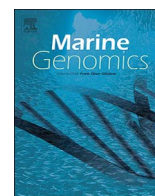




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Metagenomes from deep Baltic Sea sediments reveal how past and present environmental conditions determine microbial community composition

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ABSTRACT

Microbial communities that lived near the sediment surface in the past become slowly buried and are the source of deep subsurface communities thousands of years later. We used metagenomes to analyse how the composition of buried microbial communities may change to conform to altered environmental conditions at depth. Sediment samples were collected from down to 85 m below sea floor during the Integrated Ocean Drilling Program Expedition 347, “Baltic Sea Paleoenvironment”. The sediments vary in age, organic carbon content, porewater salinity, and other parameters that reflect the changing Baltic environment from the last ice age and throughout the Holocene. We found microorganisms capable of energy conservation by fermentation, acetogenesis, methanogenesis, anaerobic oxidation of methane, and reductive dehalogenation. Glacial sediments showed a greater relative abundance of genes encoding enzymes in the Wood-Ljungdahl pathway and pyruvate:ferredoxin oxidoreductase than Holocene sediments. Relative abundance of genes conferring salinity tolerance was found to correlate with the present salinity, even in deep late-glacial sediment layers where salinity has increased since the sediment was deposited in a freshwater lake > 9000 years ago. This suggests that deeply buried and isolated sediment communities can slowly change in composition in response to geochemical changes that happen long after deposition.

1. Introduction

Deep seafloor sediment is a vast microbial habitat on Earth (Kallmeyer et al., 2012) with unique characteristics that differentiate it from other environments (Jørgensen and Marshall, 2016). Throughout most areas of the seabed that lack significant advective fluid flow, the source of energy for microbial communities is organic matter laid down at the time the sediment was deposited. Subsistence on this aged, increasingly recalcitrant organic carbon means that deep subsurface microorganisms live under strong energy limitation and grow very slowly relative to sediment microbes at the seafloor and in other high-energy environments (Hoehler and Jørgensen, 2013; Jørgensen and Marshall, 2016; Kallmeyer et al., 2012; Lever et al., 2015). Previous studies have shown that subsurface sediments harbour distinct bacterial and archaeal communities (Chen et al., 2017; Parkes et al., 2014; Teske, 2013; Teske et al., 2014). However, the physiological characteristics that equip these microbes for the challenges of deep subsurface life are largely unknown. Moreover, it is unclear to which extent deep subsurface microbial communities grow and change in response to changing geochemical conditions, or whether they merely represent a

persistent fraction of the surface community that assembled at a time of higher energy availability and cell turnover.

The Integrated Ocean Drilling Program (IODP) Expedition 347, “Baltic Sea Paleoenvironment”, in 2013 provided an excellent opportunity to address these basic questions in subsurface microbial ecology (Andrén et al., 2015). The Baltic Sea environment has a very dynamic history, having transitioned from a period of freshwater and low organic carbon deposition in the Baltic Ice Lake at the end of the last glaciation to the modern brackish-marine period with high organic carbon (Andrén et al., 2011). These climatic changes are reflected in the sediment record, and IODP 347 was the first scientific drilling expedition to the Baltic to retrieve high-resolution sediment cores documenting this history. The freshwater to marine salinity shift is still reflected today in the pore water salinity in many locations, as seawater ions from the Holocene Baltic have not had sufficient time to fully penetrate the deep glacial sediments (Fig. 1) (Andrén et al., 2015).

The Baltic Sea is thus an excellent natural laboratory for understanding how microbial communities in the deep subsurface are influenced by sediment age, energy availability, and changing salinity over time. Holocene sediments with high organic carbon content can here be

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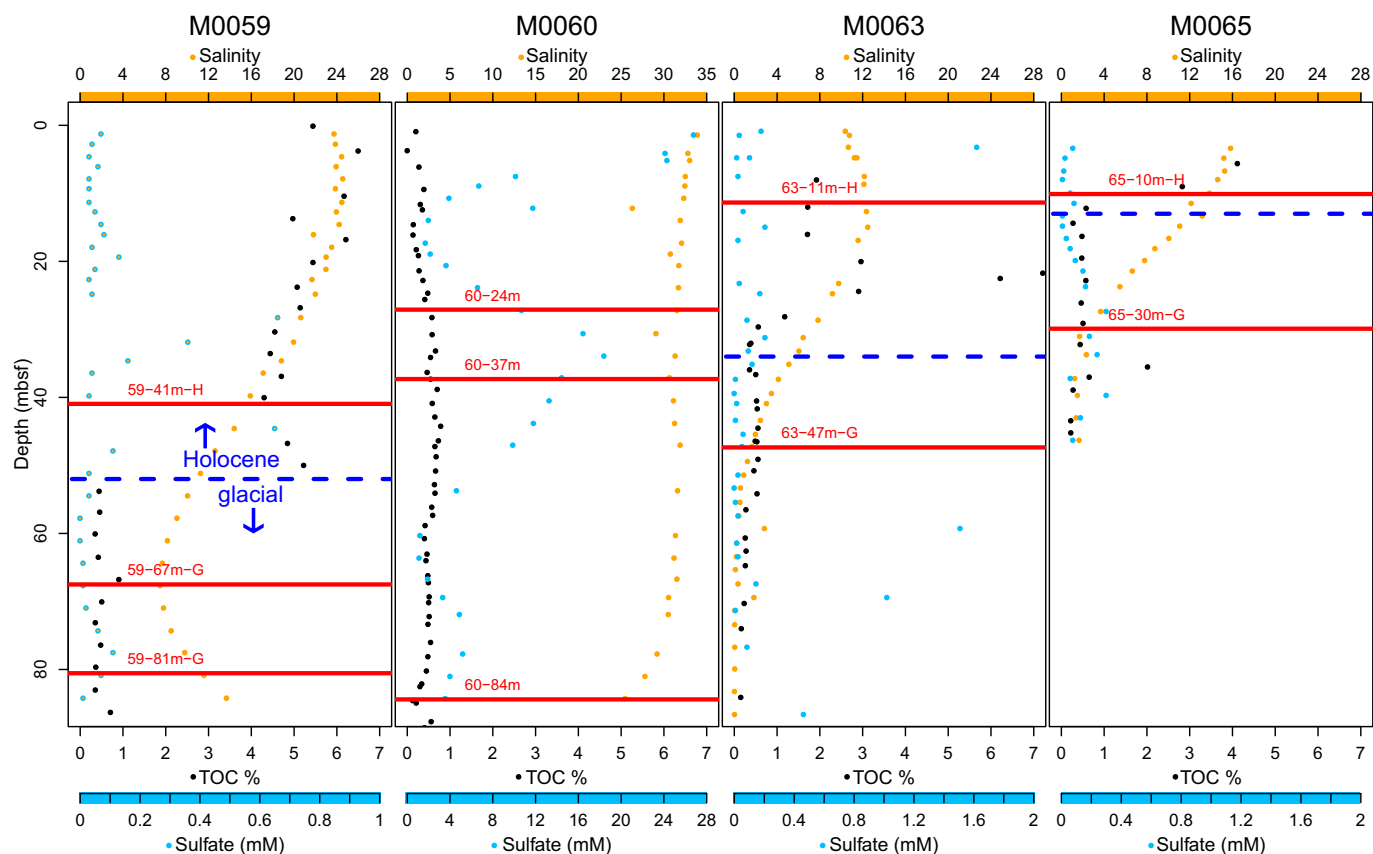


Fig. 1. Geochemical data for all boreholes sampled for this study. Data include salinity (orange points), sulfate (blue points), and total organic carbon (TOC, black points). Note the very low sulfate concentrations for three of the sites. Red horizontal lines indicate depths and core numbers of samples used for metagenomic sequencing. Dashed blue horizontal lines show the approximate depth of the Holocene/Ice Lake transition. All data are taken from the IODP Expedition 347 report (Andr en et al., 2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

compared to older glacial sediments with low organic carbon content. The old glacial sediment layers are likely to have a lower energy turnover than young Holocene sediments as a consequence of their lower organic carbon content. Furthermore, the remaining organic matter in the glacial sediment is much older and therefore more likely to be recalcitrant towards microbial degradation, making for a more energy-limited environment (Hoehler and J rgensen, 2013; J rgensen and Marshall, 2016; Middelburg, 1989). It was an important goal of this study to understand whether the microbes in these two sediment types had very different physiological capabilities.

One possible explanation for such differences could be that there were different founding microbial communities at the time the sediment was originally deposited. Since deposition, the communities have been isolated and buried deep down over thousands of years but they may still reflect their founding communities, as microbes in deep Baltic sediment have been shown to persist from shallower depths (Starnawski et al., 2017). Alternatively, the buried microbial communities may have changed composition with consequences for the communities' collective function in accordance with their present chemical environment. The step-up in salinity of the Baltic Sea from limnic to brackish-marine about 9000 years ago and the subsequent diffusion of seawater ions down into former glacial lake sediments provide an outstanding opportunity to test these two hypotheses. A previous study (Lyra et al., 2013) showed that the main factor influencing present-day microbial communities in the Baltic is palaeosalinity, but due to the shallow depths cored (< 5 m below seafloor) all samples were also affected by modern salinity due to seawater ions that have diffused into the sediments since its deposition. A set of pelagic 16S rRNA gene sequences (Herlemann et al., 2011) and metagenomes (Dupont et al., 2014) across a Baltic salinity gradient transect showed that salinity is an important

factor in determining microbial community composition in the present-day Baltic. Deep drilling samples offered the opportunity to collect samples from below the diffusion front of modern seawater ions into underlying limnic sediment, to see whether changing salinity over time has made an impact on the salinity adaptations of deep, slow-growing microbial communities. Adaptations conferring salinity tolerance in extant microbes in sediment that was originally deposited in freshwater would be an indication that the community composition is a function of its present rather than of its past environment. Therefore, another goal of our study was to determine whether the microbial communities and their associated physiological characteristics are a function of the environment at the time of deposition or of the present *in situ* environment.

We use metagenomes to determine differences in microbial functional gene relative abundance and taxon relative abundance at various depths in the Baltic seabed. The depths were chosen across both Holocene and glacial sediments to represent a range of past and present salinities and organic carbon contents. We ascribe trends in the relative abundance of genes encoding enzymes related to osmoregulation, methanogenesis, anaerobic methane oxidation, acetate metabolism, fermentation, and DNA repair to either the modern environment of the subsurface communities or the past environment of the founding surface communities based on the abundance of genes conferring salinity tolerance in sediment that was deposited under freshwater or brackish conditions. In recent years, metagenomes have been successfully used to study microbial community structure and potential function in deep marine sediments (Biddle et al., 2008, 2011; Gaboyer et al., 2015; Kawai et al., 2014) and shallow Baltic Sea sediments (Reyes et al., 2017; Starnawski et al., 2017; Thureborn et al., 2013), but this is the first study to produce metagenomes from deep Baltic sediments

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