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DISSERTATION

Arctic planktonic foraminifera pelagic carbonate production and sedimentation under changing environmental conditions

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“Spieglein, Spieglein an der Wand
Hätt′ nie gedacht, dass das passiert
Dass auf der Welt und hier im Land
Mal so ein scheiß Virus grassiert”

Schöne Grüße von Zuhause - VERSENGOLD

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Feel my heart now, I made it
Reaching things now I never thought possible
Here I am now, I made it”

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Abstract

The Arctic Ocean is substantially affected by ongoing warming and resulting loss in sea ice. Climatic change further influences biological processes. Altogether, this can result in a modification of the marine carbon cycle. Changes in the marine carbon cycle can affect the climate, also beyond the area of the Arctic Ocean, for example by changing the amount of carbon dioxide in the atmosphere and contributing to the greenhouse effect. Changing conditions of both climate and carbon saturation in the water affect marine organisms producing and storing carbon, which is transported towards the sediments and stored on longer time scales after their deaths. One of those organisms are planktonic foraminifera, calcite shell-building marine protists. Global estimates show that the mass flux of their produced calcite from the surface ocean to the deep ocean and into the sediments contribute to a considerable amount of total pelagic calcite fluxes, with high regional variability. Accordingly, estimates of foraminifera calcite mass production in the Arctic Ocean are prerequisite to evaluate the effects of present-day and future Arctic Ocean changes on the contribution of planktonic foraminifera calcite production for the carbon cycle. For this, moreover, thoroughly understanding of abiotic and biotic factors driving the productivity of planktonic foraminifera and the produced calcite mass is essential. To evaluate how the ongoing oceanic change could modify production of calcite by planktonic foraminifera, knowledge on controlling factors of planktonic foraminifera mass production is needed.

In order to unravel the effects of changes in the Arctic Ocean on planktonic foraminifera, this thesis presents studies on planktonic foraminifera from all over the Arctic and Subarctic Ocean, working with samples from both within the water column and from the sediments. The produced calcite mass is determined by comprehensive measurements of shell size and weight of all in the Arctic and Subarctic Ocean abundant species of planktonic foraminifera. Measurements on shell weights on samples from plankton nets, sediment traps and sediment cores from a total of 13 locations are used to further calculate foraminifera calcite mass fluxes in the water column and foraminifera calcite mass accumulation in the sediments using published data from all over the Arctic and Subarctic Ocean. On average, a contribution of 5.4 to 30 % of planktonic foraminifera to total $CaCO_3$ mass is determined. Local values reach contributions of up to 89 %. These results show the relevance of considering planktonic foraminifera in the context of the marine carbon cycle of the Arctic Ocean.

Investigating planktonic foraminifera mass fluxes of the most abundant species of the Arctic Ocean, *Neogloboquadrina pachyderma*, from the upper water column indicates that the production of calcite shells is happening within the upper 300 m of the water column. The flux of sinking shells below is attenuated by dissolution, strongest directly below the base of the productive zone, and of relevance in about the following 300 m depth. The strong seasonality in temperature of the Arctic realm is reflected in the seasonality of planktonic foraminifera mass fluxes shown by sediment trap data spanning over one year. Nevertheless, there are differences in flux magnitude on an interannual basis that cannot be explained by temperature and related parameters like solar insolation and sea ice extent, nor by food availability in terms of chlorophyll α concentration. This is similar in the regional variability that is present in the mass accumulation of planktonic foraminifera in the sediments: There is an overall trend connected to distinct water masses in terms of temperature, but it cannot explain the exact variability. It is hypothesized that the quality of available food is important for the productivity of planktonic foraminifera, but the data produced in the context of this thesis does not allow to test this.

As the driving processes of the productivity of planktonic foraminifera is still not fully understood, it is not possible to make clear statements on how the ongoing climate change will affect foraminifera calcite mass production. However, this thesis shows that changes in the species composition, which have been shown to already occur with the present-day temperature increase, can affect the mass produced by planktonic foraminifera due to species-specific different shell weights. Moreover, if the climatic change affects the primary production in the Arctic Ocean, likely also the productivity of planktonic foraminifera will be affected.

Overall, this thesis provides new details on the calcite mass production of planktonic foraminifera in the Arctic and Subarctic Ocean. It is shown that they are a relevant contributor to fluxes of $CaCO_3$ from the pelagic zone towards the sediments. This makes planktonic foraminifera an important component of the marine carbon cycle, which needs to be further constrained to understand how ongoing climate change will influence their contribution to drawdown of carbon.

Zusammenfassung

Der Arktische Ozean ist von fortschreitender Erwärmung und daraus resultierendem Verlust von Meereis stark beeinflusst. Der Klimawandel wirkt sich auch auf biologische Prozesse aus. Insgesamt kann dies zu einer Veränderung des marinen Kohlenstoffkreislaufs führen. Diese Veränderungen können das Klima beeinflussen, über die Region des Arktischen Ozeans hinaus, beispielsweise durch eine Veränderung der Kohlenstoffdioxidkonzentration in der Atmosphäre und damit einer Beeinflussung des Treibhauseffektes. Sich ändernde klimatische Bedingungen und Veränderungen in der Kohlenstoffkonzentration im Wasser wirken sich auf Meeresorganismen aus, die Kohlenstoff produzieren und speichern. Durch ihr Absinken nach ihrem Tod wird dieser Kohlenstoff in die Tiefe transportiert und langfristig im Sediment abgelagert. Einer dieser Organismen sind planktonische Foraminiferen, kalzitschalenbildende Protisten. Globale Schätzungen zeigen, dass der Massenfluss des von ihnen produzierten Kalzits von der Meeresoberfläche in die Tiefsee und dessen Ablagerung in Sedimente einen relevanten Teil des gesamten pelagischen Kalzitflusses ausmacht. Gleichzeitig gibt es eine hohe regionale Variabilität. Dementsprechend sind Schätzungen der Kalzitproduktion von Foraminiferen im Arktischen Ozean die Voraussetzung für die Bewertung der Auswirkungen heutiger und zukünftiger Veränderungen im Arktischen Ozean auf den Beitrag der Kalzitproduktion von planktonischen Foraminiferen zum Kohlenstoffkreislauf. Darüber hinaus ist hierfür ein gründliches Verständnis der abiotischen und biotischen Faktoren, die die Produktivität der planktonischen Foraminiferen und die produzierte Kalzitmasse antreiben, unerlässlich. Um zu beurteilen, wie der derzeitige Klimawandel die Produktion der Foraminiferen verändern könnte, ist es notwendig zu wissen, was ihre gegenwärtige Massenproduktion ausmacht.

Um die Auswirkungen des Wandels im Arktischen Ozean auf planktonische Foraminiferen zu entschlüsseln, werden in dieser Arbeit Untersuchungen an planktonischen Foraminiferen aus dem gesamten arktischen und subarktischen Ozean vorgenommen, wobei sowohl Proben aus der Wassersäule als auch aus den Sedimenten verwendet werden. Die produzierte Kalzitmasse wird durch umfassende Messungen der Schalengröße und den Schalengewichts aller im Arktischen und Subarktischen Ozean vorkommenden Arten planktonischer Foraminiferen bestimmt. Messungen der Schalengewichte an Proben aus Planktonnetzen, Sedimentfallen und Sedimentkernen von insgesamt 13 Standorten werden verwendet, um die Kalzitmassenflüsse der Foraminiferen in der Wassersäule und die Kalzitmassenakkumulation der Foraminiferen in den Sedimenten anhand veröffentlichter Daten aus dem gesamten Arktischen und Subarktischen Ozean zu berechnen. Im Durchschnitt wird ein Anteil von 5,4 bis 30 % der planktonischen Foraminiferen an der gesamten $CaCO_3$-Masse ermittelt. Lokale Werte erreichen Anteile von bis zu 89 %. Diese Ergebnisse zeigen, wie wichtig es ist, planktonische Foraminiferen im Zusammenhang mit dem marinen Kohlenstoffkreislauf des Arktischen Ozeans zu betrachten.

Die Untersuchung der Massenflüsse von planktonischen Foraminiferen der häufigsten Art des Arktischen Ozeans, *Neogloboquadrina pachyderma*, in der oberen Wassersäule zeigt, dass die Produktion von Kalzitschalen in den oberen 300 m der Wassersäule stattfindet. Der Fluss der absinkenden Schalen wird durch Auflösung abgeschwächt. Diese ist direkt unterhalb der produktiven Zone am stärksten und in den folgenden 300 m Tiefe von Bedeutung. Die starken jahreszeitlichen Schwankungen der Temperatur in der Arktis spiegeln sich in den jahreszeitlichen Schwankungen der Massenflüsse planktonischer Foraminiferen wider, die sich aus Daten

aus Sedimentfallen über ein Jahr hinweg ergeben. Dennoch gibt es zwischen den Jahren Unterschiede in der Größenordnung der Flüsse, die weder durch die Temperatur und damit verbundene Parameter wie Sonneneinstrahlung und Meereisausdehnung, noch durch die Nahrungsverfügbarkeit in Form der Chlorophyll-α-Konzentration erklärt werden können. Ähnlich verhält es sich mit der regionalen Variabilität bei der Massenakkumulation von planktonischen Foraminiferen im Sediment: Es gibt einen allgemeinen Trend, der mit bestimmten Wassermassen und deren Temperatur zusammenzuhängen scheint, aber er kann die Variabilität nicht genau erklären. Aufgrund von Hinweisen aus einer früheren Studie wird die Hypothese aufgestellt, dass die Qualität der verfügbaren Nahrung für die Produktivität der planktonischen Foraminiferen wichtig ist, aber die im Rahmen dieser Arbeit gewonnenen Daten erlauben es nicht, dies im Detail zu prüfen.

Da die treibenden Prozesse der Produktivität planktonischer Foraminiferen noch immer nicht vollständig verstanden sind, ist es nicht möglich, eindeutige Aussagen darüber zu treffen, wie sich der anhaltende Klimawandel auf die Kalzitproduktion der Foraminiferen auswirken wird. Diese Arbeit zeigt jedoch, dass Veränderungen in der Artenzusammensetzung, die nachweislich bereits mit dem heutigen Temperaturanstieg einhergehen, die von planktonischen Foraminiferen produzierte Masse aufgrund von artspezifisch unterschiedlichen Schalengewichten beeinflussen können. Wenn der Klimawandel die Primärproduktion im Arktischen Ozean beeinflusst, wird wahrscheinlich auch die Produktivität der planktonischen Foraminiferen beeinträchtigt.

Insgesamt liefert diese Arbeit neue Details über die Kalzitmassenproduktion planktonischer Foraminiferen im arktischen und subarktischen Ozean. Es wird gezeigt, dass sie einen wichtigen Beitrag zum Fluss von $CaCO_3$ aus der pelagischen Zone in die Sedimente leisten. Dies macht die Organismen zu einer wichtigen Komponente des marinen Kohlenstoffkreislaufs, die weiter eingegrenzt werden muss, um zu verstehen, wie der laufende Klimawandel den Beitrag planktonischer Foraminiferen zur Speicherung von Kohlenstoff im tiefen Ozean und Ozeansediment beeinflussen wird.

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Chapter 1

Introduction

1.1 Climate and environmental change in the Arctic Ocean

The Arctic Ocean is affected by ongoing climatic change (Najafi et al., 2015; Notz and Stroeve, 2016), with average annual air temperature constantly increasing within the past 50 years (Overland et al., 2019). Today's air temperatures are about 2° C above the average values from pre-industrial times (Overland et al., 2019). In line with increasing air temperatures, the extent of sea ice in the Arctic is shrinking, reaching a loss of more than 30 % of summer sea ice extent between 1979 and 2013 (Meier et al., 2014) and of more than 8 % during winter between 1979 and 2018 (Stroeve and Notz, 2018). The observed temperature increase in the Arctic Ocean is stronger than on global average due to polar amplification (Serreze and Barry, 2011). Climate feedback mechanisms – mechanisms where climatic change results in further enhancement of the ongoing climate change – are the cause of the polar amplification (Serreze and Barry, 2011). One of these feedbacks is the albedo feedback, where the albedo, the reflectivity of a surface, is changed: Warmer surface air temperatures cause a reduction of sea ice, decreasing the albedo. By this, the oceanic heat uptake and therefore the sea surface temperature increases, resulting in further warming and followingly further ice loss (Perovich and Polashenski, 2012). Also cloud and water vapour formation increase with higher heat transport caused by warming and lower sea ice extent over summer. Higher humidity and cloud concentration enhance the greenhouse effect, and the caused further warming leads to further sea ice melt and evaporation, making this another accelerating feedback mechanism in the area of the Arctic Ocean caused by increased temperatures (Kapsch et al., 2013).
A change in sea ice is not only relevant for the temperature regime, but can also play a role for the primary production, as decreased sea ice results in an increase of light availability in surface waters (Perovich and Polashenski, 2012). Whether there is a positive, negative or no trend of primary productivity with ongoing climate change is still under investigation, as e.g. nutrient availability, which could be influenced by the decrease of sea ice, is a relevant factor as well (Vancoppenolle et al., 2013).
Primary production is one component of the marine carbon cycle, which is relevant for both climatic and environmental conditions in the Arctic Ocean. Often, a main subject of the debate on ongoing changes in the Arctic carbon cycle is the thawing of permafrost zones in the Arctic realm, as it can result in the release of carbon dioxide or methane into the atmosphere, amplifying the ongoing temperature increase (Bowden, 2010; Biskaborn et al., 2019). Carbon input from thawing permafrost as well as riverine input and a changed primary productivity caused by climatic change are factors possibly affecting the carbonate saturation in the Arctic Ocean differently in the future, likely influencing organisms building a calcite shell (Mucci et al., 2010).
The Arctic Ocean is of relevance for the carbon cycle, as it is an ocean basin with high uptake of atmospheric CO_2 due to its low temperatures (Steinacher et al., 2009;

Miller et al., 2014). Higher uptake of atmospheric CO_2 caused by higher CO_2 concentrations in the atmosphere can increase the acidification of the Arctic Ocean, increasing dissolution of calcifying organisms (Yamamoto-Kawai et al., 2009). Decreasing sea ice can increase the gas exchange between atmosphere and ocean in the Arctic, further amplifying the present acidification (Steiner et al., 2013). A modelling study on Arctic Ocean acidification by Luo et al., 2016 indicates that ongoing changes of the acidity of the ocean can result in long-term condition changes: While the surface ocean is in direct exchange with the atmosphere, the deep ocean is not, delaying changes at depth in contrast to at the surface. At the same time, once the deep ocean acidifies, it will stay in this state for timescales of millennials (Luo et al., 2016). This is a threat to calcifying organisms whose calcification is hampered or that even dissolve under high acidic conditions ($pH < 7.7$; Davis et al., 2017), possibly occurring in the future according to the results from Luo et al., 2016 (minimum pH of 7.6).
Future climate models show that the warming trend in the Arctic will continue even under low-emission-scenarios. This can also have impacts on a global scale as it is possible that a changing Arctic Ocean results in chanced ocean and atmospheric circulation (Overland et al., 2019). Overall, climate change in the Arctic Ocean is amplifying due to feedback mechanisms, which can also result in changes of environmental conditions. Therefore, thoroughly understanding of present-day conditions and possible impacts of changes in the climate and environment of the Arctic Ocean is important.

1.2 Research area: The Arctic and Subarctic Ocean

The focus of this thesis are the Arctic and the Subarctic Ocean. There is no consistent definition of these oceans, which are based on the latitude and the position of the Arctic Circle, the average temperature and the presence and absence of trees (Nuttall and Callaghan, 2000). Here, we follow the definition of Osherenko and Young, 2005 and define the Arctic Ocean as everything between 60 to 90° N. The Subarctic Ocean is defined as everything between 45 to 60° N.
Major relatively warm surface ocean currents are entering the Arctic Ocean from the Pacific Ocean via the Bering Sea and Chuckchi Sea and from the Atlantic Ocean via the Fram Strait and the Barents Sea (Anderson and Macdonald, 2015; Fig. 1.1). Rivers from the surrounding continents, precipitation and melting sea ice add fresh water to the Arctic Ocean (Aagaard et al., 1981). The inflowing warm surface currents cool down in the high Arctic Ocean due to low air temperatures, increasing the density of the water. Through sea ice formation, the salinity of the water increases further. The water of high density sinks downwards in the high Arctic Ocean, flowing back towards the Atlantic Ocean via the western Fram Strait as the East Greenland Current and via the Baffin Bay as a deep water current (Fig. 1.1; Aagaard et al., 1981; Drange et al., 2005). Parts of the central Arctic Ocean are covered by perennial sea ice, while other areas of it are only covered during the period of maximum sea ice extent in late February to March (Meier et al., 2014). The Fram Strait and the Greenland Sea are seasonally (Winter) covered by sea ice in the areas of Arctic water currents. The western and southern parts, mainly fed by Atlantic water, remain ice free, as also do the most of the Arctic-influenced areas during summer (Drange et al., 2005). The extent of sea ice is not only relevant for the regulation of temperature and primary productivity, but also influences particle fluxes, which are highest at the ice edge (Hebbeln and Wefer, 1991). The study area of this thesis is spanning over the entire Arctic Ocean, further including data and studies from the Subarctic Ocean,

for example from the Labrador Sea. The different conditions caused by Atlantic and Arctic waters being present in different parts of the Arctic Ocean are of relevance for the climate and environmental system of the region. It is furthermore an advantage as different conditions and their influence on the ecology of the region can be analysed on samples from a narrow region, like in the Fram Strait (Hebbeln et al., 1998).

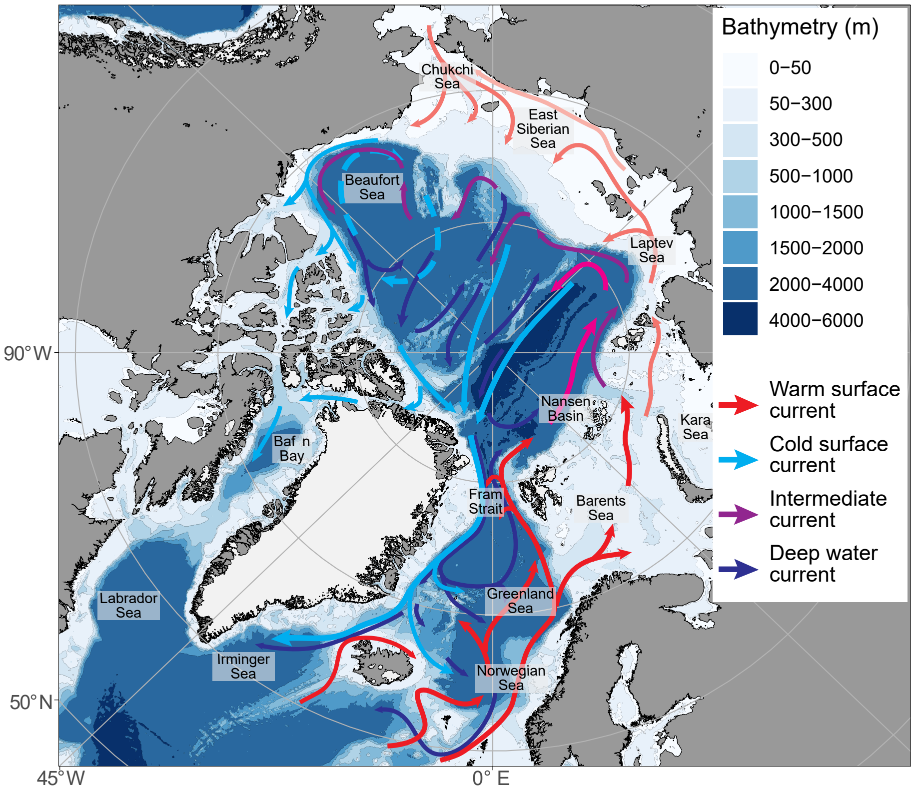

FIGURE 1.1: Overview map on the Arctic and Subarctic Ocean, the study area of the thesis. Names of the major basins and regions are indicated. The arrows show the major currents of the region, with different colors representing currents at different depths and of different temperature. Land polygons from Natural Earth Data (CC0), bathymetry from Amante and Eakins, 2009 using ggOceanMaps in R (Vihtakari, 2021), and currents from Anderson and Macdonald, 2015.

1.3 Arctic marine carbon cycle

Carbon is stored in oceans, especially the deep oceans, in large quantities (Sigman and Boyle, 2000). This is also the case in the Arctic Ocean. The transport of carbon from the atmosphere into the ocean and towards depth is driven by carbon pumps (Fig. 1.2), which are a relevant part of the overall marine carbon cycle. There are two types of carbon pumps: the physical carbon pump, and biological carbon pumps.
The solution pump is a physical pump related to solubility of CO_2 in the water: The lower the temperature and the salinity of the water, the higher the solubility and the storage capacity of CO_2 (Weiss, 1974). This results in an overall larger storage of carbon in the form of CO_2 in the deep ocean, as temperatures tend to decrease with

increasing depth (Fig. 1.2; Volk and Hoffert, 1985). Accordingly, the Arctic Ocean is a major sink of atmospheric CO_2: The cooled surface water can absorb more atmospheric CO_2 than in warmer regions, and due to the deep water formation, the CO_2 is transported towards the deep ocean (Heinze et al., 1991). Ongoing water temperature increase of the Arctic Ocean can affect this pump, reducing the capacity of CO_2 uptake (Sarmiento and Le Quéré, 1996; Joos et al., 1999; Miller et al., 2014).

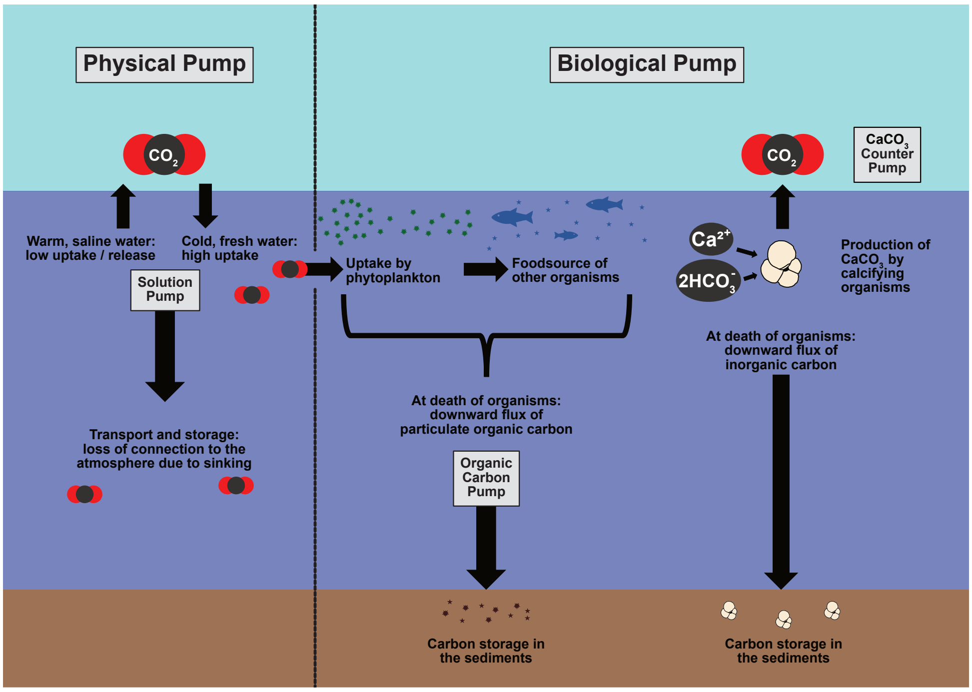

FIGURE 1.2: Schematic overview on the carbon pumps, transporting carbon from the atmosphere into the ocean and inside of the ocean towards depth. The physical pump and biological pumps are differentiated, including the role of planktonic foraminifera. Graphic based on schematic from Heinze et al., 1991.

The biological carbon pump is driven by biological activity in the ocean. Carbon is fixed in phytoplankton and other photosynthesising organisms in the photic zone, the surface waters in which sunlight is available (Riebesell et al., 2009). Phytoplankton, in turn, serves as food source for other organisms, producing organic carbon soft tissue (Heinze et al., 1991). At the death of the organisms, ranging from phyto- and zooplankton to large animals, the particulate organic carbon (POC) is sinking, finally being buried in the ocean sediments, denoted as the organic carbon pump (Fig. 1.2; Heinze et al., 1991; Riebesell et al., 2009; Henehan et al., 2017). On top of passive fluxes of dead material and fecal pellets, zooplankton like copepods actively migrating between water depth intervals contribute to the organic carbon pump (Darnis and Fortier, 2012). The amount of dissolved carbon in the surface water is reduced by the organic carbon pump, and POC is stored in the sediments on long time scales. At the same time, by lowering surface water pCO_2, the potential for further uptake of atmospheric CO_2 increases (Volk and Hoffert, 1985; Sigman and Boyle, 2000). Current changes in the Arctic climate and environment might affect the biological carbon pump, e.g. by changes in the primary production (Carmack

et al., 2006) or slowdown of particle transport towards depth due to meltwater induced stratification (von Appen et al., 2021).
The formation of inorganic carbon by calcifying organisms like planktonic foraminifera, coccolithophores and pteropods is another aspect of the biological carbon pump. The formation of $CaCO_3$ from Ca^{2+} and HCO_3^- releases CO_2, denoted as the $CaCO_3$ counter pump (Fig. 1.2; Frankignoulle et al., 1994). Even though the formation of $CaCO_3$ releases CO_2, with the death of calcifying organisms, it is still a potential for drawdown of carbon when the sinking shells are buried in sediments. By this, on geological time scales, carbon can be fixed in the sediments (Zeebe, 2012). For the potential of this drawdown in the Arctic Ocean, ongoing changes need to be considered. Acidification caused by higher uptake of atmospheric CO_2 can cause lower calcification rates of calcifying organisms (Yamamoto-Kawai et al., 2009). In the Canadian Artic Archipelago, undersaturation with respect to aragonite, was already detected recently (Beaupré-Laperrière et al., 2020). Steinacher et al., 2009 show that changes in precipitation and ice melt could result in surface waters locally becoming corrosive for aragonite in the Arctic Ocean. On long-term time scales, when the deep ocean becomes acidic and $CaCO_3$ stored in sediments is dissolved, the acidification can be neutralized (Boudreau et al., 2018). A changed biological productivity (Carmack et al., 2006; Perovich and Polashenski, 2012) and shifts in species composition of calcifying organisms (Tesi et al., 2021; Greco, Werner, et al., 2021), can result in an increase of calcification. Possibly resulting in either less $CaCO_3$ formation due to acidification, or higher $CaCO_3$ production due to higher biological productivity, the current climate change in the Arctic Ocean can affect the $CaCO_3$ counter pump in both directions (Steinacher et al., 2009). Accordingly, better understanding of the different influences on the carbonate producers is needed to evaluate the potential of carbon drawdown by the sinking of calcite formed in the upper water column in the Arctic and Subarctic Ocean.
The two biological carbon pumps do not act independently: The downward flux of organic carbon is often coupled to suspended mineral grains and the downward flux of inorganic carbon (De La Rocha and Passow, 2007). The $CaCO_3$ counter pump is linked to primary productivity, as e.g. shell formation of organisms relies on food availability. To disentangle the different effects on the marine carbon cycle under changing climatic conditions, it is therefore imperative to understand the biological processes of the contribution of the different organisms to the biological carbon pumps and how different changing conditions influence them in the Arctic and Subarctic Ocean.

1.4 Pelagic carbonate production in the Arctic

The most important pelagic carbonate producers in the Ocean are pteropods, coccolithophores and planktonic foraminifera (Schiebel, 2002; Bednaršek et al., 2012; Buitenhuis et al., 2019; Knecht et al., 2023). This study will focus on the role of planktonic foraminifera for the carbon cycle. It is nevertheless important to know the relevance of the other organisms in the Arctic Ocean. Pteropods, pelagic gastropods forming an aragonite shell (Lalli and Gilmer, 1989) can be an important contributor to mass fluxes of carbonate in the pelagic zone: Globally, they form 6 to 89 % of total carbonate fluxes (Bednaršek et al., 2012; Buitenhuis et al., 2019; Knecht et al., 2023). Similar high ranges in their contribution has been detected in the eastern Fram Strait (11 to 77 %) (Bauerfeind et al., 2014). Despite their partly high contribution to carbonate fluxes in the water column, they are of small relevance for the long term storage of carbon at the sea floor, as aragonite is more prone to dissolution than calcite (Mucci, 1983). In the eastern Fram Strait, in contrast to the high pteropod contribution to carbonate mass in the water column, they only form about 5 % of it at the sea floor (Bauerfeind et al., 2014). Coccolithophores, unicellular organisms, conduct both photosynthesis and therefore contribute to the organic carbon pump and produce a calcite shell, contributing to the $CaCO_3$ counter pump as well (Westbroek et al., 1993). While global estimates assume that the flux of these coccoliths on average contributes to about 8 % of total $CaCO_3$ fluxes (Buitenhuis et al., 2019), a contribution of less than 1 % is estimated for the eastern Fram Strait (Bauerfeind et al., 2009). For other areas of the Arctic Ocean, no estimates on the contribution of pteropods and coccolithophores to carbonate production in the upper water column and carbonate storage at the sea floor is present. This thesis focuses on planktonic foraminifera only, assuming that the role of coccolithophores and pteropods for the long-term storage of carbon is only of minor relevance in the Arctic Ocean based on the here presented numbers.

Planktonic foraminifera are marine protists (unicellular eukaryotes) and part of the zooplankton (Eynaud, 2011; Harada, 2016). They form a shell of calcium carbonate by sequentially adding chambers next to each other (Kucera, 2007; Fig. 1.3), with new calcite covering all present champers whenever a new chamber is formed (Schiebel and Hemleben, 2005). Protected by the shell is a unicellular body. Planktonic foraminifera can maintain a rather stable position in the water column (Hemleben et al., 1989). The depth habitat of planktonic foraminifera varies among species e.g. based on their food preference and light dependence (Schiebel and Hemleben, 2017), as well as within species based on regionally different environmental conditions (Greco et al., 2019). As soon as foraminifera die, their shell starts sinking towards the ocean floor, where it can be buried in ocean sediments when not influenced by dissolution. On a global scale, it has been estimated that their calcite mass downward flux constitute 23 to 56 % of total carbonate fluxes from the upper water column towards the ocean floor (Schiebel, 2002). However, a more recent estimate gives an average contribution of only 1.5 % (average of 0.011 Gt $CaCO_3$ yr^{-1}) of surface carbonate fluxes being formed by planktonic foraminifera shells (Knecht et al., 2023). The global average estimated mass of planktonic foraminifera accumulating at the sea floor is 0.71 Gt $CaCO_3$ yr^{-1} (Schiebel et al., 2007). In the Arctic Ocean in the area influenced by the West Spitsbergen current, planktonic foraminifera made up about 4 to 34 % (range of 2.3 to 7.9 mg $CaCO_3$ m^{-2} d^{-1}) of total $CaCO_3$ fluxes downwards from the upper 100 m of the water column (Anglada-Ortiz et al., 2021). Information on their contribution to the carbonate transport at further depth and the carbonate storage at the sea floor in the Arctic Ocean is lacking.

High ranges in previous estimates of the contribution of planktonic foraminifera to total $CaCO_3$ production on a global scale and the lack of data from the Arctic Ocean makes it important to further constrain the mass production of planktonic foraminifera. By this, better understanding of both the release of CO_2 during the calcite shell formation, and the drawdown of carbon when shells are buried in sediments, could be achieved. This study will only focus on the contribution of planktonic foraminifera to the inorganic carbon production, even though they also contain organic carbon that is of relevance for the overall carbon cycle (Schiebel and Movellan, 2012).

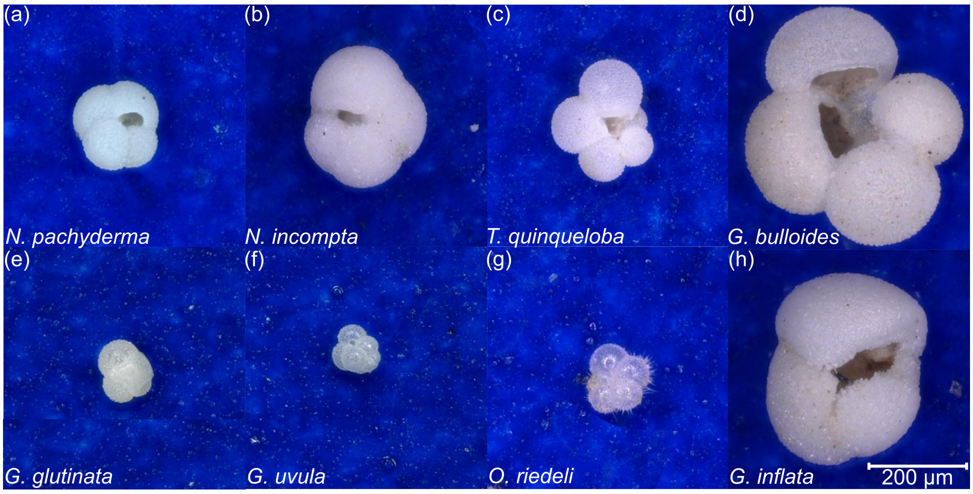

FIGURE 1.3: Overview on the planktonic foraminifera species from the Arctic and Subarctic realm. Shells are retrieved from a sediment trap in the eastern Fram Strait (a, e, f, g) and a sediment core from the Labrador Sea (b, c, d, h). The scale in (h) is for all images.

1.4.1 Subarctic and Arctic planktonic foraminifera species

The species abundance of planktonic foraminifera in the Arctic and Subarctic Ocean is limited, with only up to ten out of 50 extant species (Brummer and Kucera, 2022) being found there. These are *Neogloboquadrina pachyderma, Neogloboquadrina incompta, Turborotalita quinqueloba, Globigerina bulloides, Globigerinita glutinata, Globigerinita uvula, Orcadia riedeli, Globorotalia inflata, Turborotalita humilis and Globorotalia crassaformis* (Schiebel et al., 2017; Fig. 1.3). The species abundances vary spatially and seasonally (Volkmann, 2000; Pados and Spielhagen, 2014; Meilland et al., 2020; Greco, Werner, et al., 2021).

The most dominant species of the Arctic Ocean is *N. pachyderma* (Carstens et al., 1997; Volkmann, 2000; Schiebel et al., 2017; Anglada-Ortiz et al., 2021). *Neogloboquadrina pachyderma* is a non-spinose species and an opportunistic feeder, mainly feeding on phytoplankton, but also able to feed on zooplankton (Kohfeld et al., 1996; Bergami et al., 2009; Manno et al., 2012; Taylor et al., 2018; Greco, Morard, et al., 2021). During gametogenesis, *N. pachyderma* sometimes builds a thick calcite crust around its shell, resulting in higher shell weights and better preservation in sediments in contrast to other species (Vilks, 1975; Kohfeld et al., 1996; Bauch et al., 1997; Simstich et al., 2003). Its shell size, based on samples from the Fram Strait, ranges from 110 to 230 µm (Stangeew, 2001; Fig. 1.3). The average shell weight of *N. pachyderma* in samples from the water column is 6.3 µg, with clear weight differences between crusted (5.5 µg) and non-encrusted (2.0 µg) shells (Kohfeld et al., 1996; Kohfeld, 1998; Stangeew, 2001).

T. quinqueloba makes up only 2 to 10 % of planktonic foraminifera abundances in the cold areas of the Arctic Ocean (Volkmann, 2000), but 40 to 85 % in the areas influenced by inflowing relatively warmer Atlantic water like the eastern Fram Strait and the Barents Sea (Carstens et al., 1997; Volkmann, 2000; Pados and Spielhagen, 2014). It is a spinose and possibly symbiont bearing species (Schiebel et al., 2017). In the Fram Strait, its maximum abundance is present in the upper 100 m of the water column (Pados and Spielhagen, 2014). With an average shell size of 90 to 150 µm, *T. quinqueloba* is slightly smaller than *N. pachyderma* (Stangeew, 2001; Fig. 1.3a, c). Its average shell weight is 1.1 µg (Schiebel and Hemleben, 2000). The frequency with which *T. quinqueloba* is found in sediments is lower than in the water column, likely due to dissolution (Berger, 1970; Volkmann, 2000).

The other eight species found in the Arctic and Subarctic Ocean only make up small quantities of total planktonic foraminifera abundance in the area. With increasing influence of the warmer Atlantic waters, their relative abundance increases. Data from the Fram Strait indicates a range in the abundance of those Atlantic species of 0 to 27 % (Greco, Werner, et al., 2021). As shown in Fig. 1.3, they differ in shell size, with *G. glutinata, G. uvula* and *O. riedeli* being the smallest species of the region, *N. incompta* having a similar size as *N. pachyderma* and *T. quinqueloba*, and *G. bulloides* and *G. inflata* being larger. The species also differ in shell weight: *G. bulloides* from the water column has an average shell weight of 6.3 µg, *G. glutinata* of 4.2 µg and *N. incompta* of 3.7 µm (Schiebel and Hemleben, 2000; Schiebel et al., 2007).

Overall, despite the rather low diversity of planktonic foraminifera species in the Arctic and Subarctic Ocean, species are relevant to consider: The relative abundance of different species is connected to different environmental conditions, and the present species differ in shell size and weight. This is important for their contribution to the carbon cycle, which depends on the produced mass of $CaCO_3$. It is also of relevance in relation to the ongoing climate changes in the Arctic Ocean.

1.4.2 Possible future scenarios of Arctic planktonic foraminifera production

There is clear indication that the productivity and species abundances of planktonic foraminifera are influenced by environmental factors like water temperature, sea ice concentration, carbonate chemistry and trophic conditions (Jensen, 1998; Žarić et al., 2005; Pados and Spielhagen, 2014; Meilland et al., 2020; Ramondenc et al., 2022). Therefore, changes in these conditions driven by climate change in the Arctic could change productivity and species abundances of planktonic foraminifera in this region. Different species of planktonic foraminifera are associated with different temperature regimes (Kucera, 2007) due to differing temperature tolerances (Žarić et al., 2005). In the Subarctic and Arctic Ocean, planktonic foraminifera abundances and the flux of their shells towards the ocean floor follow the seasonal temperature pattern, peaking during summer (Jensen, 1998; Ramondenc et al., 2022). Therefore, increasing summer temperatures in the Arctic Ocean in the context of recent climate change could result in increased production of planktonic foraminifera.

It is likely that the relative abundances of planktonic foraminifera species in the Arctic and Subarctic Ocean change with changing temperatures. For example, higher abundances of the Atlantic *G. uvula* were detected in summer surface water samples in the Barents (Meilland et al., 2020). Changes in species abundances in the Fram Strait between 1985 and 2015 show that increasing temperatures result in an increase in Atlantic species in the Arctic realm, the so-called Atlantification (Tesi et al., 2021), and in lower abundances of *T. quinqueloba* in contrast to up to now still stable abundances of *N. pachyderma* in areas of high ice export (Greco, Werner, et al., 2021). This is not only crucial for the biogeography of planktonic foraminifera, but might also result in changes in their contribution to the carbon cycle, with different species having different shell sizes and weights. With both *T. quinqueloba* and most of the Atlantic species having lower shell weights than the Arctic *N. pachyderma*, it is likely that the carbonate mass production of planktonic foraminifera in the Arctic realm decreases with increasing water temperatures if the shell flux as such remains stable. As the sinking speed of shells increases with increasing shell weight, lighter shells are affected more by dissolution (Schiebel and Hemleben, 2005), possibly further diminishing the transport of carbon by planktonic foraminifera towards depth in the context of warming of the Arctic Ocean.

Production rates and downward fluxes of planktonic foraminifera increase in line with chlorophyll α concentration (Jonkers and Kucera, 2015; Rembauville et al., 2016), indicating the role of food availability for their productivity. There are furthermore indications of the quality of food having an influence on foraminifera productivity (Meilland et al., 2020). Food availability for planktonic foraminifera has been linked to the melting of sea ice in the Fram Strait, resulting in highest abundances of planktonic foraminifera at the sea ice margin (Pados and Spielhagen, 2014). Consequently, impacts of ongoing climate changes on the extent of sea ice and the phytoplankton productivity (Carmack et al., 2006; Perovich and Polashenski, 2012) could impact the mass production of calcite by planktonic foraminifera in the Arctic Ocean. Depending on the direction of change in phytoplankton productivity, and the effect of changing sea ice extent on nutrient availability, foraminifera mass production could both increase or decrease with the ongoing changes.

To constrain the influences of ongoing climate change in the Arctic Ocean on the role of planktonic foraminifera for the carbon cycle, present-day mass production of planktonic foraminifera calcite and its drivers need to be constrained. Accordingly, understanding of the mass produced in the pelagic zone and the mass arriving at the sea floor, possibly buried in the sediments, is needed. It has been shown that to estimate the calcite mass production of planktonic foraminifera, their shell flux and their average shell mass needs to be constrained (Kiss et al., 2021). Research has shown that temperature, productivity and growth conditions (combination of all environmental factors) can influence the calcification intensity of planktonic foraminifera (Weinkauf et al., 2016). Studies show general linkage between individual environmental factors and planktonic foraminifera productivity, but this far do not quantify the relationship to enable an estimation of foraminifera shell and mass production based on environmental conditions (Jensen, 1998; Žarić et al., 2005; Pados and Spielhagen, 2014; Jonkers and Kucera, 2015; Rembauville et al., 2016; Schiebel et al., 2017; Meilland et al., 2020; Ramondenc et al., 2022). Specific data on the controls of temporal and spatial variability in the productivity and calcite mass fluxes towards the sea floor by planktonic foraminifera in the Arctic and Subarctic Ocean is lacking.

Water conditions, differing with depth, can influence the shell weight of planktonic foraminifera by modulating calcification intensity (Weinkauf et al., 2016), and dissolution can occur in the upper water column (Sulpis et al., 2021). Indications of such dissolution of planktonic foraminifera shells has been quantified on a global scale (Schiebel et al., 2007), but regional data on how much foraminifera shell mass flux is reduced by dissolution directly below their productive zone in the Arctic and Subarctic Ocean is lacking. Therefore, in order to estimate the mass flux of planktonic foraminifera based on data from the upper water column, we need to know the depth at which planktonic foraminifera calcite production takes place, as well as the depth where fluxes towards the ocean floor begin. For *N. pachyderma*, a variable depth habitat of 25 to 280 m has been detected in the Arctic Ocean (Greco et al., 2019). However, there are indications that planktonic foraminifera, including *N. pachyderma*, perform ontogenetic vertical migration, meaning that they move to further depth towards the end of their life cycle, the period of the final and strongest calcification (Arikawa, 1983; Hemleben et al., 1989; Stangeew, 2001; Manno and Pavlov, 2014). On the contrary, other studies from the Arctic Ocean show the occurrence of calcification and foraminifera in their terminal life stage at all depths within their depth habitat (Kohfeld et al., 1996; Simstich, 1999; Volkmann and Mensch, 2001). Summarizing, it remains unresolved at which depth exactly the calcification of *N. pachyderma* takes place, and information on the calcification depth of other species of the region is lacking.

To assess the contribution of calcite produced by planktonic foraminifera to the carbon cycle, their deposition at the sea floor needs to be constrained. Data on mass accumulation is scarce: Moy et al., 2009 present shell weights of *N. pachyderma* in sediment cores from the Southern Ocean and Zarkogiannis et al., 2019 shell weights of *G. bulloides* from the North Atlantic. The only study from the Arctic Ocean determined shell weights of *N. pachyderma* from the Barents Sea (Berben et al., 2014). Next to the quantification of the mass accumulation of planktonic foraminifera in the sediments of the Arctic and Subarctic Ocean, its spatial and temporal variability over the region and what is defining it is yet unresolved.

Overall, there are large gaps concerning mainly the biology of planktonic foraminifera and its impact on the carbonate production of the calcifiers. This also means we lack information how a changing climate would influence them and their contribution to the carbon cycle (Roy et al., 2014). Moreover, how the carbon cycle and specifically calcifying organisms react to a change of oceanic acidification is still unknown (de Villiers, 2005). Up to now, modelling of this system is scarce and not sufficient in terms of spatial and temporal resolution (Findlay et al., 2015; Luo et al., 2016; Sulpis et al., 2019). Better understanding of foraminifera flux and transferring it into climate models would be important (Roy et al., 2014).

1.5 Thesis Objectives

The overarching goal of this thesis is to understand the driving force of the carbonate production by planktonic foraminifera in the Subarctic and Arctic Ocean and to calculate the mass of both carbonates produced in the water column and accumulated at the ocean floor. Through this, the assessment on how the ongoing climate change influences the contribution of planktonic foraminifera to the marine carbon cycle will be improved.

The first step to achieve this is to understand the calcite production of planktonic foraminifera in the upper water column. A main component of this is to know where exactly the calcification is occurring: Is it spanning over the whole depth habitat, or is it fixed to the deepest depths of it, because foraminifera perform ontogenetic vertical migration, moving downwards when growing? This is not only relevant in terms of differing water conditions at different depths that might influence the growth of shell (Carstens and Wefer, 1992), but also in terms of dissolution within the upper water column, driven by respiration of organic carbon (Schiebel et al., 2007; Sulpis et al., 2021). Samples of planktonic foraminifera from different depth intervals in the water column retrieved by plankton nets are here analysed in terms of foraminifera abundances, shell weight and shell size to understand where calcite production occurs and how it changes with depth. By this, the following hypothesis will be tested:

H1 The depth habitat of planktonic foraminifera is variable and dissolution is a relevant influence in the upper water column, making it important to constrain the depth of their productive zone and the depth where their flux towards the sediments starts.

It is important to understand what is driving the mass of calcite produced by planktonic foraminifera. Based on what is presented in section 1.4, it is likely that shell weight differs between distinct species and among species due to different environmental conditions. Better understanding on shell weight differences, also possibly influenced by dissolution in the water column and at the ocean floor, should be achieved by measuring shell weights of planktonic foraminifera from the water column and in the sediments in the Arctic and Subarctic Ocean. To understand the variability in foraminifera shell mass over time and space, plankton net samples (variation with depth and over space), sediment trap samples (variation with depth and over time) and sediment core samples (variation over space on longer time scales) are analysed. To estimate foraminifera mass fluxes, it is important to constrain the variability of the shell flux (Kiss et al., 2021). This thesis aims to quantify the effects of possible drivers of foraminifera shell flux, and especially relate it to the conditions in the Subarctic and Arctic Ocean. Samples from sediment traps, representing foraminifera mass flux over a time period of at least one year, are analysed in relation to environmental drivers (e.g. temperature, sea ice, solar insolation, chlorophyll α concentration) to test the following hypothesis:

H2 Planktonic foraminifera mass fluxes are defined by their shell flux, which is driven by water temperatures and food availability (i.e. primary productivity).

This thesis aims to better understand the role of planktonic foraminifera in the Arctic and Subarctic Ocean for the marine carbon cycle. Accordingly, the overarching hypothesis to be tested in this thesis is:

H3 A relevant amount of total $CaCO_3$ produced in the Arctic and Subarctic Ocean and stored in its sediments is formed by planktonic foraminifera. Planktonic foraminifera are therefore important organisms in the marine carbon cycle.

This will be done based on the calculated and estimated mass production of planktonic foraminifera that can be done after answering the hypotheses H1 and H2. These results will be compared to published data on total production of $CaCO_3$ in the research area to understand the overarching contribution of planktonic foraminifera to the carbon cycle.

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Chapter 2

Methodology

This chapter presents a review on the methodologies used in my own work in relation to methods used in the literature. Details on the individual methods are presented in the chapters presenting the research work and results (chapter 4, 5 and 6).

2.1 Sampling

Living and dead sinking planktonic foraminifera can be retrieved from the water column using plankton nets (Fig. 2.1a). With a multiple closing plankton net, sampling can be conducted at different water depth intervals at the same site (Sameoto et al., 2000). The collected material represents the plankton community in in the water column at the exact sampling site. While high vertical resolution can be achieved, sampling with plankton nets is restricted on horizontal resolution as well as on the temporal scale. This is especially true in the Arctic, where sampling, due to the extent of sea ice, is restricted to summer months almost exclusively (Greco et al., 2019). In the context of this research, as well as in most data from plankton net sample used for the analysis presented in chapter 4, a Hydro-Bios multinet with an opening of 0.25 m^2 has been used (Weikert and John, 1981). For the samples analysed in Kohfeld et al., 1996, likewise included in chapter 4, a MOCNESS system (Wiebe et al., 1976) has been deployed for sampling. These systems have an opening of at least 0.5 m^2. The opening size is accounted for when giving numbers of organisms found in the nets, but it can nevertheless influence the amount of material trapped with the net upon sampling (Sameoto et al., 2000). Much more relevant for the trapping efficiency of microorganisms, though, is the mesh size of the net: The smaller the mesh size, the more material is trapped. This is of relevance in the study of planktonic foraminifera when abundant species are smaller than the used mesh size (Jensen, 1998). The sampling conducted in the context of this thesis was done with a 55 µm and 100 µm mesh size, respectively. The reason for this difference is that sampling was conducted in the context of different sampling campaigns and with different initial goals in the sampling work. Other studies, used in the compilation of published data in chapter 4, sampled with minimum mesh sizes ranging from 63 to 150 µm (Table 4.1). Further variation in sampling is present in the sampled depth intervals, both in terms of the height of each interval (minimum of 15 m and maximum of 1000 m) and the absolute maximum depth (80 to 2000 m; metadata linked in Table 4.1, Table 4.2). Differences in the sampling depth intervals can influence the precision in determining where planktonic foraminifera calcification is happening (section 4.2.2). With sampling in the upper water column, plankton nets can retrieve living and dead planktonic foraminifera. Directly after sampling, living foraminifera can be identified based on the presence and colour of the cytoplasm within the calcite shell (Meilland et al., 2022). When samples cannot be analysed directly after retrieval, staining with a rose-Bengal ethanol mixture can be used. Used directly after sampling, this makes organic compounds like the cytoplasm of the foraminifera visible in dried samples (Schönfeld et al., 2013). This method is subject to inaccuracies, as remaining cytoplasm in already dead foraminifera is stained as well (Schönfeld et al., 2013). In the data worked on for this thesis, distinction of living and dead foraminifera was done directly after sampling in data sets from two sampling campaigns (MSM44, MSM66). This was not possible during the sampling of the third data set used in this thesis, which is why staining with rose-Bengal was done there. In the studied published data, staining with rose-Bengal was used in some studies (Volkmann, 2000; Stangeew, 2001). Other studies did not distinguish between living and dead foraminifera at all, making an assessment of changes with depth of living foraminifera impossible.

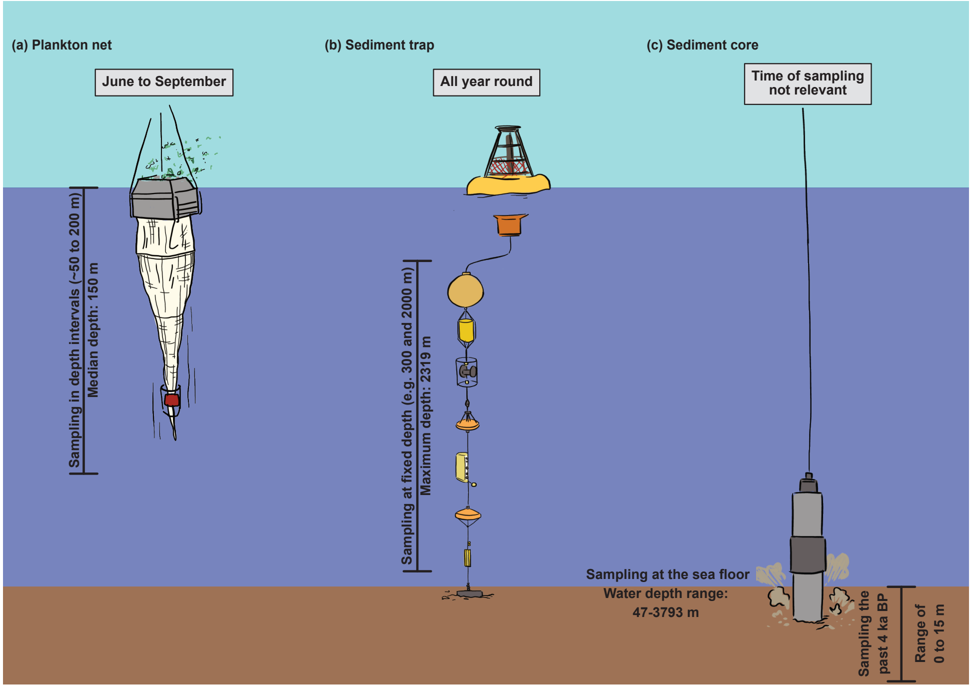

FIGURE 2.1: Overview on the three used methods to sample planktonic foraminifera from the water column and in sediments. The time period in which sampling in the Subarctic and Arctic realm was done in the used samples is indicated, as well as the relevant depth intervals of sampling. Illustrations of the sampling devices copyright: Alison McCreesh.

Sampling of planktonic foraminifera on longer time scales is done with sediment traps (Fig. 2.1b). Moored to the sea floor, they remain at a fixed position, collection sinking particles at different depth intervals in collector cups rotating with time, such that defined time intervals are sampled sequentially (Zeitzschel et al., 1978). In contrast to samples from plankton nets, distinction of alive and dead foraminifera upon trapping is not possible here. The advantage of this sampling method is the possibility to sample throughout a whole year and beyond. Sediment traps enable long-term monitoring of sinking particles at a fixed position (e.g. in the Fram Strait; Soltwedel et al., 2005). The sampling device used for this study and in Jensen, 1998, from which data is included in the study presented in chapter 5, is a modified automatic Kiel sediment trap with a sampling area of 0.5 m² and 20 collector cups. In the sampling set-up, differences were present in the sampled depth intervals (Table 5.1). The trapping depth is important to consider in terms of dissolution occurring at different depth intervals (Sulpis et al., 2021), and influences from resuspension of material from the ocean floor (Lalande et al., 2016). The trapping intervals per collector cup are slightly different between the studied stations. The larger the sampling interval, the harder a direct comparison with average environmental conditions, at least when they vary within the time period of sampling into one cup. After retrieval, the samples are split to analyse different components separately. On the samples worked on for this thesis, splits of either 1/8 or 1/16 were analysed. This was the same in most samples from Jensen, 1998 as well, but also smaller splits (up to 1/128) were analysed. The smaller the analysed split, the less likely it is to have a representative amount of foraminifera shells in the sample, especially in time periods of overall low abundances of foraminifera (Jensen, 1998).

Planktonic foraminifera shells accumulating at the sea floor are retrieved by sampling of sediment cores (Fig. 2.1c). In the context of this work, the focus is set on the past four thousand years before present (ka BP, present defined as 1950 CE; chapter 6). The determination of age depends on the used age model and is overall subject to uncertainties (Lacourse and Gajewski, 2020). The age of samples is not the main focus of this research work, which makes uncertainties in the exact age determination less relevant. Nevertheless, relevant assumptions on sedimentation rates are based on the age of sediments. The sediment cores analysed for this study have been dates using AMS ^{14}C dating. Between the studied sediment cores from the literature, the sampling resolution varies, with sampling being done in intervals from every centimetre (e.g. in data from Sarnthein et al., 2003), every second centimetre (e.g. the sediment cores analysed for this thesis) to every fifth centimetre (e.g. in data from Duplessy et al., 2001). More influence on the conducted analysis is based on counting foraminifera shells from different size fractions (Table B.1). As already described for sampling with plankton nets, the larger the size fraction, the higher the chance to underestimate the total amount of planktonic foraminifera because smaller shells are not analysed. In the for this study analysed samples, foraminifera were picked either from the whole sample in the size fraction >106 µm, or from a split of it (1/4 to 1/32, Table 6.1) depending on the total amount of planktonic foraminifera shells in the sample. Other studies also analysed splits of samples, with varying quantities, depending on the number of foraminifera shells present in the sample (Jensen, 1998; Sarnthein et al., 2003; Jackson et al., 2022).

2.2 Isolation of planktonic foraminifera shells

Planktonic foraminifera from the different sample types were picked from dried samples. They were identified to the species level based on Brummer and Kucera, 2022 and counted using a Zeiss Stemi 2000 binocular microscope. Species names in data from other studies deviating from the names given in Brummer and Kucera, 2022 were aligned to this definition. This is mainly of relevance regarding the species *N. pachyderma* and *N. incompta*: Formerly, these species were labelled as *N. pachyderma* sinistral and dextral (e.g. in Volkmann, 2000; Stangeew, 2001), instead of being treated as the separate species they were identified as later-on (Darling et al., 2006). In samples where the number of foraminifera per sample was high, smaller splits were analysed to reduce the number of shells that need to be extracted (e.g. in

Jensen, 1998; Sarnthein et al., 2003). In chapter 4, only data on the most abundant Arctic species, *N. pachyderma*, is presented. However, all foraminifera shells were retrieved from the samples from campaign PS93.1, distinguished to the species level, counted and shell size (section 2.3) and shell weight (section 2.4) were measured. This data is available online (see appendix C).

2.3 Shell size measurements

The size of individual foraminifera shells from samples analysed in this thesis was measured using a KEYENCE VHX-6000 digital microscope. Measurements were done on the umbilical view of each shell. Images of the shells were taken with the microscope under a 200x magnification. The size was measured using the Keyence Software, distinguishing the foraminifera shell from the background of the micropaleontological slide based on the colour (white shell on a blue background, Fig. 1.3). The measured size parameters are minimum and maximum diameter, perimeter and area. In other studies, size measurements were also conducted on the umbilical view, but without a measurement software (e.g. Stangeew, 2001), which, due to time restriction, can result in fewer size measurements. In most studies, shell sizes were not measured, but sometimes shells were divided into different size classes by sieving (e.g. Jensen, 1998; Kohfeld et al., 1996).

2.4 Shell weight measurements

Shell weights of planktonic foraminifera from samples worked on in the context of this thesis were measured on 1 to 200 foraminifera shells per sample, measuring different species from distinct samples individually. The measurements were done using a Sartorius SE2 ultra-micro balance (nominal resolution of 0.1 µg; chapter 4, chapter 5), a Sartorius XM1000P micro balance (nominal resolution of 1 µg; chapter 6; large bulk samples from sediment cores), and a Sartorius Cubis®II ultra-micro lab balance (nominal resolution of 0.1 µg; chapter 6; individual shell size measurements). Measurements were mainly done on bulk samples without considering size ranges to increase the precision of weight measurements for light samples. Therefore, average shell weights of each species in each sample were determined dividing the weight of all shells in the sample by the number of shells in it. Not considering size ranges, these averages could partly present over- or underestimations if a few unusual small or large shells were part of the sample.
For the weight measurements, foraminifera shells were placed in aluminium weighing boats. Beforehand, these were weighted four times to increase the precision of the measured weight. Foraminifera shells were then placed in the weighing boats. This was either done using a brush and water, leaving the samples in the room for at least 24 hours before weighing to let the water evaporate, or without water, measuring the weight directly. The weight measurement of the foraminifera shells was then repeated four to 15 times, using the average weight of all measurements for further analysis. Table 2.1 shows the effect of the repetitions on the standard deviation of the measured weight: The higher the number of repetitions, the lower the standard deviation. With the clearly higher standard deviation in samples from sediment cores, which were weighted with a nominal resolution of 1 µg in contrast to a resolution of 0.1 µg in the other measurements, it becomes visible that the precision of the scale is important to conduct most precise measurements. In other studies presenting shell weight data, the methodologies were similar, using an ultra-micro balance

with a resolution of 0.1 µg and measuring mainly bulk samples. In Stangeew, 2001, shells larger than 250 µm, hence the likely heavier shells, were measured individually, while others were measured in bulk samples.

TABLE 2.1: Standard deviation of the weight measurements of planktonic foraminifera shells in relation to the average weight of the samples and the number of repetitions that were done upon each weight measurement. The shown weight does not represent individual shell weights, but average weights of all measured bulk samples.

	Number of repititions	**Average weight [µg]**	**Average standard deviation**
All sample types		127.9	0.8
Plankton net	10 - 15	26.3	0.2
Sediment trap	6	58.7	0.6
Sediment core	4	416.7	1.9

2.5 Calculation of planktonic foraminifera calcite mass flux

Mass fluxes of planktonic foraminifera calcite from the water column towards the ocean floor and mass accumulation rates in the sediments were calculated based on shell weights and shell abundances. For in this study newly analysed samples, this was done based on the measured shell weights. Average weights from the here conducted measurements were then used to estimate the calcite mass flux of planktonic foraminifera using shell abundances from published data. The details on the calculations and the used weights for this are given in the respective sections (section 4.2.3, section 5.2.2, section 6.2.4).

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Chapter 3

Outline of manuscript

This dissertation presents three manuscripts (in different stages of publication) in a cumulative format. The research focuses on the contribution of planktonic foraminifera to the marine carbon cycle in the Arctic Ocean. In the following overview of the manuscripts, a short summary, the authors contributions, and a comprehensive overview of my own contribution to each of the presented work is given.

3.1 Upper-ocean flux of biogenic calcite

TELL, F., JONKERS L., MEILLAND J., and KUCERA M.: *Upper-ocean flux of biogenic calcite produced by the Arctic planktonic foraminifera Neogloboquadrina pachyderma*, 19 (20), 4903-4927, https://doi.org/10.5194/bg-19-4903-2022, 2022.

Short summary The study presents an assessment of the productive zone of the Arctic planktonic foraminifera *N. pachyderma* using plankton net samples from all over the Arctic and Subarctic Ocean, with a focus on the Nordic Seas and Baffin Bay. A regionally variable productive zone is detected. Attenuation of the mass flux towards depths occurs below the base of the productive zone, with a mean loss rate of 6.6 % per 100 m. This is important to consider in total estimates of mass fluxes of planktonic foraminifera settling downwards.

Author contributions The study was designed by all authors. FT carried out the laboratory work with help from JM and the data analysis with help from LJ. All authors contributed to the interpretation and discussion of the results. FT wrote the paper with contributions from MK, LJ and JM.

Detailed own contributions For this study, I isolated planktonic foraminifera shells from 37 samples collected with plankton nets during the PS93.1 campaign and measured their size and weight, as described in the sections 2.2, 2.3 and 2.4. I harmonized size measurements done by B. Lübben, the technician of the working group, on foraminifera shells retrieved during the campaigns MSM44 and MSM66. I sought out published data on the planktonic foraminifera *N. pachyderma* from plankton net samples from the research area and transformed the collected data sets into one. Based on the results from the conducted shell weight measurements, I calculated the base of the productive zone and the foraminifera mass flux towards depth from alldata sets. I conducted the statistical analysis presented in the manuscript using the scripting language R, and likewise produced all figures. I prepared the first draft of the manuscript, and in the further process, included and incorporated remarks from all co-authors. Moreover, I managed the submission process of the manuscript, compiling responses to reviewers during the review process and finalizing the manuscript for publication.

3.2 Drivers of planktonic foraminifera calcite flux in the Nordic Seas

TELL, F., JONKERS L., MEILLAND J., NÖTHIG, E-M., and KUCERA, M.: *Drivers of planktonic foraminifera calcite flux in the Nordic Seas*, in preparation for submission for publication, 2023.

Short summary The analysis of planktonic foraminifera mass fluxes from sediment trap data is done in connection to environmental data on water temperature, solar insolation, sea ice concentration and chlorophyll α concentration. While all parameters can be connected to the detected seasonal variability, no explanation of large interannual magnitude changes is possible based on these parameters. The research nevertheless gives an overview on the present variability and the importance of the mass flux variability of planktonic foraminifera in the Nordic Seas towards depth.

Author contributions The study was designed by FT, MK, JM and LJ. Access to the data and further information on the HAUSGARTEN samples was given by EN. FT carried out the laboratory work on the platonic foraminifera with help from JM. Data analysis was conducted by FT with help from LJ. All authors contributed to the interpretation and discussion of the results. FT wrote the paper with contributions from LJ, JM, EN and MK.

Detailed own contributions I isolated planktonic foraminifera shells from 40 samples from sediment traps and determined them to the species level (section 2.2). I conducted size measurements of shells (section 2.3) with P. M. Nadar, a student helper, who was instructed and supervised by me throughout his work. Measurements of shell weights (section 2.4) were done by myself. I harmonized published data from three sediment trap stations in the Nordic seas with my data. I collected additional environmental data from satellite data (chlorophyll α, sea surface temperature) and the world ocean atlas (MLD) and used the data to calculate average values of the parameters in the vicinity of the studied sediment trap stations. With advice from my co-authors, I performed all statistical analysis myself using the scripting language R, and produced all figures. The first draft of the manuscript was written by myself. The manuscript was thoroughly discussed with all co-authors and their additions and comments were incorporated by me to write the final version.

3.3 Carbonate burial of planktonic foraminifera

TELL, F., DE VERNAL, A., JONKERS L., MEILLAND J., RAPP, S. K., and KUCERA, M.: *Carbonate burial of planktonic foraminifera in the Arctic Ocean during the late Holocene*, in preparation for submission for publication, 2023.

Short summary We calculated the average mass accumulation rate of planktonic foraminifera during the past 4000 years before present from data on planktonic foraminifera from sediment cores from the Central Arctic Ocean, the Nordic Seas and the Labrador Sea. It is shown that on average, they contribute to 30 % of total $CaCO_3$ accumulation. Even though water temperature can overall be related to regional differences, it cannot explain the presented variability in foraminifera accumulation rates, neither can parameters of productivity or total mass accumulation. The data shows that dissolution at the sea floor is not important in the research area.

Author contributions The study was designed by all authors. FT carried out the laboratory work on the platonic foraminifera with help from AdV. SKR compiled the data base on published sediment core data on planktonic foraminifera with support from FT. Data analysis was conducted by FT with help from LJ. All authors contributed to the interpretation and discussion of the results. FT wrote the paper with contributions from LJ, JM, AdV, SKR and MK.

Detailed own contributions For this manuscript, I isolated planktonic foraminifera from 64 samples from three sediment cores from the Labrador Sea. I counted all shells after the determination to the species level and measured bulk weights in subsets of the sample as well as the total sample (section 2.4). I further conducted shell size measurements on 88 shells from the samples. I used a data base on published sediment cores compiled by S. K. Rapp (as part of a bachelor thesis from 2020, which was supported by me). I updated this data base with newly published data. After bringing all published data together, I used the results from shell weight measurements to calculate mass accumulation rates in all sediment cores. I retreived data on sea surface temperatures from the World Ocean Atlas and satellite data on the chlorophyll α concentration and calculated average values from these data sets for all relevant locations in this study. Using the scripting language R, I performed statistical analysis to decipher the relationship between the data sets, and produced all presented figures. Followingly, I wrote the first draft of the manuscript and discussed it with the co-authors. I included their additions and incorpoerated their comments to write the final version of the manuscript, presented in this thesis.

Chapter 4

Upper-ocean flux of biogenic calcite produced by the Arctic planktonic foraminifera *Neogloboquadrina pachyderma*

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Abstract With ongoing warming and sea ice loss, the Arctic Ocean and its marginal seas as a habitat for pelagic calcifiers are changing, possibly resulting in modifications of the regional carbonate cycle and the composition of the seafloor sediment. A substantial part of the pelagic carbonate production in the Arctic is due to the calcification of the dominant planktonic foraminifera species *Neogloboquadrina pachyderma*. To quantify carbonate production and loss in the upper water layer by this important Arctic calcifier, we compile and analyse data from vertical profiles in the upper water column of shell number concentration, shell sizes and weights of this species across the Arctic region during summer. Our data is inconclusive on whether the species performs ontogenetic vertical migration throughout its lifecycle, or whether individual specimens calcify at a fixed depth within the vertical habitat. The base of the productive zone of the species is on average located below 100 m and at maximum at 300 m and is regionally highly variable. The calcite flux immediately below the productive zone (export flux) is on average 8 mg $CaCO_3$ m^{-2} d^{-1}, and we observe that this flux is attenuated until at least 300 m below the base of the productive zone by a mean rate of 6.6 % per 100 m. Regionally, the summer export flux of *N. pachyderma* calcite varies by more than two orders of magnitude and the estimated mean export flux below the twilight zone is sufficient to account for about a quarter of the total pelagic carbonate flux in the region. These results indicate that estimates of the Arctic pelagic carbonate budget will have to account for large regional differences in the export flux of the major pelagic calcifiers and confirm that substantial attenuation of the export flux occurs in the twilight zone.

4.1 Introduction

The world's oceans play an important role in the global carbon cycle, which is at present strongly influenced by anthropogenic carbon emissions (Friedlingstein et al., 2019). The solubility of CO_2 in water is dependent on temperature, being higher at lower water temperatures. Therefore, on a global basis, the oceanic take-up of atmospheric CO_2 is especially high in the colder Arctic Ocean (Steinacher et al., 2009; Miller et al., 2014). Next to the redistribution of dissolved CO_2 by ocean circulation, the surface-ocean carbon is also removed and sequestered in the deep ocean and ocean sediments by the two major carbon pumps: the biological carbon pump and the so called 'counter pump'. The biological carbon pump transports particulate organic carbon that is fixed by photosynthesis into the deep ocean where a small part of it can be buried in the sediments (Riebesell et al., 2009; Henehan et al., 2017). In contrast, the $CaCO_3$ counter pump exports biogenic carbonate produced by calcifying organisms such as pteropods, coccolithophores and planktonic foraminifera from the productive zone. Initially, CO_2 is released during calcification, but on longer time scales, a large part of the carbon fixed in biogenic carbonate is buried in the sediments and stored on geological time scales (Zeebe, 2012; Bauerfeind et al., 2014; Salter et al., 2014; Schiebel et al., 2018).

From among the pelagic calcifiers, planktonic foraminifera, calcite shell-building marine protists, are globally responsible for an estimated $CaCO_3$ sedimentation at the sea floor of 0.71 Gt yr^{-1}, accounting for more than a quarter of the global pelagic calcite flux (Schiebel, 2002). Their contribution is likely even higher in the high-latitude oceans, where the main pelagic calcite producers, the Coccolithophoridae, are less abundant (Baumann et al., 2000; Daniels et al., 2016). For example, at the Northern Svalbard margin, summertime calcite fluxes inferred from standing stocks of planktonic foraminifera at 100 m depth form about 4 - 34 % of total $CaCO_3$ fluxes in that area (Anglada-Ortiz et al., 2021).

With ongoing global warming, the Arctic habitat is changing, becoming more hospitable for subpolar species (Wassmann et al., 2015). Pelagic calcifiers, including foraminifera, react sensitively to the ongoing transformation of their pelagic habitat (e.g. Field et al., 2006; Schiebel et al., 2018; Jonkers et al., 2019), and show increasing standing stocks in the North Atlantic (Beaugrand et al., 2013). Therefore, it is likely that continued warming and associated ecological transformation of the Arctic Ocean and its adjacent seas will also lead to changes in the carbonate counter pump and the biological carbon pump. This could have consequences for the capacity of the Arctic to take up atmospheric carbon dioxide, as well for the seawater chemistry including the nature of the sediments and thus the habitat for benthic life in this region.

In many parts of the ocean, a considerable portion of the biogenic carbonate is dissolved in the upper layer of the ocean because of processes like digestion by predators or dissolution by metabolic CO_2 released during microbial degradation of biomass surrounding the biomineral (Sulpis et al., 2021). Therefore, estimates of carbonate production and export require observations from the water column, immediately below the zone where the production occurs. Moored sediment traps provide direct observations on the seasonal cycle of biogenic carbonate flux. However, they intercept export fluxes towards the ocean floor and are typically anchored deeper than the productive zone (Wolfteich, 1994; Jensen, 1998; Jonkers et al., 2010), hence record a potentially attenuated export flux. Also, sediment trap records are too scarce in the Arctic (Soltwedel et al., 2005) to resolve the large spatial variability in planktonic foraminifera abundances and thus calcite fluxes (Volkmann, 2000b; Greco et al., 2019). Next to observations from sediment traps, planktonic foraminifera calcite fluxes can also be estimated from vertically resolved net tow profiles of standing stocks in the upper water column (Schiebel and Hemleben, 2000). Vertical profiles provide only a snapshot of the flux at the time of sampling. Also, due to the extensive sea ice cover, the time of sampling by research vessels in the Arctic is almost completely restricted to the summer season (Greco et al., 2019). However, vertically-resolved net tow profiles of shell number concentration in the water column allow us to characterise the zone in the upper water layer where carbonate production occurs and thus to quantify the new production and export production as well as the rate of loss beneath it (Sulpis et al., 2021), provided that the profiles extend to below the productive zone.

The dominant planktonic foraminifera species in the Arctic Ocean is *Neogloboquadrina pachyderma* (Carstens et al., 1997; Volkmann, 2000b; Schiebel et al., 2017; Anglada-Ortiz et al., 2021). Like all extant planktonic foraminifera, the species builds its shell by sequential addition of increasingly larger chambers, such that the largest amount of calcification occurs during the final stages of its life. In addition, this species is known to often add at the end of its life cycle a calcite crust that covers all chambers of the last whorl (Kohfeld et al., 1996; Bauch et al., 1997) and can be so thick that it accounts for most of the mass of the shell (Stangeew, 2001c). Encrusted specimens dominate sedimentary assemblages (Vilks, 1975; Kohfeld et al., 1996; Volkmann, 2000a) as encrusted shells are more resistant to dissolution.

These observations imply that understanding and quantifying the carbonate production and loss in the upper water layer by this dominant Arctic foraminifera requires understanding its vertical habitat. Many extant species of planktonic foraminifera, including *N. pachyderma*, have been suggested to perform ontogenetic vertical migration (OVM; Hemleben et al., 1989), with juvenile specimens inhabiting surface waters and slowly sinking as they mature until the depth at which the last chambers or crusts are formed. Such ontogenetic migration may cause the depth where most calcification takes place to be below the main depth habitat. It is therefore imperative to also consider the vertical pattern of calcification. Cytoplasm-bearing specimens of *N. pachyderma* occur from the surface down to about 300 m water depth, with typically an abundance maximum around 100 m (Volkmann, 2000b; Stangeew, 2001c; Greco et al., 2019). The variability of the preferred depth habitat depends on the local environmental conditions like presence of sea ice and productivity (Greco et al., 2019).

Previous work is inconclusive as to whether *N. pachyderma* performs OVM. Some studies provide evidence for an extensive OVM with the majority of calcite addition occurring towards the deep end of the habitat (Arikawa, 1983; Stangeew, 2001c; Manno and Pavlov, 2014), while other studies are inconclusive (Pados et al., 2015) or indicate that calcification up to the terminal stage may occur at any depth within the habitat (Kohfeld et al., 1996; Simstich, 1999; Volkmann and Mensch, 2001). Here we make use of a large collection of vertically resolved abundance profiles of *N. pachyderma* in the Arctic and Subarctic, combining published data with new observations, to i) resolve the calcification behaviour of the species, ii) estimate its summertime calcite export flux, and iii) its attenuation below the production zone. To distinguish the production and export zones and to determine the average depth of calcification of *N. pachyderma*, we analyse vertical profiles of the abundance of cytoplasm-bearing and empty shells, shell size spectra and mean shell weights. The results allow us to constrain the spatial variability in the calcite production of *N. pachyderma* in the Arctic Ocean during summer periods, and quantify the shell dissolution within the upper water column.

4.2 Material and methods

4.2.1 Planktonic foraminifera samples

This study is based on a combination of existing and new data from vertically resolved profiles of plankton net samples from the Arctic Ocean and adjacent seas (Table 4.1; Fig. 4.1). We used all data from the studies by Kohfeld et al., 1996, Bauch et al., 1997, Kohfeld, 1998, Volkmann, 2000b, Stangeew, 2001c, Schiebel, 2002, Simstich et al., 2003, Pados and Spielhagen, 2014 and Greco et al., 2019, containing information on at least one of the three parameters abundance, shell size or weight : size ratio of the planktonic foraminifera *N. pachyderma*, resulting in a data set of 112 depth profiles. As data on shell size and weight, which are important for estimates of calcite mass flux, are scarce in existing publications, we have extended the dataset by 36 new vertical profiles taken during expeditions in the Baffin Bay (MSM44, July 2015 and MSM66, July 2017) and in the Fram Strait (PS93.1, July 2015; Table 4.2, Fig. 4.1). All of the new profiles consist of samples from five depth intervals (Table 4.3), sampled with a multiple closing plankton net (Hydro-Bios, Kiel) with an opening of 0.25 m² and a mesh size of 100 µm during the MSM44 and MSM66 cruises and 55 µm during PS93.1. Shell number concentrations of various planktonic foraminifera species from five depth profiles from PS93.1 are published in Greco, Werner, et al., 2021. Here we recounted the number of shells of *N. pachyderma* in those profiles, generated new counts from three further profiles in the same expedition (PS93/011-3, PS93/016-3, PS93/017-3), and added measurements on shell size and weight on shells from all eight profiles.

Samples from the Baffin Bay were either processed on board or stored at -80 °C until processed onshore. All foraminifera were manually removed from each sample and counted. The counts were made separately for cytoplasm-bearing shells and empty shells, differentiated during the processing of the wet samples. As recently deceased foraminifera can still contain cytoplasm, this leads to a bias in the numbers in favour of individuals interpreted as being alive upon sampling. Shell size (maximum diameter) was measured with the software ImageJ on pictures taken through a SteREO Discovery.V8 microscope. Samples from the Fram Strait were stained using a Rose Bengal/ethanol (96 %) mixture to enable the differentiation of empty and cytoplasm-bearing shells. The samples were stored at 4 °C until processing. They were then washed over a 250 µm and 63 µm sieve. The residues were dried on filter paper and the foraminifera were separated from the dried residues. In accordance with data from earlier studies, white or transparent shells were classified as empty (e.g. Fig. 4.2e), all other (pink) shells as cytoplasm-bearing (e.g. Fig. 4.2f), assumed to represent specimens that were alive during retrieval. As rose Bengal might be staining recently dead specimens because of remaining cytoplasm in the shells (Schönfeld et al., 2013), there is a possible bias towards too high numbers of cytoplasm-bearing shells. Maximum shell diameter, perimeter and area of the two-dimensional cross-section of each individual in the umbilical view were measured with a KEYENCE VHX-6000 digital microscope. As heavily calcified shells of *N. pachyderma* tend to be less lobate than non-encrusted specimens, the ratio of perimeter and area can indicate the foraminifera shell shape (Fig. 4.2e-g): the more calcified the shell, the lower the ratio. The total weight of all shells was determined for each sample separately for shells that were considered empty and those that were considered cytoplasm-bearing, using a Sartorius SE2 ultra-micro balance (nominal resolution of 0.1 µg).

TABLE 4.1: Overview of the used samples of vertical plankton net data of *N. pachyderma*. At M21/4 and M21/5, the profile numbers in brackets indicate the number of individually labelled and taken profiles, which were combined into fewer profiles due to sampling at the same position at different depth intervals, as indicated by the number before the brackets. (Last access for all PANGAEA links is 30 May and 30 April 2022.)

Campaign	**Region**	**Start Date (dd.mm.yyyy)**	**Number of profiles**	**Mesh / minimum sieving size [µm]**	**Reference**	**Data Source**
EN199	Greenland Sea	26.07.1989	1	150	Kohfeld (1998)	Original publication
M21/4	Norwegian Sea, Greenland Sea, Fram Strait	28.06.1992	14 (29)	100	Schiebel (2002)	From `https://doi.org/10.1594/PANGAEA.75647` to `PANGAEA.75676`
M21/5	Norwegian Sea, Greenland Sea	05.07.1992	6 (14)	100	Schiebel (2002)	From `https://doi.org/10.1594/PANGAEA.75719` to `PANGAEA.75732`
M39/4	Labrador Sea	12.07.1997	8	63	Stangeew (2001)	`https://doi.pangaea.de/10.1594/PANGAEA.706908`
MSM09/2	Baffin Bay	05.09.2008	8	100	Greco et al. (2019)	`https://doi.pangaea.de/10.1594/PANGAEA.905270`
MSM44	Baffin Bay	02.07.2015	13	100	This study	
MSM66	Baffin Bay	24.07.2017	15	100	This study	
NEWP-92	Fram Strait	27.07.1992	2	150	Kohfeld et al. (1996)	`https://doi.pangaea.de/10.1594/PANGAEA.905270`
NEWP-93	Fram Strait	27.07.1993	2	150	Kohfeld et al. (1996)	`https://doi.pangaea.de/10.1594/PANGAEA.905270`
ARK-IV/3 (PS11)	Nansen Basin	08.07.1987	10	160	Bauch et al. (1997)	Original publication
ARK-X/1 (PS31)	Norwegian Sea	10.07.1994	2	125	Simstich et al. (2003)	`https://doi.pangaea.de/10.1594/PANGAEA.81987`

ARK-X/2 (PS31)	Norwegian Sea	10.07.1994	1	125	Simstich et al. (2003)	`https://doi.pangaea.de/10.1594/PANGAEA.82001`
ARK-XI/1 (PS36)	Laptev Sea	03.08.1995	16	125	Volkmann (2001)	`https://doi.pangaea.de/10.1594/PANGAEA.91119`
ARK-XIII/2 (PS44)	Fram Strait, Barents Sea	27.06.1997	15	125	Volkmann (2001)	`https://doi.pangaea.de/10.1594/PANGAEA.136881`
ARK-XV/1 (PS55)	Greenland Sea	11.07.1999	9	63	Stangeew (2001)	`https://doi.pangaea.de/10.1594/PANGAEA.706908`
ARK-XV/2 (PS55)	Fram Strait	25.07.1999	8	63	Stangeew (2001)	`https://doi.pangaea.de/10.1594/PANGAEA.706908`
ARK-XXVI/1 (PS78)	Fram Strait	25.06.2011	10	100	Pados and Spielhagen (2014)	`https://doi.pangaea.de/10.1594/PANGAEA.905270`
PS93.1 (ARK-XXIX/2.1	Fram Strait	02.07.2015	8	63	This study	

The ratio between the total weight and the mean maximum diameter (size) is here used as an indicator of the mean calcification intensity. Upon sampling, no direct differentiation between shells with or without a crust was done. Encrusted shells are identified by their larger weight than non-encrusted shells, different shell texture and less lobate shape (Fig. 4.2g).

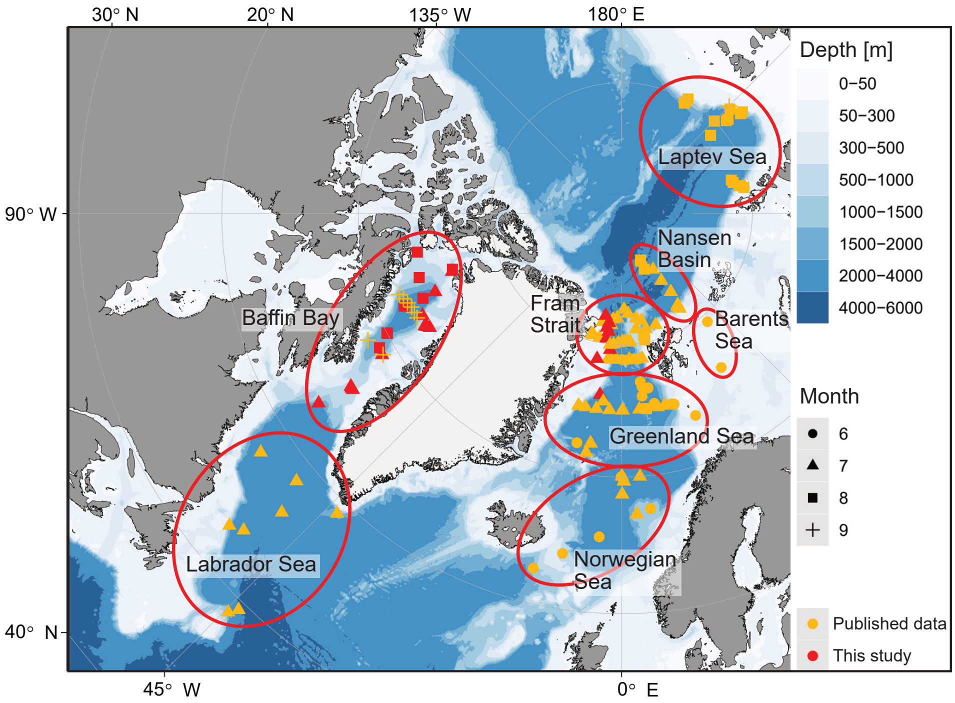

FIGURE 4.1: Overview on the research area with different regions (circled in red) sampled during different research cruises. Published data (orange) and new data (red) used in this study as well as the sampling periods (symbols) are marked. Land and glacier polygons from Natural Earth Data (CC0), bathymetry from Amante and Eakins, 2009, using ggOceanMaps in R (Vihtakari, 2021).

4.2.2 Productive zone

To determine the depth range where shell calcification occurred and below which the export began, the base of the productive zone (BPZ) of *N. pachyderma* was defined for each profile by considering the changes in shell abundance with depth. Following the concept of Peeters and Brummer, 2002, the BPZ is the depth where the shell abundance begins to substantially decline. It was calculated after Lončarić et al., 2006:

$$Z_{BPZ} = \frac{C_n - C_{exp}}{C_{n-1}}(Z_n - Z_{n-1}) + Z_{n-1} \tag{4.1}$$

where C_n is the concentration of shell numbers within the transition zone (i.e. the last depth interval before the rapid decline in shell abundance) which was defined visually for every profile as exemplarily shown in Fig. 4.2a, C_{exp} is the average shell abundance, weighted by the thickness of the sampled depth interval, in all depths below C_n, C_{n-1} is the foraminifera abundance in the depth interval above C_n. Z_n represents the top of sampling depth of the transition zone, and Z_{n-1} its bottom.

TABLE 4.2: Overview on the numbers of depth profiles used in the study, with varying numbers depending on the studied parameter.

Total profiles		148
	published data	112
	new profiles added by this study	36
Profiles to determine BPZ		126
	calculated after Lončarić et al., 2006	86
	determined by range end	40
Profiles with size measurements		23
Profiles with calcification intenstiy measurements		13
Profiles with calcification intensity trend		8
	cytoplasm-bearing shells	5
	empty shells	5
	nonencrusted shells	3
	(heavily) encrusted shells	3
Profiles to calculate mass flux		147

The equation applies to cases where the shell number concentration decreases with depth. Where this is not the case (such as where there is a distinct subsurface maximum), the equation cannot be used as the estimated BPZ would appear to lie below the depth interval of the transition zone. This was the case in 37 out of 126 profiles. In addition, in three profiles, the transition zone corresponded to the uppermost sampling layer, and the equation could not be applied. For those 40 profiles, the BPZ was defined as the bottom depth of the transition zone (Fig. 4.2a, $Z_{\text{BPZ (range end)}}$). This can result in a bias towards the estimated BPZ being located below the actual position. This bias is restricted by the overall sampling interval (median: 50 m) and has no effect on our flux estimates which are based on average shell abundances below the BPZ. In ten profiles, calculation of the BPZ was not possible as no clear transition zone was present within the sample range, including two profiles in which the abundance was zero at the total station. The maximum sampling depth of those profiles was between 180 m and 300 m, implying that the transition zone either occurred in the bottom interval or was not yet reached. Because of this ambiguity, these profiles were not used for the BPZ analysis. For profiles where abundance data were available for only one or two depth intervals at the surface (9 Profiles), estimation of the BPZ was not possible either. In total, the BPZ was determined in 126 profiles and the different methods to define BPZ were separated in the interpretation. For an overview on the number of profiles that were available for the different calculations, see Table 4.2.

The above definition of the BPZ does not rely on the separation of living (cytoplasm-bearing) and dead (empty) shells during sampling, a parameter that was not systematically recorded. The separation is ambiguous as cytoplasm decomposition takes time after death and individuals already dead could still be considered as living due to the presence of residual cytoplasm (Schiebel et al., 1995). This ambiguity is larger at greater depth, where the probability of finding living specimens becomes smaller.

TABLE 4.3: Overview on the sampled depth intervals from the stations of MSM44, MSM66 and PS93.1. Abundances of *N. pachyderma* of profiles marked with (*) are also published in Greco, Werner, et al., 2021, but counts presented in the studies were done independently from that publication.

Campaign	Event	Longitude	Latitude	Date	Net depth intervals (m)
MSM44					
	GeoB19906-2	-57.982	63.074	02.07.2015	0 - 100, 100 - 200, 200 - 300, 300 - 500, 500 - 700
	GeoB19912-2	-57.450	65.720	03.07.2015	60 - 80
	GeoB19913-1	-57.127	65.705	03.07.2015	0 - 100, 100 - 200, 200 - 300, 300 - 400, 400 - 500
	GeoB19913-2	-57.127	65.705	03.07.2015	60 - 80
	GeoB19914-2	-57.442	65.715	03.07.2015	60 - 80
	GeoB19915-2	-56.774	65.707	04.07.2015	60 - 80
	GeoB19922-3	-60.286	72.736	07.07.2015	60 - 80
	GeoB19923-1	-60.120	72.779	07.07.2015	0 - 100, 100 - 200, 200 - 300, 300 - 400, 400 - 500
	GeoB19923-2	-60.120	72.779	07.07.2015	60 - 80
	GeoB19924-2	-59.768	72.870	07.07.2015	60 - 80
	GeoB19925-2	-59.253	73.000	07.07.2015	60 - 80
	GeoB19929-2	-67.218	74.575	10.07.2015	0 - 100, 100 - 200, 200 - 300, 300 - 400, 400 - 500
	GeoB19929-3	-67.218	74.575	10.07.2015	60 - 80
MSM66					
	GeoB22304-2	-59.477	68.903	24.07.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22308-2	-62.887	72.968	26.07.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22313-2	-71.091	76.294	30.07.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22323-2	-71.827	76.386	03.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22327-2	-79.308	74.166	05.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22329-2	-66.91	73.544	06.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22333-2	-72.477	73.826	07.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22360-3	-63.032	70.000	19.08.2017	0 - 60, 60 - 90, 90 - 120, 120 - 150, 150 - 180
	GeoB22361-2	-67.000	72.000	19.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200

	GeoB22361-3	-67.000	72.000	19.08.2017	0 - 60, 60 - 90, 90 - 120, 120 - 150, 150 - 180
	GeoB22361-4	-67.000	72.000	19.08.2017	0 - 60, 60 - 90, 90 - 120, 120 - 150, 150 - 180
	GeoB22362-2	-62.892	70.000	20.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22363-3	-62.892	70.000	20.08.2017	0 - 30, 30 - 60, 60 - 90, 90 - 120, 120 - 150
	GeoB22363-4	-62.892	70.000	20.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22365-2	-61.081	69.000	20.08.2017	0 - 20, 20 - 50, 50 - 100, 100 - 150, 150 - 200
	GeoB22365-3	-61.081	69.000	20.08.2017	0 - 30, 30 - 60, 60 - 90, 90 - 120, 120 - 150
PS93.1					
	PS 93.1 11-3	-6.963	80.382	02.07.2015	0 - 20, 20 - 80, 80 - 140, 140 - 200, 200 - 230
	PS 93.1 16-3	-7.341	81.217	03.07.2015	0 - 50, 50 - 100, 100 - 220, 220 - 390, 390 - 600
	PS 93.1 17-3	-6.587	81.595	04.07.2015	0 - 20, 20 - 90
	PS 93.1 20-3 (*)	-8.901	82.096	05.07.2015	0 - 15, 2.6 - 80, 80 - 220, 220 - 320, 320 - 600
	PS 93.1 24-2 (*)	-6.365	80.913	07.07.2015	0 - 15, 15 - 55, 55 - 175, 175 - 350, 350 - 550
	PS 93.1 30-3 (*)	-4.844	79.554	09.07.2015	0 - 35, 35 - 160, 160 - 250, 250 - 350, 350 - 500
	PS 93.1 39-3 (*)	-9.612	78.748	12.07.2015	0 - 50, 50 - 150, 150 - 180, 180 - 260, 260 - 350
	PS 93.1 46-2 (*)	-6.812	76.085	15.07.2015	0 - 75, 75 - 150, 150 - 350, 350 - 430, 430 - 500

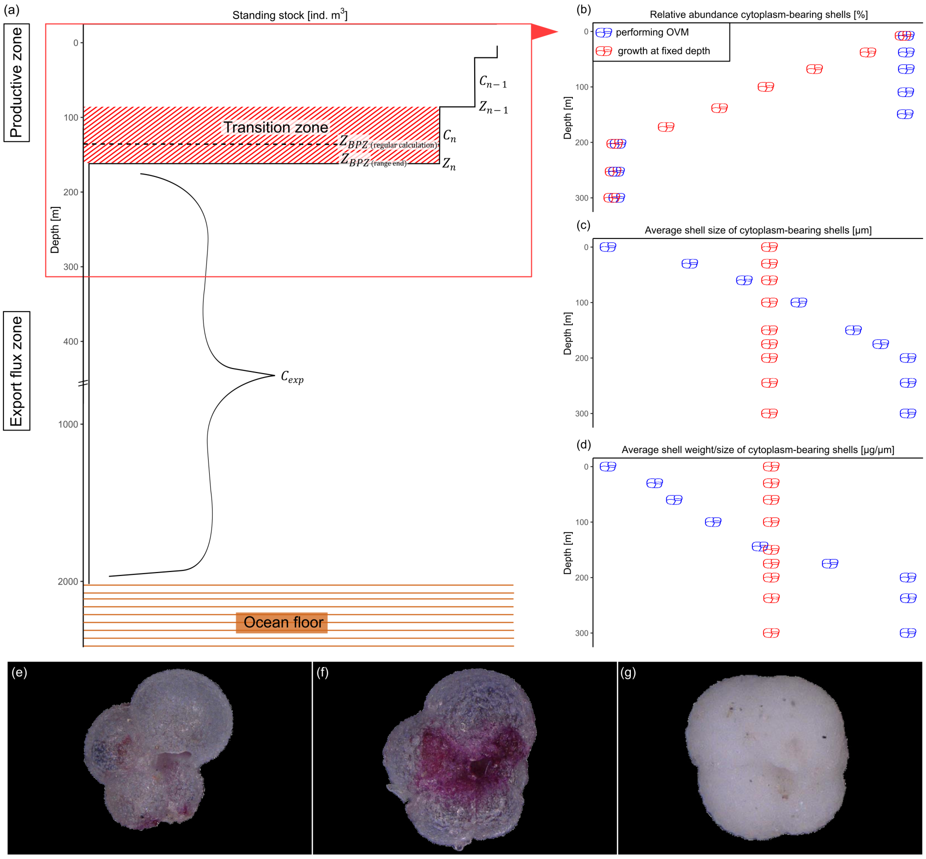

FIGURE 4.2: Schematic overview on the studied shell parameter. Shown values are constructed numbers to represent the concept of the study and not measured values. (a) change of standing stock of planktonic foraminifera with increasing depth. The parameters used to calculate the base of the export zone (Z_{BPZ}) after Lončarić et al., 2006 are shown: The transition zone represents the area in which the foraminifera shell abundance (C_n) rapidly changes, with rather stable abundances in the area below (C_{exp}). Z_n and Z_{n-1} represent the start and end depth of the transition zone, in which the calculated BPZ is located. For details on the calculation, see sect. 4.2.2. Panels (b), (c) and (d) show the change of average (b) relative abundance of cytoplasm-bearing shells, (c) average shell size and (d) average calcification intensity (shell weight / size) of cytoplasm-bearing shells with increasing water depth within the productive zone. Blue symbols represent the ideal situation if *N. pachyderma* performs ontogenetic vertical migration (OVM) throughout its lifecycle, while red shell symbols indicate the expected trend when individual specimens grow their shell at a fixed depth. Panels (e), (f) and (g) show different types of encrustation of *N. pachyderma*, with (e) representing a non-encrusted shell, (f) the beginning of encrustation and (g) thick encrustation with a clearly different and more rounded shape.

Nevertheless, where available, we used the proportion of cytoplasm-bearing and empty shells as another indicator of the maximum extent of the productive zone. To investigate at which depth of the productive zone the calcification of *N. pachyderma* occurred and if the species performed OVM, we considered the vertical profiles of the following parameters: (i) relative abundance of empty shells, (ii) shell size and (iii) mean calcification intensity expressed as the shell weight : size ratio. The reason for using those parameters is that if *N. pachyderma* performed OVM and premature mortality were zero, empty shells would only be present at the bottom of the productive zone, where the specimens would reach their maturity, while the abundance of cytoplasm-bearing shells would be 100 % at all depths above (Fig. 4.2b). At the same time, shell size and calcification intensity would increase constantly with increasing depth, reaching maximum values only at the base of the productive zone. In contrast, if individual specimens did not migrate during their life cycle, the fraction of the population dying would be equal across the productive zone. Assuming that empty shells only sink, this would lead to a linear decrease in relative abundance of cytoplasm-bearing shells. Because foraminifera of any life stage would be present in equal proportions at all depths, the average shell size and weight of cytoplasm-bearing specimens should stay constant with increasing depth (Fig. 4.2b-d).

4.2.3 Export flux zone

When the bottom of the productive zone is known (or estimated), the abundance of shells below that depth can be used to estimate the export flux by taking the sinking velocity into account (Schiebel and Hemleben, 2000). Assuming that the organic matter content of foraminifera is negligible, the calcite flux can subsequently be calculated using (average) shell weight

$$Calcite\,mass\,flux = average\,shell\,weight \cdot shell\,number\,concentration \cdot sinking\,velocity \tag{4.2}$$

where shell weight is the measured average weight of shells below the productive zone, as these are representative of the export flux. Whenever possible, the measured average shell weight was used, but for samples where no weight data is available, we used regional mean values. In regions where some weight data were available (Fram Strait, Labrador Sea, Greenland Sea, Norwegian Sea), average weights were calculated from samples of those regions alone. In all other regions, the overall mean weights from our data were used. This method is likely to underestimate present variability. To evaluate possible effects on mass flux from distinct shell types, fluxes based on average weights of either only encrusted and empty or non-encrusted and cytoplasm-bearing shells from below the productive zone were calculated as well. Shell abundance was calculated as the number of shells, divided by the sampled depth range and multiplied by the area of the net opening (as an estimate for the volume of sampled water). Sinking velocity was calculated after Takahashi and Bé, 1984:

$$Foraminifera\,sinking\,velocity(md^{-1}) = 10^{2.06} \cdot shell\,weight^{0.64} \tag{4.3}$$

using the same (average) weights as described above.
The residence time of *N. pachyderma* in the productive zone was then estimated based on the standing stock within the productive zone (ind. m^{-2}) divided by the shell flux (ind. m^{-2} d^{-1}).

4.2.4 Statistical analysis

Statistical analyses were performed using R v. 3.6.1 (R Core Team, 2022). To compare measured parameters between cytoplasm-bearing and empty shells, a Welch's t-test was performed. The analysis of trends within the productive zone was done within the beforehand individually calculated range of the productive zone of the stations.

Linear regression models were used to detect the effects of depth and sampling location on the different parameters. As the data of shell size and calcification intensity is not normally distributed, it was log-transformed before these analyses. Since the depth of the BPZ varies among the profiles, analyses were performed using tow intervals standardised to the depth of the productive zone. Some intervals extend to below the BPZ. In these cases, the tow interval represents >100 % of the depth of the productive zone.

4.3 Results

4.3.1 Shell abundances and the productive zone

The average shell abundance of *N. pachyderma* in our dataset is 25 ind. m^{-3} (Table 4.4). Shell abundances show either a maximum within the upper 50 m, or in the depth zone below, reaching down to 150 m (exemplarily shown in Fig. A.1). Those distinct patterns are distributed rather equally among all profiles and regions. Below the depth of maximum shell abundance, there is a rapid decrease in all profiles, until the abundances stabilise above 300 m water depth.
Empty shells of *N. pachyderma* are present across the entire sampled depth range (Fig. 4.3a) In the majority of the profiles, the BPZ is located between 100 m and 150 m (Fig. 4.3b). Based on the calculation after Lončarić et al., 2006, the median BPZ is situated at 124 m water depth. At stations where the BPZ could only be defined as the end of the depth range of the transition zone, its median depth is 136 m. Irrespective of how calculated, the BPZ varies among different stations and regions, with the lowest median water depth of 100 m in the Baffin Bay, and the highest median value of 160 m in the Barents Sea (Table 4.4), with variability within the regions being as large as among the regions. The minimum calculated BPZ is 15 m in a profile from the Fram Strait (PS93/020-3) and the minimum BPZ determined by the end of the net range is 20 m in a profile from the Baffin Bay (MSM09/2 466-2). The deepest BPZs reach 300 m and correspond to the pattern visible in the relative abundance of empty shells (Fig. 4.3a). Within the productive zone, the average shell number concentration of *N. pachyderma* is 42.27 ind. m^{-3}, below the productive zone, it is 6.52 ind. m^{-3} (Table 4.4).

4.3.2 Shell sizes

The average maximum diameter of *N. pachyderma* in our samples is 150 µm (Table 4.4). Shells from the Baffin Bay with a mean size of 146.5 µm (sampling mesh size: 100 µm) are smaller than shells from the Fram Strait (only data from PS93.1) that have a mean size of 180 µm (sieving size: 63 µm; Table 4.4, Fig. 4.4). A Welch's t-test shows that this difference is significant ($p < 0.001$). Cytoplasm-bearing shells within the estimated productive zone of each station in samples from PS93.1 are on average bigger than empty ones (mean sizes of 188.2 µm and 166.2 µm, respectively; Fig. 4.4a). A Welch's t-test shows that this difference is significant in eight of 14 individual samples ($p \leq 0.006$). At station PS93/024-2 in the topmost net (0-15 m), empty shells were significantly bigger ($p = 0.035$) than cytoplasm-bearing ones. Below the productive zone, two of 16 individual sampling positions contain empty shells that are on average significantly bigger than those filled with cytoplasm ($p < 0.01$). In all other samples, the differences were not statistically significant. In both regions, shells below the productive zone are significantly, if only slightly, bigger than within the productive zone (Welch's t-test: $p < 0.001$), with averages of 150 µm and 153 µm,

TABLE 4.4: Overview on measurements on different shell parameters from the different sampling areas of the study. Next to each indicated value, the 95 % confidence interval (CI) is given in italics. It is calculated assuming normal distribution, and the number of samples (n) used to calculate each parameter is given in brackets.

	Shell abundance [ind. m^{-3}]						**BPZ [m]**		**Shell size [µm]**			**Shell weight (µg)**			**Mean mass flux [mg $CaCO_3$ m^{-2} d^{-1}]**					
	Mean	95% CI (n)	Mean productive zone	95% CI (n)	Mean export flux zone	95% CI (n)	Median	95% CI (n)	Mean	Median	95% CI (n)	Mean	Median	95% CI (n)	100 m	95% CI (n)	Below BPZ	95% CI (n)	Deepest sampling position	95% CI (n)
Arctic (all samples)	25.4	4.3 (825)	42.3	6.1 (404)	6.5	0.0 (360)	112.7	10.8 (127)	150.0	143.4	0.5 (40275)	3.4	2.3	0.3 (330)	40.8	10.3 (173)	8.0	3.0 (126)	4.4	2.3 (126)
Baffin Bay	50.9	11.9 (176)	90.4	24.0 (71)	16.4	6.6 (77)	100.0	28.3 (22)	146.5	140.6	0.5 (36070)				85.5	26.1 (44)	22.7	14.3 (21)	13.7	12.8 (21)
Barents Sea	0.6	0.3 (10)	0.6	0.4 (7)	0.5	0.3 (3)	160.3	51.8 (2)							0.7	0.6 (2)	0.5	0.5 (2)	0.5	0.5 (2)
Fram Strait	11.3	2.0 (265)	19.5	3.6 (126)	3.2	0.9 (120)	100.0	16.7 (44)	180.0	172.1	1.6 (4205)	3.0	2.1	0.4 (193)	18.3	5.3 (50)	3.9	1.6 (44)	1.6	0.9 (44)
Greenland Sea	45.2	19.7 (110)	79.2	36.5 (56)	9.9	4.3 (45)	116.1	27.7 (14)				3.0	3.0	0.5 (40)	66.6	45.4 (23)	17.1	10.6 (14)	8.0	4.1 (14)
Labrador Sea	8.7	6.3 (38)	14.2	11.5 (20)	2.6	1.5 (18)	153.0	59.7 (8)				4.4	2.8	0.8 (97)	6.6	3.4 (8)	2.4	2.0 (8)	4.3	4.8 (8)
Laptev Sea	2.0	0.5 (81)	2.8	0.8 (41)	0.7	0.2 (35)	139.7	31.9 (15)							4.3	1.7 (16)	1.0	0.4 (15)	0.5	0.4 (15)
Nansen Basin	20.0	5.9 (50)	35.8	7.1 (26)	2.9	0.9 (24)	106.4	36.8 (10)							34.8	7.9 (10)	5.1	1.2 (10)	2.3	1.6 (10)
Norwegian Sea	26.8	14.4 (95)	42.7	23.2 (57)	2.8	1.0 (38)	125.8	51.4 (12)							19.1	8.8 (20)	3.0	2.5 (12)	1.8	1.3 (12)

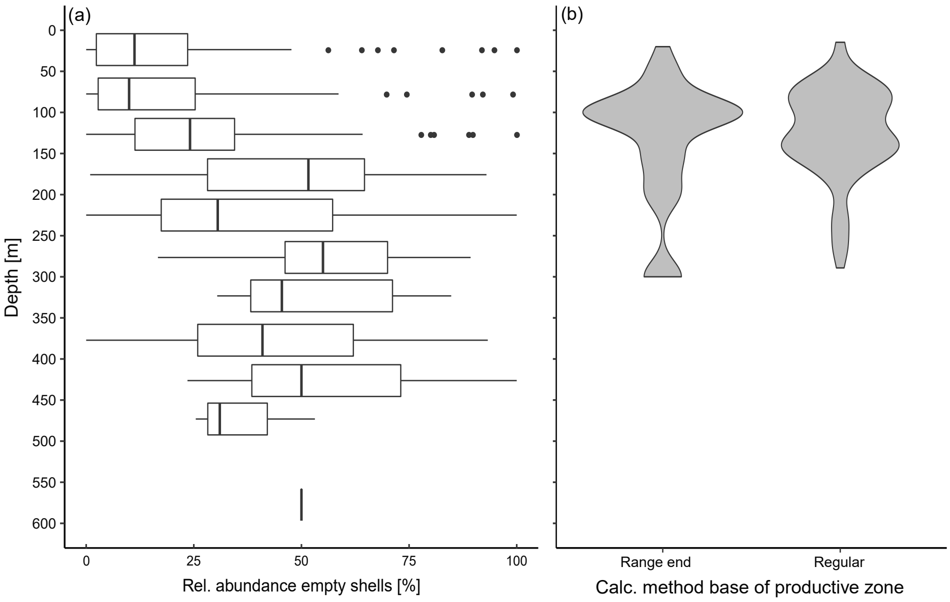

FIGURE 4.3: (a) Vertical Profile of relative abundance of empty shells at all stations of the study in which empty and filled shells were distinguished. The boxes represent the interquartile range (IQR) of the relative abundance at the given depth, and the vertical bar represents the median. Outliers, shown as points, are values beyond $1.5 \cdot IQR$ of each site of the box, and lines represent the range within $1.5 \cdot IQR$. The line at 600 m depth represents the abundance of empty shells in one single sample, as sampling in all other stations did not reach to that depth. (b) Range of the base of the productive zone (BPZ), divided by the way they were determined: "Range end" shows all samples in which the maximum depth of the net of the transition zone was defined as the BPZ, while "Regular" shows all samples in which the equation from Lončarić et al., 2006 to estimate BPZ could be applied, as described in sect. 4.2.2).

respectively (Fig. 4.4b). Statistical analysis indicates that there is no significant linear increase in average size within the productive zone (Fig. 4.5, Baffin Bay: $p = 0.399$, Fram Strait empty: $p = 0.199$, Fram Strait cytoplasm-bearing: $p = 0.627$). We find no evidence for lunar periodicity in the shell size of *N. pachyderma* in our samples.

4.3.3 Shell calcification intensity

Across both new data and literature data, the mean shell weight of *N. pachyderma* per sample ranges from 0.1 µg (potentially referring to fragments of shells from the Fram Strait, data from Kohfeld, 1998) to 20.8 µg (shells from the Labrador Sea, data from Stangeew, 2001c). The overall average weight is 3.4 µg (median: 2.3 µg, Table 4.4) and the average calcification intensity (weight / size) 0.013 µg/µm (median 0.010 µg/µm). Shell weight and calcification intensity of non-encrusted shells are lower than of (heavily) encrusted shells. Similarly, cytoplasm-bearing shells are lighter and have a lower calcification intensity than empty shells (Fig. 4.6). The differences become smaller below the productive zone. A Welch's t-test shows that the difference between the calcification intensity of cytoplasm-bearing and empty shells from PS93.1 is significant, both within ($p < 0.001$) and below ($p = 0.004$) the productive zone, with empty shells being always stronger calcified.

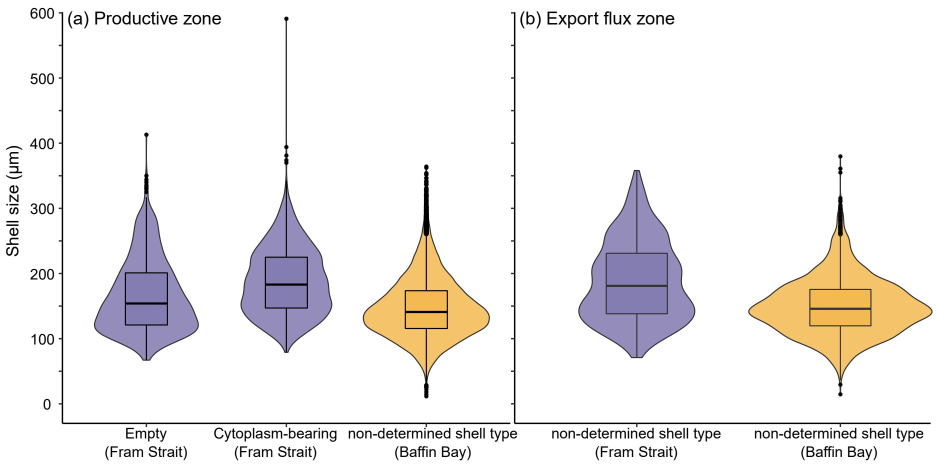

FIGURE 4.4: Overview of shell sizes of *N. pachyderma* from the Fram Strait (blue) and the Baffin Bay (orange), contrasting empty, cytoplasm-bearing and non-determined shells (a) within the productive zone, and (b) in the export flux zone. Shell types are also not distinguished in (b) in samples from the Fram Strait as we assume all shells collected below the productive zone to represent specimens that were dead during retrieval. The boxes and bars represent the interquartile range as explained in the caption of Fig. 4.3

Shell size parameters can be used to infer the presence of crust by a less lobate periphery (Fig. 4.2e-g) in samples where it has not been checked visually: Lower perimeter : area ratios indicate rounder, likely more encrusted, shells. Indeed, both within and below the productive zone, empty shells from PS93.1 are significantly rounder than cytoplasm-bearing shells (Welch t-test, $p < 0.001$), suggesting that empty shells are more encrusted than cytoplasm-bearing shells (Fig. A.2). We observe no statistically significant difference in the roundness of shells between cytoplasm-bearing shells within and below the productive zone ($p = 0.9$), but empty shells from below the productive zone are significantly rounder than those within the productive zone ($p < 0.001$; Fig. A.2). While differences within samples from the Fram Strait could be partly due to differences in sampling methods among the different studies and authors, large regional differences between the Fram Strait, the Greenland Sea and the Labrador Sea (Fig. 4.6) are likely reflecting real variability, because many of the involved studies used the same methodology.

Ten out of 18 profiles show a clear tendency towards higher calcification intensity with depth (Fig. 4.7). In seven profiles, no clear trend with depth can be detected in calcification intensity. Those profiles are all from the samples of PS93.1, four of them of empty and three of cytoplasm-bearing shells. One profile of non-encrusted shells from the Fram Strait shows lower calcification intensity at deeper depth. The involved sample size is too small to allow statistical analysis.

4.3.4 Shell mass flux

The overall mean calcite mass flux of shells of *N. pachyderma* below the BPZ in each profile based on actual weights or, where not measured, average weight of shells from below the productive zone, is 8.0 mg $CaCO_3$ m^{-2} d^{-1} (20.1 mg $CaCO_3$ m^{-2} d^{-1} based on weights of encrusted/empty shells only; 4.5 mg $CaCO_3$ m^{-2} d^{-1} based on weights of non-encrusted/filled shells only; in the following, those two values will always be given in brackets without further stating this specification). Although in some profiles, the flux seems to increase further below the BPZ, the majority of the profiles shows almost no change or a decrease in mass flux (Fig. 4.8). When calculated for shell number concentrations at the deepest net of each profile, the average calcite mass flux is further reduced by a half to 4.4 mg $CaCO_3$ m^{-2} d^{-1} (10.7 mg $CaCO_3$ m^{-2} d^{-1}; 2.4 mg $CaCO_3$ m^{-2} d^{-1}). The average loss rate in fluxes of $CaCO_3$ from the net below the base of the productive zone and the deepest sampling position of each profile is 6.6 % per 100 m (8.9 % per 100 m; 9.5 % per 100 m), the median loss is 9.1 % per 100 m (19.4 % per 100 m; 19.4 % per 100 m). The highest variations and most extreme values of changes with depth are present in the Baffin Bay, the Fram Strait and the Labrador Sea (Fig. A.3). Scaling the calcite mass loss for every pair of depth intervals below the BPZ (Fig. 4.9b) reveals that high values (and high variability of values) are limited to the 300 m depth interval below the BPZ, with both mean values and variability decreasing with depth. Weight measurements from the profiles of PS93.1 indicate that this loss is both driven by a decrease in shell mass and shell number concentration (Fig. 4.9a).

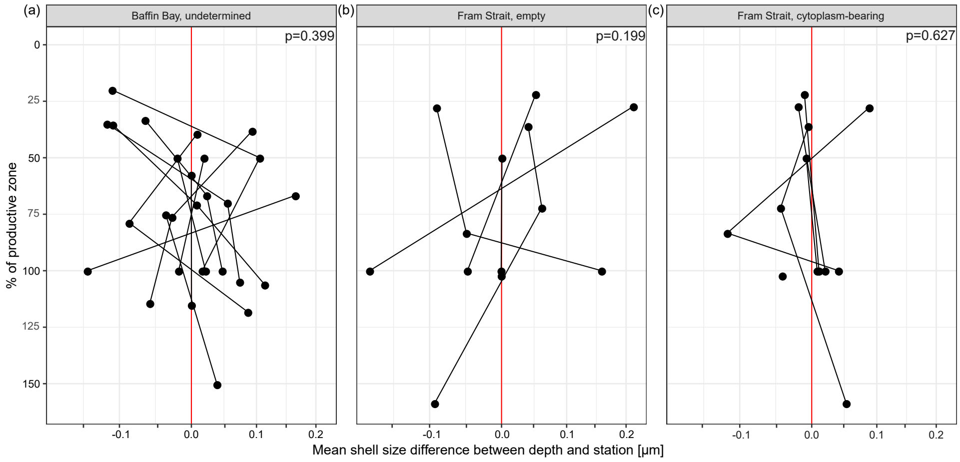

FIGURE 4.5: Mean of difference in mean shell size at the individual station and depth and the overall mean of the station, plotted against the percentage of the depth interval on the overall depth of the productive zone. 100 % equals the total depth of the productive zone, 50 % half of the depth of the productive zone. More than 100 % are reached where the sampling interval ends below the BPZ. The plot is divided into different types of shells (undetermined, empty, cytoplasm-bearing) and the two regions from which size measurements are present (Baffin Bay, Fram Strait). Consider that the samples do not represent all samples from the region shown in Fig. 4.1, but only those from (a) MSM44 and MSM66 and (b, c) PS93.1. The red line indicates the position at which no difference between the mean of the depth and the overall station exists. Only the depth interval within the estimated productive zone of each station is shown. p-values show the effect of increasing proportion of productive zone on shell size.

Irrespective of how (at which depth) the flux was calculated, the estimated mass fluxes varied among the 147 profiles by more than three orders of magnitude (Fig. 4.10). This variability has some regional components: the highest flux below the productive zone (156.9 mg CaCO$_3$ m^{-2} d^{-1}; 398.6 mg CaCO$_3$ m^{-2} d^{-1}; 83.4 mg CaCO$_3$ m^{-2} d^{-1}) was determined for a station in the central Baffin Bay (Fig. 4.11a). In the Greenland Sea, some stations also show high values (fluxes with a maximum of 66.64 mg CaCO$_3$ m^{-2} d^{-1} based on individual measurements). Those two regions have the highest average fluxes (both about 20 mg CaCO$_3$ m^{-2} d^{-1} at the base of the productive zone based on individual measurements). In comparison, average fluxes are low in the Barents Sea, Fram Strait, Labrador Sea, Laptev Sea and Norwegian Sea (< 5 mg CaCO$_3$ m^{-2} d^{-1}, Table 4.4).

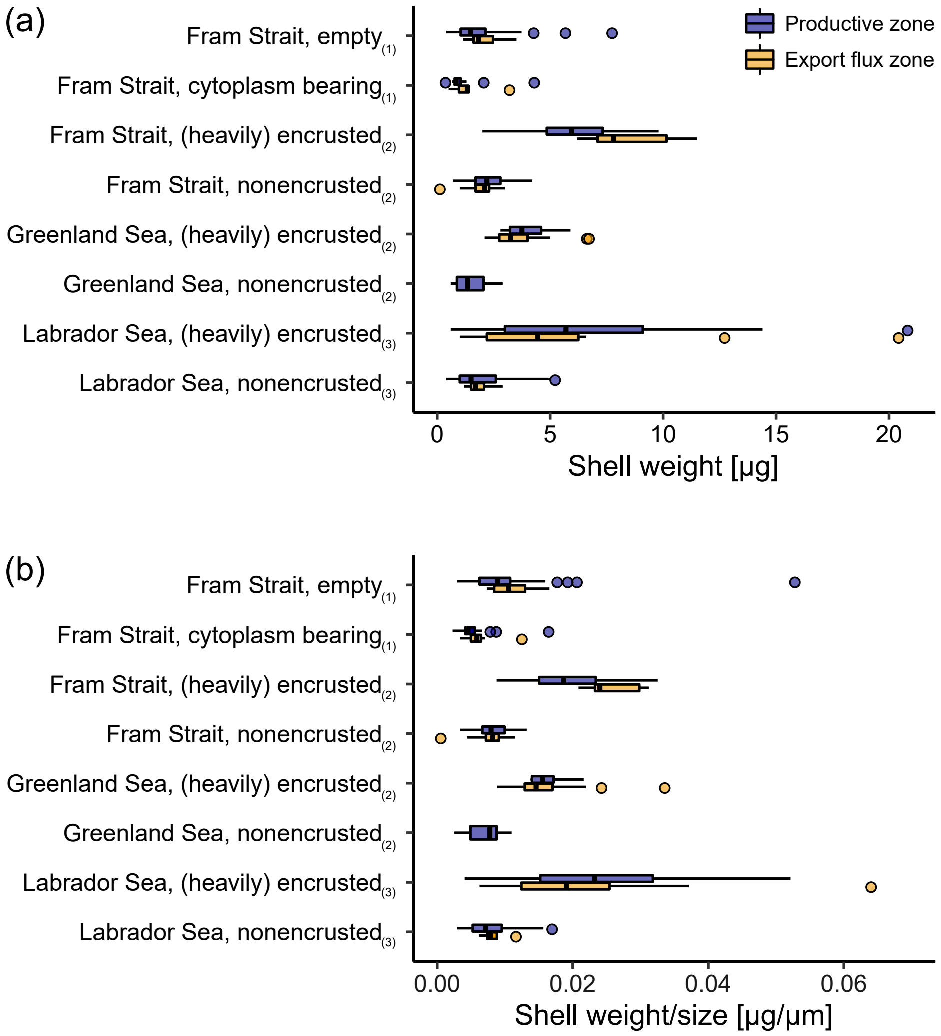

FIGURE 4.6: Overview on (a) average shell weight and (b) calcification intensity (weight / size) from shells with a different status. In this study (1), differentiation was made between cytoplasm-bearing and empty shells on shells $\geq$ 63 µm, while Kohfeld, 1998 (shells $\geq$ 150 µm; (2)) and Stangeew, 2001c (shells $\geq$ 63 µm; (3)) distinguished between (heavily) encrusted and non-encrusted shells. Besides, different sampling regions are distinguished. Blue boxes show the parameter within the productive zone of each station, orange boxes the values from samples taken below the estimated productive zone of each station. The boxes and bars represent the interquartile range as explained in the caption of Fig. 4.3.

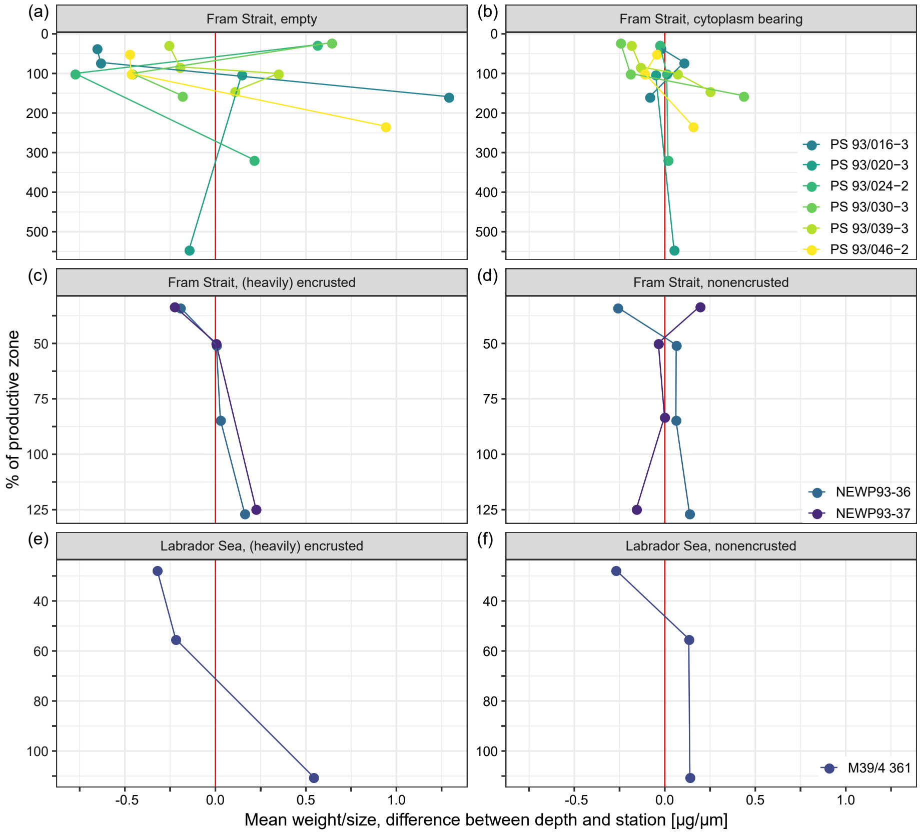

FIGURE 4.7: Mean of the difference in average calcification intensity (weight / size) at individual stations and depths and the overall weighted mean of each station within the productive zone, plotted against the percentage of the depth interval on the overall depth of the productive zone. 100 % equals the total depth of the productive zone, 50 % half of the depth of the productive zone. More than 100 % are reached where the sampling interval ends below the BPZ. Differentiation of shell types is done between cytoplasm-bearing and empty shells from Fram Strait samples of this study (a, b), while Kohfeld, 1998 (c, d) and Stangeew, 2001c (e, f) distinguished between (heavily) encrusted and non-encrusted shells in samples from the Fram Strait and the Labrador Sea. The red line indicates the position at which no difference between the mean of the depth and the overall station exists, different colours are used to make the shape of change in individual profiles visible.

4.3.5 Residence time

The calculated residence time of *N. pachyderma* based on standing stock within and shell fluxes below the productive zone ranges from < 1 to 79 days, excluding three extreme values of 182 (MSM09/2 455-7, Baffin Bay), 373 (M21/4 MSN697 and MSN-698, Norwegian Sea) and 655 days (M39/4 366, Labrador Sea) (Fig. 4.12). The median residence time is 4 days (1.8 days using average weights of encrusted and empty; 3.1 days using average weights of non-encrusted and cytoplasm-bearing average weights for the calculation of shell flux, in which sinking velocity based on shell mass is incorporated). The 95 % confidence interval ranges from 3 to 5.1 days (1.2 days to 2 days (encrusted and empty); 2.2 days to 3.5 days (non-encrusted and cytoplasm-bearing)), with a geometric mean of 3.9 days (1.5 days (encrusted and empty) 2.8 days (non-encrusted and cytoplasm-bearing)).

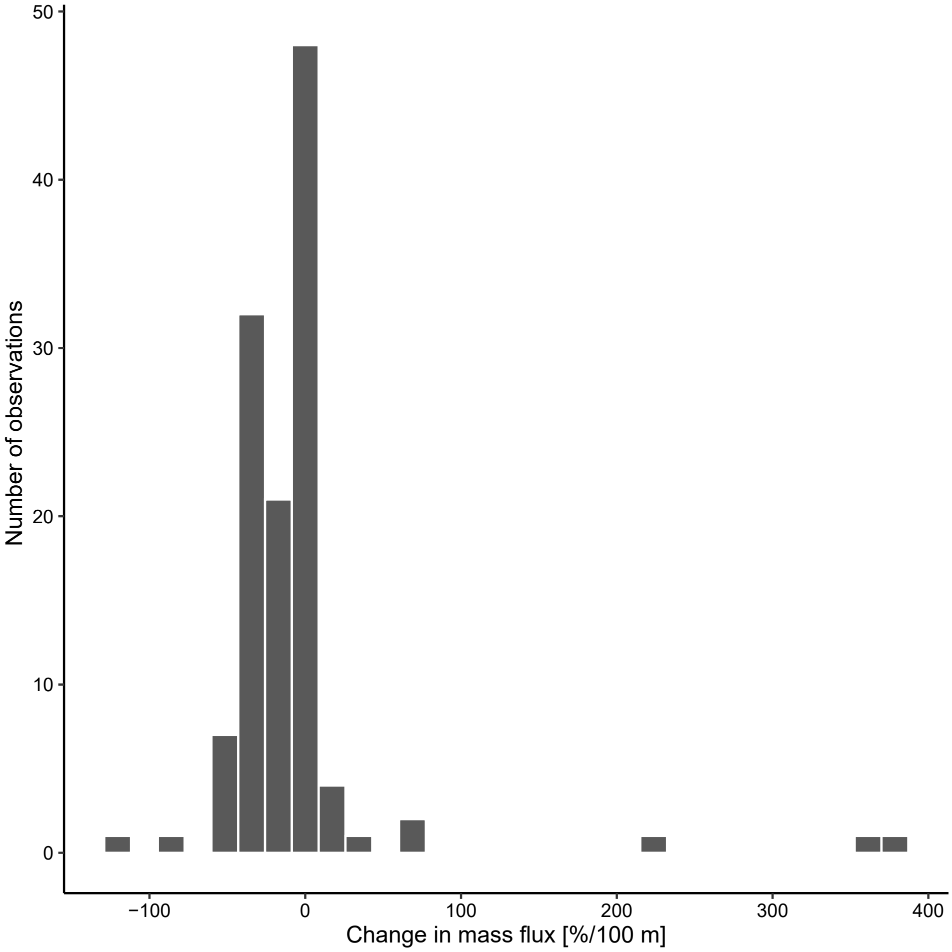

FIGURE 4.8: Change in mass flux between the net directly below the calculated base of the productive zone and the deepest net of sampling of each station.

4.4 Discussion

4.4.1 Productive zone and export flux zone

Our analysis of observations from plankton net samples indicates that the productive zone of *N. pachyderma* in the Arctic and Subarctic realm reaches down to about 113 m water depth (median of all samples: 125 m for where calculation after Lončarić et al., 2006 was possible and 136 m where it was defined as the range end). Greco et al., 2019 have shown that the habitat depth of *N. pachyderma* varies substantially. A variation in the depth interval of maximum abundances of *N. pachyderma* is also presented by Carstens and Wefer, 1992 and Carstens et al., 1997, where a connection between distinct water masses and temperature regimes is drawn. Our dataset corroborates these observations and indicates that the base of the productive zone of

N. pachyderma is also highly variable and reflects the habitat depth (vertical distribution of living specimens). Like Greco et al., 2019, we observe that even if there would be a general pattern of habitat depth and BPZ position being driven by environmental factors, as also proposed by Carstens et al., 1997, it is overlain by considerable variability, even among profiles collected in the same region and around the same time. This means that the observed BPZ variability cannot be driven by the water-column structure alone.

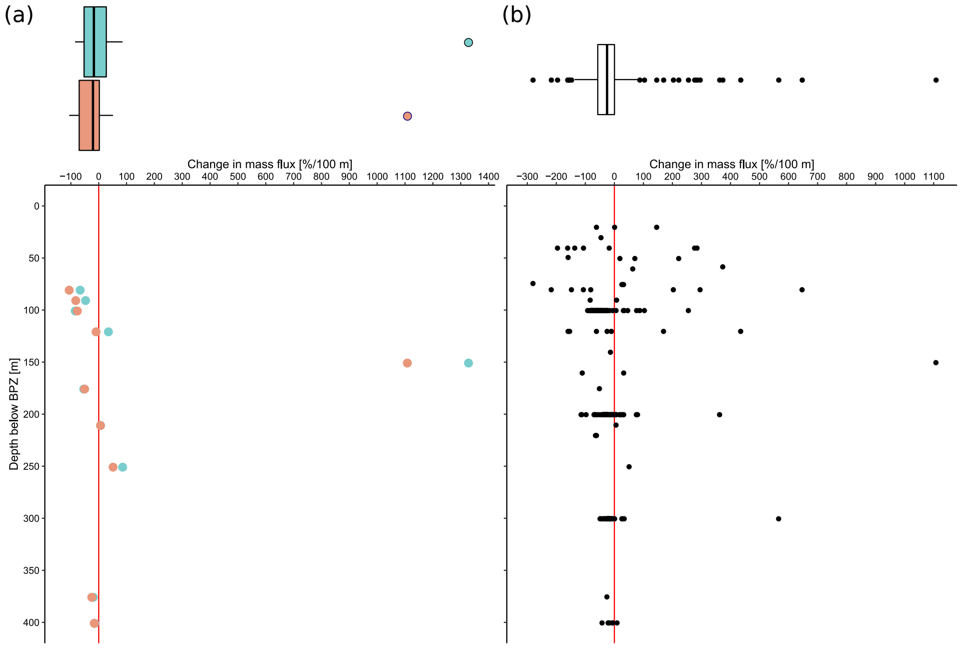

FIGURE 4.9: Flux loss with depth per 100 m in %, calculated between different sampling intervals located below the interval including the base of productive zone, plotted against the distance between the maximum sampling depth of the individual interval and the end of the net including the base of the productive zone. (a) is a comparison of loss in shell number concentration (blue) and shell mass (orange) in PS93.1 samples from the Fram Strait, (b) shows the loss in mass flux at all samples, estimated based on average shell weight and shell number concentration. The boxes and bars on top of the plots represent the interquartile range as explained in the caption of Fig. 4.3 and are plotted against the same x-axis as the plot below.

Some of the variability in the BPZ estimates may reflect patchiness in the distribution of planktonic foraminifera populations (Siccha et al., 2012). Meilland et al., 2019 observed that a patchy distribution is mainly present on a horizontal scale, with vertical distribution remaining rather stable. Nonetheless, a horizontally patchy distribution could affect the calculated BPZ in samples from the same region: In profiles with very low shell abundances (< 10 ind. m^{-3}, sometimes even < 1 ind. m^{-3}), the estimate of the BPZ position may be affected by non-representative estimates of population density. Thus, large abundance differences, caused by a patchy distribution, which has been reported to be best developed for species occurring with high abundances in the Arctic (Meilland et al., 2020), could cause large differences in estimated BPZ and display a variability in the results which may not be representative for the actual situation.

In addition, the vertical resolution of the compiled plankton net profiles (15 m to 175 m within the upper 300 m depth, Table 4.3), has a marked impact on the precision on the estimated position of the BPZ. Thus, some of the variability in the BPZ position could arise from differences in sampling methods. The BPZ estimate is also affected by the shape of the pattern of change of shell abundance with depth. Where the transition between the productive and the export zone is too gradual, the estimated depth of the BPZ is associated with larger uncertainty.

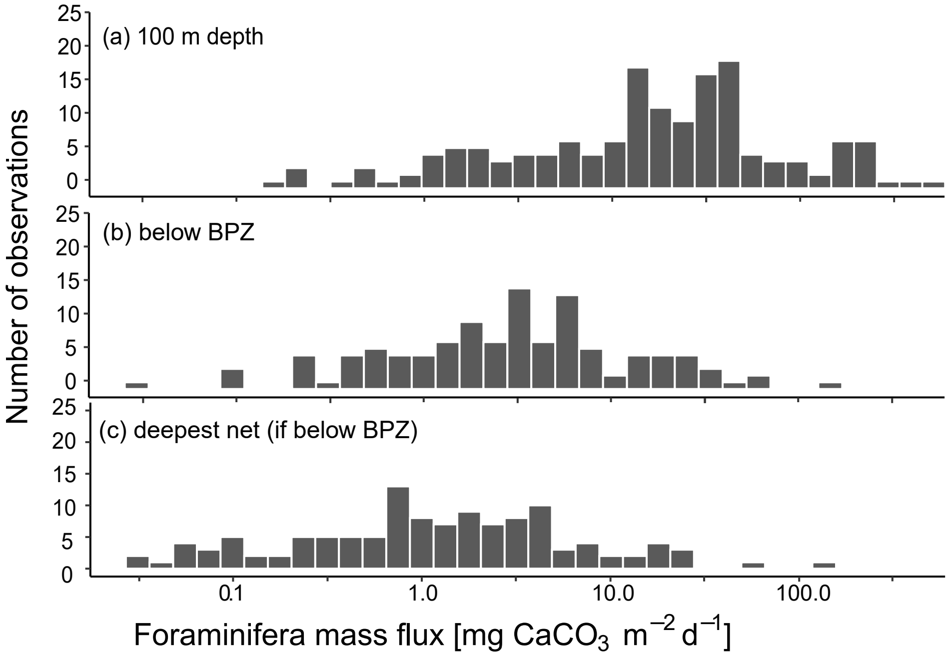

FIGURE 4.10: $CaCO_3$ mass flux of planktonic foraminifera *N. pachyderma*, calculated based on shell weights of individual samples, and, where no weight measurements are present, based on average weights from the region or all samples included in this study. Consider the logarithmic scale of the x-axis. (a) shows the fluxes at around 100 m depth (maximum sampling depths of nets: 75 - 100 m), (b) the flux in the net below the calculated base of productive zone (BPZ) of the individual stations and (c) at the deepest net of each station including all stations where that is located below the BPZ. The exact width of sampling intervals differs between individual sampling locations. Details on this are shown in Table 4.3 for profiles added in the study, and in the references listed in Table 4.1.

Some profiles show a pattern of an apparent gain in foraminifera mass flux below the inferred BPZ (Fig. 4.9). Our analysis of PS93.1 samples indicates that both higher shell abundances and shell weight below the productive zone are present at some of the stations. Higher shell weight could be explained by the loss of lighter, thinner shells due to dissolution, leading to a higher bulk weight at deeper depth. Gains in fluxes due to higher shell number concentrations are poorly constrained at depths below the BPZ, as the number of shells present in deeper nets is very low (Fig. A.1a-e). A high percentage gain in flux might in some cases only represent a difference of a few shells, which is not related to an actual higher flux but to methodological uncertainties of sampling, hence is not significant.

In summary, the calculated BPZ in each profile is associated with some uncertainty.

However, the spatial variability in the position of the BPZ is larger than the uncertainty and hence a real characteristic of the ecology of *N. pachyderma*. The location of the BPZ below 100 m in many profiles and never below 300 m is robust considering the range in vertical sampling resolution (Fig. A.1). Explicitly considering the variability in the depth of the BPZ increases the leads to improved estimates of the shell flux of *N. pachyderma* from plankton net samples.

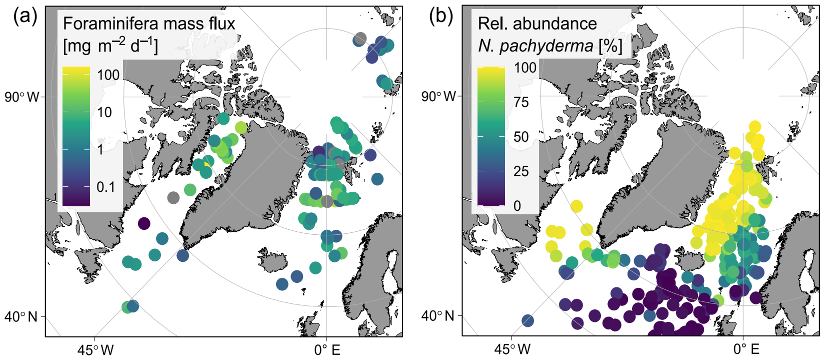

FIGURE 4.11: Regional overview on (a) foraminifera $CaCO_3$ mass flux of planktonic foraminifera *N. pachyderma* during summer (sampling period from June to September, varies among stations as shown in Fig. 4.1) below the estimated productive zone. Fluxes were calculated based on shell abundances determined in plankton net samples. Shell weights are either from direct measurements or based on average weights from the region of sampling. Consider that values are plotted on a logarithmic scale to visualise the huge regional variability. (b) shows the relative abundance of the species *N. pachyderma* found in sediment cores (data from ForCenS data set, Siccha and Kucera, 2017).

4.4.2 Calcification depth

While empty shells are already present in the sampling intervals close to the surface, and the relative abundance of empty shells tends to increase with increasing depth in the productive zone (Fig. 4.3), shell size does not systematically change with depth (Fig. 4.5). These observations speak against the presence of extensive OVM by *N. pachyderma* in the studied area (Fig. 4.2). This is consistent with observations of no clear change in shell sizes of the species with increasing depth in the Barents Sea presented by Ofstad et al., 2020. In contrast, Stangeew, 2001c and Manno and Pavlov, 2014 described higher abundances of small sized shells in the upper water column close to the surface in *N. pachyderma* from the Fram Strait. However, even in those two studies, some large shells were present in surface samples. Plankton net data from the Nansen Basin from Carstens and Wefer, 1992 show higher abundances of small sized shells below 100 m depth, which the authors linked to the impact of different water masses in the area. Thus, different conditions at different water depths and/or within different water masses can influence both the abundances of planktonic foraminifera (Carstens et al., 1997) and their assemblage size distribution, which could lead to size differences at different depths. The lack of any pattern in shell size in our data does not provide an indication of OVM, and trends in size visible in other studies could in fact be driven by distinct water conditions, and not or not alone by the performance of OVM. Our data also does not present a strong systematic change in size with lunar day, as it was detected in previous studies (Schiebel et al., 2017). However, our shell size data do not cover the entire lunar cycle, preventing drawing firm conclusions on the influence of the lunar cycle on the shell size of *N. pachyderma*.

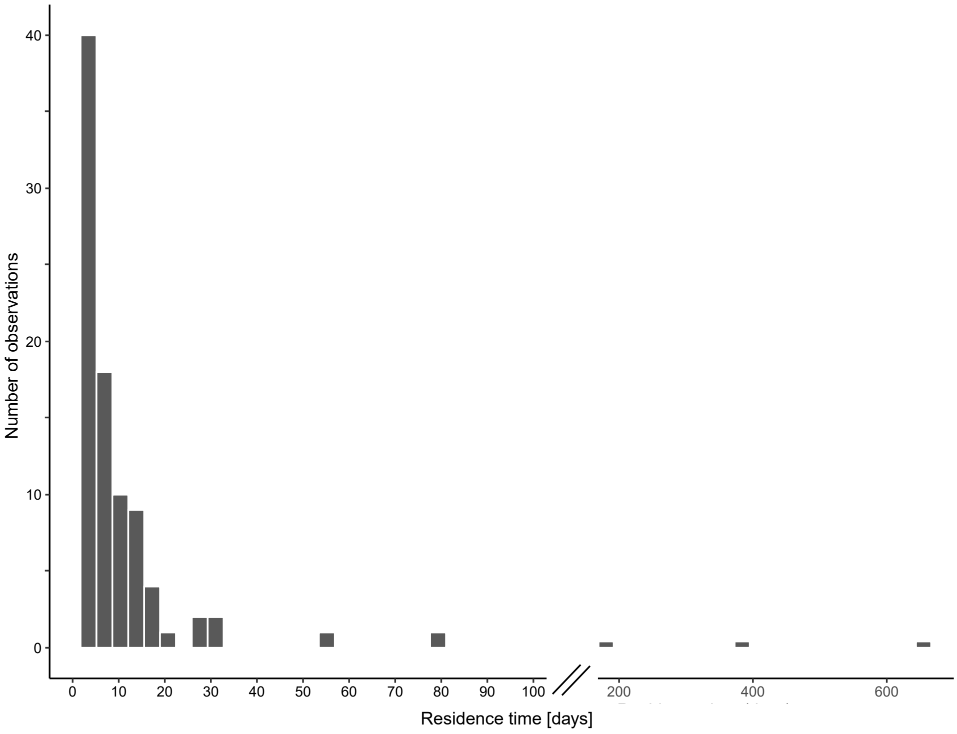

FIGURE 4.12: Residence time of empty shells of *N. pachyderma* within the productive zone in days, calculated based on the standing stock within the productive zone and the shell flux below the base of the productive zone, calculated with average shall masses below the productive zone. Consider the break in the x-axis between 100 and 200 days.

The likely important role of local environmental parameters on the terminal shell size is also reflected in the differences in shell size between empty and cytoplasm-bearing shells. Empty shells should be representative of specimens that have completed their life cycle. Therefore, shell growth at a constant depth throughout the life cycle of an individual should result in on average larger empty than cytoplasm-bearing shells at all depths. However, we only find such a difference in one of fourteen samples, and on the contrary, significantly bigger cytoplasm-bearing shells occurred in eight of fourteen samples. On the other hand, the calcification intensity of empty shells is significantly higher than for shells bearing cytoplasm in all but one sample, and their shape is significantly more rounded, further indicating strong calcification. This shows that at least in the case of the studied *N. pachyderma*, shell size measured as the maximum diameter of the shell is not an ideal indicator for maturity, but a highly variable parameter among individual specimens that might reflect variation in environmental conditions during the life cycle of the individual foraminifera. In contrast, the consistently observed stronger calcification intensity of empty shells at all depths and their distinct shape rules out that empty shells in the upper water column only represent specimens affected by premature death, i.e. before reproduction. The stronger calcification compared to cytoplasm-bearing shells is a clear indicator for a completed life cycle, as this species is known to often be associated with the development of a thick terminal calcite layer or crust (Bé, 1960; Kohfeld et al., 1996). In Stangeew, 2001c, where the presence of OVM is concluded based on shell sizes, the area of occurrence of strongly encrusted shells was observed to range from surface to 300 m depth, suggesting reproduction occurred across this whole depth range and not only at its base.

Ten out of 18 of the here studied profiles indicate an increase in calcification intensity with increasing depth within the productive zone (Fig. 4.7), which would speak in favour of OVM. However, with the other half of the profiles not displaying any trend with depth, we must conclude that there is no clear signal for OVM being present or absent. If OVM would be present across all specimens of *N. pachyderma* in the Arctic and Subarctic realm, it would need to be very limited in the depth range to not be clearly visible in our data. In regions where the productive zone ranges from about 50 m to 120 m water depth, the resolution of the studied vertical profiles might be not sufficient to detect it.

The occurrence of heavily calcified empty shells at all depths indicates that many specimens of *N. pachyderma* reach the final stage in their life cycle, building their final thicker crust, at all depths within their depth habitat. The same conclusion was also favoured by Kohfeld et al., 1996. These authors in addition hypothesised that the local conditions at a given depth not only affect the final size but also calcification intensity. Indeed, like size, calcification intensity in planktonic foraminifera has been shown to reflect parameters like temperature, productivity and optimum growth conditions (e.g. Weinkauf et al., 2016). Those parameters could also cause trends in the calcification intensity with depth, without necessarily being driven by strict OVM.

The sampling period of our data has to be considered when evaluating changes of size and calcification intensity with depth: Depending on the life span of *N. pachyderma*, which could be longer than one or two months (Carstens and Wefer, 1992; Kohfeld et al., 1996), it is possible that the samples contain individuals from multiple generations that were produced during different environmental conditions. Furthermore, sinking shells of *N. pachyderma* can be transported over considerable distances, as e.g. shown by von Gyldenfeldt et al., 2000, whose results would indicate a transport of 25 - 50 km in the upper 1000 m, resulting in the possibility of some of the encountered specimens being advected from areas with a different hydrography. Because environmental conditions can have an impact on shell size and calcification intensity (e.g. Weinkauf et al., 2016), advection could blur signs of OVM if the life span of *N. pachyderma* is long relative to the speed of advection. Even though the residence time is not a direct measure of life span, since it only reflects the average time that foraminifera > 90 µm spent alive in the productive zone and hence excludes the time it takes to reach maturity, it can provide a first order approximation. The majority of the estimated residence times is below 10 days. Longer estimates are likely due to lack of precision at low shell counts, but we note that they are not inconsistent with the life span observed in culture (Spindler, 1996). Thus, the median calculated residence time of about four days in our data suggests that the life span of the sampled *N. pachyderma* is either too short to be strongly affected by environmental variability, or that the population size is constant at short time scales and hence unlikely to be influenced by changes in environmental conditions. Therefore, we conclude that the possible blurring of signs of OVM would be rather small, and the lack of a clear trend indicating OVM at all stations can be seen as a reliable result.

In summary, our data on the presence of OVM are inconclusive. The occurrence of empty shells as well as those with high calcification intensity at all depths of the productive zone indicates that *N. pachyderma* does not seem to change its depth habitat during life, while increasing shell calcification could indicate the performance of OVM. Since it seems unlikely that the entire population of the species participates in OVM, we speculate that only a small portion of the specimens follows this behaviour. Indeed, Meilland et al., 2021 suggested such performance of OVM only by a fraction of all specimens within a population for several tropical species in the central Atlantic, and our data would appear to indicate a similar mode of population dynamics for the Arctic *N. pachyderma*. Although our data can neither confirm nor rule out the performance of OVM in *N. pachyderma* in the research area, we can define the calcification zone as the entire upper 300 m of the water column, based on the estimates of the BPZ and the fact that strongly calcified shells can be found within the whole water column above the BPZ.

4.4.3 $CaCO_3$ shell mass flux

Knowing the position and variability of the productive zone of *N. pachyderma* in the Arctic, we use data on shell abundances below the productive zone and average shell weights to estimate the calcite flux of *N. pachyderma* in each profile. Estimates of calcite fluxes based on observations from plankton nets are based on two major components that affect the calculations: (i) The (average) shell weight that is used for calculating calcite mass fluxes from shell fluxes and the sinking speed of the shells, and (ii) the depth for which the export fluxes are calculated.

Shell weight varies strongly between different shell types (non-encrusted vs. encrusted) and regions. The shell weight is also influenced by shell size, and the estimates for samples that lack weight measurements are therefore uncertain. Next to possible regional differences in shell sizes, a further source of uncertainty arises from different mesh sizes across the compiled datasets, with higher average shell weights at coarser mesh sizes. Since we determined and considered weight measurements on samples from the smallest (63 µm) and coarsest (150 µm) mesh sizes, the average that is used in this study is likely representative for most of the samples in the analysed dataset, where the majority of the profiles are based on sampling with mesh sizes of 100 µm to 125 µm (Table 4.1).

Using weights of encrusted, empty shells results in calcite fluxes that are three to five times higher (average of 10.7 mg $CaCO_3$ m^{-2} d^{-1}) than estimates based on overall average weights (average of 4.4 mg $CaCO_3$ m^{-2} d^{-1}) or weights of non-encrusted, cytoplasm-bearing shells (average of 2.4 mg $CaCO_3$ m^{-2} d^{-1}). However, our observations indicate that not all specimens build a thick crust before reproducing or dying and some still contain remainders of cytoplasm while already sinking. Therefore, flux calculations based on averages of all shell types should be more realistic then only using weights of encrusted, empty shells.

The highest estimated calcite fluxes in our data set are present in the Baffin Bay (average of 13.7 mg $CaCO_3$ m^{-2} d^{-1}; Table 4.4) and the Greenland Sea (average of 8.0 mg $CaCO_3$ m^{-2} d^{-1}; Table 4.4). We do not have any weight measurements from the Baffin Bay, hence use overall averages to calculate fluxes for data from there, as explained in the method section (sect. 4.2.2). Our data on shell sizes from the Baffin Bay indicate that the shells are systematically smaller than those from the Fram Strait, from where a large number of samples on which weights were measured are taken from. Therefore, the calculated calcite fluxes in the Baffin Bay could be overestimated. As we also see variability in shell weights in samples of similar sizes when sampled at different regions, it would also be hard to establish any size-weight relationship that would be accurate for a region where we lack data. Greenland Sea samples are based on the average weights of samples from the same region, but weight measurements are done on a larger minimum shell size (150 µm) than other counts from the region (mainly using 100 µm mesh size), which could also cause some overestimation.

Interestingly, large differences in flux estimates also emerge from calculations on different depth intervals. We show that flux estimates based on an export flux level of 100 m, as done in previous estimates (e.g. Schiebel, 2002), are overestimating the export, because a large part of the population below 100 m down to 300 m is still alive. Calcite mass fluxes based on shell number concentration immediately below the BPZ indicate values that are about five times smaller (8.0 mg $CaCO_3$ m^{-2} d^{-1} below BPZ in contrast to 40.8 mg $CaCO_3$ m^{-2} d^{-1} at 100 m depth; Table 4.4), indicating that the commonly used level of 100 m (Schiebel, 2002) would not be appropriate for the whole Arctic. Next, we observe that the export flux is attenuated below the BPZ (Fig. 4.9) and average mass fluxes at the deepest sampled net are reduced by a half compared to fluxes directly below the BPZ (average of 4.4 mg $CaCO_3$ m^{-2} d^{-1} at the deepest net). The vertical distribution and amount of this calcite flux loss are similar to observations in other parts of the ocean (Schiebel et al., 2007; Sulpis et al., 2021). Thus, our estimated BPZ seems to be consistent. Sulpis et al., 2021 and Schiebel et al., 2007 ascribe high losses in $CaCO_3$ in the upper water column to indiscriminate digestion by large plankton feeders or CO_2 release due to degradation of residual cytoplasm in the shells or in particles to which empty shells may be attached during sinking. Indeed, Greco, Morard, et al., 2021 hypothesised that *N. pachyderma* is during life associated with sinking aggregates, which would lead to a situation where even after the foraminiferal cytoplasm is released during reproduction, the empty shell may remain in contact with organic matter. Our data indicate that flux attenuation is driven by both a reduction in shell mass and in shell number concentration (Fig. 4.9a). Dissolution can result in both of these losses, as both a reduction in weight of strongly calcified shells and a total dissolution of thinner shells is possible due to this process.

Notwithstanding the exact mechanisms, our results indicate a substantial attenuation of calcite flux of Arctic *N. pachyderma* below the productive zone, with an average loss of about 6.6 % per 100 m. In contrast to other regions, the strong limitation of fluxes in the Arctic to the summer period has to be considered (Bauerfeind et al., 2009; Jonkers et al., 2010). It has been shown that pulsed high fluxes are less prone to dissolution in the upper water column (Klaas and Archer, 2002; Schiebel, 2002; Sulpis et al., 2021). Therefore, the loss of planktonic foraminifera $CaCO_3$ in the upper water column of the Arctic ocean might be lower than in regions with the same mean annual flux distributed throughout the year.

Based on a compilation of plankton tow data and taking 100 m as the BPZ, Schiebel, 2002 reported total planktonic foraminifera calcite flux estimates in the North Atlantic of about 100 mg $CaCO_3$ m^{-2} d^{-1}. This value is more than three times higher than the average calcite export flux by *N. pachyderma* in our dataset at that depth (29.5 mg $CaCO_3$ m^{-2} d^{-1}, averaging over regional averages to account for all regions equally). The difference could be explained by foraminifera building a thicker shell in the North Atlantic, or simply by higher shell abundances. Lower shell abundances in our data already result from methodological effects: By sampling *N. pachyderma* only, we underestimate the total flux of planktonic foraminifera in all regions where abundances of other species are also relevant, like the Greenland Sea and the Norwegian Sea (Fig. 4.11b). Besides, coarser mesh sizes can underestimate shell number concentrations and hence lead to lower flux values. A comparison of abundances of *N. pachyderma* in our compilation derived from the same region, but sampled with different mesh sizes, shows that its abundance is on average 27 % lower when a coarser then 63 µm mesh size (100 µm, 125 µm, 150 µm) is used, because small shells are not sampled. These observed estimates of a reduction in the abundances is comparable to the results by Carstens et al., 1997, who detected a reduction in foraminifera abundances of 7 % to 40 % with increasing mesh size. The flux given by Schiebel, 2002 is based on data from sampling with a 100 µm mesh size. Our data from the western Fram Strait indicates that in this region, the abundance of larger (>125 µm, >150 µm) shells is on average 56 % lower than what is sampled with a mesh size of 100 µm. With 49 out of 148 stations in our dataset having a mesh size coarser than 100 µm, the lower flux estimates in our compilation are likely at least partly underestimated, compared to fluxes consistently based on sampling with a mesh size of 100 µm, but the difference is unlikely to be larger than one third.

Besides, different BPZ at the distinct research areas could lead to different values at 100 m depth. We show that 100 m can be too shallow to estimate the fluxes in the Arctic, but cannot judge the effect of a possibly deeper or varying productive zone in the North Atlantic (Schiebel et al., 1995) on flux estimates. Taking all possible biases in our flux estimation as well as effects on the flux from Schiebel, 2002 into account, our estimates cannot be considered as substantially deviating from his flux estimates for the North Atlantic.

An opportunity to further validate our calcite flux estimates is given by a recent study from the Northern Svalbard margin by Anglada-Ortiz et al., 2021, who reported total foraminifera calcite fluxes of 2.3 mg $CaCO_3$ m^{-2} d^{-1} to 7.9 mg $CaCO_3$ m^{-2} d^{-1} based on data from living planktonic foraminifera in the upper 100 m of the water column. It has to be considered that this might not represent the export flux zone, as at least two of the studied profiles show increasing shell abundance below 100 m. Nevertheless, considering that the planktonic foraminifera assemblages reported by those authors contained only about 50 % *N. pachyderma*, their minimum reported flux is similar to the range of the estimates in our data set for the Barents Sea at 100 m (0.39 mg $CaCO_3$ m^{-2} d^{-1} to 1.86 mg $CaCO_3$ m^{-2} d^{-1} using different weight averages for the calculation). The fact that our estimates are still slightly below those from Anglada-Ortiz et al., 2021, taking the abundance of *N. pachyderma* into account, could be explained by the different mesh sizes: Anglada-Ortiz et al., 2021 sampled with a mesh size of 90 µm, while sampling was done with a mesh size of 125 µm in our data from that region (Table 4.1). Moreover, the samples analysed in our study were taken in June, while those from Anglada-Ortiz et al., 2021 represent fluxes in August, which often represents the most productive period of planktonic foraminifera in the Arctic Ocean (Jensen, 1998). Overall, this comparison confirms the high local and seasonal variability in fluxes of *N. pachyderma* in the (Sub)Arctic realm (Fig. 4.11a) and suggests that the estimated flux values in our study are broadly in line with earlier individual observations.

To set the estimated flux of *N. pachyderma* into relation to total $CaCO_3$ fluxes of both aragonite and calcite, we compare our results with data from sediment traps in the Greenland Basin (Bodungen et al., 1995), the Fram Strait (Hebbeln, 2000; Bauerfeind et al., 2009) and the Lomonosov Ridge (Fahl and Nöthig, 2007). As all of our data originate from the summer season, and the shell flux in the Arctic and Subarctic is highly seasonal (Jensen, 1998), we compare our data with daily $CaCO_3$ fluxes from June to September only. The total range of $CaCO_3$ fluxes is similar to the flux we observe in *N. pachyderma* in plankton nets, with fluxes of *N. pachyderma* being mostly located at the lower end (Fig. 4.13). Using a mean daily mass flux of *N. pachyderma* at the greatest sampled depths of each net of 4.43 mg $CaCO_3$ m^{-2} d^{-1}, the species would make up about 23 % of total $CaCO_3$ flux (18.89 mg $CaCO_3$ m^{-2} d^{-1}) measured in the sediment traps. This is in line with global estimates from Schiebel et al., 2007 giving a contribution of planktonic foraminifera to overall $CaCO_3$ fluxes of about 25 %. Our result is further in line with an estimated contribution of planktonic foraminifera to total calcite fluxes in the Atlantic Ocean of 19 % by Kiss et al., 2021, but lower than estimates from Salmon et al., 2015 of a contribution of up to 40 % to total $CaCO_3$ fluxes. For the Southern Ocean, higher contributions (34 - 49 %) have been estimated (Salter et al., 2014).

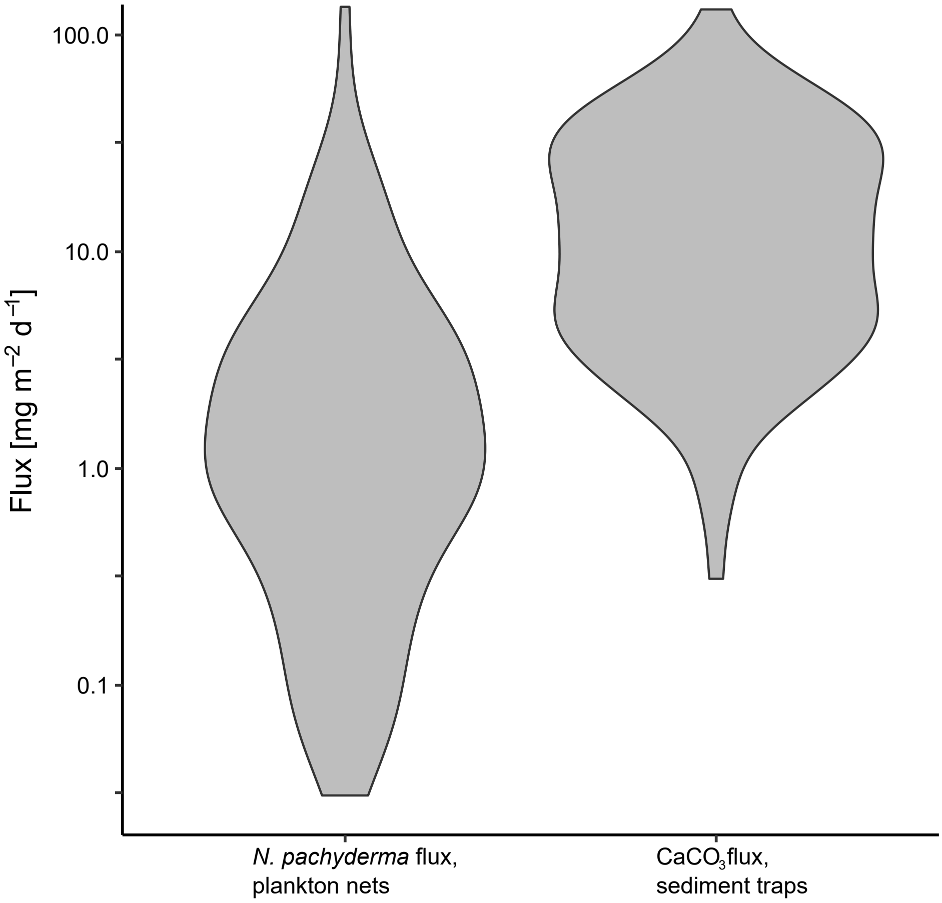

FIGURE 4.13: Comparison of daily mass flux of *N. pachyderma* in plankton nets and $CaCO_3$ in sediment traps plotted on a logarithmic scale. Sediment trap data is from sediment traps in the Fram Strait (Hebbeln, 2000; Bauerfeind et al., 2009), the Greenland Basin (Bodungen et al., 1995) and the Lomonosov Ridge (Fahl and Nöthig, 2007)

A direct comparison of fluxes of planktonic foraminifera from samples from within the same region with total $CaCO_3$ fluxes in the region indicates a lower contribution of planktonic foraminifera in the Eastern (> 0° E) Fram Strait (10 %) and a higher contribution in the western part (< 0° E) of the Greenland Sea (50 %) to total $CaCO_3$ fluxes. For this comparison, we subdivided the regions by longitude to account for the different influences of Atlantic and Arctic waters, which play an important role for the abundances and habitats of planktonic foraminifera in this region (Pados and Spielhagen, 2014). The contribution of 10 % of planktonic foraminifera $CaCO_3$ fluxes to total $CaCO_3$ fluxes in the Fram Strait is in line with the lower end of estimated contribution of planktonic foraminifera to total $CaCO_3$ fluxes at the Northern Svalbard margin (4 - 34 %; Anglada-Ortiz et al., 2021). The higher contribution of planktonic foraminifera $CaCO_3$ fluxes to total $CaCO_3$ fluxes in the Greenland Sea is in the range of the estimates from Salter et al. (2014) from the Crozet Plateau in the Southern Indian Ocean, indicating that it falls within globally realistic ranges. The previously described possible effect of coarser mesh size decreasing flux estimates has to be considered, meaning that the values of planktonic foraminifera $CaCO_3$ fluxes from our dataset provide a minimum range.

Overall, our data indicates that the production of $CaCO_3$ by planktonic foraminifera in the Arctic Ocean has a similar share to total fluxes as in other regions. We also see large variability with some Arctic regions showing much lower contribution than in other oceans and the global average. It has to be stressed, however, that our estimates are only for a single (albeit often the most abundant) species and the total flux of planktonic foraminifera in the studied region must be higher. The contribution of planktonic foraminifera to the Arctic carbonate budget may therefore be larger than the numbers given here. Moreover, even though the aragonite-producing pteropods are abundant in the Arctic and their shells are preserved in sediment trap samples (Bauerfeind et al., 2014; Busch et al., 2015), most of the aragonite flux dissolves prior to burial in the sediment because the majority of the Arctic seafloor is located below the aragonite compensation depth (Jutterström and Anderson, 2005). Our calculation of an apparent 23 % contribution of planktonic foraminifera to the summertime export flux of carbonate is thus likely translated into a larger share of the burial flux, making the calcite flux by planktonic foraminifera highly relevant for the Arctic oceanic carbon cycle.

4.5 Conclusion

Our compilation of vertically resolved data on the dominant Arctic planktonic foraminifera *N. pachyderma* reveals that the base of the productive zone of this species is on median located at about 113 m depth, but shows large regional variability and locally reaches down to 300 m. Our analyses show that it is important to constrain the base of the productive zone to estimate fluxes in the export flux below: using a constant 100 m depth to estimate fluxes leads to a fivefold flux overestimation in contrast to the flux at the top of the export zone. We can conclude that in the absence of knowledge on the position of the BPZ, using 300 m depth should provide a conservative, yet more realistic estimate of the *N. pachyderma* export flux in the Arctic realm than using the formerly often used depth of 100 m. Within the productive zone, our data are inconclusive whether *N. pachyderma* performs ontogenetic vertical migration throughout its lifecycle. We observe empty and strongly encrusted shells, hence specimens that have completed their life cycle, at the whole depth range, and do not see any pattern of increasing shell size. Nevertheless, as a systematic increase in calcification intensity with depth is present at some stations, we speculate that OVM is performed by at least a small part of the community.

The overall average calcite mass flux of *N. pachyderma* based on measured average shell weights (average of 3.4 µg) and shell number concentrations (average of 25 ind. m^{-3}) is estimated to be 8 mg $CaCO_3$ m^{-2} d^{-1} directly below the base of the productive zone in the Subarctic and Arctic Ocean. Below the base of the productive zone, the flux is on average attenuated at a rate of 6.6 % per 100 m at least within the following 300 m depth. This attenuation is driven by a reduction in shell number concentration and in weight, which is probably mainly driven by dissolution of thinner, less calcified shells.

Notwithstanding uncertainties in flux estimates due to high regional variability, coarser mesh sizes with underrepresentation of total shell abundance and the lack of weight measurements in some regions, our estimates are in line with previous global studies and local studies from adjacent areas. Comparison with data from sediment traps shows that *N. pachyderma* is on average responsible for 23 % of total pelagic carbonate fluxes in the Subarctic and Arctic realm, with a regional variability of ten to 50 %, indicating an even bigger share of total planktonic foraminifera especially in Subarctic regions, where *N. pachyderma* only makes up 50 % of the total population.

Author contributions The study was designed by all authors. FT carried out the laboratory work with help from JM and the data analysis with help from LJ. All authors contributed to the interpretation and discussion of the results. FT wrote the paper with contributions from MK, LJ and JM.

Data availability All data created for this study, including calculations made on published data, is available on PANGEA (`https://doi.pangaea.de/10.1594/PANGAEA.941250`). The data source of abundances from published data are also listed in Table 4.1, and shell weights from the M39/4 expedition are listed as PANGEA references (Stangeew, 2001a; Stangeew, 2001b).

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Chapter 5

Drivers of planktonic foraminifera calcite flux in the Nordic Seas

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Abstract The Nordic Seas play an important role for the carbon cycle as they act as a major sink of atmospheric CO_2. One component contributing to the marine carbon cycle is the production of pelagic carbonates, among others by planktonic foraminifera. Ongoing climate change could influence their productivity, resulting in a change of the carbon cycle in this region. In this study, we analyse the mass fluxes of planktonic foraminifera based on sediment trap data from newly analysed samples in the Fram Strait and published data in the Norwegian and Greenland Sea to understand and quantify the drivers of their mass production to enable understanding the role of climate change. Our data shows that the mass flux of planktonic foraminifera, mainly defined by the shell flux, has a strong seasonal variation in the Nordic Seas, with high fluxes during summer and low fluxes during winter. While a close relationship of foraminifera fluxes to temperature is present, this factor cannot explain all of the variability, especially not the interannual variability between summer seasons. Our analysis indicates that the availability of food and its quantity are important drivers of the planktonic foraminifera mass flux variability, without us being able to further quantify this with the data at hand. On average, the planktonic foraminifera mass flux in the studied sediment traps contributes to 5.4 % of total $CaCO_3$ fluxes. Further contribution likely comes from pteropods, mostly dissolving before being stored at the sea floor, and coccolithophores. With high deviation between estimates of $CaCO_3$ fluxes of the different carbonate producers and total $CaCO_3$ fluxes, further quantification is necessary here to understand the possible influence of ongoing Arctic warming on the Arctic marine carbon cycle.

5.1 Introduction

The Nordic Seas are one of the major oceanic sinks of atmospheric CO_2 (Takahashi et al., 2002). At the same time, the whole Arctic and Subarctic realm underlie ongoing climate change at a high pace due to polar amplification (Serreze and Barry, 2011), facing warming and shrinking sea ice especially during summer (Meier et al., 2014). When atmospheric CO_2 is transferred into surface oceans, oceans act as a CO_2 sink, redistributing it by circulation. The physical and biological carbon pump transport carbon (C) towards the deep ocean and ocean sediments. When particulate organic carbon (POC) is fixed in organisms by photosynthesis, it is transported to depth at the death of the organisms (Riebesell et al., 2009; Henehan et al., 2017). On the contrary, during the calcification process of organisms like pteropods, coccolithophores and planktonic foraminifera, surface ocean alkalinity is reduced and CO_2 is released into the atmosphere, denoted as the $CaCO_3$ counter pump (Frankignoulle et al., 1994). Nevertheless, when those organisms die, their shells sink downwards to the sediments. Specimens reaching the sediment will then bury carbon fixed in their shells on geological time scales (Zeebe, 2012; Salter et al., 2014).

Data from the eastern Fram Strait from sediment traps at the HAUSGARTEN observatory show that on average, 11 to 77 % of $CaCO_3$ fluxes are formed by pteropods (Bauerfeind et al., 2014; Busch et al., 2015). Despite this high contribution to the overall carbonate fluxes, only about 5 % of $CaCO_3$ being stored at the seafloor is formed by pteropods, indicating their dissolution in the water column or at the seafloor (Bauerfeind et al., 2014; Busch et al., 2015; Sulpis et al., 2021). In the same research area, Coccolithophores only form < 1 % of $CaCO_3$ fluxes in the upper water column (Bauerfeind et al., 2014). Planktonic foraminifera contribute to the calcite flux to a greater extent than the coccolithophores in the sediment traps at the HAUSGARTEN observatory (Ramondenc et al., 2022). Even though data on their shell flux in this region is available (Ramondenc et al., 2022), information on their contribution to $CaCO_3$ fluxes is lacking. On a global scale, planktonic foraminifera are estimated to be responsible for 32 to 80 % of $CaCO_3$ sedimentation at the sea floor (0.71 Gt yr^{-1}; Schiebel, 2002; Schiebel et al., 2007). Local estimates of their $CaCO_3$ mass flux for the Subarctic and Arctic realm, based on plankton nets deployed during summer, give an average of 8 mg $CaCO_3$ m^{-2} d^{-1} below the productive zone, accounting for about one quarter of total carbonate fluxes (Tell et al., 2022). Likewise using plankton net data, Anglada-Ortiz et al., 2021 give a contribution of planktonic foraminifera to total $CaCO_3$ fluxes of 4 to 34 % at the North Svalbard Margin, while pteropods contribute to 66 to 96 % of $CaCO_3$ fluxes in the upper water column.

Planktonic foraminifera shell fluxes in the Subarctic and Arctic realm show a seasonal pattern with maximum fluxes occurring between August and October and declining until a minimum around January (Jensen, 1998b; Jonkers et al., 2010; Ramondenc et al., 2022). A study from the Cape Blanc upwelling area indicates that the mass flux of planktonic foraminifera and its variability is mainly defined by the variability in foraminifera shell fluxes, while changes in shell weight only play a role on interannual timescales (Kiss et al., 2021). However, the controls of foraminifera shell flux are overall poorly constrained. Besides the knowledge on the intra-annual variability in shell fluxes, Jensen, 1998b has shown interannual variability in the Nordic Seas and regional differences in foraminifera fluxes between the Greenland Sea and the Norwegian Sea. In addition, a tendency of foraminifera shells being smaller during colder periods was detected in samples from the Nordic Seas (Jensen, 1998b). This could also be associated with lower shell weights influencing mass fluxes of planktonic foraminifera, but data on this is lacking. In terms of driving factors of the detected variability in foraminifera fluxes, both global and regional analyses indicate foraminifera shell fluxes following the pattern of chlorophyll α concentration and peaking at the same time, which could be relevant in terms of food source of foraminifera (Jonkers and Kucera, 2015; Rembauville et al., 2016). Pados and Spielhagen, 2014 show that in the Fram Strait, the extent of sea ice is a relevant factor in terms of food availability for planktonic foraminifera. Highest abundances are present at the sea ice margin, in contrast to lower abundances in areas of permanent sea ice cover and abundances on a medium level in the open ocean. Still, detailed studies on the relevance of different driving factors and their relationship to foraminifera mass fluxes are lacking.

This study aims to define the drivers of planktonic foraminifera calcite mass fluxes in the Subarctic and Arctic realm based on sediment trap data from the HAUSGARTEN observatory in the Fram Strait and three sediment trap moorings in the Nordic Seas from Jensen, 1998b. Shell flux and shell mass of relevant foraminifera species are analysed to identify the factors that form the variability in $CaCO_3$ mass fluxes produced by planktonic foraminifera within the seasonal cycle. Foraminifera mass fluxes are assessed at different depth intervals to assess the potential effects of dissolution and advection. To then understand influences on and drivers of the mass flux of planktonic foraminifera, environmental parameters are considered: sea surface temperature, solar insolation, variability in the depth of the mixed layer depth, sea ice concentration, chlorophyll α concentration and POC flux. We moreover assess the contribution of planktonic foraminifera to total $CaCO_3$ mass fluxes in the research area to quantify their relevance for the carbon cycle.

5.2 Material and methods

5.2.1 Sediment trap samples of planktonic foraminifera

This study is based on data from a sediment trap mooring in the HAUSGARTEN observatory in the eastern Fram Strait (79° 00.24′ N, 04°1.81′ E) operated by the Alfred-Wegener-Institute Helmholtz Center for Polar and Marine Research, complemented by published data from three further sediment trap stations located in the Greenland and Norwegian Sea from Jensen, 1998b (Fig. 5.1, Table 5.1). The HAUSGARTEN observatory is a Long-Term Ecological Research (LTER) observatory that has been monitoring particle sedimentation using moored sediment traps in the eastern Fram Strait since August 2000 (Soltwedel et al., 2005). We here use samples from the period of 24.06.2014 to 15.07.2015 (mooring FEVI30). The data from Jensen, 1998b spreads over the time period from 06.08.1991 to 15.07.1995, with a break between 1993 to 1994 (Table 5.1). We define samples with a flux of 0 individuals (ind.) m^{-2} d^{-1} in the moorings OG5, NB6 and NB7, as given in the data published on PANGAEA, as no data, as indicated in the publication of Jensen, 1998b. We further exclude the data from the deep trap (3000 m) of the station NB from our analysis, as the occurrence of benthic foraminifera and spicules as well as signals from other plankton groups at this trap indicate that the particle fluxes are strongly affected by resuspension and lateral advection and thus are not representative for sinking fluxes alone (Andruleit, 1995; Jensen, 1998b).

The central area of the HAUSGARTEN observatory is located in the ice-free part of the eastern Fram Strait which is defined by warm and nutrient-rich Atlantic water transported by the West Spitsbergen Current (WSC, Fig. 5.1; Soltwedel et al., 2005). In contrast, the western Fram Strait, partly ice-covered throughout the year and strongly influenced by ice drifting out of the central Arctic Ocean, is defined by the cold and fresh water of the East Greenland Current (EGC; Soltwedel et al., 2005; Bauerfeind et al., 2009). The hydrographic conditions in the Norwegian Sea are similar to the eastern Fram Strait, as they are driven by the Norwegian Current which transitions into the WSC. Average sea surface temperatures in the Norwegian Sea are slightly higher than in the eastern Fram Strait. The Greenland Sea is mainly influenced by the EGC and the Jan Mayen Current (JMC; Swift, 1986; Bodungen et al., 1995a).

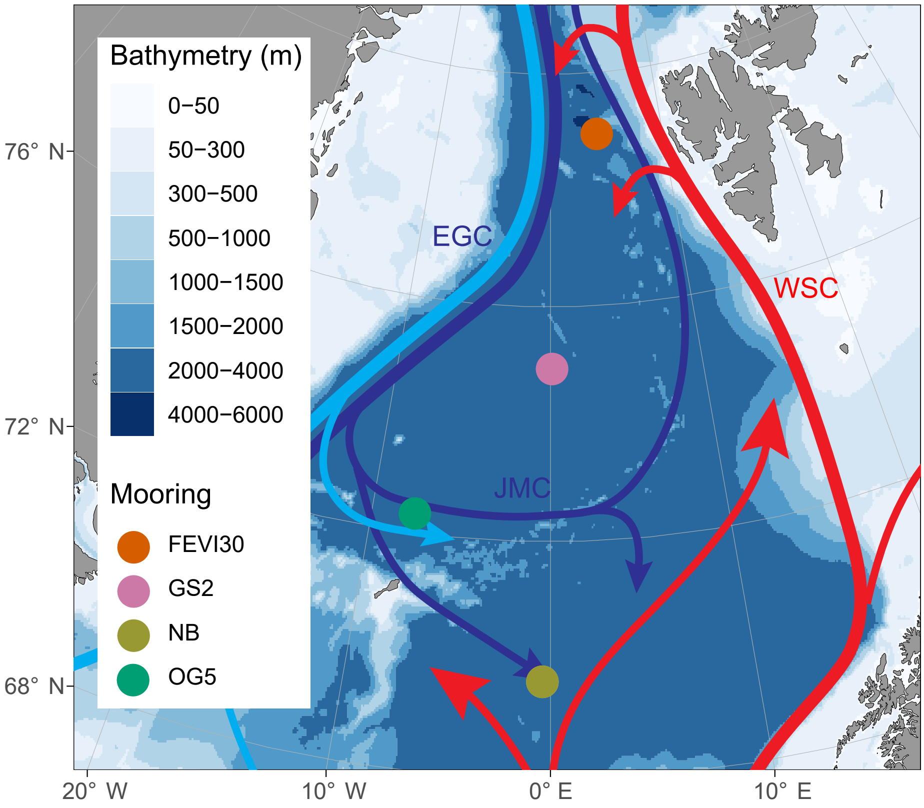

FIGURE 5.1: Location of sediment traps in the Nordic Seas. FEVI30 indicates the sediment trap in the HAUSGARTEN observatory analysed for this study, the other three points show locations of traps analysed by Jensen, 1998b. Red arrows indicate warm surface currents including the West Spitsbergen Current (WSC), light blue arrows cold surface currents (East Greenland Current, EGC) and dark blue arrows cold deepwater currents (Jan Mayen Current, JMC). Land polygons from Natural Earth Data (CC0), bathymetry from Amante and Eakins, 2009; using ggOceanMaps in R (Vihtakari, 2021), and currents from Anderson and Macdonald, 2015.

TABLE 5.1: Information on the sediment trap locations used in this study.

Mooring	**Latitude**	**Longitude**	**Sampling period**	**Water depth [m]**	**Trap depths [m]**	**No. of samples per depth**	**Source**	**Data source**
OG5	72.38	-7.71	06.08.1991 - 10.07.1992	2624	500, 1000, 2300	20	Jensen, 1998a; von Bodungen et al., 1995b	`https://doi.org/10.1594/PANGAEA.56002`; `https://doi.org/10.1594/PANGAEA.72222`
NB6	69.69	-0.47	06.08.1991 - 07.07.1992	3270	500, 1000	20	Jensen, 1998a; Thomsen and von Bodungen, 2001	`https://doi.org/10.1594/PANGAEA.55991`; `https://doi.org/10.1594/PANGAEA.60035`
NB7	69.69	-0.47	08.07.1992 - 02.10.1993	3270	500, 1000	20	Jensen, 1998a	`https://doi.org/10.1594/PANGAEA.56001`
GS2	75.00	0.00	03.06.1994 - 15.05.1995	3720	300, 900, 2100	19	Jensen, 1998a	
FEVI30	79.01	4.03	24.06.2014 - 15.07.2015	2517	213, 2319	20	This study	

The collection of sinking particles at FEVI30 was done with two modified automatic Kiel sediment traps installed in a bottom-tethered long-term mooring (Bauerfeind et al., 2014). We here analyse samples from two trap depths, in the following labelled as the shallow (213 m) and deep (2319 m) trap. The aperture of the sediment traps is 0.5 m^2. It has been shown that particles are transported from distances of up to 34 km around the mooring, and that the overall catchment area is variable due to changes in current velocities and directions on short-term time-scales (Bauerfeind et al., 2009; Wekerle et al., 2018). Sample collection was done by 20 liquid-tight collector cups, filled with filtered and sterilised water from the North Sea. For adjustment of salinity to 40 psu, NaCl was added. Poisoning with mercury chloride was done to get a 0.14 % solution (average pH at splitting: 7.7). The interval of collection was 15 to 21 days during the summer period (May to September) and 15 to 31 days during the winter period (October to April, Table 5.2). After their retrieval, the sediment trap samples were stored refrigerated at the Alfred-Wegener-Institute Helmholtz Center for Polar and Marine Research.

TABLE 5.2: Overview on sampling periods of the sediment trap at HAUSGARTEN observatory (Fram Strait). The asterisk (*) indicates a sample that was contaminated during splitting and therefore not available for analysis.

Station	**Sample Number**	**Duration [days]**	**Date**	**Trap depth [m]**	**Split**
FEVI 30	1	21	24.06.14 - 15.07.14	213, 2319	1/8, 1/8
FEVI 30	2	16	15.07.14 - 31.07.14	213, 2319	1/8, 1/8
FEVI 30	3	15	31.07.14 - 15.08.14	213, 2319	1/8, 1/8
FEVI 30	4	16	15.08.14 - 31.08.14	213, 2319	1/8, 1/8
FEVI 30	5	15	31.08.14 - 15.09.14	213, 2319	1/8, 1/8
FEVI 30	6	15	15.09.14 - 30.09.14	213, 2319	1/8, 1/8
FEVI 30	7	31	30.09.14 - 31.10.14	213, 2319*	1/8, 1/8
FEVI 30	8	15	31.10.14 - 15.11.14	213, 2319	1/8, 1/8
FEVI 30	9	15	15.11.14 - 30.11.14	213, 2319	1/8, 1/8
FEVI 30	10	31	30.11.14 - 31.12.14	213, 2319	1/8, 1/8
FEVI 30	11	31	31.12.14 - 31.01.15	213, 2319	1/8, 1/8
FEVI 30	12	28	31.01.15 - 28.02.15	213, 2319	1/8, 1/8
FEVI 30	13	31	28.02.15 - 31.03.15	213, 2319	1/8, 1/8
FEVI 30	14	15	31.03.15 - 15.04.15	213, 2319	1/16, 1/8
FEVI 30	15	15	15.04.15 - 30.04.15	213, 2319	1/16, 1/8
FEVI 30	16	15	30.04.15 - 15.05.15	213, 2319	1/16, 1/8
FEVI 30	17	16	15.05.15 - 31.05.15	213, 2319	1/16, 1/8
FEVI 30	18	15	31.05.15 - 15.06.15	213, 2319	1/16, 1/8
FEVI 30	19	15	15.06.15 - 30.06.15	213, 2319	1/16, 1/8
FEVI 30	20	15	30.06.15 - 15.07.15	213, 2319	1/8, 1/8

Samples were split in eight or 16 aliquots for further processing (Table 5.2). Sample FEVI30-7 from the deep trap was contaminated during the splitting process and therefore could not be analysed. Foraminifera shells were individually picked from the wet sample with a pipette, washed with tap water and dried at 50 °C overnight. Foraminifera species were determined based on the taxonomy of Brummer and Kucera, 2022. Fragments of foraminifera shells that could be identified as parts of foraminifera shells based on the chamber structure were defined as undetermined shells. Very small shells of which species determination was difficult fall in this category as well. Size measurements were conducted with a KEYENCE VHX-6000 digital microscope, measuring the minimum and maximum diameter of individual shells using the KEYENCE software, and shell weights were measured per sample and species with a Sartorius SE2 ultra-micro balance (nominal resolution of 0.1 µg). At maximum, 200 shells were used for one measurement. Of samples containing more than 200 shells, only up to 200 shells out of it were measured, visually selecting a representative variety of shells present in the sample for the measurement. In 23 samples, weight measurements were not conducted on all species. This concerned different species differently (*N. incompta* in 15 samples, *T. quinqueloba* in 1 sample, *G. bulloides* in 7 samples, *G. glutinata* in 4 samples, *G. uvula* in 3 samples and *O. riedeli* in 1 sample). Total $CaCO_3$, $CaCO_3$ excluding aragonite from pteropods and POC fluxes were determined in all samples from FEVI30 as described in Bauerfeind et al., 2009. For the sediment trap stations from Jensen, 1998b, data on total $CaCO_3$ and POC fluxes is available for the stations OG5 (data from von von Bodungen et al., 1995b) and NB6 (data from Thomsen and von Bodungen, 2001), but not for the stations NB7 and GS2.

5.2.2 Analysis of planktonic foraminifera fluxes

To understand what is defining the variability in planktonic foraminifera mass fluxes, we study the variability of planktonic foraminifera shell flux (ind. m^{-2} d^{-1}) in samples from all four sediment trap stations. The variability of shell size and average shell mass of planktonic foraminifera over time and with depth is analysed in samples from FEVI30. For the data from Jensen, 1998b, only information on the proportion of different shell size classes are available for the stations OG5 and NB7, but not on exact shell sizes or shell weights. Besides overall variability of shell flux, size and weight, their variability within the most relevant species of planktonic foraminifera in the research area is assessed.

$CaCO_3$ mass fluxes of planktonic foraminifera (mg $CaCO_3$ m^{-2} d^{-1}) at sediment trap FEVI30 were calculated based on the foraminifera shell flux and the average weight of the different species in the sample, under the assumption that the foraminifera shells do only, if at all, contain little organic matter (Mezger et al., 2019). Where weight measurements of the species in a sample are lacking, which is the case in a few samples from FEVI30 and all samples from Jensen, 1998b, the average weight of the species from all samples was used to estimate the mass flux. Doing so, we assume that shell size and calcification intensity of the planktonic foraminifera is similar at the different sampled stations and that seasonal variability can be considered negligible. As regional differences in foraminifera shell size between the Fram Strait and the Baffin Bay have been indicated in a previous study (Tell et al., 2022), we cannot preclude that there are regional differences, which is why this assumption will be accounted for in the interpretation of the results. Possible seasonal variability is analysed for the FEVI30 samples, and the result of this analysis will be accounted for as well. The data from Jensen, 1998b is based on analysis of samples > 63 µm, while no foraminifera shells were excluded based on grain size in samples from FEVI30. Less than 1 % of the shells from FEVI30 have a minimum diameter < 63 µm (199 out of 22,073 analysed shells). The proportion of shells in the size class from 63 to 125 µm is slightly higher in samples from FEVI30 than in samples from OG5 and NB7 (48 % in contrast to 36 %) and the proportion of larger shells slightly lower (51 % in contrast to 57 % at OG5 and 61 % at NB7 in the size class 125 to 250 µm, and 1 % in contrast to 7 % at OG5 and 3 % at NB7 in the size class 250 to 500 µm). The $CaCO_3$ flux at stations OG5, GS2 and NB is therefore likely to present a minimum estimate, resulting in a conservative estimate of the importance of planktonic foraminifera for the $CaCO_3$ budget. To quantify trends in foraminifera shell fluxes within the water column and possible effects of dissolution on the foraminifera shell and mass flux, fluxes as well as shell size and weight at different depth intervals were compared.

To determine possible drivers of the mass flux of planktonic foraminifera, data on environmental parameters were gathered for each upper sediment trap. We do so as the production of foraminifera shells, which might be influenced by environmental conditions, is happening in the first 300 m depth (Volkmann, 2000; Stangeew, 2001; Greco et al., 2019; Tell et al., 2022). Planktonic foraminifera present a seasonal pattern in fluxes similar to temperature patterns in the Nordic Seas (Jensen, 1998b; Ramondenc et al., 2022). As no in situ temperature measurements are present for the sediment trap stations from Jensen, 1998b, we use satellite data on sea surface temperature (SST; data from NOAA NMFS SWFSC ERD, NOAA CoastWatch West Coast, [data set]) to analyse the relationship of planktonic foraminifera mass fluxes and water temperature. The satellite data with a resolution of 4x4 km was retrieved from a 1x1° grid surrounding the location of each sediment trap, calculating the average SST for each time step present in the satellite data (resolution of 8 days) for the whole area. At FEVI30, we complement this data with direct temperature measurements from the conductivity-temperature-depth (CTD) casts of the mooring (data from Bauerfeind et al., 2016). As this measurement is conducted throughout the water column, we used the average values from the upper 213 m, the area in which shells collected in the upper trap are formed. Linked to temperature are the mixed layer depth (MLD) and the solar insolation. Data on MLD is present on long-term averages in the World Ocean Atlas 2018, determined based on a density threshold (Boyer et al., 2018). We analysed MLD at the different sampling locations from the time period from 2005 to 2017 for comparison with foraminifera fluxes at sediment trap station FEVI30, and from the period of 1981 to 2010 for the other three sediment trap stations, as those are the time intervals present in the World Ocean Atlas for the MLD that include each sampling period of our analysed stations. Solar insolation at the different sediment trap stations throughout the year was calculated as a function of date and latitude using the solar constant of 1361 W m^{-2} (Thekaekara and Drummond, 1971). The concentration of sea ice is not only another parameter linked to temperature, but has also been shown to be relevant for abundances of planktonic foraminifera in the Fram Strait by Pados and Spielhagen, 2014. To test the correlation of total planktonic foraminifera mass fluxes and sea ice concentration, we used satellite data on the sea ice concentration with a resolution of 25 x 25 km from Fetterer et al., 2017. We calculated the average sea ice concentration in a 1x1° grid in this data around the position of each sediment trap for the relevant time period. Rembauville et al., 2016 have shown that foraminifera fluxes increase with increasing chlorophyll α concentration. Meilland et al., 2020 further indicated that it is not only the quantity of chlorophyll α, but especially the quality of available food that is of importance for foraminifera productivity. Estimates of chlorophyll α concentration from remote sensing are only available since 1998, hence only for the sampling period of FEVI30. To get an impression of average chlorophyll α concentration with the seasons at the different stations, we further analysed the average monthly chlorophyll α concentration from 2003 to 2021 in the 1x1° grid around each sediment trap location, also including FEVI30 to compare the average value with the exact measurements. All data on chlorophyll α concentration was derived from NASA/GSFC/OBPG, [data set]. To further evaluate productivity in direct connection to the flux of planktonic foraminifera, we made use of measurements of POC fluxes at FEVI30, OG5 and NB6 from the sediment trap samples themselves. To evaluate the effect of the different drivers on the mass flux of planktonic foraminifera, Spearman's Rank correlation coefficients (Spearman, 1904) were calculated, as foraminifera mass flux are not normally distributed. All statistical analyses were performed using R v. 4.2.1 (R Core Team, 2022).

5.3 Results

5.3.1 Defining factors of the variability of foraminifera mass flux

Neogloboquadrina pachyderma, *Turborotalita quinqueloba* and *Neogloboquadrina incompta* are the most abundant species in the four time series and together make up over 90 % of the total shell flux (Table 5.3). All other species are present at abundances below 8 %. We hence concentrate our analysis on the three most abundant species.

TABLE 5.3: Relative abundances (%) of planktonic foraminifera species at the different sediment trap stations and all stations together over the whole sampling period, weighted by the shell flux in different samples.

Species	**All stations**	**FEVI30**	**OG5**	**GS2**	**NB**
N. pachyderma	53.4	38.0	84.7	51.2	39.7
N. incompta	8.3	9.2	2.0	3.5	18.7
T. quinqueloba	31.3	41.9	13.2	43.9	26.1
G. bulloides	0.4	0.1	0.0	0.0	1.5
G. glutinata	2.6	3.7	0.0	0.2	6.4
G. uvula	3.1	3.2	0.0	1.4	7.7
O. riedeli	0.4	0.4	NA	NA	NA
Undetermined	0.9	3.5	0.1	0.0	0.0

5.3.1.1 Variability in foraminifera shell flux

The average shell flux of planktonic foraminifera in the studied sediment traps over a time period from August in the first year of sampling to May in the second year of sampling ranges from 83 to 560 ind. m^{-2} d^{-1} (Table 5.4). It is following a seasonal pattern, with maximum values being reached between July and November (838 to 4363 ind. m^{-2} d^{-1}), and minimum fluxes occurring from January to April (0.0 to 7.6 ind. m^{-2} d^{-1}; Table 5.4; Fig. 5.2). This pattern is visible in all three studied species, with more variability in *N. incompta*, connected to uncertainties caused by its overall lower shell flux.

At mooring FEVI30, there is a trend of increasing foraminifera shell fluxes with depth all over the sampling period with only one exception (Fig. 5.3). At GS2, shell fluxes tend to be higher at the shallow trap. At the other two stations, both increases and decreases in shell fluxes with depth occur.

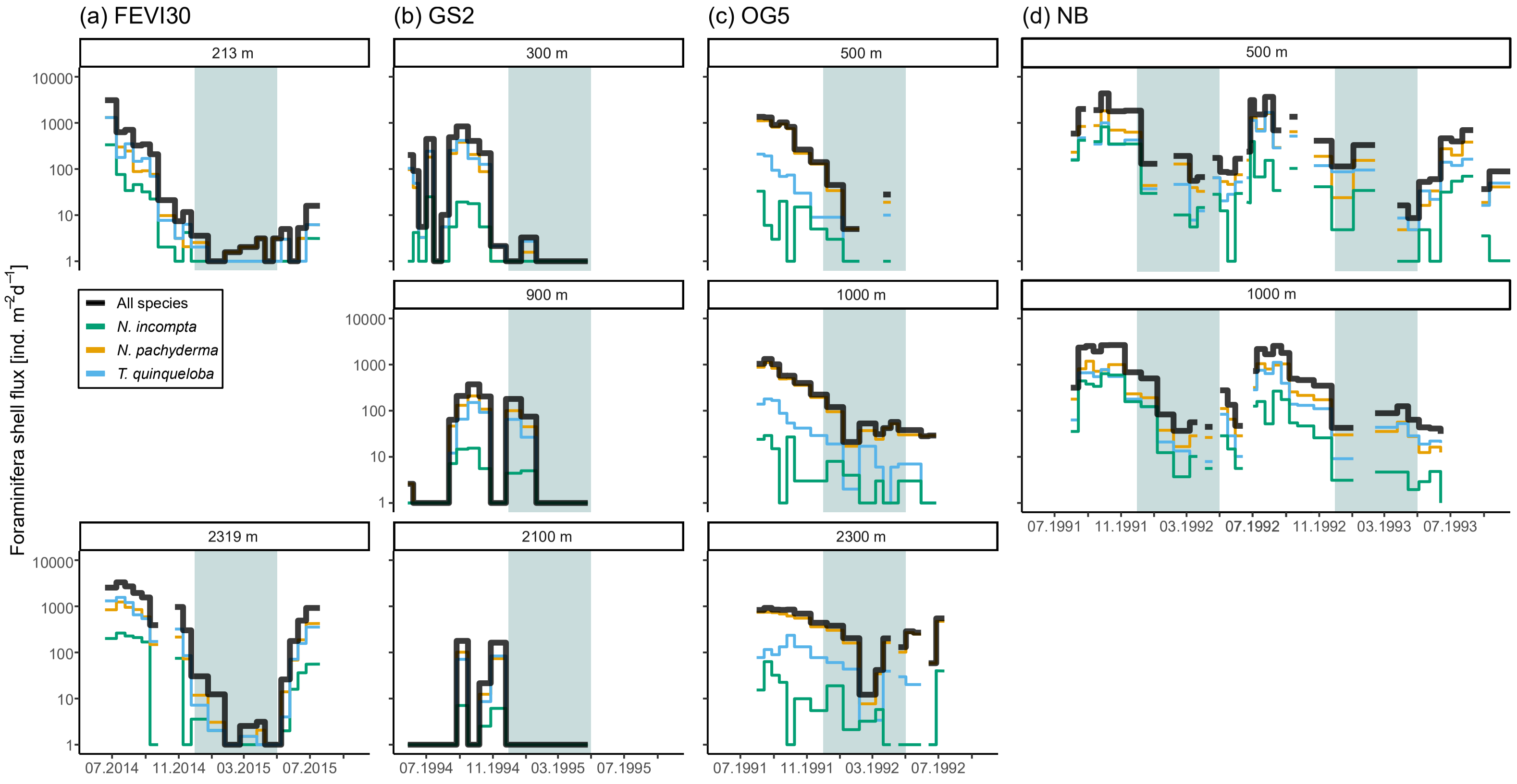

FIGURE 5.2: Shell flux of planktonic foraminifera at the different sediment traps of the study, divided into sampling depths. The total shell flux of all species and the flux of the three most abundant species, *N. pachyderma*, *T. quinqueloba*, and *N. incompta*, are shown in different colours. The y-axis is plotted on a logarithmic scale, adding +1 to all values to enable visualisation of fluxes with values of zero. Winter and spring (December to May) are marked with a light blue shading.

TABLE 5.4: Minimum, maximum and average shell flux of planktonic foraminifera (ind. m^{-2} d^{-1}) at the different sediment trap stations and sampling depths of the study. The given average represents the average from August in the first year of sampling to May in the second year of sampling to enable comparability between the different stations that overall sampled different time intervals.

Shell flux	Min.	Max.	Average (August y1 - Mai y2)
FEVI30	0.0	3309	98
GS2	0.0	838	83
OG5	0.0	1352	335
NB	7.6	4363	560

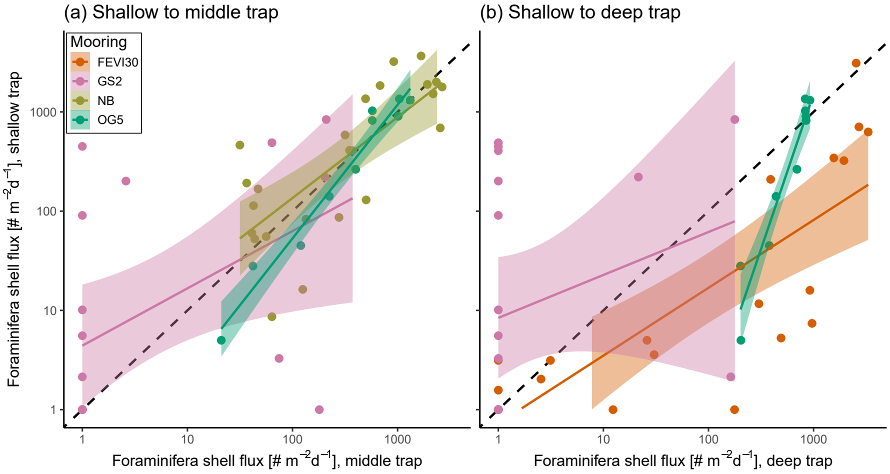

FIGURE 5.3: Comparison of foraminifera shell flux at the shallow (213 m, 300 m, 500 m) and the (a) middle (900 m, 1000 m) and (b) deep (1000 m, 2100 m, 2300 m, 2319 m) sediment trap of each mooring of the study. The black dashed line indicates the line where fluxes are the same at both depth intervals. All points above this line indicate higher fluxes at the shallow trap, all points below higher fluxes at the deeper trap. The coloured lines show the linear regression model for each sediment trap station, the shadings the 95 % confidence interval. Fluxes are plotted on a logarithmic scale, adding +1 to all values to enable visualisation of fluxes with values of zero.

5.3.1.2 Variability in foraminifera shell size and weight

Shell sizes of planktonic foraminifera in samples from all sampled depths of FEVI30 and OG5 decreased by about 18 % (24 and 35 µm, respectively) from summer (June to August) to autumn (September to November; Fig. 5.4). At the shallow trap of FEVI30, this seasonal change was smaller (7 %). At NB7, average shell sizes between summer and autumn 1992 only differ by 1 % (0.75 µm), but foraminifera shells were 30 % larger (44 µm) in summer 1993 (Fig. 5.4c). The changes in size were similar at the different depth intervals of station NB7. At FEVI30, foraminifera shell sizes on average were 8 to 19 % smaller at further depth within the same time interval, at NB7, they were 4 to 7 % smaller. At OG5, the average shell size in samples from further depth was 4 to 17 % larger. Planktonic foraminifera shell weight data are only available for the Fram Strait time series. On average, shell weights were 33 % (0.5 µg) higher during summer (Fig. 5.5). The change in shell weight with depth at the same time interval is larger than that, with shells at 2319 m being 55 % (1.2 µg) lighter during summer than at 213 m depth, and 39 % (0.5 µg) lighter during autumn. Contrasting the different species reveals that while *T. quinqueloba* on average is the largest of the three most abundant species in all timeseries, *N. pachyderma* is the heaviest according to the data from sediment trap FEVI30 (Table 5.5).

TABLE 5.5: Average shell weight (µg) and shell size (µm) of different species of planktonic foraminifera at the different sediment trap stations, weighted by the shell flux in each sample. Values for all species together are further weighted by the abundance of the different species in each sample. Shell sizes of the stations OG5 and NB7 are based on average values from size classes the shells were classified into, and not from detailed size measurements, as done on samples from FEVI30.

	Avg. shell weight [µg]	**Avg. min. diameter [µm]**	**Avg. Max. diameter [µm]**	**Avg. size from mesh size group [µm]**	
		FEVI30		**OG5**	**NB7**
All species	1.5	132.9	161.3	168.9	150.4
N. pachyderma	2.3	136.1	164.5	168.1	144.0
N. incompta	1.5	127.0	155.7	175.0	157.0
T. quinqueloba	1.3	143.0	172.8	172.6	159.6
G. bulloides	4.1	172.6	214.7		
G. glutinata	1.2	127.2	153.2		
G. uvula	0.3	90.7	109.8		
O. riedeli	0.4	102.2	123.9		
Undetermined	0.6	100.9	130.2		

5.3.1.3 Contribution of planktonic foraminifera mass flux to total $CaCO_3$

Mass fluxes of planktonic foraminifera at FEVI30 range from 0.0 to 7.1 mg $CaCO_3$ m^{-2} d^{-1} over the whole time series, with a summer (June to October) average of 2.7 mg $CaCO_3$ m^{-2} d^{-1} (Table 5.6). Mass fluxes for the other stations were calculated based on average shell weights from FEVI30. As changes in shell size at the different stations are different, and we cannot draw a direct conclusion on the effect of different shell sizes on different shell weights, this is the best possible estimate, even though our data indicates that shell mass varies over time and even more between depth intervals. Based on the average weights from data from FEVI30, the magnitude of mass fluxes at the moorings OG5, GS2 and NB is similar to the fluxes from FEVI30 (Table 5.6). The overall average mass flux of planktonic foraminifera at all studied sediment traps from August to May in preceding year at each deepest sampling position is 0.5 mg $CaCO_3$ m^{-2} d^{-1}.

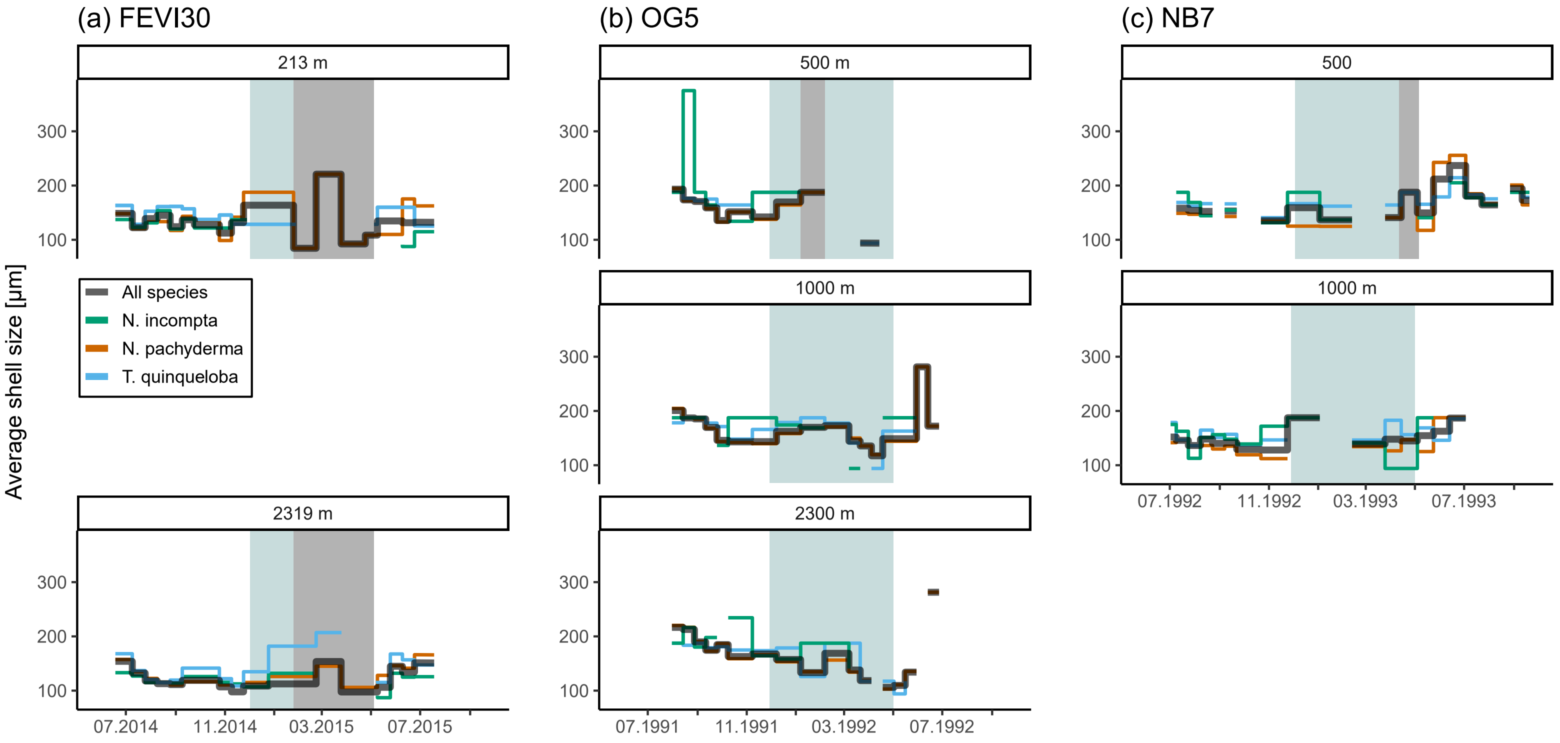

FIGURE 5.4: Average and species-specific shell size of all planktonic foraminifera in the sediment traps FEVI30, OG5 and NB7 over time of sampling. Size information on samples from FEVI30 represents individual measurements of the minimum diameter on all shells in all samples. Size data for OG5 and NB7 are based on the average size of each determined size class (63 - 125 µm, 125 - 250µm, 250 - 500 µm). Areas marked in grey represent periods of overall low foraminifera shell fluxes (<10 ind. m^{-2} d^{-1}), making accurate determination of average sizes difficult. The flux of *N. incompta* in the sample from August 1991 at OG5 at 500 m depth was also below this threshold, reducing the representability of the average size of this species at this point in time. The light blue shading indicates winter and spring (December to May).

On average, planktonic foraminifera mass fluxes make up 5.4 % of total fluxes of $CaCO_3$ at the sediment trap stations FEVI30, OG5 and NB6 (data on $CaCO_3$ lacking at GS2 and NB7) at all depth intervals. At FEVI30, the contribution at the shallow trap is lower than at the deep trap looking at the contribution to total $CaCO_3$, but higher at the shallow trap looking at the contribution to $CaCO_3$ without the aragonite from pteropods (Fig. 5.6a). At OG5, the contribution to total $CaCO_3$ fluxes is slightly higher at the shallow trap (Fig. 5.6) and there is no difference with depth at station NB6 (Fig. 5.6c).

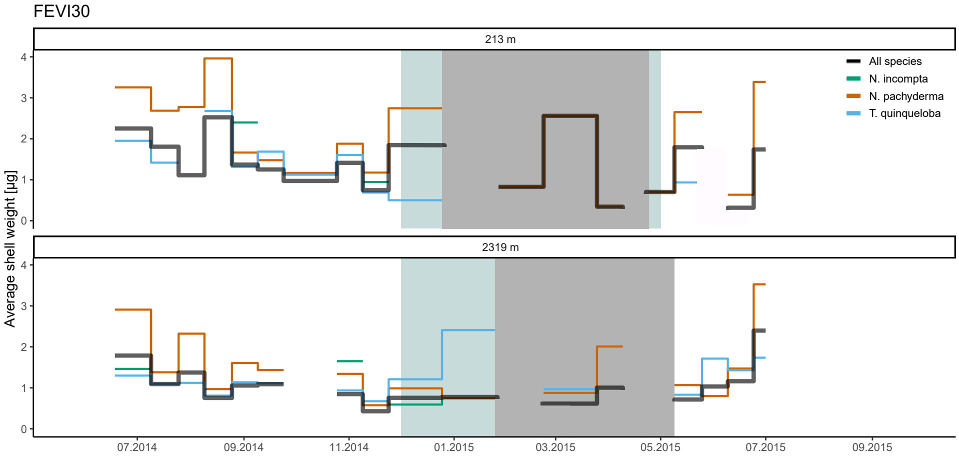

FIGURE 5.5: Average shell weight of all species in the samples from sediment trap station FEVI30, as well as of the most abundant species *N. pachyderma*, *T. quinqueloba*, and *N. incompta*, plotted against the time of sampling. Areas marked in grey represent periods of low foraminifera shell fluxes (> 10 ind. m^{-2} d^{-1}), the light blue shading indicates winter and spring (December to May).

5.3.2 Environmental drivers of foraminifera mass flux

As described in section 5.3.1, the most abundant species of planktonic foraminifera follow the same seasonal pattern of fluxes over the whole sampling period without clear species succession. We therefore analyse environmental influences on foraminifera mass fluxes for the total assemblage of species in the data. As stated in the methods section, we furthermore focus on fluxes in each shallowest trap, as this is closest to the depth where planktonic foraminifera shells are produced, hence where environmental factors can mostly influence their productivity and thereby their mass flux. The locations of the four sediment trap stations of this study differ in environmental conditions in terms of average sea surface temperature, sea ice concentration and mixed layer depth in the period sampled by all traps (August to May; Fig. 5.7d-f). The average concentration of chlorophyll α is on a similar level at all stations (Fig. 5.7c), while average POC fluxes in the shallow sediment trap are higher at station FEVI30 (Fig. 5.7b). Average overall mass fluxes of planktonic foraminifera are lowest at FEVI30 and highest at NB (Fig. 5.7a). It has to be considered that highest fluxes at FEVI30 occurred in July 2014 (Fig. 5.2a), which is not represented in the here shown average, and that this maximum reached at FEVI30 is similar to the maximum of NB (Table 5.6).

TABLE 5.6: Minimum, maximum and average mass flux of planktonic foraminifera (mg $CaCO_3$ m^{-2} d^{-1}) at the different sediment traps of the study and different depth intervals. The given average represents the average from August in the first year of sampling to May in the second year of sampling to timewise enable comparability between the different stations. The summer average represents the average in the months June to October to show the average of the most productive period.

Station	**Depth [m]**	**Minimum**	**Maximum**	**Average (August y1 - May y2)**	**Summer average (June - October)**
FEVI30	213	0.0	7.1	0.2	2.7
	2319	0.0	4.6	0.2	1.6
GS2	300	0.0	1.5	0.2	0.5
	2100	0.0	0.3	0.1	0.1
OG5	500	0.0	2.8	0.6	1.8
	2300	0.0	1.9	0.9	1.8
NB	500	0.0	7.7	0.9	2.2
	1000	0.1	4.5	1.0	1.4

All over the studied stations, the mass flux of planktonic foraminifera is linearly correlated with total $CaCO_3$ fluxes, POC with the sea ice concentration at GS2 and OG5. All parameters but sea ice concentration are significantly correlated with sea surface temperature (Fig. 5.8). That the correlation is not significant for the sea ice concentration is related to the missing sea ice concentration at the location of mooring NB, without which this correlation is also significant.

Peaks in foraminifera mass fluxes occur in line with peaks in the sea surface temperature, as well as in the solar insolation and minimum in the mixed layer depth (Fig. 5.9). Sea ice concentration minimum is in line with the foraminifera mass flux maximum at GS2 and OG5, while the sea ice concentration at FEVI30 constantly decreases from July 2014 to July 2015. This means that at FEVI30, highest foraminifera mass fluxes are present in the period of highest sea ice concentration. The long-term average chlorophyll α concentration shows the tendency of peaking slightly before the peak in foraminifera mass flux occurs at all stations. Measurements from the time of sampling from FEVI30 show chlorophyll α concentrations up to ten times higher in July 2015 in comparison to July 2014. POC fluxes at FEVI30 follow the seasonal pattern as well, with the peak in summer 2015 occurring before the peak in planktonic foraminifera mass fluxes. At OG5, they decrease towards winter, without increasing in the preceding summer. At NB, the overall seasonal pattern in POC fluxes is blurred by periods of higher fluxes from October to December and in April in between the overall less productive winter period.

Calculation of a linear regression model between the mass flux of planktonic foraminifera and the total $CaCO_3$ flux, POC flux, sea surface temperature, sea ice concentration, chlorophyll α concentration, mixed layer depth and the solar insolation, working with logarithmic values of all parameters to account for their non-linearity, gives only a significant influence from total $CaCO_3$ flux and the mixed layer depth. As total $CaCO_3$ flux contains the foraminifera flux, we then looked at the mixed layer depth alone, which results in a R^2-value of 0.4 ($p < 0.00$).

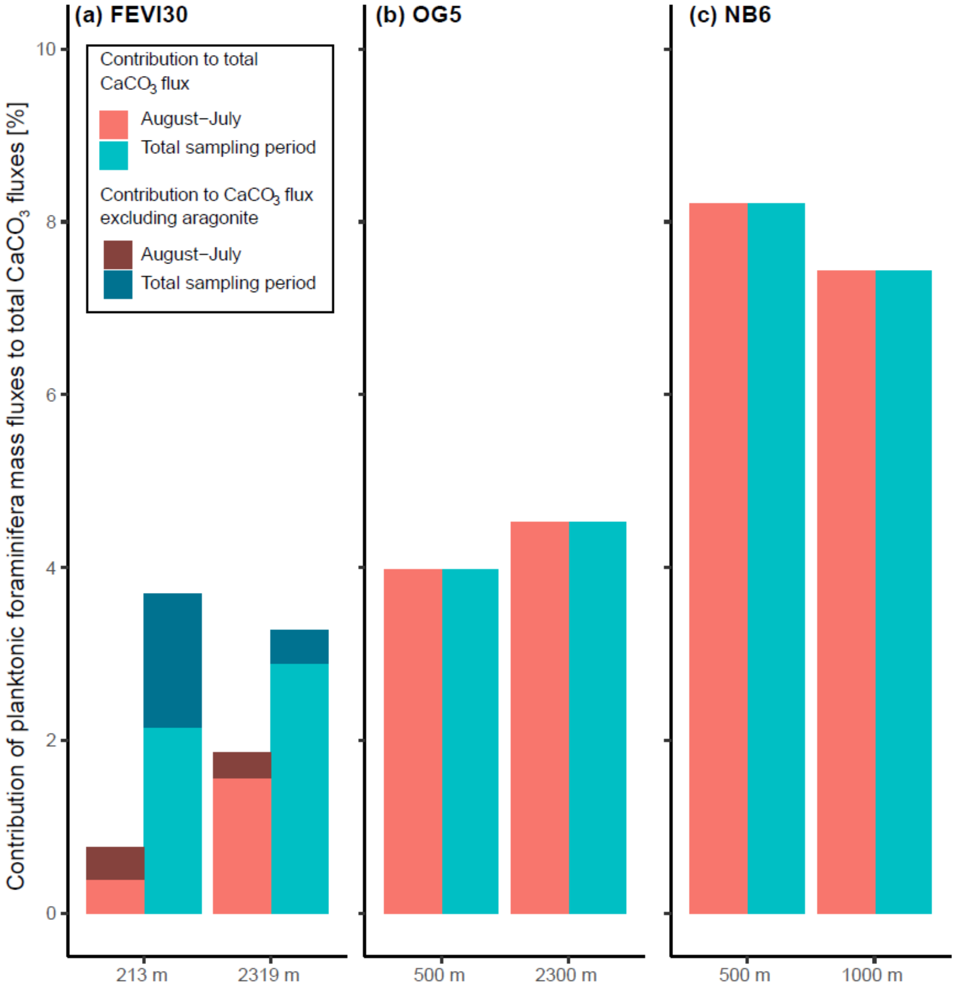

FIGURE 5.6: Contribution of planktonic foraminifera mass flux to the total $CaCO_3$ flux at the three moorings where this information was available, shown for both the whole sampling period of each trap (blue) and to enable direct comparability for August in the first year of sampling to July in the preceding year (red) for different depth intervals (at OG5 and NB6, these two periods were the same). In (a), the contribution to total $CaCO_3$ excluding the aragonite from pteropods exceeding the contribution to $CaCO_3$ including aragonite is indicated by the darker bars.

5.4 Discussion

5.4.1 Defining the variability of foraminifera mass flux

Our data confirms that the variability in the mass flux of planktonic foraminifera is mainly defined by variability in the shell flux, as previously shown by Kiss et al., 2021. On an intra-annual scale, shell fluxes vary by about three orders of magnitude at the studied sediment trap stations in the Nordic Seas (Fig. 5.2), while shell size and shell weight at maximum vary by one order of magnitude (Fig. 5.4, Fig. 5.5). Kiss et al., 2021 further show that on interannual scales, shell weight is more relevant for the total mass flux variability of planktonic foraminifera. As our data on shell size and weight never cover more than one year at the same sampling location, we are not able to define an effect of variation in shell weight in contrast to variation in shell fluxes on interannual time scales. Nevertheless, shell size and shell weight tend to change with the seasons in our data, becoming smaller and lighter during winter. Several studies present indications that shell size and calcification intensity of planktonic foraminifera are influenced by water temperature, resulting in smaller and less calcified shells in times of lower temperatures (Carstens and Wefer, 1992; Kohfeld et al., 1996; Weinkauf et al., 2016; Ofstad et al., 2020). The cause of this influence might not be the temperature alone, but also the low food availability in colder periods hampering growth. Further effect on shell weight might be based on the reproduction of planktonic foraminifera mainly happening during the productive summer period in the research area (Carstens et al., 1997; Volkmann, 2000; Pados and Spielhagen, 2014). The most abundant species of the region, *N. pachyderma*, sometimes builds a thick calcite crust in the context of its gametogenesis (Kohfeld et al., 1996). If reproduction mainly occurs during the productive period in summer and autumn, average shell weights would be higher in this time. On the contrary, during winter, when reproduction is limited, crustation might not occur as often, leading to lower average shell weights. That the change in shell weight in foraminifera shells from FEVI30 between summer and winter is stronger than in shell size can be explained by shell size not necessarily increasing significantly when the thick crust is added (Tell et al., 2022), or by a change in the reproductive behaviour from sexual to asexual reproduction (Meilland et al., 2022).

5.4.2 Accuracy in planktonic foraminifera mass flux estimation

Even though the variability in foraminifera shell mass is minor in contrast to the variability in shell flux, it is a relevant component to determine the overall mass fluxes. Our data shows the importance of constraining shell weight as detailed as possible if mass fluxes are estimated based on shell flux data. With the different species-specific shell weights (Table 5.1) not having the same ranking as the species abundance (Table 5.3), it is necessary to use species-specific average weights when no measurements of weights are present for a studied sample. Nevertheless, even with knowing species-specific weights and their abundance in all here studied sediment trap samples, our estimates in mass flux have components of inaccuracy.

The weights used to determine the mass flux at FEVI30 are species-specific shell weights that were extrapolated to the total mass per species based on counts, and not measured on all picked shells. The measured species-specific weights on average differ by about 3 µg. Therefore, the used average weights are imprecise, especially when using them for distinct samples. All shell weights we used here are from the sediment trap FEVI30 and based on hundreds of specimens pooled together. As it has been shown that temperature can influence the shell weight of foraminifera (Carstens and Wefer, 1992; Kohfeld et al., 1996; Weinkauf et al., 2016; Ofstad et al., 2020), the differences in temperature averages at the studied stations (Fig. 5.7) could have an effect on average weights. On top of that, as stated in the methods section, the slightly lower proportion of smaller shells in samples from FEVI30 can result in a bias towards too low estimates of foraminifera mass fluxes in the other samples.

The detected decrease in shell weight with depth is important to consider for the accuracy of the mass flux estimates. As the used average shell weight to determine fluxes in the samples from Jensen, 1998b is based on samples from all depths, mass fluxes at shallow sampling depths from the stations from Jensen, 1998b might be underestimated, while fluxes at further depth are overestimated by about 50 %, which is the decrease in weight with depth detected in samples from FEVI30 during the productive season.

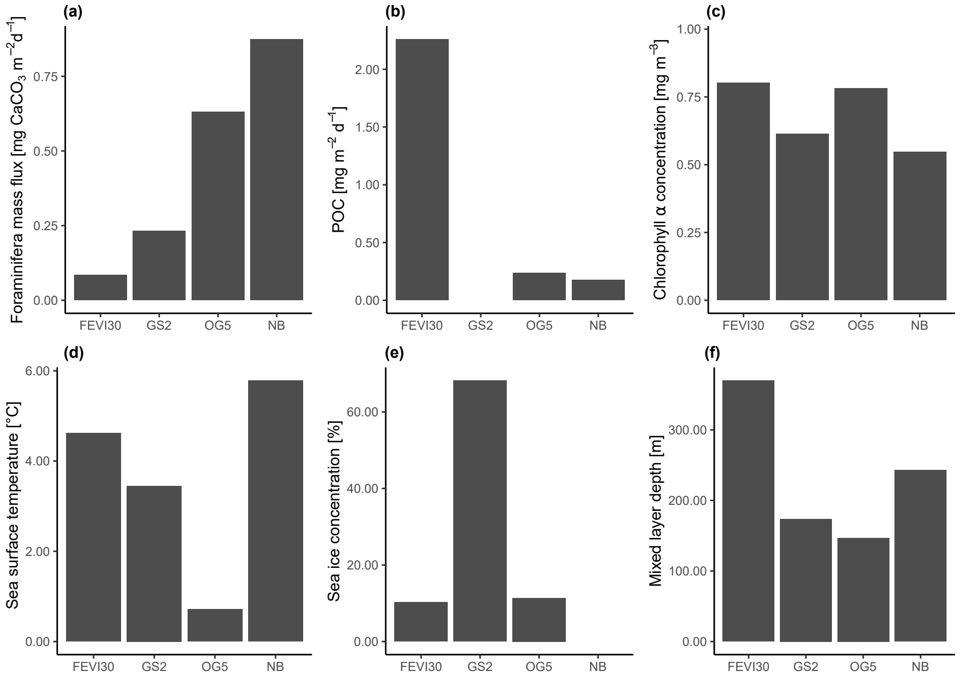

FIGURE 5.7: Averages of (a) planktonic foraminifera mass flux at the shallowest trap depth and (b-f) different environmental parameters at all sediment trap stations in the time period from August in the first year of sampling to May in the second year of sampling. (a), (b) and (e) show values representing the exact time period of sampling at each trap, while (c), (d) and (f) represent long-term average values as described in the methods section. The chlorophyll α concentration (c) from FEVI30 represents the average from the actual sampling period of the station. POC fluxes show fluxes from the same sediment traps as the foraminifera mass fluxes, displaying values from each shallow sediment trap.

However, we do not know if the magnitude of change at the other locations would be the same, without knowing the reasons for the change. An effect of dissolution is unlikely, as shell fluxes at FEVI30 increase with depth. We further assume that dissolution would result in an increase in the average shell weight, as thin shells dissolve faster, leaving only the heavier shells behind. A possible explanation of differences in shell weights with depth can be the detected lateral advection at the HAUSGARTEN observatory, where the samples from FEVI30 come from (Lalande et al., 2016). Lateral advection can bring shells formed under different environmental conditions into the deep trap, resulting in a divergent average shell weight. Lalande et al., 2016 further have shown that the trapped material in the deep sampling position contains resuspended material from the Barents Sea. This material could be affected by dissolution differently, as well as containing shells formed under different conditions, hence bringing lighter shells into the deeper trap.

While our data shows no clear indication of dissolution of the foraminifera with depth, the examined shells might still have been influenced by dissolution before the weight measurements: With an average pH of 7.7 during splitting after sample retrieval, dissolution is not unlikely to affect the shells, especially considering that the weight measurements were conducted four to five years after sample retrieval. There is no information on the pH at sample retrieval for the samples from Jensen, 1998b. If the pH would be different, that could, besides environmental influences, be an explanation for the different proportion of size classes between samples from FEVI30 and data from Jensen, 1998b, as described in the methods section (section 5.2.2).

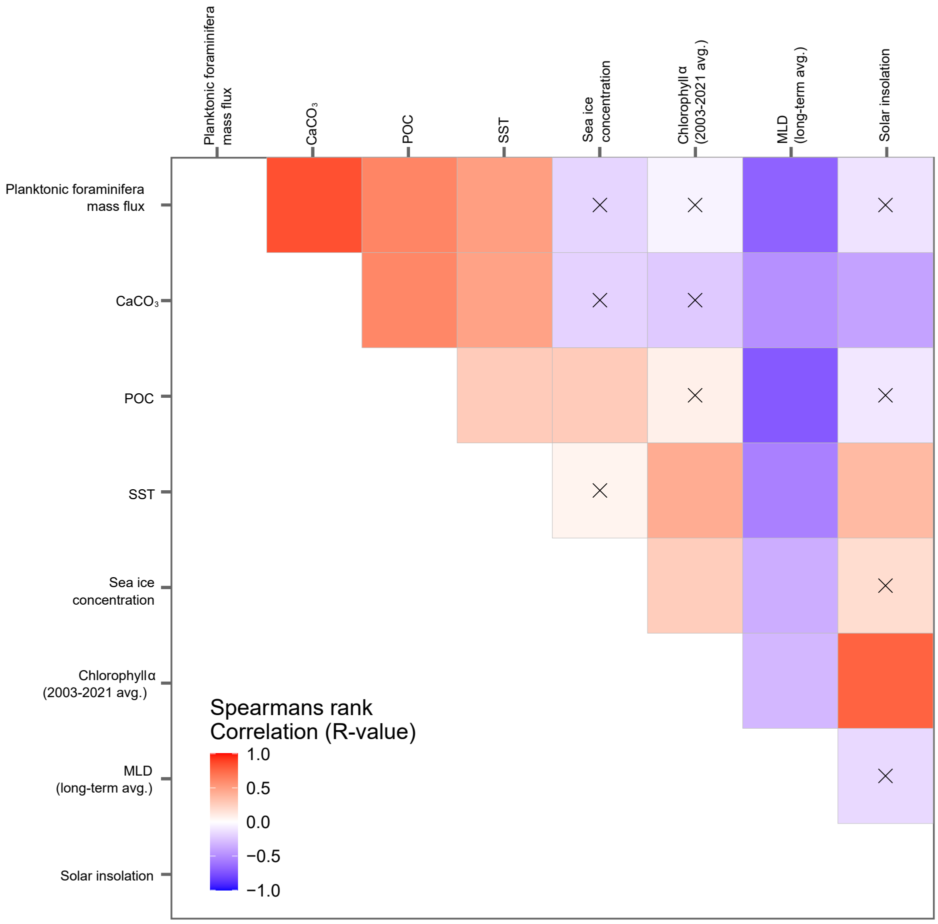

FIGURE 5.8: Spearman's rank correlation between the mass flux of planktonic foraminifera at all sediment trap stations of the study and different possible drivers of the mass flux, as well as correlations between the other parameters. Values marked with an x are not significant ($p > 0.05$).

The higher shell fluxes at the deep trap of FEVI30 (Fig. 5.3) can partly be explained by the depth of the shallow trap: It has been shown that the productive zone of *N. pachyderma* can reach down to 300 m, with a maximum of 289 m in samples from the Fram Strait (Tell et al., 2022). With a sampling depth of 213 m, it is therefore likely that foraminifera fluxes in the shallow trap represent an underestimation, as foraminifera shells are still produced below the depth of trapping. This can result in higher fluxes at further depth. However, we also see a gain in foraminifera shell fluxes in some samples from the moorings OG5 and NB. Here, the depth of the trap cannot be the explanation, as the shallow traps of these moorings were located at 500 m depth, hence below the shown end of the productive zone of *N. pachyderma* (Tell et al., 2022).

The tendency of higher fluxes at greater depth was also shown in sediment traps in other parts of the Arctic and Subarctic realm by Bodungen et al., 1995a and Thomsen et al., 2001 at the Barents Sea margin and by Fahl and Nöthig, 2007 at the Lomonosov Ridge. It can further be explained by the described lateral advection at the HAUSGARTEN observatory, which could cause higher fluxes at further depth (Lalande et al., 2016). von Gyldenfeldt et al., 2000 estimated flux trajectories of *N. pachyderma* and *T. quinqueloba* in the eastern Fram Strait based on sediment trap data, showing that transportation over distances of up to 300 km is possible. The current system of the Nordic Seas and the Fram Strait with both warm Atlantic and cold Arctic surface water currents, together with colder bottom water currents (Anderson and Macdonald, 2015; Fig. 5.1), might lead to differences in shell fluxes at different trapping depths, as temperatures can have an effect on the productivity. Scholten et al., 2001 furthermore indicate an overall trapping bias from sediment traps, causing higher flux values at deeper trapping positions.

The average sinking velocity of the foraminifera shells in our samples, based on the average shell weight and the equation by Takahashi and Bé, 1984 is 124 m d^{-1}. Regarding the distances between the different sampling depths, that would mean shells need about 10 to 20 days to sink from the shallow to the deep trap depth. In combination with the different flow regimes that could form fluxes of different magnitudes due to variable environmental conditions and transport foraminifera shells over some lateral distances, this can explain the gain in shell flux we see in some of the samples of all traps.

While shell fluxes in almost all samples from FEVI30 increase with depth, and in almost all samples from GS2 decrease with depth, there is no systematic tendency at the moorings OG5 and NB. Large plankton feeders' indiscriminate digesting or dissolution caused by CO_2 generated during organic matter degradation are two potential causes of a reduction in flux with depth (Schiebel et al., 2007; Sulpis et al., 2021). The pattern of changes with depth only deviates slightly from the line indicating no change with depth (Fig. 5.3). Therefore, systematic dissolution at all traps can be precluded. The variability can further be an indicator for the variable water conditions in the area, in connection with lateral advection.

On top of these inaccuracies in planktonic foraminifera mass flux estimates due to imprecision in the used shell weight, analytical error can furthermore be caused by the analysed splits of samples. Looking at 1/8 or 1/16 of each sample, it is likely to have a few more or less shells in the analysed sample then on what would be the overall shell number in the sample. This especially can change estimates in periods of low fluxes (number of shells counted < 5), where already a few shells more or less make a difference of several orders of magnitude.

5.4.3 Environmental drivers of planktonic foraminifera mass fluxes

As planktonic foraminifera from the Arctic and Subarctic realm form in the upper water column (Volkmann, 2000; Stangeew, 2001; Greco et al., 2019; Tell et al., 2022), meaning that their productivity is based on conditions in that depth zone, we focus our analysis of environmental parameters as possible drivers of foraminifera mass fluxes on this zone. Section 5.4.2 shows that, for a final assessment of mass fluxes reaching the ocean floor, changes of fluxes with depth have to be considered on top of the drivers of the productivity in the upper water column.

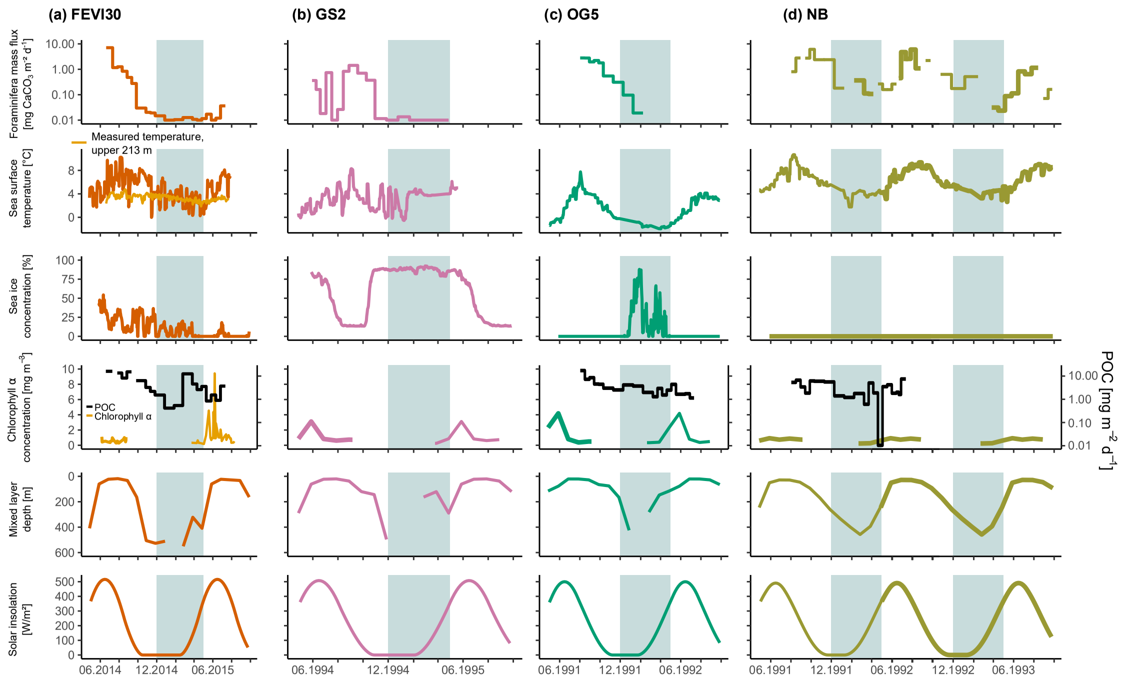

FIGURE 5.9: Mass flux of planktonic foraminifera at the different sediment trap stations in each upper trap (213 m, 300 m, 500 m), sea surface temperature, sea ice concentration, chlorophyll α concentration and particulate organic carbon (POC), mixed layer depth and solar insolation. Foraminifera mass fluxes and POC fluxes are plotted on a logarithmic scale, adding +0.01 to all values to enable visualisation of fluxes with values of zero. Chlorophyll α concentration in the plots (b-d), the mixed layer depth and the solar insolation represent long-term averages as described in the methods section. The light blue shading indicates December to May.

The overall pattern of planktonic foraminifera mass fluxes is the same as the pattern of all studied parameters, with peak values during summer, and minima during winter, connected to the seasonal cycle of insolation and temperature in the research area. Žarić et al., 2005 and Lombard et al., 2009 have shown that planktonic foraminifera have a certain tolerance range of temperatures. Our data shows that foraminifera fluxes, especially at the stations further influenced by Arctic water, strongly increase with increasing temperatures, indicating that temperature is relevant for foraminifera to be productive. Though, the increase in fluxes occurs at different temperatures at the different stations, suggesting that there is at least not a fixed temperature threshold valid at all regions for the (Sub)Arctic species that needs to be reached to trigger high productivity. None of the difference in average values of sea surface temperature, sea ice concentration, mixed layer depth, POC flux or chlorophyll α concentration at the locations of sediment trap stations directly reflects the difference present in foraminifera mass fluxes at the different stations (Fig. 5.7).

The time period analysed for average values is restricted to August in the first year of sampling to May in the preceding year due to the lack of samples from periods longer than that at all stations together. The maximum flux present at FEVI30 in July 2014 is close to the maximum flux reached at mooring NB (Table 5.6). Respectively close to each other are the average temperatures at the two stations (Fig. 5.7). However, temperature differences cannot directly explain differences in flux magnitude during the productive period in different years (Fig. 5.9), so temperature does not seem to govern the magnitude of planktonic foraminifera mass fluxes within the productive season. A similar conclusion has been drawn by Jonkers et al., 2010 on sediment trap data from the Irminger Sea, assuming that it is not temperature itself, but changing stratification, light intensity and the closely related availability of food that is relevant for foraminifera flux variability. The impact of stratification is visible in our data set as well, with the onset of fluxes only occurring after the mixed layer depth being located close to the surface (roughly upper 200 m), hence within the productive zone of the Arctic species (Tell et al., 2022).

Increasing light intensity and the position of the mixed layer depth are relevant factors for the overall biological productivity, especially in terms of primary production relying on nutrients and light for photosynthesis (Kirk, 1994). Therefore, the parameters can be related to the food source of planktonic foraminifera. Previous studies indicate that *N. pachyderma*, the most abundant foraminifera species in the research area, is an opportunistic feeder: It has been suggested to be feeding on phytoplankton (Kohfeld et al., 1996; Carstens et al., 1997; Volkmann, 2000; Bergami et al., 2009; Pados and Spielhagen, 2014; Taylor et al., 2018; Greco, Morard, et al., 2021), but can also feed on crustaceans (Manno et al., 2012). Greco, Morard, et al., 2021 have shown that *N. pachyderma* is overall associated with diatom-fuelled sinking aggregates, supporting the idea of its opportunistic feeding behaviour. Such opportunistic feeding behaviour would mean that both the concentration of chlorophyll α and POC fluxes can influence the productivity and hence mass fluxes of planktonic foraminifera. Our data is in line with that, with both chlorophyll α concentration and POC fluxes tending to be high directly before peaks of planktonic foraminifera mass fluxes (Fig. 5.9). While the peaks of foraminifera mass flux and chlorophyll α concentration occur in line with each other, the exact variability in magnitude between years cannot be linked between them. This might be due to the fact that the food sources of the foraminifera vary, not exclusively being restricted to phytoplankton which is represented by chlorophyll α. Furthermore, Meilland et al., 2020 indicated that the quality of the food is likely more relevant than its quantity. Such a measure is missing in our data at hand, and could be a possible explanation of different magnitudes in foraminifera mass fluxes under similar chlorophyll α concentration but resulting from different phytoplanktonic groups or species. It has been shown that the extent of sea ice is an important factor for phytoplankton blooms in the Arctic, resulting in dynamic availability at different depths (Trudnowska et al., 2021). This might likewise play a role for the productivity of planktonic foraminifera feeding on phytoplankton. Additionally, Greco, Morard, et al., 2021 detected that the productivity and population dynamics of *N. pachyderma* might be influenced by parasitism. Parasitism could cause lower mass fluxes in periods with good conditions in terms of food availability, hence blur the signal in trends of chlorophyll α concentration and POC fluxes in contrast to the foraminifera mass fluxes. Therefore, it might be a further variable defining the overall variability.

Sea ice is important to consider as an influence on planktonic foraminifera mass fluxes in those parts of the Nordic Seas that are at least seasonally covered by sea ice (in our study, all stations but NB). Pados and Spielhagen, 2014 have shown that while planktonic foraminifera do not form under sea ice, their abundance in the sea ice margin is higher than in the open ocean. This further underlines the relevance of food availability for planktonic foraminifera productivity: While below sea ice, primary productivity is hampered due to the lack of light, it can be higher close to the sea ice due to nutrients released during ice melt. Increasing primary productivity could increase food availability for planktonic foraminifera and hence increase their mass production. This effect could also explain why foraminifera fluxes at FEVI30 in July 2014 are higher than in July 2015, while sea ice concentration was lower in July 2015. Moreover, we cannot preclude that foraminifera found in the sediment traps are shells that have been frozen into the sea ice and are released during its melt. It is possible that foraminifera frozen in the ice survive and reproduce when being released from the ice and get in contact with food, as it has been shown for *N. pachyderma* in Antarctica (Dieckmann et al., 1991). This could result in higher fluxes with some delay after the beginning of the ice melt. This effect would be stronger in periods of high sea ice concentration in the area close to FEVI30, as higher sea ice concentration also means higher melt rates during summer.

Next to these biotic factors, the water flow regime at the trap position is likely of relevance for the variability we can see in the foraminifera mass fluxes. Station GS2 is located between the main inflow of warm Atlantic and outflow of cold Arctic surface currents, and further influenced by cold Arctic deep currents (Fig. 5.1). Those different water masses can cause huge shifts in the water conditions, in terms of temperature as well as in terms of food availability. On top of water movement that can result in poor trapping of material during some periods, this might explain the strong deviation in flux patterns less clearly related to water temperatures we see at GS2.

Overall, the seasonal regime of the Nordic Seas in terms of insolation and temperature is of relevance for the seasonal pattern in planktonic foraminifera mass fluxes in the region. Though, the interannual variability and strong regional differences are possibly related to the availability and quality of food and the reproduction rate connected to sexual or asexual reproduction. In the more northern and colder regions, sea ice has to be considered as an influence factor on the food availability. The data of our study indicates those connections, without enabling a detailed quantification of drivers of the mass fluxes. For this, more detailed studies on the role of food of planktonic foraminifera on their productivity, as well as on the impacts on particle transport and trapping efficiency, would be needed.

5.4.4 Relevance of foraminifera mass flux for total carbonate storage

The average mass flux of planktonic foraminifera at all depths of the studied sediment traps in the Nordic Seas from August in the first year of sampling to the preceding May is 0.5 mg $CaCO_3$ m^{-2} d^{-1}. Previous estimates on foraminifera mass fluxes from the region are based on plankton net sampling during the productive summer period (Anglada-Ortiz et al., 2021; Tell et al., 2022). From June to October, the average mass flux at the shallow sediment traps is 1.8 mg $CaCO_3$ m^{-2} d^{-1}. This is below the estimates from Anglada-Ortiz et al., 2021 from the North Svalbard Margin (2.3 to 7.9 mg $CaCO_3$ m^{-2} d^{-1}) and Tell et al., 2022 from the Subarctic and Arctic Ocean (8 mg $CaCO_3$ m^{-2} d^{-1}). With up to 10 % higher abundances of foraminifera shells larger than 125 µm in samples from OG5 and NB7 in contrast to FEVI30 (section 5.2.2), it is possible that the used average shell weights to estimate fluxes from these traps result in an underestimation. Nevertheless, the maximum foraminifera mass fluxes present in our data (Table 5.6) are within the presented range of the previous studies from Anglada-Ortiz et al., 2021 and Tell et al., 2022. The median foraminifera shell flux at FEVI30 (20 ind. m^{-2} d^{-1}) is similar to the median shell fluxes at the HAUSGARTEN observatory between 2007 to 2017 (Ramondenc et al., 2022). Comparing median shell fluxes during the different seasons shows that while the magnitude at FEVI30 was similar to the overall values from 2007 to 2016 in winter and spring, fluxes were higher in fall and especially higher in summer 2014 in contrast to the long-term median. Average water temperatures in the upper 213 m in the sampling period of 2014 and 2015 were almost equal to the average from 2004 to 2012 (von Appen et al., 2019). Therefore, we conclude that the data we present here from FEVI30 is representative for a productive year of average temperatures in the area. The present deviation in the average mass fluxes in contrast to earlier studies from the region highlights the strong seasonal variation in the study area that needs to be considered for total fluxes, which is lacking in studies based on plankton nets. The importance of assessing planktonic foraminifera fluxes all over the year instead of only during the productive summer period also becomes apparent looking at the contribution of planktonic foraminifera to total $CaCO_3$ fluxes: The average contribution of 5.4 % in all here studied sediment traps is below the estimate of 23 % from Tell et al., 2022 based on summer samples and at the lower end of the range presented in Anglada-Ortiz et al., 2021 of 4 to 34 %. However, during the productive summer, peak values of 20 to 25 % are reached at the examined stations (FEVI30, OG5, NB6), one sample at NB6 even reaching a contribution of 75 %. To evaluate the role of planktonic foraminifera to the storage of carbon in form of $CaCO_3$ in the sediments, it is further important to consider the composition of $CaCO_3$ fluxes. At FEVI30, the contribution of aragonite, hence pteropods, to the total $CaCO_3$ flux over the whole sampling period is 42 % at the shallow and 16 % at the deep trap. This stresses that pteropods are much more affected by dissolution. Former studies on samples from the HAUSGARTEN observatory show a very variable contribution of pteropods ranging from 7 to 75 %, as well as the strong decrease in pteropods with depth (Bauerfeind et al., 2014; Busch et al., 2015). There is no information on the abundances and mass flux production of pteropods from the sediment traps GS2, NB and OG5. The contribution of planktonic foraminifera to the $CaCO_3$ flux excluding pteropods is still only about 4 % in the data from FEVI30. Highest fluxes of pteropods occur from September to December in the research area (Ramondenc et al., 2022), meaning after the productive period of planktonic foraminifera. Accordingly, even if it is likely that pteropods also make up a relevant part of $CaCO_3$ flux at the other studied trap locations, there must be further material making up the total

$CaCO_3$ flux. Bauerfeind et al., 2009 estimated coccolithophores to only form < 1% of the $CaCO_3$ at the HAUSGARTEN observatory. Calculating average mass fluxes of coccolithophores for the moorings OG5 and NB6 using counts from Andruleit, 1995 based on Young and Ziveri, 2000 gives an average annual contribution of 2 and 6 % to total $CaCO_3$ fluxes, respectively. This estimate, though, has to be regarded cautiously, as the method is prone to errors of up to 50 % (Young and Ziveri, 2000). As we lack information on coccolithophores at FEVI30, we can only use this information to speculate about their contribution to the total $CaCO_3$ flux. But even assuming that the coccolithophore contribution was higher than at OG5, with a contribution of 42 % by pteropods and 3 % by planktonic foraminifera, this does not add up to 100 %. Without having studied the whole trapping material, we are not able to disentangle this discrepancy. Nevertheless, it is important to consider that the estimates of contributions to total $CaCO_3$ fluxes are prone to errors. In all cases, samples are picked from a split, which can result in different amounts of $CaCO_3$ in the splits looking at the organisms and in the split used to determine total $CaCO_3$. Moreover, mass fluxes of the organisms are always estimated extrapolating average weight values to species counts, which might not be precise enough. On top of that, only organisms that can be identified as the respective species group are counted, which means particles of broken organism shells are not included in the total mass estimate. With the possibility of foraminifera shells sinking in aggregates (Greco, Morard, et al., 2021) and large quantities of sinking fecal particles detected at the HAUSGARTEN observatory (Lalande et al., 2013), there is a potential of shells being partly dissolved and not detectable in the samples anymore. Besides, we here compare data from different traps, as we do not have information on all carbonate producers from the same trap. All these inaccuracies could explain at least part of the discrepancy between the mass fluxes of the different organism groups and the total $CaCO_3$ flux. For better assessment, an overarching study, working with all organism groups on samples from the same trap, would be needed. Similar discrepancies between estimates of carbonate contribution by different calcifiers and the total carbonate flux has also been detected in a recent study by Knecht et al., 2023, likewise concluding that more detailed studies would be needed to disentangle the details.

With the mixed effect of increasing fluxes with depth due to lateral advection, and dissolution of shells below the productive zone, we assume that fluxes calculated based on samples from deeper traps are most representative for the mass flux of planktonic foraminifera finally reaching the ocean floor and therefore contribution to the storage of carbon. To assess the role of the planktonic foraminifera mass flux for the carbon cycle on short time scales, an evaluation of the release of CO_2 during the formation of $CaCO_3$ in contrast to the carbon in it reaching the ocean floor is needed. Based on Smith and Mackenzie, 2016, during the production of 1 mol of $CaCO_3$, 0.66 mol of CO_2 are released. Therefore, the average planktonic foraminifera mass flux of 0.5 mg $CaCO_3$ m^{-2} d^{-1} (5 µmol $CaCO_3$ m^{-2} d^{-1}) at all stations of our study together would result in a release of 3.2 µmol CO_2 m^{-2} d^{-1} (containing 0.9 µmol / 0.010 mg Carbon), while the $CaCO_3$ reaching the ocean floor contains 0.6 µmol m^{-2} d^{-1} Carbon (0.007 mg C). Smith and Gattuso, 2011 state that whether $CaCO_3$ results in a source or sink of CO_2 depends not only on the production and storage rate of $CaCO_3$, but further on different water conditions in precipitation and dissolution, which we cannot evaluate further with our available data. Nevertheless, our data shows how important the release of CO_2 caused by the $CaCO_3$ counter pump and the production of foraminifera shells is for the carbon cycle regarding short time scales and especially the surface and subsurface. It has to be considered that these estimates only look at the calcite shell of planktonic foraminifera, without taking the role of the organic soft tissue of planktonic foraminifera for the carbon cycle into account, which also is a relevant component of carbon fixation (Schiebel and Movellan, 2012).

5.4.5 Implications of climate change on planktonic foraminifera mass flux

Our data shows clear differences in species-specific shell weight of planktonic foraminifera (Table 5.5). Therefore, a change in species assemblages can affect the $CaCO_3$ fluxes to the deep sea even when total foraminifera abundances remain stable. It has been shown that the so-called 'Atlantification', a warming Arctic and Subarctic resulting in increasing abundances of Atlantic species in the Nordic Seas (Kraft et al., 2013; Andrews et al., 2019; Tesi et al., 2021) is currently affecting foraminifera species abundances in the Fram Strait (Greco, Werner, et al., 2021) and the Barents Sea (Meilland et al., 2020). Depending on how species composition will change, this can affect the contribution of planktonic foraminifera to the carbon cycle. With the most Atlantic species being lighter than the currently most abundant *N. pachyderma*, it is likely that the overall mass flux will decrease in the future, if it is not balanced out by an overall increase in foraminifera productivity due to changes in the primary production.

5.5 Conclusion

Our data confirms that the variability in planktonic foraminifera mass flux is mainly defined by the variability in the foraminifera shell flux, even though shell weights tend to be lower during winter, which is likely an effect of lower temperatures and the connected missing or different reproduction during this time period. Even though the present seasonal variability in planktonic foraminifera mass fluxes in the Nordic Seas closely follows the seasonal pattern of temperature, interannual changes in the magnitude of the fluxes cannot be explained by temperature or temperature-related parameters like sea ice concentration and the mixed layer depth. It is likely that the availability and quality of food is an important factor for this. To further assess this effect, more detailed studies on the feeding behaviour and the role of food quantity and quality for planktonic foraminifera productivity would be necessary. The average mass flux of planktonic foraminifera in the Nordic Seas at depths of 1000 to 2319 m from August in the first year of sampling to May in the second year of sampling is 0.5 mg $CaCO_3$ m^{-2} d^{-1}, which is about 5.4 % of total $CaCO_3$ fluxes in the area. With uncertainties in the mass estimation due to lacking weight information from stations other than the northernmost station FEVI30, and a relevant quantity of $CaCO_3$ fluxes being formed by pteropods which are dissolved before long-term storage at the sea floor, this still makes planktonic foraminifera a relevant contributor to $CaCO_3$ export and hence the oceanic carbon cycle in the Subarctic realm. With ongoing climate change influencing species abundances and assemblages, which can result in changes in the mass of $CaCO_3$ formed, it is important to further constrain the role of planktonic foraminifera for the overall carbon cycle both in terms of CO_2 release during the formation of $CaCO_3$, carbon fixation in the living shell of the foraminifera and carbon storage at the sea floor during accumulation of shells on long-term time scales.

Author contributions The study was designed by FT, MK, JM and LJ. Access to the data and further information on the HAUSGARTEN samples was given by EN. FT carried out the laboratory work on the platonic foraminifera, with help from JM. Data analysis was conducted by FT with help from LJ. All authors contributed to the interpretation and discussion of the results. FT wrote the paper with contributions from LJ, JM, EN and MK.

Data availability All data created for this study is available on PANGAEA (`https://doi.pangaea.de/10.1594/PANGAEA.957172`). The data sources of the published data are linked in Table 5.1.

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Chapter 6

Carbonate burial of planktonic foraminifera in the Arctic Ocean during the late Holocene

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Abstract Large amounts of carbonate are buried in the world's ocean, among them the Arctic Ocean. Planktonic foraminifera play a relevant role for the storage of $CaCO_3$ in the sediments, contributing to the long-term storage of carbon. In this study, we quantify this contribution of planktonic foraminifera to total storage of $CaCO_3$ during the past 4000 years before present in the Arctic and Subarctic Ocean, an area strongly affected by ongoing climate change. We measure foraminifera shell weights in samples from three sediment cores of the Labrador Sea, and we used species-specific shell weights to evaluate mass accumulation rates in the Arctic and Subarctic Ocean from published and newly produced data. The average mass accumulation rate all over the studied sediment cores and time interval is 0.09 g $CaCO_3$ cm^{-2} ka^{-1}. On average, the contribution to total $CaCO_3$ in the studied sediment cores is 30 %. While spatial differences in the mass accumulation rates seem to be overall related to different water temperature regimes, the surface water temperature cannot explain all detected variability. As present-day chlorophyll α concentrations as a parameter of productivity are not correlated to the foraminifera mass accumulation rates, and the foraminifera accumulation rates are unrelated from total mass accumulation rates, we lack a distinct explanatory parameter for the present differences. Nevertheless, with the relevant contribution to total $CaCO_3$ stored in the sediments, which regionally is ranging from 5 to 89 %, we can show that planktonic foraminifera are an important organism group to consider when disentangling the marine carbon cycle in the Arctic and Subarctic Ocean.

6.1 Introduction

More than 38,000 Pg of the carbon that circulates in our Earth's system is stored in the deep oceans and ocean sediments (Sigman and Boyle, 2000). The vertical transport of carbon from the surface towards the deep ocean and its sediments is largely driven by the biological carbon pumps (Zeebe, 2012). Organic carbon is transported towards the sediments when organisms die and their soft tissue sinks downward, and CO_2 is released during the remineralization of this organic carbon (Heinze et al., 1991). When organisms form shells out of $CaCO_3$, CO_2 is released to the surface ocean, increasing its alkalinity, denoted as the carbonate counter pump (Frankignoulle et al., 1994). This is happening on short-term time scales. On million-year time scales, though, the sinking of $CaCO_3$ produced by organisms in the surface ocean results in carbon removal when being buried in the sediments (Zeebe, 2012). This is relevant for the stabilisation of the carbon cycle on longer time scales, as ocean acidification can be reduced by the dissolution of $CaCO_3$ buried in sediments (Sulpis et al., 2018). As the solubility of CO_2 increases with decreasing temperatures, the uptake of atmospheric CO_2 in the Arctic Ocean realm is high (Steinacher et al., 2009; Miller et al., 2014). Climate warming causing a decrease in sea ice cover and enhanced atmosphere-ocean exchanges in the Arctic, but also an increase in water temperatures could thus have an impact on the carbon cycle in the Arctic Ocean (Berner et al., 2005; Meier et al., 2014).

Among the major contributors to the sedimentation of $CaCO_3$ are planktonic foraminifera, single-celled protists forming a calcite shell and living in the upper water column. On a global scale, they have been shown to be responsible for about 32 to 80 % of the deep ocean calcite budget with a sedimentation of 0.71 Gt yr^{-1} (Schiebel, 2002; Schiebel et al., 2007). A recent study on the planktonic foraminifera production in the upper water column gives a contribution of planktonic foraminifera to global carbonate fluxes of only 1.5 % (0.001 Gt yr^{-1}, Knecht et al., 2023). Within the water column, a contribution of 23 % has been shown in the Arctic and Subarctic Ocean during summer months (Tell et al., 2022). The contribution is lower considering foraminifera production throughout the year in the Nordic Seas, with planktonic foraminifera only making up about 5 % of the total $CaCO_3$ flux at 1000 to 2300 m depth (Tell et al., 2023). Estimates of the overall mass accumulation of planktonic foraminifera in the sediments of the Arctic and Subarctic Ocean are lacking. Previous studies have shown variations in the dissolution of planktonic foraminifera in the sediments of the Fram Strait during the past millennia (Zamelczyk et al., 2013), and that dissolution of shells occurs before being stored in the sediments in the Baffin Bay (Stehman, 1972). At the same time, the Arctic and Subarctic Ocean have been shown to be strongly influenced by pulsed fluxes of planktonic foraminifera during the summer months (Jensen, 1998; Tell et al., 2023). Such high fluxes can result in higher preservation in sediments (Schiebel, 2002; Schiebel and Hemleben, 2000). Recent global estimates on the magnitude of dissolution of $CaCO_3$ at the seafloor are lacking information from the Arctic Ocean (Sulpis et al., 2018).

This study aims to quantify the accumulation of calcite from planktonic foraminifera (g $CaCO_3$ cm^{-2} ka^{-1}) in the Arctic and Subarctic Ocean during the past four thousand years before present (ka BP, with present being defined as 1950 CE), thus to quantify its contribution to the carbon cycle. We also investigate the causes in the variability of magnitude of mass accumulation. Dissolution of foraminifera shells is strongest at the sediment surface, as the vulnerability to dissolution decreases with shells being filled with fine-grained material during their burial (Huber et al., 2000). Therefore, we assume that mass accumulation rates are higher at locations of high sedimentation rates, where dissolution is hampered. Moreover, the primary productivity is likely to determine the accumulation rates of planktonic foraminifera because it is relevant for the productivity of the foraminifera themselves (Jonkers and Kucera, 2015; Rembauville et al., 2016), and also influences the dissolution at the sea floor. The higher the flux of organic particles towards the sediments, the higher the dissolution, as metabolic processes release CO_2 (Huber et al., 2000).

We here compare rates of planktonic foraminifera mass accumulation with sedimentation rates and total mass accumulation rates in sediments to disentangle their effects on the calcite storage. We further analyse regional differences in foraminifera mass accumulation in connection to influences of distinct water masses and the calcite saturation at the seafloor, temperature regimes and productivity in terms of chlorophyll α concentration. A comparison of accumulation rates in the sediments with recent estimates on foraminifera productivity from the water column in the research area then allows us to make a first estimate on the influence of dissolution in this region.

6.2 Material and methods

The data used in this study are from sediment cores of the Subarctic and Arctic Ocean (Fig. 6.1). They include published data from cores located north of 58° N that contain information on the abundance of planktonic foraminifera in relation to the amount of sediment and its accumulation and have a robust age model or at least several dated levels. Only sediment cores with at least one sample within the past 4 ka BP were selected. This time interval was chosen to enable a large spatial spread of data despite the low sedimentation rates in some parts of the Arctic Ocean (de Vernal et al., 2013; de Vernal et al., 2020). Nevertheless, we are aware of the fact that this interval corresponding to the late Holocene, though not being influenced by extreme climatic shifts, has not been stable and experienced some climatic changes (e.g. Spielhagen et al., 2011). In total, with these criteria, data from 29 sediment cores could be retrieved from publications (Table B.1, data from Pagels, 1991; Bauch, 1993; Nørgaard-Pedersen et al., 1998; Jensen, 1998; Bauch, 1999; Kunz-Pirrung, 2003; Duplessy et al., 2001; Rasmussen et al., 2003; Sarnthein et al., 2003; Gurvich and Vlasova, 2004; Spielhagen, 2004; Labeyrie and Jennings, 2005; Spielhagen et al., 2011; Taldenkova et al., 2013; Werner et al., 2013; Berben et al., 2014; Jennings et al., 2015; Perner et al., 2018; Griem et al., 2019; de Vernal et al., 2020; Zehnich et al., 2020; Syring et al., 2020; Jackson et al., 2022).

To increase the regional extent further into the Labrador Sea, planktonic foraminifera from three sediment cores were analysed for this study: HU2008-029-004 TWC (in the following labelled TWC004, 61.46° N, 58.04° W; further information on the core in Gibb et al., 2015), MD99-2227 (58.21° N, 48.37° W; further information on the core in Fagel et al., 2004) and HU91-045-93BX (in the following labelled BX93, 50.2° N, 45.68° W). Individual shell size and weight of different planktonic foraminifera species in samples from those three cores were analysed in detail, as this information is lacking for other studies from the Subarctic and Arctic realm. Sediment core BX93 is located outside the above defined latitudinal range, but was added to increase the number of samples for shell size and shell weight measurements, and be able to make a regional comparison of those parameters.

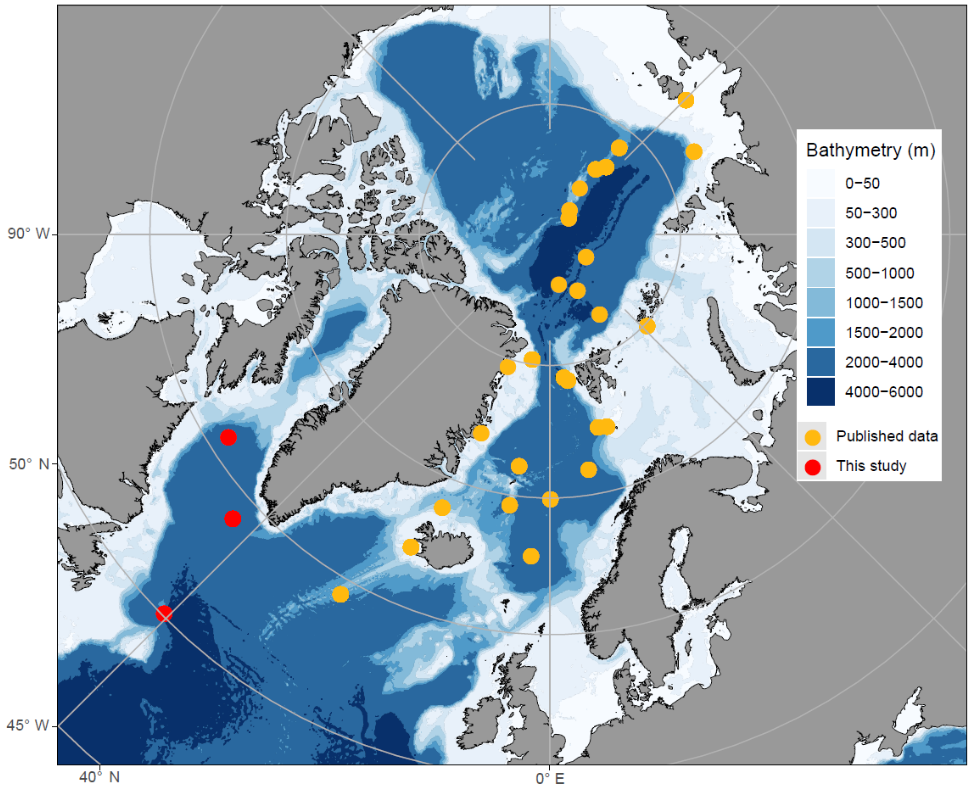

FIGURE 6.1: Overview map with all sediment cores used in this study, combining new data from the Labrador Sea (red) with published data from all over the Arctic and Subarctic Ocean (orange). Land polygons from Natural Earth Data (CC0), bathymetry from Amante and Eakins, 2009 using ggOceanMaps in R (Vihtakari, 2021)

6.2.1 Planktonic foraminifera samples

In total, 64 samples from the three Labrador Sea cores were analysed (Table B.1). Planktonic foraminifera were extracted out of the dried sediment of the size fraction > 106 µm. Samples were split depending on the total amount of material in it, and 1/8, 1/16 or 1/32 of the sample was analysed, extracting all shells of planktonic foraminifera from the split (average of 300 shells per sample, minimum 66 shells, Table 6.1). Fragments of shells were extracted whenever identification of a foraminifera shell was possible based on the visible structure of several chambers. Planktonic foraminifera were determined to the species level when possible based on the taxonomy by Brummer and Kucera, 2022 and counted. Fragments of shells, broken and further unidentifiable shells were counted separately. Measurements of shell weight were done using a Sartorius XM1000P micro balance (nominal resolution of 1 µg). The bulk weight of all foraminifera shells in each sample was measured. To increase the precision, weight measurements were done four times, and the average weight of all measurements per sample is used for further analysis. Furthermore, to determine a range of individual shell weights of different species, two to 40 shells per species were measured on 37 samples of the three sediment cores, depending on the number of species in the sample. We cannot preclude that shells were entirely empty, but they were cleaned from sticking particles as much as possible under the binocular with a brush.

TABLE 6.1: Overview on the three Labrador Sea cores analysed for this study. The given ages indicate modelled ages based on linear interpolation as described in section 6.2.3

Sediment core	Sampling interval [m]	Age [ka BP]	Split	Foraminifera shells picked
TWC004	0.00 - 0.01	0.02	1	1479
TWC004	0.02 - 0.03	0.34	1	1591
TWC004	0.04 - 0.05	0.64	1/4	470
TWC004	0.06 - 0.07	0.96	1/4	463
TWC004	0.08 - 0.09	1.23	1/4	320
TWC004	0.01 - 0.11	1.39	1/4	868
BX93	0.00 - 0.02	1.19	1/16	632
BX93	0.02 - 0.04	1.27	1/16	331
BX93	0.04 - 0.06	1.34	1/16	532
BX93	0.06 - 0.08	1.41	1/16	746
BX93	0.08 - 0.10	1.48	1/16	1208
BX93	0.10 - 0.12	1.55	1/16	375
BX93	0.12 - 0.14	1.62	1/16	285
BX93	0.14 - 0.16	1.69	1/16	310
BX93	0.16 - 0.18	1.76	1/16	146
BX93	0.18 - 0.20	1.83	1/16	593
MD-2227	0.02 - 0.03	0.83	1/8	326
MD-2227	0.04 - 0.05	0.90	1/8	440
MD-2227	0.06 - 0.07	0.97	1/8	357
MD-2227	0.08 - 0.09	01.05	1/8	490
MD-2227	0.12 - 0.13	1.17	1/16	259
MD-2227	0.14 - 0.15	1.23	1/16	289
MD-2227	0.16 - 0.17	1.29	1/8	314
MD-2227	0.18 - 0.19	1.34	1/16	256
MD-2227	0.22 - 0.23	1.46	1/16	215
MD-2227	0.24 - 0.25	1.52	1/16	254
MD-2227	0.26 - 0.27	1.58	1/16	326
MD-2227	0.28 - 0.29	1.64	1/16	197
MD-2227	0.32 - 0.33	1.76	1/32	186
MD-2227	0.34 - 0.35	1.82	1/16	423
MD-2227	0.36 - 0.37	1.88	1/32	178
MD-2227	0.38 - 0.39	1.94	1/32	163
MD-2227	0.42 - 0.43	02.06	1/32	200
MD-2227	0.44 - 0.45	2.12	1/32	191
MD-2227	0.46 - 0.47	2.18	1/32	156
MD-2227	0.48 - 0.49	2.24	1/32	239
MD-2227	0.52 - 0.53	2.36	1/32	146
MD-2227	0.54 - 0.55	2.42	1/32	121
MD-2227	0.56 - 0.57	2.48	1/32	96
MD-2227	0.58 - 0.59	2.54	1/32	96
MD-2227	0.62 - 0.63	2.64	1/32	132
MD-2227	0.64 - 0.65	2.68	1/16	141
MD-2227	0.66 - 0.67	2.72	1/16	220
MD-2227	0.68 - 0.69	2.76	1/32	114

MD-2227	0.72 - 0.73	2.86	1/32	87
MD-2227	0.74 - 0.75	2.92	1/32	116
MD-2227	0.76 - 0.77	2.98	1/16	119
MD-2227	0.78 - 0.79	03.04	1/16	94
MD-2227	0.82 - 0.83	3.14	1/32	152
MD-2227	0.84 - 0.85	3.18	1/32	116
MD-2227	0.86 - 0.87	3.22	1/16	125
MD-2227	0.88 - 0.89	3.26	1/32	112
MD-2227	0.92 - 0.93	3.36	1/32	93
MD-2227	0.94 - 0.95	3.42	1/32	81
MD-2227	0.96 - 0.97	3.48	1/32	156
MD-2227	0.98 - 0.99	3.54	1/32	95
MD-2227	1.02 - 1.03	3.64	1/32	109
MD-2227	1.04 - 1.05	3.68	1/32	181
MD-2227	1.06 - 1.07	3.72	1/32	129
MD-2227	1.08 - 1.09	3.76	1/16	66
MD-2227	1.12 - 1.13	3.84	1/16	126
MD-2227	1.14 - 1.15	3.88	1/16	123
MD-2227	1.16 - 1.17	3.92	1/16	124
MD-2227	1.18 - 1.19	3.96	1/32	125

To assess the size and weight of the different species more precisely, individual measurements of shell size parameter (minimum and maximum diameter) were done with a KEYENCE VHX-6000 digital microscope on 88 foraminifera shells from five samples from the three sediment cores from the Labrador Sea (from 0 to 0.01 m and 0.1 to 0.11 m in TWC004, from 0 to 0.02 m in BX93 and 0.08 to 0.09 m and 0.34 to 0.35 m in MD-2227, choosing samples with several shells per species). Individual shell weight was measured on 82 of those shells with a Sartorius Cubis®II ultra-micro lab balance (nominal resolution of 0.1 µg). Before weighing, the shells were left in the room for at least 24 hours to acclimate with the room, and for the water that was used to place them in the weighing boats to evaporate. The shells were selected randomly from the samples, though it is likely that there was a bias towards larger and heavier shells, as shells that were easily distinguishable to the species level were picked.

6.2.2 Sediment core chronology

To establish a chronology for sediment core BX93, AMS ^{14}C dating was done at the radiocarbon laboratory at the Alfred-Wegener-Institute Helmholtz Center for Polar and Marine Research with the Mini Carbon Dating System (MICADAS) on two samples (from 0.04 to 0.06 m and 0.12 to 0.14 m) of shells of mixed planktonic foraminifera species (sample weight of 2 and 2.5 mg, respectively; Table 6.2). The age of all other samples in the sediment core was determined based on linear interpolation between the measured ages (Table 6.1). New age-depth models based on linear interpolation between measured ages was also done for samples from the sediment core MD99-2227, where dating was done every 10 cm (Fagel et al., 2004), and for the cores PS87/023, PS87/055, PS87/070, PS87/079 and PS87/099, where dates were obtained at 1-2 cm intervals (de Vernal et al., 2020). The chronology of TWC004 is from van Bellen et al., 2019. As this study aims to understand the recent storage of planktonic foraminifera and their $CaCO_3$ shell mass in ocean sediments without looking into details of changes during the past, we did not harmonise the chronology of all sediment cores but worked with the published chronology. This might cause discrepancies in the age models, but has no impact on our analysis, as the focus of the study is to detect overall regional trends in the roughly defined time frame, and as variability within the cores over time is assessed.

TABLE 6.2: Radiocarbon dates for the sediment core BX93. The numbers in the brackets define the error range.

Name Core	Sampling interval [m]	F ^{14}C	Age [ka BP]
BX93	0.04 - 0.06	0.847 (0.008)	1.336 (77)
BX93	0.12 - 0.14	0.818 (0.008)	1.619 (77)

6.2.3 Mass accumulation of planktonic foraminifera

The mass accumulation of planktonic foraminifera (MAR$_{PF}$) in all sediment cores was calculated multiplying the accumulation rate of planktonic foraminifera (AR$_{PF}$) with shell weight (Ehrmann and Thiede, 1985):

$$MAR_{PF}\,[g\,CaCO_3\,cm^{-2}\,ka^{-1}] = AR_{PF}\,[ind.\,cm^{-2}\,ka^{-1}] \cdot shell\ weight\,[g] \tag{6.1}$$

Calculations of the MAR$_{PF}$ of the three sediment cores from the Labrador Sea are based on the measured bulk shell weights of the individual samples. For all other sediment cores, we used the average shell weight determined from the Labrador Sea cores. Where species were distinguished, species-specific shell weights were used. Planktonic foraminifera accumulation rate that was not provided from published data is calculated as the product of the mass accumulation rate (MAR) of the sample and the concentration of planktonic foraminifera (c$_{PF}$) per gram of dry sediment (ind. g^{-1}):

$$AR_{PF}\,[ind.\,cm^{-2}\,ka^{-1}] = MAR\,[g\,CaCO_3\,cm^{-2}\,ka^{-1}] \cdot c_{PF}\,[ind.\,g^{-1}] \tag{6.2}$$

The MAR is the product of the dry bulk density (DBD) and the linear sedimentation rate (LSR)

$$MAR\,[g\,cm^{-2}\,ka^{-1}] = DBD\,[g\,cm^{-3}] \cdot LSR\,[cm\,ka^{-1}] \tag{6.3}$$

and the LSR is determined based on the determined age of the sediments

$$LSR\,[cm\,ka^{-1}] = \frac{d_2\,[cm] - d_1\,[cm]}{a_2\,[ka\,BP] - a_1\,[ka\,BP]} \tag{6.4}$$

where d$_1$ and a$_1$ are the depth (cm) and age (ka BP) of one sample, and d$_2$ and a$_2$ of a second sample located below the first sample in the sediment core.

6.2.4 Analysis of influences on planktonic foraminifera mass accumulation

To assess possible drivers of the detected MAR$_{PF}$, we correlated it with the overall sedimentation rate and mass accumulation rate from sediment cores. By doing this, we aim to show if increases in MAR$_{PF}$ only occur when the overall MAR increases, or if changes in the accumulation of planktonic foraminifera occur independently from the overall sedimentation rate. Further, correlations between MAR$_{PF}$ and the deposition depth were calculated to assess differences between shelf and deep-ocean areas: the foraminifera productivity in shelf areas is much lower (Schiebel and Hemleben, 2017), but dissolution in the water column could lead to lower MAR_{PF} rates at deeper sampling locations, as calcite dissolution increases with increasing pressure and decreasing temperatures (Hancock et al., 2007). In addition to the deposition depth, the average Ω calcite (solubility ratio of calcite, indicating undersaturation when $\Omega < 1$) was calculated after Lewis et al., 1998 using data from GLODAPv2.2022 (Key et al., 2015; Olsen et al., 2016; Lauvset et al., 2022). The data represents average values from a 2x2° grid with each sediment core location in its centre. The resolution was chosen based on the resolution of the available data. No data was available for 5 out of the 33 sediment cores. To account for influences on the productivity of planktonic foraminifera, we analysed the relationship and correlation between planktonic foraminifera mass accumulation rates and surface water temperature and the concentration of chlorophyll α, as these parameters can be connected to present variability in foraminifera mass fluxes (Tell et al., 2023). Sea surface temperature data are from the World Ocean Atlas 2018 (Locarnini et al., 2019). We used the average temperature between 1955 to 2010 during summer months. The average chlorophyll α concentration was derived from NASA/GSFC/OBPG, [data set], calculating the average chlorophyll α concentration for the whole time period from 2003 to 2021 in a 1x1° grid with each sediment core sampling position in its centre. We are aware that the foraminifera found in the sediments were formed before the recent years, likely under slightly different conditions then what is represented by the modern averages. Therefore, the analysis can only be seen as a first impression on possible influencing factors. In the 11 sediment cores having total $CaCO_3$ mass accumulation rates available (see Table B.1), the proportion of planktonic foraminifera is calculated.

As the data is not normally distributed, we calculated Spearman's Rank correlation (Spearman, 1904) to check for linear correlations. Furthermore, local polynomial regression fitting was visualised to show possible non-linear relationships between the different parameters and the mass accumulation of planktonic foraminifera. All statistical analyses were performed using R v. 4.2.1 (R Core Team, 2022).

6.3 Results

6.3.1 Planktonic foraminifera shell mass

To estimate the mass accumulation rate of planktonic foraminifera in the sediments, information on the shell weight of the species that can be found in Arctic and Subarctic sediments is needed. The average shell weight of all planktonic foraminifera species present in the sediment cores from the Labrador Sea is 4.8 µg for bulk measurements and 6.5 µg for individual shell measurements (Table 6.3). The average bulk weight differs by up to 1.5 µg between the three sediment cores from the Labrador Sea (3.9 µg in TWC004, 5.4 in MD99-2227 and 4.8 µg in BX93). Overall, the shell weight in individual shells tends to be higher than values from bulk measurements, which at least partly is an analytical effect, as shells easy to distinguish on the species level, i.e. tendentially larger shells, were picked for the individual measurements. The standard deviation in individual weight measurements is larger than in the bulk measurements, being almost of the same order as the average value (Table 6.3). Both in the individual and the bulk weight measurements, species-specific weight clearly differs. With 0.8 µg in bulk measurements (no individual measurements conducted), *Globigerinita uvula* is the lightest species, while *Globorotalia inflata* (12.8 µg in bulk, 14.7 µg in individual measurement) and *Globigerina bulloides*

(8.4 µg in bulk, 13.8 µg in individual measurement) are the heaviest species. All other species (*Neogloboquadrina pachyderma*, *Turborotalita quinqueloba*, *Neogloboquadrina incompta* and *Globigerina glutinata*) have shell weights between 4.0 and 5.6 µg in the individual measurements (2.4 to 4.9 µg in bulk measurements). There is no systematic trend in the average shell weight with age of the samples (Fig. 6.2). In sediment core BX93 and MD99-2227, changes in the weight of *G. bulloides* and *G. inflata* with time are larger than in other species. However, there is no a clear trend, neither in shell weights from the total sample nor in weights of the different species. Hence, the difference between distinct species of planktonic foraminifera remains uniform over time.

TABLE 6.3: Size and weight of planktonic foraminifera in the three studied cores from the Labrador Sea, and average percentages of species in 17 out of the 33 sediment cores in which foraminifera were determined to the species level. The shell weight was both measured as a bulk (two to 40 shells per sample and species), and individually (82 shells from different samples). The shell size was measured on 88 shells.

	Shell size from individual shells [µm]	**Shell weight from individual shells [µg]**	**Shell weight from bulk [µg]**	**Relative abundance in all cores [%]**
Total average	278.4	6.5	5.2	
N. pachyderma	252.6	5.6	5.3	55.7
T. quinqueloba	245.0	4.1	3.9	11.2
N. incompta	283.0	5.0	4.4	2.3
G. glutinata	250.3	5.0	3.1	0.8
G. bulloides	430.0	13.8	10.3	0.4
G. uvula	NA	NA	1.1	0.3
G. inflata	392.5	14.7	13.2	0.0
Undetermined/ broken shells	NA	NA	3.8	0.1

The most abundant species in samples of the study is *N. pachyderma* (Table 6.3). Its abundance shows some variation over time within the different sediment cores. It is lowest in the Labrador Sea and highest in the Fram Strait (consider that information on species abundance from the central Arctic Ocean are lacking; Fig. 6.3a). Of further relevance are *T. quinqueloba* and *N. incompta*, while other species, on average, record less than 1 %. In sediment core DS97-2P from the Reykjanes Ridge, the abundance of *G. bulloides*, *G. glutinata* and *G. uvula* is larger than 10 %. In sediment core IK9373-10 from the Laptev Sea, the species *Turborotalita clarkei* is also common. However, it is not present in the samples from the Labrador Sea, and we do not have weight information for this species.

Overall, we conclude that with the high standard deviation in the individual shell measurements, it is likely more accurate to work with bulk measurements to estimate overall mass accumulation rates of planktonic foraminifera, as bulk measurements have been conducted on a larger quantity of samples (individual measurements on 82 shells, bulk measurements on 2201 shells in 195 bulk samples). The differences in shell weight of the species of the region show that this is important to be considered. With no clear trend over the time interval considered in this study, we see the overall average shell weight of the studied cores as most representative to be used to calculate mass accumulation rates for sediment cores where data on shell weight is lacking.

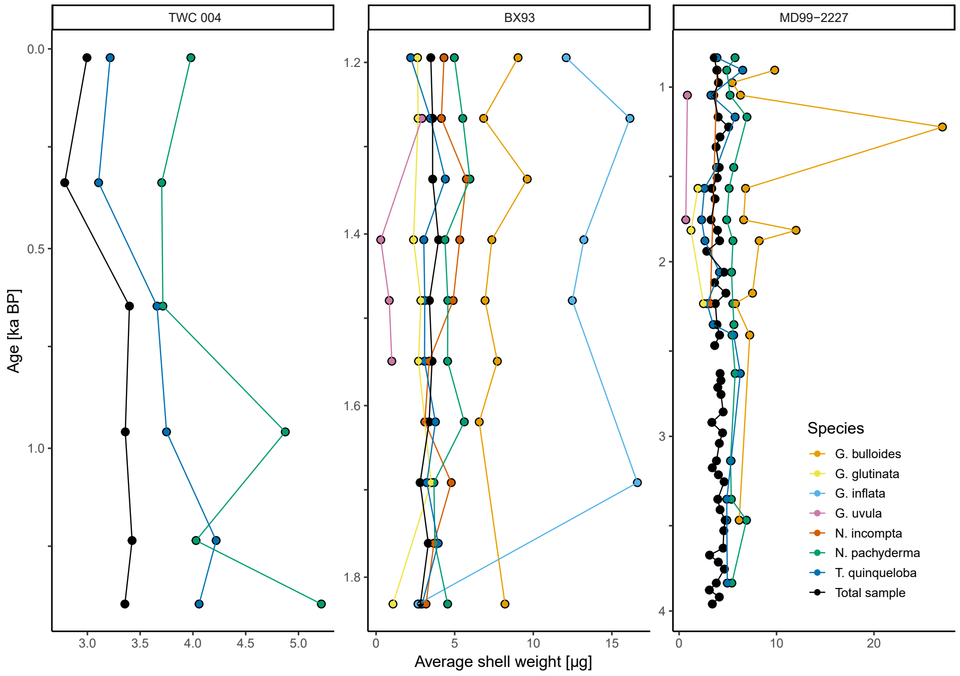

FIGURE 6.2: Average foraminifera shell weight from bulk measurements of different planktonic foraminifera species in the three sediment cores from the Labrador Sea plotted against age. The thicker black line and black dots indicate the overall average weight. The samples from core TWC004 contained more than the two plotted species, but no separate weight measurements were done those species. Consider the differences in values both on the x- and y-axis.

6.3.2 Carbonate mass accumulation of planktonic foraminifera in the sediments

The average mass accumulation rate of planktonic foraminifera over all studied sediment cores spanning at maximum over the past 4 ka BP is 0.09 g $CaCO_3$ cm^{-2} ka^{-1}, and the median is 0.01 g $CaCO_3$ cm^{-2} ka^{-1} (Table 6.4). A mass accumulation rate of 0.00 g $CaCO_3$ cm^{-2} ka^{-1}, indicating the lack of preserved planktonic foraminifera shells, is present all over the sediment core PS2644-5 from the Denmark Strait, which spans over a time period of 0.26 to 3.95 ka BP. The maximum average mass accumulation of 8.81 g $CaCO_3$ cm^{-2} ka^{-1} is recorded in the sediment core 23411-5 from the Norwegian Sea. Comparison with total $CaCO_3$ accumulation rates in the 11 sediment cores where this metrics is available (Table B.1) shows that the average contribution of planktonic foraminifera to it is 30 %, the median contribution is 5 % (Table 6.4). Two groups can be distinguished: Sediment cores from the central Arctic Ocean (S1524-1, PS2166-2, PS2177-1, PS2195-4) present a contribution of 46 to 89 % of planktonic foraminifera to the total $CaCO_3$ accumulation, while the contribution in the sediment cores from the Labrador Sea (BX93, MD99-2227), the eastern

Fram Strait (MSM/05-712-2, MSM05/5-723-2), the Nansen Basin (PS1521-15) and the Laptev Sea (PS51/154-11) is between 0 to 5 %. The highest average contribution to total $CaCO_3$ accumulation rates is not present in the sediment core with the highest planktonic foraminifera mass accumulation (sediment core 23411-5), but in a core that has a lower than average foraminifera mass accumulation rate (0.04 g $CaCO_3$ cm^{-1} ka^{-1}; sediment core PS1524-1 from the Nansen Basin).

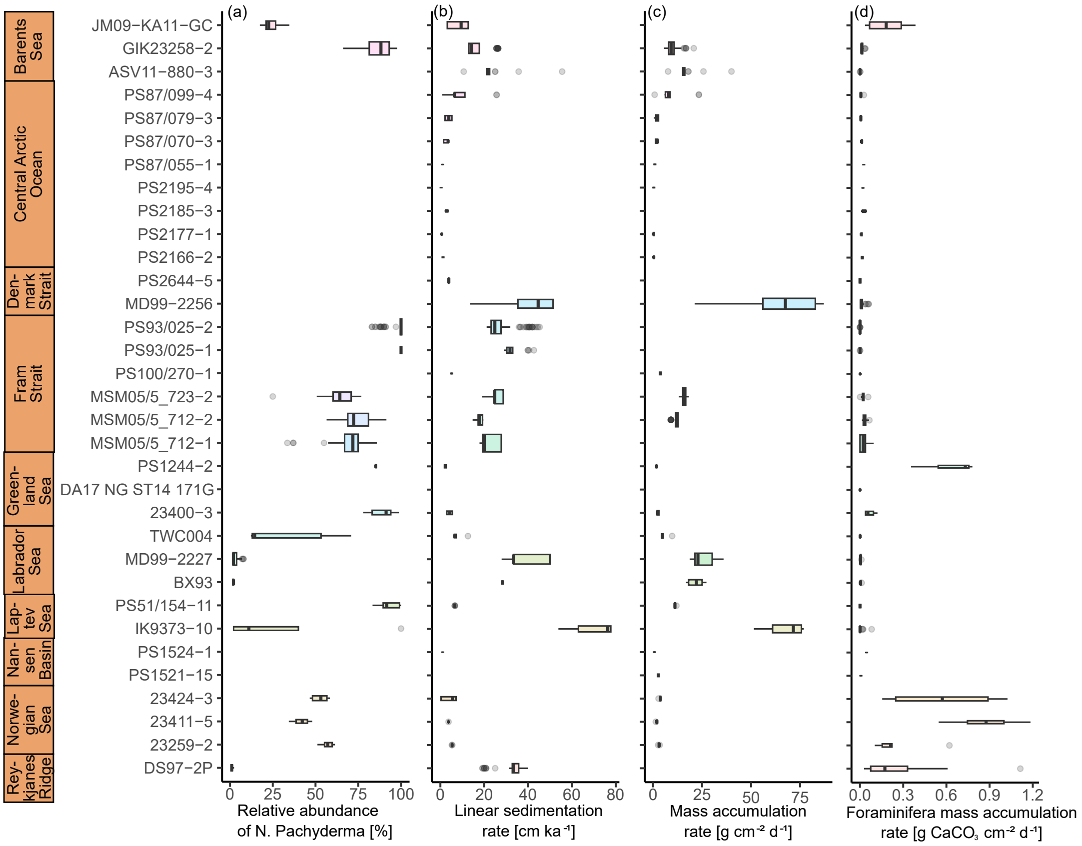

FIGURE 6.3: Range of (a) relative abundance of *N. pachyderma*, (b) linear sedimentation rate, (c) mass accumulation rate and (d) planktonic foraminifera mass accumulation rate in all the sediment cores analysed in the study, sorted by regions (as labelled on the left). The boxes represent the interquartile range (IQR) of the given value in each sediment core and the vertical bar represents the median. Outliers, shown as points, are values beyond 1.5 × IQR of each side of the box, and lines represent the range within 1.5 × IQR. The width of each box represents the number of samples per sediment core, with the thickest width representing the core including the most samples. Sediment core PS93/025, before handled as one core, is plotted here divided into its two parts (1 and 2). Where no boxes are plotted in (a), foraminifera were not determined to the species level.

The variation in the foraminifera mass accumulation rate within each sediment core over the studied time period is small in most of the cores (Fig. 6.3d). Only in 6 out of 33 sediment cores, the interquartile range is large, while in all other cores, the values are similarly low (between 0.00 and 0.10 g $CaCO_3$ cm^{-2} ka^{-1}). The sediment cores with a strong variability are all from different regions, besides the three cores from the Norwegian Sea all presenting higher ranges in the foraminifera mass accumulation over the past 4 ka BP. The linear sedimentation rate and the total mass accumulation rate show higher variability between the different sediment cores (Fig. 6.3b, c). Comparing the average foraminifera mass accumulation in the studied sediment cores over different time intervals does likewise not indicate any strong changes within the past 4 ka BP (Fig. 6.4b-e). Strongest variations are present in the Norwegian Sea with a rather low foraminifera mass accumulation of 0.09 g $CaCO_3$ cm^{-2} ka^{-1} from 3 to 4 ka BP in contrast to an accumulation rate of 0.57 g $CaCO_3$ cm^{-1} ka^{-1} in the period from 1 to 2 ka BP in sediment core 23259-2. At the Reykjanes Ridge, the foraminifera mass accumulation in the most recent sample (0 to 1 ka BP, sediment core DS97-2P) was only 0.03 g $CaCO_3$ cm^{-2} ka^{-1} in contrast to an average of 0.30 g $CaCO_3$ cm^{-2} ka^{-1} in the three time intervals before. In one sample from the Barents Sea (JM09-KA11-GC), the foraminifera mass accumulation increased from 0.05 g $CaCO_3$ cm^{-2} ka^{-1} between 3 to 4 ka BP to 0.28 g $CaCO_3$ cm^{-2} ka^{-1} in the most recent interval from 0 to 1 ka BP. At all other positions, the average planktonic foraminifera mass accumulation was rather stable during the past 4 ka BP.

TABLE 6.4: Average, median, minimum and maximum planktonic foraminifera mass accumulation in all studied sediment cores, and the contribution of foraminifera to total $CaCO_3$ mass accumulation. The calculation accounts for each sediment core equally, independent from the number of samples in the core.

	Average	**Median**	**Minimum**	**Maximum**
Foraminifera mass accumulation [g $CaCO_3$ cm^{-2} ka^{-1}]	0.09	0.01	0	0.80
Proportion on total $CaCO_3$ accumulation [%]	30	5	0	89

The average mass accumulation of planktonic foraminifera within the past 4 ka BP in the Arctic and Subarctic Ocean shows regional variability: Highest accumulation rates (> 0.5 g $CaCO_3$ cm^{-2} ka^{-1}) are present in the Norwegian Sea and the influence area of warm surface currents, decreasing towards the north and areas of further influence of cold Arctic currents (values between 0.001 and 0.1 g $CaCO_3$ cm^{-2} ka^{-1}; Fig. 6.4a). In the central Arctic Ocean, values are similar. Towards the shelf areas (Laptev Sea, Barents Sea, western Fram Strait and Greenland Sea; water depths $\leq$ 300 m at the coring positions), mass accumulation rates are close or equal to 0 g $CaCO_3$ cm^{-2} ka^{-1}. In the Labrador Sea, average mass accumulation rates of planktonic foraminifera are similar to those in the central Arctic Ocean (0.005 to 0.001 g $CaCO_3$ cm^{-2} ka^{-1}), increasing towards the south.

6.3.3 Drivers of planktonic foraminifera carbonate mass accumulation

The analysis of possible parameters defining the mass accumulation rate of planktonic foraminifera in the Arctic and Subarctic realm was conducted using average values from all sediment cores, as the goal is to decipher regional influences and overall causes. As described in the paragraphs above, the variability over the time span of the past 4 ka BP is rather small within most of the cores. Therefore, we assume average values to be representative for the mass accumulation at the individual locations. We further assume that it is valid to compare the average values from the past 4 ka BP with recent average environmental data, as past changes have not been large in terms of foraminifera mass accumulation rates. We nevertheless are aware of the ongoing climatic change in the Arctic that hampers this assumption.

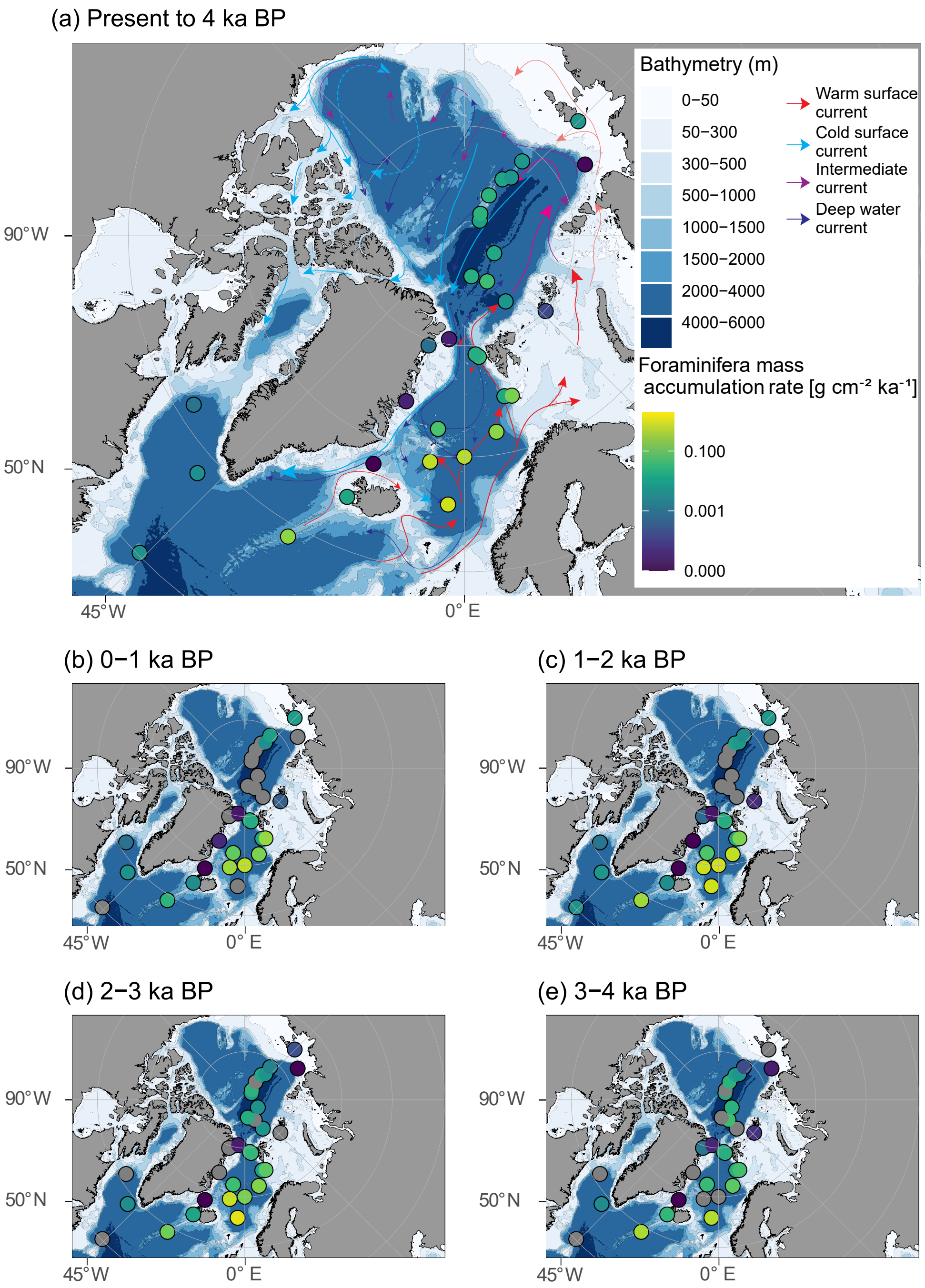

FIGURE 6.4: (a) Average mass accumulation rate of planktonic foraminifera in sediments of the last four millennia in the Arctic and Subarctic Ocean, (b-e) divided into four time intervals. Grey circles indicate no data. Land polygons from Natural Earth Data (CC0), bathymetry from Amante and Eakins, 2009 using ggOceanMaps in R (Vihtakari, 2021), and currents from Anderson and Macdonald, 2015.

Figure 6.3b-d indicates that the variability present in the mass accumulation rate of planktonic foraminifera is different to the linear sedimentation rate and the total mass accumulation rate in each individual sediment core. Consequently, high total accumulation rates seem to not always occur at the same time as high planktonic foraminifera accumulation rates. The linear correlation model using Spearman's Rank correlation shows a significant correlation between the total mass accumulation and the foraminifera mass accumulation ($R = -0.43$, $p = 0.033$; Fig. 6.5b), but no correlation of foraminifera accumulation with linear sedimentation rate ($p = 0.093$; Fig. 6.5). High planktonic foraminifera mass accumulation rates tend to occur at low sedimentation and total mass accumulation rates, as shown by the local polynomial regression fitting (Fig. 6.5a-b).

To check for possible influences of dissolution at the sediment surface interface, we analysed the relationship of planktonic foraminifera mass accumulation rates with the depth of each sampling location and the Ω calcite. Overall, foraminifera mass accumulation rates increase with increasing depth, which is significant after Spearman's Rank correlation ($R = 0.43$, $p = 0.014$; Fig. 6.5c). The local polynomial regression fitting visualises that this increasing trend is limited: While foraminifera rates are higher than at smaller depths from about 1600 to 3300 m, they are again low at depths below 3400 m (Fig. 6.5c). Low accumulation rates at deeper depths could be an indication of dissolution, which we checked looking at the average Ω calcite at each position. In all but one position (of PS2195-4 from the central Arctic Ocean), Ω calcite is > 1, which means that the water is oversaturated with calcite, not forcing dissolution of the foraminifera calcite. There is no significant linear correlation of foraminifera mass accumulation and the Ω calcite at depth ($p = 0.270$), and no further indication of any clear relationship (Fig. 6.5d).

Mass accumulation rates of planktonic foraminifera are significantly correlated with the average sea surface temperature during summer months: The higher the surface temperature, the higher the planktonic foraminifera mass accumulation rate ($R = 0.4$, $p = 0.046$; Fig. 6.5e). A similar relationship as with the depth is present between foraminifera mass accumulation and the sea surface temperature: It increases towards about 10 °C, but at higher temperatures, it is close to values reached at temperatures between -2 and +5 °C (Fig. 6.5e). The average chlorophyll α concentration at the coring positions is not significantly correlated to the mass accumulation rate of planktonic foraminifera ($p=0.660$; Fig. 6.5f). At most locations, the average chlorophyll α concentration between 2003 to 2021 has values between 0.5 and 1.5 mg m^{-3}, while high foraminifera accumulation rates only occur when the chlorophyll α concentration is between 0.6 and 1.0 mg m^{-3}.

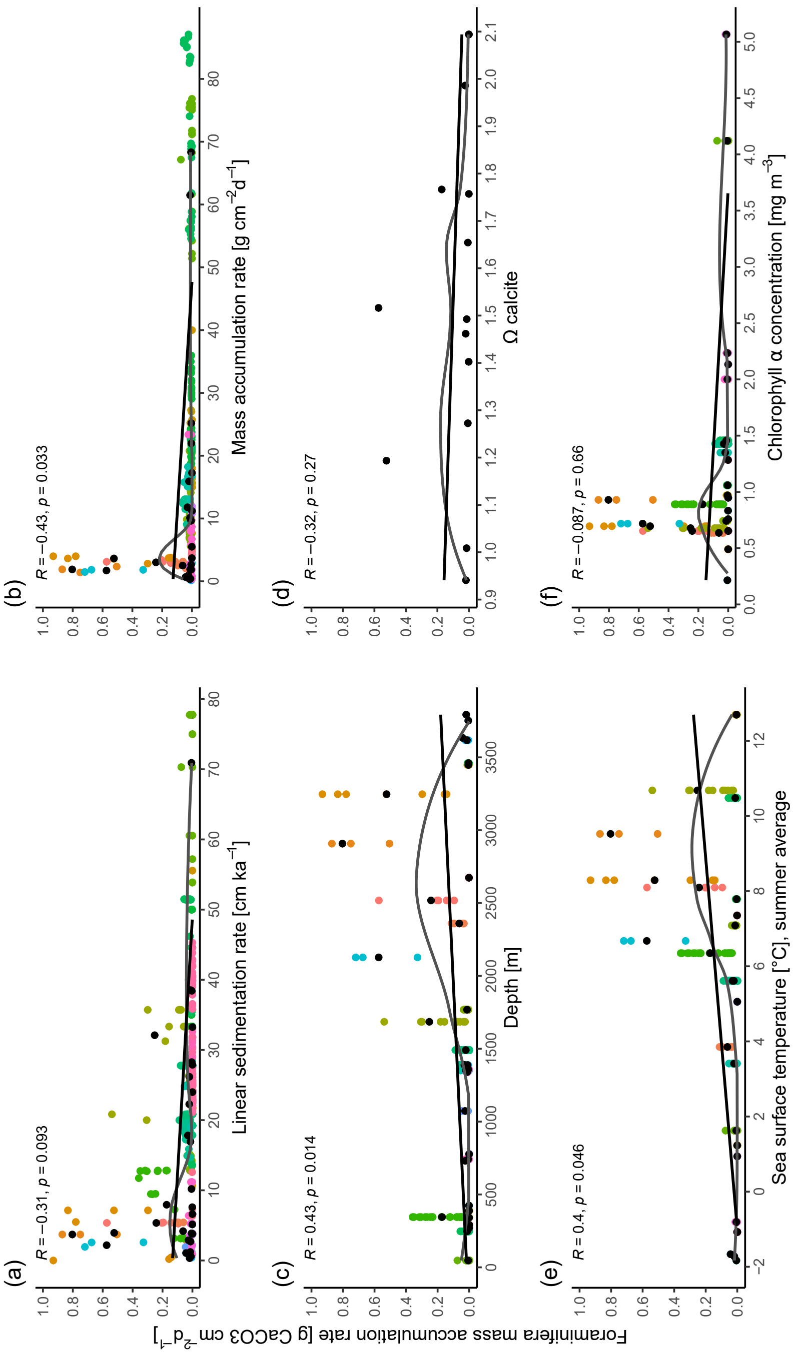

FIGURE 6.5: Relationship of planktonic foraminifera mass accumulation with (a) the linear sedimentation rate and (b) the total mass accumulation rate of each sediment core, (c) the deposition depth, (d) average Ω calcite, (e) average sea surface temperature during summer months and (f) average chlorophyll α concentration. The black dots indicate average values per sediment core, while the coloured dots are values from individual samples within the different cores. Consider that the environmental data from (d-f) are long-term averages from modern measurements. The black lines indicate the linear correlation between the shown parameter, as represented by the given R- and p-values from Spearman's Rank correlation, while the grey lines show the local polynomial regression fitting.

6.4 Discussion

6.4.1 Influences on planktonic foraminifera mass accumulation

The mass accumulation rate of planktonic foraminifera in the Arctic and Subarctic Ocean during the past 4 millennia varies over space, and furthermore over time at a few locations. The overall average foraminifera mass accumulation rate in the research area ranges from 0 to 0.8 g $CaCO_3$ cm^{-1} ka^{-1}. Our data indicates that highest average mass accumulation rates of planktonic foraminifera occur in the part of the Nordic Seas driven by relatively warm and saline Atlantic surface currents (Fig. 6.4). Moreover, planktonic foraminifera mass accumulation rates are positively correlated with the average summer sea surface temperatures. This is in line with previous results indicating that temperature and related parameters like sea ice extent and food availability play determinant roles on planktonic foraminifera populations both in terms of species abundances and calcite mass production (Žarić et al., 2005; Jonkers et al., 2010; Pados and Spielhagen, 2014; Jonkers and Kucera, 2015; Rembauville et al., 2016; Tell et al., 2023). Although foraminifera mass fluxes are clearly related to the temperature, they are not necessarily high under higher temperature regimes - there are also several sediment cores from areas of higher average summer temperatures with low foraminifera mass accumulation rates (Fig. 6.5e). This indicates that temperature is not the only relevant parameter, as it has also been discussed in Tell et al., 2023. Our data does not indicate a correlation to the chlorophyll α concentration, which would be an indicator of food availability and overall biological productivity. The analysed chlorophyll α concentration represents an average over 18 years, which have been influenced by significant warming in the Arctic (Overland et al., 2019), while the sediment cores represent much longer time scales. There are indications for changes in the primary production in the Arctic Ocean, which makes the present-day average less comparable to the information from the past 4 ka BP in the sediment cores (Ardyna and Arrigo, 2020). Moreover, using the total average chlorophyll α concentration could blur out plankton blooms of high intensity only occurring during short time periods in the Arctic and Subarctic Ocean (Oziel et al., 2017). As planktonic foraminifera, among them the in the Arctic important *N. pachyderma*, can be opportunistic feeder (Bergami et al., 2009; Taylor et al., 2018; Greco et al., 2021), a lack of correlation between the planktonic foraminifera mass accumulation and the average annual chlorophyll α concentration not necessarily indicates that the availability of food is not a relevant influence for the foraminifera productivity. If they also use other food sources, they could be independent from chlorophyll α concentration, and still dependent on the overall availability of food.

Sulpis et al., 2021 have shown dissolution of $CaCO_3$ to be strong close to the surface and at about 2000 to 3000 m depth in the Subpolar North Atlantic. Jutterström and Anderson, 2005 report that the majority of the Arctic Ocean is oversaturated with calcite, not causing strong dissolution of calcite shells. The planktonic foraminifera mass accumulation rate in the here studied sediment cores tends to be higher at deeper coring positions, but is low again at the deepest position. At the same time, average Ω calcite at the ocean floor from recent data confirm the finding of Jutterström and Anderson, 2005, showing that only one sediment core has been retrieved from a location which is undersaturated in respect to calcite at depth (Fig. 6.5f). This sediment core is from the central Arctic Ocean, and also from one of the deepest sampling positions. With the low foraminifera mass accumulation rates at locations of similar depths (from the central Arctic Ocean as well, plus two from the Nansen Basin and one core from the Labrador Sea), it is possible that dissolution occurred at those locations. It has to be considered that the Ω calcite values presented here are from recent measurements, while the foraminifera mass accumulation rate in the cores is influenced by the conditions during the past 4 ka BP. Even though our data indicates no strong changes over this time period, it has not been entirely stable. If Ω calcite has been higher in the past (e.g. slightly < 1 in contrast to slightly > 1 nowadays), dissolution could have affected the foraminifera mass accumulation. As calcite dissolution increases with higher pressure and lower temperatures, i.e. with depth (Jutterström and Anderson, 2005), it is likely that effects of dissolution would mostly have occurred at the deep sampling locations.

A possible contributor to the significant positive correlation between planktonic foraminifera mass accumulation and depth is that is has been shown that the productivity of planktonic foraminifera is overall lower in shelf areas in contrast to in the open ocean (Schmuker, 2000; Sousa et al., 2014). Schmuker, 2000 did not only connect this to the living depth of the foraminifera, but also to effects of lateral advection in shelf areas, transporting foraminifera to deeper areas before they are finally deposited.

Our data indicates that planktonic foraminifera mass accumulation rates do not increase with increasing rates of sedimentation and total mass accumulation, but are mostly independent from that (Fig. 6.3b-d, Fig. 6.5a-b). This means that the productivity and accumulation of planktonic foraminifera is independent from the accumulation of other particles. It furthermore shows low impact of dissolution in the study area: dissolution would affect foraminifera shells more in case of low total accumulation rates due to longer exposition to the surrounding environment at the sediment surface (Huber et al., 2000). Furthermore influencing the dissolution of planktonic foraminifera shells at the sea floor is the accumulation rate of organic carbon, as upon its respiration, CO_2 is released, possibly causing dissolution (Archer, 1991). We cannot preclude such effects.

A further way to assess the magnitude of dissolution in the water column is to compare the mass accumulation rate of planktonic foraminifera in the sediments with foraminifera mass flux rates within the water column. Tell et al., 2023 presented estimates of average daily foraminifera mass fluxes in the Nordic Seas over one year. Interpolation of these daily mass accumulation rates over 1000 years results in about 0.04 g $CaCO_3$ cm^{-1} ka^{-1} (standard deviation of 0.05 Table 6.5). To enable most direct comparison, we compare these values with the foraminifera mass accumulation rates in the top of the sediment cores from similar locations, using the sediment cores closest to each sediment trap position. Even though our data indicates that changes over the in the sediment cores studied time period are small, looking at the most recent sample is the most direct possible comparison with data from the water column. The rates of foraminifera mass accumulation in the top sample of sediment cores from the Fram Strait are close to estimated mass fluxes from the sediment trap data from this region (Table 6.5). In the Greenland Sea and the Norwegian Sea, mass accumulation rates calculated based on sediment trap data is much lower than the estimates from sediments (Table 6-5). Either similar or higher accumulation rates in the sediments in comparison to in the water column provide arguments against strong dissolution at the sea floor in the research area, as dissolution would result in clearly lower foraminifera mass in the sediments than in the water column. Higher sedimentation rates in the sediments could be caused by higher productivity in the region during the time period which is represented in the values from the sediments. It is further important to consider that the numbers from the sediment traps are based on interpolation. By this, we assume that the foraminifera mass fluxes detected during one year of sampling per sediment trap location is representative for the past 1000 years. Already the data from the sediment traps used for this comparison indicate differences in mass fluxes between two years (Tell et al., 2023). Therefore, interpolating over such a long period comes with high inaccuracy. Nevertheless, further comparison of the foraminifera mass accumulation rate in the sediments with data on mass fluxes from the Arctic and Subarctic Ocean of the most abundant Arctic species *N. pachyderma* from the upper water column presents a similar distribution of fluxes: High fluxes are present in the Nordic Seas and the eastern Fram Strait, and lower fluxes closer to the shelves and in the western Fram Strait (Tell et al., 2022). Overall, the comparison with data from the water column indicates that the estimates of foraminifera mass accumulation in the sediments are representative for the present-day situation in the Arctic and Subarctic Ocean. It further supports the indication of, if any, low influence of dissolution in the region.

TABLE 6.5: Planktonic foraminifera mass accumulation rates in the top sample of a few sediment cores from the Fram Strait, Greenland Sea and Norwegian Sea, and calculated mass accumulation rates based on sediment trap data from Tell et al., 2023. The number in the brackets in the interpolated values indicates the standard deviation.

Region	**Sediment core**	**Age top of sediment core [ka BP]**	**MAR_{pf} top of sediment core [g $CaCO_3$ cm^{-2} ka^{-1}]**	**Reference sample**	**MAR_{pf} reference sample [g $CaCO_3$ cm^{-2} ka^{-1}]**
Eastern Fram Strait	MSM05/5_712-1	-0.06	0.07	Sediment trap FEVI30	0.04 (0.06)
Eastern Fram Strait	MSM05/5_712-2	0.42	0.02	Sediment trap FEVI30	0.04 (0.06)
Eastern Fram Strait	MSM05/5_723-2	-0.06	0.02	Sediment trap FEVI30	0.04 (0.06)
Greenland Sea	23400-3	0.62	0.10	Sediment trap OG5	0.03 (0.02)
Norwegian Sea	23424-3	0.00	0.53	Sediment trap NB	0.04 (0.06)

6.4.2 Relevance of planktonic foraminifera mass accumulation for total carbonate storage

The average mass accumulation rate of planktonic foraminifera over the Arctic and Subarctic Ocean we calculated for the past four millennia is 0.09 g $CaCO_3$ cm^{-2} ka^{-1}. This value is based on average shell weights of specimens collected in samples from the Labrador Sea sediment cores. These average values have uncertainties. First, our measurements show a deviation in shell weights between measurements in bulk foraminifera shells and individual shells of about 1.7 µg on average (Table 6.3). This might partly be an effect of measuring larger and heavier shells individually, but we can still not preclude that using bulk weights for the mass accumulation rate determination results in an underestimation. At the same time, especially the individual measurements present high uncertainties, caused by strong differences in shell weights of shells of the same species. Therefore, the used average shell weights are overall only able to give a rough estimate of the mass accumulation rate. Using average shell weights from the Labrador Sea sediments may be another source of uncertainty because we measured the shells in the > 106 µm fraction, while the data of 8 out of the 29 sediment cores analysed is based on foraminifera shells in the > 63 µm fraction (Table B.1). Hence, applying the average shell weight from the Labrador Sea cores to those samples overestimates the mass accumulation. As the smallest shell in the measured shells from the Labrador Sea has a shell size of 120 µm, we can only assume what difference in shell weight results from shell size differences. In our measurements, the difference in shell weight of *N. pachyderma* with a maximum diameter of 200 µm and 250 µm, respectively, is almost 3 µg, which is a doubling in shell weight. This effect cannot be as large towards smaller shell sizes, as there would then be no shells smaller than 100 µm. That shell weights are much higher towards high shell sizes can be explained by the fact that upon adding calcite, new calcite layers are always formed around all existing shells, hence when another chamber is added to an already larger shell, the shell weight increases even more (Schiebel and Hemleben, 2005). Due to the lacking data on shell weights from shells < 106 µm, as well as the lacking information on the size distribution in the sediment cores that present data on shells > 63 µm, we cannot assess the detailed influence of using average shell weights from our data for all sediment cores, but only assume that the used average weights result in an overestimation.

Beyond these methodological caveats, the geographical distribution of planktonic foraminifera must be considered. Several studies indicate that under warm water temperature, calcification rates and hence foraminifera shell weights are higher than under low temperatures (Carstens and Wefer, 1992; Kohfeld et al., 1996; Weinkauf et al., 2016; Tell et al., 2022). With the Labrador Sea cores being located further south than most of the sediment cores studied here (Fig. 6.1), it is likely that the average shell weight and mass accumulation rate are overestimated. Within the three sediment cores, there is some difference in the average shell weight, which can partly be related to differences in species abundances and least heavy Atlantic species being present in the northernmost core TWC004. The average weight of *N. pachyderma* is also slightly different between the three cores. As in the average weight of all shells of the core, it is highest in the core MD99-2227, which is located in the middle of the three cores from the Labrador Sea, hence a clear relationship of latitude or temperature cannot be drawn. Therefore, the average rates of planktonic foraminifera mass accumulation of this study have to be regarded as rough estimates with uncertainties that could both lead to underestimation and overestimation.

Setting the average mass accumulation rate in relation to total $CaCO_3$ accumulation rate shows that planktonic foraminifera make up about 30 % (median: 5 %). Our data indicates regional differences, with a high importance of planktonic foraminifera in the high Arctic and the Greenland Sea (contribution of 46 % and higher), and lower relevance in the Fram Strait, the Nansen Basin, the Labrador Sea and the Laptev Sea. It has to be considered that to evaluate regional differences in further detail, more data would be needed, as we only have information on the total $CaCO_3$ accumulation from 11 sediment cores. The median value of the contribution and the estimates from the Fram Strait are in line with estimates from sediment trap data from the Nordic Seas presented in Tell et al., 2023. 5 % of the total $CaCO_3$ seem modest. However, the carbonate stored in the sediments is not only derived from biogenic $CaCO_3$ produced in the ocean, but also contains detrital carbonates. Such detrital carbonates can be related to erosion and released with meltwater from land ice or sea ice (Hebbeln, 2000) and occur frequently in sediments from the Arctic (Spielhagen et al., 1997). This would mean that for the formation of $CaCO_3$ in the ocean and hence the marine carbon cycle, planktonic foraminifera are still of relevance. Furthermore, our data indicate that planktonic foraminifera are especially important in the high Arctic Ocean, likely because productivity of other organisms as well as input of detrital carbonates is lower here (Jin et al., 2012; de Vernal et al., 2013; de Vernal et al., 2020).

6.5 Conclusion

Using foraminifera shell weights measured on three sediment cores from the Labrador Sea, we calculated mass accumulation rates of planktonic foraminifera in the Subarctic and Arctic Ocean during the past four millennia. The average accumulation rate is 0.09 g $CaCO_3$ cm^{-2} ka^{-1}, but differs regionally in line with the patterns of currents, in relation with the properties of the water masses, including their temperature regimes. Even though temperature seems to be relevant, it cannot explain the total pattern in foraminifera mass accumulation rate. Present-day concentration of chlorophyll α can also not explain the variability, but we cannot preclude other parameters of biological productivity and food availability to be important. Overall, our data do not indicate strong calcium carbonate dissolution, and the accumulation rates of planktonic foraminifera appear independent from total mass accumulation rates in the studied sediment cores that are characterized by variable amounts of detrital inputs. The foraminifera accumulation rates in sediment cores are within the range of estimates based on the study of sediment traps in the Fram Strait, but deviate in the Greenland and Norwegian Sea where the calculated rates in the sediments exceed those estimated from fluxes in the water column. On average, planktonic foraminifera mass accumulation rate in the Subarctic and Arctic realm make up about 30 % of total $CaCO_3$ present in the sediments from the region. This contribution has high regional variability, and the median contribution of planktonic foraminifera mass to total $CaCO_3$ accumulation is only 5 %. Still, with a contribution of up to 89 % in some regions, planktonic foraminifera are relevant to consider in terms of the carbon cycle in the Subarctic and Arctic Ocean.

Author contributions The study was designed by all authors. FT carried out the laboratory work on the platonic foraminifera with help from AdV. SKR compiled the data base on published sediment core data on planktonic foraminifera with support from FT. Data analysis was conducted by FT with help from LJ. All authors contributed to the interpretation and discussion of the results. FT wrote the paper with contributions from LJ, JM, AdV, SKR and MK.

Data availability All data created for this study is available on PANGAEA (`https://doi.pangaea.de/10.1594/PANGAEA.958156`). The data sources of the published data are linked in Table B.1.

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Chapter 7

Extended discussion

The Arctic Ocean is currently undergoing strong climatic and environmental changes, reinforced by polar amplification (Serreze and Barry, 2011). The marine carbon cycle is a relevant influencing factor of the climate, as it can for example release or take-up atmospheric CO_2, and is likewise affected by ongoing changes (Steinacher et al., 2009; Friedlingstein et al., 2019). Therefore, it is important to constrain these influences in further detail. How much mass of carbon is produced by planktonic foraminifera in the Arctic and Subarctic Ocean and what are controlling factors of this production, as well as how the ongoing changes could have an impact on the state of the art, will be discussed in the following based on the precedingly presented results.

7.1 Planktonic foraminifera mass estimates from different sample types

Data from plankton nets, sediment traps and sediment cores show large variation in the mass accumulation rate of planktonic foraminifera in the research area of the Subarctic and Arctic Ocean (Fig. 7.1). Accumulation rates of close to zero occasionally occur in all regions, at least in the plankton net data. The highest accumulation rates are present in the Greenland Sea, the eastern Fram Strait and the Barents Sea. These results are all based on data from plankton net sampling, which, in the research area, was only conducted from June to September, the high productive period of planktonic foraminifera in the Arctic and Subarctic Ocean (Jensen, 1998; Ramondenc et al., 2022). This means that calculating a 1000-year average based on daily mass production from summer results in overestimation. Also interpolation to 1000 years from sediment trap data is likely prone to error, even if the data represents the whole seasonal cycle. With high variability in the sediment trap data itself (section 5.3.1.1), it is unlikely that the average mass flux per year did not change over 1000 years. The calculated flux data indicate higher foraminifera mass production in the Nordic Seas and the Baffin Bay in contrast to lower productivity in the central Arctic Ocean. The high values in the Baffin Bay are only from plankton data, probably influenced by using average shell weights for the calculation that are not representative for the region (section 4.4.3), and therefore presenting an overestimation. Higher values of planktonic foraminifera mass accumulation in the Nordic Seas are visible in different sample types. Data from the central Arctic Ocean is mostly from sediment core data. The regional differences are important to consider when assessing the foraminifera mass production in the whole research area and possible climatic influences. Figure 7.1 furthermore shows how different samples from the individual sample type are distributed over the research area, with e.g. information on the high Arctic being only based on sediment core data, meaning that we do not have any data on recent foraminifera production in the water column there. This underlines the potential of combining different sample types for estimates of foraminifera on a wider regional extent, notwithstanding the inaccuracies resulting from comparison of data sampled during different time intervals. This is especially important in regions like the Arctic Ocean, where sampling is hampered by the extent of sea ice and the overall remote location of the large central Arctic Ocean (Bluhm et al., 2011). Accordingly, even if analysing different sample types together makes direct comparison of estimated values difficult, it is the only potential to get information on a large regional extent in the research area.

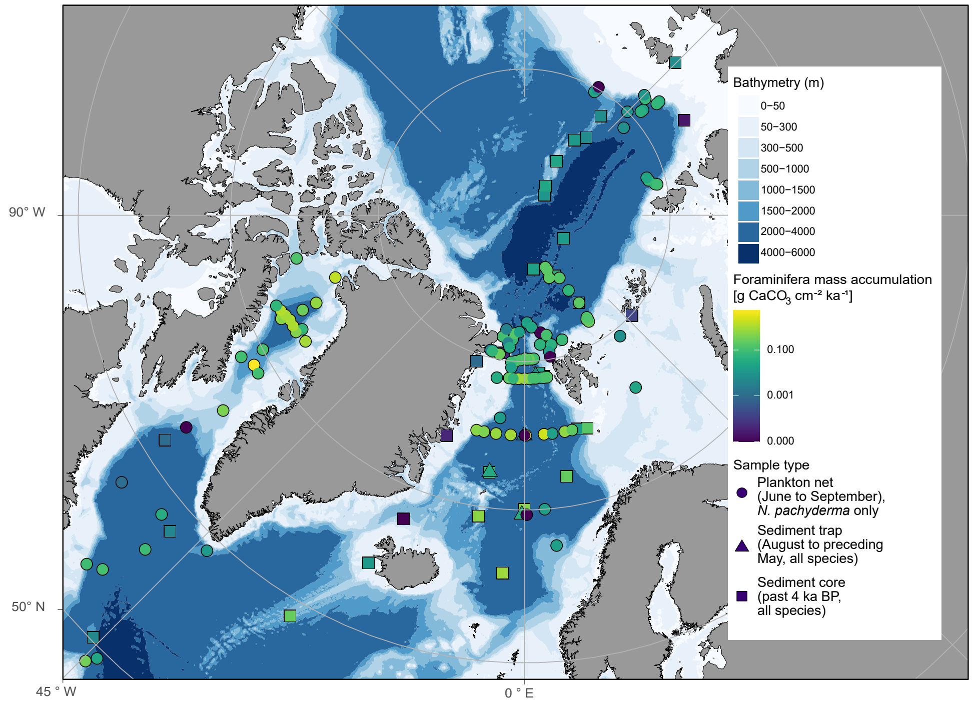

FIGURE 7.1: Mass accumulation rate of planktonic foraminifera in the Subarctic and Arctic realm based on data from different sample types. The accumulation rates of *N. pachyderma* from plankton net samples (data from chapter 4) from summer months and from sediment traps (data from chapter 5) from August to the preceding May are based on multiplying the detected mass production with 365 years for an annual value and with 1000 for the value for the accumulation rate per 1000 years. The accumulation rate is plotted on a logarithmic scale. Land polygons from Natural Earth Data (CC0), bathymetry fromAmante and Eakins, 2009 using ggOceanMaps in R (Vihtakari, 2021).

The overall average mass production of planktonic foraminifera from all samples shown in Fig. 7.1 is lognormal distributed, with a geostrophic mean of 0.05 g $CaCO_3$ cm^{-2} ka^{-1} (μ = -2.97, σ = 2.25) and the 68 % interval of the mass production ranging from, 0.01 to 0.49 g $CaCO_3$ cm^{-2} ka^{-1}. The extreme spread in values is caused by the plankton net data, with an arithmetic average being 10 times larger than the values from sediment traps and sediment cores. Leaving out the summer-biased samples from plankton nets, the average mass accumulation is 0.05 g $CaCO_3$ cm^{-2} ka^{-1} (median: 0.02 g $CaCO_3$ cm^{-2} ka^{-1}). This underlines the importance of studying planktonic foraminifera fluxes towards the and at the sea floor, as processes of dissolution can diminish the mass produced in the surface ocean (Schiebel, 2002; Sulpis et al., 2019). While a global estimate indicates that only about 25 % of the calcite produced by planktonic foraminifera in the surface oceans is accumulated at the sea floor (Schiebel, 2002), the study on *N. pachyderma* from the Arctic and Subarctic Ocean presents an average loss of about 19.8 % in the upper water column (loss of 6.6 % per 100 m in the 300 m below the productive zone; section 4.4.3). Assuming no further loss at deeper intervals, this would result in 80.2 % of the produced foraminifera accumulating in the sediments. With that, the mass accumulation rate of planktonic foraminifera at the sea floor based on mass fluxes from plankton net data results in 0.24 g $CaCO_3$ cm^{-2} ka^{-1}, which is still higher than the results from the other sampling types. This indicates the importance of considering the sampling bias when only using data from June to September. Data from the HAUSGARTEN observatory in the eastern Fram Strait indicates that about 99 % of total mass fluxes of foraminifera in the surface ocean towards the sediments are formed between June and September (chapter 5). Together, this can explain the high deviation in the mass accumulation rates based on plankton net data compared to data from sediment traps and sediment cores. This is because sediment trap and sediment core data represent foraminifera mass produced during the whole seasonal cycle, whereas plankton net data only represents the productive summer months. Moreover, samples from plankton nets are likely less affected by dissolution.

7.2 Role of Arctic planktonic foraminifera in the marine carbon cycle

The average mass accumulation rates of planktonic foraminifera can be used to estimate their Arctic Ocean wide production of $CaCO_3$. Multiplying the average value from sediment traps and sediment cores (leaving out data from plankton nets due to the apparent overestimation) with the area of the Arctic Ocean of 14.7x10^6 km² (Shiklomanov et al., 2000) gives an accumulation rate of 0.78 t $CaCO_3$ cm^{-2} ka^{-1}. This is much lower than the global estimate from Schiebel et al., 2007 of 0.71 Gt $CaCO_3$ yr^{-1}. Even when including the data from plankton nets, which is the sample type the values from Schiebel et al., 2007 are based on, the value is still clearly lower (3.47 t $CaCO_3$ cm^{-2} ka^{-1} / 0.000000003 Gt $CaCO_3$ cm^{-2} ka^{-1}). This could be an indication that the mass accumulation of planktonic foraminifera in the Arctic Ocean is much lower than on a global scale. Deviation between our data and data from other studies has also been detected in comparison with data from the Arctic and the Atlantic Ocean (section 4.4.3, section 5.4.4). Nevertheless, the high extent of assumptions and interpolation in the here presented numbers have to be kept in mind, which can amplify deviations. No distinction between shelf and open ocean area has been made in the calculation. Though, both the in chapter 6 presented data and previous data (Schiebel and Hemleben, 2017) show that there is (almost) no production of planktonic foraminifera in the shelf area. Further indication of inaccuracy in the mass determination comes from the large gap between estimates of mass produced by calcifying organisms and total $CaCO_3$ in sediment traps (thoroughly discussed in section 5.4.4). Therefore, the here presented values might underestimate the mass of $CaCO_3$ produced by planktonic foraminifera.

To assess the overall role of planktonic foraminifera in the Subarctic and Arctic Ocean for the carbon cycle, the different time intervals of the biological carbon pump have to be considered. While exchange of carbon in the surface waters is mostly relevant on short time intervals of centuries, on 100,000-year time scales, the exchange and transport towards the sediments is more relevant (Zeebe, 2012). In the surface water, the release of CO_2 during the formation of $CaCO_3$ is important, with a production of about 0.66 mol CO_2 per 1 mol produced $CaCO_3$ (Smith and Mackenzie, 2016). At the same time, planktonic foraminifera incorporate carbon into their living shell (Schiebel and Movellan, 2012). This means they also contribute to the biological carbon pump, and if not degraded in the upper water column after their death directly, to the transport of carbon from the surface to the deep ocean. In the upper water column, the productivity of planktonic foraminifera is a factor to consider in terms of release of CO_2 that is potentially emitted into the atmosphere. The lower the productivity, the lower the CO_2 release (Zeebe, 2012). Nevertheless, on longer time scales, planktonic foraminifera are an important contributor to carbon drawdown towards the deep ocean, where it is stored long-term. With data on the carbon mass of the living cell of the foraminifera lacking, it is hard to make an estimate on the total mass of this drawdown. However, the here presented numbers of the produced mass of $CaCO_3$ from foraminifera shells give an estimate that can be of use for future calculations of a carbon budget of planktonic foraminifera from the Arctic and Subarctic Ocean.

7.3 Relevance of findings under changing climate scenarios

The planktonic foraminifera shell weight measurements presented in this thesis of distinct planktonic foraminifera species from the research area indicate that shell weight is important to consider in connection to the shown change in relative abundance of different species, that is likely to continue with ongoing warming (Greco, Werner, et al., 2021). With decreasing abundances of the Arctic *N. pachyderma* and Subarctic *T. quinqueloba*, and increasing abundances of the Atlantic species like *G. uvula*, *G. glutinata* and *G. bulloides*, the overall produced shell mass could change. It is challenging to give this change a clear direction, as some Atlantic species are lighter than the Arctic species, while others are heavier (Table 7.1). If *N. pachyderma* would be mostly replaced by light species like *G. uvula* and *G. glutinata*, the total produced mass would be reduced, while it would increase if *G. bulloides* and *G. inflata* displace it, under the assumption of a constant overall foraminifera shell flux (Fig. 7.2). This research work did not analyse any possible species abundance changes in the connection of changing climatic conditions. Greco, Werner, et al., 2021 only present overall values of the Atlantic species *G. glutinata*, *G. bulloides*, *N. incompta*, *G. uvula* and *O. riedeli* together, which tend to increase. There are indications of increasing abundances of *G. uvula* from the Barents Sea (Meilland et al., 2020), but this is only a snapshot, both temporal and regional, so no overall conclusions on the development of the produced shell mass can be drawn from this result. Nevertheless, the present large differences in shell weights of distinct species of planktonic foraminifera from the Subarctic and Arctic Ocean and species moving northwards from the Atlantic Ocean make an influence of climatic change on the mass production of $CaCO_3$ by planktonic foraminifera in the research area very likely (Fig. 7.2).

The described effects of species-specific shell weights on the mass production assume that the overall abundance, i.e. the productivity of planktonic foraminifera, is not changing over time. The analysis of environmental drivers of foraminifera mass production indicates that this might not be the case. Sediment trap data from the Nordic Seas demonstrate the in previous studies indicated relationship of planktonic foraminifera with the water temperature (Jensen, 1998; Žarić et al., 2005) of increased productivity in warmer periods (section 5.4.3). However, the analysis shows that it is not possible to directly quantify changes in foraminifera mass production by water temperature. Thus it is not possible to directly assume an increased mass production of planktonic foraminifera in the Arctic and Subarctic Ocean in the context of the present-day warming trend of the Arctic and the projected warming in the future (Overland et al., 2019). If the onset of the warmer summer period, hence the onset of increasing foraminifera productivity, occurs earlier in the year due to the warming, and production stays high longer towards winter, it is, nevertheless, possible that the warming trend results in higher mass production (Fig. 7.2).

TABLE 7.1: Average shell weights of Arctic and Subarctic planktonic foraminifera species from different sample types. Data from plankton nets is presented section 4.3.2 (*N. pachyderma*) and appendix C, data from sediment traps in section 5.3.1.2 and data from sediment cores in section 6.3.1.

Average shell weight [µg]	**Plankton net samples**	**Sediment trap samples**	**Sediment core samples**
All species	1.1	1.5	4.8
N. pachyderma	1.6	2.3	4.9
T. quinqueloba	1.0	1.3	3.7
N. incompta	0.9	1.5	4.3
G. glutinata	0.9	1.2	2.4
G. bulloides	1.1	4.1	8.4
G. uvula	1.1	0.3	0.8
O. riedeli	0.9	0.4	NA
G. sacculifer	NA	NA	12.8

Increasing temperatures in the Arctic Ocean are not only relevant in terms of water temperature, but connected to further parameters of change. One of this is the ongoing substantial loss in sea ice (Meier et al., 2014; Stroeve and Notz, 2018). The combination of higher temperatures and lower sea ice extent could result in an increase in the primary productivity (Carmack et al., 2006; Perovich and Polashenski, 2012; Fig. 7.2). Lewis et al., 2020 show that supply of nutrients is a main factor of change in primary production. This can be related to sea ice and release of nutrients during ice melt, but also to river discharge, which is influenced by changing climatic conditions on land (Lewis et al., 2020). Husherr et al., 2017 show that increased ocean acidification, likewise associated with the ongoing climate change, is likely to reduce the biomass of algae in the Arctic Ocean (Fig. 7.2). This means that the current changes in the Arctic Ocean possibly do not result in a one-direction-change of the primary production, which makes it difficult to assess the effect of changes on planktonic foraminifera. It is getting even more complex due to the finding that not only the food availability, but presumably also the food quality is driving the mass flux of $CaCO_3$ produced by planktonic foraminifera towards the sediments (Meilland et al., 2020; section 5.4.3). With the current data gap of food quality on foraminifera biology and uncertainties of mixed effects of climate change on the primary productivity, it is not possible to draw direct conclusions on how the persistent change of the Arctic Ocean affects the carbonate mass production of planktonic foraminifera in terms of changing primary productivity (Fig. 7.2). However, water temperature, sea ice and ocean acidification likely affect the primary productivity and thus the food source of planktonic foraminifera in the Arctic Ocean, which makes them important components of the total mass of $CaCO_3$ that is produced by planktonic foraminifera. Even without being able to give the change a direction, this thesis shows that these factors are important to consider and that the ongoing climate change will likely affect the foraminifera productivity.

Acidification and dissolution are important factors in the context of transport and sedimentation of foraminifera calcite shells at the ocean floor. Studies on the present-day Arctic Ocean saturation of calcite (Jutterström and Anderson, 2005; Chierici and Fransson, 2009), and a future modelling study (Luo et al., 2016) indicate that most of the Arctic Ocean is not undersaturated in respect to calcite, and that undersaturation will also not occur in the context of overall increasing acidification in the future. The analysis of present-day conditions has shown that there is one location in the central Arctic Ocean that is undersaturated in respect to calcite (section 6.4.1). Therefore, it is possible that planktonic foraminifera in small regional extent of the Arctic Ocean can be affected by dissolution at the sea floor (Fig. 7.2), which, with the ongoing change, might increase. Overall, though, dissolution due to a changed state of the Arctic Ocean itself is likely not having large impact on the future mass accumulation of planktonic foraminifera. However, changes in species abundances and total mass flux produced in the upper water column could change the dissolution in that zone. The impact of dissolution on spinose species of planktonic foraminifera is larger than on non-spinose species (Berger, 1970). In the research area, spinose species are *T. quinqueloba*, *G. bulloides* and *O. riedeli*. If these species increase in abundance in contrast to the non-spinose Arctic *N. pachyderma*, the dissolution of foraminifera shells in the upper water column could increase, resulting in lower transport of calcite towards the sediments. Also the magnitude of fluxes from the upper water column downwards is relevant for the intensity of fluxes, as dissolution minimizes with increasing amount of material sinking downwards at the same time (Klaas and Archer, 2002; Schiebel, 2002; Sulpis et al., 2021). If the beforehand discussed possible effects on foraminifera productivity from changing climate conditions and related factors lead to higher fluxes during certain time periods, more shells would arrive at the sea floor before being dissolved (Fig. 7.2). In contrast, dissolution can increase if the amount of organic carbon attaching to the sinking foraminifera shells, as hypothesized by Greco, Morard, et al., 2021, increases (Fig. 7.2): During the degradation of organic carbon, CO_2 is released, which can cause local dissolution (Sulpis et al., 2021). Comprising, while acidification is likely not strongly increasing dissolution of planktonic foraminifera shells in the Arctic Ocean, changes in total foraminifera productivity as well as in mass fluxes of organic carbon can affect the $CaCO_3$ mass production by planktonic foraminifera in the research area. To give this change a sign, more details on the changes of both foraminifera mass fluxes and total organic carbon fluxes would be necessary.

To sum up, the ongoing climate change in the Arctic and Subarctic Ocean can result both in an increase in planktonic foraminifera calcite mass production (caused e.g. by higher abundances of heavy Atlantic species, longer warm periods and possibly higher quality and quantity of food) and in a decrease of foraminifera calcite mass production (caused e.g. by higher abundances of light Atlantic species or stronger dissolution in the upper water column due to higher amounts of organic carbon and its degradation; Fig. 7.2). The studies presented in the context of this thesis help to further understand the driving factors of planktonic foraminifera mass productivity: Water temperature is an overarching factor influencing components like sea ice and primary productivity. The latter seems to be an important driver of the observed variability in planktonic foraminifera shell mass production. While this thesis contributes to a better understanding of these factors, it is still not possible to quantify the strength of the driving factors in further detail. Moreover, there are still many unknowns in the consequences of the climatic change in relation to primary productivity in the research area, which are relevant for the $CaCO_3$ mass production by planktonic foraminifera.

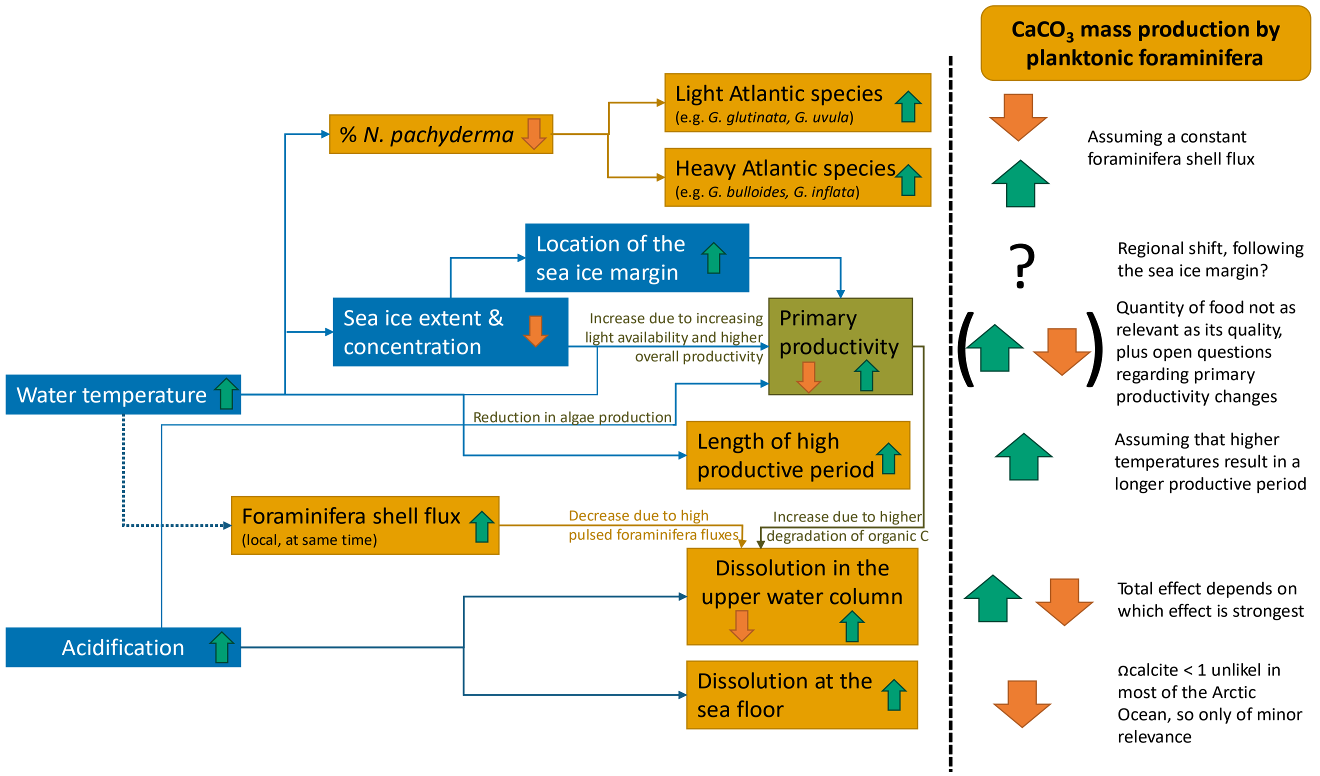

FIGURE 7.2: Schematic overview on possible influences of chancing conditions in the Arctic and Subarctic Ocean in the CaCO$_3$ mass produced by planktonic foraminifera. Effects caused by higher water temperature and higher acidification are shown. The indicated trends in the foraminifera mass production (right of the dashed black line) are based on the results from the chapters 4, 6 and 5. The arrows indicate possible trends in both climatic and environmental conditions and in the foraminifera productivity. The shown trends in both climatic and environmentally influenced parameters and the foraminifera productivity are simplified and not as linear in one direction in reality.

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Chapter 8

Conclusion and outlook

The research conducted in the context of this thesis shows that to understand the mass flux of planktonic foraminifera in the Arctic and Subarctic Ocean towards the ocean floor and its role for the marine carbon cycle, a complex of factors needs to be considered. From the upper water column towards the sediments, the productivity and accumulation can be influenced and driven by various abiotic and biotic factors, which interact with the ongoing changes in the Arctic. Analysis of a combination of new and published data on planktonic foraminifera from plankton nets, sediment traps and sediment cores were conducted to test the hypotheses presented in section 1.5 and are summarized here again:

H1 The depth habitat of planktonic foraminifera is variable and dissolution is a relevant influence in the upper water column, making it important to constrain the depth of their productive zone and the depth where their flux towards the sediments starts.

The results show that *N. pachyderma*, the most abundant planktonic foraminifera in the Arctic Ocean, has a highly variable productive zone, ranging from 15 to 300 m. Shell weight and shell size of planktonic foraminifera shells retrieved with plankton nets from different depth intervals do not indicate extensive ontogenetic vertical migration. This means that the heavy calcification at the end of the life cycle of the foraminifera is not fixed to the deepest point of the productive zone of this species, but individual calcification occurs at various depths within the total productive zone. Below the productive zone, substantial attenuation of downward mass fluxes of *N. pachyderma* of about 6.6 % per 100 m has been detected in the 300 m water column below the end of the productive zone. Comparison of the calculated mass flux of planktonic foraminifera with previous studies indicates clear differences in the estimated average results. In connection to the detected attenuation, this supports the importance to constrain the productive zone of planktonic foraminifera if their mass flux towards the sediments should be assessed based on data from plankton nets from the upper water column.

H2 Planktonic foraminifera mass fluxes are defined by their shell flux, which is driven by water temperatures and food availability (i.e. primary productivity).

Planktonic foraminifera shell weights tend to be higher during the high productive summer months in the Arctic Ocean (Fig. 5.5), and significant differences in the shell weight of distinct species of planktonic foraminifera exist (Table 7.1). However, the analysis of planktonic foraminifera mass fluxes from sediment trap data (chapter 5) shows that the shell flux is what actually defines the present variability, both intra-and interannually. The increase of mass fluxes of planktonic foraminifera occurs parallel to the onset of insolation, increasing temperatures and increasing chlorophyll α concentration. However, none of these parameters can explain the present differences in mass flux magnitude between different years (section 6.3.2). Accordingly, they are not the only drivers and they cannot be used for quantifying mass fluxes of planktonic foraminifera under varying climatic and environmental conditions. With the data at hand, it was unfortunately not yet possible to detect drivers that can explain the changes in magnitude. It is hypothesized that the quality of the food available is of relevant influence, but this could not have been tested in this context.

H3 A relevant amount of total $CaCO_3$ produced in the Arctic and Subarctic Ocean and stored in its sediments is formed by planktonic foraminifera. Planktonic foraminifera are therefore important organisms in the marine carbon cycle.

Planktonic foraminifera in the Arctic and Subarctic Ocean on average contribute to 5.4 to 30 % of total $CaCO_3$ (section 4.4.3, section 5.3.1.3, section 6.3.2). Locally, contributions of up to 89 % (section 6.3.2) were detected. Planktonic foraminifera overall are a relevant contributor to total $CaCO_3$, especially in its storage in ocean sediments for longer time scales, which is a relevant factor of carbon storage in the marine carbon cycle. This is especially the case in regions where large parts of $CaCO_3$ mass production is formed by aragonitic pteropod shells which dissolve at the sea floor, like it is the case in the Fram Strait (Bauerfeind et al., 2014).

While this thesis was able to disentangle some of the unknowns regarding the mass production of calcite by planktonic foraminifera in the Arctic and Subarctic Ocean and its role for the marine carbon cycle, new questions arise from the here presented research work, indicating possible future directions of research in this field. One main component would be to quantify the influences on planktonic foraminifera mass flux variability over time and space regarding the climatic and environmental driving factor. As discussed in section 7.2, it is still uncertain how primary productivity will evolve in the future under ongoing climatic change (Carmack et al., 2006; Lewis et al., 2020). Regarding planktonic foraminifera, the most relevant question based on the results presented in chapter 5 is: What role does the quality of food actually play for the variability in productivity? While current indications of the food quality to be an important driver are based on samples from the field (Meilland et al., 2020), detailed laboratory studies monitoring the effect of different food sources on their productivity would be needed for quantification. Examples of laboratory studies on planktonic foraminifera and effects of different growing condition already exist (e.g. Spindler et al., 1984; Hemleben et al., 1985; Bijma et al., 1990; Greco et al., 2020). To quantify the effect of the food quality on the productivity, similar studies with varying food sources would be needed. For thoroughly understanding of the effect on foraminifera productivity, reproduction of foraminifera in the laboratory culture would be necessary. This is a challenge regarding the fact that up to now, despite observation of reproduction in the laboratory (Davis et al., 2020; Meilland et al., 2022), reproduction of a second generation of planktonic foraminifera has not been achieved in culture yet (Schiebel and Hemleben, 2017). Culture studies of planktonic foraminifera could furthermore add details on the observations of seasonal temperature effects on the shell mass (chapter 5).

This work gives an overview on the mass of $CaCO_3$ produced by planktonic foraminifera in the Arctic and Subarctic Ocean in relation to total $CaCO_3$. Though, data from sediment traps (chapter 5) indicate large gaps between estimates of mass production by calcifying organisms like planktonic foraminifera and the total $CaCO_3$ settling flux. If we want to understand how ongoing climate change in the Arctic Ocean affects this component of the carbon cycle, knowledge on all components that sum up to the total $CaCO_3$ is needed. To close the existing gap between organism-individual and total $CaCO_3$ settling flux estimates, research on different organism groups from the same location would be needed. On top of that, the bulk sample, which is used to determine the total $CaCO_3$ content, needs to be studied thoroughly to be able to detect possible reasons of deviations between bulk samples and sample splits used for studying individual organism groups. This could then be used to evaluate causes of existing gaps, and possibly help to correct existing results such that more precise understanding of the contribution of planktonic foraminifera and other organisms to the deposition of $CaCO_3$ at the sea floor could be achieved. Doing so, overall evaluation on how ongoing climate change could affect the marine carbon cycle in respect to production of $CaCO_3$ would be possible.

For the overarching goal of estimating a carbonate budget of planktonic foraminifera in the Arctic and Subarctic Ocean, as discussed in section 7.1, more information is needed on the organic carbon that is produced by planktonic foraminifera. Existing knowledge (e.g. from Schiebel and Movellan, 2012) would need to be extended to better understand this component for the different species of planktonic foraminifera in the research area. Besides, to evaluate if the production of $CaCO_3$ in the upper water column in the end results in higher release of carbon towards the atmosphere or higher storage at the sea floor, assessment of the water conditions at which calcification and dissolution occur would be needed (Smith and Gattuso, 2011). Combining these different estimates and data sets could enable more detailed assessment of the role of planktonic foraminifera for the marine carbon cycle.

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Appendix A

Upper-ocean flux of biogenic calcite produced by the Arctic planktonic foraminifera *Neogloboquadrina pachyderma*

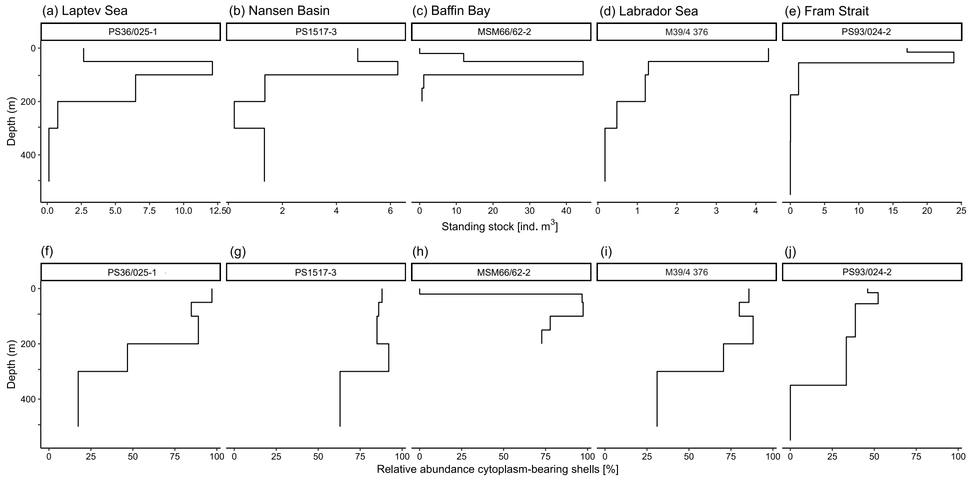

FIGURE A.1: Example of vertical profiles of abundances of *N. pachyderma* at five different sampling locations from different parts of the Arctic Ocean. (a-e) show absolute shell number concentration (ind. m^{-3}) of *N. pachyderma*, (f-j) relative abundance of cytoplasm-bearing shells of *N. pachyderma*.

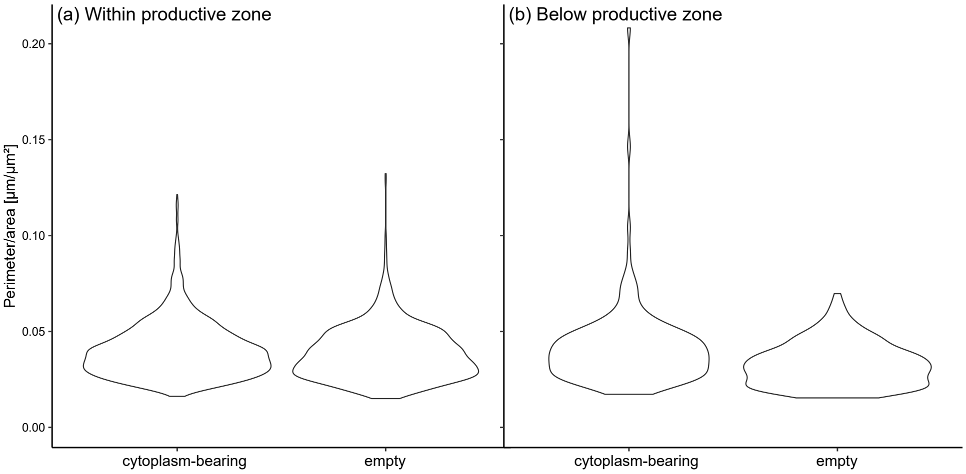

FIGURE A.2: The ratio of perimeter to area in individual shells of *N. pachyderma* in samples from PS 93.1, divided by the status (cytoplasm-bearing and empty). (a) represents the shells from within the calculated productive zone of the individual stations, (b) those from below the productive zone.

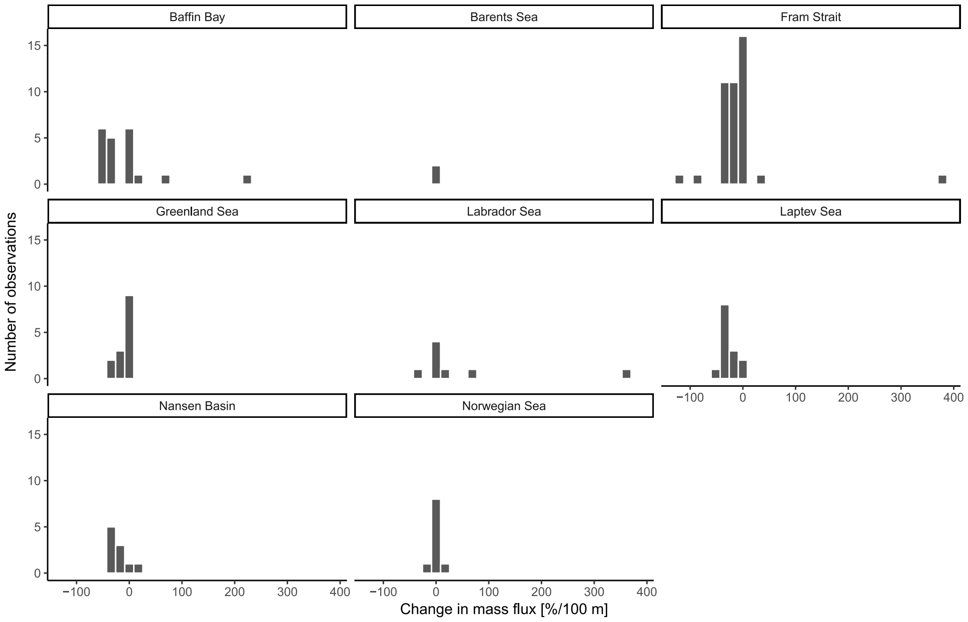

FIGURE A.3: Change in shell flux between the net directly below the calculated base of the productive zone and the deepest net of sampling of each station, divided by the different regions of sampling.

Appendix B

Carbonate burial of planktonic foraminifera in the Arctic Ocean during the late Holocene

TABLE B.1: Overview on the 33 sediment cores used in this study, combining published data with three sediment cores from the Labrador Sea added in this study.

Sediment core	**Lat.**	**Lon.**	**Depth [mbsf]**	**Age min [ka BP]**	**Age max [ka BP]**	**No. of samples > 4 ka**	**Size fraction [μm]**	**$CaCO_3$ data available**	**Reference**	**Data source**
23259	72.0	9.3	2518	0.09	14.77	5	63-500	No	Jensen, 1998	data from original publication
23400	72.4	7.8	2630	0.62	12.38	6	63-500	No	Jensen, 1998	data from original publication
23411	65.8	3.5	2908	1.55	14.56	4	63-500	No	Jensen, 1998	data from original publication

23424	70.0	0.1	3247	0.00	2.58	7	63-500	No	Jensen, 1998	data from original publication
ASV11-880-3	79.9	47.1	388	0.00	9.80	18	100	No	Duplessy et al. (2001); Gurvich & Vlasova (2004)	`https://doi.pangaea.de/10.1594/PANGAEA.657129`; `https://doi.pangaea.de/10.1594/PANGAEA.135089`
DA17 NG ST14 171G	74.1	-19.4	341	0.00	12.20	3	63	No	Jackson et al. (2022)	`https://doi.org/10.22008/FK2/VOCGWD/8R7RHG`
DS97-2P	58.9	-31.3	1685	0.00	52.00	44	100	No	Rasmussen et al. (2003); Perner et al. (2018)	`https://doi.org/10.1016/S0377-8398(02)00115-9`; `https://doi.pangaea.de/10.1594/PANGAEA.898384`
GIK23258-2	75.0	14.0	1768	0.70	13.99	52	150	No	Sarnthein et al. (2003)	`https://doi.pangaea.de/10.1594/PANGAEA.114682`
HU2008-029-002BX/TWC004	61.5	-58.0	2668	0.02	1.39	6	106	No	This study	
HU91-045-093BX	50.2	-45.7	3448	1.19	1.83	10	106	Yes	This study	Chronology from `https://doi.pangaea.de/10.1594/PANGAEA.905402`
IK9373-10	75.3	135.2	47	0.75	2.32	20	63	No	Bauch (1999); Kunz-Pirrung (2003)	`https://doi.pangaea.de/10.1594/PANGAEA.56012`; `https://doi.pangaea.de/10.1594/PANGAEA.90611`
JM09-KA11-GC	74.9	16.5	345	0.05	11.79	24	100-1000	No	Berben et al. (2014)	`https://doi.pangaea.de/10.1594/PANGAEA.901872`
MD99-2227	58.2	-48.4	3460	0.76	3.96	48	106	Yes	This study	Chronology from `https://doi.pangaea.de/10.1594/PANGAEA.839124`

MD99-2256	64.3	-24.2	247	0.19	17.37	39	150	No	Jennings et al. (2015); Labeyrie & Jennings (2005)	https://doi.pangaea.de/10.1594/PANGAEA.864063; https://doi.pangaea.de/10.1594/PANGAEA.864056; https://doi.pangaea.de/10.1594/PANGAEA.253587
MSM05/5_712-1	78.9	6.8	1491	0.00	02.07	159	100-250	No	Spielhagen et al. (2011)	https://doi.pangaea.de/10.1594/PANGAEA.755092
MSM05/5_712-2	78.9	6.8	1389	0.42	8.84	64	100-250	Yes	Werner et al. (2013)	https://doi.pangaea.de/10.1594/PANGAEA.770168
MSM05/5_723-2	79.2	5.3	1351	0.00	12.03	110	100-250	Yes	Werner et al. (2016)	https://doi.pangaea.de/10.1594/PANGAEA.849329
PS100/270-1	79.5	-18.1	423.6	0.75	10.21	2	63-500	No	Syring et al. (2020)	https://doi.pangaea.de/10.1594/PANGAEA.921171
PS1244-2	69.4	-8.7	2127	0.25	567.00	4	125-500	Yes	Bauch (1993)	https://doi.pangaea.de/10.1594/PANGAEA.82294; https://doi.pangaea.de/10.1594/PANGAEA.82283
PS1521-15	82.9	32.1	3752	2.22	170.00	2	125-500	Yes	Pagels (1991)	https://doi.pangaea.de/10.1594/PANGAEA.388803
PS1524-1	85.4	26.4	3634	03.07	75.30	2	125-500	Yes	Pagels (1991)	https://doi.pangaea.de/10.1594/PANGAEA.388867; https://doi.pangaea.de/10.1594/PANGAEA.388782
PS2166-2	86.9	59.7	3618	2.40	70.82	2	125-500	Yes	Nørgaard-Pedersen et al. (1998)	https://doi.pangaea.de/10.1594/PANGAEA.398997
PS2177-1	88.0	134.9	1388	02.07	69.30	3	125-500	Yes	Nørgaard-Pedersen et al. (1998)	https://doi.pangaea.de/10.1594/PANGAEA.398998

PS2185-3	87.5	144.2	1073	02.03	51.00	3	125-500	No	Spielhagen et al. (2004)	https://doi.pangaea.de/10.1594/PANGAEA.206405
PS2195-4	86.3	9.6	3793	2.79	115.07	1	125-500	Yes	Nørgaard-Pedersen et al. (1998)	https://doi.pangaea.de/10.1594/PANGAEA.399000
PS2644-5	67.9	-21.8	777	0.26	84.97	14	150	No	Griem et al. (2019)	https://doi.pangaea.de/10.1594/PANGAEA.904033
PS51/154-11	77.3	120.6	270	0.55	17.30	10	63	Yes	Taldenkova et al. (2013)	https://dx.doi.org/10.1016/j.marmicro.2012.06.007
PS87/055-1	85.7	148.8	731	3.64	46.00	1	106	No	de Vernal et al. (2020)	https://doi.org/10.1073/pnas.2008996117
PS87/070-3	83.8	146.1	1340	2.58	10.04	7	106	No	de Vernal et al. (2020)	https://doi.org/10.1073/pnas.2008996117
PS87/079–3	83.2	141.4	1359	1.72	5.45	12	106	No	de Vernal et al. (2020)	https://doi.org/10.1073/pnas.2008996117
PS87/099–4	81.4	142.2	741	1.17	3.32	11	106	No	de Vernal et al. (2020)	https://doi.org/10.1073/pnas.2008996117
PS93/025	80.5	-8.5	290	0.02	10.63	123	100-250	No	Zehnich et al. (2020)	https://doi.pangaea.de/10.1594/PANGAEA.923845

Appendix C

Data

In the following, all data sets produced in the context of this thesis are listed, giving access to all data.

Planktonic foraminifera from plankton nets All data in supplement to chapter 4 is available on PANGAEA: `https://doi.org/10.1594/PANGAEA.941250`.
The data sets include the in the context of this thesis conducted counts of *N. pachyderma* from plankton net samples from the campaigns MSM44, MSM66 and PS93.1, shell size measurements from MSM44, MSM66 and PS93.1, shell weight measurements from PS93.1, and the calculated base of productive zone and mass flux of *N. pachyderma* from both produced new data sets and published data.
In addition, all other species of planktonic foraminifera present in the PS93.1 samples were counted, the average shell weight per species and sample was measured and shell sizes were measured individually. This data was not further analysed as the focus of the here presented research using plankton net data was set on *N. pachyderma*. The data is available here: `https://doi.org/10.5281/zenodo.7581517`.

Planktonic foraminifera from sediment traps All in the context of this thesis newly produced data in supplement to chapter 5 is available on PANGEA: `https://doi.pangaea.de/10.1594/PANGAEA.957172`.
The data includes counts, shell size and shell weight measurements of all species of planktonic foraminifera, and fluxes of total $CaCO_3$ and POC at the sediment trap FEVI30 at the HAUSGARTEN observatory.
In the context of the research for this thesis, planktonic foraminifera from another sediment trap at the HAUSGARTEN observatory, TDLT2014, were analysed. This data was not included in the analysis of chapter 5 as a comparison of the shell counts from the samples with initial foraminifera shell counts directly after sample retrieval indicated high deviation. Therefore, dissolution affecting the shells in the time period between their retrieval (2015) and the beginning of the analysis in the context of this study (2020) is assumed. The data on shell counts per species, average shell weights per sample and species, and individual shell sizes is nevertheless available here: `https://doi.org/10.5281/zenodo.7581700`.

Planktonic foraminifera from sediment cores Shell counts, shell weight and shell size measurements on samples from the Labrador Sea (both as bulk and individual measurements), used for the study presented in chapter 6, are available on PANGAEA: `https://doi.pangaea.de/10.1594/PANGAEA.958156`.

Appendix D

Science communication on the Arctic Ocean

As all scientific work presented here was supported by the German Research Foundation (DFG), hence public funds, I take it for granted to not only make all acquired scientific data and results available to the public, but also to reach out to the general public about the outcome of the research and the importance of understanding the ongoing climate change in the Arctic Ocean. Therefore, I took several opportunities of scientific outreach activities and got in touch with different groups of people. A comprehensive overview on the outreach activities I did during the three years of my research in the context of this dissertation is given below. It presents different ways of doing scientific outreach and the advantages of different methods I discovered.

Online workshops for school children In the course of the covid-19 pandemic, it was only possible to get in touch with interested people online. One of these formats set up in Germany for school children was the digital door (Digitale Drehtür). Together with colleagues from the ArcTrain research training group, Johanna Hingst, Linda Thielke and Jan-Hendrik Malles, I conducted three online-courses about the ongoing climate change in the Arctic and its role for the global climate crisis. Even though taking place online, a major part of the courses was to encourage the children to work together in groups. We created a group work in which they collected everything they already knew about the Arctic on sketches I had drawn before the course (Fig. D.1). It was impressive to see their knowledge, and further increase their curiosity.
The university of Bremen also set up different types of online programs during the pandemic. In the course of the digital children university, I made a video call with an entire school class, where I gave insights in my daily work as a scientist and answered many questions about going on a research vessel, working in a laboratory and the Arctic as my research area. During the online open campus of the university, I took part in a virtual speed dating of the *MARUM – Center for Marine Environmental Sciences* as one of the institutes of the university, and likewise presented my daily work as a scientist.

Science videos and podcast To give children the chance to do some experiments about the Arctic and Arctic sea ice at home, which was especially valuable during the pandemic, together with Johanna Hingst, Luisa von Albedyll and Valentin Ludwig, I produced three videos showing experiments with water and ice. These videos were published via the university during the digital children university, and were furthermore made available via the YouTube channel of ArcTrain. The videos

were used by one school class, which we later-on met (virtually) to discuss their observations and the connection to the real Arctic Ocean. The video in which I explain one of the experiments and the scientific background can be found here: `https://youtu.be/jcrbNOsg6-4`
Another video project I was part of was a project from the *MARUM – Center for Marine Environmental Sciences* in cooperation with the kindergartens of Bremen. A group of children from the kindergarten came to the institute and got insights into doing scientific research on marine science by doing some small experiments themselves. Together with my colleague Dr Julie Meilland, I showed them how to look through a binocular and study extremely tiny organisms. The children were impressed by the different shapes of foraminifera and other organisms like mollusks, and it was great to see how children younger than six years already can understand main concepts about the ocean and its organisms. The video, showing the visit of the children and explaining why it is valuable to give already young children the chance to visit a research institute and to trigger their curiosity, is available here: `www.kita.bremen.de/aktuelles/projekte-kooperationen/naturwissenschaftliche-bildung-23412`
An online format, mainly run by scientists from the Alfred-Wegener-Institute for Polar and Marine Research, is the YouTube channel *Science for the living room (Wissenschaft fürs Wohnzimmer)*. In this format, scientists give live talks about their research on YouTube, so people can watch it from home. I gave a talk about planktonic foraminifera and their role for the carbon cycle and followingly answering questions from the audience. This video is available on YouTube: `https://youtu.be/Nhf9y2M-REY`
Similar to videos, podcasts are an important online medium nowadays. I got the chance to give an interview in *The Science Pawdcast*, a podcast interviewing scientist from all over the world every week, giving insights on how people get involved in science, what their research is about and why it is important. I introduced my work as a PhD student in this format. Later-on, I got in touch with the host of the podcast again, who started Twitter live talks twice a week on top of the recorded podcast. I was invited to one of these live sessions, and once more talked about my research work and motivation as a scientist. The podcast interview was already interesting, but the live talk was even more exciting, as people listening could ask questions directly, which shows me that they are really interested in learning more.

The podcast episode is available here: `https://bunsenbernerbmd.buzzsprout.com/413041/7404022-season-2-episode-52-2020-hot-or-not-cats-vs-dogs-and-franziska-tell-on-the-arctic-ocean`
And the recording of the live show here: `https://bunsenbernerbmd.buzzsprout.com/413041/10449953-spaces-unleashed-bonus-content-with-phd-candidate-fransika-tell-on-tiny-ocean-wonders`

Museum talks and exhibitions A place to reach a scientifically interested general public are (natural) museums. I participated in a “Soapbox Science” event in the climate exhibition of Bremerhaven (Klimahaus Bremerhaven), where I was standing in the exhibition area about the Arctic to give visitors an overview on the role of the Arctic climate for the regional climate in Northern Germany. It was really interesting to offer people, mostly children and their parents, the chance to ask me about more information than what is shown in the exhibition. People were not used to the format and mostly a little bit shy, but it was nevertheless an interesting experience and some curious questions were asked. I furthermore gave a talk about working with planktonic foraminifera and their role for the climate system in the overseas museum Bremen (Übersee Museum), and later-on in the city library of Bremen (Stadtbibliothek Bremen). For the national history museum of Münster (LWL Museum für Naturkunde), I gave an interview about doing scientific research on the climate with samples from the ocean and about climate change, which was exhibited in line with photographs and material provided by *MARUM – Center for Marine Environmental Sciences* in a special exhibition about the climate (15.06.2022 - 14.01.2024).

FIGURE D.1: One of the self-drawn schematics about "Living beings and vegetation in the Arctic" for the digital online courses for school children. Visualizing the context of the group work focus seemed to be helpful, and the simple sketches encouraged them to add their own sketches to the image to show what they already know and what they are interested in learning more about during the course.

Science goes PUBlic A very special format to reach out to the general public is the project *Science goes PUBlic*. It is a format of short talks in pubs in Bremen and Bremerhaven giving people insights into scientific research. In this context, I once more gave a talk about planktonic foraminifera, how to analyse them and why studying them is relevant in the field of climate sciences. Talking in front of an audience without any presentation and in a dim room instead of the usual seminar rooms or lecture halls was a special experience. The most valuable of the format was to get in contact to the people directly after the talk. I was impressed about their curiosity and the many questions they asked about biology, climate change and many more.

Blogs about research experiences During the whole time period of my PhD, I was part of the ArcTrain blog team. The ArcTrain blog gives insights into scientific research of the international research training group on the Arctic Oceans, on the daily life of scientists and on connecting scientists from Germany and Canada. Articles are written in up to three languages (English, German, French). I have written several articles, and together with Lina Madaj and Valentin Ludwig and later-on with Simon Wett took care of editing and posting articles written by different ArcTrain members. In connection to that, I also helped managing the ArcTrain twitter account.

ArcTrain blog: `https://arctrain.de`
Twitter: `https://twitter.com/IRTG_ArcTrain`

Moreover, during a 2.5 months research stay in Montréal under the guidance of Dr Anne de Vernal, I have written a personal blog about my experiences in doing research at another institute and living in a foreign country. This blog can be found here: `https://www.marum.de/Franziska-Tell/Page11612.html`
Blogging is the least direct method of scientific outreach, and you often do not know how many people read the articles in detail. But it is a good training for writing in other than the scientific style, and both for the ArcTrain and my personal blog, I got feedback from people that were very interested in getting insights in the experiences of scientists.