A 43 kyr record of protist communities and their response to oxygen minimum zone variability in the Northeastern Arabian Sea

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ABSTRACT

An extensive oxygen minimum zone (OMZ) occurs in the northeastern (NE) Arabian Sea where sedimentary records show evidence of alternating strong and weak OMZs that correlate with North Atlantic climate variability during the last glacial–interglacial cycle. OMZs are expanding world-wide, but information on long-term OMZ-ecosystem interactions is mainly limited to fossilized species, notably foraminifera. Here, we provide a first comprehensive ancient sedimentary DNA record of both fossilizing and non-fossilizing protists and their response to OMZ variability in the NE Arabian Sea over the last 43 ka. Protist communities changed significantly during strong vs. weak OMZ conditions coincident with interstadials and stadials respectively. Dinoflagellates were identified as significant indicator taxa for strong OMZs during glacial as well as interglacial interstadials, whereas diatoms were significant indicators for strong OMZs only during glacial interstadials. The chlorophyte *Chlorella* was found to be the main phototrophic protist in nutrient-depleted surface waters during glacial stadials. Notably, strong OMZ conditions shaped past protist communities by creating isolated habitats for those capable of sustaining oxygen depletion either by adapting a parasitic life cycle (e.g. apicomplexans) or by establishing mutualistic connections with others (e.g. radiolarians and mixotrophic dinoflagellates) or by forming cysts (e.g. colpodeans). Notably, a long-term increase in eutrophication and a decrease in the diatom/dinoflagellate ratio was observed during the late Holocene favoring the pelagic component of the marine food web. A similar scenario could be expected in the context of predicted worldwide expansion of coastal OMZs associated with global climate change.

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1. Introduction

1.1. Oxygen minimum zone (OMZ)

Over geological timescales, recurring changes in the ocean oxygenation have resulted in multiple biotic crises with concomitant changes in marine ecosystems and climate balance (Wright et al., 2012). Over the last few decades, decline in oxygen concentrations has been observed throughout much of the world ocean's interior and is predicted to continue in the context of coastal eutrophication and global warming (Helm et al., 2011; Keeling et al., 2010). Upwelling of nutrients promote the formation of plankton blooms. Oxygen consumption through bacterial degradation of this sinking biomass and thermal stratification of the water column contribute to a decreased oxygen availability leading to the formation and expansion of oxygen minimum zones (OMZs) at mid water depths (∼150–1300 m) (Schulz et al., 2002). Selective pressure under OMZ conditions has been observed in unicellular eukaryotes (protists), which are major components of the oceanic food chain and are important contributors to and consumers of pelagic productivity (Burkill et al., 1993; Strom and Welschmeyer, 1991; Worden et al., 2015). Photosyn-

thetic protists are major primary producers inhabiting the photic zone, while bacterivorous and planktivorous heterotrophs bridge the prokaryotic component of the food web to higher trophic levels and follow the distribution of autotrophic protists. Mixotrophs being capable of autotrophy and phagotrophy, have a much wider distribution across the water column (Sherr and Sherr, 1994) and can be directly exposed to oxygen stress at intermediate depth (Jing et al., 2015). Shoaling of the upper boundaries of the OMZs can affect protist habitats and *vice versa*, changes in the distribution of primary producers and consumers can affect the oxygen demand and, hence the distribution of OMZs.

1.2. Modern observations: OMZ vs protists

The northeastern Arabian Sea experiences semi-annual monsoonal wind reversals contributing to two periods of heightened surface productivity: during the southwest (SW) monsoon (June–September) and during the northeast (NE) monsoon (November–February) (Parab et al., 2006). Strong SW monsoonal winds lead to north-eastward drift of nutrient-rich surface waters from Oman to the Pakistan margin causing high primary productivity (Andruleit et al., 2000; Schulte and Muller, 2001; Schulz et al., 2002). While during NE monsoon sea surface cooling activates the convection processes causing deep mixing of subsurface waters. This process leads to injection of nutrients to surface waters bolstering high winter pelagic productivity (Madhupratap et al., 1996). Microscopic cell counts and pigment analysis revealed that during the SW monsoon when nitrate concentrations are high, diatoms become dominant along with prymnesiophytes (Parab et al., 2006). By the end of the SW monsoon, sinking biomass of decaying diatom blooms provides substrate for microbial degradation, which causes rapid oxygen consumption at intermediate depth and intensification of the OMZ (Parab et al., 2006; Schulz et al., 2002). During this period, nitrate concentrations become undetectable and a shift from diatoms and prymnesiophytes to dinoflagellates below the shallow pycnocline is observed (Parab et al., 2006). In the oxygenated surface waters, where nitrate is below detection limits, pico-cyanobacterial populations then become dominant (Parab et al., 2006). During the NE monsoon, low nitrate concentration causes the replacement of a mixed diatom-dinoflagellate population by the nitrogen-fixing cyanobacterium *Trichodesmium*. A combination of low phytoplankton biomass and high ammonium concentrations further suggest that active grazers prevent the establishment of diatom-dinoflagellate blooms in the eastern Arabian Sea during the NE Monsoon. In May, just prior to the start of the SW Monsoon, nutrient enrichment associated with the demise and decay of *Trichodesmium* blooms along with coastal upwelling of nitrates stimulate the growth of both diatoms and dinoflagellates (Parab et al., 2006).

Information on these OMZ-ecosystem interactions in the Arabian Sea and elsewhere is mainly based on such recent observations, modeling experiments, and fossilized foraminifera (Blackford and Burkill, 2002; Madhupratap et al., 1996; Parab et al., 2006; von Rad et al., 1999). A holistic overview of past OMZ-protist interactions is lacking world-wide since the majority of the above-mentioned protist taxa do not fossilize. However, even in the absence of microfossils, genetic signatures of past planktons were found to be preserved in the marine geological records and can be used to reconstruct marine ecosystem changes caused by environmental perturbations (Coolen et al., 2013; Inagaki et al., 2005; Lejzerowicz et al., 2013).

1.3. Coring location in northeastern (NE) Arabian Sea

Records close to the Indus Canyon show that during the last glacial–interglacial cycle the NE Arabian Sea witnessed alternate

strong and weak OMZs (Banakar et al., 2010; von Rad et al., 1995; Schulz et al., 1996), which makes it an ideal location to study long-term protist-OMZ interactions. For this study, we used highly resolved profiling of sedimentary protist 18S ribosomal RNA genes at centennial-scale resolution to reconstruct the interplay between past OMZ variability and protist community structures over the last glacial–interglacial cycle in the NE-Arabian Sea. The core used for this study was obtained from the centre of the OMZ on the continental slope, NW of the Indus Canyon (Orsi et al., 2017). Geochemical analysis revealed a distinct pattern of laminated, organic carbon-rich intervals comparable to those present in previously studied cores, which were obtained in close vicinity and at comparable water depths within the OMZ (von Rad et al., 1995).

Here, integrated analysis of the sedimentary DNA and paleoceanographic proxy data revealed unprecedented details about long-term effects of OMZ conditions on protist communities. Similar approaches could potentially reveal insights about long-term OMZ-ecosystem interactions at important OMZ locations other than the Arabian Sea.

2. Methods

2.1. Sample collection and storage

For this study, a 13-m-long Piston core 11C spanning 43 kyr of deposition was obtained during R/V Pelagia cruise 64PE300 from the center of the OMZ (566 m depth) on the continental slope NW of the Indus Canyon (23°N; 66°E). Subsamples (214 two-cm-thick intervals) for DNA and geochemical analysis were taken aseptically inside the ancient DNA-dedicated clean lab at the Woods Hole Oceanographic Institution (WHOI) as described in detail recently (Orsi et al., 2017). In that study, the same intervals of this core have been used to reveal to what extent the sub-seafloor microbiome was shaped by past OMZ conditions (Orsi et al., 2017).

2.2. Age model

Radiocarbon dates were obtained for the Holocene interval from mixed planktonic foraminifera or monospecific *Orbulina universa* samples (Orsi et al., 2017). Calibration was performed using Calib 7.1 with a reservoir age of 565 ± 35 radiocarbon years (Stuiver and Reimer, 1993). For pre-Holocene sediments, the age model is based on correlative tie points from XRF-derived Br record in core 64PE300-11C to the high-resolution total organic carbon records of nearby core SO90-136KL (Schulz et al., 1998). Linear interpolation was used to determine ages for each individual sample.

2.3. Bulk geochemistry

The intact archived core sections were scanned for bulk elemental composition using an ITRAX^{TM} micro-XRF scanner with a molybdenum x-ray tube with a step-size of 200 μm for an exposure time of 10 s^{-1}. Bromine variability was used as proxy for organic matter (Ziegler et al., 2008). Total organic carbon (TOC), $\delta^{13}C$, $\delta^{15}N$, and C/N were analyzed using a Delta Plus stable light isotope mass spectrometer from 214 freeze-dried and carbonate-free sediment samples spanning the entire core as described in detail elsewhere (Orsi et al., 2017).

2.4. Sedimentary DNA extraction and analysis

Inside the ancient DNA-dedicated lab at WHOI, genomic DNA was extracted and purified from 5–10 g of wet weight sediment after Direito et al. (2012) with modifications described for this core in detail recently (Orsi et al., 2017). This protocol was repeated without the addition of sediment and the resulting extract was used as a control for contamination during extraction