UNIVERSITY OF COLOGNE

Biogeography and its impact on benthic heterotrophic protists – Investigations from the littoral to the deep sea

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“The more clearly we can focus our attention on the wonders and realities of the universe about us, the less taste we shall have for destruction.” – Rachel Carson

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Contents

Abstract

Biogeography is the study of the distribution of biodiversity and the processes resulting in spatial patterns. Knowledge on biogeography is crucial for the understanding of ecosystem functions and evolutionary processes. But, if biogeographical concepts, established for macroorganisms, also apply for microbial communities is far from being clarified. Protists (unicellular eukaryotes) are the most common and most diverse eukaryotes on Earth and play a key role in the microbial food web by transferring carbon to higher trophic levels. However, their diversity and distribution in marine sediments, especially in the deep sea, is yet not fully understood. The overall aim of this study was to extend the knowledge on biogeographical distribution patterns of protist communities at the ocean floor considering different spatial scales to understand ecological and evolutionary processes within this vast environment.

By combining the molecular technique of amplicon sequencing with live-countings, direct microscopical observations and cultivation-based approaches, benthic protist communities along depth transects around multiple islands and seamounts of the Azores archipelago were investigated. Strong differences between communities from different depths and islands were found, indicating a separation of communities on islands shelfs/seamounts from communities inhabiting the surrounding deep-sea areas, favouring speciation processes on islands/seamounts.

The deep-sea areas surrounding islands and seamounts are complex environments, characterised by large geological features and diverse microhabitats, possibly enhancing the evolution of a diverse protist community, specially adapted to the complex and harsh prevailing conditions. Within this study, the composition and distribution of deep-sea protist communities in bathyal, abyssal and hadal depths were analysed. Amplicon sequencing of the V9 18S rDNA of sediment samples from three different abyssal regions in the North Atlantic Ocean and the Caribbean Sea, revealed high variations in the structure of protist communities at large spatial scales. In addition, spatial patterns at local scales were found by comparing community compositions of sediment samples taken ~1 m apart from each other. The OTU (operational taxonomic units) richness decreased with sediment depth which correlated with decreasing TOM (total organic matter) contents, when looking at a vertical scale in different sediment layers of the same sediment core. The only exception was one station where sedimented macroalgae (*Sargassum*) were found on the deep-sea floor, possibly influencing the microbial communities directly or indirectly.

A global study, comparing 11 regions in the Atlantic and Pacific Ocean, showed that different ocean basins harbour unique protist communities with high rates of endemism, being distinct from surface water communities. A high genetic novelty was found within the deep-sea samples, indicating a specific deep-sea nanofauna, but it also underlines the need to extend common reference databases using cultivated protist strains.

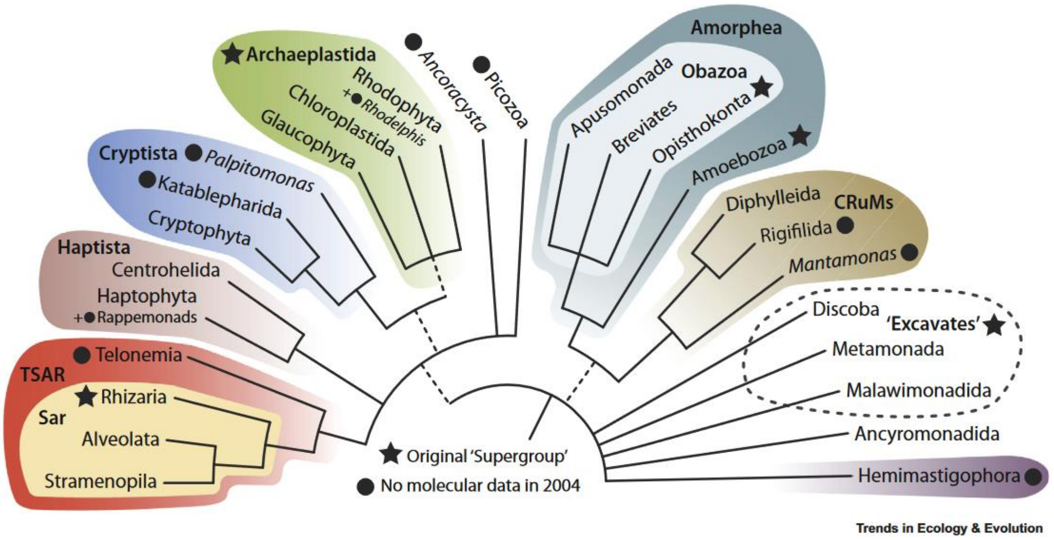
Within this study, two protist groups, with clonal cultures from surface waters and the deep sea, were investigated more in detail to examine their biogeographical distribution and ecological adaptations. Fourteen strains of Percolomonadida were isolated and cultivated, including two new families, four new genera and ten newly described species. Phylogenetic analyses indicated a separation by ecological traits of the marine families Lulaidae and Barbeliidae from the Percolomonadidae with representatives from different meso- and hypersaline waters. The isolation and cultivation of 39 strains of *Cafeteria*-like flagellates led to the reorganization of the Cafeteriaceae with nine newly described species being added to the two already known species. Within the Percolomonadida as well as the Cafeteriaceae, single species seemed to be globally distributed in marine surface waters and the deep sea and were able to survive varying environmental conditions (salinity and hydrostatic pressure). However, most species seemed to be locally restricted in their distribution.

Overall, the combination of various different methods enabled a broad overview on the diversity and distribution of benthic protist communities from the sublittoral down to the deep sea and showed that different islands of the Azores harbour distinct protist communities. Spatial distribution patterns were observed at local, regional and global scales in the deep sea, indicating that protist communities are shaped by the heterogeneity of the deep-sea floor. Detailed analyses of single taxonomic groups gave new insights into their biogeographical distribution and adaptations to different environmental conditions. The present thesis underlines the complex biogeographical distribution patterns of protist communities at different spatial scales, probably shaped by heterogenous environments with changing, extreme conditions, which require specific ecological adaptations.

General Introduction

Diversity and Function of Protists

Protists (unicellular eukaryotes) are probably the most diverse and most common eukaryotes on Earth, with a widespread distribution throughout the eukaryotic tree of life (Figure1) (Adl et al., 2019; Archibald et al., 2017; Burki et al., 2020; Patterson, 1999). As most of this diversity is yet uncultured, it is extremely difficult to fully resolve the phylogenetic position of many protist groups and to understand their ecological role. They developed a variety of different feeding types and trophic modes including phototrophy, heterotrophy, saprotrophy, parasitism and symbioism, which are associated to their large number of diverse functions in the food web (Worden et al., 2015).



Trends in Ecology & Evolution

Figure 1. The eukaryotic tree of life after Burki et al. (2020) based on a consensus of recent phylogenomic studies. The colours correspond to the currently used "supergroups". Multifurcation shows unresolved branching orders among lineages. Dashed lines reflect uncertainties about the monophyly of groups. Groups marked by an asterisk were considered as "supergroup" in former versions of the supergroup model. Circles show lineages where no molecular data were available when the supergroup model emerged.

Among the heterotrophic feeding modes of protists, predation is the best-studied mode in marine systems including predation on viruses, bacteria, archaea, algae, as well as on other heterotrophic protists (e.g. by several ciliates) or even on metazoans (e.g. by foraminiferans and radiolarians) (Sherr and Sherr, 2002; Swanberg and Caron, 1991). The nano- (2-20 µm) and microfauna (20-200 µm) of the marine pelagial for instance can consume up to 62% of the daily algal production (Schmoker et al., 2013). Ecologically especially important for the microbial food web, is the bacterial grazing by protists as it controls bacterial abundances and channels organic carbon and nutrients to higher trophic levels (Azam et al., 1983; Sorokin and Paveljeva, 1972). Thereby, bacterial and archaeal communities are structured due to selective grazing (Bonkowski, 2004; Jousset, 2012; Jürgens and Massana, 2008). The concept of organic matter and nutrient transfer to higher trophic levels in the microbial food web is called 'microbial loop' and describes a linear chain from dissolved organic matter via bacteria, nanoflagellates and microfauna to higher trophic levels (Azam et al., 1983). Since the initial conceptualization of the microbial loop, additional aspects and connections within the microbial food web have been discovered, leading to the idea of a far more complex structure, in which microbial eukaryotes are involved in a wide range of interactions and occupy multiple trophic levels (Figure 2).

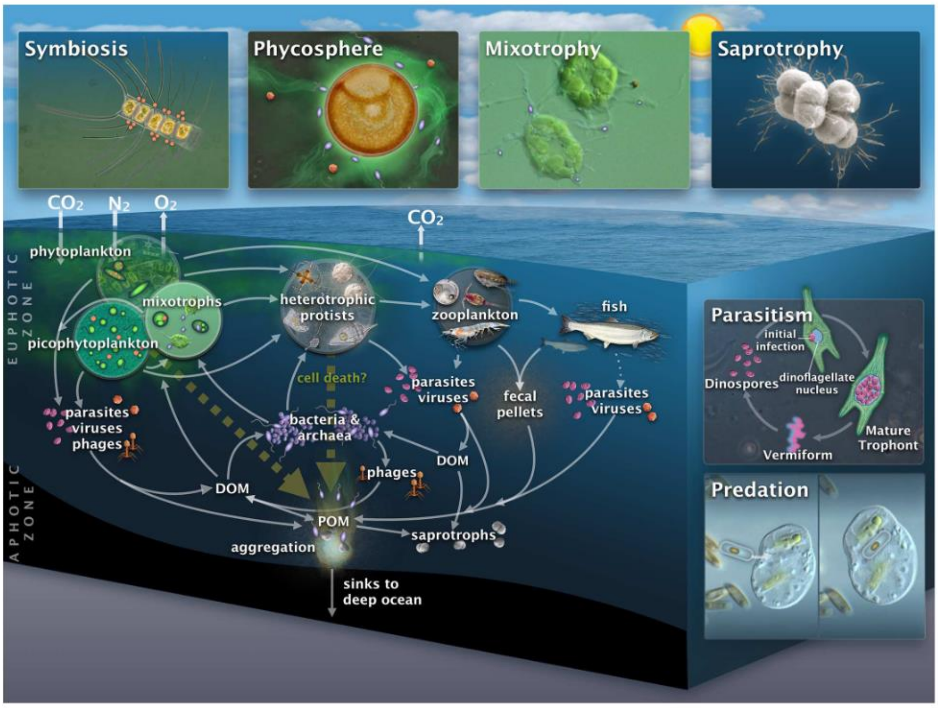


Figure 2. Model of the pelagic food web in the euphotic zone of the ocean in which microbes of the three domains of life interact. Inlets show trophic modes and interactions in which protists are involved (Worden et al., 2015).

Mixotrophy, the ability to combine photosynthetic and predatory-based nutrition, was recognized as abundant trophic mode among marine protists (Bird and Kalff, 1986; Flynn et al., 2019; Stoecker et al., 2017). Parasitic and mutualistic symbionts have shown to be highly diverse and abundant in marine ecosystems, but are still largely uncharacterised (de Vargas et al., 2015; Scheckenbach et al., 2010). While microbial food webs in marine surface waters are well studied, less is known about the structure and functioning of microbial food webs in marine sediments, especially in the deep sea.

Environmental Conditions in the Deep Sea

Two thirds of the Earth’s surface is covered by ocean and over 90% of these waters are deeper than 200 m, making the deep-sea floor the largest benthic habitat on our planet (Gage and Tyler, 1991). However, the deep sea is probably also the least investigated habitat, because it is extremely remote and difficult to access. Less than 1% of the deep-sea floor has been sampled so far (McClain, 2007). The prevailing conditions in the deep-sea realm are challenging for life, as the absence of light, low temperatures around 2 °C and the high hydrostatic pressure, raising by 1 bar with every 10 m depth. Topographically, the deep sea is a highly complex environment with features such as mid-ocean ridges, fracture zones and seamounts shaping it at the landscape level. The number of seamounts alone is estimated between 30,000 and over 100,000 globally (Danovaro et al., 2014) of which only a tiny fraction has been directly sampled so far (Kvile et al., 2014). But there are also smaller geological features such as hydrothermal vents, cold seeps, cold-water coral reefs, pockmarks and faults shaping the deep-sea floor at more local spatial scales (Levin and Sibuet, 2012; Watling et al., 2013).

Due to the absence of photosynthesis, the carbon supply in the deep sea mainly depends on sinking material from surface waters (Johnson et al., 2007; Lampitt et al., 2001). As the carbon flux decreases with increasing depth (Berelson, 2001; Pace et al., 1987; Suess, 1980), the deep sea was formerly considered as a food-poor environment with a low biomass and low abundances of organisms (e.g. Rex et al., 2006). However, recent studies emphasized the role of extensive and rapid sedimentation events of macroalgae (like brown algae of the genus *Sargassum*) for carbon sequestration, which could have been overlooked by former sedimentation trap surveys (Figure 3) (Baker et al., 2018; Krause-Jensen and Duarte, 2016). A global estimate suggested that macroalgae sequester about 173 TgC per year of which about 90% is exported to the deep sea (Krause-Jensen and Duarte, 2016). How these carbon sources can be utilized by deep-sea organisms, especially the nano- and microfauna, is not very well studied so far. As food fall events can take on different dimensions and depend on region and season (Billet et al., 1983; Dierssen et al., 2009; Lampitt, 1985; Rice et al., 1994), they shape the spatial heterogeneity of the deep-sea floor.

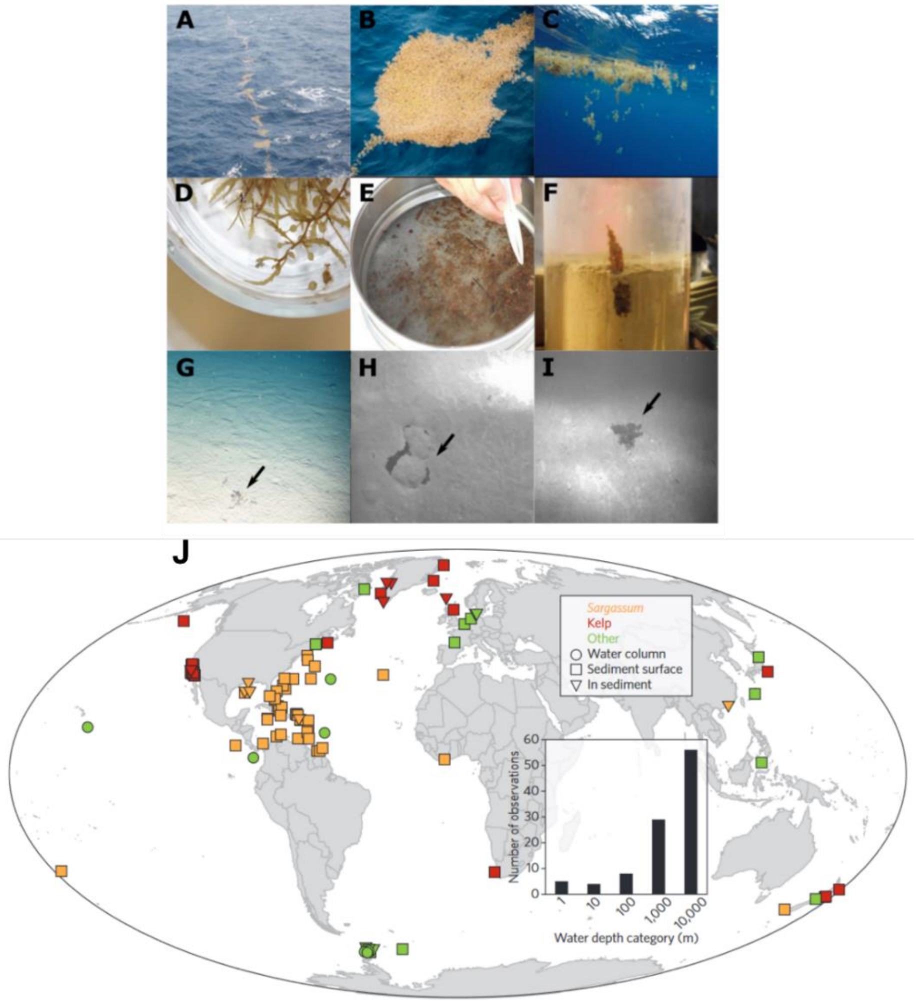


Figure 3. Macroalgae as food source in the deep sea (**A-I** from Baker et al. (2018); **J** from Krause-Jensen and Duarte (2016)). **A, B** showing rows and mats of *Sargassum* algae floating on the ocean surface, beginning to sediment **(C)**. **D-F:** Samples of *Sargassum fluitans* collected during a cruise of RV Sonne. Pieces of *Sargassum* were found in samples of the epibenthic sledge **(E)** and in a sediment core of the multicorer **(F)**. **G-I:** Photos of the deep-sea floor taken by a camera-equipped epibenthic sledge **(G)** and an autonomous underwater vehicle **(H, I),** showing patches of *Sargassum* algae on the deep-sea floor. **J:** Map of locations where macroalgal carbon storage was observed by sediment traps in the water column, on sediment surfaces or buried in the sediment. Colours indicate different macroalgae types. Inlet shows the number of observations per depth.

Microhabitats in the deep sea are shaped by scattered distributed food resources and other factors such as sediment characteristics, geological and biogenic structures and small-scale disturbances (Grassle and Maciolek, 1992; Grassle and Morse-Porteous, 1987; Jumars, 1976). These ecological niches should have favoured the evolution of a diverse, heterogenous protist community at the deep-sea floor, specially adapted to the harsh and complex prevailing conditions.

Biogeography of Marine Protists

Next-generation sequencing methods such as amplicon sequencing enabled large-scale investigations on species richness and distribution patterns and unveiled an enormous diversity of microbial eukaryotes (e.g. de Vargas et al., 2015; Edgcomb et al., 2002; Obiol et al., 2020). Massive amounts of data have been produced and showed that especially marine communities differ severely from soil and freshwater communities with almost no overlap between marine and terrestrial systems (Singer et al., 2021). However, marine, benthic protist communities have received only little attention in comparison to pelagic ones (Bik et al., 2012; Cordier et al., 2022; Forster et al., 2016). Most benthic studies focused on diversity hotspots such as hydrothermal vent systems (Edgcomb et al., 2002; López-García et al., 2003) or anoxic basins (Dawson and Pace, 2002; Stoeck et al., 2003; Takishita et al., 2005), but coastal and deep-sea environments showed to have a comparable diversity with high genetic novelties (Bik et al., 2012; Gong et al., 2015; Massana et al., 2015; Pawlowski et al., 2011; Scheckenbach et al., 2010). Especially deep-sea sediment communities were found to be extremely diverse, exceeding the diversity of the pelagic realm of the ocean at least by threefold (Cordier et al., 2022). In addition, previous studies suggest the existence of a specific nano- and microfauna in abyssal sediments (Arndt et al., 2003; Scheckenbach et al., 2005; Schoenle et al., 2017). One study by Scheckenbach et al. (2010) found significant differences in the community structure of protists of three abyssal plains, indicating distribution patterns on a large-scale level probably shaped by ecological factors. Another study by Bik et al. (2012) showed that shallow water communities are distinct from deep-sea communities, with some taxa maintaining a eurybathic range and a wide deep-sea distribution, while the majority of taxa were regionally restricted.

Knowledge on the biogeography of organisms, their abundances, distribution and diversity across temporal and spatial scales, is fundamental as it is linked to the function of ecosystems and gives important information on evolutionary mechanisms regulating diversity (Brown et al., 2002; Levin, 1992). For microorganisms, the critically discussed ‘Everything is everywhere, but the environment selects’ hypothesis, initially established by Beijerinck, states that small organisms (< 2 mm) are not limited in their dispersal and will have a cosmopolitan distribution as long as their environmental requirements are met (Baas-Becking, 1934; Beijerinck, 1913; Fenchel and Finlay, 2004; Finlay, 2002; Kellogg and Griffin, 2006). However, this theorem is challenged as traditional methods of species identification, based on morphotypes were supplemented by new molecular methods which have uncovered widespread crypticity, phylogeographical patterns and a restricted dispersal in many microbial species (Foissner, 2006; Lachance, 2004; O'Malley, 2007; Telford et al., 2007). A global study on bathyal and abyssal seafloor bacteria showed that even prokaryotes show a high rate of endemism, especially among rare taxa, while high abundant taxa more likely showed a cosmopolitan distribution (Bienhold et al., 2016). Similarly, eukaryotic microbial communities in most habitats consist of diverse, very abundant taxa of which a few species are dominant, and many low abundant species, the so called "rare species" (Logares et al., 2014). Rare taxa are reservoirs of functional and genetic diversity, but they are also more likely influenced by environmental factors and sudden changes (Lynch and Neufeld, 2015; Pedrós-Alió, 2012; Zhang et al., 2018).

Depth-dependent distribution patterns of benthic protists are only rarely studied so far in the marine realm. One study by Guardiola et al. (2016) analysed the structure of sediment communities along a slope and an adjacent submarine canyon in the Mediterranean Sea. Along depths from 900 to 1750 m, they found significant changes in the community composition with depth, season and between the canyon and the slope. Another study by Hausmann et al. (2002) used a semi-quantitative cultivation approach to investigate communities along a transect in the Mediterranean Sea ranging from 156 to 4617 m depths, showing a quantitative change with increasing depths, as well as a qualitative change in the taxonomic composition of benthic communities. However, distribution patterns of protists from the surface down to the deep-sea realm in the world's oceans are far from being resolved. One of the most influential theories within ecological biogeography is the 'theory of island biogeography' first stated by McArthur and Wilson in 1967, predicting that (i) larger islands have more species at equilibrium, because of high colonization rates and low extinction rates and (ii) islands with greater distance to the mainland have less species at equilibrium, since they have lower colonization rates. Later, the theory was revised to the 'general dynamic theory of oceanic island biogeography' by Whittaker et al. (2008), describing the relationship between immigration, speciation and extinction in relation to the change of island characteristics through time. Pinheiro et al. (2017) adopted the theory to marine organisms and since then it was applied to e.g. reef fish (Mazzei et al., 2021; Pinheiro et al., 2017), gastropods (Hachich et al., 2015) and marine meiofauna (George, 2013), but if it is also applicable to microbial organisms is still under debate (Dickey et al., 2021). Surrounding deep-sea areas, with their harsh environmental conditions, could act as dispersal barrier for benthic protist species living on island shelfs or seamounts and the islands/seamounts could become so called 'trapping stones' (George, 2013). On the other hand, if benthic protist species are able to distribute via the deep-sea floor, islands/seamounts could also serve as ‘stepping stones’ (Hubbs, 1959; McArthur and Wilson, 1967) or ‘staging posts’ (Cecca, 2002; Rosen, 1983), connecting populations and enabling the constant gene flow over large distances.

Overall, biogeography is a central aspect for the understanding of evolution (Richardson, 1981), because a crucial mechanism of evolutionary processes is genetic isolation. But biogeographical patterns of marine protists, shaped by the heterogeneity of their surrounding habitat, are still far from being understood. Especially small-scale distribution patterns at horizontal and vertical-scales in the deep sea, or from the shallow littoral zone down to the dee-sea floor, need to be resolved to understand the mechanisms driving evolutionary processes in this vast and under-explored environment.

Aims

The main objective of this study was to better understand biogeographical distribution patterns of protist communities at the ocean floor and to resolve ecological and evolutionary processes linked to these patterns. Therefore, we sampled different regions of the Atlantic Ocean including depths from sublittoral down to abyssal sediments to investigate the diversity and biogeographical distribution of the inhabiting nano- and microfauna at large and small, vertical and horizontal spatial scales by environmental sequencing. We aimed to resolve their spatial distribution and ecological adaptations to different environmental conditions by investigating single taxonomic groups more in detail.

The following questions were addressed:

1.) Are benthic deep-sea protist communities genetically isolated from communities in shallower depths due to their specific adaptations to deep-sea conditions?
2.) Are there large- and small-scale distribution patterns of benthic protists present at the deep-sea floor?
3.) Do different deep-sea regions harbour unique protist communities?
4.) How are protist species adapted to the conditions prevailing in the deep sea?

To answer these questions, protist communities along depth transects from sublittoral down to abyssal depths around different islands and seamounts of the Azores were analysed by a combination of live-counting, direct observations, cultivation-based approaches and an amplicon sequencing approach (Chapter 1, 2). Deep-sea communities from bathyal, abyssal and hadal depths, from different regions of the world’s ocean, were investigated with the aim to resolve distribution patterns of benthic microbial communities at local, regional and global scales in the deep sea and to answer the question if different regions of the deep sea, harbour unique protist communities (Chapter 3, 4). Clonal cultures of single taxonomic groups were used to analyse their biogeographical distribution and ecological adaptations to different environmental conditions, like different salinity concentrations and high hydrostatic pressures like those prevailing in the deep sea (Chapter 5-9).

Summary of Chapters

The findings presented in the framework of this thesis are structured in two parts, each represented by four or five chapters. The first part focuses on the diversity and biogeographic distribution of protist communities at the ocean floor. Patterns of spatial distribution were revealed at large and small, horizontal and vertical scales as well as from sublittoral down to abyssal depths. The second part of this thesis covers the biogeography, phylogeny and autecological adaptations of protists from surface waters and the deep sea to resolve evolutionary processes in different taxonomic groups and to understand their ecological role.

Part 1

Biogeographical Patterns of Protist Diversity in the Deep Sea at Horizontal and Vertical Scales and in Relation to Increasing Depth

Chapter 1: Changes in the Abundance and Taxonomic Composition of Benthic Heterotrophic Protists from Atlantic Sublittoral to Deep-Sea Sediments

To investigate how benthic protist communities change with increasing depth, their abundance and taxonomic composition was analysed in sediment samples from sublittoral down to abyssal regions, taken around two seamounts and three islands of the Azores archipelago. By this, it was shown that protist abundances decreased significantly and community composition changed with increasing depth. While some species were found in samples from all depths, others seemed to be restricted to lower depths. This indicates that most protist species are restricted to certain depths and that there is a specific deep-sea nano- and microfauna, specially adapted to the prevailing conditions. *Published in Diversity, doi: 10.3390/d14030164*

Chapter 2: Differences between Benthic Protist Communities from the Sublittoral to the Deep Sea at the Azores Islands Revealed by Environmental Sequencing

The diversity and distribution of benthic protist communities in sublittoral to deep-sea sediments from the Azores islands were investigated using amplicon sequencing of the V9-region on the 18S rDNA. Thereby, it was found that protist community composition significantly differed in different investigated depths with communities from three different depths zones clustering separate from each other (50 m, 150-500 m and 1000-2000 m). Distinct protist communities were found at the three islands, indicating that the surrounding deep-sea areas may act as a barrier for the dispersal of some species inhabiting the island shelfs, possibly leading to a limited gene flow between populations of the different investigated islands favouring speciation processes. *Published in Microorganisms, doi: 10.3390/microorganisms11071664*

Chapter 3: Horizontal and Vertical Small-Scale Patterns of Protist Communities at the Atlantic Deep-Sea Floor

Diversity and distribution of protist communities in abyssal sediments of the Atlantic Ocean were investigated using amplicon sequencing of the V9-region on the 18S rDNA. Only a low amount of OTUs (operational taxonomic units) were shared between the three investigated abyssal regions, showing patterns of protist diversity at large spatial scales. The analysis of samples taken from sediment cores, separated by ~1 m, showed differences in the protist community structure, indicating a distinct eukaryotic microbial diversity even at small horizontal scales. Protist community composition varied also at a vertical scale, in different investigated sediment layers (upper 2 mm, 1 cm, 2 cm, 3 cm). These findings indicate that deep-sea protist communitites are shaped by the heterogeneity of the deep-sea floor. *Published in Deep-Sea Research Part I: Oceanographic Research Papers, doi: 10.1016/j.dsr.2021.103515*

Chapter 4: High and Specific Diversity of Protists in the Deep-Sea Basins Dominated by Diplonemids, Kinetoplastids, Ciliates and Foraminiferans

DNA metabarcoding and cultivation-based surveys on 20 sediment samples from 11 regions in the Pacific and Atlantic Ocean were used to investigate deep-sea protist communities and their role in the deep ocean. Next to the traditionally considered foraminiferans, other groups such as diplonemids, kinetoplastids and ciliates were found to be highly diverse and clearly exceeded the diversity of metazoans. Different ocean basins harboured distinct protist communities, as well as communities from bathyal, abyssal and hadal depths showed large differences in OTU richness. This study showed that benthic protist communities in the deep sea are highly specific, locally diverse and only share little overlap with pelagic communities, underlining their importance for shaping seafloor communities. *Published in Communications Biology, doi: 10.1038/s42003-021-02012-5*

Part 2

Biogeography, Phylogeny and Autecological Adaptations of Marine Protists Exemplified Using Single Taxonomic Groups

Chapter 5: Diversity and Phylogeny of Percolomonads Based on Newly Discovered Species from Hypersaline and Marine Waters

To resolve evolutionary relationships within the group of percolomonads (Heterolobosea), the morphology, 18S rDNA phylogeny and salinity tolerance of seven percolomonad cultures from marine waters and saline, athalassic waters were investigated. Five new percolomonad species and three new genera were described. The species *Percolomonas doradorae,* isolated from a hypersaline inland lake in the Atacama Desert, showed the broadest salinity tolerance with salinities from 23-150 PSU (practical salinity units), while the other species showed a narrower salinity tolerance around marine conditions. This indicates that *P. doradorae* is adapted to a wide range of environmental conditions (including marine) and could be widely distributed, while the other investigated species might be limited to one habitat type. *Published in European Journal of Protistology, doi: 10.1016/j.ejop.2021.125808*

Chapter 6: Biogeography, Autecology and Phylogeny of Percolomonads Based on Newly Described Species

Seven new strains of percolomonads (Heterolobosea) were isolated from marine waters and hypersaline environments in the Atacama Desert. We investigated their morphology, 18S and 28S rDNA concatenated phylogeny, salinity tolerance and biogeographic distribution by comparing the cultivation-based approach with environmental sequencing data. Two new families, a new genus and five new species were described. *Percolomonas adaptabilis,* isolated from the Atlantic Ocean, seemed to be globally distributed in marine surface waters and showed a broad tolerance against high salinity concentrations in its environment, indicating that it might not be limited to marine habitats. The other species seemed to be more restricted in their distribution, probably influenced by environmental factors such as temperature, depth or oceanic region. *Published in Journal of Eukaryotic Microbiology, doi: 10.1111/jeu.12930*

Chapter 7: Global Comparison of Bicosoecid *Cafeteri*a-like Flagellates from the Deep Ocean and Surface Waters, with Reorganization of the Family Cafeteriaceae

The phylogenetic relationships within the Cafeteriaceae (Stramenopiles) were reorganized by investigations on 29 *Cafeteria*-like protist strains from marine surface waters and the deep sea from all over the world's ocean. Besides morphological analyses, a concatenated phylogeny (18S rDNA, 28S rDNA) resulted in a separation of the Cafeteriaceae into two already known species (*Cafeteria roenbergensis* and *C. mylnikovii*) and six newly described species. Comparisons of V9 18S rDNA data of the new strains with environmental sequencing data from the deep sea and surface waters, showed that *C. burkhardae* seemed to be globally distributed, while the other species seemed to be more locally restricted, indicating biogeographical distribution patterns within the Cafeteriaceae. *Published in European Journal of Protistology, doi: 10.1016/j.ejop.2019.125665*

Chapter 8: *Cafeteria* in Extreme Environments: Investigations on *C. burkhardae* and Three New Species from the Atacama Desert and the Deep Ocean

Ten additional strains of the genus *Cafeteria* (Stramenopiles) were isolated from extreme environments as the deep sea and athalassic waters in the Atacama Desert. Morphological and molecular analyses (18S rDNA and 28S rDNA) revealed three new species, however most of the strains were associated with the already described species *C. burkhardae*. Salinity tolerance experiments showed that only strains of *C. burkhardae* and *C. baltica* were able to tolerate salinities up to 150 PSU, indicating that these species are adapted to a broad range of salinities and could inhabit a variety of different habitats, including hypersaline environments. *Published in European Journal of Protistology, doi: 10.1016/j.ejop.2022.125905*

Chapter 9: Survival of Marine Heterotrophic Flagellates Isolated from the Surface and the Deep Sea at High Hydrostatic Pressure: Literature Review and Own Experiments

Cultivated protist strains belonging to different taxonomic groups (bicosoecids, kinetoplastids, choanoflagellates, ancyromonads, euglenids, chrysomonads and cercozoans), isolated from marine surface waters and the deep sea, were tested for their ability to survive high hydrostatic pressures (up to 670 bar). Barotolerant behaviour was demonstrated for several different flagellate species isolated from the surface, indicating that these species might be able to survive in the deep-sea realm. Survival and barophilic behaviour of protist strains isolated from the deep sea supports that these species originate from active deep-sea communities and indicates their genetic adaptation to deep-sea conditions. *Published in Deep-Sea Research Part II: Topical Studies in Oceanography, doi: 10.1016/j.dsr2.2017.04.022*

Part 1

Biogeographical Patterns of Protist Diversity in the Deep Sea at Horizontal and Vertical Scales and in Relation to Increasing Depth

Chapter 1: Changes in the Abundance and Taxonomic Composition of Benthic Heterotrophic Protists from Atlantic Sublittoral to Deep-Sea Sediments

Published publication

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Chapter 2: Differences between Benthic Protist Communities from the Sublittoral to the Deep Sea at the Azores Islands Revealed by Environmental Sequencing

Published publication

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Chapter 3: Horizontal and Vertical Small-Scale Patterns of Protist Communities at the Atlantic Deep-Sea Floor

Published publication

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Chapter 4: High and Specific Diversity of Protists in the Deep-Sea Basins Dominated by Diplonemids, Kinetoplastids, Ciliates and Foraminiferans

Published publication

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Part 2

Biogeography, Phylogeny and Autecological Adaptations of Marine Protists Exemplified Using Single Taxonomic Groups

Chapter 5: Diversity and Phylogeny of Percolomonads Based on Newly Discovered Species from Hypersaline and Marine Waters

Published publication

Carduck, S., Nitsche, F., Rybarski, A., **Hohlfeld, M.**, Arndt, H., **2021**. Diversity and Phylogeny of Percolomonads Based on Newly Discovered Species from Hypersaline and Marine Waters. *European Journal of Protistology 80, 125808. doi: 10.1016/j.ejop.2021.125808*

Chapter 6: Biogeography, Autecology and Phylogeny of Percolomonads Based on Newly Described Species

Published publication

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Chapter 7: Global Comparison of Bicosoecid *Cafeteria*-like Flagellates from the Deep Ocean and Surface Waters, with Reorganization of the Family Cafeteriaceae

Published publication

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Chapter 8: *Cafeteria* in Extreme Environments: Investigations on *C. burkhardae* and Three New Species from the Atacama Desert and the Deep Ocean

Published publication

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Chapter 9: Survival of Marine Heterotrophic Flagellates Isolated from the Surface and the Deep Sea at High Hydrostatic Pressure: Literature Review and Own Experiments

Published publication

Živaljić, S., Schoenle, A., Nitsche, F., **Hohlfeld, M.**, Piechocki, J., Reif, F., Shumo, M., Weiss, A., Werner, J., Witt, M., Voss, J., **2018**. Survival of Marine Heterotrophic Flagellates Isolated from the Surface and the Deep Sea at High Hydrostatic Pressure: Literature Review and Own Experiments. *Deep-Sea Research Part II 148, 251-259. doi: 10.1016/j.dsr2.2017.04.022*

Conclusive Summary and Perspectives

The biogeography and diversity of communities is inseparably linked to the function of ecosystems and their ecological and evolutionary processes (Cardinale et al., 2012; Levin, 1992). The overall aim of this dissertation was to extend the current knowledge on biogeographical distribution patterns of marine protists. The present thesis gives new insights for defining the biogeography of marine protists at large and small, horizontal and vertical scales, from the shallow littoral down to the deep-sea floor, as well as its link to speciation processes. The work conducted within this thesis should add important contributions to the knowledge on the structure of deep-sea protist communities and their potential importance for the functioning of deep-sea ecosystems.

Using the Azores islands in the North Atlantic Ocean as a model region, the composition and distribution of benthic heterotrophic protist communities in sediments from sublittoral down to the deep sea around three islands (Flores, Terceira, Santa Maria) and two seamounts (Princess Alice Bank, Formigas Bank) were investigated in this study. The Azores are an isolated, geologically recent archipelago, comprising nine islands which emerged between 8 million and 250,000 years ago. Combining direct microscopical observations, live-counting, a cultivation-based approach and an amplicon-sequencing approach of the V9 18S rDNA, showed that protist community structure changed with increasing depth, with significant differences between communities from the sublittoral, upper bathyal and deeper zones (Chapter 1, 2). Abundances of benthic protists, belonging to all size classes and all major taxonomic groups, decreased with increasing depth, indicating that a high number of species might be restricted to lower depths. Representatives of some taxonomic groups were found in samples from all depths, like kinetoplastids, bicosoecids, cercozoans and foraminiferans, indicating their wide distribution and adaptation to a broad range of different environmental conditions (Chapter 1). In the amplicon sequencing approach, high numbers of ASVs (amplicon sequence variants) were detected being unique to either the sublittoral or upper bathyal in comparison to deeper zones, indicating the restricted distribution of many species which lack adaptations to deep-sea conditions (Chapter 2). Those species might be limited in their distribution, because they cannot distribute via the deep-sea floor to adjacent islands or seamounts. The number of individuals which could not be assigned to any taxonomic group during live-counting increased in depths below 1000 m, showing the distinct characteristics of deep-sea protist communities with a high number of so far undiscovered species. Some taxonomic groups with low abundances in the live-counting approach, like cercozoans and amoebozoans, dominated in the cultivation approach, indicating rare species, sampled in low concentrations, which are easily overlooked by other methods. Similar to the live-counting approach, the cultivation-based approach showed a steep decrease of cultivable morphotypes at depth over 300 m. This points towards a shift in the community structure with increasing depths, which might be coupled to the observed absence of microphytobenthos below 300 m leading to a diminishing nutrient availability (Chapter 1). Cultivation-based approaches are highly selective due to the defined cultivation conditions (e.g. temperature, atmospheric pressure, food sources), but they have the advantage to allow for detailed morphological and molecular characterization of species and the detection of low abundant taxa (Schoenle et al., 2016). However, species appearing in culture are not necessarily actively thriving at the sampling site. They could also have hatched from cysts. Direct microscopical live-observations can give insights into the active protist community and allow for abundance estimations and identification of morphotypes, but they are also limited due to the short available time frame (Jeuck and Arndt, 2013). High-throughput sequencing methods are a powerful tool and allow for large-scale investigations of the diversity and distribution of protist communities, but there are still some unresolved problems like their strong dependence on the coverage of reference databases and different copy numbers of the 18S ribosomal gene in different protist groups (Weber and Pawlowski, 2013). Therefore, a combination of different methods was used in the present study to gain a comprehensive view of the protist community structure (Jeuck et al., 2017; Schoenle et al., 2016). Moreover, as derived from mock community analyses, high-throughput sequencing methods produce high amounts of “noisy” reads, underlining the need of strict filtering criterions and the inclusion of a mock community in each sequencing run (Catlett et al. 2020; Chapter 2).

ASVs from the three Azores islands were dominated in all depths by dinoflagellates, ciliates and radiolarians. While dinoflagellates and ciliates seemed to be strongly influenced by depth, radiolarians probably belonged to pelagic taxa, descended from the water column (Chapter 2). One major challenge in the analysis of sediment communities is, that the sediment is a ‘DNA reservoir’ containing not only the DNA of the inhabiting species, but also extracellular DNA and DNA from cysts (Corinaldesi et al., 2011; Pawlowski et al., 2011). Screening the data for pelagic ASVs is difficult, as many taxonomic groups contain both, pelagic and benthic species and the reference databases are not yet sufficient to discriminate between them. Future investigations on marine sediments could include the analysis of mRNA to retrieve the active fraction of the protist community (Pawlowski et al., 2022). Within this study, differences between protist community structures of the three investigated Azorean islands were revealed. Thereby, the oldest island Santa Maria (8.12 mya, Borges et al., 2009) harboured the highest richness (824 ASVs) and the highest number of unique ASVs (558 ASVs), while the island Terceira (3.52 mya) showed a lower unique diversity with 332 ASVs and the youngest island Flores (2.16 mya) had the lowest unique diversity with 160 ASVs, fitting to the concept of island biogeography, which states that older islands, up to a certain point, harbour a higher species richness (Whittaker et al., 2008). A biogeographical isolation of species on islands/seamounts could have supported speciation processes leading to unique protist communities. Similar patterns were reported from the Atacama Desert, where different hypersaline inland lakes harbour different stramenopile and choanoflagellate species due to their isolated position (similar to islands in the ocean), which have led to an isolation of communities followed by radiation of species (Arndt et al., 2020; Schiwitza et al., 2018, 2021). Future analyses of protist communities from other islands and seamounts of the Azores, as well as of other Macaronesian islands could be used to reinforce the observed patterns. Additionally, further studies on pelagic communities in different depths between the islands/seamounts are needed to analyse the overlap between benthic and pelagic communities and find genotypes which are strictly benthic to further elucidate the observed distribution patterns.

The deep-sea floor surrounding islands and seamounts is a complex environment with large geological features (Watling et al., 2013) and diverse microhabitats (Grassle and Maciolek, 1992; Grassle and Morse-Porteous, 1987; Jumars, 1976), which are largely uncharted. Within the present study, the structure and dispersal of protist communities in bathyal, abyssal and hadal depths were analysed (Chapter 3, 4). Deep-sea nanofauna communities from three abyssal sights (4000 – 5134 m) in the Caribbean Sea and the North Atlantic Ocean were analysed by amplicon sequencing of the V9 18S rDNA, focusing on horizontal and vertical distribution patterns (Chapter 3). Our data revealed high variations in the structure of protist communities between the three abyssal regions indicating patterns of protist distribution at large spatial scales. Differences in the community composition of sediment samples taken from the same multi-corer deployment (separated by ~ 1 m) point towards a distinct microbial community even at a local horizontal scale. Therefore, future diversity studies of benthic protist communities should be based on several sediment cores per station to overcome the problem of patchiness in the deep sea. At a vertical scale, in different sediment layers, the number of OTUs decreased with sediment depth, correlating with decreasing TOM contents in the sediment. The only exception was one station were clumps of macroalgae (*Sargassum*) were observed at the deep-sea floor. At this station the TOM content did not decrease with sediment depths and the protist communities of the different sediment layers showed a high similarity to each other, indicating that the *Sargassum* algae could have enriched the sediment directly with organic matter leading to a higher OTU richness. These results are the bases for further studies on the influence of deposited macroalgae on deep-sea microbial food webs, using in-situ long-term experiments, exposing *Sargassum* algae labelled with stable isotopes on the deep-sea floor. Thereby, the macroalgae carbon could be traced through the microbial food web and the influence on the species richness and abundance could be analysed.

On a global scale, comparing 11 deep-sea regions in the Atlantic and Pacific Ocean, with first data on hadal protist communities, few dominant OTUs (with high read abundances) exhibited a cosmopolitan distribution, while most taxa were rare (low read abundances) and showed high rates of endemism (Chapter 4). This supports the existence of large-scale distribution patterns of protist diversity. About 50% of OTUs were unique to only one station and less than 1% occurred in all examined stations. Large differences were found between communities from bathyal, abyssal and hadal regions. Likely, there are multiple processes linked to the heterogeneous conditions of the deep-sea floor, shaping protist communities. Comparisons with the Tara Ocean dataset, covering the diversity of the sunlit ocean (de Vargas et al., 2015), revealed fundamental differences to the benthic deep-sea dataset presented in this study. Hyperdiverse lineages, containing more than 1000 OTUs, were detected within the diplonemids, kinetoplastids, foraminiferans, dinoflagellates, ciliates, marine alveolates (MALV-groups) and cryptophyceans, together covering more than half of all OTUs, revealing an underestimated complexity of deep-sea microbial food webs. Only 2.4% of the OTUs could be assigned with a 100% similarity to a reference sequence from the database, indicating a high genetic novelty and a specific deep-sea nanofauna. However, it also underlines the need to extent our common reference databases especially with morphologically and molecularly characterised deep-sea isolates. Cultivated protist strains can be used as model organisms, investigating ecological adaptations to environmental conditions (e.g. salinity, hydrostatic pressure), biogeographical distributions and speciation processes.

Within the present study, two protist groups were examined in more detail, the Percolomonadida (Heterolobosea) and the Cafeteriaceae (Stramenopiles). The current phylogeny of percolomonads was extended and further resolved by 14 new strains, with two new families, four new genera and ten newly described species (Chapter 5, 6).

Morphological investigations showed only slight differences between the species, supporting the assumption that the group consists of a cluster of several cryptic species (Tikhonenkov et al., 2019). Genetically, the strains showed a high diversity with pairwise distances of the 18S rRNA gene of up to 23% to the closest already described species. The separation between the Percolomonadidae, with several representatives from meso- and hypersaline athalassic waters, and the marine families Barbeliidae and Lulaidae in the phylogenetic analyses, indicates a separation by ecological traits. To investigate the biogeographical distribution of percolomonads, the V9 marker region on the 18S rDNA of the strains was compared to two global, marine amplicon sequencing datasets, the Tara Ocean dataset (de Vargas et al., 2015), covering the sunlit ocean, and the benthic deep-sea dataset presented in this thesis (Chapter 6). Thereby, the V9-sequences of seven species were absent in the two metabarcoding datasets (*Barbelia atlantica*, *B. pacifica*, *Nonamonas montiensis*, *N. santamariensis*, *Lula levis*, *L. jakobsenorum*, *Percolomonas cosmopolitus*), indicating their restricted distribution. Sequences 100% identical to the V9-region of *P. doradorae*, isolated from a hypersaline (> 50 PSU) lake in the Atacama Desert (Chile), were detected in one station of the Tara Ocean study. This indicates that this species might be also distributed in the marine environment and might not be limited to one habitat type, further supported by its wide salinity tolerance range (23-150 PSU) observed in this study (Chapter 5). Although the V9-region is not always species specific (e.g. for some *Cafeteria* species, see Chapter 7 or Placididea, Rybarski et al. 2021), the V9 sequences of the Percolomonadida showed clear differences with p-distances between 2% and 36%.

Percolomonas adaptabilis showed a global V9-distribution in surface waters, coupled with a broad salinity tolerance range (2-150 PSU), indicating its cosmopolitan distribution, which might not be limited to the marine realm. The occurrence of V9-sequences of three different percolomonad species in the benthic deep-sea dataset indicates that Percolomonadida species might not be restricted to surface waters, but could also occur at the deep-sea floor.

Similar distribution patterns as for the Percolomonadida were found for the genus *Cafeteria* (Chapter 7, 8). While one species, *Cafeteria burkhardae*, seems to have a cosmopolitan distribution in marine surface waters and deep-sea sediments, the distribution of the other species of this genus seems to be more locally restricted (Chapter 7). *Cafeteria* was found to be one of the most common and ecologically significant heterotrophic nanoflagellates in marine plankton (Obiol et al., 2021). Within the present study, investigations on 39 cultivated strains from all over the world have led to a reorganization of the family Cafeteriaceae with nine new species being added to the two already known species *C.*

roenbergensis and *C. mylnikovii*. Cultures being isolated from marine surface waters, brackish waters, the deep sea and meso- to hypersaline inland waters in the Atacama Desert, demonstrate the broad range of environmental conditions that this genus is able to cope with. However, since most protists are able to produce cysts when the conditions deteriorate (Atkins et al., 1998), this does not necessarily mean that the species were active at the sampling sites. Though, cultures can be used to test for ecological adaptations (to e.g. salinity, hydrostatic pressure). Strains of *C. baltica* (from brackish waters) and *C. burkhardae* (from marine conditions) were able to survive salinities of up to 150 PSU in the salinity tolerance experiment and all investigated species were able to tolerate a salinity decrease to very low saline waters (Chapter 8). Pressure experiments with *Cafeteria* strains from surface waters and the deep sea showed that strains of *C. burkhardae* and *C. biegae* were able to survive high hydrostatic pressures of up to 550 bar, which is the prevailing pressure at 5500 m depth (Chapter 9). Besides, representatives of chrysomonads, cercomonads, choanoflagellates and kinetoplastids were able to survive high pressures of over 400 bar, indicating their ability to thrive under deep-sea conditions. Even barophilic behaviour was observed for several species isolated from the deep sea (*C. burkhardae*, *Rhynchomonas nasuta*), indicating their genetic adaptation to high pressures. Future studies could include direct observations of the behaviour and locomotion of nanoflagellates under different hydrostatic pressure conditions to gain more insights on how species are affected by abiotic pressure stress. In similar studies on deep-sea ciliates, the behaviour of all investigated ciliate species was significantly influenced by exposure to high pressures (Živaljić et al., 2020a, 2020b). Moreover, it would be interesting to investigate the genes involved in the adaptation to deep-sea conditions by comparative transcriptome analyses of surface water and deep-sea strains, being exposed to atmospheric and high hydrostatic pressures.

Within this study, the integrative use of amplicon sequencing with cultivation-based approaches, live-counting and direct microscopical observations gave a broad overview on the composition, diversity and distribution of marine protist communities with new insights into ecological and evolutionary processes. Detailed analyses of cultivated protist strains of single taxonomic groups enabled for a deeper understanding of their ecological adaptations and biogeographical distribution. The present thesis underlines the heterogeneity of protist communities at the ocean floor with spatial distribution patterns at local, regional and global scales and gives a new view on the genetic diversity and complexity of deep-sea protist communities.

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Subpublications and Records of Achievement

Part 1

Chapter 1: **Hohlfeld, M.**, Arndt, H. (2022) Changes in the Abundance and Taxonomic Composition of Benthic Heterotrophic Protists from the Atlantic Sublittoral to Deep-Sea Sediments. *Diversity, 14, 164. doi: 10.3390/d14030164*

The study was designed and results were achieved by the author of the present thesis together with Prof. Dr. Hartmut Arndt. The author performed the bioinformatic analyses and wrote the manuscript.

Chapter 2: **Dünn, M.**, Arndt, H. (2023) Distribution Patterns of Benthic Protist Communities Depending on Depth Revealed by Environmental Sequencing—From the Sublittoral to the Deep Sea. *Microorganisms, 11, 1664. doi: 10.3390/microorganisms11071664*

The study was designed by the author and Prof. Dr. Hartmut Arndt. The author was involved in sampling, performed the laboratory work, bioinformatic analyses and wrote the manuscript.

Chapter 3: **Hohlfeld, M.**, Schoenle, A., Arndt, H. (2021) Horizontal and Vertical Small-Scale Patterns of Protist Communities at the Atlantic Deep-Sea Floor. *Deep-Sea Research Part I, 171, 103515. doi: 10.1016/j.dsr.2021.103515*

The study was planned by the author of the present thesis together with Prof. Dr. Hartmut Arndt. Bioinformatic analyses of metabarcoding data were performed by the author under guidance of Dr. Alexandra Schoenle. The author wrote the manuscript. Sequencing data were obtained during author's master thesis.

Chapter 4: Schoenle, A., **Hohlfeld, M.**, Hermanns, K., Mahé, F., de Vargas, C., Nitsche, F., Arndt, H. (2021) High and Specific Diversity of Protists in the Deep-Sea Basins Dominated by Diplonemids, Kinetoplastids, Ciliates and Foraminiferans. *Communications Biology, 4, 501. doi: 10.1038/s42003-021-02012-5*

The study was designed by Dr. Alexandra Schoenle and Prof. Dr. Hartmut Arndt. The author performed the laboratory work of the environmental sequencing process and was involved in establishing the in-house reference database.

Part 2

Chapter 5: Carduck, S., Nitsche, F., Rybarski, A., **Hohlfeld, M.**, Arndt, H. (2021) Diversity and Phylogeny of Percolomonads Based on Newly Discovered Species from Hypersaline and Marine Waters. *European Journal of Protistology, 80, 125808. doi: 10.1016/j.ejop.2021.125808*

The study was designed by Dr. Sarah Carduck and Prof. Dr. Hartmut Arndt. The author performed the phylogenetic analyses and helped with the data collection and editing of the manuscript.

Chapter 6: **Hohlfeld, M.**, Meyer, C., Schoenle, A., Nitsche, F., Arndt, H. (2022) Biogeography, Autecology and Phylogeny of Percolomonads Based on newly Described Species. *Journal of Eukaryotic Microbiology, 00, e12930. doi: 10.1111/jeu.12930*

The conception and writing were conducted by the author of the present thesis under guidance of Prof. Dr. Hartmut Arndt. The author was involved in the sampling and isolated and established several cultures. Phylogenetic analyses and salinity experiments were carried out by the author. Electron and light microscopy were performed by the author, Brigitte Gräfe and Claudia Meyer. The biogeographical analysis was carried out by the author and Dr. Alexandra Schoenle.

Chapter 7: Schoenle, A., **Hohlfeld, M.**, Rosse, M., Filz, P., Wylezich, C., Nitsche, F., Arndt, H. (2020) Global Comparison of Bicosoecid *Cafeteria*-like Flagellates from the Deep Ocean and Surface Waters, with Reorganization of the Family Cafeteriaceae. *European Journal of Protistology, 73, 125665. doi: doi.org/10.1016/j.ejop.2019.125665*

The study was planned and written by Dr. Alexandra Schoenle under guidance of Prof. Dr. Hartmut Arndt. The author was involved in the cultivation and molecular work of several cultures.

Chapter 8: Schoenle, S., **Hohlfeld, M.**, Rybarski, A., Sachs, M., Freches, E., Wiechmann, K., Nitsche, F., Arndt, H. (2022) *Cafeteria* in Extreme Environments: Investigations on *C. burkhardae* and Three New Species from the Atacama Desert and the Deep Ocean. *European Journal of Protistology, 85, 125905. doi: 10.1016/j.ejop.2022.125905*

The study was planned and written by Dr. Alexandra Schoenle together with Prof. Dr. Hartmut Arndt. The author was involved in the cultivation, the molecular work and the salinity experiment of several cultures.

Chapter 9: Živaljić, S., Schoenle, A., Nitsche, F., **Hohlfeld, M.**, Piechocki, J., Reif, F., Shumo, M., Weiss, A., Werner, J., Witt, M., Voss, J., Arndt, H. (2018) Survival of Heterotrophic Flagellates Isolated from the Surface and the Deep Sea at high Hydrostatic Pressure: Literature Review and Own Experiments. *Deep-Sea Research Part II, 148, 251-259. doi: 10.1016/j.dsr2.2017.04.022*

The study was conceptualized and written by Dr. Suzana Živaljić together with Prof. Dr. Hartmut Arndt. The author isolated and established several cultures and was involved in the performance of the pressure experiments.

Erklärung gemäß §7 Absatz 8 der Promotionsordnung

„Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation selbstständig und ohne die Benutzung anderer als der angegebenen Hilfsmittel und Literatur angefertigt habe. Alle Stellen, die wörtlich oder sinngemäß aus veröffentlichten und nicht veröffentlichten Werken dem Wortlaut oder dem Sinn nach entnommen wurden, sind als solche kenntlich gemacht. Ich versichere an Eides statt, dass diese Dissertation noch keiner anderen Fakultät oder Universität zur Prüfung vorgelegen hat; dass sie - abgesehen von unten angegebenen Teilpublikationen und eingebundenen Artikeln und Manuskripten - noch nicht veröffentlicht worden ist sowie, dass ich eine Veröffentlichung der Dissertation vor Abschluss der Promotion nicht ohne Genehmigung des Promotionsausschusses vornehmen werde. Die Bestimmungen dieser Ordnung sind mir bekannt. Darüber hinaus erkläre ich hiermit, dass ich die Ordnung zur Sicherung guter wissenschaftlicher Praxis und zum Umgang mit wissenschaftlichem Fehlverhalten der Universität zu Köln gelesen und sie bei der Durchführung der Dissertation zugrundeliegenden Arbeiten und der schriftlich verfassten Dissertation beachtet habe und verpflichte mich hiermit, die dort genannten Vorgaben bei allen wissenschaftlichen Tätigkeiten zu beachten und umzusetzen. Ich versichere, dass die eingereichte elektronische Fassung der eingereichten Druckfassung vollständig entspricht."

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Education

since 03/2019	**PhD in Biology** at University of Cologne, Germany
10/2015 – 07/2018	**M.Sc. in Biological Science** at University of Cologne, Germany
10/2012 – 09/2015	**B.Sc. in Biology** at University of Cologne, Germany
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Employments

since 03/2019	**Research associate** in the working group of Prof. Dr. Hartmut Arndt, University of Cologne, Institute of Zoology, General Ecology
11/2015 – 02/2019	**Research assistant** in the working group of prof. Dr. Hartmut Arndt
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External Internships and Expeditions

05/2020 – 06/2020	**Baltic Sea Expedition** EMB238 on the Elisabeth Mann Borgese
08/2018 – 10/2018	**Azores Expedition** M150 on the RV Meteor
08/2017 – 08/2017	**Atlantic Expedition** M139 on the RV Meteor
03/2017	**Internship** at IOW Leibniz Institute for Baltic Sea Research, Warnemünde, Germany
08/2014 – 09/2014	**Internship** at Taricaya Ecoreserve, Madre de Dios, Peru

Conferences and Workshops

12-15/07/2022	**41st Meeting of the German Society of Protozoology**, Bergisch Gladbach, Germany. Talk: *“Patterns of protist diversity from sublittoral to abyssal sediments in the Atlantic Ocean and consequences for speciation processes”*

23-25/02/2021	**40th Meeting of the German Society of Protozoology**, Online. Talk*:” Vertical distribution patterns of benthic protists in the deep sea -influenced by sedimented macroalgae?”*
03-06/03/2020	**39th Meeting of the German Society of Protozoology**, Kaiserslautern, Germany. Talk: *“Extended phylogeny of* Percolomonas*-like flagellates from marine and hypersaline environments”*
28-29/11/2019	**Workshop on Applied Machine Learning in Taxonomy**, Munich, Germany
28/07-02/08/2019	**VIII ECOP-ISOP Joint Congress**, Rome, Italy. Talk: *“ILLUMINAting the deep sea – patterns of protist diversity in abyssal depths”*
20-22/02/2019	**38th Meeting of the German Society of Protozoology**, Vienna, Austria. Talk: *“Small- and large-scale patterns of protists from the abyssal sea floors in the Caribbean Sea and the southern North Atlantic Ocean”*
27/02-02/03/2018	**37th Meeting of the German Society of Protozoology**, Cologne, Germany
21-24/02/2017	**36th Meeting of the German Society of Protozoology**, Meißen, Germany. Poster: *“Potential contribution of protist communities of surface-floating* Sargassum *algae to deep-sea communities in the southern North Atlantic”*
03-06/03/2015	**34th Meeting of the German Society of Protozoology**, Magdeburg, Germany

Society Memberships

German Society for Protozoology (DGP)
International Society of Protistologists (ISOP)

Awards

12-15/07/2022	**Oral Presentation Award 1st Place** at the 41th Meeting of the German Society for Protozoology (DGP), Bergisch Gladbach, Germany
28/07-02/08/2019	**Holz-Conner Award** at the VIII European Congress of Protistology -ISOP Joint Meeting, Rome, Italy
20-22/02/2019	**Oral Presentation Award 2nd Place** at the 38th Meeting of the German Society for Protozoology (DGP), Vienna, Austria