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Deep-sea ciliates: Recorded diversity and experimental studies on pressure tolerance

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ABSTRACT

Microbial eukaryotes play an important role in biogeochemical cycles not only in productive surface waters but also in the deep sea. Recent studies based on metagenomics report deep-sea protistan assemblages totally different from continental slopes and shelf waters. To give an overview about the ciliate fauna recorded from the deep sea we summarized the available information on ciliate occurrence in the deep sea. Our literature review revealed that representatives of the major phylogenetic groups of ciliates were recorded from the deep sea (> 1000 m depth): Karyorelictea, Heterotrichea, Spirotrichea (Protohypotrichia, Euplotia, Oligotrichia, Choreotrichia, Hypotrichia), Armophorea (Armophorida), Litostomatea (Haptoria), Conthreep (Phyllopharyngea incl. Cyrtophoria, Chonotrichia, Suctoria; Nassophorea incl. Microthoracida, Synhymeniida, Nassulida; Colpodea incl. Bursariomorphida, Cyrtolophosidida; Prostomatea; Plagiopylea incl. Plagiopylida, Odontostomatida; Oligohymenophorea incl. Peniculia, Scuticociliatia, Hymenostomatia, Apostomatia, Peritrichia, Astomatia). Species occurring in both habitats, deep sea and shallow water, are rarely found to our knowledge to date. This indicates a high deep-sea specific ciliate fauna. Our own studies of similar genotypes (SSU rDNA and *cox1* gene) revealed that two small scuticociliate species (*Pseudocohnilembus persalinus* and *Uronema* sp.) could be isolated from surface as well as deep waters (2687 m, 5276 m, 5719 m) of the Pacific. The adaptation to deep-sea conditions was investigated by exposing the ciliate isolates directly or stepwise to different hydrostatic pressures ranging from 1 to 550 atm at temperatures of 2 °C and 13 °C. Although the results indicated no general barophilic behavior, all four isolated strains survived the highest established pressure. A better survival at 550 atm could be observed for the lower temperature. Among microbial eukaryotes, ciliates should be considered as a diverse and potentially important component of deep-sea microeukaryote communities.

1. Introduction

The deep sea represents the world's largest biome on earth. However, there is still a huge lack of understanding concerning biodiversity and ecology of the deep-sea floor. The abyssal sea floor (3000–6000 m) covers around 54% of the earth surface and is the most common benthic environment with remarkably constant conditions (Gage and Tyler, 1991). Deep-sea organisms have to cope with extreme environmental conditions including low food availability, low temperatures, permanent darkness and high hydrostatic pressure.

Microbial eukaryotes or protists play an important role in the ocean matter flux in productive surface waters and are major components of biogeochemical cycles. Controlling half of the primary production, heterotrophic flagellates and ciliates are extremely important for remineralization of nutrients in the ocean (Azam and Malfatti, 2007; Landry and Calbet, 2004). Although there is a high variability of

recorded abundances, surface waters are typically inhabited by 10^5 bacteria and 10^3 protists per milliliter (Azam and Malfatti, 2007). Considering the order of geographic magnitude of the deep sea, little is known about protists in these depths (e.g. Edgcomb et al., 2002; Scheckenbach et al., 2005, 2010). Studies mainly concentrated on deep-sea areas with extreme environmental conditions like hydrothermal vents and cold seeps (Alexander et al., 2009; Edgcomb et al., 2009). Comparison of the microbial community structure of shelf and deep-sea habitats showed differences in protistan assemblages (Countway et al., 2007). Genetic approaches like next-generation sequencing and clone libraries have turned out to be reliable tools in identifying previously unknown protistan lineages in the deep sea (Edgcomb et al., 2002; López-García et al., 2001). Deep-sea organisms are dependent on sinking detritus. Besides being a food source such aggregations may serve as transportation vehicle to the deep sea for different protozoan species (Alldredge and Silver, 1988; Arndt et al., 2003; Bochkansky

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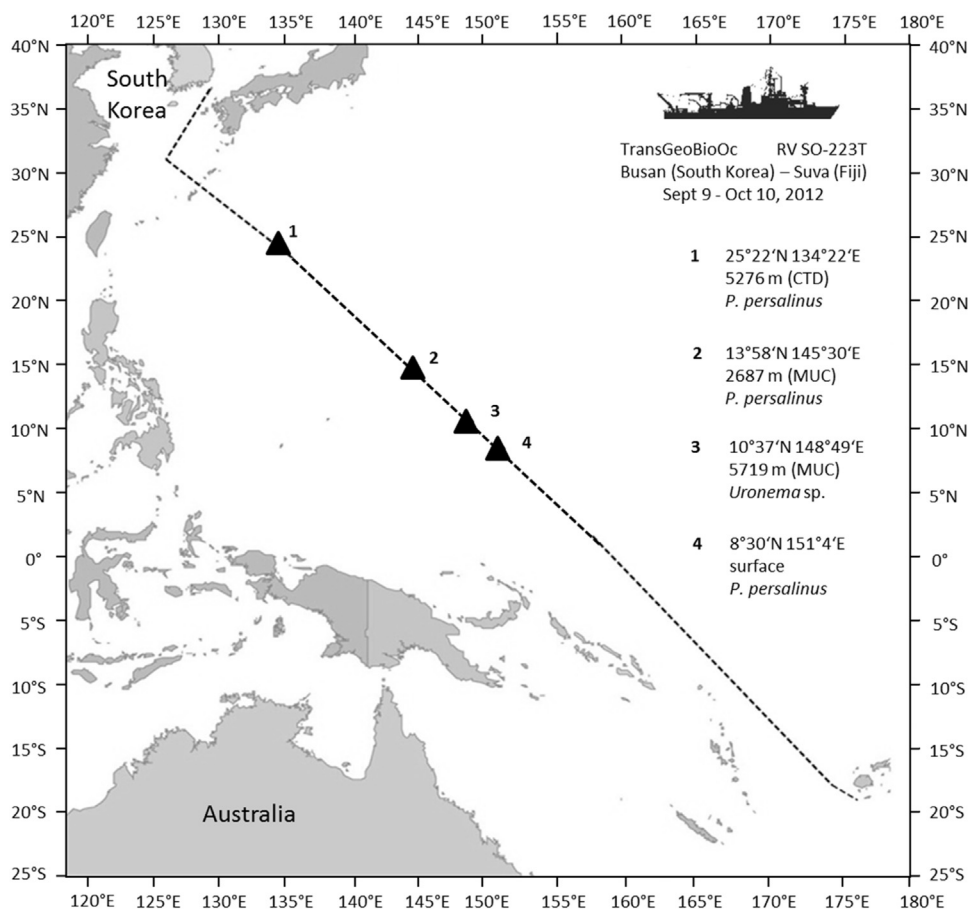


Fig. 1. Station map - Locations of four sampling stations during the research cruise RV Sonne I SO 223-T from Busan, South Korea, to Suva, Fiji (Sept 9 – Oct 10, 2012). Geographical positions, depth, sampling procedure and isolated ciliate species are given for each station.

et al., 2017; Caron et al., 1982; Lochte and Turley, 1988) in addition to sinking carcasses (Dayton and Hessler, 1972; Smith, 1985). Protists are known to encyst to overcome periods of unfavorable environmental conditions. This process potentially plays an important role for survival in the deep sea (Atkins et al., 1998).

Protist records from the deep sea are mainly available for foraminiferans (Danovaro et al., 2010; Gooday and Jorissen, 2012; Pawlowski et al., 2011b), while there is surprisingly little information available regarding the diversity of ciliates in the deep sea. Several studies indicate the presence of ciliates in deep-sea sediments (e.g. Pawlowski et al., 2011a). Furthermore, ciliates have been found as epibionts on benthic deep-sea arthropods (Bartsch and Dovgal, 2010; Sedlacek et al., 2013). Large-scale studies demonstrated a close link between benthic biodiversity and ecosystem functioning in the deep sea (e.g. Danovaro et al., 2008a). They estimated that a biodiversity loss of 20–30% can result in a 50–80% reduction of key processes of deep-sea ecosystems. Therefore, it is important to understand the role of ciliated protists as a potentially very important group of abyssal microbial food webs. Earlier studies had shown that deep-sea protists like heterotrophic flagellates are able to survive pressures up to 300 atm (Atkins et al., 1998). Some flagellates and ciliates even preferred moderate pressure (Kitching, 1957; Turley et al., 1988). The ciliate *Tetrahymena* is able to survive deep-sea pressures of up to 250 atm (Hemmingsen, 1982; Hemmingsen and Hemmingsen, 1983).

To give an overview about the ciliate fauna recorded from the deep sea, we summarized the available information on ciliate occurrence in the deep sea. Species occurring in both habitats, deep sea and shallow waters, are rarely found to our knowledge to date. The isolation of two scuticociliates commonly found in surface waters isolated from the deep sea raised the question whether or not the same ciliate species or even genotypes might populate surface as well as deep-sea waters.

Thus, there might be a possible exchange or permanent sedimentation of surface individuals to the deep. Therefore, we monitored possible pressure tolerances and discussed distribution mechanisms.

2. Material and methods

2.1. Sampling

Samples were taken with a Multi-Corer system and a Seabird SBE *9plus* CTD from the North Pacific Ocean as well as the South Pacific Ocean during the RV Sonne I cruise SO-223T (9th September – 8th October 2012) from Busan, South Korea, to Suva, Fiji (see Fig. 1). Samples of the Multi-Corer system were taken from the overlaying water as well as from the upper 2 mm sediment layer by means of a sterile syringe. A closing mechanism at the top and bottom of the cores reduces the risk of contamination with organisms and cysts from upper water layers and, thus, a contamination should be negligible. Subsamples of a few milliliters of the sediment suspension were cultivated into 50 ml tissue-culture flasks (Sarstedt, Nümbrecht, Germany) filled with 30 ml autoclaved sea water. In addition, 500 ml aliquots of the overlaying water were incubated in 650 ml tissue-culture flasks. All cultures were supplied with sterilized quinoa grains as an organic food source for autochthonous bacteria. Furthermore, surface water was collected to compare surface with deep-sea isolates. These samples were also transferred to 50 ml tissue culture flasks filled with 30 ml autoclaved sea water and two quinoa grains.

Four ciliate strains isolated from different depths were investigated: *Pseudocohnilembus persalinus* HFCC (Heterotrophic Flagellate Cultures Cologne) 816 (0 m), *Pseudocohnilembus persalinus* HFCC 814 (2687 m), *Pseudocohnilembus persalinus* HFCC 822 (5276 m) and *Uronema* sp. HFCC 823 (5719 m). The isolates were cultivated in 50 ml tissue culture flasks (Sarstedt, Nümbrecht, Germany) filled with 30 ml Schmaltz-Pratt

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