



Research paper

Modern planktic foraminifers in the high-latitude ocean



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ABSTRACT

Planktic foraminifers can be sensitive indicators of the changing environment including both the Arctic Ocean and Southern Ocean. Due to variability in their ecology, biology, test characteristics, and fossil preservation in marine sediments, they serve as valuable archives in paleoceanography and climate geochemistry over the geologic time scale. Foraminifers are sensitive to, and can therefore provide proxy data on ambient water temperature, salinity, carbonate chemistry, and trophic conditions through shifts in assemblage (species) composition and the shell chemistry of individual specimens. Production and dissolution of the calcareous shell, as well as growth and remineralization of the cytoplasm, affect the carbonate counter pump and to a lesser extent the soft-tissue pump, at varying regional and temporal scales. Diversity of planktic foraminifers in polar waters is low in comparison to lower latitudes and is limited to three native species: *Neogloboquadrina pachyderma*, *Turborotalita quinqueloba*, and *Globigerina bulloides*, of which *N. pachyderma* is best adapted to polar conditions in the surface ocean. *Neogloboquadrina pachyderma* hibernates in brine channels in the lower layers of the Antarctic sea ice, a strategy that is presently undescribed in the Arctic. In open Antarctic and Arctic surface waters *T. quinqueloba* and *G. bulloides* increase in abundance at lower polar to subpolar latitudes and *Globigerinita uvula*, *Turborotalita humilis*, *Globigerinita glutinata*, *Globorotalia inflata*, and *Globorotalia crassaformis* complement the assemblages. Over the past two to three decades there has been a marked increase in the abundance of *Orcadia riedeli* and *G. uvula* in the subpolar and polar Indian Ocean, as well as in the northern North Atlantic. This paper presents a review of the knowledge of polar and subpolar planktic foraminifers. Particular emphasis is placed on the response of foraminifers to modern warming and ocean acidification at high latitudes and the implications for data interpretation in paleoceanography and paleoclimate research.

1. Introduction

1.1. Modern environment and climate change

The marine environment and climate of the Arctic and Antarctic have changed considerably over the course of the Cenozoic, including long-term cooling and more rapid turnovers caused by plate tectonics and large-scale circulation patterns (e.g., Lawver et al., 1992; Zachos et al., 2001; Brinkhuis et al., 2006; Moran et al., 2006; Sluijs et al.,

2006). Temperatures in polar regions have been relatively high for a prolonged period since the beginning of the Holocene and are still rising, causing shifts in ecosystem limits (Loarie et al., 2009; IPCC, 2013). Higher than modern sea surface temperatures (SSTs) during the last interglacial maximum (MIS 5.5), about 125 thousand years (125 ka) ago, were accompanied by reduced ice volume and corresponding sea level rise (e.g., Kopp et al., 2009; Rohling et al., 2014). Freshening of polar surface waters has been observed along with past and modern climate warming and sea ice retreat (e.g., Haas et al., 2008;

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Spielhagen and Bauch, 2015; Haumann et al., 2016). Climate model projections indicate an asymmetric warming between the Arctic and Southern Ocean, with an early response in the Arctic and a delayed response in the Southern Ocean: Northern polar regions are projected by modeling studies to be subjected to warming mostly through persistent Atlantic Meridional Overturning, also referred to as polar amplification (e.g., Manabe and Stouffer, 1980; Manabe et al., 1991; Meehl et al., 2007). The polar amplification in the northern hemisphere is much larger than in the southern hemisphere (Masson-Delmotte et al., 2006) since deep mixing and cooling by the Antarctic ice sheet causes the polar Southern Ocean to take up heat without equivalent surface warming. Nevertheless, poleward shift of the Antarctic Circumpolar Current (ACC) and resulting changes in temperature and salinity of the respective water bodies occurred during the 1990s and 2000s (e.g., Böning et al., 2008; Sokolov and Rintoul, 2009; Meijers et al., 2012, Haumann et al., 2016).

Polar regions are heavily affected by climate change (e.g., Greene et al., 2008; Turner and Overland, 2009). Continental and marine polar ecosystems are characterized by reduced diversity in comparison to lower latitude ecosystems, rendering them particularly susceptible to environmental perturbation and changes in species distribution (e.g., Hansen et al., 2013; Venables et al., 2013; Watanabe et al., 2014). Depending on the tolerance range of each species to a given environmental pressure their distribution limits can change at varying pace (Loarie et al., 2009). Modern changes in climate and ocean chemistry over the past 200 years of industrialization may resemble past changes in species composition over glacial-to-interglacial time-intervals of climate warming in the southern Indian Ocean, and at a pace that compromises acclimatization of the marine plankton (cf. Field et al., 2006; Lohbeck et al., 2012; Meilland, 2015). In addition to changes affecting native species, the migration of subarctic species into the Arctic Ocean is assumed to occur through reduction in sea ice, increased eddy activity in the ice-free Arctic Ocean and enhanced organic matter production and flux (Serreze et al., 2007; Watanabe et al., 2014). Shifts in biogeochemical regimes can affect the production of coccolithophores and planktic foraminifers and ultimately perturb the marine carbonate budget and CO₂ turnover (Salter et al., 2014). Understanding of modern and past processes critically depends on regional assessments of species dynamics at sub-annual timescales.

1.2. Planktic foraminifers at high latitudes

Approximately 50 planktic foraminifer morphospecies populate the modern ocean, but of these only *Neogloboquadrina pachyderma*, *Turborotalita quinqueloba*, and *Globigerina bulloides* are frequent in the polar oceans (e.g., Bé, 1960a; Kennett, 1968; Vilks, 1970; Tolderlund and Bé, 1971; Hemleben et al., 1989; Eynaud, 2011). Consequently, modern planktic foraminifer diversity in the polar oceans is low in comparison to lower latitudes, and high standing stocks are dominated by a few species (Stehman, 1972; Carstens et al., 1997; Žarić et al., 2005). Molecular genetics has revealed that the dominant polar morphospecies *N. pachyderma* possibly includes seven different genotypes (Darling et al., 2006), out of which Types I and IV represent Arctic and Antarctic species, respectively. The other five genotypes dwell at sub-polar latitudes and in upwelled waters (Darling and Wade, 2008). In addition, the right coiling (dextral) sibling *Neogloboquadrina incompta*, which had long been assumed to be a right coiling morphotype of *N. pachyderma*, has now been shown to be an entirely different species abundant at subpolar to temperate latitudes (Darling et al., 2006). Likewise, other morphospecies include different genotypes with specific ecological demands and regional distribution patterns. These findings have much improved the understanding and applicability of polar planktic foraminifers as proxies of paleoclimate and paleoceanographic significance (Darling and Wade, 2008). In addition, technological advances of mass spectrometers and elemental analyzers facilitate analyses of a wide range of element ratios including trace elements and

isotopes of entire planktic foraminifer tests and single chambers, used to reconstruct past environments including water temperature, salinity, and trophic condition (e.g., Nürnberg, 1995; Bauch et al., 1997; Volkman and Mensch, 2001; Mortyn and Charles, 2003; Meland et al., 2006; Pados et al., 2015; Hagemann, 2017). Apart from being recorders of hydrology and climate change, planktic foraminifers affect marine carbonate and atmospheric CO₂ budgets through calcification of their tests and their differential impacts on the biological carbon pump and carbonate counter pump (e.g., Salter et al., 2014; Schiebel and Hemleben, 2017).

1.3. Effect of changing modern and past ecosystems and climates on planktic foraminifer test calcite production and CO₂ turnover

Over the past decades, pH of surface seawater has decreased from pH 8.2 to pH 8.1, i.e., 30% more acidic, and will further acidify in the near future (e.g., Caldeira and Wickett, 2003). Surface ocean acidification (OA) has been highest in the subpolar North Atlantic and Southern Oceans with a decrease of up to 0.11 and 0.10 pH units, respectively, whereas OA has been lowest in the subtropical South Pacific with a decrease of about 0.04 pH units (Key et al., 2004; Boyer et al., 2013). Calcareous plankton counteract the atmospheric CO₂ increase by reducing their calcification rates and hence CO₂ production (i.e., the carbonate counter pump) resulting in a reduction of shell calcite mass in planktic foraminifers at low (De Moel et al., 2009 Arabian Sea) and high latitudes (Moy et al., 2009, Southern Ocean). However, reduced calcification and calcite mass of the individual calcareous skeletons are limited to a threshold beyond which certain species might become extinct (Hsieh et al., 2005; Orr et al., 2005; Lohbeck et al., 2012). The efficiency of the planktic foraminifer carbonate counter pump may hence depend on the degree to which different species react to the changing environment and seawater pH. Disconcertingly, species' reactions to ecosystem change are nonlinear over the time interval of increasing concentration of greenhouse gases in the atmosphere and surface ocean since the late 20th century (e.g., Hsieh et al., 2005; Field et al., 2006). This review briefly presents the ecology of polar and subpolar planktic foraminifers at the species level, and discusses the current knowledge and recent findings on their biogeochemistry, and implications for paleoceanography and climate change.

2. Polar and subpolar planktic foraminifer species

Modern polar and subpolar morphospecies include *N. pachyderma*, *T. quinqueloba*, *G. bulloides*, *Orcadia riedeli*, *Globigerinita uvula*, *Globigerinita glutinata*, *N. incompta*, *Turborotalita humilis*, *Globorotalia crassaformis*, and *Globorotalia inflata*, sorted from the highest to lowest polar affinity (Fig. 1). *Orcadia riedeli*, *G. uvula*, and *N. incompta* are increasingly documented from higher latitudes over the past few years (Meilland, 2015; Meilland et al., 2016). *Turborotalita humilis*, *G. crassaformis* and *G. inflata* are present to the south of the Subantarctic Front during summer (Salter et al., 2014). Morphospecies are briefly discussed for their genotypes. The patchy distribution of the subpolar to subtropical species *Beella megastoma* is not discussed in the following due to its rare occurrence in the modern ocean. Paleoceanographic implications of the presence of *B. megastoma* in the North Atlantic are discussed by Bauch (1994), see also Schiebel and Hemleben, 2017).

Fig. 1 is a 1.5-column fitting image.

2.1. *Neogloboquadrina pachyderma*

Neogloboquadrina pachyderma has a bipolar distribution with the two Genotypes I and IV dominating polar assemblages in the northern and southern hemispheres, respectively (e.g., Bé, 1977; Darling et al., 2000; Darling et al., 2004; Darling and Wade, 2008; André et al., 2014). The Antarctic *N. pachyderma* Genotype IV hibernates in brine channels within sea ice surviving salinities up to 82 PSU, and almost exclusively

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