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The importance of sea ice for exchange of habitat-specific protist communities in the Central Arctic Ocean

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ABSTRACT

Sea ice is one of the main features influencing the Arctic marine protist community composition and diversity in sea ice and sea water. We analyzed protist communities within sea ice, melt pond water, under-ice water and deep-chlorophyll maximum water at eight sea ice stations sampled during summer of the 2012 record sea ice minimum year. Using Illumina sequencing, we identified characteristic communities associated with specific habitats and investigated protist exchange between these habitats. The highest abundance and diversity of unique taxa were found in sea ice, particularly in multi-year ice (MYI), highlighting the importance of sea ice as a unique habitat for sea ice protists. Melting of sea ice was associated with increased exchange of communities between sea ice and the underlying water column. In contrast, sea ice formation was associated with increased exchange between all four habitats, suggesting that brine rejection from the ice is an important factor for species redistribution in the Central Arctic. Ubiquitous taxa (e.g. *Gymnodinium*) that occurred in all habitats still had habitat-preferences. This demonstrates a limited ability to survive in adjacent but different environments. Our results suggest that the continued reduction of sea ice extent, and particularly of MYI, will likely lead to diminished protist exchange and subsequently, could reduce species diversity in all habitats of the Central Arctic Ocean. An important component of the unique sea ice protist community could be endangered because specialized taxa restricted to this habitat may not be able to adapt to rapid environmental changes.

1. Introduction

Sea ice is a major factor that structures the polar ecosystem, which is characterized by strong seasonality. Large amounts of sea water undergo a yearly cycle of freezing and melting leading to variations in physical and biogeochemical properties of the surface ocean and the sea ice. Thus, polar organisms must be well adapted to this strong seasonality in terms of their life cycle, ecology and physiology. Unicellular eukaryotes that live within the water column or sea ice habitats are the primary energy source for all trophic levels in the marine ecosystem (Søreide et al., 2013; Kohlbach et al., in press) and account for a large proportion of total primary production and carbon flux (Andreassen et al., 1996; Michel et al., 2002; Riedel et al., 2008; Boetius et al., 2013; Fernández-Méndez et al., 2015).

The main habitats of the Central Arctic Ocean (CAO) have been impacted by current climate induced changes with large implications for biological processes and energy fluxes. In particular, the sea ice decline (Comiso, 2003; Comiso et al., 2008) and a thinner, younger ice pack (Maslanik et al., 2011; Laxon et al., 2013; Kwok and Rothrock, 2009) has major implications for the Arctic ecosystem. These changes resulted in more light being transmitted through sea ice (Nicolaus et al., 2012) which enhanced the photosynthetic production of sea ice algae and phytoplankton (Arrigo et al., 2014a; Arrigo and van Dijken, 2015). Due to earlier sea ice retreat, the timing of spring phytoplankton blooms has shifted (Leu et al., 2011). Because phytoplankton is incorporated in the sea ice (Niemi et al., 2011), a time shift may also alter the sea ice community structure of the following spring sea ice bloom. Thus, a thinning sea ice cover and loss of multi-year ice (MYI, sea ice that survived at least one summer) (Comiso, 2012) can influence sea ice and pelagic community structure and habitat exchange with further implications for species diversity, food web dynamics (Carmack and Wassmann, 2006; Wassmann, 2008; Hilligsøe et al., 2011; David et al., 2015; Hardge et al., submitted) and carbon sequestration (Boetius et al., 2013). Furthermore, due to sea ice thinning and melt pond proliferation, the abundance and diversity of freshwater genera (e.g. *Chlamydomonas* and *Ochromonas*), could increase in sea ice and melt ponds (Kilias et al., 2014b), and thus, most likely contribute significantly

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to primary productivity in the Central Arctic Ocean (Fernández–Méndez et al., 2015). Shifts in community composition were observed in the Canadian Arctic Ocean and Fram Strait, where large plankton cells were displaced by small cells possibly as a result of Ocean freshening and warming (Li et al., 2009; Tremblay et al., 2009; Nöthig et al., 2015).

In-depth knowledge about protist community structure and exchange between the variable habitats of the CAO is still lacking, particularly in melt ponds (Kilias et al., 2014b; Fernández–Méndez et al., 2015) and under-ice water (UIW) (Arrigo et al., 2012; Laney and Sosik, 2014). The two main habitats of the CAO, the water column and sea ice, are inhabited by different protist communities. While mainly Dinophyceae are common in the water column (Booth and Horner, 1997; Jensen and Hansen, 2000; Kilias et al., 2014a), the sea ice is mainly dominated by Bacillariophyceae (Poulin et al., 2011; Comeau et al., 2013). However, little is known about the overall degree of protist exchange and the driving forces that trigger exchange between the habitats (Niemi et al., 2011). It is likely that the habitats are connected with each other via brine channels in the sea ice matrix. Sea ice algae can be released into the under-ice water (UIW) during sea ice melt (von Quillfeldt, 2000; Boetius et al., 2013) and pelagic protists can be incorporated into the sea ice matrix during sea ice formation (Ackley et al., 1987; Gradinger and Ikävalko, 1998; Różańska et al., 2008; Niemi et al., 2011). In addition, the melting of snow during the Arctic summer leads to large melt ponds on the ice floes (Sankelo et al., 2010), which generally are not connected to the UIW. However, with the tendency towards FYI, the under-ice or sea ice communities can evolve into communities of open or frozen melt ponds (Lee et al., 2011). Therefore, the spatial dynamics of protist communities in the Arctic Ocean are affected by sea ice thinning, as they are primarily controlled by changes in the surrounding physical environment rather than by active immigration or emigration. However, existing knowledge about habitat-restriction or habitat-exchange is only based on the analysis of conventional approaches, such as: light microscopy (e.g. Ackley et al., 1987; Gradinger and Ikävalko, 1998; Różańska et al., 2008; Lee et al., 2011; Niemi et al., 2011; Poulin et al., 2011). This knowledge is especially important in the context of climate change, as species restricted to one habitat might be more vulnerable to climate change (Myers et al., 2000; Lovejoy and Potvin, 2011; Thaler and Lovejoy, 2015), because they are highly adapted to a specific living environment in terms of their life cycle and physiology. In contrast, widely distributed species might be less affected, because of their ability to adapt to fast changing environmental conditions. The assessment of rare and habitat-specific taxa, as well as the protist exchange between the habitats (i.e. number of unique or shared taxa) is best analyzed with molecular methods. The fast improvement of next-generation sequencing allows the identification of rare and small-sized species, which lack morphological features, and are both often overlooked using light microscopy.

In this study, we sequenced protist communities in deep-chlorophyll maximum water (DCM), under-ice water (UIW), sea ice (ICE) and melt pond water (MW) sampled in the Central Arctic Ocean (CAO) during summer of the record sea ice minimum year 2012. We provide a comprehensive overview of habitat-specific protist community composition and elucidated the exchange of protists between the habitats by assessing the number of shared operational taxonomic Units (OTUs), as well as the driving forces of exchange. We tested the following hypotheses:

1) Different habitats in the ice-covered Arctic Ocean harbor unique, habitat-specific protist taxa.
2) Ubiquitous species that occur in all habitats still have habitat-preferences.
3) Sea ice melting triggers protist exchange between various habitats of the CAO.

2. Material and methods

2.1. Sampling

Seven ice stations were sampled in the Eurasian Basin of the CAO during *RV Polarstern* expedition "IceArc" in 2012 (PS80, 5 August to 29 September 2012) (Fig. 1, Table 1). A total of seven seawater samples from the DCM, seven UIW samples, eight ice cores and seven MW samples were collected in different water masses, which were distinguished based on Jones et al., 1998 (Table 1).

Water samples were collected with Niskin bottles (12 L) attached to a CTD (conductivity, temperature, depth) rosette from the DCM, which varied between 10 m and 50 m (Table 1). Two liters subsamples were taken in PVC bottles. UIW samples were collected during the 2012 IceArc expedition with a Masterflex® E/S™ portable sampler pump. The tube was marked every meter and was placed with a weight 1 m under the ice. For molecular analysis, 2 L of water was filtered through Isopore Membran Filters (Millipore, Billerica, MA, USA) with pore sizes of 10 μm, 3 μm and 0.4 μm to ensure collection of all protist cell sizes. Filters were stored in Eppendorf tubes at −80 °C.

First-year ice (FYI) and multi-year ice (MYI) cores (Table 1) were drilled with a Kovacs 9 cm inner diameter corer (Kovacs Enterprise, Roseburg, USA). Four ice cores were drilled per station: two 'physical cores' for determining physico-chemical parameters, one 'biological cores' for analyzing biological communities and one "biogeochemical core" for nutrient analyses. The 'biological cores' were sectioned in 10 to 20 cm intervals and melted in 0.2 μm filtered sea-water to minimize osmotic stress to protists during the melting process (Miller et al., 2015). Melting of sea ice was conducted under low light conditions at 4 °C for 24–48 h. The samples were pooled from the entire core and

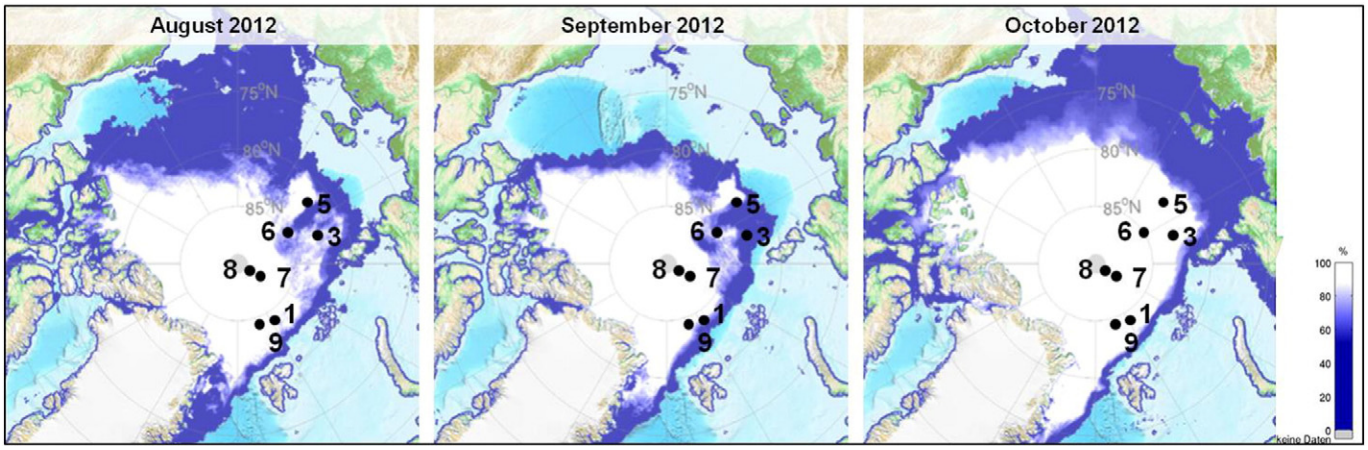

Fig. 1. Position of ice stations sampled during the RV Polarstern expedition IceArc to the central Arctic in 2012. For exact sample positions see Table 1. At each ice station, sampling of deep-chlorophyll maximum water layer depth, under-ice water, sea ice cores and melt pond water took place. The maps show monthly mean sea ice concentrations for August, September and October (map from meereisportal.de). October is presented to illustrate the increase in sea ice concentration at the end of the season.