$ ratios lower than 1. Nevertheless, when $\frac{\mathrm{DHA}}{\mathrm{EPA}}$ was compared between stations, the ratio remained around 1, indicating that not only EPA but also DHA (commonly found in dinoflagellates) was present in high concentration in "bulk" nematodes. DHA values reached up to almost 20% of the total FA content and it was already shown that although nematodes are able to biosynthesise highly unsaturated FA (HUFAs), they hardly ever biosynthetize DHA (Honnens et al., 2014; Leduc and Probert, 2009), pointing to a selective feeding behaviour. This FA is an

important constituent of all organisms and in the benthic system it may represent food sources with high refractory material content (which might be rich in DHA) rather than dietary dinoflagellates. Thus, higher values of markers for "fresh" diatom input (16:1ω7 and EPA) were observed at SG, while the other stations exhibited strong indications for a more refractory feeding behaviour (high DHA values at LC and a marked decrease from HC_BEP to HC_AEP). An important FA that should be mentioned is the PUFA 20:4ω6, present in high abundances in foraminiferans (Gooday et al., 2002; Suhr et al., 2003). While it lacked completely in *Desmodora*, this FA was present in relatively high abundances in all other "bulk" nematodes and Desmoscolecidae, suggesting a potential input of foraminiferans in their diet. Lejzerowicz et al. (2014) showed single-chambered, soft-walled monothalamous taxa as the most abundant Foraminifera encountered at the same stations of the Southern Ocean sampled as this study. Considering that foraminiferans are ubiquitous and PUFA-rich, their potential inclusion in the general nematode food diet is not surprising. Hence, we conclude that when there is high quality food available, nematodes will selectively feed on this fresh OM, whereas when food becomes limiting, they will adopt a more opportunistic feeding strategy behaviour consisted of refractory material, which enables them to feed throughout the year.

Isotope studies conducted on deep-sea nematodes from the Northeast Pacific suggested a sedimentary food source, thus mainly composed of refractory organic matter (Jeffreys et al., 2013). Hitherto, this behaviour would be more expected in food-limited environments, as was observed in the FA analyses for the LC site. Because "fresh" food is limited at this station, foraging is restricted to refractory material. Next to differences in interspecific isotope composition, differences in prey availability, nematode body size and habitat might be responsible for variation in trophic levels within the same species (Leduc et al., in press). Consequently, without the combination with stable isotope analyses, results should be interpreted with caution. Studies conducted on pelagic copepods showed that they accumulate large lipid reserves (wax esters, 16:1ω7, 18:4ω3 and EPA) as an adaptation to the pronounced seasonality and strongly pulsed food supply, but that in the Antarctic they have evolved a more opportunistic feeding behaviour, storing triacylglycerols rather than wax esters (Dalsgaard et al., 2003). FA contents of nematodes are generally much lower than in copepods (De Troch et al., 2012), and together with the dominance of typical phospholipids of biomembranes (EPA, DHA and 16:0) observed in other studies (Graeve et al., 1997), they possibly do not accumulate lipids as an energy storage. It is improbable then that they would synthesize great amounts of polyunsaturated

FA *de novo* without any need for it (Guilini et al., 2013). Thus, PUFA concentrations in nematodes from HC_BEP, HC_AEP and LC might be derived from intermediate food components, such as foraminiferans, or from feeding on refractory material (available all year round), which is poor in PUFA (Gulini et al., 2013).

### 2.4.4 Nematode function, taxon diversity and respiration

Trophic structure showed a higher number of 1B (non-selective deposit feeders) in SG and this number increased with sediment depth due to the presence of *Cervonema*, *Daptonema,* and *Sabatieria* in deeper layers of the sediment. Representatives of these genera were long and big in this study, and could easily dwell in deeper layers to avoid competition and/or feed on refractory material buried deeper down. Moens and Vincx (1997), when analysing feeding behaviour of various species, mentioned that *Daptonema setosum* (1B) had a restless and erratic feeding behaviour, interrupting periods of immobility or slow gliding with abrupt activity. Therefore, although the feeding behaviour of the other 1B genera was not yet tested, we expect low selectivity of this group. Epistratum feeders (2A) dominated the samples at all stations. At HC_BEP they were mainly present in the subsurface layer (1–2 cm), and at HC_AEP they were mainly concentrated in the superficial layers. These differences were mainly due to the genus *Microlaimus* and its migration towards superficial layers after fresh food input, indicating an opportunistic behaviour of this genus. At SG, trophic group 2A was mainly represented by the genus *Desmodora*, mostly present in the superficial layers. In general, epistratum feeders are often associated with surface sediments due to fresh OM input.

The higher total respiration rates at SG were in accordance with the higher fresh Chl*a* input, as well as with elevated nematode diversity and biomass. More diverse communities are generally linked to a higher sediment-community respiration, which in turn is also correlated to higher energy availability (Levin et al., 2001). A more diverse community is believed to be able to mineralise more carbon and optimise resource use (Pape et al., 2013a) and its response to food input can be immediate (Gage and Tyler, 1991), resulting in higher oxygen consumption (enhanced respiratory activity) after a phytoplankton bloom (Veit-Köhler et al., 2011). Sachs et al. (2009) observed a high sedimentary oxygen uptake at the Polar Front for sites underlying areas of high chlorophyll concentration in surface waters. Our results differ from respiration rates observed by Pape et al. (2013a) for the Mediterranean, where diversity did not mirror respiration

rates, but are in accordance with the general sediment community oxygen consumption results found for nematodes elsewhere (Franco et al., 2010; Levin et al., 2001; Veit-Köhler et al., 2011).

### 2.4.5 Environmental drivers of nematode standing stocks

DISTLM results for density, biomass and FA composition displayed a significant effect of the average primary productivity (avNPP) on nematode density and FA, and of sediment Chl*a* on nematode biomass. This reflects the importance of surface primary productivity and flux of OM to the seabed as major drivers of nematode community structure. It has been shown before that deep-sea communities appear to be chiefly controlled by energy availability (Levin et al., 2001; Karakas et al., 2009; Pape et al., 2013b; Pfannkuche and Lochte, 1993; Soetaert and Heip, 1989) and by diatom production at the surface (Sachs et al., 2009). Moreover, Ruff et al. (2014) observed for the same SG station a strong benthic-pelagic coupling due to the export of dense, fast-settling particles detected by the presence of intact 16S RNA, a strong indicator for fresh phytoplankton. These results corroborate the previously mentioned "diatom ooze belt" dominated by *Chaetoceros* spp. and their high carbon export capacity in SG site (Sachs et al., 2009). Next to that, in Antarctica, low degradation rates of OM may occur due to the low temperatures and low microbial activity, enabling the accumulation of OM sediments over longer periods of time (Fabiano and Pusceddu, 1998) and, consequently, its availability to the benthic organisms.

## 2.5 Conclusions

With the use of different approaches concerning surface primary productivity estimates, sediment Chl*a* and the use of FAs in combination with nematode community analysis, we integrated environmental and biological traits to unravel different aspects of benthic-pelagic coupling in the Southern Ocean. We observed that nematode standing stocks from abyssal plains of the Southern Ocean are regulated by plankton-derived food sources, though nematodes are also able to thrive on refractory material or other food sources (e.g. foraminiferans). Differences in nematode community composition as well as the increase in nematode high quality fatty acids mostly occur in relation to an increase in surface primary productivity, since certain nematode genera (e.g. *Desmodora*) seem to

be significantly favoured by the increase in labile organic matter arriving at the seabed.

As nematodes do not have lipid reserves and must feed all-year round, they will predominantly feed on fresh organic matter when present, as shown by the nematode FA composition in comparison sediment FA, but easily change to a poorer diet based on refractory material whenever fresh food becomes scarce. Food selectivity based on FA biomarkers demonstrated a preference for a diatom-based diet in "bulk" nematodes and *Desmodora* from SG, whereas at the other stations feeding on food sources other than diatoms was dominant.

FA analyses on nematodes, as well as other promising techniques, such as compound specific stable isotopes from amino acids, are still restricted by the small size of this group. "Bulk" techniques provided a good insight in this study because very contrasting stations in terms of surface productivity were used and one main feeding type (2A) dominated the samples, providing clear FA signals. Nevertheless, information about each genus feeding habit is still diluted and/or restricted to the most abundant genera.

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## 2.7 Supplementary data

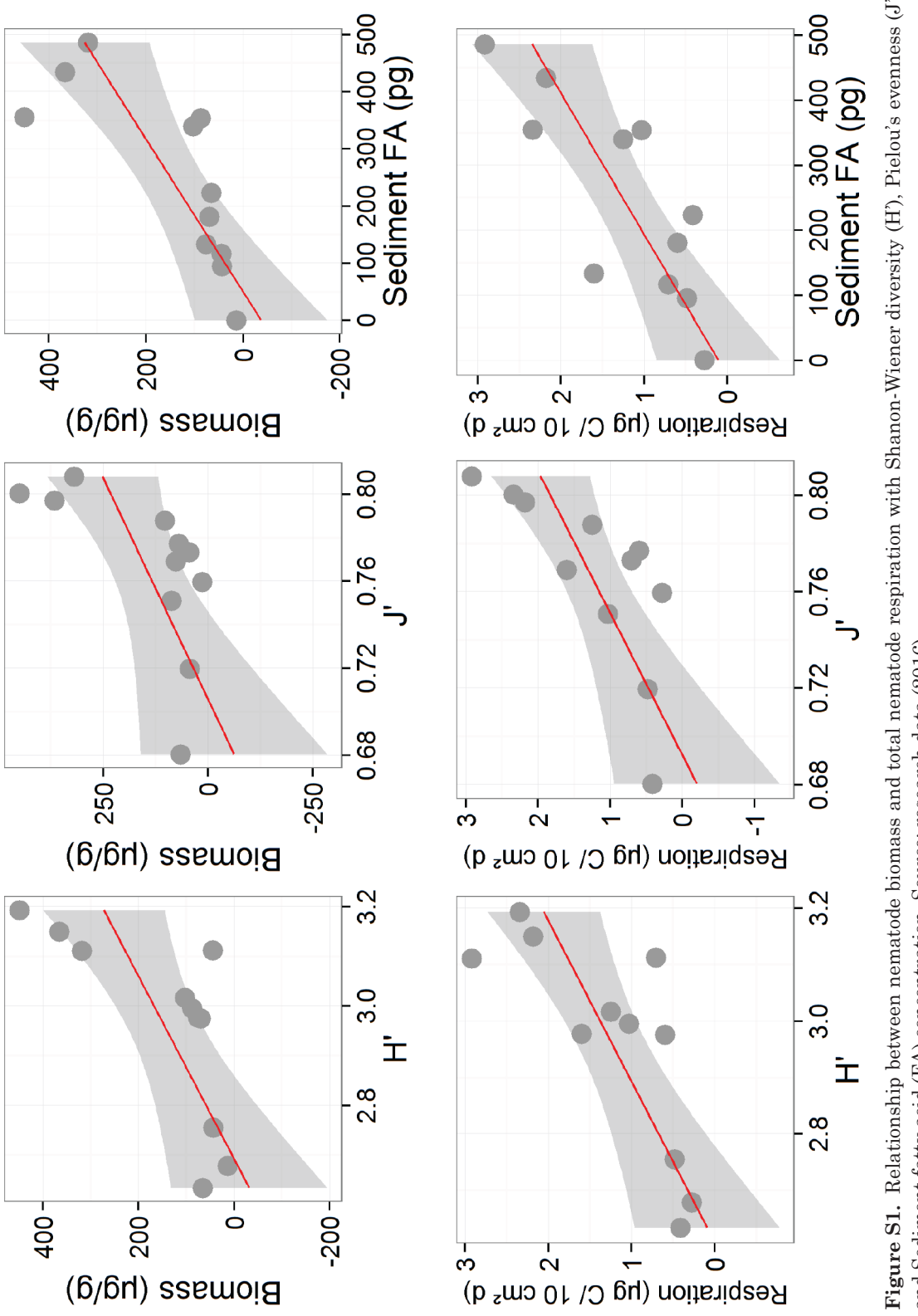


**Figure S1.** Relationship between nematode biomass and total nematode respiration with Shanon-Wiener diversity (H'), Pielou's evenness (J') and Sediment fatty acid (FA) concentration. Source: research data (2016).

**Table S1.** Univariate PERMANOVA table of results for sediment fatty acid profiles (Sediment SFAs = sediment saturated fatty acids; Sediment MUFAs = sediment monounsaturated fatty acids; Sediment PUFAs = sediment polyunsaturated fatty acids; Bacterial + planktonic FA = fatty acid bacterial- or planktonic-derived; avNPP = average net primary productivity). Values in bold and italic indicate significant differences ($p < 0.05$). Source: research data (2016).

**Sediment SFAs**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms | P(MC) |
|---|---|---|---|---|---|---|---|
| **station** | 3 | 205.93 | 68.643 | 1.2572 | 0.32 | 7360 | |
| **Res** | 7 | 382.2 | 54.599 | | | | |
| **Total** | 10 | 588.13 | | | | | |

**Sediment MUFAs**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms | P(MC) |
|---|---|---|---|---|---|---|---|
| **station** | 3 | 8980.8 | 2993.6 | 4.5469 | 0.0698 | 897 | |
| **Res** | 7 | 4608.7 | 658.39 | | | | |
| **Total** | 10 | 13590 | | | | | |

**Sediment PUFAs**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms | P(MC) |
|---|---|---|---|---|---|---|---|
| **station** | 3 | 1246.6 | 415.52 | 16.572 | | 62 | ***0.0031*** |
| **Res** | 6 | 150.44 | 25.074 | | | | |
| **Total** | 9 | 1397 | | | | | |

**Bacterial + planktonic FA**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms | P(MC) |
|---|---|---|---|---|---|---|---|
| **station** | 3 | 2401.7 | 800.57 | 9.6817 | ***0.0011*** | 4978 | |
| **Res** | 6 | 496.13 | 82.689 | | | | |
| **Total** | 9 | 2897.8 | | | | | |

**avNPP**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms | P(MC) |
|---|---|---|---|---|---|---|---|
| **station** | 3 | 2.6443E5 | 88145 | 2.0766E5 | ***0.0001*** | 302 | |
| **Res** | 7 | 2.9713 | 0.42447 | | | | |
| Total | 10 | 2.6444E5 | | | | | |

**Table S2.** Multivariate PERMANOVA two-way nested design table of results for nematode density, relative abundance, total number of genera and biomass. Significant results ($p < 0.05$) are represented in bold and italic. Source: research data (2016).

**Density (10 cm²)**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms |
|---|---|---|---|---|---|---|
| **Station** | 3 | 37403 | 12468 | 59.967 | ***0.0001*** | 9888 |
| **Slice** | 4 | 26382 | 6595.6 | 57.527 | ***0.0001*** | 9875 |
| **Replicate (station)** | 12 | 24949 | 2079.1 | 18.134 | ***0.0001*** | 9742 |
| **Station x slice** | 12 | 32817 | 2734.7 | 23.852 | ***0.0001*** | 9757 |
| **Res** | 48 | 55033 | 1146.5 | | | |
| **Total** | 79 | 1,7658E5 | | | | |

**Relative Abundance (%)**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms |
|---|---|---|---|---|---|---|
| **Station** | 3 | 21855 | 7285 | 52.691 | ***0.0001*** | 9883 |
| **Slice** | 4 | 15848 | 3962.1 | 48.888 | ***0.0001*** | 9879 |
| **Replicate (station)** | 12 | 16591 | 1382.6 | 1.706 | ***0.0001*** | 9758 |
| **Station x slice** | 12 | 20848 | 1737.4 | 21.437 | ***0.0001*** | 9771 |
| **Res** | 48 | 38901 | 810.44 | | | |
| **Total** | 79 | 1.14E+09 | | | | |

**Total number of genera (S)**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms |
|---|---|---|---|---|---|---|
| **Station** | 3 | 20286 | 6762 | 39.356 | ***0.0001*** | 9884 |
| **Slice** | 4 | 11605 | 2901.4 | 33.381 | ***0.0001*** | 9863 |
| **Replicate (station)** | 12 | 20618 | 1718.2 | 19.768 | ***0.0001*** | 9761 |
| **Stationxslice** | 12 | 12774 | 1064.5 | 12.247 | ***0.049*** | 9786 |
| **Res** | 48 | 41720 | 869.16 | | | |
| **Total** | 79 | 1.07E+05 | | | | |

**Biomass (µg dwt)**

| Source | df | SS | MS | Pseudo-F | P(perm) | unique perms |
|---|---|---|---|---|---|---|
| **Station** | 3 | 50632 | 16877 | 42.716 | ***0.0001*** | 9873 |
| **Slice** | 4 | 22217 | 5554.4 | 21.377 | ***0.0001*** | 9800 |
| **Replicate(station)** | 12 | 47413 | 3951.1 | 15.207 | ***0.0001*** | 9603 |
| **Station x slice** | 12 | 44751 | 3729.3 | 14.353 | ***0.0001*** | 9623 |
| **Res** | 48 | 1.25E+09 | 2598.2 | | | |
| **Total** | 79 | 2.90E+09 | | | | |

**Table S3.** Relative concentrations of individual fatty acid (% of total fatty acid) in "bulk" nematodes (and separate groups *Desmodora* and Desmoscolecidae) from all sampled stations (SG = South Georgia; HC_AEP = High Chlorophyll_After Eddy Pump; HC_BEP = High Chlorophyll_Before Eddy Pump; LC = Low Chlorophyll). Source: research data (2016).

| Fatty acids and ratios | Desmoscolecidae | *Desmodora* | "Bulk" nematodes | | | |
|---|---|---|---|---|---|---|
| | | | SG | HC_AEP | HC_BEP | LC |
| **14:0** | 1.1 ± 2.6 | 4.1 ± 0.2 | 2 ± 0.2 | 1.4 ± 1.7 | 3.2 ± 3.3 | 1.1 ± 1.9 |
| **antei iso 15:0** | - | - | 0.3 ± 0.2 | - | - | - |
| **iso 15:0** | - | - | 0.3 ± 0.4 | 1.2 ± 1.5 | - | - |
| **15:0** | - | - | 0.3 ± 0.9 | - | - | - |
| **16:0** | 26.1 ± 1.6 | 13.3 ± 3 | 8.6 ± 0.5 | 31.6 ± 5.8 | 20.8 ± 2.4 | 20.2 ± 6.1 |
| **16:1ω7** | 12.4 ± 1.5 | 26.4 ± 3 | 12.4 ± 1.8 | 4.6 ± 1.2 | 1.2 ± 1.2 | 2.2 ± 3.8 |
| **17:0** | - | - | 0.2 ± 0.5 | - | - | - |
| **17:1ω7** | - | - | 0 ± 0.1 | - | - | - |
| **18:0** | 15.5 ± 2.5 | 7.4 ± 2.9 | 4.5 ± 0.5 | 16.4 ± 4.4 | 9.8 ± 3.2 | 11.2 ± 4.2 |
| **18:1ω9t** | 0.8 ± 1.8 | 4 ± 0.2 | 7.5 ± 1.8 | 6.2 ± 4.7 | 4.3 ± 4.4 | 7.7 ± 0.9 |
| **18:1ω9c** | 8.1 ± 2 | 5.3 ± 0.4 | 8.9 ± 1.4 | 8.2 ± 2.2 | 6.6 ± 0.6 | 7.5 ± 1.1 |
| **18:2ω6t** | - | - | 0.9 ± 2.2 | - | - | - |
| **18:2ω6c** | - | 2.4 ± 3.2 | 0.5 ± 0.2 | - | - | - |
| **20:1ω9t** | 0.1 ± 0.2 | - | 3 ± 0.9 | - | - | 1 ± 1.7 |
| **20:1ω9c** | - | 4 ± 3.2 | 4 ± 1.4 | - | - | 1 ± 1.8 |
| **20:2ω6** | - | - | 1.5 ± 0.2 | - | - | - |
| **20:4ω6** | 17.2 ± 3.5 | - | 12.7 ± 2 | 13.7 ± 2.6 | 23 ± 5.4 | 19.9 ± 2.4 |
| **EPA(20:5ω3)** | 18.7 ± 2.8 | 18.6 ± 1 | 15.6 ± 1.8 | 5.8 ± 4.7 | 12.9 ± 0.2 | 13 ± 0.8 |
| **24:1ω9** | - | 3 ± 6.4 | 1.7 ± 0.1 | - | - | - |
| **DHA(22:6ω3)** | - | 11.5 ± 9 | 15.1 ± 1.6 | 11 ± 2.7 | 18.2 ± 2.8 | 15.1 ± 1.8 |
| **DHA/EPA** | - | 0.6 ± 0.6 | 1 ± 0.1 | 1.9 ± 0.2 | 1.4 ± 0.2 | 1.2 ± 0.3 |
| **EPA/DHA** | - | 1.61 ± 0.6 | 1 ± 0.1 | 0.5 ± 0.2 | 0.7 ± 0.2 | 0.8 ± 0 |
| **16:1ω7/16:0** | 0.5 ± 0 | 2 ± 0.5 | 1.4 ± 0.2 | 0.1 ± 0 | 0.1 ± 0 | 0.1 ± 0.2 |
| **iso 15:0+anteiso 15:0/ 15:0** | - | - | - | - | - | - |
| **ΣC16/ΣC18** | 1.6 ± 0 | 2.1 ± 0 | 0.9 ± 0.1 | 1.2 ± 0 | 1.1 ± 0 | 0.8 ± 0 |
| **ΣSFA** | 42.7 ± 5.9 | 24.9 ± 3.3 | 16.2 ± 2.3 | 50.6 ± 7.2 | 33.9 ± 2.2 | 32.5 ± 8.4 |
| **ΣMUFA** | 21.4 ± 1.4 | 42.7 ± 12.2 | 37.5 ± 1.4 | 18.9 ± 3.3 | 12.1 ± 5 | 19.4 ± 6.3 |
| **ΣPUFA** | 35.9 ± 4.5 | 32.4 ± 14.4 | 46.3 ± 3.1 | 30.5 ± 4 | 54.1 ± 2.8 | 48.1 ± 3.9 |
| | | | | | | |
| **ΣPlanktonic FA %** | 86.4 ± 7.9 | 64.1 ± 20 | 79.3 ± 3.3 | 92.9 ± 7.2 | 95.6 ± 2.2 | 95.7 ± 5.0 |
| **ΣBacterial FA %** | 1.14 ± 0 | 4.1 ± 0 | 2.8 ± 2.1 | 2.5 ± 1.5 | 3.2 ± 0 | 1.1 ± 0 |

**Table S4.** Dissimilarity (> 5 %) SIMPER routines based on the nematode (including *Desmodora* and Desmoscolecidae) individual fatty acid concentrations. Source: research data (2016).

| ***Desmodora* x Desmoscolecidae** | **%** | **Desmoscolecidae x Nematoda** | **%** | ***Desmodora* x Nematoda** | **%** |
|---|---|---|---|---|---|
| **ΣC16/ΣC18** | 26.15 | **ΣC16/ΣC18** | 32.59 | **ΣC16/ΣC18** | 18.32 |
| **EPA/DHA** | 8.27 | **ΣMUFA** | 8.12 | **ΣPUFA** | 12.38 |
| **ΣMUFA** | 7.95 | **ΣPUFA** | 7 | **C16:1w7/16:0** | 11.8 |
| **C16:1w7/16:0** | 7.64 | **EPA/DHA** | 6.94 | **C20:4w6** | 6.83 |
| **ΣSFA** | 6.81 | **DHA/EPA** | 6.82 | **EPA/DHA** | 6.12 |
| **C20:4w6** | 6.05 | **ΣSFA** | 6.4 | | |
| **DHA/EPA** | 5.86 | **DHA(22:6w3)** | 5.54 | | |
| **C16:1w7** | 5.04 | | | | |

**Table S5.** Marginal tests from the distance-based linear model (DISTLM) for genera assemblages and selected environmental variables. Chla = Chlorophyll a; Chla:phaeo = chlorophyll a: phaeopigments; Chla: TOC = chlorophyll a: total organic carbon; CPE = chloroplastic pigment equivalents; % TN = total nitrogen content; % TOC = total organic carbon content; total sedFA = total sediment fatty acid content; avNPP = average net primary productivity. Values in bold and italic indicate significant differences ($p < 0.05$). Source: research data (2016).

| **Density (10 cm²)** | **SS(trace)** | **Pseudo-F** | **P** | **Prop.** |
|---|---|---|---|---|
| **Chla** | 4337.5 | 4.6603 | ***0.0001*** | 0.34115 |
| **Chla: phaeo** | 4334.3 | 4.655 | ***0.0054*** | 0.3409 |
| **Chla:TOC** | 993.83 | 0.76315 | 0.5664 | 7.8166E-2 |
| **CPE** | 2295.3 | 1.9828 | 0.08 | 0.18053 |
| **% TN** | 1199.2 | 0.93724 | 0.4296 | 9.4316E-2 |
| **% TOC** | 1381.3 | 1.0969 | 0.3209 | 0.10864 |
| **total sedFA** | 2226.7 | 1.9109 | 0.0992 | 0.17514 |
| **avNPP** | 4639.8 | 5.1717 | ***0.0028*** | 0.36493 |

| **Biomass (µg/ g)** | **SS(trace)** | **Pseudo-F** | **P** | **Prop.** |
|---|---|---|---|---|
| **Chla** | 6443.9 | 2.6176 | ***0.0027*** | 0.22531 |
| **Chla:phaeo** | 8275.3 | 3.6644 | ***0.0052*** | 0.28935 |
| **Chla:TOC** | 2064.1 | 0.70006 | 0.8581 | 7.2171E-2 |
| **CPE** | 3806.1 | 1.3816 | 0.1018 | 0.13308 |
| **% TN** | 3405.1 | 1.2163 | 0.3035 | 0.11906 |
| **% TOC** | 2474.5 | 0.85246 | 0.5861 | 8.65E-02 |
| **total sedFA** | 3593 | 1.2931 | 0.2474 | 0.12563 |
| **avNPP** | 8153.2 | 3.5888 | ***0.0005*** | 0.28508 |

| **Total FA (pg/ ind)** | **SS(trace)** | **Pseudo-F** | **P** | **Prop.** |
|---|---|---|---|---|
| **Chla** | 2019.2 | 2.2976 | 0.0557 | 0.20337 |
| **Chla:phaeo** | 3536.1 | 4.9785 | ***0.003*** | 0.35615 |
| **Chla:TOC** | 613.61 | 0.59286 | 0.7535 | 6.1803E-2 |
| **CPE** | 838.99 | 0.83072 | 0.5569 | 8.4502E-2 |
| **% TN** | 636 | 0.61598 | 0.7947 | 6.41E-02 |
| **% TOC** | 494.81 | 0.47206 | 0.7446 | 4.98E-02 |
| **total sedFA** | 826.46 | 0.81719 | 0.5744 | 8.3241E-2 |
| **avNPP** | 3793.5 | 5.5649 | ***0.0002*** | 0.38208 |

**Table S6.** Sequential tests from the distance-based linear model (DISTLM) for genera assemblages and selected environmental variables. Chla = Chlorophyll a; Chla:phaeo = chlorophyll a: phaeopigments; Chla: TOC = chlorophyll a: total organic carbon; CPE = chloroplastic pigment equivalents; % TN = total nitrogen content; % TOC = total organic carbon content; total sedFA = total sediment fatty acid content; avNPP = average net primary productivity. Values in bold and italic indicate significant differences ($p < 0.05$). Source: research data (2016).

| **Density (10 cm²)** | **Adj R²** | **SS(trace)** | **Pseudo-F** | **P** | **Prop.** | **Cumul.** | **res.df** |
|---|---|---|---|---|---|---|---|
| **+avNPP** | 0.29437 | 4639.8 | 5.1717 | ***0.0023*** | 0.36493 | 0.36493 | 9 |
| **+Chla:Phaeo** | 0.36971 | 1663.5 | 2.0758 | ***0.0299*** | 0.13083 | 0.49576 | 8 |
| **+Chla** | 0.39028 | 984.44 | 1.2699 | 0.2432 | 7.7428E-02 | 0.57319 | 7 |
| **+Chla:TOC** | 0.42272 | 1022.7 | 1.3935 | 0.219 | 8.0441E-02 | 0.65363 | 6 |

**Best solution**

| **Adj R²** | **RSS** | **No.Vars** | **Selections** |
|---|---|---|---|
| 0.42272 | 4403.8 | 4 | 1-3; 9 |

| **Biomass (µg/ g)** | **Adj R²** | **SS(trace)** | **Pseudo-F** | **P** | **Prop.** | **Cumul.** | **res.df** |
|---|---|---|---|---|---|---|---|
| **+Chla: Phaeo** | 0.21039 | 8275.3 | 3.6644 | ***0.0047*** | 0.28935 | 0.28935 | 9 |
| **+% TN** | 0.25292 | 3231.4 | 1.5124 | 0.1704 | 0.11299 | 0.40233 | 8 |
| **+avNPP** | 0.27428 | 2564.4 | 1.2355 | 0.226 | 8.9664E-2 | 0.492 | 7 |
| **+% TOC** | 0.29803 | 2482.9 | 1.2367 | 0.2649 | 8.6817E-2 | 0.57882 | 6 |
| **+Chla:TOC** | 0.32555 | 2401.2 | 1.2448 | 0.2916 | 8.3959E-2 | 0.66277 | 5 |

**Best solution**

| **Adj R²** | **RSS** | **No.Vars** | **Selections** |
|---|---|---|---|
| 0.32555 | 9644.6 | 5 | 2; 3; 5; 6; 9 |

| **total FA (pg/ind)** | **Adj R²** | **SS(trace)** | **Pseudo-F** | **P** | **Prop.** | **Cumul.** | **res.df** |
|---|---|---|---|---|---|---|---|
| **+avNPP** | 0.31342 | 3793.5 | 5.5649 | ***0.0002*** | 0.38208 | 0.38208 | 9 |
| **+Chla: Phaeo** | 0.5168 | 2297.1 | 4.7882 | ***0.0077*** | 0.23137 | 0.61334 | 8 |
| **+% TOC** | 0.5498 | 709.1 | 1.5864 | 0.1973 | 7.142E-2 | 0.68486 | 7 |
| **+CPE** | 0.61648 | 844.18 | 2.217 | 0.0956 | 8.5025E-2 | 0.76989 | 6 |
| **+total sedFA** | 0.64372 | 516.02 | 1.4588 | 0.2416 | 5.1974E-2 | 0.82186 | 5 |

**Best solution**

| **Adj R²** | **RSS** | **No.Vars** | **Selections** |
|---|---|---|---|
| 0.64362 | 1768.7 | 5 | 2; 4; 6; 8; 9 |

# Chapter 3

# Species variability and connectivity in the deep sea: evaluating effects of spatial heterogeneity and hydrodynamic effects

Unpublished manuscript

## 3.1 Introduction

The link between biodiversity (i.e. diversity of species) and ecological processes (e.g. carbon flow, species productivity) has created a heightened interest in ecological research after large-scale human impacts were deemed responsible for declining species numbers and alterations of ecosystem properties (Loreau et al., 2001). Stretching between the coast and the abyssal plains of the deep sea, continental margins (0–4000 m) encompass the largest habitat diversity in the marine environment (Ramirez-Llodra et al., 2010). They harbour a high biodiversity, and are responsible for 90 % of the new biological productivity in oceans and seas, providing valuable food and energy resources for the marine fauna (Salgueiro et al., 2014).

It is generally accepted that many principal biological oceanographic processes, such as carbon burial and nutrient cycling, remain concentrated within continental margins (Levin and Dayton, 2009). Yet, the biodiversity of continental margins is under severe threat by commercial exploitation, ranging from fisheries, to gas, oil, and mineral extraction (Levin and Dayton, 2009; Puig et al., 2012). The direct impact of these unabated commercial activities on benthic environment and populations varies greatly, from pervasive sediment erosion, transportation and deposition, to the large-scale alteration of community composition (Puig et al., 2012). Therefore, continental margins comprise key locations to study the effects of environmental alterations on benthic biodiversity.

Understanding the processes that shape biodiversity patterns on continental margins is an important prerequisite for comprehending anthropogenic impacts in these environments. Sea-surface processes have an important effect on the benthic fauna because part of the primary production is exported from overlying waters to the deep-sea floor, mostly in the form of phytodetritus, where it serves as food source to benthic communities (Billett et al., 1983; Lins et al., 2015; Serpetti et al, 2013; Wei et al., 2010). Particulate organic carbon input in the deep sea has been regarded as one of the main factors shaping benthic community structure and functioning (Rex, 1981). Phytodetritus creates patchiness, enhancing habitat heterogeneity, and consequently promotes species coexistence (Cardinale et al., 2000). In addition, depth indirectly plays a role in structuring benthic communities, since organic matter flux is negatively related to depth, and deeper regions will consistently receive less input of labile organic matter compared to shallower regions (Danovaro et al., 2010; García et al. 2008; Lutz et al., 2007; Ramalho et al. 2014).

Probably as a consequence of this decline in food availability, decreases in abundance and biomass associated with an increase in depth on the continental slopes have been observed for all benthic size classes (mega-, macro- and meiofauna) (Flach et al., 2002; Muthumbi, et al., 2011; Rex et al., 2005; Rowe et al., 2008; Thiel, 1978).

Food availability, as well as biological factors (predation, competition, dispersal), drive small-scale (1–10 $m^2$) patterns of benthic communities (Gage, 1997) promoting alpha diversity (Levin et al., 2001). Besides, other factors also play a role in shaping benthic communities. High community differences over large spatial scales (100–1000 $m^2$; beta diversity) within continental margins have been observed both along a bathymetric gradient as well as between stations of similar depth. This indicates that beta diversity is not singularly depth-dependent (Danovaro et al., 2013; Havermans et al., 2013). Physical factors, including near-bottom currents, sediment grain-size heterogeneity, boundary constraints, hydrodynamics, human activities, and topography are also considered of particular importance for beta diversity (Levin et al., 2001). They shape biodiversity as they may reduce the effect of a dominant species through the redistribution of resources among inferior and superior competitors (Stachowicz et al., 2007), and in this way increasing species diversity.

Moreover, population dynamics and dispersal (Derycke et al., 2013; Gage, 1997; Rex et al., 2005) have been shown to affect the structuring of benthic fauna at different spatial scales. In this sense, continental margins are recognised as highly heterogeneous systems (Levin and Dayton, 2009). Most benthic species have restricted active dispersal potential, but passive dispersal may be facilitated through ocean currents, especially for species with pelagic larval stage (Etter and Bower, 2015; Gallucci et al., 2008; Lins et al., 2014; Ullberg and Ólafsson, 2003).

The lack of a pelagic larval stage in free-living nematodes, the focus group of this study, could therefore be viewed as a disadvantage to dispersal. Nevertheless, this abundant and omnipresent group of benthic metazoa is found at all depths and in all deep-sea habitats (Giere, 2009; Vincx et al., 1994). Nematodes belonging to the meiofauna (< 1 mm) exhibit high species richness and are one of the few taxa in which true cosmopolitan species may exist (Bik et al., 2010; Zeppilli et al., 2011). Some species are able to actively swim, following chemical cues, but more importantly, nematodes may be passively transported via water currents following resuspension from disturbance events (Schratzberger et al., 2004; Jensen, 1981). Molecular studies have indicated that

different nematode taxa in diverse habitats exhibit population connectivity across a wide range, with some species showing subtle but significant genetic structuring at a small spatial scale, and other species exhibiting no differentiation along large distances (> 500 km). These findings confirm a high dispersal potential and low endemism for at least some species (Derycke et al., 2005; Derycke et al., 2013). Nematodes therefore, hold ideal life traits when seeking to understand connectivity, coexistence, and benthic-pelagic coupling in the deep sea.

Depth-related factors are thought to inhibit across-depth gene flow and thus to promote speciation in some taxa; this would contribute another explanation for why the bathyal holds such a high biodiversity (Rex and Etter, 2010). While empirical data for macrofaunal molluscs, crustaceans, as well as octocorals has been found in support of this depth-differentiation hypothesis (France and Kocher, 1996; Jennings et al., 2013; Quattrini et al. 2015), it may not apply to nematodes, where repeated and regular interchanges between depths were observed (Bik et al., 2010) and which may be realised by underestimated use of near-bottom currents as dispersal vectors.

In this study, community diversity was assessed along two isobathic parallel transects at the Western Iberian Margin. Potential drivers for turnover in nematode taxonomic composition were analysed at three spatial scales: within stations, between stations from the same depth, and between the two depth transects. To evaluate potential depth-mediated differentiation, connectivity between the two bathymetric zones was investigated based on 18S rDNA sequence data of selected nematode taxa. The following hypotheses were tested:

(H1). The patchiness of food resources deposited at the seafloor results in a higher alpha diversity;

(H2). Disturbance (high hydrodynamics) increases habitat heterogeneity, resulting in a higher beta diversity;

(H3). Beta diversity between different bathymetric transects is higher than beta diversity across similar depths;

(H4). There is connectivity between shallow and deep areas.

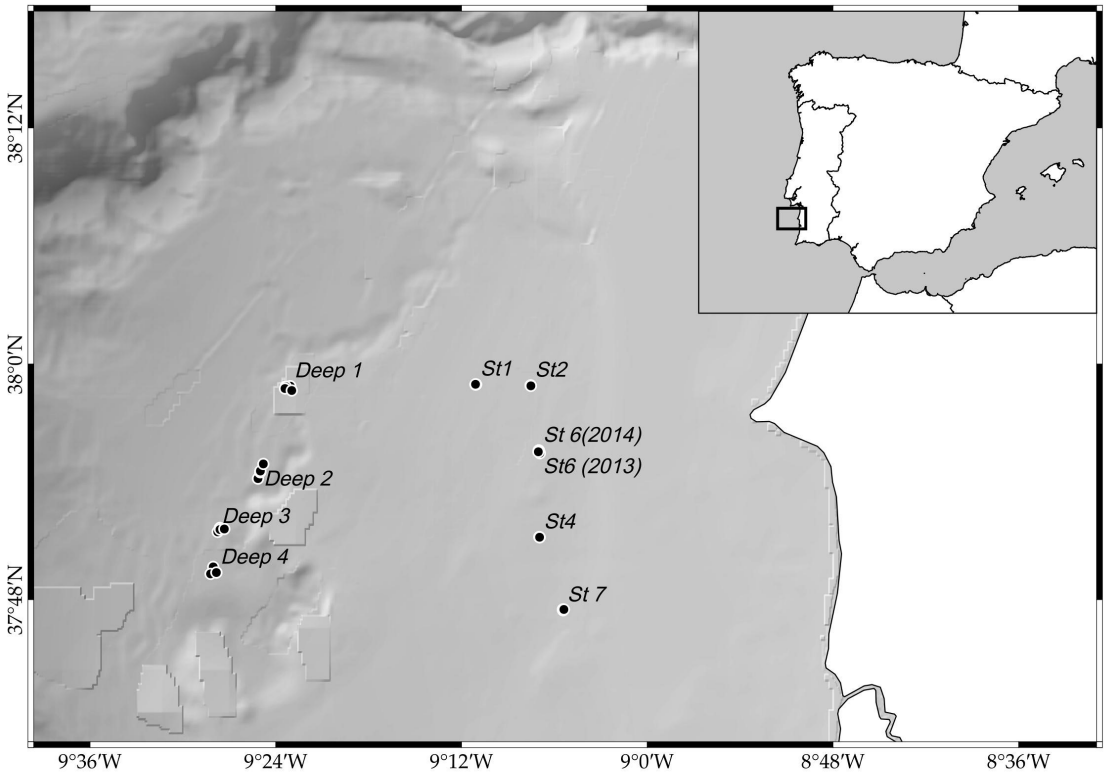


**Figure 3.1** Location of B2013/17 and B2014/15 stations. Sampling stations are represented by black circles. Source: the author (2016).

## 3.2 Material and methods

### 3.2.1 Sampling and study area

The Western Iberian Margin (WIM) is characterised by a narrow shelf and steep slope (García et al., 2008; Nolasco et al., 2013; Relvas et al., 2007). Primary production in this area increases in May–June and constitutes a significant proportion of the yearly production, reaching values higher than 90 $gCm^2y^{-1}$ (Salgueiro et al., 2014). The WIM exhibits seasonal upwelling with filaments that can penetrate more than 200 km into the open ocean, influencing not only vertical transport but also horizontal particle transport from near shore towards the open ocean (Crespo et al., 2011; Figueiras et al., 2002; Relvas et al., 2007; Salgueiro et al., 2010; Salgueiro et al., 2014). The high particle transport observed at the WIM occurs mainly due to the great hydrodynamics in the area.

This region possesses an equatorward current flow generated by thermohaline structures of water masses and wind-forcing, eddy interactions with the alongshore circulation and buoyant plumes (Relvas et al., 2007). These features, together with shelf

**Table 3.1** Sampling details. Source: research data (2016).

| Station | Deployment | Date | Depth (m) | Latitude | Longitude |
|---|---|---|---|---|---|
| S1 | 10 | 13/06/2013 | 445 | 37°58'959"N | 09°11'050"W |
| S1 | 12 | 13/06/2013 | 445 | 37°58'953"N | 09°11'094"W |
| S1 | 13 | 14/06/2013 | 445 | 37°58'967"N | 09°11'090"W |
| S2 | 15 | 14/06/2013 | 335 | 37°58'904"N | 09°07'525"W |
| S2 | 17 | 14/06/2013 | 335 | 37°58'913"N | 09°07'528"W |
| S2 | 18 | 14/06/2013 | 335 | 37°58'888"N | 09°07'513"W |
| S4 | 33 | 16/06/2013 | 325 | 37°51'171"N | 09°06'944"W |
| S4 | 34 | 16/06/2013 | 325 | 37°51'188"N | 09°06'974"W |
| S4 | 35 | 16/06/2013 | 325 | 37°51'174"N | 09°06'950"W |
| S7 | 21 | 4/06/2014 | 295 | 37°47'448"N | 09°05'430"W |
| S7 | 22 | 4/06/2014 | 294 | 37°47'494"N | 09°05'442"W |
| S7 | 24 | 4/06/2014 | 290 | 37°47'490"N | 09°05'380"W |
| S613 | 47 | 17/06/2013 | 296 | 37°55'597"N | 09°06'998"W |
| S613 | 51 | 17/06/2013 | 298 | 37°55'594"N | 09°07'001"W |
| S613 | 52 | 17/06/2013 | 298 | 37°55'594"N | 09°07'002"W |
| S614 | 10 | 3/06/2014 | 296 | 37°55'586"N | 09°06'992"W |
| S614 | 12 | 3/06/2014 | 294 | 37°55'455"N | 09°06'934"W |
| S614 | 14 | 3/06/2014 | 296 | 37°55'530"N | 09°07'031"W |
| D1 | 48 | 5/06/2014 | 906 | 37°58'871"N | 09°23'061"W |
| D1 | 49 | 5/06/2014 | 955 | 37°58'849"N | 09°23'353"W |
| D1 | 50 | 5/06/2014 | 955 | 37°58'752"N | 09°23'405"W |
| D1 | 56 | 6/06/2014 | 930 | 37°58'651"N | 09°22'967"W |
| D2 | 43 | 5/06/2014 | 939 | 37°54'163"N | 09°25'150"W |
| D2 | 44 | 5/06/2014 | 950 | 37°54'489"N | 09°25'006"W |
| D2 | 46 | 5/06/2014 | 900 | 37°54'550"N | 09°24'994"W |
| D2 | 47 | 5/06/2014 | 941 | 37°54'911"N | 09°24'803"W |
| D3 | 39 | 5/06/2014 | 996 | 37°51'450"N | 09°27'752"W |
| D3 | 40 | 5/06/2014 | 1001 | 37°51'650"N | 09°27'615"W |
| D3 | 41 | 5/06/2014 | 998 | 37°51'567"N | 09°27'606"W |
| D3 | 42 | 5/06/2014 | 950 | 37°51'595"N | 09°27'324"W |
| D4 | 51 | 5/06/2014 | 900 | 37°49'375"N | 09°27'839"W |
| D4 | 52 | 6/06/2014 | 957 | 37°49'661"N | 09°28'042"W |
| D4 | 53 | 6/06/2014 | 1006 | 37°49'307"N | 09°28'214"W |
| D4 | 54 | 6/06/2014 | 987 | 37°49'375"N | 09°27'839"W |

and coastal currents, upwelling filaments, and fronts, impact the subsurface circulation, internal waves, and consequently the transport of sinking particulate organic matter to the seabed (Álvarez-Salgado et al., 1997; Relvas et al., 2007). During the RV Belgica B2013/17 (10.06.2013–18.06.2013) and B2014/15 (02.06.2014–10.06.2014) cruises to the WIM, sediment samples for nematode and environmental analyses were taken at the slope off the southwest coast of Portugal (Fig. 3.1). The study area comprised two main transects roughly parallel to the isobaths. The first transect was 23 km, situated 294–445 m deep (further referred to as shallow transect), just beyond the shelf break; the second transect was located at the mid-slope, 19 km long, and at a water depth of 900–1006 m (named deep transect). The 'shallow' area included six stations while the 'deep' area

comprised four stations (Table 3.1). Sampling was performed using a Multicorer (MUC) equipped with four Plexiglas tubes yielding samples with a virtually undisturbed sediment surface (inner core diameter 9.8 cm).

### 3.2.2 Sediment analyses

Samples for granulometric and geochemical analyses (1 g of sediment) from the first sediment layer (0–1 cm) were frozen at -80 °C. Grain-size distribution was measured with a Malvern Mastersizer 2000 (0.02–2000 µm size range) and divided into five categories, from silt-clay to coarse sand fractions. Sediment particle-size diversity (SED) was calculated from the percent dry weight of the five size classes mentioned above using the Shanon-Wiener diversity index (Etter and Grassle, 1992; Leduc et al., 2012). Total sedimentary organic carbon (% TOC) and nitrogen (% TN) were determined with a Carlo Erba elemental analyser on freeze-dried and homogenised samples after acidification with 1 % HCl to eliminate carbonates. Total organic matter (% TOM) content was determined after combustion of the sediment samples at 550 °C.

Chlorophyll *a* (Chl*a*), chlorophyll degradation products, and carotenoids in the sediment were measured with a Gibson fluorescence detector (Wright and Jeffrey, 1997) after lyophilisation, homogenization, and extraction in 90 % acetone, and separation of the samples via reverse-phase HPLC (High-Performance Liquid Chromatography). Chloroplastic pigment equivalents (CPE: Chl*a* + phaeopigments) were used as a proxy for surface-derived primary productivity at the seafloor.

### 3.2.3 Nematode sample processing for community analyses

At each station, three to four replicate samples of the 0–1 cm layer were used for nematode analysis. Samples were fixed on board with seawater buffered 4 % formalin. Sediment was washed over 1000 µm and 32 µm sieves. The fraction retained on a 32 µm sieve was centrifuged three times using LUDOX HS40 Dupont (specific gravity 1.19) as flotation medium and then stained with Rose Bengal. In each sample, 140 nematode individuals (whenever enough present) were randomly picked out and gradually transferred to glycerine (De Grisse, 1969), mounted on glass slides and identified to genus level using relevant literature (Vanaverbeke et al., 2015; Warwick et al., 1998). Functional diversity (relative abundance of each trophic type) of nematodes was

calculated using individuals trophic levels according to Wieser (1953): selective deposit feeders (1A), non-selective deposit feeders (1B), epistratum feeders (2A) and predators (2B), complementing the 2B group with the notion of 'scavengers' (Jensen, 1987). Trophic diversity (TD) was calculated using the index proposed by Heip et al. (1985):

$$TD = \frac{1}{\sum_{i=1}^{4} qi^2}$$

where *q*i is the relative abundance of type i. Taxonomic diversity was measured using Shannon-Wiener diversity (H'), expected nematode genera (EG (80)) and Pielou's evenness (J'). Each replicate (core) value was used as a measurement of alpha diversity, while differences within stations, between stations and between transects were utilised to measure beta diversity.

### 3.2.4 Data analysis

Trends in environmental variables (% TOC, % TN, % TOM, Chl*a*, CPE, carotenes, depth, sediment grain size and SED) and univariate nematode variables (H', J', EG (80), and TD) were investigated by means of Spearman rank correlations and Draftsman plots (Anderson et al., 2007) in R (R Core Team, 2013). The nematode community data on genus level were analysed based on Bray-Curtis similarities (and Euclidean distances for the univariate data) by means of non-parametric multivariate ANOVA (PERMANOVA; Anderson et al., 2007) to assess differences between 'deep' and 'shallow' areas (2-factor nested design) and between all stations across both transects (1-factor design). The 2-factor model included 'depth' as a fixed factor and 'station' as a random factor nested in 'depth'. The 1-factor model design used 'station' as a fixed factor.

Due to the use of an unbalanced design, the type I of sum of squares was chosen for the PERMANOVA analysis to make sure all possible re-arrangements of samples are equally likely (Anderson et al., 2007). Subsequent pairwise t-tests were performed between all pairs of levels to determine where differences between each combination were found. Additionally, PERMDISP routines were used to test for homogeneity of multivariate dispersions between stations. PERMDISP results were not significant, indicating location differences through equally dispersed distances to centroids. SIMPER routines were executed based on Bray-Curtis similarity, with a cut-off of 90 % for low contributions. Dissimilarities within and between stations were compared with distances between geographical areas (km) and between depth differences. The multivariate

environmental data was first normalised (subtracted mean divided by standard deviation) and resemblance matrices were calculated based on Euclidean distances. Subsequently, PERMANOVA tests were performed using the same design as described for the multivariate nematode community data. DistLM (distance-based linear model) routines were performed to analyse and model the relationship between nematode genus community and environmental variables with correlations lower than 0.9 (Chl*a*, carotenes, CPE, % TN, silt-clay, very fine sand, medium sand and coarse sand). Highly correlated variables (% TOC, % TOM, fine sand and depth) were first transformed to cosine and if high correlations persisted they were excluded from the DistLM analysis. The DistLM model was built using a step-wise selection procedure and adjusted $R^2$ as a selection criterion. Euclidean distance was used as a resemblance measure for DistLM procedures and the results were displayed in dbRDA (distance-based redundancy analysis) plots.

### 3.2.5 Molecular phylogenetic analyses of nematodes

One sample from each of the 'shallow' stations S4 and S2 and one from the 'deep' station D4 were preserved in DESS (Yoder et al., 2006) and used for molecular analyses. The first centimetre (0–1 cm) of each core was washed with LUDOX HS40 Dupont, following the same protocol as for the community analysis (see above). One hundred nematodes were randomly picked out per sample under a stereomicroscope (50x magnification). Each individual was rinsed in sterile water, transferred to a microscope slide containing sterile water, and digitally photographed as morphological reference with a compound microscope Leica DMR and Leica LAS 3.3 imaging software. DNA extraction followed Derycke et al. (2005) using the entire specimens. PCR amplification of the nuclear small subunit (SSU or 18S) rDNA was conducted using the primers G18S4 (5'-GCTTGTCTCAAAGATTAAGCC-3') and 22R (5'-GCCTGCTGCCTTCCTTGGA-3') (Blaxter et al., 1998).

All PCR reactions were conducted using an EXT PCR Kit, with a final reaction volume of 25 µl. Each reaction contained 2 µl of template solution containing nematode genomic DNA, 15.125 µl PCR grade water, 0.125 µl of each primer (25 mM), 2.5 µl 10x of PCR buffer, 2 µl of MgCl2, 2.5 µl Loading dye, 0.5 µl dNTP 10mM and 0.125 µl DNA TopTaq polymerase. PCR amplifications were conducted for 39 cycles, each consisting of a 30s denaturation at 94 °C, 30 s annealing at 56 °C, and 30 s extension at 72 °C, with an initial denaturation step of 5 min at 94 °C and a final extension step of 10 min at 72

°C. Successful PCR reactions were identified using agarose gels stained with ethidium bromide and were sequenced with both forward and reverse primers by Macrogen Europe (The Netherlands) with the fluorescent dye terminator Sanger sequencing method. The resulting reads were assembled using Mega 6.0. Sequences were checked for contamination using the BLAST algorithm on GenBank (Benson et al., 2008). The sequences that showed contamination or were of low quality (high amount of ambiguous nucleotides) were removed from the alignment. Nematode contig sequences (consensus of forward and reverse sequences) generated during this study were aligned using the MAFFT algorithm (Katoh et al., 2009) as implemented in Geneious 9.0 (Kearse et al., 2012) at default settings (the alignment algorithm was automatically determined; scoring matrix was 200PAM / k=2; gap-opening penalty was 1.53 and the offset value was 0.123).

GenBank sequences for the most representative genera in the samples (all of the nematode class Chromadorea) were included from GenBank (Benson et al., 2008) (whenever available) to compare differences in genetic/phylogenetic diversity between different depths and locations. Sequences from Meldal et al. (2007) and from Bik et al. (2010) were used to compare generic diversity and diversity within the genus *Halalaimus*, respectively, between different habitats. For both datasets, Modeltest 2.1 (Posada and Crandall, 1998) and jModeltest (Posada, 2008) were used to determine that the best suitable model for maximum likelihood analyses of the nuclear data was according to the Akaike Information Criterion (AIC, Akaike, 1981) GTR+I+G. Reconstruction of 18S relationships was conducted using Maximum Likelihood.

The analyses were performed by means of Randomized Axelerated Maximum Likelihood (RAxML; Stamatakis, 2006) in raxmlGUI (Silvestro and Michalak, 2012) using the fast Likelihood search 1000 replicates to calculate Bootstrap support values. For the *Halalaimus* dataset, Bayesian inference was additionally applied in MrBayes (Ronquist and Huelsenbeck, 2003) to supplement topological inferences. Analyses were run for 5 000 000 generations using 6 MCMC chains. From all runs the first 25 % of sampled trees were discarded as burn-in. Consensus trees were used for illustration here and were ordered and annotated in FigTree and Geneious tree viewer and colourised in Adobe Illustrator. In the supplement tree, line thickness indicates strength of bootstrap support. The *p*-distances for each genus were calculated in MEGA 6.0 using pairwise comparisons and pairwise deletion of gaps.

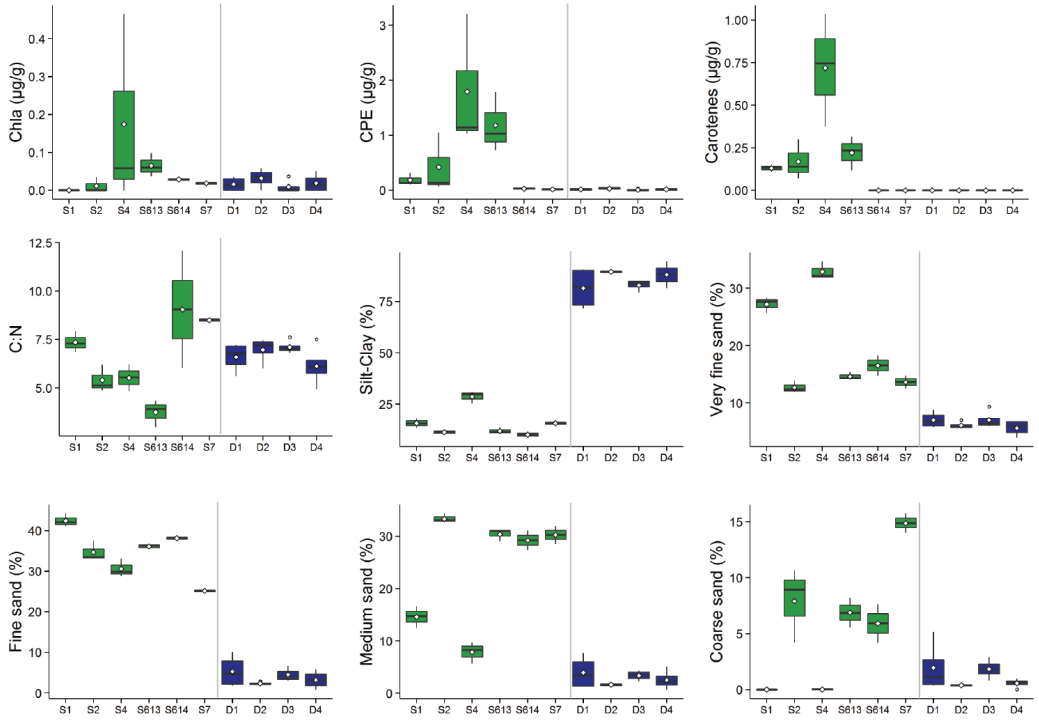


**Figure 3.2** Environmental variables used in this study per station: Chl*a* (Chlorophyll a), CPE (Chloroplastic Pigment Equivalent), Carotenes, C/N (ratio between % TOC / % TN), Silt-Clay, Very fine sand, Fine sand, Medium sand and Coarse sand. Source: research data (2016).

## 3.3 Results

### 3.3.1 Environmental parameters

Biogeochemical and granulometric properties of the sediment are shown in Figure 3.2. Sediment particle-size diversity (SED) significantly decreased ($p < 0.05$) at the 'deep' transect. The sediment composition at the 'deep' stations was mainly composed of silt-clay fractions (81–89 %), while at the 'shallow' stations fine sand (25–42 %) dominated, except for S7, where medium sand showed a higher proportion (30 %). Nested PERMANOVA results showed significant differences between depth transects and among stations within the same transect ($p < 0.05$) (Table S1). Pairwise comparisons between stations showed higher variability in sediment composition for the 'shallow' stations, where the pairs of stations [S7, S2], [S2, S614], [S2, S613] and [S614, S613] showed similar sediment characteristics (Table S1). Pairwise comparison for 'deep' stations only showed differences between D2 and D3. Within station comparison showed low variability (< 25 % deviation from the mean values) in silt-clay and very fine sand for most stations both shallow and deep (Fig. 3.2). Fine, medium, and coarse sand variability within each station was higher when compared to silt-clay and very fine sand (Fig. 3.2).

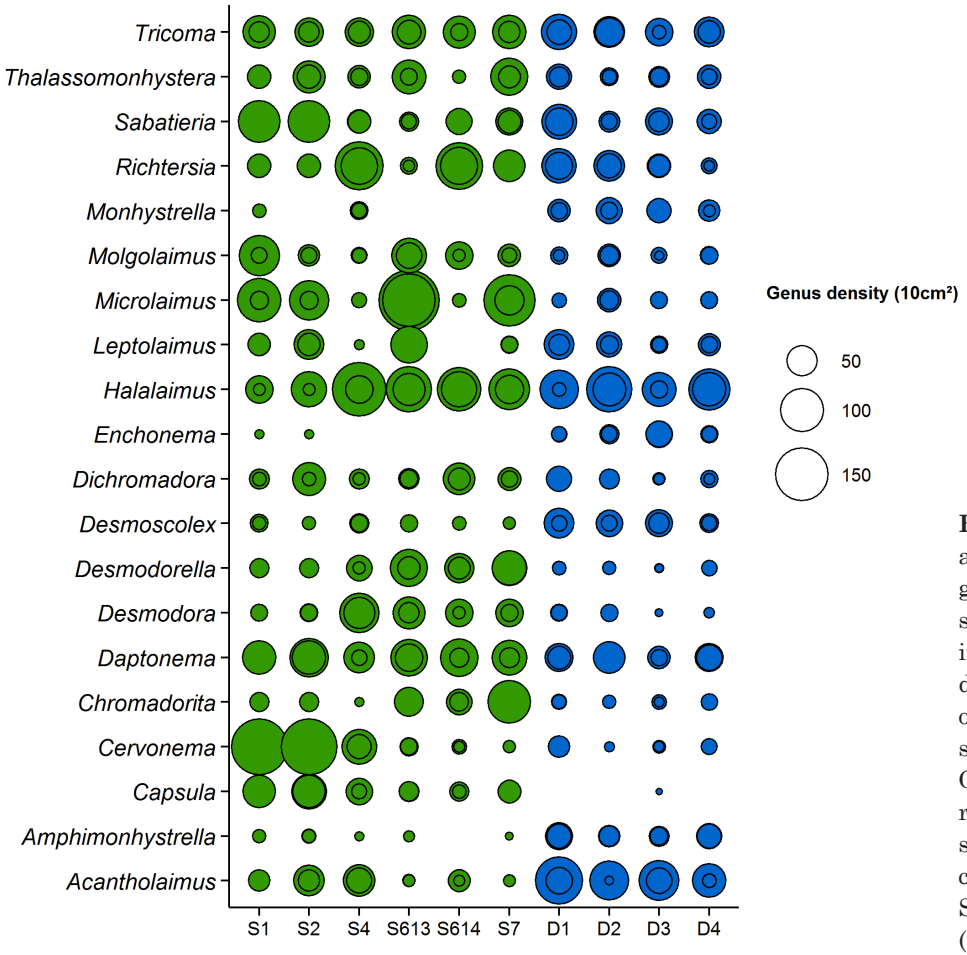


**Figure 3.3** Most abundant nematode genera (> 4 %) per station. Inner circles indicate genus density (10 cm²) and outer circles genus standard deviation. Green circles represent shallow stations and blue circles deep stations. Source: research data (2016).

Significant higher values (nested PERMANOVA, $p < 0.05$) of % TOM (Table S2), % TOC+ (Table S3) and % TN (Table S4) were observed at the deeper transect. Additionally, 'deep' stations were not significantly different from each other ($p > 0.05$) for % TOM, % TOC and % TN, while 'shallow' stations exhibited significant differences between pairs of stations for % TOM (significantly different pairs: [S1, S4], [S1, S7], [S4, S7], [S4, S2], [S4, S614] and [S4, S613]), % TOC (significantly different pairs: [S1, S4], [S4, S2], [S4, S613] and [S614, S613]) and % TN (significantly different pairs: [S1, S4], [S4, S7] and [S4, S2]). No strong variability (< 25 % deviation from the mean values) was observed within station for these three variables (Fig. 3.2). Chl*a* (0–0.17 µg $g^{-1}$), carotenes (0–0.72 µg $g^{-1}$) and CPE (0.01–1.79 µg $g^{-1}$) values were generally low. Chl*a* showed no significant differences between depth transects ($p > 0.05$) and only the pairs [S1, S7] and [S1, S614] were significantly different from each other (Table S5). In addition, Chl*a* showed high variability (> 25 % deviation from the mean values) at the 'shallow' stations, especially at S4 (Fig 3.2). Carotenes and CPE revealed significant differences between depths and among pairs of stations ($p < 0.05$). For carotenes, the pairs of stations [S1, S4], [S1, S7] and [S1, S614] were significantly different from each other (Table S6), while for CPE only the pair [S1, S613] was significantly different (Table S7). Moreover, carotenes were

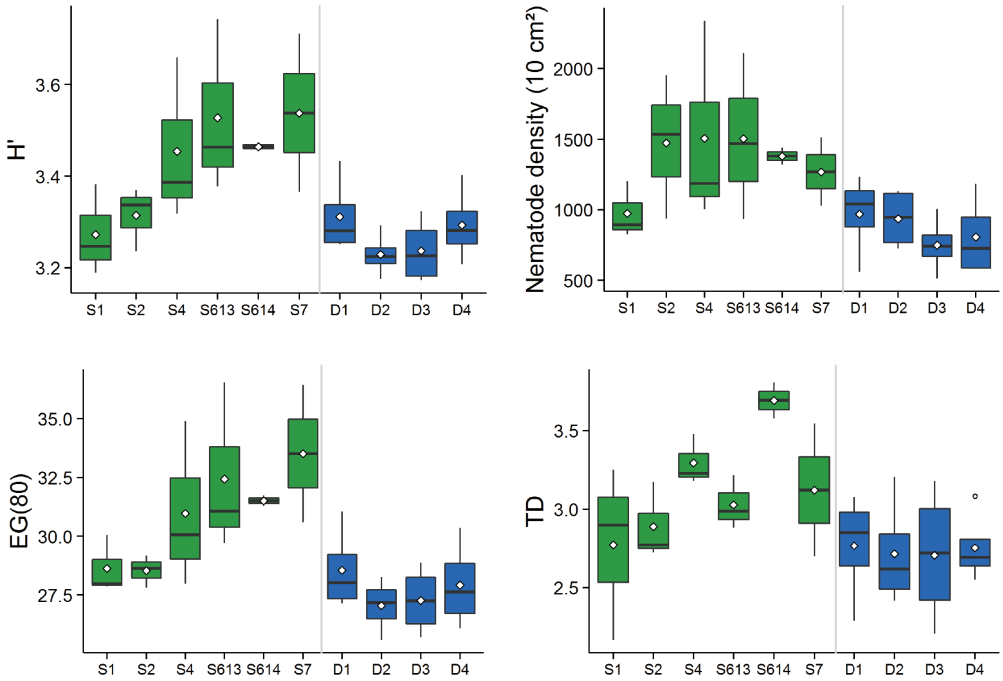


**Figure 3.4** Nematode Shannon-Wiener (H') diversity, nematode density (individuals/10 cm²), Expected number of genera (EG(80)) and trophic diversity (TD) per station. Green boxplots represent shallow stations and blue boxplots represent deep stations. Black lines represent the median, empty circles represent the mean, lower box indicates the first quartile and upper box the third quartile. Upper line shows the maximum value and lower line the minimum value. Source: research data (2016).

completely absent at the 'deep' stations (Fig. 3.2).

### 3.3.2 Nematode community structure

The most abundant nematode genera (≥ 4 %) per station are visualised in Fig. 3.3. The genera *Acantholaimus* and *Halalaimus* dominated at all 'deep' stations (7.6–11.3 % and 7.2–11.7 %, respectively), whereas the 'shallow' stations showed high variability in the most abundant genera. Among the 155 identified genera, 62 were restricted to the 'shallow' areas, and 19 genera were only found in the 'deep' stations. Most of the genera showed low occurrence, with 87 genera found at relative abundances < 1 %. Evenness (J') was not different between the two bathymetric areas and only revealed pairwise differences between D2 and D4 (Table S8). Shannon-Wiener (H') diversity at genus level varied from 3.18 (S1) to 3.74 (S613) at the 'shallow' stations and from 3.17 (D3) to 3.43 (D1) at the 'deep' transect (Fig. 3.4). In this sense, Shannon-Wiener (H') diversity was significantly higher at 'shallow' stations (nested PERMANOVA, $p < 0.05$) and the highest diversity was observed at S613 (Fig 3.4, Table S9). Pairwise comparisons revealed significant differences between the pairs [S1, S7], [S7, S2] and [S2, S614]. Besides having the highest diversity, S613 also revealed the highest replicate variability (3.52 ± 0.19).

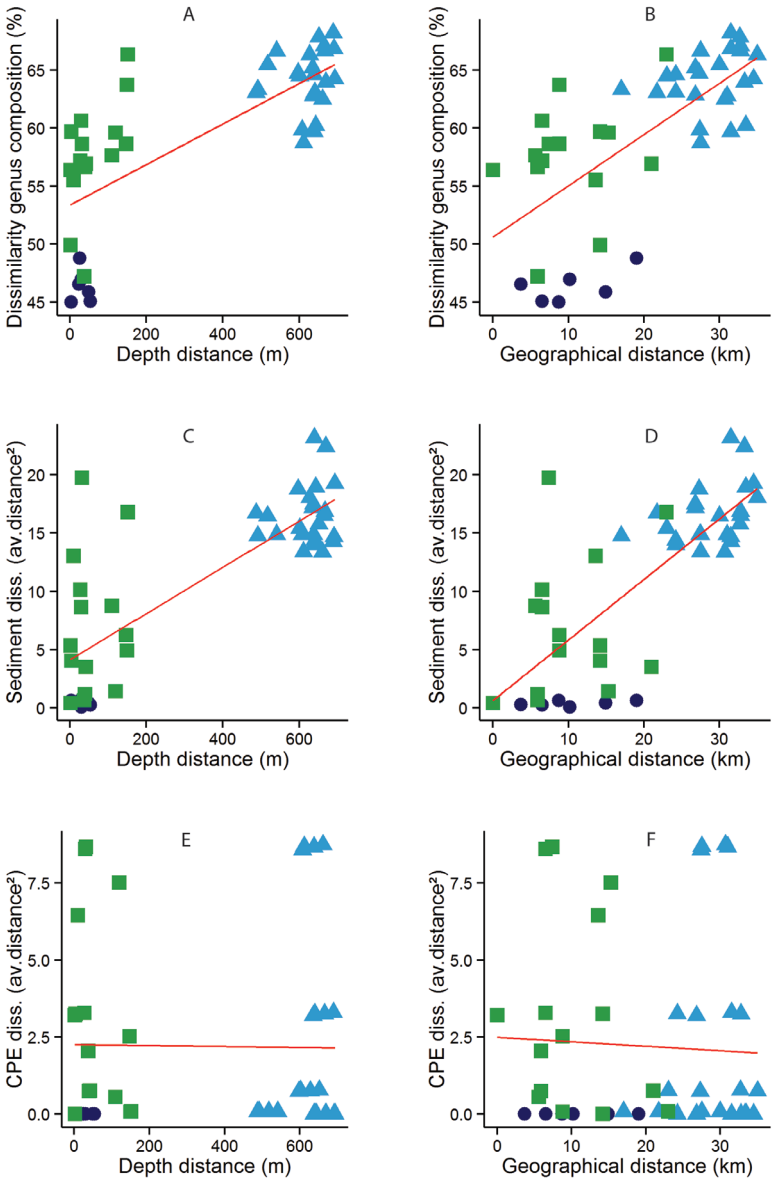


**Figure 3.5** Dissimilarity values in nematode genus composition among depth difference (A) and between geographical areas (B), in sediment composition among depth difference (C) and between geographical areas (D), and in chloroplastic pigment equivalents (CPE) among depth difference (E) and geographical areas (F). Green squares represent dissimilarities between shallow stations, dark blue circles between deep stations and light blue triangles show dissimilarities between shallow and deep. Red lines indicate linear trends. Source: research data (2016).

Expected number of genera (EG(80)) varied from 27 (S2) to 34 (S4) at the 'shallow' stations and from 25 (D2) to 31 (D1) at the 'deep' stations (Fig 3.4). Nested PERMANOVA results revealed significant higher values at the 'shallow' stations when compared to the 'deep' stations ($p < 0.05$) for EG (80) (Table S10). Pairwise comparisons showed significant differences between the pairs [S1, S7], [S1, S614], [S7, S2] and [S2, S614].

Dissimilarities between deployments within stations varied from 53–60 % (S1), 38–57 % (S2), 45–57 % (S4), 45–57 % (S613), 41–53 % (S614), and 42–58 % (S7) for the shallow stations, and 39–60 % (D1), 39–51 % (D2), 36–47 % (D3), and 44–64 % (D4) for the deep stations. In general, dissimilarity values between stations increased with increasing depth and geographical distance (Fig 3.5). SIMPER analysis revealed that the genera *Acantholaimus*, *Microlaimus*, *Richtersia*, and *Halalaimus* were mainly responsible

for the average dissimilarity (63.99 %) between the two depths. The first genus was mainly found at 'deep' areas, whereas *Microlaimus* and *Richtersia* had higher densities at 'shallow' stations. The genus *Halalaimus* showed constant average densities in both transects, but higher density fluctuations at the 'shallow' stations. Nested PERMANOVA results showed significant differences between transects and among stations ($p < 0.05$) (Table S11). Pairwise comparisons revealed no significant differences between 'deep' stations, while the pairs of 'shallow' stations [S1, S7] and [S7, S2] possessed significant differences ($p < 0.05$) in nematode genera composition. When PERMANOVA tests (one-way PERMANOVA) were calculated between all stations, 'deep' stations significantly differed from 'shallow' stations ($p < 0.05$) but the pairs [D1, S1], [D1, S4], [D2, S4], [D4, S1], and [D4, S4] were not significantly different from each other ($p > 0.05$).

Trophic diversity revealed significantly higher values at the shallow stations ($p < 0.05$) but no significant pairwise comparison ($p > 0.05$). Nested PERMANOVA results for relative abundance of trophic groups displayed significant differences between depths, but not among stations from the same depth ($p > 0.05$) (Table S12). Average similarity between 'deep' and 'shallow' areas was 80 %. SIMPER analyses revealed that differences between depths were mainly due to the higher relative abundance of selective deposit feeders (1A) at deeper stations. The shallow stations exhibited higher abundance of epistratum feeders (2A) and predators/scavengers (2B).

### 3.3.3 Correlation between nematode community structure and environmental variables

The correlation between univariate diversity values (H', J, EG (80) and TD) and environmental variables (% TN, % TOC, Chl*a*, carotenes, CPE, sediment grain size, and SED) are shown in Fig. 3.6 and Table S13. Evenness (J') was not correlated to any environmental factor. Diversity (H') was negatively correlated to silt-clay, but positively correlated to very fine-medium sand, SED, and total carbon and nitrogen. The EG (80) was negatively correlated to % TN, % TOC and silt-clay, and positively correlated to CPE, very fine sand, fine sand, medium sand and SED. Trophic diversity (TD) was negatively correlated to % TN and silt-clay, and positively correlated to Chl*a*, CPE, very fine sand, fine sand and SED.

DistLM analyses based on twelve environmental variables explained 33 % of the total nematode diversity. Silt-clay accounted for 23 % of the total variation, being

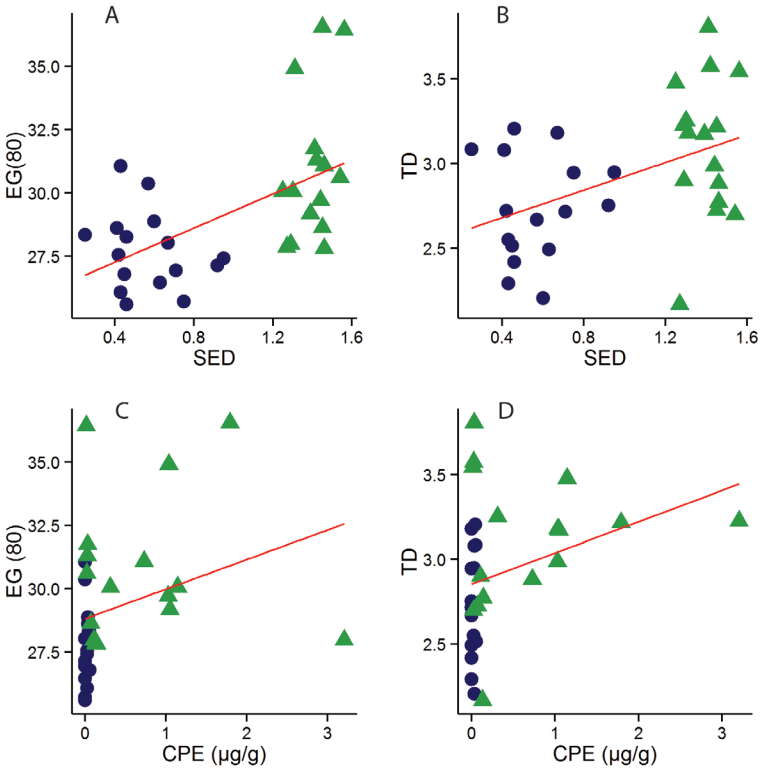


**Figure 3.6** Correlations between (A) Sediment particle-size diversity (SED) and Expected genus diversity (EG (80)), (B) between SED and Trophic diversity (TD), (C) between EG (80) and Chloroplastic Pigment Equivalents (CPE) and (D) between TD and CPE. Green triangles represent correlations for shallow stations and dark blue circles between deep stations. Red line indicate linear trends. Source: research data (2016).

responsible for most differences found between 'shallow' and 'deep' stations (Fig. 3.7A). Considerable higher silt-clay content was observed in the 'deep' stations. The other variables did not contribute significantly to the model and/or added < 5 % in explaining the total variation. When only 'shallow' stations were included in the model, the significant environmental variables explained 23 % of the total variation (Fig. 3.7B). Coarse sand was the main factor accounting for variation between 'shallow' stations (13 %). This sediment fraction showed highly fluctuating values (0.02–14.88 %) between stations of the 'shallow' areas.

### 3.3.4 Nematode molecular phylogenetic analyses

From the 300 vouchered nematodes, the success rate of sequencing was only 30 %. For 199 specimens no PCR product was detected or sequences were of low quality. Phylogenetic analyses showed that the 101 sequenced nematodes belong to seven different orders of free-living marine nematodes (Table S14). The highest genetic diversity was reported for the order Enoplida, with 25 different 18S sequences, followed by the order Plectida (19 different 18S sequences) and Desmodorida (18 different 18S sequences). The Maximum Likelihood (ML) phylogeny inferred from 18S sequences is shown in Fig. S1.

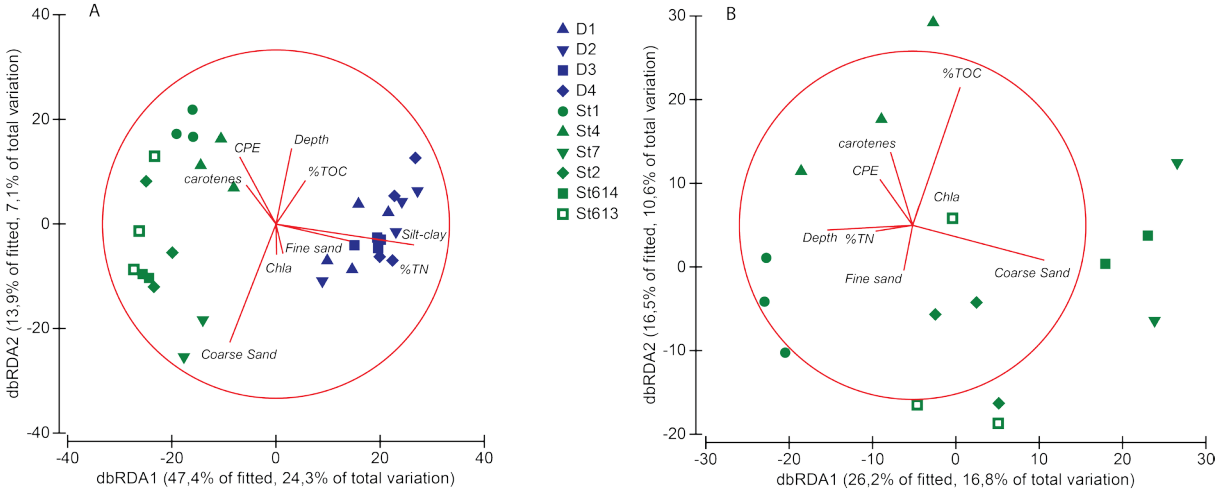


**Figure 3.7** Distance-based redundancy analysis (dbRDA) illustrating the DistLM model based on the genera assemblage data for "deep" (blue) and "shallow" (green) stations (A) and only between shallow stations (B). Fitted environmental variables are shown with their vectors (strength and direction of effect of the variable on the ordination plot). Source: research data (2016).

In general, the backbone of the Chromadorea phylogeny was poorly supported, leading to several paraphyletic or polyphyletic orders and some families, such as Plectida, Desmodorida, and Oxystominidae. Well supported were the orders Tylenchida (bootstrap support (bs) = 99), Monhysterida (bs = 100), Dorylaimida (bs = 100), Monochida (bs = 100), and Triblonchida (bs = 82). Desmodorida is polyphyletic in our analysis with the family Microlaimidae forming a well-supported clade (bs = 100). The orders Chromadorida and Enoplida represent monophyletic but extremely weakly supported groups (bs = 5 and 41 respectively), while the orders Trefusiida and Triplonchida appeared nested within Enoplida.

However, resolving the phylogenetic ties within Chromadorea was not within the scope of this article. What the consensus shows is that the 18S phylogeny supported the broad taxonomic representation of nematodes in the samples and furthermore indicated neither geographic nor depth clustering between 'deep' and 'shallow' taxa at any level of the tree topology (Fig. S1). This was moreover demonstrated within the best-represented and monophyletic (Fig. S1) genus in the dataset, *Halalaimus* (15 individuals, complemented with 42 GenBank sequences from different depths and locations globally distributed). Here, the new sequences showed no clustering related to depth or geography was observed but instead they seem randomly scattered between samples from different depths and regions (Fig. 3.8).

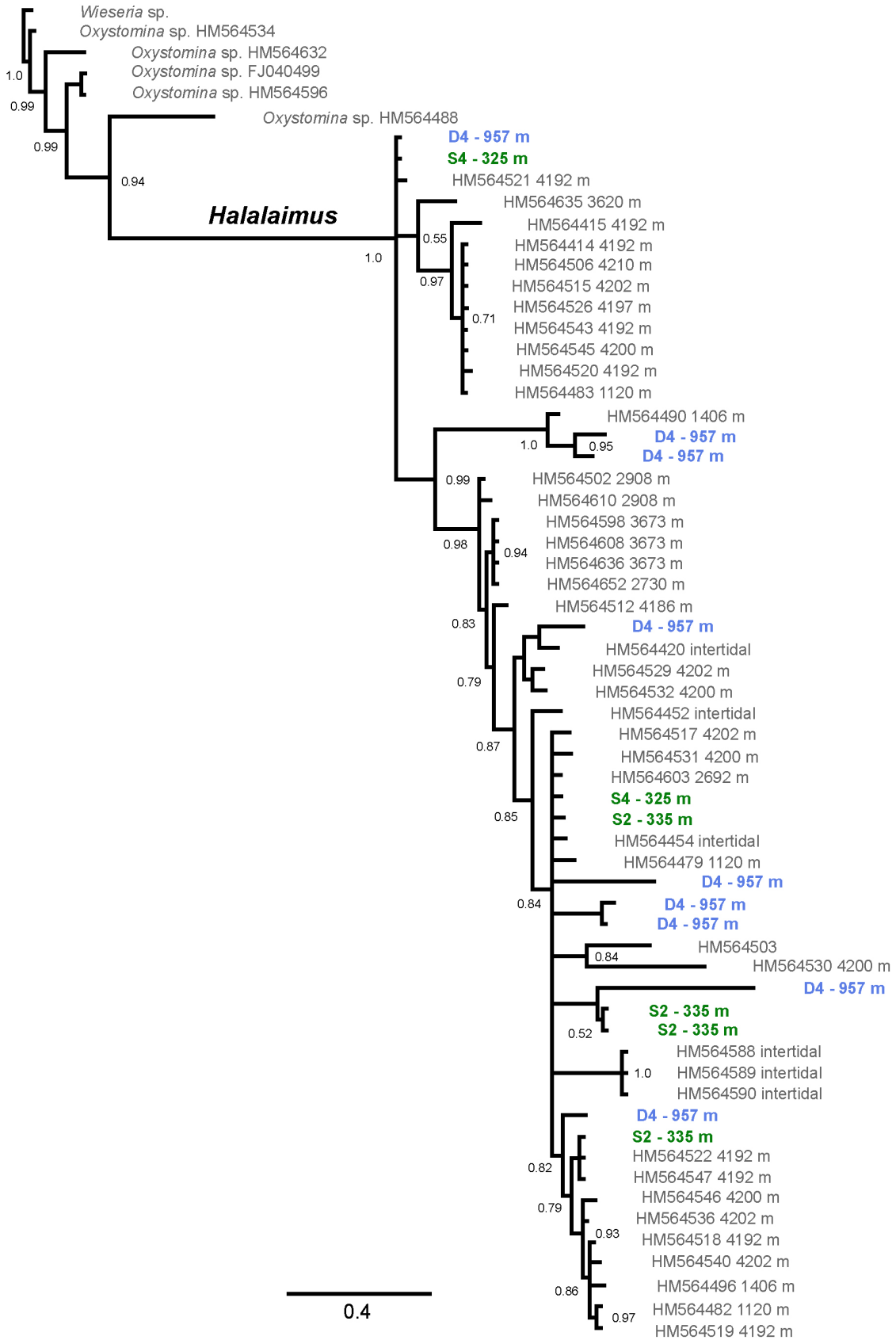


**Figure 3.8** Consensus of Bayesian inference of phylogeny of the genus *Halalaimus* based on 18S rDNA sequence fragments generated in this study and from Bik et al. (2010); node support is given as posterior probabilities (PP); nodes with PP smaller than 0.50 were collapsed. The outgroup was set to *Wieseria*. The tree shows multiple instances of close relationships between individuals collected at different depth zones. Source: research data (2016).

## 3.4 Discussion

### 3.4.1 (H1) The patchiness of food resources deposited at the seafloor results in a higher alpha diversity

In this study, the high variability of food distribution within shallow stations (Fig. 3.2) observed at the Western Iberian Margin (WIM) was positively associated with a high alpha diversity in terms of trophic group composition and genus community diversity (Fig. 3.4). The export flux and the distribution of labile organic matter on the seabed are related to the high patchiness observed in surface primary productivity (Crespo et al., 2011). As such, they are resulting from the interactions between coastline features and wind forcing, as previous studies stated (Crespo et al., 2011). In this regard, surface processes dynamic changes over time and space will also affect resource distribution (Cardinale et al., 2000). Our data can hence be connected to productivity-related processes, such as upwelling events, pulsed food export, and quality of organic matter, which are thought to indirectly affect species richness (alpha diversity). These processes act as surrogate factors of small-scale patchiness and habitat heterogeneity, shaping patterns of species diversity (Tokeshi, 1999). This idea is supported by our observed pattern of a decrease of 'labile' organic matter with an increase in depth that was also related to a lower variability of resources within and between deep stations, as well as a decline of alpha diversity (Fig. 3.6). A similar relationship between decreasing availability of 'labile' organic matter associated to a decrease in diversity was also observed by Leduc et al. (2012) for another slope at similar depths and may thus represent a general pattern at continental margins.

The generally low food input in the deep sea might favour organisms adapted to thrive in this food-deprived environment. The deposit-feeding behaviour of *Halalaimus* in this study may explain its success and reflect its high fitness in the deep sea in general (Fig. 3.3), because deposit feeding can be interpreted as an adaptation to the low food input. Taxa with this feeding mode are often dominant in deep-sea soft sediments and may replace functions otherwise performed by more specialist genera (Amaro et al., 2009; McClain et al., 2015). The presence of the epistratum feeder *Acantholaimus* in higher abundances at the deeper transect was expected (Fig. 3.3), since this genus is considered a typical deep-sea genus. *Acantholaimus* is increasing in abundance from the shelf break towards abyssal plains and dominating nematode communities at all these depths

(Vanreusel et al., 2010). Up to 51 species of *Acantholaimus* were already described (Miljutin and Miljutina, 2016) and a large number of different species can coexist (Muthumbi et al., 2011). By possessing a large variation in its mouth parts, *Acantholaimus* coexistence indicates a possible food resource partitioning (Muthumbi et al., 2011). However, whether the restriction to deep regions is solely food-related or whether other abiotic/biotic factors play a role in the distribution of *Acantholaimus* is still not clear.

A general dependency on the surface-derived organic matter arriving at the seabed has already been observed for all benthic size classes (macro-, mega-, and meiofauna) (Amaro et al., 2009; Lins et al., 2015; Veit-Köhler et al., 2013; Würzberg et al., 2011). In addition, changes in feeding habits according to the food input rate were detected across different taxonomic groups of the benthos (Amaro et al., 2009; Moens and Vincx, 1997). Our findings support this change in feeding mode, as shown by our data on the trophic composition, associated with the depth-dependent decrease in food supply (Fig. 3.6). This means that, when 'fresh' organic matter is scarce, feeding may generally rely on refractory organic material or even in facultative predatory behaviour (Fonseca and Gallucci, 2008). A similar trend was reported for the nematode genus *Pontonema*, which showed facultative predatory behaviour in the deep sea, but not in shallow water as a consequence of food deprivation in the first (Fonseca and Gallucci, 2008). These strategies enable organisms to cope with various changes in food availability and suggest a highly adaptive behaviour of deep-sea organisms, including nematodes, and the tendency to use resources complementarily (Cardinale et al., 2000; Moens and Vincx, 1997).

### 3.4.2 (H2) Disturbance (high hydrodynamics) increases habitat heterogeneity, resulting in a higher beta diversity

Distance-based linear models (DistLM) displayed a major significant effect of the silt-clay proportion on community variation when compared amongst distinct depth transects (Fig. 3.7). Higher variation in sediment composition together with an increase in sediment particle-size diversity (SED) at the 'shallow' stations were most probably related to strong near bottom current pulses already reported at the WIM (Quaresma et al., 2007). Here, the increase in sediment and nematode community dissimilarity with increasing geographical distance and depth (Fig. 3.5) indicate a rapid species turnover at the WIM. Moreover, the higher dissimilarity for both nematode community and sediment at the 'shallow' transect (Fig. 3.5) suggest higher hydrodynamics in this area. Near-bottom

currents at the WIM, varying from 0.1–0.2 m $s^{-1}$, have the capacity to erode and suspend sediment (Drago et al., 1998; Quaresma et al., 2007). In addition, it has been asserted that bottom flow at the WIM may cause high energetic conditions, resulting in areas rich in coarse sand and poor in silt-clay, which is more easily maintained in suspension (Quaresma et al., 2007). Furthermore, the WIM is known to be subjected to fisheries, applying bottom trawls down to a depth of 800 m water depth, which can also affect the continuous mixing and resuspension of surface sediments from the continental slope (ICES, 2008; Pusceddu et al., 2014). Consequently, if higher resuspension rates of sediment can occur, especially at depths shallower than 800 m, this will also affect resuspension of organisms dwelling at or within the sea bottom while increasing variability in relation to more stable environments (e.g. the deep transect).

Our study demonstrated higher trophic diversity (TD) and relative abundances of deposit feeders in the deep stations (Fig. 3.4), together with a higher hydrodynamic stability, also reflected by the finer sediment composition in relation to the shallow stations (Fig. 3.2). This decline in TD with depth, positively associated with a decline in SED was also observed by Leduc et al. (2012) for similar depths, although here SED and TD values reported, were much higher. Trophic diversity at the shallow stations showed greater variation (Fig. 3.4), illustrating higher niche differentiation across stations, reflecting the possible transient stage of this habitat. Moreover, higher prominence of opportunistic species and fast colonisers (epistratum feeders), such as *Microlaimus*, was observed at shallow stations in this study (Fig. 3.3), which were further characterised by higher food input as shown by the greater Chl*a* values. The dominance of opportunists in waters below 200 m (Muthumbi et al., 2011; Pape et al., 2013; Raes et al., 2010) has been observed in many deep-sea areas in association with disturbance events, where communities are dominated by few species during the entire recolonisation process (Lee et al., 2001). The observed high densities of *Microlaimus*, which is both tolerant to disturbance and an early coloniser (Lee et al., 2001; Moreno et al., 2008; Raes et al., 2010), are in accordance with the relatively strong hydrodynamics and possible anthropogenic disturbance effects from fisheries at the WIM, which influence the bottom dynamics at the shallower stations. Disturbance effects via either bedload movement or erosion and sedimentation of suspended load alters not only particle size, but also organic content. Effects on the benthic fauna are mainly observed on deposit feeders, with an increase in deposit feeding during transitional and depositional phases, when hydrodynamics or other disturbance effects decrease (Gage, 1997).

At the WIM the strong non-linear waves corroborate the idea of small-scale disturbance and possible colonization by organisms more suitably adapted to stress conditions. Thus, the higher alpha and beta diversity observed at the shallow stations (mainly represented by low occurrence genera) indicates that disturbance levels in this area enhance not only alpha but also beta diversity. The WIM is characterised by the alternation between strong and weak winds, which in turn drive benthic storms and upwelling processes, and consequently determines the behaviour of benthic organisms (Vitorino et al., 2002). It can be assumed that whenever conditions are more favourable, such as during weak bottom-current periods, rare genera, for instance those with long life cycles, could become more important in terms of abundance and biomass (Bongers et al., 1991). In this sense, environmental fluctuations determine the identity of the dominant competitors, which are in our study *Halalaimus* in the deep and *Microlaimus* at the shallow stations. They also provide opportunities for other species to establish (Fox, 2013). As a consequence, the observed species diversity will be a trade-off between the frequency of disturbance, providing opportunities for new species to overcome competitive exclusion, and ecosystem stability, resulting in an increase in habitat heterogeneity (Gage, 1997).

### 3.4.3 (H3) Beta diversity between different bathymetric transects is higher than beta diversity across similar depths

Sediment grain-size characteristics, an indicator for hydrodynamics, were clearly more heterogeneous between shallow stations when compared to deep stations (Fig. 3.2). Differences in hydrodynamics promote habitat heterogeneity and consequently beta diversity (Gage, 1997). Variation in near-bottom currents were hence probably the main driver responsible for among-station variation within the shallow transect. Contrastingly, the high silt-clay contribution together with the low variation within and between stations observed at the deep stations (Fig. 3.2) was associated with the lower beta diversity in this area (Fig. 3.4). As mentioned earlier, the stability of this environment, in opposition to a higher expected genus diversity (EG (80)) and TD at the shallow stations, favoured the dominance of the genera *Acantholaimus* and *Halalaimus*, commonly abundant in relatively undisturbed deep-sea soft sediments (Vanreusel et al., 2010).

In general, dissimilarity in genus composition increased with both depth and geographical distance (Fig. 3.5). Additionally in this investigation, beta diversity between depth transects was higher than within transects, although distances between stations

and transects were comparable. Other studies have shown that even small bathymetrical changes can be more important for promoting taxonomic differentiation than large geographical distances within the same depth (Havermans et al., 2013; Quattro et al., 2001). Here, the strong differences in sediment composition and food resource patchiness between transects (Fig. 3.2) were likely the main factors responsible for the higher beta diversity observed between the two transects. These findings suggest that diversity changes can be associated with both large and small-scale features. In general, beta diversity in the deep sea appears to be regulated by mechanisms of energy availability, biological interactions, disturbance, and habitat heterogeneity (Levin et al., 2001). Changes in these features at the slope occur much faster with increasing depth than with increasing isobathic distances (Rex, 1981).

While sediment grain size did not show strong variability among cores from the same station (Fig. 3.2), high among-core variation in the density of the most abundant genera was observed (Fig. 3.3). Both these most abundant genera, as well as the presence of low occurrence genera in each core implies that within-station turnover is also affected by small-scale patchiness, such as different availability, composition and size spectra of food particles (Danovaro et al., 2013), as it was shown by the increase in EG (80) and TD with increasing 'labile' organic matter (Fig. 3.6). In this study, however, food resource distribution alone, as shown by the trophic composition, does not explain the high within-station variability in diversity observed at the shallow transect.

Additional ecological factors and biotic interactions not measured here could account for the high alpha diversity observed at the WIM (> 40 % within station variation), such as competition, predation, dispersal dynamics, and patch extinction (McClain and Barry, 2010). Nevertheless, when predation levels are high, the proportion of juveniles in a community should also be high, due to constant predation and "cropping" of standing stocks (Grassle and Sanders, 1973) or due to the unsuitability of juveniles in a predator diet caused by their smaller size (dos Santos and Moens, 2011). In our study, the juvenile/ adult proportion varied from 0.8 to 1.0, indicating no differences in abundance between these groups, and may indicate possibly weak predation effects (McClain et al., 2015).

Human-induced activities, such as bottom trawling and drilling activities, were not measured in this study, but should be considered as a potential factors causing disturbance and impacting habitat heterogeneity, especially at the shallow stations studied here. Trawling activities are very common at the WIM and negative impacts on

sediment resuspension and benthos mortality were reported for other slopes, as well as a decrease in benthos abundance and species richness (Pusceddu et al., 2014; Sparks-McConkey and Watling, 2001).

### 3.4.4 (H4) There is connectivity between shallow and deep

Although we observed distinct differences in community structure between the shallow and deep stations, the large proportion of genera shared between the two depth transects may be indicative of connectivity between the two (Fig. 3.3). In our study, phylogenetic relationships within and between the genera sampled at both shallow and deep stations potentially revealed shared species and thus connectivity across depth. The precise understanding of spatial variability and the processes which drive species diversity and connectivity in the deep sea are presently still poorly understood (Danovaro et al., 2013; Etter and Bower, 2015). Deep basins are confluent at extensive depths and connected by thermohaline circulation, suggesting they do not represent completely isolated systems (Levin et al., 2001). Processes such as deep-water formation and upwelling, potentially represent means of (passive) across-depths dispersal (Brandt, 1992; Brandt et al., 2007; Kussakin, 1973; Strugnell et al., 2008). Contrastingly, for some deep-sea taxa, such as protobranch bivalves, gastropods, and some crustaceans, depth-related diversification have been observed, indicating possible depth-related barriers to dispersal (Etter and Bower, 2015; Etter et al., 2005, 2011; Havermans et al., 2013; Wilson, 1983). The depth-related population differentiation observed in these studies, however, covered larger bathymetric ranges than the ones studied here, and were mostly situated at the lower bathyal and abyss (Etter and Bower, 2015; Etter et al., 2011). Just a few studies have assessed shallow-deep connectivity using a combined morphological and molecular approach (Bik et al., 2010; Riehl and Kaiser, 2012; Van Campenhout et al., 2014; Van Gaever et al., 2009). In contrast to the molluscs and crustaceans mentioned above, selected nematodes and isopods show high degrees of connectivity across depth, suggesting taxon-specific barriers (Bik et al., 2010; Riehl and Kaiser, 2012).

In our study, phylogenetic relationships within and between the genera sampled at both shallow and deep stations did not reveal any evidence for depth-endemic lineages or isolation Fig. S1). Instead, shallow and deep specimens were intermingled in the phylogenetic reconstruction. This result indicates frequent exchange and connectivity between bathymetrically different habitats. Except for *Halalaimus*, all deep-sea nematode

genera discussed in this study were sequenced for the first time. Although the relatively conserved 18S rDNA used in this study may not be the most suitable marker to assess dispersal, evolutionary rates of this gene are unknown for the nematode genera studied. Nevertheless, the presence of identical sequences between individuals from shallow and deep habitats (Fig. 3.8) provides hints towards dispersal between depths at relatively recent evolutionary time-scales.

Our results for *Halalaimus* are in accordance with Bik et al. (2010), revealing multiple historic interchanges between habitats of different depth for multiple species. Likewise, no clear geographical structuring was observed in our phylogenetic tree, although this result could be biased due to limited taxon and geographic sampling. Whether nematode dispersal occurs passively through hydrodynamics or is active employing chemical cues and active swimming, connectivity among marine nematode assemblages can be maintained both over large (> 500 km) and small (50–100 km) geographical distances. This explains the success of these benthic organisms as colonisers (Boeckner et al., 2009; Derycke et al., 2013; Gallucci et al., 2008) and strikingly confirms the unparalleled suitability of nematodes as a model organism regarding studies on connectivity and species turnover in the deep sea.

Even though our results indicate connectivity between shallow and deep habitats, other studies have suggested endemism in deep-sea habitats (De Mesel et al., 2006; Van Campenhout et al., 2014). For example, *Halomonhystera disjuncta* was previously believed to occur in both shallow and deep habitats (Van Gaever et al., 2009), but a recent study based on 18S, COI, and ITS sequences showed that this species in fact constitutes two different lineages occupying deep and shallow environments, respectively (Van Campenhout et al., 2014). Our phylogenetic results moreover highlight the scarcity of publically available DNA sequence data for deep-sea nematodes. For example, we present here the first sequence of the genus *Microlaimus* (no records in the GenBank, searched on 3 Dec 2015). Other genera are poorly represented in public sequence depositories (e.g. *Gammanema*: two 18S sequences, *Leptolaimus*: three 18S sequences, and *Richtersia*: two 28S sequences). The use of more specific and variable markers, such as the mitochondrial CO1 or the rDNA internal transcribed spacer, was not possible within this study due to low success rate of DNA amplification. Low success rates in PCR amplification are a known issue in deep-sea nematodes, but the causes are not well understood (Bik et al., 2010). Degradation of DNA may have occurred during sample processing and could be caused by increases in temperature.

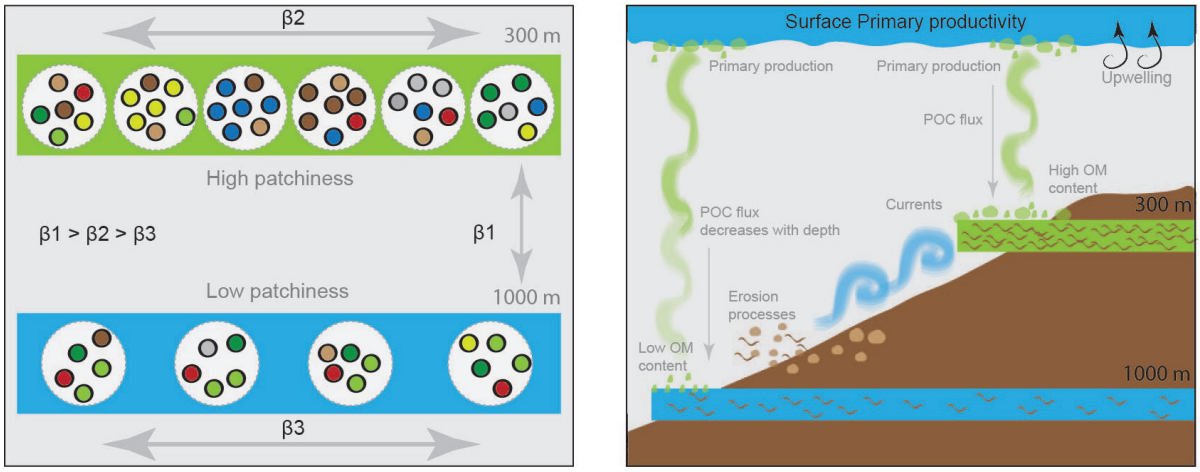


**Figure 3.9** Scheme showing (left) how beta diversity varied across stations and between bathymetrical transects, and the higher patchiness found at the 'shallow' stations, and (right) the main environmental factors responsible for beta diversity between both depth transects. Upwelling effects, primary production, currents, disturbance causing erosion processes, and decrease of POC (particulate organic carbon) with increasing depth are considered to be correlated with both alpha and beta diversity. The fate of organic matter produced at the surface varies with depth, where deeper areas will receive lower labile organic matter (OM) when compared to shallower areas. Moreover, erosion processes are illustrated through the resuspension of sediment and organisms (e.g. nematodes) into the water column as a consequence of strong hydrodynamics. Source: the author (2016).

Genetic structuring of shallow-water nematode populations was shown by Derycke et al. (2013) based on more variable markers (COI, ITS). They showed that despite being capable of long distance dispersal, nematodes may also show clear genetic differentiation at small-scales. In this study, we displayed the high dispersal capabilities and connectivity for nematodes, but those were not high enough to counteract community differentiation observed in the genera composition. Moreover, it is possible that only a small number of species show high dispersal (gene flow), while other species may have limited dispersal abilities.

## 3.5 Conclusions

Our results reported a high variability of resource distribution (Chl*a*, CPE, carotenes) and sediment composition within and between the shallow stations, associated with a high alpha and beta diversity at the WIM (Fig. 3.9). High alpha diversity was mainly related to a complementary use of food resources whereas higher hydrodynamics at shallower habitats (inferred by the high sediment heterogeneity) promoted greater variation in community structure across stations (higher beta diversity) compared to deeper areas, favouring organisms tolerant to disturbance to become more abundant.

Coarser sediment composition at the shallow stations indicated that strong near-bottom current pulses can have positive effects on the benthic fauna, promoting diversity through the creation of suitable patches. The higher beta diversity observed across transects highlights the increase in stability and dominance of particular genera with increasing depth. To conclude, phylogenetic relationships suggested connectivity between deep and shallow waters for the nematode genus *Halalaimus*.

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# 3.7 Supplement

**Table S1.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for sediment composition. Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 105.29 | 105.29 | 18.037 | **0.0027** | 3014 |
| **Station(Depth)** | 8 | 45.042 | 56.302 | 28.113 | **0.0001** | 9929 |
| **Res** | 22 | 4.406 | 0.20027 | | | |
| **Total** | 31 | 155 | | | | |

**PAIR-WISE TESTS**

Term ‘Station(Depth)‘

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 14.453 | 35 | 0.1836 |
| D1, D3 | 0.21922 | 35 | 0.9692 |
| D1, D4 | 11.404 | 35 | 0.2898 |
| D2, D3 | 28.189 | 35 | **0.0062** |
| D2, D4 | 0.74526 | 35 | 0.5423 |
| D3, D4 | 17.462 | 35 | 0.0754 |

Within level ‘SHALLOW‘ of factor ‘Depth‘

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| St1, St4 | 52.363 | 10 | **0.005** |
| St1, St7 | 14.786 | 10 | **0.0004** |
| St1, St2 | 59.548 | 10 | **0.0019** |
| St1, St614 | 54.457 | 10 | **0.0094** |
| St1, St613 | 10.274 | 10 | **0.0004** |
| St4, St7 | 15.104 | 10 | **0.0009** |
| St4, St2 | 72.374 | 10 | **0.0008** |
| St4, St614 | 7.09 | 10 | **0.0027** |
| St4, St613 | 12.505 | 10 | **0.0002** |
| St7, St2 | 27.661 | 10 | 0.0586 |
| St7, St614 | 41.579 | 3 | **0.036** |
| St7, St613 | 61.604 | 10 | **0.0049** |
| St2, St614 | 10.659 | 10 | 0.3696 |
| St2, St613 | 0.80935 | 10 | 0.4851 |
| St614, St613 | 0.81016 | 10 | 0.4904 |

**Table S2.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Total Organic Matter (%). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 28.266 | 28.266 | 290.31 | **0.0038** | 3009 |
| **Station(Depth)** | 8 | 0.75128 | 9.39E+01 | 13.912 | 0.2576 | 9951 |
| **Res** | 22 | 14.851 | 6.75E+02 | | | |
| **Total** | 31 | 31 | | | | |

PAIR-WISE TESTS

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 0.87706 | 35 | 0.4193 |
| D1, D3 | 21.165 | 35 | 0.0767 |
| D1, D4 | 15.794 | 35 | 0.1669 |
| D2, D3 | 12.268 | 35 | 0.28 |
| D2, D4 | 0.4402 | 35 | 0.6771 |
| D3, D4 | 0.94545 | 35 | 0.3727 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 11.198 | 10 | **0.0006** |
| S1, S7 | 38.705 | 10 | **0.0297** |
| S1, S2 | 11.958 | 10 | 0.2967 |
| S1, S614 | 0.69613 | 10 | 0.5416 |
| S1, S613 | 10.709 | 10 | 0.3462 |
| S4, S7 | 12.439 | 10 | **0.0016** |
| S4, S2 | 59.381 | 10 | **0.0047** |
| S4, S614 | 36.069 | 10 | **0.0393** |
| S4, S613 | 81.676 | 10 | **0.0015** |
| S7, S2 | 12.966 | 10 | 0.2842 |
| S7, S614 | 0.7778 | 3 | 0.5125 |
| S7, S613 | 21.078 | 10 | 0.1247 |
| S2, S614 | 4.62E+02 | 10 | 0.9641 |
| S2, S613 | 0.2926 | 10 | 0.7909 |
| S614, S613 | 0.13656 | 10 | 0.8965 |

**Table S3.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Total Organic Carbon (%). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 26.291 | 26.291 | 117.4 | **0.0044** | 2982 |
| **Station(Depth)** | 8 | 1.728 | 0.216 | 2.1723 | 0 | 9948 |
| **Res** | 22 | 2.1876 | 9.94E+02 | | | |
| **Total** | 31 | 31 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 6.24E+02 | 35 | 0.9543 |
| D1, D3 | 14.616 | 35 | 0.1973 |
| D1, D4 | 16.115 | 35 | 0.1581 |
| D2, D3 | 14.857 | 35 | 0.1932 |
| D2, D4 | 16.355 | 35 | 0.1534 |
| D3, D4 | 0.52802 | 35 | 0.6108 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 43.932 | 10 | **0.0127** |
| S1, S7 | 4.85E+02 | 10 | 0.9671 |
| S1, S2 | 13.419 | 10 | 0.2507 |
| S1, S614 | 2.617 | 10 | 0.0761 |
| S1, S613 | 25.712 | 10 | 0.0639 |
| S4, S7 | 21.765 | 10 | 0.1079 |
| S4, S2 | 42.708 | 10 | **0.0127** |
| S4, S614 | 20.996 | 10 | 0.1254 |
| S4, S613 | 65.162 | 10 | **0.0032** |
| S7, S2 | 0.85525 | 10 | 0.4589 |
| S7, S614 | 0.97067 | 3 | 0.4387 |
| S7, S613 | 13.943 | 10 | 0.2571 |
| S2, S614 | 25.694 | 10 | 0.0814 |
| S2, S613 | 0.49958 | 10 | 0.6447 |
| S614, S613 | 47.643 | 10 | **0.0171** |

**Table S4.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Total Nitrogen (%). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 24.328 | 24.328 | 68.19 | **0.0031** | 2975 |
| **Station(Depth)** | 8 | 27.534 | 0.34417 | 1.7061 | 0.1482 | 9942 |
| **Res** | 22 | 4.4381 | 0.20173 | | | |
| **Total** | 31 | 31 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 0.23752 | 35 | 0.8173 |
| D1, D3 | 25.534 | 35 | **0.0417** |
| D1, D4 | 0.91472 | 35 | 0.3884 |
| D2, D3 | 11.073 | 35 | 0.3213 |
| D2, D4 | 0.34137 | 35 | 0.7475 |
| D3, D4 | 11.913 | 35 | 0.2853 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 69.773 | 10 | **0.0027** |
| S1, S7 | 0.721 | 10 | 0.517 |
| S1, S2 | 0.64104 | 10 | 0.5577 |
| S1, S614 | 0.31006 | 10 | 0.7737 |
| S1, S613 | 2.198 | 10 | 0.0896 |
| S4, S7 | 59.241 | 10 | **0.0097** |
| S4, S2 | 29.036 | 10 | **0.0415** |
| S4, S614 | 24.086 | 10 | 0.0942 |
| S4, S613 | 1.21 | 10 | 0.2871 |
| S7, S2 | 0.91122 | 10 | 0.4207 |
| S7, S614 | 0.53866 | 3 | 0.6433 |
| S7, S613 | 20.931 | 10 | 0.1266 |
| S2, S614 | 0.14015 | 10 | 0.9037 |
| S2, S613 | 12.206 | 10 | 0.2896 |
| S614, S613 | 10.775 | 10 | 0.356 |

**Table S5.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Chlorophyll *a* (µg/g). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 13.669 | 13.669 | 1.149 | 0.3532 | 3010 |
| **Station(Depth)** | 8 | 93.176 | 11.647 | 12.613 | 0.246 | 9929 |
| **Res** | 22 | 20.316 | 0.92343 | | | |
| **Total** | 31 | 31 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 10.171 | 15 | 0.3465 |
| D1, D3 | 0.51803 | 4 | 0.6248 |
| D1, D4 | 0.1894 | 8 | 0.8526 |
| D2, D3 | 14.632 | 8 | 0.19 |
| D2, D4 | 0.74632 | 15 | 0.4868 |
| D3, D4 | 0.63864 | 4 | 0.542 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 11.913 | 2 | 0.2925 |
| S1, S7 | 51.545 | 4 | **0.0146** |
| S1, S2 | 1 | 1 | 0.3738 |
| S1, S614 | 12.399 | 4 | **0.0006** |
| S1, S613 | 36.177 | 4 | **0.0248** |
| S4, S7 | 0.82471 | 10 | 0.4677 |
| S4, S2 | 11.092 | 4 | 0.3355 |
| S4, S614 | 0.77009 | 10 | 0.5019 |
| S4, S613 | 0.74004 | 10 | 0.4872 |
| S7, S2 | 0.45648 | 7 | 0.676 |
| S7, S614 | 1.801 | 3 | 0.2177 |
| S7, S613 | 19.838 | 10 | 0.1387 |
| S2, S614 | 11.506 | 7 | 0.333 |
| S2, S613 | 2.51 | 7 | 0.0646 |
| S614, S613 | 15.554 | 10 | 0.2141 |

**Table S6.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Carotenes (μg/g). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms | P(MC) |
|---|---|---|---|---|---|---|---|
| **Depth** | 1 | 80.288 | 80.288 | 33.462 | | 72 | 0.1063 |
| **Station(Depth)** | 8 | 17.986 | 22.482 | 99.215 | **0.0028** | 9931 | |
| **Res** | 22 | 49.853 | 0.2266 | | | | |
| **Total** | 31 | 31 | | | | | |

PAIR-WISE TESTS

Within level 'DEEP' of factor 'Depth'

| Groups | t |
|---|---|
| D1, D2 | Denominator is 0 |
| D1, D3 | Denominator is 0 |
| D1, D4 | Denominator is 0 |
| D2, D3 | Denominator is 0 |
| D2, D4 | Denominator is 0 |
| D3, D4 | Denominator is 0 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 3.064 | 10 | **0.0351** |
| S1, S7 | 82.415 | 7 | **0.0033** |
| S1, S2 | 0.56826 | 10 | 0.6091 |
| S1, S614 | 82.415 | 7 | **0.0031** |
| S1, S613 | 15.569 | 10 | 0.1936 |
| S4, S7 | 2.905 | 7 | 0.0624 |
| S4, S2 | 27.014 | 10 | 0.0544 |
| S4, S614 | 2.905 | 7 | 0.0602 |
| S4, S613 | 24.855 | 10 | 0.0661 |
| S7, S2 | 1.935 | 7 | 0.149 |
| S7, S614 | Denominator is 0 | | |
| S7, S613 | 29.953 | 7 | 0.0617 |
| S2, S614 | 1.935 | 7 | 0.1473 |
| S2, S613 | 0.58587 | 10 | 0.584 |
| S614, S613 | 29.953 | 7 | 0.0583 |

**Table S7.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Chloroplastic Pigment Equivalents (Chl*a* + phaeopigments) in µg/g. Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 72.472 | 72.472 | 3.644 | **0.0386** | 2997 |
| **Station(Depth)** | 8 | 14.936 | 1.867 | 46.588 | **0.0045** | 9952 |
| **Res** | 22 | 88.166 | 0.40075 | | | |
| **Total** | 31 | 31 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 10.171 | 15 | 0.3529 |
| D1, D3 | 0.51803 | 4 | 0.6183 |
| D1, D4 | 0.1894 | 8 | 0.8558 |
| D2, D3 | 14.632 | 8 | 0.1964 |
| D2, D4 | 0.74632 | 15 | 0.4832 |
| D3, D4 | 0.63864 | 4 | 0.5433 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 2.271 | 10 | 0.0875 |
| S1, S7 | 19.895 | 10 | 0.1385 |
| S1, S2 | 0.72924 | 10 | 0.4989 |
| S1, S614 | 18.669 | 10 | 0.1602 |
| S1, S613 | 30.912 | 10 | **0.0403** |
| S4, S7 | 19.487 | 10 | 0.1428 |
| S4, S2 | 17.777 | 10 | 0.1559 |
| S4, S614 | 19.374 | 10 | 0.1495 |
| S4, S613 | 0.79021 | 10 | 0.4756 |
| S7, S2 | 0.98405 | 10 | 0.4014 |
| S7, S614 | 1.801 | 3 | 0.2104 |
| S7, S613 | 28.504 | 10 | 0.0662 |
| S2, S614 | 0.95874 | 10 | 0.4111 |
| S2, S613 | 17.076 | 10 | 0.1642 |
| S614, S613 | 28.251 | 10 | 0.0658 |

**Table S8.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Pielou's Evenness (J'). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 1.7584 | 1.7584 | 0.88153 | 0.4262 | 1247 |
| **Station(Depth)** | 8 | 15.683 | 1.9604 | 2.188 | 0.0632 | 9944 |
| **Res** | 25 | 22.399 | 0.89596 | | | |
| **Total** | 34 | 39.745 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 19.931 | 35 | 0.0956 |
| D1, D3 | 11.297 | 35 | 0.2983 |
| D1, D4 | 11.256 | 35 | 0.3002 |
| D2, D3 | 0.32117 | 35 | 0.7622 |
| D2, D4 | 29.688 | 35 | **0.026** |
| D3, D4 | 1.803 | 35 | 0.1239 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 21.911 | 10 | 0.0909 |
| S1, S7 | 20.528 | 35 | 0.0929 |
| S1, S2 | 15.427 | 10 | 0.1928 |
| S1, S614 | 21.028 | 10 | 0.1034 |
| S1, S613 | 25.457 | 10 | 0.0675 |
| S4, S7 | 0.55518 | 35 | 0.6057 |
| S4, S2 | 0.59708 | 10 | 0.5868 |
| S4, S614 | 0.87619 | 10 | 0.4261 |
| S4, S613 | 0.39437 | 10 | 0.7152 |
| S7, S2 | 0.16946 | 35 | 0.8768 |
| S7, S614 | 0.25975 | 35 | 0.8014 |
| S7, S613 | 0.30146 | 35 | 0.777 |
| S2, S614 | 2.61E+02 | 10 | 0.9855 |
| S2, S613 | 0.43361 | 10 | 0.6877 |
| S614, S613 | 16.224 | 10 | 0.1809 |

**Table S9.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Shanon-Wiener diversity (H'). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 51.09 | 51.09 | 7.9858 | **0.0249** | 1256 |
| **Station(Depth)** | 8 | 49.471 | 6.1838 | 2.5175 | **0.0352** | 9950 |
| **Res** | 25 | 61.407 | 2.4563 | | | |
| **Total** | 34 | 166.19 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 17.005 | 35 | 0.1341 |
| D1, D3 | 13.561 | 35 | 0.2247 |
| D1, D4 | 0.30917 | 35 | 0.7727 |
| D2, D3 | 0.17259 | 35 | 0.8632 |
| D2, D4 | 13.559 | 35 | 0.2177 |
| D3, D4 | 10.458 | 35 | 0.3349 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 15.485 | 10 | 0.1929 |
| S1, S7 | 29.366 | 35 | **0.0307** |
| S1, S2 | 0.60365 | 10 | 0.59 |
| S1, S614 | 34.028 | 10 | **0.0277** |
| S1, S613 | 20.977 | 10 | 0.1059 |
| S4, S7 | 0.83038 | 35 | 0.4515 |
| S4, S2 | 12.653 | 10 | 0.281 |
| S4, S614 | 0.24289 | 10 | 0.8264 |
| S4, S613 | 0.48703 | 10 | 0.6484 |
| S7, S2 | 26.766 | 35 | **0.0472** |
| S7, S614 | 0.89408 | 35 | 0.412 |
| S7, S613 | 0.22099 | 35 | 0.8344 |
| S2, S614 | 37.889 | 10 | **0.0169** |
| S2, S613 | 18.584 | 10 | 0.1418 |
| S614, S613 | 0.4437 | 10 | 0.6781 |

**Table S10.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for Expected genera (EG(80)). Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 94.88 | 94.88 | 91.429 | **0.0168** | 1256 |
| **Station(Depth)** | 8 | 80.234 | 10.029 | 24.215 | **0.0457** | 9941 |
| **Res** | 25 | 103.55 | 41.419 | | | |
| **Total** | 34 | 287.97 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 14.246 | 35 | 0.2047 |
| D1, D3 | 11.205 | 35 | 0.3043 |
| D1, D4 | 0.48756 | 35 | 0.6371 |
| D2, D3 | 0.24395 | 35 | 0.8117 |
| D2, D4 | 0.80301 | 35 | 0.4486 |
| D3, D4 | 0.55524 | 35 | 0.5978 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| St1, St4 | 10.783 | 10 | 0.3365 |
| St1, St7 | 33.664 | 35 | **0.019** |
| St1, St2 | 0.1162 | 10 | 0.9104 |
| St1, St614 | 40.957 | 10 | **0.0141** |
| St1, St613 | 17.301 | 10 | 0.1639 |
| St4, St7 | 12.852 | 35 | 0.258 |
| St4, St2 | 11.654 | 10 | 0.3134 |
| St4, St614 | 0.31719 | 10 | 0.7659 |
| St4, St613 | 0.50139 | 10 | 0.642 |
| St7, St2 | 36.149 | 35 | **0.0147** |
| St7, St614 | 15.434 | 35 | 0.1828 |
| St7, St613 | 0.62355 | 35 | 0.5708 |
| St2, St614 | 71.147 | 10 | **0.0016** |
| St2, St613 | 18.401 | 10 | 0.1448 |
| St614, St613 | 0.38887 | 10 | 0.7129 |

**Table S11.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for nematode community composition. Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 13517 | 13517 | 6.7478 | **0.0028** | 1259 |
| **Station(Depth)** | 8 | 15514 | 1939.2 | 1.5908 | **0.0001** | 9745 |
| **Res** | 25 | 30475 | 1219 | | | |
| **Total** | 34 | 59461 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 0.76301 | 35 | 0.7173 |
| D1, D3 | 0.9061 | 35 | 0.5444 |
| D1, D4 | 0.84413 | 35 | 0.6229 |
| D2, D3 | 10.155 | 35 | 0.4024 |
| D2, D4 | 0.86606 | 35 | 0.5949 |
| D3, D4 | 0.88881 | 35 | 0.5807 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 1.248 | 10 | 0.2218 |
| S1, S7 | 19.035 | 35 | **0.0235** |
| S1, S2 | 12.887 | 10 | 0.2012 |
| S1, S614 | 15.582 | 10 | 0.0839 |
| S1, S613 | 11.945 | 10 | 0.2625 |
| S4, S7 | 16.065 | 35 | 0.0602 |
| S4, S2 | 12.669 | 10 | 0.2076 |
| S4, S614 | 15.113 | 10 | 0.0978 |
| S4, S613 | 12.013 | 10 | 0.2592 |
| S7, S2 | 1.67 | 35 | **0.0492** |
| S7, S614 | 12.541 | 35 | 0.2045 |
| S7, S613 | 16.441 | 35 | 0.054 |
| S2, S614 | 14.735 | 10 | 0.1186 |
| S2, S613 | 0.77248 | 10 | 0.6776 |
| S614, S613 | 12.894 | 10 | 0.1995 |

**Table S12.** Table of results from the multivariate PERMANOVA two-way nested design test and pairwise t-tests for nematode trophic composition. Values in bold represent significant values. Source: research data (2016).

**PERMANOVA table of results**

(2-factor design)

| Source | df | SS | MS | Pseudo-F | P(perm) | Unique perms |
|---|---|---|---|---|---|---|
| **Depth** | 1 | 1974.6 | 1974.6 | 14.297 | **0.0013** | 1257 |
| **Station(Depth)** | 8 | 1068.2 | 133.53 | 1.2756 | 0.2391 | 9929 |
| **Res** | 25 | 2617 | 104.68 | | | |
| **Total** | 34 | 5606 | | | | |

PAIR-WISE TESTS

Term 'Station(Depth)'

Within level 'DEEP' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| D1, D2 | 0.51763 | 35 | 0.8016 |
| D1, D3 | 0.37384 | 35 | 0.8242 |
| D1, D4 | 0.71546 | 35 | 0.5998 |
| D2, D3 | 0.38009 | 35 | 0.8599 |
| D2, D4 | 0.51489 | 35 | 0.7916 |
| D3, D4 | 0.38968 | 35 | 0.8624 |

Within level 'SHALLOW' of factor 'Depth'

| Groups | t | Unique perms | P(MC) |
|---|---|---|---|
| S1, S4 | 0.58178 | 10 | 0.6937 |
| S1, S7 | 10.792 | 35 | 0.3396 |
| S1, S2 | 10.727 | 10 | 0.3577 |
| S1, S614 | 0.88803 | 10 | 0.4849 |
| S1, S613 | 0.88786 | 10 | 0.4648 |
| S4, S7 | 0.97944 | 35 | 0.4039 |
| S4, S2 | 22.706 | 10 | 0.0505 |
| S4, S614 | 0.5012 | 10 | 0.7517 |
| S4, S613 | 19.218 | 10 | 0.1004 |
| S7, S2 | 20.569 | 35 | **0.0395** |
| S7, S614 | 0.44003 | 35 | 0.8343 |
| S7, S613 | 15.491 | 35 | 0.127 |
| S2, S614 | 23.118 | 10 | 0.0549 |
| S2, S613 | 0.83393 | 10 | 0.5643 |
| S614, S613 | 20.307 | 10 | 0.1135 |

**Table S13.** Spearman correlations between the nematode univariate variables Shanon-Wiener diversity (H‘), Pielou‘s Evenness (J‘), Expected genera (EG (80)) and Trophic Diversity (TD) with sediment environmental variables. % TN= Total Nitrogen (%), % TOC=Total Organic Carbon (%), Chl*a*= Chlorophyll *a*, Carotenes, CPE= Chloroplastic Pigment Equivalents, Silt-Clay, Very Fine Sand, Fine Sand, Medium Sand, Coarse Sand and SED=Sediment Diversity. Source: research data (2016).

| | **% TN** | **% TOC** | **Chl*a*** | **Carotenes** | **CPE** | **Silt-Clay** | **Very Fine Sand** | **Fine Sand** | **Medium Sand** | **Coarse Sand** | **SED** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **H'** | **-0.38** | **-0.44** | 0.26 | 0.32 | 0.32 | **-0.46** | **0.43** | **0.41** | **0.42** | 0.3 | **0.51** |
| **J** | 0.26 | 0.12 | -0.11 | -0.09 | -0.28 | 0.19 | -0.22 | -0.26 | -0.2 | 0.04 | -0.17 |
| **EG (80)** | **-0.43** | **-0.46** | 0.25 | 0.31 | **0.36** | **-0.47** | **0.45** | **0.45** | **0.44** | 0.28 | **0.52** |
| **TD** | **-0.4** | -0.28 | **0.37** | 0.3 | **0.39** | **-0.37** | **0.48** | **0.41** | 0.34 | 0.05 | **0.4** |

**Table S14.** Sequenced nematode genera by Field ID (Identification number), taxonomic position, location and GenBank Accession numbers (AN; to be provided upon acceptance). Source: research data (2016).

| Field ID | Order | Family | Genus | Latitude | Longitude | Depth (m) | GenBank AN |
|---|---|---|---|---|---|---|---|
| 77L10H15 | Plectida | Camacolaimidae | *Camacolaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 52L27G15 | Plectida | Camacolaimidae | *Camacolaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 97L22D15 | Araeolaimida | Diplopeltidae | *Campylaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 81L18E15 | Monhysterida | Xyalidae | *Capsula* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 42L29D15 | Plectida | Ceramonematidae | *Ceramonema* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 50L26C15 | Plectida | Ceramonematidae | *Ceramonema* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 15L17C15 | Araeolaimida | Comesomatidae | *Cervonema* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 25L20C15 | Araeolaimida | Comesomatidae | *Cervonema* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 28L20C15 | Araeolaimida | Comesomatidae | *Cervonema* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 20L27D15 | Monhysterida | Xyalidae | *Daptonema* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 55L26C15 | Monhysterida | Xyalidae | *Daptonema* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 48L27G15 | Desmodorida | Desmodoridae | *Desmodora* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 56L28G15 | Desmodorida | Desmodoridae | *Desmodora* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 76L10H15 | Desmodorida | Desmodoridae | *Desmodora* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 42L27G15 | Desmodorida | Desmodoridae | *Desmodora* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 41L29D15 | Desmodorida | Desmodoridae | *Desmodorella* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 46L29D15 | Desmodorida | Desmodoridae | *Desmodorella* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 54L27G15 | Desmoscolecida | Desmoscolecidae | *Desmoscolex* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 84L10H15 | Desmoscolecida | Desmoscolecidae | *Desmoscolex* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 62L28G15 | Desmoscolecida | Desmoscolecidae | *Desmoscolex* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 93L19E15 | Chromadorida | Chromadoridae | *Dichromadora* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 93L31C15 | Plectida | Diplopeltoididae | *Diplopeltoides* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 90L11H15 | Chromadorida | Selachinematidae | *Gammanema* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 3L22D15 | Chromadorida | Selachinematidae | *Gammanema* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 51L04E15 | Chromadorida | Selachinematidae | *Gammanema* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 5L16C15 | Chromadorida | Selachinematidae | *Gammanema* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 65L05E15 | Chromadorida | Selachinematidae | *Gammanema* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 9L17C15 | Desmoscolecida | Desmoscolecidae | *Greeffiella* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 89L30C15 | Enoplida | Oxystominidae | *Halalaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 19L14G15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 60L28G15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 51L26C15 | Enoplida | Oxystominidae | *Halalaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 88L18E15 | Enoplida | Oxystominidae | *Halalaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 87L18E15 | Enoplida | Oxystominidae | *Halalaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 66L05E15 | Enoplida | Oxystominidae | *Halalaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 100L11H15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 64L28G15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 50L27G15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 99L19E15 | Enoplida | Oxystominidae | *Halalaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 77L30C15 | Enoplida | Oxystominidae | *Halalaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 65L07H15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 40L15G15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 39L15G15 | Enoplida | Oxystominidae | *Halalaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 78L30C15 | Chromadorida | Selachinematidae | *Halichoanolaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 7L13G15 | Enoplida | Enchelidiidae | *Ledovitia* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 64L27C15 | Plectida | Leptolaimidae | *Leptolaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 45L25C15 | Plectida | Leptolaimidae | *Leptolaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |

| Field ID | Order | Family | Genus | Latitude | Longitude | Depth (m) | GenBank AN |
|---|---|---|---|---|---|---|---|
| 13L27D15 | Plectida | Leptolaimidae | *Leptolaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 2L13G15 | Plectida | Leptolaimidae | *Leptolaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 53L04E15 | Plectida | Leptolaimidae | *Leptolaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 2L22D15 | Plectida | Leptolaimidae | *Leptolaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 63L28G15 | Plectida | Leptolaimidae | *Leptolaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 24L18C15 | Enoplida | Thoracostomopsidae | *Mesacanthion* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 90L31C15 | Chromadorida | Cyatholaimidae | *Metacyatholaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 14L17C15 | Monhysterida | Linhomoeidae | *Metalinhomoeus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 10L17C15 | Monhysterida | Linhomoeidae | *Metalinhomoeus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 12L13G15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 50L29D15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 56L04E15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 83L18E15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 86L18E15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 80L18E15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 63L05E15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 49L29D15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 4L22D15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 79L30C15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 43L25C15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 46L25C15 | Desmodorida | Microlaimidae | *Microlaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 1L13G115 | Desmoscolecida | Meyliidae | *Paratricoma* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 33L28D15 | Plectida | Camacolaimidae | *Procamacolaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 92L31C15 | Plectida | Camacolaimidae | *Procamacolaimus* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 21L27D15 | Plectida | Camacolaimidae | *Procamacolaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 47L29D15 | Plectida | Camacolaimidae | *Procamacolaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 52L04E15 | Plectida | Ceramonematidae | *Pselionema* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 44L27G15 | Plectida | Ceramonematidae | *Pselionema* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 38L15G15 | Plectida | Ceramonematidae | *Pselionema* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 14L13G15 | Chromadorida | Selachinematidae | *Richtersia* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 2L16C15 | Chromadorida | Selachinematidae | *Richtersia* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 23L18C15 | Chromadorida | Selachinematidae | *Richtersia* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 72L27C15 | Chromadorida | Selachinematidae | *Richtersia* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 26L14G15 | Chromadorida | Selachinematidae | *Richtersia* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 22L14G15 | Plectida | Haliplectidae | *Setoplectus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 86L30C15 | Araeolaimida | Comesomatidae | *Setosabatieria* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 70L27C15 | Araeolaimida | Diplopeltidae | *Southerniella* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 9L22D15 | Araeolaimida | Diplopeltidae | *Southerniella* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 17L13G15 | Enoplida | Ironidae | *Syringolaimus* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 60L04E15 | Enoplida | Ironidae | *Syringolaimus* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 6L16C15 | Desmoscolecida | Desmoscolecidae | *Tricoma* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 43L29D15 | Desmoscolecida | Desmoscolecidae | *Tricoma* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 41L27G15 | Desmoscolecida | Desmoscolecidae | *Tricoma* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 70L05E15 | Desmoscolecida | Desmoscolecidae | *Tricoma* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 11L27D15 | Enoplida | Oncholaimidae | *Viscosia* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 96L31C15 | Enoplida | Oncholaimidae | *Viscosia* | 37°51.171'N | 09°06.944'W | 325 | N/A |
| 72L05E15 | Enoplida | Oncholaimidae | *Viscosia* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 29L28D15 | Enoplida | Oncholaimidae | *Viscosia* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 64L05E15 | Enoplida | Oncholaimidae | *Viscosia* | 37°58.904'N | 09°07.525'W | 335 | N/A |
| 32L15G15 | Enoplida | Oxystominidae | *Wieseria* | 37°49'661'N | 09°28'042'W | 1006 | N/A |
| 8L17C15 | Monhysterida | Xyalidae | not defined | 37°51.171'N | 09°06.944'W | 325 | N/A |

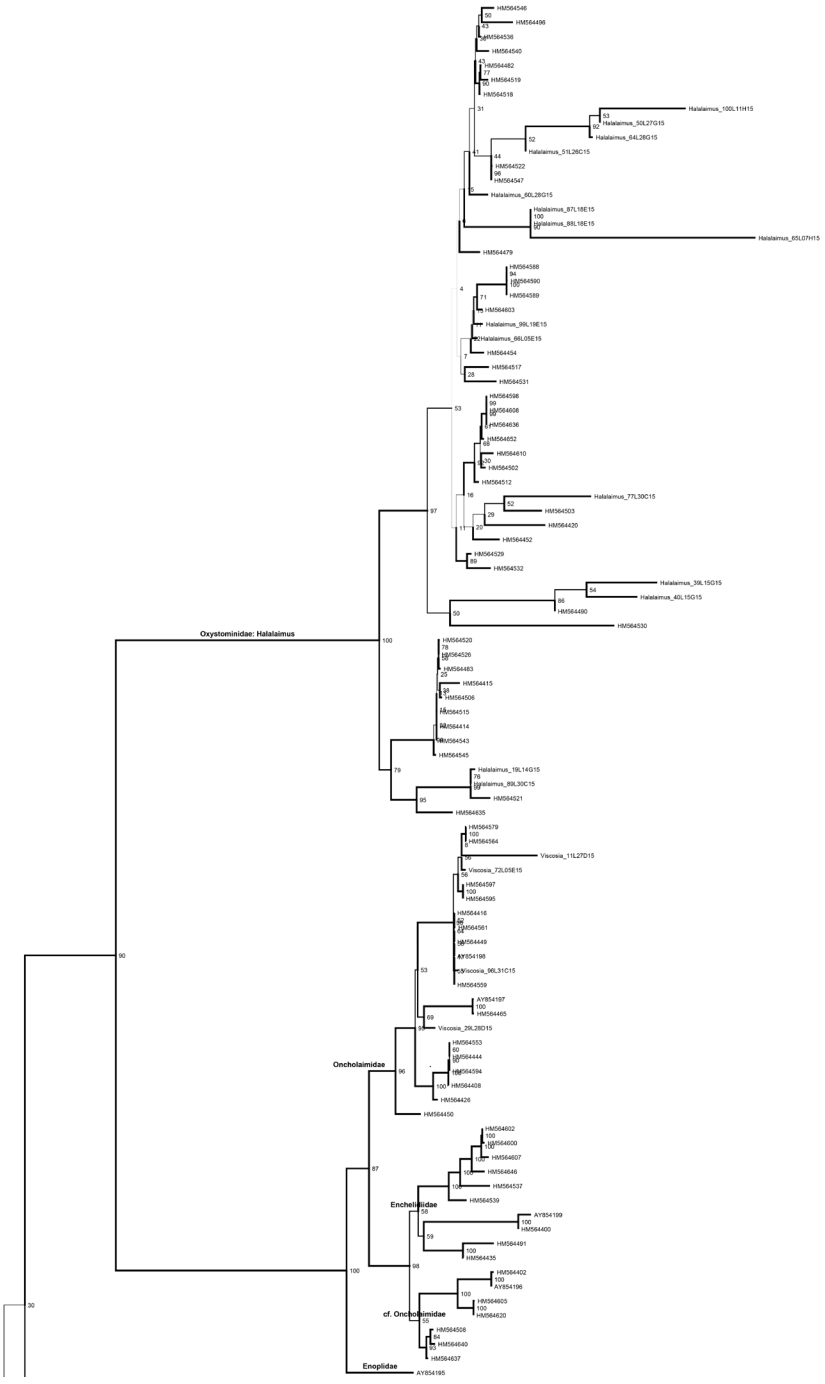


**Figure S1 part 1.** Partial-18S rDNA phylogeny of Nematoda: Chromadorea. The inferred relationships support a broad taxonomic representation of nematodes in samples from lower shelf and upper slope at the West-Iberian Margin and furthermore indicate neither geographic nor depth clustering between 'deep' and 'shallow' taxa at any level of the tree topology. Reconstruction of nematode 18S relationships was conducted using Maximum Likelihood. Bootstrap support values were generated using 1000 replicates and are presented as node support. The analyses were performed by means of Randomized Axelerated Maximum Likelihood (RAxML). Branch (line) width represents statistical support. Sequences retrieved from Genbank are represented by their Genbank Accession numbers. Orders and Families are annotated as branch labels. Continued next page.

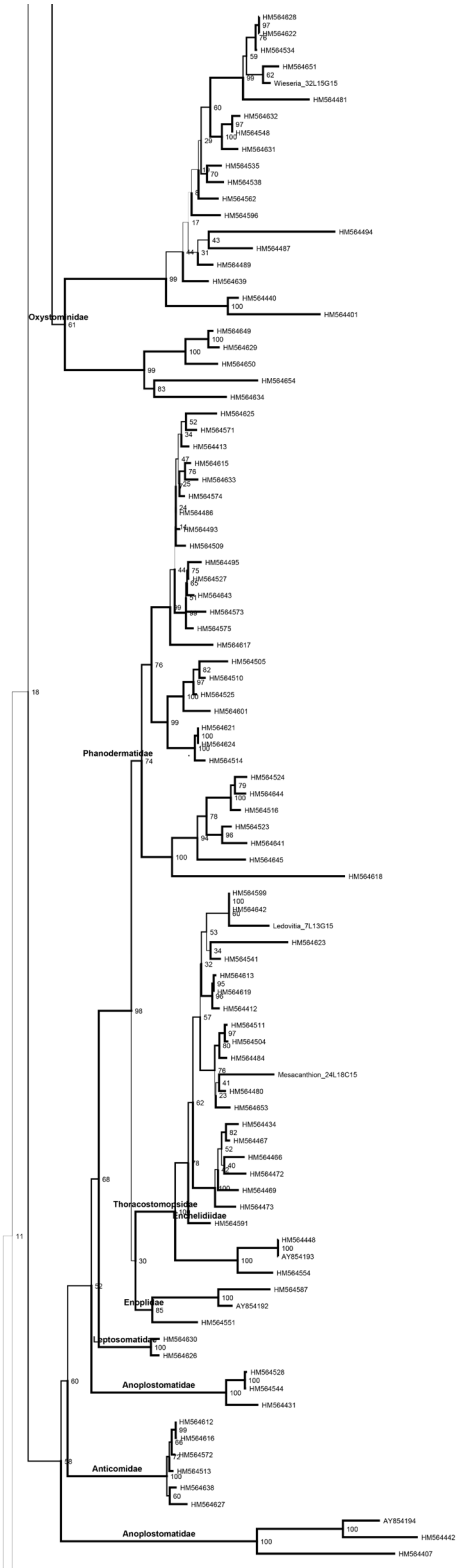


**Figure S1 part 2.** Continuation from previous page. Partial-18S rDNA phylogeny of Nematoda: Chromadorea. The inferred relationships support a broad taxonomic representation of nematodes in samples from lower shelf and upper slope at the West-Iberian Margin and furthermore indicate neither geographic nor depth clustering between 'deep' and 'shallow' taxa at any level of the tree topology. Reconstruction of nematode 18S relationships was conducted using Maximum Likelihood. Bootstrap support values were generated using 1000 replicates and are presented as node support. The analyses were performed by means of Randomized Axelerated Maximum Likelihood (RAxML). Branch (line) width represents statistical support. Sequences retrieved from Genbank are represented by their Genbank Accession numbers. Orders and Families are annotated as branch labels. Continued next page.

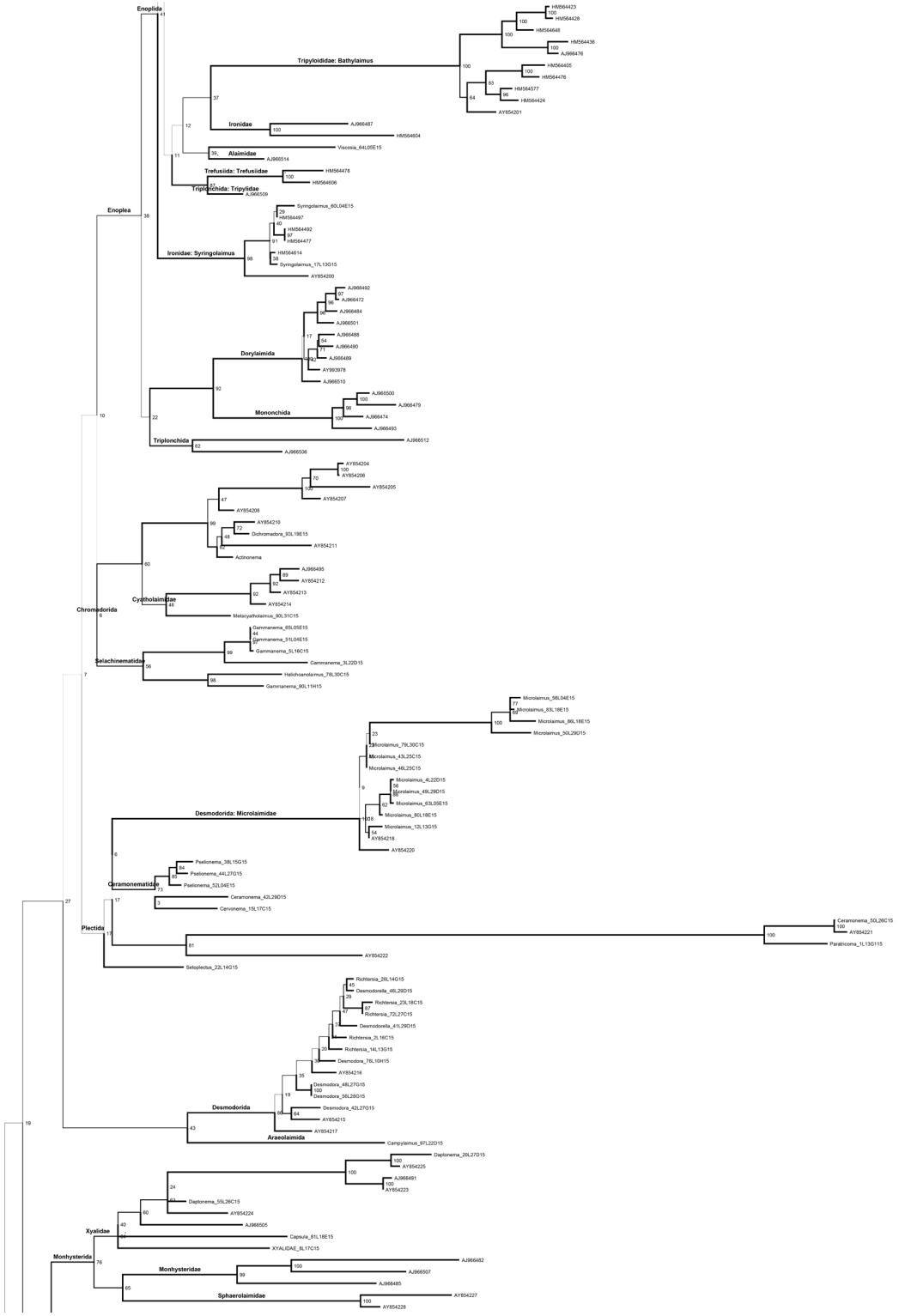


**Figure S1 part 3.** Continuation from previous page. Partial-18S rDNA phylogeny of Nematoda: Chromadorea. The inferred relationships support a broad taxonomic representation of nematodes in samples from lower shelf and upper slope at the West-Iberian Margin and furthermore indicate neither geographic nor depth clustering between 'deep' and 'shallow' taxa at any level of the tree topology. Reconstruction of nematode 18S relationships was conducted using Maximum Likelihood. Bootstrap support values were generated using 1000 replicates and are presented as node support. The analyses were performed by means of Randomized Axelerated Maximum Likelihood (RAxML). Branch (line) width represents statistical support. Sequences retrieved from Genbank are represented by their Genbank Accession numbers. Orders and Families are annotated as branch labels. Continued next page.


**Figure S1 part 4.** Continuation from previous page. Partial-18S rDNA phylogeny of Nematoda: Chromadorea. The inferred relationships support a broad taxonomic representation of nematodes in samples from lower shelf and upper slope at the West-Iberian Margin and furthermore indicate neither geographic nor depth clustering between 'deep' and 'shallow' taxa at any level of the tree topology. Reconstruction of nematode 18S relationships was conducted using Maximum Likelihood. Bootstrap support values were generated using 1000 replicates and are presented as node support. The analyses were performed by means of Randomized Axelerated Maximum Likelihood (RAxML). Branch (line) width represents statistical support. Sequences retrieved from Genbank are represented by their Genbank Accession numbers. Orders and Families are annotated as branch labels. Source: research data (2016).

# Final Considerations

## Trends in surface primary productivity and particulate organic matter flux to the seabed

The link between surface primary production and benthic communities was one of the main topics treated in this thesis. This was studied in two target areas, the Western Iberian Margin (WIM) in the North Atlantic and the Atlantic sector of the Southern Ocean (SO). The distribution of primary production in the oceans is generally patchy and this patchiness is a result of interactions between coastline features and wind forcing (Crespo et al., 2011). Both of these factors appear to be more important at the WIM than in the SO, because the former study region is located at the continental slope. Here the influence from the coast is generally high compared to the open ocean (Crespo et al., 2011). While the WIM possesses similar upwelling characteristics to other continental margins (Salgueiro et al., 2010), surface primary productivity in the SO was greatly determined by its unique regional features (Knox, 1994). The SO receives low terrestrial input and its dominant energy flow is determined by high seasonal phytoplankton surface production, followed by sinking and breakdown in both pelagic and benthic microbial loops (Griffiths, 2010; Rowe et al., 2008).

The areas studied at the WIM covered approximately 20–30 km² and were thus subjected to the same surface productivity regime (Salgueiro et al., 2014). Contrastingly, the stations located at the SO encompassed a large area (~2000 km²), showing significant differences in their net surface primary productivity (NPP) between stations. For the stations situated at the Polar Front (PF), NPP increased westwards and the South Georgia station showed the highest NPP values **(Chapters 1 and 2)**. The higher NPP at the South Georgia was already expected, as this region exhibits constant local nutrient supply throughout the year, supporting high plankton productivity (Brandon et al., 2000; Orsi et al., 1995; Whitehouse et al., 1996). Moreover, from the stations located at the PF, South Georgia is part of the so-called 'diatom ooze belt' and is the only studied station featuring a high abundance of the nutrient-rich diatom *Chaetoceros* spp., which is respon-

sible for high biogenic silica accumulation at the sea bottom (Sachs et al., 2009).

Stations located south of the PF studied in this thesis showed lower NPP values when compared to those at the PF. However, these results could be an underestimation caused by the longer ice-coverage period in winter around these stations, and consequently the lack of satellite-based Chl*a* information (**Chapter 1**). Although undetectable with satellites, these sea ice-covered areas located south of the PF are potentially regions of strong sea-ice algal production in winter and subsequent decay in the summer, which creates a shallow mixed layer of melted sea-ice algae and sea surface water, and consequently enhances primary production (Beckmann et al., 2001; Flores et al., 2011). In general, sea-ice algal productivity can account for up to 25 % of total primary production in the SO (Arrigo and Thomas, 2004).

In Chapter 1, the particulate organic carbon flux was estimated for the SO stations to assess how much labile organic matter reaches the seabed (Lutz et al., 2002; Lutz et al., 2007). The estimated particulate organic carbon flux at the stations south of the PF was clearly exceeding that estimated for the PF stations (**Chapter 1**). Nevertheless, the algorithm used to estimate carbon flux is depth-dependent and takes neither sea-ice algae production into account nor biological-pump interrelated processes, such as (dis)aggregation of organic particles (De La Rocha and Passow, 2007). This means that the contrast between the PF stations and those south of the PF could in reality be even higher. Nevertheless, the depth-dependence of this algorithm illustrates the crucial role of depth in the transfer efficiency of particulate organic carbon (De La Rocha and Passow, 2007; Lutz et al., 2007).

## Benthic-pelagic coupling

One of the aims of this thesis was to study the impact that surface primary productivity and particulate organic carbon flux to the seabed have on deep-sea benthic communities. Stations located in areas of high surface productivity in the SO showed higher benthic meiofaunal diversity, density and standing stocks (e.g. abundance and biomass) (**Chapters 1 and 2**). South of the PF, meiofauna density and diversity were highest. These southern sites can be considered more stable because of smaller influence of strong currents and due to their proximity to the Antarctic continent. The conditions

encountered there may thus favor diverse and steady communities. Moreover, at the MR and LS stations located south of the PF, high meiofauna densities were associated with extended seasonal ice coverage and elevated primary production at the seasonal ice edge (Froneman et al., 2004; Hunt et al., 2011). Concurrently, enriched isotope values of the meiofauna from Antarctica (including the same stations studied here) indicated feeding activity on sea-ice algae at deep-sea stations that were located beneath the ice cover (Moens et al., 2007; Veit-Köhler et al., 2013). Similar associations with productivity patterns in the same area could be shown for microbial communities (Ruff et al., 2014), echinoderms (Würzberg et al., 2014), as well as ostracods (Brandão et al., 2014). Although the SO represents a unique environment under the influence of complex current regimes and high seasonality (Gooday, 2002; Griffiths, 2010; Knox, 1994), the same positive correlation between surface productivity and benthic diversity and standing stocks has also been observed in different regions displaying contrasting surface productivity (Danovaro et al., 1999; Pape et al., 2013; Smith et al., 2008; Vanreusel et al., 1995). It can hence be concluded that these observations may represent a global pattern applying to all different benthic size classes (Rex et al., 2005; Wei et al., 2010).

Meiofauna densities at the South Georgia stations were up to ten times higher than those at nearby stations at the PF. This difference in density could be attributed to higher values of photosynthetic products, such as chlorophyll *a* (Chl*a*), chloroplastic pigment equivalents (CPE) and sediment fatty acids. This illustrates the potential higher nutrient flux to the benthos at South Georgia and reliance of the meiofauna on surface primary productivity as their primary food source (**Chapters 1 and 2**). The amount of organic matter that arrives at the sea floor can in conclusion be pinpointed as one of the main drivers shaping deep-sea standing stocks. The lack of correlation for the estimated POC flux with other environmental parameters and density and biomass of meiofauna could be due to the high dependence of this algorithm to the water depth. In this sense, the use of estimated POC for highly heterogeneous stations in terms of water depth is not recommended.

## Factors shaping benthic communities

While in the SO distinctness in surface primary productivity between otherwise similar areas is reflected in the benthos, other additional factors shaping diversity,

density and standing stocks become apparent where surface primary productivity is similar. Differences in organic matter arriving at the seabed could be seen in relation to depth differences between areas under similar surface primary productivity, such as the studied transects at the WIM (**Chapter 3**). It is widely accepted that especially density and biomass have a negative correlation with depth (Danovaro et al., 2010; Rex et al., 2006). The comparable surface primary productivity for both lower continental shelf and mid-slope areas in the here presented study were followed by a lower arrival of organic matter to the deeper areas, explained by the lower sediment Chl*a* values found at the mid-slope stations. Nevertheless, high variability in sediment Chl*a* at the shallow stations indicate that other productivity-related processes played a role in enhancing small-scale patchiness as well as habitat heterogeneity and alpha diversity in this habitat (Danovaro et al., 2013; **Chapter 3**; and see below). These findings depict a complex interaction of water-column features, such as surface primary productivity, depth, as well as current regimes, on the benthic communities. While here this connection could be inferred for the most dominant metazoan taxon, the nematodes, other studies indicate similar patterns for other taxonomic groups and size classes as well, thus suggesting generality of these findings (Havermans et al., 2013; Rex et al., 2006).

Alpha diversity, here defined as within-core genus diversity, was mainly determined by resource distribution (Danovaro et al., 2013). In the SO, fatty acid analyses revealed that nematodes selectively take up high quality fatty acids, named polyunsaturated fatty acids, PUFAs (Lins et al., 2015, **Chapter 2**). PUFAs are considered plankton-based and their high relative concentration in nematodes indicated a diet based on fresh phytodetritus derived from surface waters. Moreover, the high concentrations of the fatty acid 20:4ω6 found here, generally derived from foraminiferans, also suggested a potential contribution of these organisms to the nematode diet (Gooday, 2002; Suhr et al., 2003). The high concentration of 'labile' plankton-derived PUFAs in nematodes was mainly observed for nematodes at the South Georgia station. Contrastingly, the other stations located at the PF exhibited high levels of the fatty acid DHA, which potentially represents food sources with high refractory material content (Dalsgaard et al., 2003). Therefore, we can conclude that whenever high quality food is available, nematodes feed selectively, whereas when food is limited they will show a more opportunistic feeding behavior ingesting mainly refractory material.

At the WIM, resource variation also supported the dependency on surface primary productivity based on benthic assemblage diversity and trophic structure. High variation

in sediment composition and low silt-clay content observed both at the lower continental shelf at the WIM as well as at the South Georgia station strongly indicates high hydrodynamics in both areas. This high hydrodynamics may cause high-energetic conditions, resulting in areas rich in coarse sand and poor in silt-clay (Quaresma et al., 2007). In this regard, it can be assumed that if sediment can be resuspended, so can be organisms dwelling especially in the surface layers (0–2 cm) of the sediment. At the WIM, high hydrodynamics at the continental shelf stations were possibly the main driver responsible for among-station variation, supporting high habitat heterogeneity and subsequently high beta diversity among stations. In contrast, the high silt-clay content observed for stations at the mid-slope, together with the low variability within and between stations of this transect, could be the cause for low beta diversity observed in this area.

In the studies presented here it could be shown that a complex interaction of factors, such as hydrodynamic conditions and water depth, determine the distribution of the surface-derived food particles on the sea bottom and this is reflected in biodiversity patterns. Different hydrodynamic regimes were furthermore considered as important for biodiversity patterns because they have an influence on sediment characteristics.

## Nematode community composition

The model group of organisms studied in this thesis was the phylum Nematoda. Nematodes dominate the marine benthic metazoan meiofauna almost globally and across all depths in terms of abundance and diversity (Giere, 2009). The high observed generic diversity of nematodes has been valuable in numerous studies employing them as environmental indicators (Bongers and Ferris, 1999; Bongers et al., 1991). That is because there are certain recognized taxon-specific trades. Some nematode species are known to be resistant to specific disturbance levels and to heavy metals, while other species show sensitivity to pollutants (Bongers and Ferris, 1999; Bongers et al., 1991).

In the deep sea, for example, the presence of the genera *Microlaimus* and *Desmodora* indicates a moderate level of disturbance, because these genera are characterized as opportunistic and typical colonizers, showing a rapid response to enhanced in organic matter input fluxes (Vanreusel et al., 2010). For both the SO and WIM lower continental shelf stations, *Microlaimus* was the most or one of the most abundant genera

(> 5 %) (**Chapters 2 and 3**). Moreover, at the SO also vertical migration to the sediment surface was observed for *Microlaimus* probably in response to food input, showing the behavioral plasticity of this genus (**Chapter 2**).

The typical genera found in the deep sea, such as *Thalassomonhystera*, *Halalaimus*, and *Acantholaimus,* are common inhabitants of soft-bottom sediments and exhibit a wide distribution (Vanreusel et al., 2010). In this thesis, *Thalassomonhystera* revealed high abundances (14.6–21.3 %) in the SO, while for the WIM the highest relative abundance of this genus was < 5 %. This genus is commonly found in high abundances at abyssal plains, in trenches, as well as in highly productive areas, such as hydrothermal vents (Vanreusel et al., 2010). The relative contribution of *Thalassomonhystera* to the nematode community at the slope (WIM) was surprisingly low compared to the literature, but it was still one of the most abundant genera at stations dominated by fine sand, thus suggesting restrictions of this genus to certain sediment types.

While dominant in the SO, as well as at the mid-slope stations from the WIM, relative abundances of *Acantholaimus* did not exceed 3 % at the low continental shelf stations of the WIM. This genus is rarely found in shallow water, with only one species description for intertidal habitats (Platt and Zhang, 1982). This absence of *Acantholaimus* in shallow waters has been attributed to secondary displacement of *Acantholaimus* species in these habitats, following speciation in the deep sea (Bik et al., 2010). Hence, it may be possible that *Acantholaimus* has its phylogenetic origin at great depths and has colonized shallow waters. This assumption may be supported by the biogeography of this genus that shows increases in abundances with increasing depth globally except for the continental shelf and slope in Antarctica, where it exhibits high species diversity at all depths (De Mesel et al., 2006).

While *Acantholaimus* seems to be a typical deep-sea genus, *Halalaimus* appears to be cosmopolitan and very successful at both abyssal plains and continental slopes, but also in several shallow-water habitats. This genus was one of the most abundant in all environments studied in this thesis, and a high relative abundance of *Halalaimus* has been found in various other habitats as well, such as canyons, seamounts, cold seeps, trenches, as well as around corals and nodules (Vanreusel et al., 2010). Characterized as a persister, *Halalaimus* is supposed to have a narrow ecological amplitude and to be sensitive to environmental disturbances (Bongers et al., 1999). Moreover, this genus is a non-selective deposit feeder. Taxa with this feeding mode are often dominant in deep-sea

soft sediments (Amaro et al., 2009; McClain and Schlacher, 2015). The deposit-feeding behavior of *Halalaimus* can be interpreted as an adaptation to the low food input and may explain its success and high fitness in the deep sea. This feeding mode could also explain the high relative abundance of *Halalaimus* found in canyons, in comparison to other environments (Vanreusel et al., 2010; **Chapters 2 and 3**).

In this study (**Chapters 1, 2 and 3**), the importance of the most abundant genera *Microlaimus*, *Desmodora*, *Thalassomonhystera*, *Acantholaimus,* and *Halalaimus* varied with region and studied depth. Moreover, the factors influencing genus distribution mainly comprised disturbance effects and dependency of food resources. While *Microlaimus* and *Desmodora* are mainly found in moderately disturbed environments with high organic matter input, *Thalassomonhystera* and *Halalaimus* seem to be mostly found in either stable or productive environments. Until present, it is still not clear which environmental factors drive the distribution of *Acantholaimus*. Although characterized as an epistratum feeder, no correlation of abundance/diversity patterns of this genus with organic matter was observed. This indicates that other factors, such as the amount of mineralizable carbon, may play a role in the distribution of *Acantholaimus* (Soetaert and Heip, 1995).

## Connectivity and dispersal in the deep sea

Nematodes, despite lacking a larval stage, can disperse throughout their whole life stage either passively by drifting in the water column or through bedload movement, or actively using chemical cues (Boeckner et al., 2009; Galucci et al., 2008). In addition, dispersal capabilities could be species-specific, since some nematode species have adaptation to avoid being eroded in the water column (Fonsêca-Genevois et al., 2006; Lins et al., 2013). In this regard, both strong genetic differentiation as well as long distance dispersal may contribute to the high diversity observed in nematode species worldwide. In this thesis, the potential of selected nematode taxa for maintaining connectivity across a depth gradient was analysed.

Two important aspects related to beta diversity (species turnover) are connectivity and dispersal (Danovaro et al., 2013; Etter and Bower, 2015). In general, faunal dispersal over large geographical distances appears to be favoured by the physical

uniformity of the deep sea at extensive depths (France and Kocher, 1996). Therefore, deep-sea ecosystems seem not to represent completely isolated systems (Levin et al., 2001). In fact, deep-sea diversity appears to be controlled by the same mechanisms of energy availability, biological interactions, disturbance and heterogeneity as other major ecosystems (Levin et al., 2001). Depth or depth-related factors on the contrary seem to impose dispersal limitations on selected taxa, such as on some crustaceans and molluscs (France and Kocher, 1996; Havermans et al., 2013; Jennings et al., 2013). For other taxa, such as nematodes from the order Enoplida however, regular interchanges between shallow and deep waters could be detected genetically (Bik et al. 2010). In this thesis, nematodes collected at different depths from the WIM revealed no evidence for depth-endemic lineages or isolation. Therefore, species collected at different bathymetrical transects were intermingled in the phylogenetic reconstruction, indicating exchange between lower continental shelf and mid-slope for this genus (**Chapter 3**).

In this study congruent morphological and molecular results were gained pointing towards low numbers of geographical and depth 'endemics' (**Chapters 2 and 3**). Nevertheless, even though clear differences in environmental variables display distinct habitats at the WIM between stations at lower continental shelf and mid-slope, geographical distances as well as bathymetrical distances were minor (20–30 km). Derycke et al. (2013) revealed that subtle to strong genetic differentiation within a 50–100 km spatial scale can occur, but also that connectivity among marine nematodes can be maintained across large geographical distances (> 500 km). In the SO, only few species were found at single stations, though this result could be entirely due to subsampling of less common species and not due to real endemism (**Chapter 2**). This picture was supported by the results obtained from DNA sequences where phylogenetic tree topologies clearly reject regional or depth endemism but instead show interchanges between shallow and deep areas. Specifically for *Halalaimus* no distinct depth-specific clades were observed. The phylogenetic results rather suggest that nematodes living at lower continental shelf and mid-slope at the WIM are part of the same fauna (**Chapter 3**).

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