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# Modern planktic foraminifers in the high-latitude ocean

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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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> increase by reducing their calcification rates and hence CO<sub>2</sub> 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

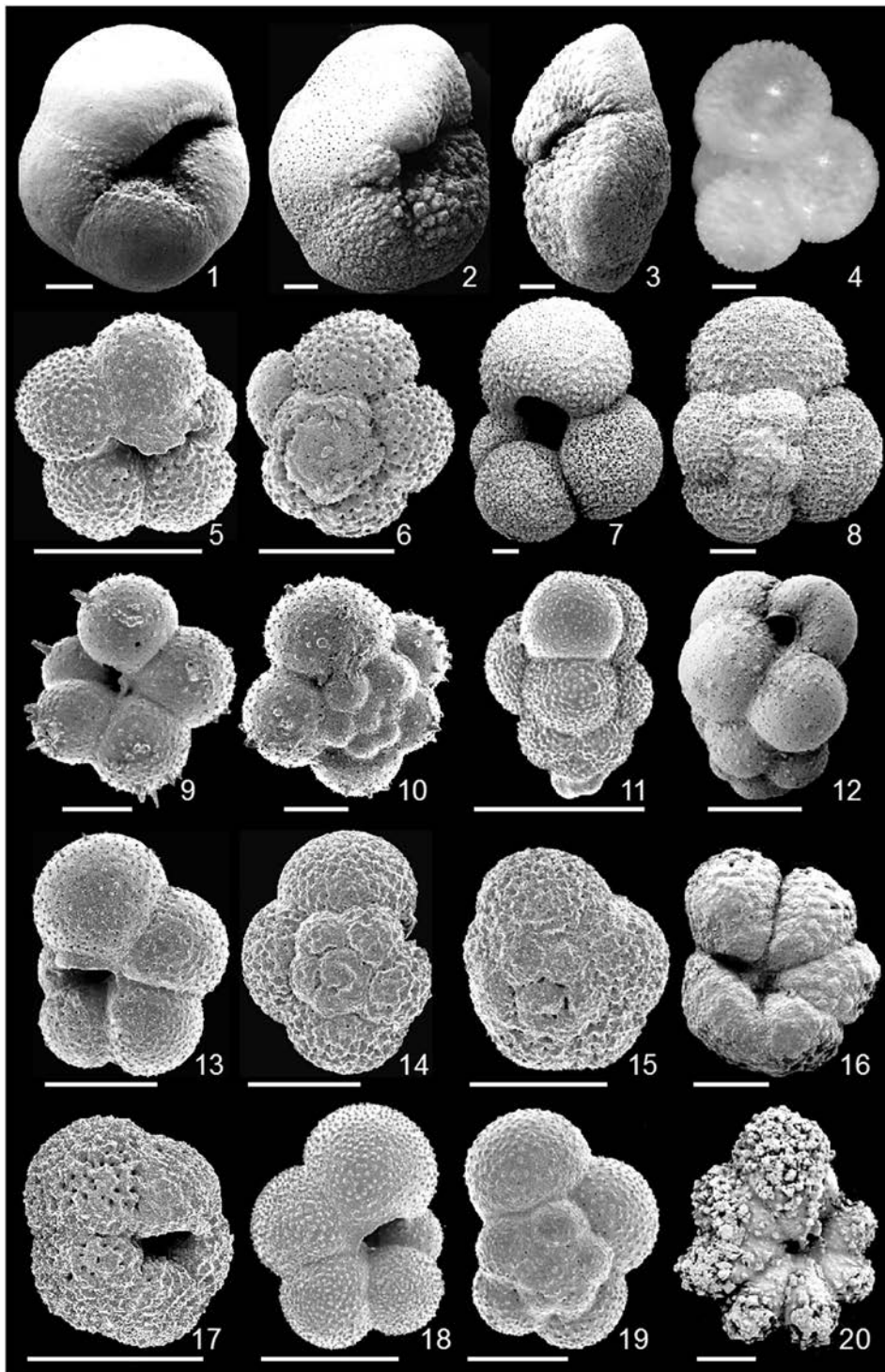


Fig. 1. Modern polar and subpolar planktic foraminifer species. 1 *G. inflata* with calcite veneer, 2–3 *G. crassaformis*, 4 *G. glutinata*, 5–6 *T. quinqueloba*, 7–8 *G. bulloides*, 9–10 *O. riedeli* with remnants of broken spines, 11–12 *G. uvula*, 13–14 *N. incompta*, 15–16 and 20 *T. humilis*, 17–18 *N. pachyderma* with thick calcite crust (17). 1,2,3,7,12,15 from sediment trap off Crozet. 5,6,8,9,10,11,13,14,17,18,19 from plankton net hauls in the southern Indian Ocean. 4,15,16,20 from plankton net hauls in the North Atlantic. 9,10 courtesy Springer Verlag. 4 is an incident light micrograph, all others are scanning electron micrographs. Bars 50  $\mu\text{m}$ .

feeds on diatoms (Spindler and Dieckmann, 1986; Dieckmann et al., 1991; Spindler, 1996). Predominantly large individuals occur at very high standing stocks within the lower layers of the sea ice, and there is no evidence of *N. pachyderma* reproducing when overwintering within sea ice. A maximum of 1075 individuals of *N. pachyderma* was enumerated from one liter of Antarctic new ice (Dieckmann et al., 1991). Average standing stocks of *N. pachyderma* in the sea ice range from 190 to 320  $\text{ind l}^{-1}$  (Spindler and Dieckmann, 1986; Dieckmann et al., 1991), which is up to 1000 times higher than total planktic foraminifer (all species) standing stocks in the adjacent water column (see also Bergami et al., 2009). In the lower 10 cm of ice in the Weddell Sea total

planktic foraminifer standing stocks of 461  $\text{ind l}^{-1}$  have been observed in August to October 2013 (Monti-Birkenmeier et al., 2017). These are exceptionally high standing stocks. Typically, standing stocks in the open surface ocean range up to several hundred individuals per cubic meter (Schiebel and Hemleben, 2017).

The overwintering strategy observed in the Antarctic *N. pachyderma* Genotype I has not yet been observed in Arctic sea ice, which may be caused by differences in sea ice formation (Spindler, 1991). However, the dynamics of sea ice formation in the Arctic Ocean have been changing over the past decades along with anthropogenic  $\text{CO}_2$  emissions and transient climate warming (Notz and Stroeve, 2016). If



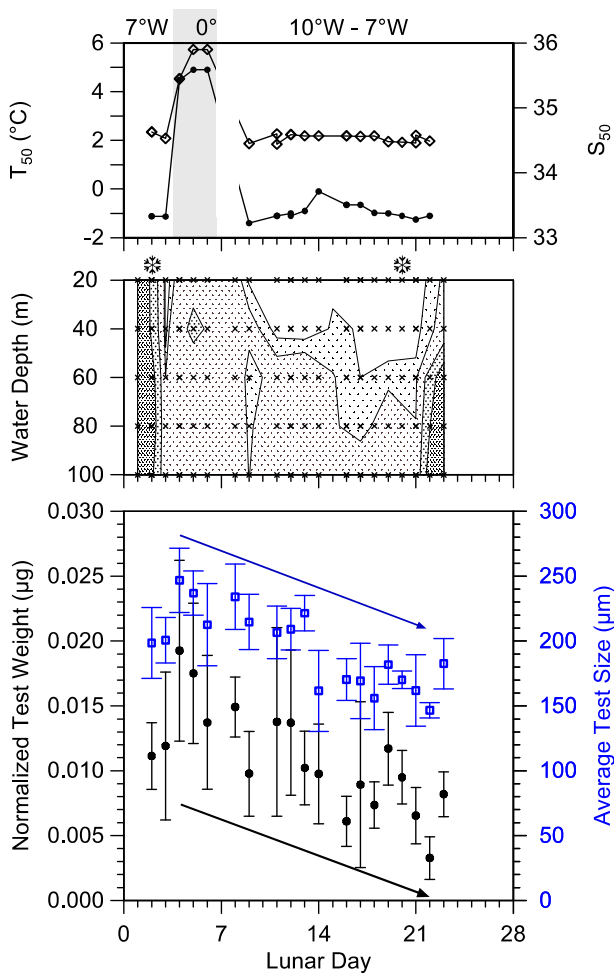


Fig. 2. Population dynamics of *N. pachyderma* in the northern North Atlantic. *Lower Panel*: Development of mean size (minimum diameter) and normalized weight ( $\mu\text{g}$  per  $1\ \mu\text{m}$  minimum test diameter) of individual tests of *N. pachyderma* over one synodic lunar cycle (synodic lunar day, LD zero to LD28) at the 40–60 m water depth interval in the Norwegian-Greenland Sea, sampled in 1989 (RV Meteor cruise 10/3) and 1993 (RV Meteor 26/3, LD14 only) at about  $72^\circ\text{N}$ . From LD4 after the full moon (LD zero), test size and weight decrease until LD22 (arrows). Before LD4, maximum standing stocks (shading corresponds to  $> 50$ ,  $> 100$ ,  $> 500$ , and  $> 1000$  individuals  $\text{m}^{-3}$  of sampled seawater) in the upper 100 m of the water column (*middle panel*) were composed of rather small tests close to the ice edge (ice crystal symbol). During the synodic lunar cycle until LD21 (one week after the new moon), adult *N. pachyderma* gradually descended to waters below 60 m depth. From LD22, increasing numbers of growing individuals indicate a new generation of *N. pachyderma* (cf. Volkmann, 2000b). Water depths give the lower levels of the analyzed 20-m depth intervals. *Upper panel*: Temperature and salinity at 50 m water depth ( $T_{50}$  and  $S_{50}$ , dots and diamonds, respectively) were rather stable and low in the main sampling area around  $72^\circ\text{N}$  and  $10^\circ\text{W}$  -  $7^\circ\text{W}$ . Warmer and saltier conditions to the east (around zero meridian, shaded in gray) indicate southern sourced waters transported north by the Norwegian Atlantic Current. After Garnier (2015).

modern Arctic *N. pachyderma* Type I begins to display an overwintering behavior similar to the Antarctic Type IV, it would indicate that this survival strategy developed before the Arctic and Antarctic genotypes evolved into different species.

High standing stocks of *N. pachyderma* during the short polar summer in Arctic waters occur close to the ice edge (Fig. 2).

When the salinity of Arctic surface waters off the ice edge is low due to melt-water effects, *N. pachyderma* quantitatively descends to subsurface waters below the surface freshwater lense, and may serve as a proxy for the state of ambient seawater (e.g., temperature, salinity, and trophic condition) indicated by changes in the chemical composition (stable isotopes and cations) of the shell calcite (Carstens and Wefer, 1992; Carstens et al., 1997; Volkmann, 2000a; Spielhagen et al., 2011).

Planktic foraminifer production in the water column beneath the sea ice is typically lower than in ice free areas (Pados and Spielhagen, 2014; Watanabe et al., 2014), although considerable under-ice productivity and export of algae can occur at the regional scale (Boetius et al., 2013).

*Neogloboquadrina pachyderma* is characterized by opportunistic reproduction and alimentation strategies (i.e., diatoms; Anderson et al., 1979). It is considered one of the most competitive species among the planktic foraminifers and best adapted to environmental conditions, in particular short productive windows, in the polar summer (cf. Jonkers et al., 2010). Similar strategies also render *N. pachyderma* competitive in upwelling areas. *Neogloboquadrina pachyderma* from upwelling regions and marginal seas are represented by five to six genotypes, which are different from the polar ones (Bauch et al., 2003; Darling et al., 2006; Darling and Wade, 2008; André et al., 2014). In the open northern North Atlantic, a monthly reproductive cycle of *N. pachyderma* is highlighted by cyclic abundance of test-size cohorts (Fig. 2) assumed to be triggered by the synodic lunar cycle (Volkmann, 2000b).

An increasingly thick calcite crust covers the ontogenetic shell of *N. pachyderma* from shallow toward deeper waters, which enhances the preservation potential of the tests during sedimentation whilst simultaneously affecting the average chemical composition of tests (Bauch et al., 1997; Simstich et al., 2003; Kozdon et al., 2009). Calcite crusts possibly form when mature individuals descend to the deeper water column during ontogeny over a synodic lunar cycle, while smaller and lighter individuals remain in surface waters (Fig. 2). Crust formation and test calcite mass do not appear to be significantly affected by temperature and salinity of ambient seawater, but rather by ontogenetic stage and test size (Fig. 2).

Fig. 2 is a single-column fitting image.

The stable isotope ( $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ) signals and cation (Metal-to-Ca) ratios of tests of *N. pachyderma* produced beneath the sea ice differ from those produced in ice free waters, probably caused by limited air-sea exchange and a shallow habitat under the sea ice (Hendry et al., 2009; Pados and Spielhagen, 2014; Xiao et al., 2014). When descending in the water column and adding a calcite crust to the distal shell,  $\delta^{18}\text{O}$  signatures of tests get heavier (i.e., more positive), and tests from surface sediments usually have higher  $\delta^{18}\text{O}$  values than tests from the surface water column (Stangeew, 2001; Simstich et al., 2003; Kozdon et al., 2009). The same is true for *T. quinqueloba* (Stangeew, 2001; Simstich et al., 2003). Consequently,  $\delta^{18}\text{O}$  data of whole tests are not a good representation of the entire ontogenetic development of individuals, and are possibly biased toward the final ontogenetic stage and formation of a calcite crust (cf. Fig. 1-16 and -17). Therefore, high-resolution data of the different early and late ontogenetic stages of tests would be needed to correctly decipher changes in the polar environment from chemical data (stable isotopes and cation ratios) of any planktic foraminifer test (Kozdon et al., 2009).

## 2.2. *Turborotalita quinqueloba*

*Turborotalita quinqueloba* is probably one of the most frequent modern planktic foraminifer species in the modern global ocean. The polar to subpolar Atlantic and North Pacific host the cryptic *T. quinqueloba* Genotype II, as well as various subtypes (Darling et al., 2000; Darling and Wade, 2008; André et al., 2014). In the Arctic Ocean, high standing stocks of *T. quinqueloba* of hundreds of individuals ( $> 63\ \mu\text{m}$ ) per cubic meter of seawater near the sea ice margin (Carstens et al., 1997) are supported by enhanced primary production and food availability (Volkmann, 2000a). The vertical distribution of *T. quinqueloba* follows the distribution of water bodies. In the warm Atlantic-sourced waters of the West Spitsbergen Current and in the Barents Sea, *T. quinqueloba* comprises up to 85% of the total planktic foraminifer assemblage in surface waters (Volkmann, 2000a, 2000b). Depending on salinity and the availability of prey, highest standing stocks occur at 100–150 m water depth close to the sea-ice margin, and in subsurface waters at 50–100 m depth in open waters distant from the ice margin

(Carstens et al., 1997; Volkman, 2000b). Maximum-standing stocks under the sea-ice may occur as deep as 150–200 m (Carstens et al., 1997). In contrast, *T. quinqueloba* may occur at an abundance of only 2–10% of the planktic foraminifer assemblage dominated by *N. pachyderma* in polar-sourced waters of western Fram Strait and outer Laptev Sea (Volkman, 2000b). *Turborotalita quinqueloba* and *N. pachyderma* dominate the typically small-sized cold-water assemblages in high latitudes (Carstens et al., 1997; Volkman, 2000b; Eynaud, 2011). The abundance of *T. quinqueloba* generally decreases from high to low latitudes (e.g., Parker, 1962; Vincent and Berger, 1981). Cyclic abundance of *T. quinqueloba* indicates a synodic lunar reproduction cycle (Volkman, 2000b).

### 2.3. *Globigerina bulloides*

*Globigerina bulloides* is characteristic of both upwelling environments in lower latitudes and seasonally enhanced primary production at mid and high latitudes (e.g., Bé and Tolderlund, 1971; Thiede, 1975; Naidu and Malmgren, 1996; Schiebel et al., 2001). Out of various genotypes of *G. bulloides* (e.g., Darling and Wade, 2008; Sears et al., 2012; Morard et al., 2013; André et al., 2014), the two Subtypes IIa and IIb have a bipolar distribution. Thus, gene flow between northern and southern high latitudes must have existed (Darling et al., 2000), similar to *T. quinqueloba* and *N. pachyderma*. Different genotypes of *G. bulloides* may indicate both enhanced production of algal prey at temperate to high latitudes during spring and upwelling conditions at low to mid latitudes.

*Globigerina bulloides* is an opportunistic species, which often dominates planktic foraminifer live assemblages, test flux, and ocean floor sediment assemblage at mesotrophic and eutrophic conditions (e.g., Sautter and Thunell, 1989). It is an important archive of biogeochemical information in paleoceanography (e.g., Fischer and Wefer, 1999; Hillaire-Marcel and de Vernal, 2007). *Globigerina bulloides* bears no symbionts and typically dwells above the thermocline within the upper 60 m of the water column of sub-polar to temperate water bodies. The distribution of *G. bulloides* in surface waters may be modified by hydrologic conditions and the availability of prey. In addition to its general ecologic demand, other biological prerequisites, i.e., reproduction strategy (synodic lunar), may influence the depth distribution of *G. bulloides* (Schiebel et al., 1997).

### 2.4. *Orcadia riedeli*

*Orcadia riedeli* is a rare cosmopolitan species of the polar to tropical oceans, attributed to surface waters of enhanced productivity and availability of prey (Brummer et al., 1988; Meilland, 2015; Meilland et al., 2017). *Orcadia riedeli* has been previously reported from the sea surface of the temperate eastern North Atlantic Ocean and the Atlantic sector of the Southern Ocean (Holmes, 1984). Although not recorded from early sampling campaigns in the Indian sector of the Southern Ocean (Bé and Tolderlund, 1971; Bé and Hutson, 1977), more recent studies in a similar region just north of the Subtropical Front report that *O. riedeli* may account for up to 7% of the total planktic foraminifer standing stock in surface waters (Meilland, 2015; Meilland et al., 2017), potentially indicating an expansion of its geographical range.

### 2.5. *Globigerinita uvula*

Although abundant in the polar to temperate oceans *Globigerinita uvula* decreases in numbers toward lower latitudes (Schiebel and Hemleben, 2000; Bergami et al., 2009). *Globigerinita uvula* includes two genotypes, the subpolar Genotype II and the subtropical Genotype I (André et al., 2014). In general, *G. uvula* displays an opportunistic behavior to seasonally enhanced phytoplankton production in spring. *Globigerinita uvula* represents up to 0.5–1.2% of the total live planktic foraminifer species assemblage in marginal Arctic Seas (Volkman,

2000a) compared to 5% (> 100 µm) during spring and early summer in the temperate NE Atlantic (Schiebel et al., 1995). However, as a rather small-sized species, *G. uvula* may occur more frequently in the test-size assemblage < 100 µm than > 100 µm. The distribution of *G. uvula* in the South Atlantic and southern Indian Oceans is similar to northern hemisphere waters (cf. Kemle-von-Mücke and Hemleben, 1999; Schiebel and Hemleben, 2000). More recently, in the austral summer 2012, *Globigerinita uvula* was reported as one of the dominant planktic foraminifer species in the Indian sector of the Southern Ocean, occurring between the Subantarctic Front (SAF) and the Polar Front (PF) and south of the PF (Meilland et al., 2016; Meilland et al., 2017). In marginal basins such as the southern Bay of Biscay, *G. uvula* is most abundant in surface waters in spring (Retailleau et al., 2011).

### 2.6. *Globigerinita glutinata*

*Globigerinita glutinata* is one of the most frequent species in the modern global ocean. In general, *G. glutinata* decreases in abundance from lower to higher latitudes (Schiebel and Hemleben, 2017). When transported to subpolar and polar regions with surface currents, *G. glutinata* may occur in the Fram Strait (75°N) during summer (Stangeew, 2001, West Spitsbergen Current), and may form considerable proportions of the sediment assemblages (Fig. 4, included with *Globigerinita* spp.). At lower latitudes, production of *G. glutinata* is related to nutrient entrainment and food (e.g., diatoms) production at depths of the seasonal thermocline (e.g., Schiebel et al., 2001). This may also be the case in surface waters of the Labrador Sea south of Greenland (up to 59°N), where *G. glutinata* formed about half of the planktic foraminifer assemblage in summer, around shallow (< 50 m) thermocline depths (Stangeew, 2001).

### 2.7. *Globorotalia inflata*

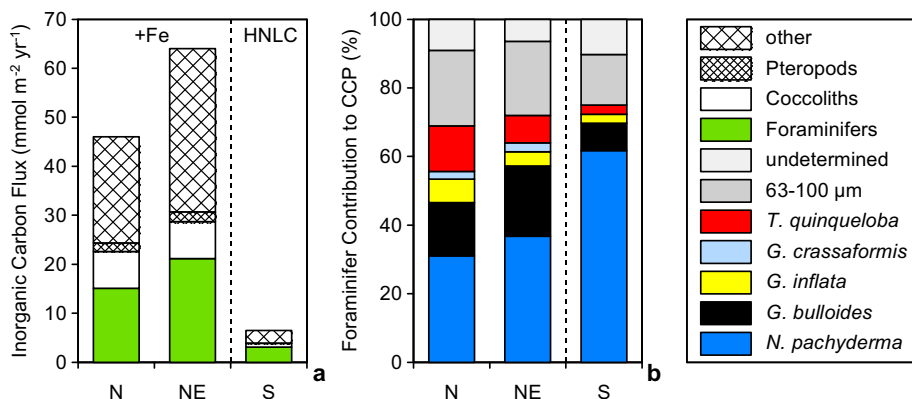
*Globorotalia inflata* is most frequently observed in subpolar to subtropical waters and is often associated with hydrologic fronts and eddies. Genotypes I and II of *G. inflata* produce two different morphotypes that occur with an allopatric distribution equatorward and poleward of the Subpolar Front, respectively (Morard et al., 2011). *Globorotalia inflata* Genotype I occurs at mid latitudes and has an opportunistic behavior to regionally enhanced trophic conditions in the surface and subsurface water column (cf. Lončarić et al., 2007; Storz et al., 2009), which may also be the case in Genotype II from higher latitudes. Due to enhanced regional standing stocks and a high fossilization potential, *G. inflata* is frequently employed as an archive in paleoceanography (e.g., Dittert et al., 1999; Niebler et al., 1999; Lončarić et al., 2006). During enhanced phytoplankton production in spring the cytoplasm of *G. inflata* often has a greenish or orange stain caused by the consumption of chrysophytes and diatoms, respectively (Hemleben et al., 1989). In addition to its distribution in pelagic waters, *G. inflata* may dominate the planktic foraminifer fauna in surface to subsurface strata in hemipelagic to neritic waters characterized by regionally enhanced food availability (Retailleau et al., 2012). *Globorotalia inflata* follows a monthly reproduction cycle.

### 2.8. *Turborotalita humilis*

*Turborotalita humilis* dwells in the tropical and subpolar surface ocean (e.g., Holmes, 1984). It is frequent at the northern limit of the North Atlantic subtropical gyre, associated to the Azores-Front Current-System (Schiebel et al., 2002). Similar blooms of *T. humilis* occurred in surface waters off the Canary Islands in spring 1997 and in spring 2006 in the western Mediterranean Sea (cf. Schiebel and Hemleben, 2017).

### 2.9. *Globorotalia crassaformis*

*Globorotalia crassaformis* is a cosmopolitan species that dwells in



**Fig. 3.** (a) Varying annual inorganic carbon ( $\text{CaCO}_3$ ) fluxes in iron fertilized (+ Fe) and low-iron (HNLC) waters according to sediment trap data from north (N), northeast (NE), and south (S) of Crozet Plateau in the southern Indian Ocean (Salter et al., 2014). Planktic foraminifer tests and shell fragments contribute most of the compound specific particles, followed by coccoliths and pteropods. 'Other' inorganic carbon flux may include fragments of larger organisms, and coccolith within fecal pellets. (b) Near Crozet, *N. pachyderma* is a major contributor to the species-specific shell calcite production and carbonate counter pump (CCP). Planktic foraminifer tests of the 63–100  $\mu\text{m}$  size-fraction are not classified. Absolute and relative fluxes of planktic foraminifers, coccolithophores, and pteropods may vary even stronger on a larger regional scale than between the + Fe and HNLC water around Crozet Plateau (Salter et al., 2014, Rembauville et al., 2016a).

subsurface waters around 200–400 m depth in the tropical and subtropical ocean, and ascends to the surface ocean at higher latitudes (cf. Parker, 1962). The subsurface habitat of *G. crassaformis* is associated with enhanced primary production in surface waters and oxygen-depleted waters below the surface mixed layer of the ocean (Kemle-von-Mücke and Hemleben, 1999). In proximity to the Crozet Plateau in the subpolar Indian Ocean, adult individuals of *G. crassaformis* were recorded in sediment traps during summer (Salter et al., 2014). The exclusively adult individuals may have been transported from lower latitudes by reached maturity without reproducing. In addition to an external trigger induced by the synodic lunar cycle, reproduction is probably supported by ecological conditions such as quality and quantity of prey, as well as temperature and salinity of ambient seawater (e.g., Bijma et al., 1992). The distribution of *G. crassaformis* in the high-latitude South Atlantic resembles that of the southern Indian Ocean.

### 3. Planktic foraminifer carbon biogeochemistry in high latitudes

The biological carbon pump consists of two separate but interacting components; the soft-tissue pump (Volk and Hoffert, 1985) and the carbonate counter pump (Heinze et al., 1991). The soft-tissue pump is the downward flux of particulate organic carbon (POC) to the deep-ocean. The fraction of POC that sinks beyond the ventilation depth (depth of maximum winter mixing) drives a reduction in partial pressure of carbon dioxide in the surface ocean that is compensated by oceanic uptake of atmospheric  $\text{CO}_2$  (Sigman and Boyle, 2000). In contrast, the carbonate counter pump can increase the partial pressure of  $\text{CO}_2$  in surface waters through calcite production (see Section 3.2). Although frequently neglected, the effective sequestration of atmospheric  $\text{CO}_2$  into the deep-ocean by the biological carbon pump is mediated by the relative magnitudes of these two opposing processes (Antia et al., 2001; Salter et al., 2014). Foraminifers, like other calcifying plankton, are key to this balance since they produce both particulate organic carbon as biomass and calcite as tests.

#### 3.1. Planktic foraminifer test flux and the soft-tissue pump

The organic carbon pump of soft tissue (i.e., cytoplasm) has so far been assumed virtually non-existent in planktic foraminifers (e.g., Watanabe et al., 2014), since sedimentation of planktic foraminifers occurs primarily as empty tests with little to no cytoplasm remains. Planktic foraminifer shell-bound inorganic carbon ( $\text{CaCO}_3$ ) constitutes, on average, about three times the biomass-bound organic carbon of the same individual (Schiebel and Movellan, 2012). When processes such as production, transportation, remineralization, and dissolution of organic and inorganic carbon are accounted for, the sub-surface flux of organic carbon biomass associated to planktic foraminifer (i.e., the soft-tissue pump) is only about 10% of the biomass in the productive surface

mixed layer of the ocean (Schiebel and Movellan, 2012). Foraminifers potentially influence POC export indirectly through calcite mineral ballasting. Previous studies have shown that bulk calcite fluxes are positively correlated with POC fluxes (Klaas and Archer, 2002), indicating that the associations of calcite minerals with organic aggregates and fecal pellets may provide excess density, which promotes the settling of POC. However, foraminifer and coccolith calcite are likely to interact differently with organic aggregates. Sediment trap studies that have partitioned bulk  $\text{CaCO}_3$  fluxes across different calcite bearing organisms indicate weak associations of foraminifer- $\text{CaCO}_3$  with POC flux in the Southern Ocean (Salter et al., 2014; Rembauville et al., 2016a). This is likely explained by the rapid export of large and heavy foraminifer tests that settle as individual particles. Experimental studies support this by showing that foraminifer tests are not incorporated into organic aggregates like the much smaller coccoliths, and may even in some cases collide with organic particles inducing disaggregation (Schmidt et al., 2014). These studies seem to suggest a small role for foraminifer in sequestering atmospheric  $\text{CO}_2$  into the deep-ocean that can be neglected in comparison with other organisms such as diatoms (Leblanc et al., 2012; Buitenhuis et al., 2013), which have been directly quantified as major flux vectors of the soft-tissue pump in the Southern Ocean (Salter et al., 2012; Rembauville et al., 2015; Rembauville et al., 2016b). Nevertheless, organic carbon of planktic foraminifers is systematically exported from the surface mixed layer to the subsurface ocean (cf. Boltovskoy and Lena, 1970; Schiebel and Movellan, 2012). Therefore, quantitative data on fossil planktic foraminifer assemblages may be employed to complement  $\delta^{13}\text{C}$  data as a proxy of the biological carbon pump of the past oceans (e.g., Broecker, 1971; Hilting et al., 2008).

#### 3.2. Planktic Foraminifers and the carbonate counter pump

The precipitation of  $\text{CaCO}_3$  by foraminifers and other calcite (coccolithophores) and aragonite (pteropods) bearing organisms liberates  $[\text{CO}_2]$  in surface waters according to the equation  $\text{Ca}^{2+} + 2\text{HCO}_3^- \rightarrow \text{CaCO}_3 + \text{CO}_2 + \text{H}_2\text{O}$  (Fig. 3). This is somewhat counter-intuitive since the inorganic carbon concentration decreases as the reaction proceeds. The chemical equilibrium described above also shows that one mole of  $\text{CO}_2$  is generated for each mole of  $\text{CaCO}_3$  produced, but this is incorrect due to the buffering capacity of seawater: Calcite precipitation decreases total dissolved inorganic carbon ( $\text{TCO}_2$ ) and total alkalinity (TA) in a ratio of 1:2. The buffering capacity of seawater means that it gets more acidic because the decrease in total alkalinity exceeds that of total inorganic carbon and results in an increase in  $[\text{CO}_2]$  (Zeebe, 2012). Consequently, the ratio of released  $\text{CO}_2$  to precipitated carbonate ( $\psi$ ) is a function of mixed layer inventories of  $\text{TCO}_2$ , TA, and temperature, being higher at low temperatures (Frankignoulle et al., 1994). This effect needs to be considered to correctly quantify the effect of calcification on  $\text{CO}_2$  release (e.g., Salter



et al., 2014). Dissolution of calcite works in a reverse manner. Thus,  $\text{CaCO}_3$  must be produced above the ventilation depth, and transported below it, in order to reduce atmospheric  $\text{CO}_2$  sequestration associated to the soft-tissue pump, a process termed the carbonate counter pump (Heinze et al., 1991). On the timescales discussed above, the ocean's carbonate pump only leads to shifts in the vertical distribution of  $\text{TCO}_2$  and TA, and not to changes in their inventories. Therefore, similar to the soft-tissue pump, the carbonate counter pump can modulate atmospheric  $\text{CO}_2$  concentrations on timescales of 100–1000 years due to global mixing of the oceans. On much longer timescales, the burial of  $\text{CaCO}_3$  in marine sediments represents a major mechanism to remove carbon from the ocean-atmosphere system (Zeebe, 2012).

Since most foraminifers live in the surface ocean and sink rapidly to depth, they have the potential to contribute to the carbonate counter pump. In waters around the Crozet Plateau in the Southern Ocean, a foraminifer-dominated carbonate counter-pump is estimated to offset atmospheric  $\text{CO}_2$  sequestration from the soft-tissue pump by up to 30% (Salter et al., 2014) (Fig. 3). However, the production and flux of planktic foraminifer shell-bound carbon is known to vary on a regional scale (e.g., Schiebel, 2002; Jonkers and Kucera, 2015). For example, the carbonate counter pump around the Kerguelen Plateau is much weaker and dominated by coccolith-derived calcite (Rembauville et al., 2016a), a difference seemingly related to the position of the Subantarctic Front (cf. Fig. 3). Likewise, production of pteropods and their aragonite shells varies according to environmental conditions, following, for example, the quantity and quality of prey (cf. Schiebel et al., 2002; Buitenhuis et al., 2013; Salter et al., 2014).

Fig. 3 is a 1.5-column fitting image.

The contribution of foraminifers to the carbonate counter pump also heavily depends on the composition of the flux-assembly, and in particular the presence of small and large species. The size distribution of different species is important since larger tests contain more calcite biomass per individual and thus release more  $\text{CO}_2$  than smaller tests. Regional comparisons of the carbonate counter pump effect in the Southern Ocean demonstrate it is in part regulated by shifts from small species like *N. pachyderma* (mean test size  $166 \pm 32 \mu\text{m}$ ) to larger ones such as *G. bulloides* ( $247 \pm 32 \mu\text{m}$ ) and *G. inflata* ( $337 \pm 93 \mu\text{m}$ ), which in turn is related to iron availability and productivity niches (Salter et al., 2014; Rembauville et al., 2016a). Some species also show seasonal variation in size-normalized weights (SNWs), which are frequently applied as a proxy of test thickness and/or calcification rates. For example, in the Southern Ocean near Crozet, *N. pachyderma* and *G. bulloides* show approximately a seasonal 2-fold range in SNWs whereas that of *T. quinqueloba* remains relatively constant (Salter et al., 2014) (Fig. 3). These differences may be related to temporal dynamics in food-supply, calcification depth and  $\text{CO}_2$  concentration. Poleward of the polar fronts in Antarctic and North Atlantic waters, assemblages are dominated by *N. pachyderma* displaying differential production of its ontogenetic shell and calcite crust (e.g., Simstich et al., 2003). Ontogenetic calcification must take place within the ventilated zone in the surface mixed layer in order to affect atmospheric  $\text{CO}_2$ . However, dwelling depth and precipitation of shell calcite in high latitudes are affected by regional salinity changes in surface waters due to sea-ice melting in addition to other environmental effects (e.g., Carstens and Wefer, 1992; Volkmann, 2000b), as well as ontogenetic changes in depth-distribution as shown for *N. pachyderma* (Fig. 2). Similarly, subsurface dwelling individuals of other species may be important components of foraminifer-derived  $\text{CaCO}_3$  flux (e.g., Salter et al., 2014) although their effect on  $\text{CO}_2$  equilibria may be negligible if they do not produce calcite in the surface ocean. In order to correctly quantify the impact of foraminifers on the carbonate counter pump it is therefore imperative to adopt a species-centered approach that considers test size, size-normalized weights, vertical distribution patterns, and niche dynamics (Fig. 2).

### 3.3. The effect of carbonate chemistry on planktic foraminifer calcification

Bicarbonate ( $\text{HCO}_3^-$ ) is the main source (~90%) of carbonate for planktic foraminifer shell calcite formation, followed by carbonate ions ( $\text{CO}_3^{2-}$ , about 10%), and minor amounts of  $\text{H}_2\text{CO}_3$ , and  $\text{CO}_2$  (Zeebe and Wolf-Gladrow, 2001). In turn, planktic foraminifer precipitation of the shell calcite is affected by  $\text{CO}_2$  concentration and pH of ambient seawater. Precipitation of test calcite is highest at high carbonate ion concentration ( $[\text{CO}_3^{2-}]$ ) and high pH (Moy et al., 2009). Consequently, high  $[\text{CO}_2]$  and low pH ( $< 8.2$ ) cause decreased precipitation of shell calcite. In addition to reduced calcite production at increasing partial pressure of  $\text{CO}_2$ , dissolution of shell calcite during sedimentation in the subsurface water column causes production of increasingly thinner and lighter tests (e.g., Broecker and Clark, 2001; Barker and Elderfield, 2002; Schiebel et al., 2007). The ongoing rise in atmospheric  $\text{CO}_2$  causes increasing  $[\text{CO}_2]$  and decreasing pH in the surface and deep water column and thinning of planktic foraminifer shells at high latitudes (e.g., Caldeira and Wickett, 2003; De Moel et al., 2009; Moy et al., 2009; Roy et al., 2015). As a negative feedback, rapid modern anthropogenic  $\text{CO}_2$  increase (Thomas et al., 2007) is counteracted by the reduction of planktic foraminifer calcification and consequent decreased contribution to the carbonate counter pump. The same systematics of carbonate concentrations and calcification rates are probably valid to varying degrees in other plankton functional types like coccolithophores and the flux of coccolith-bound carbon (e.g., Riebesell et al., 2000; Lohbeck et al., 2012; Buitenhuis et al., 2013; O'Brien et al., 2013), and pteropods (e.g., Orr et al., 2005; Bednaršek et al., 2012).

### 3.4. Variability of planktic foraminifer calcification over geologic time-intervals

Modern Subantarctic waters are a major sink of atmospheric  $\text{CO}_2$  (Takahashi et al., 2002). In contrast, Antarctic waters poleward of the Polar Front (PF) are a source of  $\text{CO}_2$  from upwelled waters to the atmosphere. North Atlantic subpolar and polar (i.e., Arctic) waters also act as a major sink of atmospheric  $\text{CO}_2$ , which is exported to depth by downwelling of surface waters and therefore leads to neither an increase in surface seawater  $\text{CO}_2$ , nor to major changes in surface marine pH. Consequently, polar planktic foraminifers in Arctic and Subarctic waters produce more calcite mass and thicker shells than in Antarctic and Subantarctic waters. In addition to differences in planktic foraminifer calcite production and original shell thickness, stronger dissolution in the carbonate ion ( $\text{CO}_3^{2-}$ ) depleted subsurface Southern Ocean (Sarmiento and Gruber, 2006) leads to further loss in shell calcite mass and thinning of shells when compared to the Arctic and northern North Atlantic waters. The production of ontogenetic calcite crusts on top of the tests of Southern Ocean *N. pachyderma* is probably reduced in comparison to tests from the North Atlantic and Arctic Oceans (cf. Simstich et al., 2003; Schiebel and Hemleben, 2017).

Regional increases in planktic foraminifer shell calcite production and export in the Subantarctic Ocean are stimulated by iron availability and primary production (i.e., prey for the foraminifers), and cause a strengthened carbonate counter pump. As a consequence, the production and flux of carbonate in naturally iron-fertilized waters reduce the overall amount of  $\text{CO}_2$  transferred to the deep modern ocean by up to one third (Salter et al., 2014). The role of planktic foraminifers in mediating the carbonate counter pump may have been even stronger during glacial time intervals when aeolian deposition fertilized large areas of the Subantarctic (e.g., Martínez-García et al., 2011, 2014). The average test size of polar and subpolar planktic foraminifers did not significantly change over time-intervals of global climate change over the Cenozoic, i.e., the past 65 Ma (Schmidt et al., 2004). In contrast, test size of the dominating polar planktic foraminifer *N. pachyderma* increased over the past 1.1 Ma and has been maximum over the late Quaternary, i.e., the past 250 ka (Yamasaki et al., 2008). It can hence be assumed that polar planktic foraminifer carbonate turnover is affected



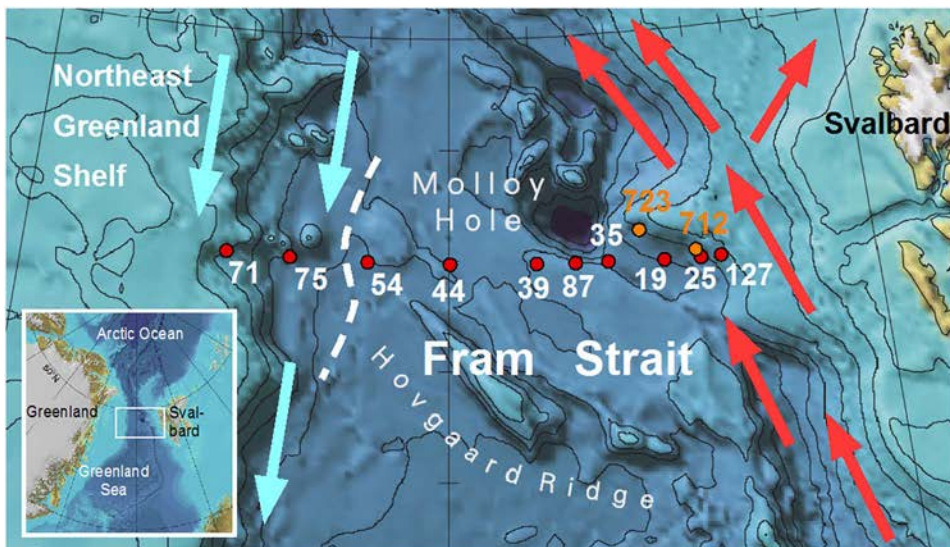
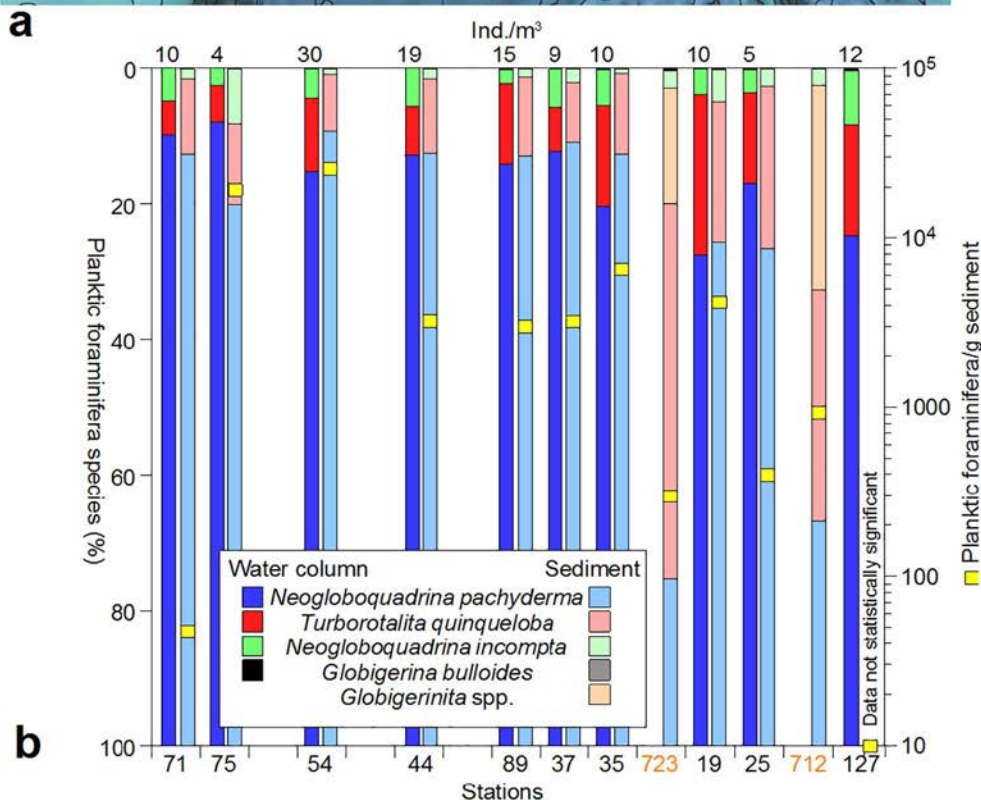


Fig. 4. Planktic foraminifers in plankton and sediment samples from the Fram Strait. (a) Bathymetric map and surface current pattern of the Fram Strait ([www.ibcao.org](http://www.ibcao.org)) showing locations of plankton tows and sediment surface samples (red dots; see Pados and Spielhagen, 2014). Samples from sediment cores MSM5/5-712 and -723 (orange dots and numbers; Spielhagen et al., 2011, Werner et al., 2016). The sea-ice margin in late June to early July 2011 is shown by the stippled white line. The northward flow of warm, saline Atlantic Water (red arrows) and low-saline, cold, ice-covered surface waters from the Arctic Ocean (blue arrows). (b) Absolute ( $\text{Ind./m}^3$ , on top of panel) and relative abundances of most frequent planktic foraminifer species (100–250- $\mu\text{m}$  test-size fraction) in plankton tow samples (bright colors) and sediment surface samples (pale colors) at stations shown in (a). Plankton data are cumulative for the uppermost 500 m. For details see Pados and Spielhagen (2014). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



by climate change and exerts both positive (biological carbon pump) and negative (carbonate counter pump) feedbacks on atmospheric  $\text{CO}_2$  sequestration. The effect of modern changes in climate and  $\text{CO}_2$  budgets on foraminifers and other biota needs to be monitored and ideally assessed by high-resolution time-series analyses.

#### 4. Comparing live and fossil species assemblages

The basic principle for quantitative reconstructions of paleoceanographic parameters from microfossil distribution includes the assumption that the composition of the surface seafloor sediment represents modern conditions in the overlying water column. Considering planktic foraminifers, reconstruction by methods such as modern analog techniques (MATs) applies largely to the uppermost 500 m of the water column. Reliability is tested by comparison of planktic foraminifer counts in both sediment and water samples from the same location. In

the following, we present an example from the Fram Strait (Pados and Spielhagen, 2014). The Fram Strait is a confined high-latitude passage with steep bathymetry between Greenland and Svalbard, which is exposed to strong currents and seasonality (Fig. 4). As such, planktic foraminifer population dynamics from the Fram Strait may serve as a good example to be compared to other high-latitude systems, each with its inherent regional and temporal characteristics.

Results from a transect at  $79^\circ\text{N}$  across the Fram Strait (Fig. 4a) show good conformity of species distributions in the corresponding samples (Fig. 4b), which are dominated by *N. pachyderma*. The relative abundance of subpolar *T. quinqueloba* is significantly higher in samples from the eastern than western Fram Strait, reflecting strong northward advection of southern sourced Atlantic waters along the western Svalbard-Barents Sea continental margin. Differences in assemblage counts from sediment and water samples (e.g., *T. quinqueloba* at Stations 71 and 75, Fig. 4a) may have various reasons: Sediment samples integrate species

distributions over time periods, which may range from years to several millennia, depending on sedimentation rates. In contrast, data from plankton-net samples represent snapshots affected by seasonal and longer-term environmental and climate conditions not necessarily corresponding to the period of maximum planktic foraminifer production and sedimentation, which is particularly true for high-latitude waters (Fairbanks and Wiebe, 1980; Schiebel, 2002; Kohfeld et al., 1996; Pados and Spielhagen, 2014). Thus, seasonal changes in water mass characteristics at particular sites, including ice coverage, may result in differences in the relative abundances of species. Furthermore, seasonal production may be decoupled at the species-scale as observed for *T. quinqueloba* and *N. pachyderma* (Jonkers et al., 2010). Accordingly, plankton tows may include varying species assemblages at the inter-annual scale and longer time-intervals of environmental change (cf. Carstens et al., 1997; Volkman, 2000a, 2000b, versus Pados and Spielhagen, 2014).

Considering the high relative abundances of *T. quinqueloba* in some plankton tow samples from the eastern Fram Strait (Carstens et al., 1997; Volkman, 2000a, 2000b), abundances of this species in surface sediments from Stations 19 and 25 are surprisingly low (Fig. 4). The apparent mismatch most likely results from generally low sedimentation rates in Arctic deep-sea environments, which lead to comparatively high total numbers of planktic foraminifers in the surface samples (Fig. 4b). In addition, differential dissolution of the thin-shelled *T. quinqueloba* may reduce proportions particularly in comparison to the often more thick-shelled and dissolution-resistant *N. pachyderma*. At a few sites with high accumulation rates on the western continental margin of Svalbard, however, sediment surface samples contain up to 70% of subpolar foraminifers (Fig. 4b; Spielhagen et al., 2011; Werner et al., 2016). At these sites (Fig. 4a, Stations 712 and 723) dilution by terrestrial input is high and total numbers of planktic specimens in the sediment are low (Fig. 4b). Here, surface sediments were deposited over the past few decades and experienced a pronounced warming of the Atlantic waters. Accordingly, planktic foraminifer assemblages include significantly higher proportions of subpolar species over polar species (Spielhagen et al., 2011, Werner et al., 2016). At high-accumulation rates samples from the pre-industrial period, including the Little Ice Age, contain only 15–40% subpolar species.

At other sites, with typical Holocene sedimentation rates of 2–4 cm ky<sup>-1</sup> in the central and eastern Fram Strait (Nørgaard-Pedersen et al., 2003), sediment surface samples are composed of a mixture of assemblages from both industrial and pre-industrial times. These assemblages contain only minor amounts of planktic foraminifers deposited during the last 100 years of rapid warming. An additional effect of bioturbational mixing of surface sediments and dilution of the most recent surface sediments results in low relative abundances of subpolar foraminifers in high-latitude samples. Most likely, the majority of tests in these samples were deposited during pre-industrial times, when advection of Atlantic Water was weaker, temperatures were lower, and less subpolar species were dwelling in the eastern Fram Strait. To conclude, relative abundances in the water column strongly depend on the season of sampling, whereas surface sediment samples are biased by sediment mixing. Therefore, year-round sediment trap samples are needed to understand the relations between both live individuals and fossil tests from sediment assemblages in areas of strong seasonality and changing vertical fluxes.

Fig. 4 is a 1.5-column fitting image.

#### 4.1. Phenology of polar planktic foraminifers

Seasonality of planktic foraminifers is most pronounced at mid to high latitudes, following phytoplankton succession and trophic pathways, i.e., the availability of prey (e.g., Bé, 1960b; Schiebel and Hemleben, 2005; Fraile et al., 2009). In polar oceans, high planktic foraminifer production occurs during the short summer, when high solar irradiance and temperatures sustain enhanced primary and

secondary production (e.g., Fischer et al., 1988; Kretschmer et al., 2016). Consequently, changing seasonality between warmer and colder climate stages affects the timing, quality (i.e., species) and quantity of planktic foraminifer production (Spielhagen et al., 2011; Feldmeijer, 2014; Kretschmer et al., 2016). During colder climates like glacial stadials and Heinrich Events, spring conditions are assumed to start later than during interstadials and interglacials (Kretschmer et al., 2016). Delayed spring conditions at varying environmental conditions might affect biological production and planktic foraminifer assemblages. To which degree modern changes in SSTs and the Arctic Ocean environment also affect the seasonal production and phenology of planktic foraminifers (cf. Kretschmer et al., 2016) needs to be assessed by time series analyses of faunal assemblages.

#### 4.2. Planktic foraminifer species turnover during time intervals of rapid climate warming

During time intervals of rapid climate warming, and changes in atmosphere and ocean circulation (Denton et al., 2010), species may be increasingly transported by currents from the temperate mid-latitude ocean to higher latitudes. For example, the rare modern mid-latitude species *Beella megastoma* repeatedly occurred in the Norwegian-Greenland Sea during glacial Terminations TII, TIII, and TV leading from Marine Isotope Stage (MIS) 6 to MIS 5 around 130 ka, MIS 8 to 7 around 243 ka, and MIS 12 to 11 around 424 ka, respectively (Bauch, 1996). These short-lived incursions of non-native species during short-term events of climate change and circulation turnover have also been observed in species other than *B. megastoma*.

A large-scale hydrologic revolution similar to the late Pleistocene Terminations TI, TII, and TIV may have caused the occurrence of *G. crassaformis* in waters off the Kerguelen Plateau during the climate transition from MIS 32 to 31 around 1.081 Ma (cf. Venz and Hodell, 2002; Meilland, 2015). Modern *G. crassaformis* have been found as far south as the Crozet Islands in austral summer, but not poleward of the Crozet Islands (Salter et al., 2014). In contrast to its subsurface habitat at lower latitudes, *G. crassaformis* inhabits surface waters when being transported to high latitudes, possibly following its food source (cf. Schiebel and Hemleben, 2017). The same distribution pattern is followed by *N. pachyderma*, which is limited to seasons and depth habitats by alimentation and ambient seawater salinity at the regional scale (e.g., Carstens et al., 1997; Volkman, 2000a; Pados and Spielhagen, 2014).

Before ~1900 CE, 10% to 40% of planktic foraminifers in the western Fram Strait between Svalbard and Greenland around 79°N were subpolar species (e.g., *T. quinqueloba* and *N. incompta*), whereas 60% to 90% were polar species (e.g., *N. pachyderma*, Spielhagen et al., 2011). In comparison, assemblages of the past 100 years are increasingly composed of subpolar (i.e., ‘warmer’) species, which is an inversion of the subpolar/polar species ratio, reaching 66% subpolar individuals in the surface sediment sample on average. The percentage of subpolar individuals is closely related to the distribution of water bodies, with low values in Arctic waters and high values in Atlantic Waters. Highest subpolar foraminifer fluxes and percentages in samples from the Modern Period indicate a strongly increased influence of warm Atlantic Waters advected from the Norwegian Sea to the north (Spielhagen et al., 2011). The changes in planktic foraminifer assemblages are confirmed by transfer (SIMMAX) calculations. SSTs calculated from Mg/Ca measurements confirm increasing temperatures associated with a stronger influence of Atlantic Water off western Svalbard over the Modern Period. Until about 1850 CE, average summer Atlantic Water SSTs varied between 2.8 °C and 4.4 °C (SIMMAX). Since 1890 CE, planktic foraminifer assemblages include more temperate species, and provide SIMMAX-calculated temperatures, which are about 2 °C higher than during the previous 2 ky, i.e., at a range of 4.1 °C to 6.0 °C (Spielhagen et al., 2011). A strong Atlantic Water warming event in the Arctic Ocean in the 1990s caused a

shoaling of the Atlantic Water core, an enhanced heat flux to the surface (Steele and Boyd, 1998), and decreasing sea ice (Comiso et al., 2008). Paleooceanographic interpretation of planktic foraminifers would hence need to consider regional differences in depth distribution and phenology at the species level, and account for the entire individual chemical signature of the shell (e.g., Spielhagen and Erlenkeuser, 1994; Elderfield et al., 2002; Pados et al., 2015).

## 5. Conclusions

Planktic foraminifer assemblages in the polar oceans have changed over the past 150 years, following exposure to major changes in high-latitude environments such as rising temperatures and increasingly sea-ice free regions. Species diversity has increased over the past decades. Formerly rare and lower-latitude species such as *O. riedeli*, *U. uvula*, *G. crassaformis* and *N. incompta* are increasing components of high-latitude assemblages. Foraminifers are mainly limited by the availability of their algal prey, and thus major changes in distribution patterns display changes in primary production. Any shifts in assemblage structure of the planktic food chain and trophic conditions impacts carbon turnover. Both positive (biological carbon pump) and negative (carbonate counter pump) feedbacks with increasing CO<sub>2</sub> concentration in the atmosphere and ocean may occur at regional to basin scale. These changes are not unique in Earth history and appear to be a recurring phenomenon during times of rapid climate change such as the Quaternary glacial terminations. Employing foraminifer proxies of past changes of the polar environment at high temporal resolution, as well as monitoring the current change of the polar oceans and atmosphere, provides a natural indicator and early warning system of global climate change.

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