



Regional-scale drivers of marine nematode distribution in Southern Ocean continental shelf sediments

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ABSTRACT

Many marine meiofauna taxa seem to possess cosmopolitan species distributions, despite their endobenthic lifestyle and restricted long-distance dispersal capacities. In light of this paradox we used a metacommunity framework to study spatial turnover in free-living nematode distribution and assess the importance of local environmental conditions in explaining differences between communities in surface and subsurface sediments of the Southern Ocean continental shelf. We analysed nematode community structure in two sediment layers (0–3 cm and 3–5 cm) of locations maximum 2400 km apart. We first focused on a subset of locations to evaluate whether the genus level is sufficiently taxonomically fine-grained to study large-scale patterns in nematode community structure. We subsequently used redundancy and variation partitioning analyses to quantify the unique and combined effects of local environmental conditions and spatial descriptors on genus-level community composition. Macroecological patterns in community structure were highly congruent at the genus and species level. Nematode community composition was highly divergent between both depth strata, likely as a result of local abiotic conditions. Variation in community structure between the different regions largely stemmed from turnover (i.e. genus/species replacement) rather than nestedness (i.e. genus/species loss). The level of turnover among communities increased with geographic distance and was more pronounced in subsurface layers compared to surface sediments. Variation partitioning analysis revealed that both environmental and spatial predictors significantly explained variation in community structure. Moreover, the shared fraction of both sets of variables was high, which suggested a substantial amount of spatially structured environmental variation. Additionally, the effect of space independent of environment was much higher than the effect of environment independent of space, which shows the importance of including spatial descriptors in meiofauna and nematode community ecology. Large-scale assessment of free-living nematode diversity and abundance in the Southern Ocean shelf zone revealed strong horizontal and vertical spatial structuring in response to local environmental conditions, in combination with (most likely) dispersal limitation.

1. Introduction

Meiofauna and nematodes in particular are important components of offshore seafloor communities and their macroecological diversity and distribution patterns are used as a proxy for general seafloor conditions and ecosystem functions (Danovaro et al., 2008; Leduc et al., 2013; Zeppilli et al., 2016). However, there is but little insight on the larger-scale drivers for nematode distribution and community composition. Many marine meiofauna species are traditionally believed to possess wide geographic distributions (Boeckner et al., 2009; Giere, 2009), which is attributed to their small body size and large population sizes, in combination with ocean currents facilitating long-distance dispersal. However, multi-marker gene sequencing of focal taxa (e.g.,

Mollusca, Gastrotricha; Jörger et al., 2012; Kieneke et al., 2012) recently revealed the presence of a substantial amount of cryptic diversity and the existence of multiple genetic lineages within morphologically defined species boundaries (Hauquier et al., 2017; Jörger et al., 2012). Hence, previously reported global or ubiquitous species distributions based on morphological taxon delineation alone might represent several lineages with more restricted range sizes (Derycke et al., 2013). This revived the discussion on endobenthic meiofaunal invertebrates being effectively dispersal-limited at larger geographic scales, despite the relatively homogeneous nature of the marine ecosystem, the presence of homogenising ocean currents, and the absence of geographic barriers to exchange of organisms (Srivastava and Kratina, 2013). Large-scale taxonomic inventories of meiofauna groups are therefore

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needed to evaluate the validity of this paradox and to assess the structuring roles of more regional (e.g., dispersal from a regional species pool) and local (e.g., environmental habitat, biotic interactions) processes on community assembly (cf. Fonseca et al., 2014; Leduc et al., 2012).

In this respect, the metacommunity concept (Holyoak et al., 2005; Leibold et al., 2004) provides a useful theoretical starting point. As species diversity is governed by processes operating at different spatial and temporal scales (Cornell and Harrison, 2013; Holyoak et al., 2005; Ricklefs, 1987), several attempts have been made to disentangle the interplay between local and regional processes (Holyoak et al., 2005; Leibold et al., 2004). In the metacommunity theory, communities are defined as sets of local assemblages that are affected by local- as well as regional-scale dynamics, including the dispersal of multiple, potentially interacting species. Depending on how much emphasis is put on environmental heterogeneity, the degree of functional equivalence among species and dispersal rate, (meta-) community dynamics were traditionally divided into four main paradigms, namely neutral models, patch dynamics, mass effects and species sorting (see Cottenie, 2005; Leibold et al., 2004; Logue et al., 2011 for a detailed assessment). Several studies characterised metacommunities based on how well they conform to these four paradigms, or alternatively and more recently, at what point and for which spatial scale deterministic and stochastic processes become more important (e.g., Chase and Myers, 2011; Cottenie, 2005; Declerck et al., 2011; Vellend et al., 2014; Viana et al., 2016). A substantial amount of these studies focused on habitat patches with relatively discrete geographical boundaries such as lake and pond ecosystems (Beisner et al., 2006; Vanschoenwinkel et al., 2007), and highlighted the importance of local species-sorting dynamics in explaining community turnover (i.e. β -diversity). In these cases, compositional variation between communities largely stemmed from associations between species and local environmental conditions. At the same time, historical processes and dispersal limitation were shown to explain patterns of restricted distributions in some lacustrine groups that were previously believed to possess unlimited dispersal capacities, such as diatoms (Soininen, 2007; Verleyen et al., 2009). While the application and validation of the metacommunity theory are ever-increasing, empirical studies in marine metacommunities are rare compared to terrestrial and lacustrine habitats, and mostly focus on taxa with a larval development or a pelagic propagule stage which facilitates long-distance dispersal (e.g., Moritz et al., 2013: benthic polychaetes; Okuda et al., 2010: macroalgae, benthic invertebrates and molluscs). In the few studies available for the marine realm, local environmental conditions appeared to explain the vast majority of the β -diversity patterns through the process of species sorting, while dispersal limitation was of secondary importance as a result of the strong connectivity between ocean basins (Heino et al., 2015 and references therein; but see McClain et al., 2012).

We focus on free-living nematode communities on the continental shelf of the Atlantic sector of the Southern Ocean, at a spatial scale which spans the Scotia Arc, the Antarctic Peninsula and the eastern Weddell Sea (Fig. 1). Free-living nematodes are the most abundant and speciose marine metazoan taxon in various seafloor sediments (Heip et al., 1985; Lamshead and Boucher, 2003), including the Antarctic continental shelf (De Mesel et al., 2006; Hauquier et al., 2015, 2016). Since they do not possess pelagic larvae, their dispersal is mainly mediated by passive transportation through hydrodynamics in the water column (Boeckner et al., 2009; Moens et al., 2013; Thomas and Lana, 2011) in which case nematodes residing in surface sediments have a higher probability of resuspension and transportation than those digging deeper into the seafloor. This in turn has important implications for their long-distance dispersal capacities. Several studies have reported cosmopolitan species ranges in nematodes (e.g., Zepilli et al., 2011), and ascribe community variation between sites in light of the sedimentary properties of the different habitat patches (parallel to the “everything is everywhere” hypothesis for microorganisms; Moens

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

The approach of this study was twofold. First, we tested to what extent (macro-) ecological patterns differ between the genus and species level and whether nematode species are as widely distributed as genera. This was done for five stations across the Scotia Arc and Weddell Sea where a hierarchical sampling strategy was adopted for two sediment depth layers (surface 0–3 cm and deeper 3–5 cm). Second, these data were combined with existing datasets on nematode genus composition in the Southern Ocean to (i) investigate community variation at a scale ranging from a few 100 m to as much as 2400 km, and link the patterns observed to local environmental conditions while considering the underlying spatial configuration, and (ii) test whether nematodes residing deeper in the sediments express different distribution patterns than surface-dwelling taxa that are less protected from bottom dynamics and passive transportation by ocean currents in the area (e.g., the Weddell gyre; Deacon, 1979).

2. Methods

2.1. Sampling area

Nematode community samples were collected during scientific expeditions ANT-XXVII/3 and ANT-XXIX/3 of the German RV *Polarstern* in austral summer 2011 and 2013, respectively (Gutt, 2013; Knust et al., 2012). A multicorer (MUC, 12 cores, inner diameter 57 mm, surface area 25.52 cm²; Barnett et al., 1984) was used to gather undisturbed sediment-water interface samples at continental shelf depths (~240–520 m) at locations along the Scotia Arc and the Antarctic Peninsula, and in the eastern Weddell Sea. Eleven locations are included in this study (see Table 1, Fig. 1), of which five were used to investigate macroecological patterns at both genus and species level. These latter ones were South Georgia (SG), King George Island (KG), South Orkneys (SO), off Auståsen (AUS) and Bendex (BX). The first three are located in the vicinity of Scotia Arc and South Shetland islands and are named after their geographical reference, while the latter two are situated at the eastern Weddell Sea continental shelf (AUS = off Auståsen ice rise, BX = arbitrary name assigned upon time of sampling) (Knust et al., 2012). Detailed information on the other stations can be found in Hauquier et al. (2015, 2016). Two of these (LW & LS) were situated in an area east of the Antarctic Peninsula where the ice shelf collapsed prior to 2002 (Hauquier et al., 2016). The other stations were distributed near the Antarctic Peninsula tip (JE & ET) and the South Shetland Islands (DC & DE) (Hauquier et al., 2015). Despite the lack of obvious geographical barriers between most of the locations covered in this study and the presence of large-scale oceanic currents (Fig. 1), both sides of the Weddell Sea are separated by a vast area of deep-sea habitat, while locations near the Peninsula are influenced by different oceanographic regimes (Hauquier et al., 2015, 2016).

2.2. Sampling strategy

2.2.1. Comparison of patterns at different taxonomic levels

Within the five locations used for both genus and species assessment (Table 1), a hierarchical sampling design was adopted to collect specimens at three spatial levels and two vertical depth strata. Between-location distances range from approximately 15 km (AUS & BX) to almost 2300 km (BX & KG) as the crow flies, which constitutes the largest spatial scale. From each MUC deployment, three individual cores were selected (two for AUS). The distances between these cores in the MUC frame were measured and ranged from a few tens of centimetres to 1 m. This is considered the second spatial scale, namely between cores within locations. This intra-site comparison is warranted given that

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