Meilland et al. present an interesting study on the population dynamics of modern planktic foraminifera in the Western Barents Sea. As planktic foraminifera are a sensitive indicator of environmental changes in the Arctic, a region particularly affected by global temperature changes, the authors address a relevant scientific question within the scope of BG. The authors use a novel multiproxy approach combining the use of plankton net, core-top, molecular biology, environmental parameters and phytoplankton characterization. The manuscript has certainly been improved in response to the previous referees' comments. However, in my opinion, it still needs some minor revisions. I further suggest that the manuscript is read and corrected by an English native speaker or a professional author service due to numerous linguistic issues, only some of which I have listed below. In some places, they make following the manuscript difficult. I am looking forward for the authors' response and further discussion.

A: First of all we would like to thank the reviewer for her/his very helpful and constructive comments. The manuscript has been checked by two native English speaker and improved. We hope this new version of it will be satisfying.

# General comments:

Your vertical plankton hauls sampled only the uppermost 100 m, while for example, N. pachyderma can live as deep as 280 m (Greco et al., 2019). This might perhaps partly explain the discrepancy between living and fossil assemblages and should be discussed in the manuscript.

A: we sampled down to 700 m depth for 7 of the 9 studied stations and found very low abundances below 100 m depth (<5 ind.m<sup>-3</sup>) including for *N. pachyderma* abundances (< 1.25 ind.m<sup>-3</sup>). We added this information to the manuscript and will make those counts available on Pangea as well.

The authors interchangeably use terms such as "fossil assemblages", "core-top assemblages" or "assemblages in surficial sediments". It is not clear whether all these terms mean the same or not. Please be more consistent in using these terms.

A : we went through the manuscript and change terms in order to be consistent.

Another issue is that some information given in Material and Methods are repeated in the Results (see specific comments below but please also check the entire manuscript for repetitions).

A : we removed these sections from the results

Specific/technical comments:

Keywords: I suggest adding "planktonic foraminifera" as a keyword

A: We added "planktonic foraminifera" in the keyword

# 1. Introduction

The introduction is somewhat mixed-up. Paleoceanographic information is mixed with modern assemblage studies, habitat depth mixed with seasonal variability, foraminifera with other

organisms... In some places, too much details is given (e.g., 104 tow hauls in Greco et al. 2019). Suddenly the Southern Indian Ocean pops out... Please consider rewriting to better structure this section.

A : we worked on the introduction in order to structure it better and keep what we consider important information.

40: Add a comma after "As a response"

A: comma added

45-46: Either "Such phenomenon (...) is" or "Such phenomena (...) are"

A: correction made

48-51: I suggest deleting the sentence "Eynaud (2011) noticed..." as irrelevant to the study of modern assemblages.

A: we deleted the sentence

54: Change "observed PF by the means of plankton tows," to "analyzed PF collected with plankton tows". Please note that Pados and Spielhagen (2014) analyzed both forams living in Polar and Atlantic waters and used both plankton tows and core top samples.

A : we replaced the sentence

73: Change "planktonic foraminifera" to PF (be consistent in using the abbreviations that you introduced)

A: correction made

79: Change "planktonic foraminifera from a same species" to "PF of the same species"

A: correction made

2. Oceanographic setting

84: Change "Spitsbergen Banken and shallow Bjørnøya; Storfjordrenna and Bjømøyrenna glacial troughs" to "Storfjordrenna and Bjørnøyrenna glacial troughs separated by shallow Spitsbergen Banken". Please verify if it's Spitsbergen Banken or Spitsbergenbanken.

A: we made the corrections L.91 and after verification in the literature, decided to use Spitsbergenbanken (correction also made L.102 for this term)

87: Nothing is written about the currents carrying Arctic Water to the study area.

A: Indeed we didn't mention Arctic Water in the paper as none of the discussed samples were collected in this water layer. Arctic Waters were only encountered twice during the cruise and mixed with NwAW (Giraudeau et al., 2016).

From 88 onwards: To my understanding, the Oceanographic section should only contain the state-of-the-art on the subject. If the authors performed some oceanographic measurements, please move the information to "Material and Methods" and "Results" sections.

A : we changed these sections of the manuscript accordingly

98: "above described" => "described above"

A: correction made

3. Material and Methods

112 and elsewhere: You use either "Spitsbergen", "Spitzbergen" or "Spitzberge". Please unify. To my knowledge, "Spitsbergen" is the English spelling, while "Spitzbergen" is German and "Spitzberg" French.

A: we thank the reviewer for this observation and unified using Spitsbergen

118: Change "collection" to e.g., "sampling strategy"

A: we amended following the reviewer's comment

124: "All living PF" – if they were preserved with ethanol, they were not living anymore. Change to, e.g., "All foraminiferal tests containing coloured cytoplasm ("living")...". Where the samples stained with Rose Bengal? If so, this should be mentioned. Otherwise, how were they coloured?

A: the net samples were not stained and individuals that was living at the moment of the sampling (the one we call "living") were distinguished by the natural coloration of their cytoplasm. We therefore choose not keep this sentence intact.

130: "separately numbered" => "counted separately"

A: correction made

137: "Individual" => "The individuals"

A: correction made

146: Referee#2 suggested using "core-top" instead of "subfossil". I think it also concerns the term "fossil".

A : we disagree and would prefer to keep fossil here.

147: INSU<sup>1</sup> – please check if the journal accepts footnotes.

A: we removed the footnote and place detailed the accronym INSU directly in the text.

149: Delete "the more horizontal" – something is horizontal or not, it can't be more or less horizontal.

# A: we replaced horizontal by "even"

149-150: Change "The core-top sediment (0- 0.5 cm slice)" to "The uppermost 0.5 cm of the core"

# A: we replaced following the Reviewer's suggestion

152-156: Please rewrite the two sentences so that they are more related to each other.

A: this section has been modified

# 4. Results

162: CTD, not CDT! "5 values" – what values? Please specify.

# A: correction and specification made

163-166: The paragraph gives absolutely no information about the results and most (if not all) the info were already given in the methods.

A: the paragraph has been slightly rewritten but kept as we think it provides guidance to the reader.

169: The highest PF concentrations were found at the edge of the NwCW range (station 7) so I would refrain from saying that the highest concentrations were found in NwCW.

A: we changed the sentence to precise highest concentrations were found at the edge of the NwCW.

173: It should be specified which species are considered polar and which subpolar by the authors.

A: We used the SCOR WG138 taxonomy for this study where only *N. pachyderma* is described as a polar species. As the used taxonomy is mentioned in the Material and Methods, we would rather not comment on it in this section.

188: "analyse" => "analysis" or "analyses"

# A: corrected

194-195: The information in brackets was already given in the methods and is unnecessary here.

# A: we removed the breckets

195: "successfully" – I assume you wouldn't mention them at all in the manuscript if they were unsuccessful.

A: we removed "successfully"

204: Is it exactly equal (down to  $0.00000001 \mu m$ ) or close enough to saz that the siye distribution of the picked tests is szmmetric?

A : we added precisions to the text

206:  $\mu m => \mu g$ 

A: correction made

207:  $\mu g => \mu g/\mu m \text{ (or } \mu g^* \mu m^{-1})$ 

A: correction made

209: "slightly (but not significantly)" – this is not very specific, please rephrase by, e.g., giving some numbers

A: we mentioned the Figure 6 once again here.

212-215: This was already written in the methods.

A: we removed it from this section

217: Please add station numbers to Figure 7.

A : Figure 7 amended

218: I would rather write that N. pachyderma was the most abundant species. Dominance suggests that it reached >50% which is the case only in one station.

A: we agree with the Reviewer and corrected

5. Discussion

234-236: I don't understand the sentence. Please rephrase.

A: we changed the sentence

238: In my opinion, low abundances at the two ends of the transect do not suggest patchiness. Low abundances in the middle of the transect would suggest it.

A : we disagree with the reviewer

274: Shouldn't it be station 7 instead of 8?

A: we made the correction

275: The location of the Polar Front should be marked in Figure 1.

A: we prefer to keep Figure 1 as simple as possible and would rather not add the location of the Polar front. We cited Oziel et al., 2017 here, presenting very accurate data for it. Moreover, our transect don't cross the polar front.

# 6. Conclusions

363-365: Please specify that the percentages concern the living (plankton haul) population.

A : we provided this additional information

A: we did the correction

# Population dynamics of modern planktonic foraminifera in the western Barents Sea

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Abstract. This study reports on diversity and distribution of planktonic foraminifera (PF) in the Barents Sea Opening (BSO). Populations of PF living in late summer (collected by means of stratified plankton tows) and recently deposited individuals (sampled by interface corer) were compared. High abundances reaching up to 400 ind.m<sup>-3</sup> in tow samples and 8000 ind.cm<sup>-3</sup> in surface sediments were recorded in the centre of the studied area while low abundances were observed in coastal areas, likely due to continental influences. The living and core-top assemblages are mainly composed of the same four species Neogloboquadrina pachyderma, Neogloboquadrina incompta, Turborotalita quinqueloba and Globigerinita uvula. The two species G. uvula and T. quinqueloba dominate the upper water column, whereas surface sediment assemblages display 20 particularly high concentrations of N. pachyderma. The unusual dominance of G. uvula in the water sample assemblages compared to its low proportion in surface sediments might be the signature of 1) a seasonal signal due to summer phytoplankton composition changes at the BSO, linked to the increase of summer temperature at the study site, and/or 2) a signal of a larger time-scale and wider geographical reach phenomenon reflecting poleward temperate/subpolar species migration and consecutive foraminiferal assemblage diversification at high latitudes due to global change. Protein concentrations were measured on single specimens and used as a proxy of individual carbon biomass. Specimens of all species show the same trend, a northward decrease of their size-normalized-protein concentration. This suggests that foraminiferal biomass is potentially controlled by different constituents of their organelles (e.g. lipids). The coupling of data from plankton tows, protein measurements and surface sediments allows us to hypothesise that PF dynamics (seasonality and distribution) are decoupled from their metabolism.

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5 Keywords: planktonic foraminifera, living and dead communities, latitudinal distribution, protein content, seasonality, atlantification, Barents Sea

#### 1 Introduction

Polar areas are sensitive to global temperature changes, particularly in the Arctic where warming occurs faster than in the rest of the world and has accelerated over the past 50 years (Shepherd, 2016). This Arctic amplification appears to be mainly caused by sea-ice loss under increasing CO<sub>2</sub> (Dai et al., 2019). Recently increased advection of Atlantic Water into the Barents Sea modifies its physico-chemical properties (Smedsrud et al., 2013), which directly affect the entire cosystems in the region. Higher temperatures lead to increased rates of planktonic primary production (Vaquer-Sunyer et al., 2013) and increased CO2 concentrations are expected to have a fertilization effect on marine autotrophs (Holding et al., 2015). Not only is productivity increasing, but spring and summer blooms are also occurring earlier in the European Arctic Ocean (Oziel et al., 2017). As a response, some taxa of calcifying groups (i.e. foraminifera, coccolithophores, molluses and echinoderms; Beaugrand et al., 2013) exhibit a poleward movement in agreement with expected biogeographical changes under sea temperature warming. Both satellite images (Smyth et al., 2004; Burenkov et al., 2011) and in situ measurements (Dylmer et al., 2013; Giraudeau et al., 2016; AMAP 2018) have shown rapid expansion of temperate species of coccolithophores in the Arctic. For example, Emiliania huxleyi shows a striking poleward shift (>5°) in the distribution of its blooms (Neukermans et al., 2018). This phenomenon, called "atlantification" (Årthun et al., 2012), is expected to impact every trophic level of the food web, from small phytoplankton, species (Neukermans et al., 2018) to larger organisms (Dalpadado et al., 2012). Recent studies have investigated the ecology and biodiversity of planktonic foraminifera from the high-latitude North Atlantic (e.g. Schiebel et al., 2017). The species N. pachyderma comprises more than 90% of recent assemblages (i.e. found in surface sediments) from the Polar Region, North of Iceland (Kucera et al., 2005). Rather few studies on living planktonic foraminifera (PF) communities 65 have focussed on (sub-) Arctic regions. Plankton tows also show that N. pachyderma is dominant species in Arctic (~90%) followed by T. quinqueloba (5%) (Volkmann, 2000; Pados and Spielhagen, 2014), Through the compilation of population density profiles from 104 stratified plankton tow hauls collected in the Arctic and the North Atlantic Oceans, Greco et al. (2019) investigated the ecology of N. pachyderma. In particular, the variability of its habitat depth, and underlined the knowledge gap on its ecological preferences. In the western subpolar North Atlantic (Irminger Sea), the production of N. pachyderma shows two peaks, in spring and late summer, while winter shows a low production (Jonkers et al., 2010; 2013). The diversity of PF has increased in polar waters over the past decades, even though it remains low in comparison to lower latitudes, due to the poleward migration of warm-water species (Schiebel et al., 2017). A similar process appears to occur in the southern hemisphere (Meilland et al., 2016). Some species from lower latitudes are described as new components of poleward assemblages. The shift of PF assemblages to warmer conditions, since the pre-industrial stage, has been very recently 75 highlighted more globally in the Northern hemisphere (Jonkers et al., 2019). These major modifications in PF distribution patterns display changes more related to primary production than to water temperature itself (e.g. Jonkers et al., 2010; Schiebel

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Supprimé: Eynaud, (2011) noticed that the species N. pachyderma, the most characteristic high-latitude taxon, dominates the past interglacial assemblages for the last 1.8 Ma. while the subpolar species Turborotalia quinqueloba records northward penetration of Atlantic warm water masses in the Arctic, especially during interglacial periods.

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Supprimé: observed PF by the means of plankton tows, in the cold and fresh Polar waters of the Fram Strait during early summer. They report a large dominance of N. pachyderma and a co-occurrence of T. quinqueloba, accounting for 90 and 5% of all tests, respectively. Volkmann, (2000) also documented this large dominance of N. pachyderma and the co-occurrence with T. quinqueloba, overall in the Arctic

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et al., 2017). Planktonic foraminifera, being sensitive to ambient water geochemistry, are considered good indicators of the polar changing environments (Schiebel et al., 2017). More studies on living PF communities in the Arctic regions are needed to assess the spatial and temporal variability in their population dynamics and to better constrain the today's polar and subpolar species ecological preferences.

Taking the opportunity of a cruise dedicated to the exploration of the physical oceanography of the western Barents Sea (MOCOSED 2014 cruise), we investigated the connections between the spatial variability of living PF, phytoplankton communities (Giraudeau et al., 2016), and the hydrological system through a South-to-North transect, between Northern Norway and Spitsbergen [68-76]°N. Along this transect, we compared PF living faunas (from plankton tow) to the assemblages found on the sea floor (from core-top sediments) in order to investigate eventual recent changes in their population dynamics.

130 This latitudinal transect also gave us the opportunity to quantify protein concentrations of individual living PF in this area for the first time and along a physico-chemical gradient to see if and how it varies and explore how planktonic foraminifera from a same species may adjust to different environments.

## 2. Oceanographic setting

The studied area covers the western Barents Sea margin, i.e. Barents Sea Opening (BSO), where the surface and intermediate ocean circulation, are characterised by the confrontation of the North Atlantic and the Arctic Waters (Figure 1). The seasonal and interannual dynamics of these two water masses, interacting with the complex topography of the western margin (Storfjordrenna and Bjørnøyrenna glacial troughs separated by shallow Spitsbergenbanken), determine the position of the Polar Front (Loeng, 1991). The Norwegian Atlantic Current (NwAC) carries Atlantic Water into the Barents Sea. Along the western Barents Sea margin, Atlantic Water is transported to the Fram Strait by the West Spitsbergen current (Skagseth et al., 2008; Oziel et al., 2017; Figure 1).

In the southern part of the transect a strong thermohalocline clearly underlined a surface mixed layer of about 30-35 m depth.

This cline slightly deepened northwards and blurred out north of 74.5°N where no stratification was observed in the water column. From South to North of the transect: i) high temperatures and low salinities reflected the Norwegian Coastal Water (NwCW), which is also enriched in Chl-a. The relatively warm NwCW (8.5 to 11°C) extended northwards up to 74.5°N overlying the colder Norwegian Atlantic Water (NwAW). Less saline (33.5) to the South, NwCW became saltier (34.9) in the vicinity of the Spitsbergenhanken; ii) at the northern end of the transect, the NwAW penetrated the Barents Sea through the Storfjordrenna trough with temperatures from 6 to 8°C and an open marine salinity of 35.1 (Giraudeau et al., 2016).

The Chl-a content followed the hydrological pattern described above (Figure 2 c). Relatively high concentrations (mean ≈ 0.8 mg.m³) were located in the surface mixed layer composed of NwCW. The highest values around 1.25 mg.m³ were recorded off the Norwegian coast. Chl-a content decreased northwards (north of 74.5°N) and reached ≈ 0.4 mg.m³ in the upper layer (0-60m) of the well-mixed NwAW. The composition of the phytoplankton community observed in surface water at 7 stations along the studied transect was essentially dominated by three algal groups; Fuco-flagelattes (25 to 43%; major component Phaeocystis pouchetii), Prasinophytes (15 to 30%; major components Micromonas pusilla and Bathycoccus pusilla) and

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Prymnesiophytes (13 to 24%; major component *Emiliana huxleyi*) (Giraudeau at al., 2016). Three other features are noteworthy (Figure 2 d): i) the dominance of dinoflagellates (24%) at the southernmost station of the transect (close to the Norwegian coast) contrasted with their total absence in the well mixed NwAW, North of 74.5; ii) the presence of diatoms (10-20 %) in the surficial NwCW, but rare (<5%) to the North; iii) the constant increase in relative abundance of Cyanobacteria from < 5% to more than 15% along the South-to-North transect.

3. Material and Methods

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In late summer 2014, from August 8 to September 20, the SHOM (French Hydrographic Office) operated the oceanographic cruise MOCOSED 2014, on board the "R/V *Pourquoi pas2*". Along a 700 km South-to-North transect from the Norwegian (68°N) to the Spitsbergen (76°N) coasts, investigations of hydrological processes at the BSO were carried out coupled with the exploration of the phytoplankton and foraminiferal communities using a total of 32 vertical casts deployed  $\approx$  20 km apart from each other (Figure 1 and 2).

# 3.1. Living planktonic foraminifera from stratified plankton samples (MultiNet)

Living PF were collected at 7 of the 32 CTD South-to-North transect stations (#3 to #9), and at 2 stations (#1 and #2) located West-to-East ≈ 20 km apart from the central point of the main South-to-North CTD transect (Figure 1; Table 1), using a 185 stratified plankton tow (MultiNet Hydro-Bios type Midi, opening of 0.25 m<sub>s</sub><sup>2</sup>) equipped with five nets (mesh size 100 μm to avoid nets clogging in case of intense phytoplankton bloom). This sampling strategy was used in order to observe the potential effect of latitudinal changes but also of bathymetry, longitudinally, on PF distribution. At each station, one vertical haul sampled five successive water layers from the sea surface to 100 m depth. A second hauls has been deployed for the stations 1, 3, 4, 5, 6, 7 and 8, to collect material down to 700 m depth (Table 1), For each of the depth intervals (0-20 m, 20-40 m, 40-60 m, 60-80 m, 80-100 m; 0-100 m, 100-200 m, 200-300 m, 300-500 m and 500-700 m), the filtered water volume was measured by means of a flowmeter attached to the MultiNet mouth. Each MultiNet sample was preserved in a 250 mL vial with ethanol (90%) buffered with hexamethylenetetramine until processing at the land-based laboratory. Back at the laboratory, MultiNet samples were washed over a 100 µm mesh, all foraminifera were removed from the sample and dried in an oven at 50 °C. All living PF, distinguished by their coloured cytoplasm visible through the shell, were picked, stored in counting cells and identified at the species level, following the SCOR WG138 taxonomy as implemented in Siccha and Kucera (2017). Empty tests, considered as dead individuals were counted separately. Correlations following a non-metric multidimensional scaling ordination (NMDS) were carried out with the R package Vegan (Oksanen et al., 2013). Using the Bray-Curtis distance these correlations were tested between PF species absolute concentrations, the latitude of the station and parameters of the ambient waters (temperature, salinity, Chl-a concentration). Results are given in relative abundances (% of the total, live or dead fauna) or in absolute abundances in number of individuals per m<sup>3</sup> of filtered water (ind.m<sup>-3</sup>).

Protein biomass and test size measurements

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For protein extraction and measurement, a few living individuals (≈60) were picked on board from out of the shallowest water samples at stations 3 to 9 immediately after sampling. Only shells that were completely filled with cytoplasm were selected. After picking, individuals were immediately cleaned with a brush and filtered seawater to remove all particles, including organic matter, that were stuck to the test. The individuals were stored in a 1.5 mL Eppendorf vial and analysed on board, using the bicinchoninic acid (BCA) method as explained in Meilland et al., (2016). Morphometric analyses on single foraminiferal tests were carried out at the University of Angers with an automated incident light microscope (Bollmann et al., 2004; Clayton et al., 2009) at a resolution of 1.4 μm². Images were analysed for their two-dimensional (silhouette) morphometry (Beer et al., 2010), including minimum test diameter, which is the shortest distance from wall to wall that passes through the centre of the proloculus (the initial chamber of a foraminifer). Protein-to-size relations were determined for the minimum diameter of each test providing size-normalized protein content (SNP) for data analyses. Foraminifera protein concentrations were linearly normalized to 1 μm minimum test diameter, being aware of any unavoidable errors related to non-linear increments of biomass at volumetric test growth (cf. Beer et al., 2010).

## 3.2. Fossil planktonic foraminifera assemblages from core-tops (Multitube)

230 At 5 sites of the main CTD transect, an interface corer (Multitube type Oktopus GmbH, Institut National des Sciences de l'Univers, division of Brest, France) was used to obtain simultaneously 8 short sediment cores (less than 1 m in length) (Figure 1; Table 1). At each station, the core with the more even and undisturbed water-sediment interface was selected. The uppermost 0.5 cm of the core, was sampled and fixed with 95 % ethanol. Samples were stained with Rose Bengal, reacting with cytoplasm, to distinguish PF still bearing cytoplasm (fresh or in degradation) and thus very recently deposited from sossil PF without cytoplasm. Stained shells of foraminifera probably reflect the spring and summer population of the year of sampling, even though the exact degradation time of cytoplasm is still poorly constrained (Schönfeld et al., 2013). The core-top sediments were wet sieved using a 100 µm mesh and the foraminifera were identified using the same SCOR WG138 taxonomy in order to be directly comparable to the plankton tow samples.

# 4. Results

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## 4.1. Planktonic foraminifera diversity and distribution in the water column

Data from the 7 stations of the South-to-North CTD transect with 5 depth values per station, were compiled to display the repartition of PF absolute abundances (for total assemblage and species-specific) in the upper 100 meters of the vertical section across the BSO. Abundances of living specimens below 100 m depth were very low (total concentration <5 ind.m<sup>3</sup>) and are therefore not discussed. Data from station 1 (Western) and station 2 (Eastern) located 20 km on either side of the S-N transect, were compared to the data of station 6 at the middle of the transect.

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Supprimé: thus we cannot be precise on the time-scale pointed out by Rose Bengal-stained specimens. Based on the hydrology, sites depth (Table 1), and sediment oxidation over the studied area, we can reasonably think that Rose Bengal coloration is in our situation highlighting spring and summer population that recently felt. The discussion will be based on this assumption.

For the purpose of this study, the core-top sediment has been wet sieved on a 100 µm mesh (same as the plankton net mesh size), and analysed for the planktonic foraminiferal assemblages. Every picked planktonic foraminifer has been identified consistently with those collected by plankton tows.

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Total concentrations of living PF fauna varied between 0 and 400 ind.m<sup>-3</sup> (Figure 3). Along the South-to-North CTD transect, the highest concentrations were all observed above 20 m water depth, in the surface mixed layer of the well stratified water area, i.e. at the edge of the NwCW. The two stations located at the south and north extremities of the transect (# 3, off the Norwegian coast, and #9, off the Spitsbergen coast) displayed low densities (10 to 50 ind.m<sup>-3</sup>). At station 1, located above the Barents Sea margin slope, the maximum abundance of 220 ind.m<sup>-3</sup> was recorded in a deeper habitat (20-40 m, Figure 3). Station 2, located inside the Barents Sea, was very poor in PF (<10 ind.m<sup>-3</sup>). In total, 10 species were observed. The studied area was characterised by high abundances of subpolar to polar species (Figure 4), listed in descending order: Globigerinita uvula (45%), Turborotalita quinqueloba (26%), Neogloboquadrina incompta (15%) and Neogloboquadrina pachyderma (9%). There was a notable presence of the temperate water species Globigerina bulloides (3%), and negligible percentages (<1%) of Globigerinita glutinata, Neogloboquadrina dutertrei, Globigerinoides ruber, Globigerinoides sacculifer and Orcadia riedeli.

In the surface waters of the South-to-North transect (0-20 m depth), except at the septentrional station 9, *G. uvula* was the most abundant species reaching 64 % of the total fauna at station 7. The second most abundant species, *T. quinqueloba* dominated the PF fauna only at station 9, with 45 % of the total assemblage and 26 ind.m<sup>-3</sup>. Both *G. uvula* and *T. quinqueloba* have a patchy repartition with two patches of maximum abundances located in the first 0-20 m, at station 4 and 7 for *G. uvula* (175 and 245 ind.m<sup>-3</sup>, respectively) and at station 5 and 7 for *T. quinqueloba* (53 and 80 ind.m<sup>-3</sup>, respectively). The northern and common patch for both species is the more intense. In the 20-40 m deep layer at station 1 (West of the transect), these two species showed also relatively high concentrations (121 ind.m<sup>-3</sup> for *G. uvula*, and 30 ind.m<sup>-3</sup> for *T. quinqueloba*). The two other major species *N. pachyderma* and *N. incompta* and similarly low relative abundances (4 to 22%, and 8 to 25%, respectively). For both species, maximum absolute abundance of about 40-45 ind.m<sup>-3</sup> occurred in the central part of the transect between [72-74°N].

The NMDS analysis of species abundances with regard to environmental parameters (latitude of the station, temperature, salinity, Chl-a concentration) indicates that none of the species-specific distribution displays a significant correlation to any of the tested variables (p-values > 0.1). NMDS documents distributional affinity (Figure 5), with N. pachyderma and N. incompta plotting in the same area and T. quinqueloba and G. uvula plotting separately from each and also from the N. pachydermatN. incompta area.

# 4.2. Planktonic foraminifera protein biomass

315 Individual protein content (BCA method) and associated test minimum diameter were measured for a total of 272 specimens of the 4 major species, including 32 specimens of Neogloboquadrina pachyderma, 58 Neogloboquadrina incompta, 72 Globigerinita uvula and 110 Turborotalita quinqueloba. A 5 to 25 individuals per species were selected at each sampled depthinterval of the 7 stations along the S-N transect, paying careful attention to sample the whole size range of the populations. At

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station 7, the protein extraction was successful for only one specimen of *N. pachyderma*. Therefore, no value is display for this species at this station in Figure 6.

Minimum diameters of the 272 selected tests cover a large size range, from 65 to 315 μm with a median value of 160 μm. *N. incompta* is the biggest species with a median of 200 μm, and *G. uvula* the smallest with a median of 110 μm (Table 2). For each studied species, the mean size is close enough to the median size to say that the size distribution of the picked tests is symmetric, thus making us confident that our test selection represents properly the natural test size range of each studied species. The biomass of a single individual normalized by its test size (SNP), averages out about 0.0055 μg of protein per μm of foraminiferal shell diameter. It varies depending on species from 0.0004 (*G. uvula*) to 0.0426 μg μm. (*T. quinqueloba*). The SNP of all 4 species displays a porthward decrease from 70 to 74° (Figure 6). *T. quiqueloba* and *G. uvula* have slightly (but not significantly) higher relative protein concentrations than *N. pachyderma* and *N. incompta* (Figure 6).

## 4.3. Planktonic foraminifera diversity and distribution in surface sediments

355 Concentrations of planktonic foraminifera with colourless empty tests varied from a maximum of 6200 ind.cm<sup>-3</sup> at station 4 (71.3°N) to a minimum of 200 ind.cm<sup>-3</sup> at the septentrional station 9 (Figure 7 a). Neogloboquadrina pachyderma was the most abundant species (31 to 59%) along the entire transect. Assemblages were more mixed at the two ends of the transect where N. pachyderma was less abundant. The assemblage at the southernmost point also contained Turborotalita quinqueloba (33%) and Neogloboquadrina incompta (24%). While at the northernmost point, station 9, T. quinqueloba (23%) co-occurred with Globigerinita uvula (25%).

Concentrations of planktonic foraminifera bearing a coloured cytoplasm (Figure 7 b) varied from 100 to 300 ind.cm<sup>-3</sup>. All along the transect, the relative abundance of <u>coloured</u> *N. pachyderma* remained between 10 and 26 %. The species *T. quinqueloba* occurred everywhere above 20% and up to 40% South of 72°N. The central station 6 was <u>dominated by *G. uvula*</u> (38%). North of 74°, the fauna was balanced between *N. incompta* (33 and 9 %) and *G. uvula* (8 and 34%).

## 5 5. Discussion

Distribution pattern of living planktonic foraminifera at the Barents Sea Opening

In the late summer of 2014 the hydrology at the BSO was characterised, by a strong water stratification with a 30 m thick Chla enriched lens of NwCW that to the north overlapped with the NwAW (saltier and colder) from 69.8°N to 74.5°N. Further north, a well-mixed water column with characteristics of the NwAW occupied the Storfjordrenna Trough. Here a coccolithophore bloom and the highest concentration of cyanobacteria were recorded in the upper water column (Giraudeau et al., 2016). Despite these marked features the pattern of planktonic foraminifera abundance did not correlate with any of the studied environmental parameters (Figure 5). These observations confirm the low influence of commonly imputed parameters Supprimé: represent

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Supprimé: Interface undisturbed cores were retrieved from 5 stations of the South-to-North CTD transect (Table 1) to investigate the core-top sediment (0-0.5 cm slice). The dead PF assemblages were studied making the difference between Rose Bengal-stained showing recently dead individuals still bearing a non-degraded cytoplasm after post-mortem deposition, and colourless empty tests of individuals dead for longer periods of time. §

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such as temperature, salinity and primary production on PF density (Schiebel et al., 2017). In accordance with the conclusions of Retailleau et al., (2018) conclusions, multiples indications, however suggest a possible role of water turbidity in PF abundance variation. The highest densities of PF occurred in the 0-20m upper water layer between 70.5 and 74.5°N. Their very low abundances (total concentration < 5 ind.m<sup>-3</sup>) below 100 m depth suggest a shallow depth habitat for individuals in the region, especially for *N. pachyderma* which was recently reported to live between 25 and 280 m depth in the north Atlantic Arctic region (Greco et al., 2019). Very low abundances were also recorded nearby the Norwegian and Spitsbergen coasts. The low abundances at the two ends of the studied transect could reflect planktonic foraminifera patchiness pattern of distribution (Meilland et al., 2019) or highlight the fact that waters under continental influences (nutrient-enriched, more turbid) likely hamper the foraminiferal production. In line with this, the abrupt decrease in abundances from West to East (stations 2, to 6, to 1) may be ascribed to the decrease in depth of the Bjømøyrenna Trough up to the Barents Sea shelf (from 1850 to 430 m), as foraminifera are suspected to avoid neritic waters over continental shelves (Schmuker, 2000).

The remarkable point of our results is the dominance of Globigerinita uvula. This species, described as a temperate to polar species (Schiebel and Hemleben, 2017), is known to account for less than 2% of the assemblages in marginal Arctic Seas based on material collected with a 63 µm plankton net mesh size (Volkmann, 2000). Neogloboquadrina pachyderma is considered the dominant species in polar regions, making up more than 90% of the total planktonic foraminifera assemblages (e.g. Schiebel 420 et al., 2017). The high densities of G. uvula recorded at the BSO in 2014 seem to contradict the former statements but are consistent with a recent study reporting G. uvula as one of the dominant species in southern high latitudes, South of the Polar Front (Meilland et al., 2017). A possible explanation could be the warming experienced by the western Barents Sea (SST anomalies  $\approx +2^{\circ}$ C) and its increase in salinity (SSS anomalies  $\approx +0.3$ ) over the last decades (Dobrynin and Pohlmann, 2015). These hydrological changes impact the plankton dynamics and biogeography, with a northward shift of the natural range of biological communities (Barton et al., 2016). Thus, the species distribution of planktonic foraminifera could be affected by an eventual expansion of subpolar/temperate species towards high latitudes leading to phytoplankton composition changes, in response to sea temperature warming under global climate change. Our observations from the North Polar Region support the shift of planktonic foraminifera assemblages to warmer conditions already asserted from North Atlantic (Jonkers et al., 2019) and from the southern Indian Ocean data (Meilland et al., 2017). However, a single observational dataset is the Barents Sea is not sufficient to robustly validate this assumption and a second hypothesis for the dominance of G. uvula in our sampling area could be a response to specific phytoplankton composition and ambient water conditions by pulsed reproduction events only in summer conditions. This seasonal pattern is known to occur in polar regions for Turborotalita quinqueloba (Schiebel and Hemleben, 2017). In fact, this species is the second dominant one in our late summer 2014 samples. As observed in this study, T. quinqueloba is also known to display high concentrations in the Barents Sea and western Spitsbergen (Volkmann 2000) and to co-occur with the typically polar species Neogloboquadrina pachyderma in the high-latitude cold-water assemblages (Volkmann, 2000; Eynaud, 2011).

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Discrepancy between the species-specific distribution patterns was observed in late summer 2014 at the BSO. The low abundances of *Neogloboquadrina pachyderma* and *Neogloboquadrina incompta* consistent over the studied area versus the patchy distribution and high densities of *Globigerinita uvula* and *Turborotalita quinqueloba*, suggest differences in the ecological strategy and behaviour between these two pairs of species. The patchy pattern of planktonic foraminifera distribution has been observed before (Boltovskoy, 1971; Siccha et al., 2012; Meilland et al., 2019) suggesting that high densities are not exclusively constrained by the physical structure of the (sub-) surface layers.

Potential differences in diet preferences could explain the observed species distribution in late summer 2014 at the BSO. Both *G. uvula* and *T. quinqueloba* are thought to follow food availability and primary production (Volkmann 2000, Schiebel and Hemleben 2017). However, we observed no correlation between their distribution and Chl-a concentrations (Figure 5). In late summer 2014, *G. uvula* and *T. quinqueloba* showed high concentrations especially at station 7, located at the crossroads of the Atlantic (NwAW) and Arctic waters flowing out of the Storfjordrenna (Figure 1), at the edge of the polar front (Oziel et al., 2017). From this location to the northern station, the concentration of phytoplankton was relatively low and the phytoplankton community showed singular characteristics, in comparison to the southern part of the transect: fuco-flagelattes became dominant and diatom concentrations decreased. The fuco-flagelatte blooms (mainly *Phaeocystis pouchetii* in late summer 2014; Giraudeau et al., 2016) are well known to occur in the Barents Sea (Wassmann et al., 1990; Vaquer-Sunyer et al., 2013). Our hypothesis is thus that high densities of *G. uvula* and *T. quinqueloba* are due to food composition (quality) rather than food concentrations (quantity). This also implies that satellite-derived chlorophyll concentrations, considered as potential indicators of algal bloom, may not always be good indicators to perceive foraminiferal concentration and distribution.

Planktonic foraminifera protein concentration, potential marker of their metabolism

Proteins are the main component of zooplankton biomass (Corg) in all oceanographic regions, from the tropics to polar areas (e.g., Percy and Fife 1981; Donnelly et al., 1994; Kumar et al., 2013; Yun et al., 2015). Their role is essential to organisms' growth and their concentration and composition likely reflect the environment individuals grew in and how well they adjust to it. Based on previous studies, the protein concentration of PF can be used as a proxy of its biomass (Corg) and foraminiferal biomass should remain the same for a given test size (Schiebel and Movellan, 2012). However, in our study, the SNP (size normalized protein content) of PF decreases with higher latitude and hence with decreased in Chl-a concentration and temperature. The size of individuals picked for these analyses remains however constant. This observation suggests that foraminifera metabolisms (i.e. ability to consume/degrade food and to grow) is decreasing towards the north. This would be consistent with the observation of lower metabolism for zooplankton with decreasing salinity and temperature in the Arctic (Alcaraz et al., 2010). Proteins are the main component of zooplankton biomass (Corg) closely followed by lipids. Lipids in zooplankton organisms are very variable geographically, showing a latitudinal pattern with high percentages in polar areas and low percentages in warm tropical waters. Lipids percentages, also display seasonal features, with higher values in summer than in winter (Falk-Petersen et al., 1999; Mayzaud et al., 2011; Kumar et al., 2013). It is thus possible that a part of energy (biomass

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/ C<sub>org</sub>) of the PF collected along the South-to-North transect shifts from being stocked as protein in warmer waters to being stocked as lipids in colder waters. This strategy would allow foraminifera to resist the cold to potentially overwinter. This hypothesis is supported by analogous observations made on different size fraction of zooplankton in the Southern Indian Ocean showing variability in protein and lipid percentages among the 80 to 200 µm populations (Harmelin-Vivien et al., 2019) and also by observations made on pteropods in the Arctic (Kattner et al., 1998; Phleger et al., 2001; Böer et al., 2005). The fact that higher SNP of foraminifera were observed where Chl-a is higher is compatible with the fact that polar organisms rely on their protein catabolism when food is easily accessible rather than on their lipid storage (Brockington & Clarke 2001). It has also been shown that a single organism in a cold environment is able to switch between predominantly protein or lipid catabolism across its life (Mayzaud, 1976). This suggests that individuals from the same species can display more or less proteins for the same biomass in different locations. With the reduction of PF protein concentration (and likely metabolism) going north, one could expect lower abundances. However, we observe no link between PF concentrations, which appeared to be species specific, and protein concentrations (evolving similarly for all four species) suggesting a decoupling between individuals metabolism and densities.

Discrepancy between upper water column and interface sediment samples

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The PF species compositions recorded during the late summer 2014 in the water column and in surface sediments are similar while species relative abundances are drastically different. Indeed, the living fauna (collected by plankton net) displays large relative and absolute abundances of the two species Globigerinita uvula and Turborotalita quinqueloba whereas the fossil assemblages (found in core-tops) are largely dominated by Neogloboquadrina pachyderma or, at the southernmost station, codominated by T. quinqueloba and N. pachyderma (Figure 7 a). Affected by differential settling velocities (200 and 500 m.day<sup>-1</sup> in normal conditions), water depth and test sizes of different species, the foraminiferal fluxes exported from the upper productive surface and reaching the sea bottom depend on direction and intensity of currents (Takahashi and Bé, 1984). Lateral advection may transport shells over long distances > 25 km for N. pachyderma and > 50 km for T. quinqueloba, respectively (Von Gyldenfeldt et al., 2000). Lateral advection of shells is also strengthened by water stratification that increases resident time at the shear boundary between water masses (Kuhnt at al. 2013). The BSO has a complex hydrography with the buoyant NwCW flowing northwards above the NwAW that is entering eastwards the Barents Sea when cold BSAW is flowing westwards. In such areas, the PF settling velocities and extension of lateral advection poorly constrained. Consequently, the sediment core records cannot match exactly with the place and/or the intensity of production (Von Gyldenfeldt et al., 2000; Jonkers et al., 2015). However, considering potential lateral advection of shells, Pados and Spielhagen, (2014) observed from a study through the dynamic Fram Strait that the distribution pattern obtained by plankton tows was clearly reflected on the sediment surface, and that the assemblage on the sediment surface can be used as an indicator for modern planktonic foraminiferal fauna. This suggests that the large discrepancy between upper water column and interface sediment samples collected at the BSO in late summer 2014 should be taken into consideration. As a sedimentation rate of  $1.3 \pm 0.6$  mm.yr<sup>-1</sup> has been recently measured in the Storfjordrenna outlet [76°N-17°E], close to our station 9 (Fossile et al., 2019), the core-top Supprimé: are supposed to Supprimé: his Supprimé: a Supprimé: a Supprimé: N Supprimé: densities Supprimé: surficial Supprimé: smear Supprimé: superposed Supprimé: present Supprimé: creeping Supprimé: are completely unknown Supprimé: aware of the eventual Supprimé: concluded Supprimé: upper

sediments may have recorded less than a decade. Even though sedimentation rates are likely to vary along the transect, we hypothesise that the sea surface-bottom differences in the foraminiferal assemblages along the South-to-North transect at the BSO might reflect a community change within a short period of time (about a decade).

Furthermore, the analysis of sediment from the 5 core tops demonstrated important differences between the assemblages of fossil fauna and recently settled tests (likely coming from surface Spring/Summer production), i.e. Rose-Bengal stained tests bearing not yet decomposed cytoplasm. For example, at 71.3°N, the percentages of coloured T. quinqueloba and G. uvula are twice as high as the ones observed for the fossil faunas (Figure 7). At 72.9°N in the surface sediment, G. uvula reaches up to 570 38% of the coloured assemblages (Figure 7 b) whereas it never exceeds 25% in the non-coloured ones (Figure 7 a). The high abundance of the two species G. uvula and T. quinqueloba in the living fauna as well as in the recently settled shells, but not in the fossil faunas suggest that they may present a seasonal character with a production period focussed in late summer as a response to environmental and trophic conditions. This is supported by previous studies in the Arctic where T. quinqueloba has been found to dominate assemblages sampled in August (Carstens et al., 1997; Volkmann, 2000) but not in June/ early 575 July (Pados and Spielhagen, 2014), and by sediment trap observations from the subpolar North Atlantic where T. quinqueloba reaches its maximum in autumn (Jonkers et al., 2010). The dominance of N. pachyderma in the fossil faunas collected at the BSO and its low but constant presence in the coloured shells of surface sediment and plankton tow sampled in late summer 2014 suggests that this species may demonstrate a regular production throughout the year. Neogloboquadrina pachyderma production appears to be yearly sustained and constant in the area whereas other species clearly respond to a local seasonal 580 signal.

## 6. Conclusion

The sampling and analytic approaches deployed during the MOCOSED14 cruise and combining the use of plankton net, coretop, molecular biology (protein measurement), environmental parameters and phytoplankton characterisation provides us with a unique dataset to better constrain the distribution of planktonic foraminifera within the highly complex studied area of the western Barents Sea.

The observed abundances of PF in the studied area are high offshore and the lower densities were recorded nearby the Norwegian and Spitsbergen coasts. These observations highlight the fact that waters under continental influences (nutrient-enriched, more turbid) are rather inhospitable for PF production. The PF species composition observed at the BSO is diverse, with more than 10 different species in the net samples including Globigerinita uvula (45%), Turborotalita quinqueloba (26.2%), Neogloboquadrina incompta (15%) and Neogloboquadrina pachyderma (8.9%). The two species G. uvula and T. quinqueloba dominate the living (water sample) population and display highly patchy abundances suggesting they occur in late summer in response to physico-chemical conditions and related specific primary productivity. The dominance of G. uvula in water samples could also be a signal of the temperature increase experienced over the last decades in the Barents Sea and

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the North Atlantic Ocean, Further sampling in the area is thus needed to <u>test</u> this hypothesis. The species *N. pachyderma* and *N. incompta* show low densities but a continuous distribution pattern in the water samples. They also dominate the core-top assemblages suggesting that both species present a more consistent production over the course of spring-summer season.

Unlike their species specific abundances pattern of distribution, size-normalized protein concentrations of all four major species decrease with the increasing latitude (and a decrease in temperature and Chl-a concentration). This observation leads us to hypothesise that 1) PF abundance and metabolism are decoupled and 2) foraminifera metabolism in the North of the studied region is lower than in the South. It opens the following question: Can individuals of the same species balance the ratio between their protein and lipid concentrations (major components of zooplankton Corg) in order to adapt to environmental conditions (e.g. temperature)? Further analyses on planktonic foraminifera lipid concentration and composition are thus needed and would help us to better understand the metabolism of these organisms and their fate in a context of climate change.

## Data availability

Data will be made available on request to the main author until their online publication on PANGAEA (https://pangaea.de/).

## 630 Author contributions

JM and HH designed the study. JM, VH, ID and JS generated the data and carried out the analyses. TG provided access to the MOCOSED 2014 cruise. All authors contributed to writing the manuscript.

## Competing interests

The authors declare that they have no conflict of interest.

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**Table 1:** Location (Latitude and Longitude), sampling date and water depth, of the 9 MultiNet and 5 Multitube stations, incremented from South to North (stations 1 and 2 being positioned aside the main transect mid-point #6). Stations where phytoplankton analyses were performed are also indicated.

			Sample collection				Code de champ modifié		
Station	Latitude (°N)	Longitude (°E)	Date	Depth of sampling site (m)	Multinet (0-100 m)	Multinet (0-700 m)	Phytoplankton	Multitub	e
3	69,845	13,879	22.08.14	2675	х	x	х	х	
4	71,308	13,942	23.08.14	1940	x	x	x	x	
5	72,138	14,098	23.08.14	1253	x	x	x		
1	72,893	11,762	16.08.14	1839	x	x			
6	72,897	14,207	24.08.14	990	x	x	х	x	
2	72,912	19,487	17.08.14	430	x				
7	73,736	14,376	24.08.14	1320	x	x	x		
8	74,537	14,508	25.08.14	1978	x	x	x	x	
9	75,602	14,705	26.08.14	445	x		x	x	

Table 2: Descriptive statistics [minimum, maximum, average, and median values in  $\mu$ m] of the minimum (i.e. the shortest) diameter of all the 272 BCA measured specimens, per species.

distribution	

Species	Minimum	Average	Median	Maximum
All	65.12	158.45	160.2	315.18
G. uvula	65.5	108.8	108.8	160.8
T. quinqueloba	65.12	166.13	166.56	249.18
N. incompta	75.08	191.29	196.66	280.46
N. pachyderma	100.7	184.3	180.7	315.18

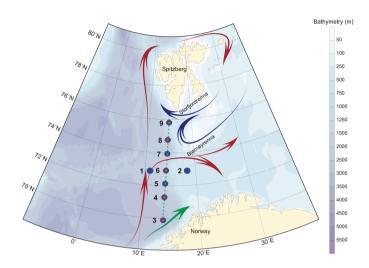


Figure 1: Sampling map of the MOCOSED cruise in the western Barents Sea with schematic surface circulation (red arrows = Atlantic Water; blue arrows = Arctic Water; green arrow = Norwegian Coastal Current; adapted from Oziel et al., 2017).

Little green dots display the 32 CTD/Niskin stations along the South-to-North transect; large blue circles show the location of the 9 MultiNet stations; medium red circles underline the 5 multicore stations.

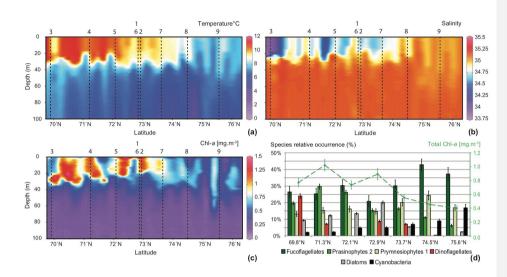


Figure 2: South-North, 0-100 m deep sections across the Barents Sea Opening, compiled from data of the 32 CTD casts: (a) 840 Temperature (°C); (b) Salinity; and (c) Chl-a concentrations (mg.m-3). Vertical dashed lines and associated numbers correspond to the location of the MultiNet hauls. The lower right panel (d) displays pigment concentrations translated into the relative abundances of the major phytoplankton species at 7 sampling stations along the transect (Giraudeau et al., 2016).

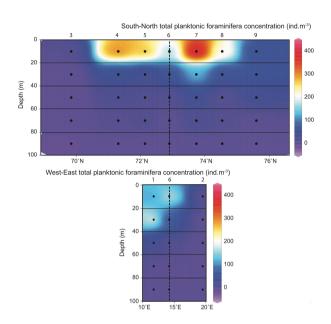


Figure 3: Distribution of planktonic foraminifera total abundances (ind.m<sup>-3</sup>) in the 0-100 m depth section across the Barents

845 Sea Opening (upper panel) and in the West-East transect (stations 1, 6 and 2; lower panel). Station names are indicated above vertical alignments of 5 dots representing the middle points of the 5 net sampling intervals.

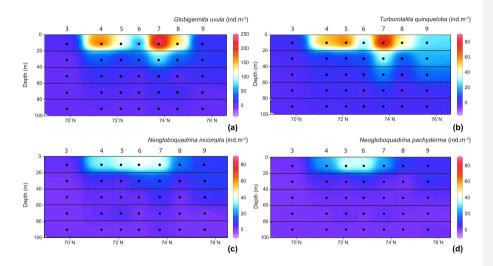
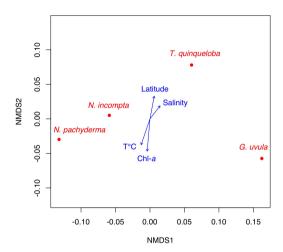
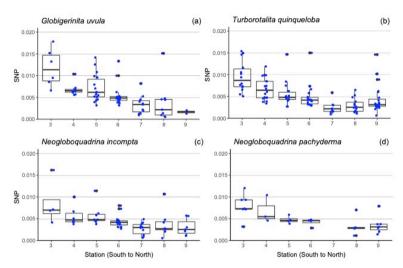


Figure 4: Distribution of the four major species abundances (ind.m<sup>-3</sup>) in the 0-100 m depth section across the Barents Sea Opening. (a) For *Globigerinita uvula* with species abundances (z-axes) going from 0 to 250 ind.m<sup>-3</sup>; (b) for *Turborotalita* quinqueloba (c) Neogloboquadrina incompta (d) and Neogloboquadrina pachyderma values goes from 0 to 80 ind.m<sup>-3</sup>. Station names are indicated above vertical alignments of 5 dots representing the middle points of the 5 net sampling intervals.



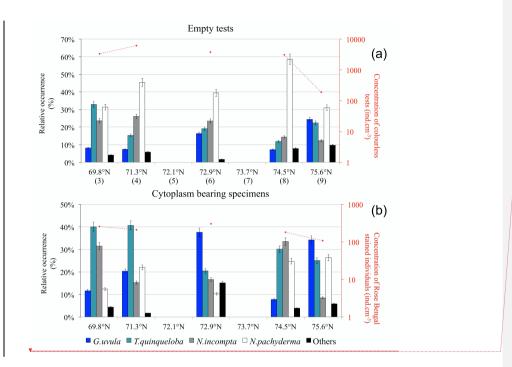
**Figure 5:** Standard nonmetric multidimensional scaling ordination analysis (NMDS) of planktonic foraminifera species distribution (red dots) with temperature, salinity, Chl-*a* and station location as factor (blue arrows).



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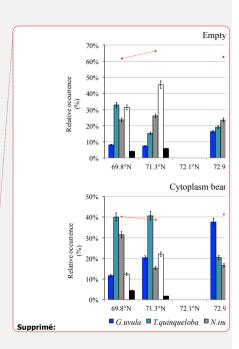
Figure 6: Boxplot of the size normalized protein biomass (SNP,  $\mu g.\mu m^{-1}$ ), along the South-to-North transect (from station 3 = 69.8°N to station 9 = 75.6°N) (a) for *Globigerinita uvula* (b), *Turborotalita quinqueloba* (c), *Neogloboquadrina incompta* (d) and *Neogloboquadrina pachyderma*. Blue dots highlight the data dispersion. Potential outliers were removed such as data for *N. pachyderma* at station 7 as analyses were only run on one individual. Thick lines indicate median, boxes extend to interquartile range (IQR) and whiskers indicate  $1.5^{\circ}IQR$ 

Mis en forme : Anglais (G.B.)



**Figure 7:** Relative species occurrence (% of the total fauna) of planktonic foraminifera found in the upper 0.5 cm core-top sediment (histograms) and total concentration of individuals per cm<sup>3</sup> of dry sediment (logarithmic Y axis on the right): (a) colourless empty tests (stations numbers are in brackets) and (b) individuals bearing a Rose Bengal coloured cytoplasm.

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