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

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**Abstract.** This study reports on species diversity and distribution of planktonic foraminifera (PF) at the Barents Sea Opening (BSO). PF populations living in late summer (collected by means of stratified plankton tows) and recently settled individuals (sampled by interface corer) were studied and compared. High abundances reaching up to 400 ind.m$^{-3}$ in tow samples and 8000 ind.cm$^{-3}$ in surface sediments were recorded in the centre of the studied area while low abundances were observed in coastal areas, likely hampered by continental influences. The living and subfossil (i.e. core-top) assemblages are mainly composed of the four same species *Neogloboquadrina pachyderma, Neogloboquadrina incompta*, *Turborotalita quiqueloba* and *Globigerinita uvula*. The two species *G. uvula* and *T. quiqueloba* largely dominate the upper water column whereas surface sediment assemblages display especially high concentrations of *N. pachyderma*. The unusual dominance of *G. uvula* in the water sample assemblages compared to its low occurrence 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 wide geographical reach phenomenon inducing poleward temperate/subpolar species migration and consecutive foraminiferal assemblage diversification at high latitudes under global climate forcing. Protein concentrations were measured on single specimens and used as a proxy of individual carbon biomass. Specimens of all species show the same trend, i.e. a northward decrease of their size-normalized-protein concentration suggesting foraminiferal biomass to be potentially controlled by different constituents of their organelles (e.g. lipids). The originality of coupling data from plankton tows, protein measurements and surface sediments allows us to hypothesise that PF dynamics (seasonality and distribution) is decoupled from their metabolism.

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**Keywords:** living and dead communities, latitudinal distribution, protein content, seasonality, atlantification

## 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 $CO_2$ (Dai et al., 2019). Recent increased advection of Atlantic Water in the Barents Sea modifies its physico-chemical properties (Smedsrud et al., 2013), which gets directly reflected in the entire ecology of the region. Higher temperatures lead to increased rates of planktonic primary production (Vaquer-Sunyer et al., 2013) and increased $CO_2$ concentrations are expected to have a fertilization effect on marine autotrophs (Holding et al., 2015). Enhanced primary production is accompanied by lateral shifts of the spring and summer phytoplankton blooms in the European Arctic Ocean (Oziel et al., 2017). The increased intrusion of warming Atlantic Water in the Barents Sea also affects phytoplankton composition. Some taxa of different calcifying groups (i.e. foraminifera, coccolithophores, molluscs and echinoderms; Beaugrand et al., 2013), and non-calcifying groups (i.e. radiolarians; Bjørklund et al., 2012) exhibiting 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 recorded 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). Such phenomenon, called "atlantification" (Årthun et al., 2012), is expected to impact every trophic levels of the food web, from small phytoplanktonic species (Neukermans et al., 2018) to larger organisms as fish (Dalpadado et al., 2012). For instance, invasive subpolar shelf fish communities expand northwards in the Barents Sea when the Arctic shelf fish community retracted northward to deeper polar basin (Fossheim et al., 2015). Recent studies have investigated the ecology and biodiversity of planktonic foraminifera from the high-latitude North Atlantic (i.e. Schiebel et al., 2017). 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. The species *N. pachyderma* comprises more than 90% of recent assemblages (i.e. found in surface sediments) from the Polar Region, North of Iceland (MARGO data base; Kucera et al., 2005). Rather few studies on living PF communities have concentrated on (sub-) Arctic regions. Pados and Spielhagen (2014) observed 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. 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) deeply investigated the ecology of *N. pachyderma*. In particular, the variability of its habitat depth, and finally underlined the knowledge gap on its

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ecological preferences. In the western subpolar North Atlantic (Irminger Sea), the maximum production of *N. pachyderma* shows two peaks, in spring and late summer, while winter shows a low production (Jonkers et al., 2010; 2013). Following the extensive review of Schiebel et al., (2017), diversity of planktonic foraminifera has increased in polar waters over the past decades, even though it remains low in comparison to lower latitudes. Some species from lower latitudes are described as new components of formerly high-latitude assemblages (Southern Indian Ocean; Meilland et al., 2016). The shift of planktonic foraminifera assemblages to warmer conditions, since the pre-industrial stage, has been very recently highlighted more globally in the Northern hemisphere (Jonkers et al., 2019). These major modifications in PF distribution patterns display changes more in primary production than in water temperature itself (e.g. Jonkers et al., 2010; Schiebel et al., 2017). More studies on living PF communities in the Arctic regions are highly 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. Planktonic foraminifera, being sensitive to ambient water geochemistry, are considered as good indicators of the polar changing environments (Schiebel et al., 2017).

Taking the opportunity of a cruise dedicated to the exploration of the physical oceanography of the western Barents Sea (MOCOSED 2014 cruise, onboard the R/V *Pourquoi pas ?* - operator SHOM, the French Hydrographic Office), we investigated the connections between the spatial variability of living planktonic foraminifera, 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, it was also possible to compare living faunas (in plankton tow samplings) to the PF assemblages found on the sea floor (from core-top sediments) in order to investigate eventual recent changes in PF population dynamics and to quantify Living PF (LPF) individual protein concentrations as a proxy of their metabolism and organic carbon biomass.

## 2. Oceanographic setting

The studied area covers the western Barents Sea margin, i.e. Barents Sea Opening (BSO), where surface and intermediate ocean circulations 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 (Spitsbergen Banken and shallow Bjørnøya; Storfjordrenna and Bjømøyrenna glacial troughs), determine position and meandering 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 then transported to the Fram Strait by the West Spitsbergen current (Skagseth et al., 2008; Oziel et al., 2017; Figure 1).

## 3. Material and Methods

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 pas ?*". Along a 700 km South-to-North transect from the Norwegian

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(68°N) to the Spitzberg (76°N) coasts, investigations of hydrological processes at the BSO were carried out coupled with the exploration of the phytoplankton and foraminiferal communities (Figure 1).

### 3.1. Conductivity Temperature Density (CTD) and phytoplankton analyses

Vertical profiles of temperature, salinity and fluorescence were obtained along the main South-to-North transect. A total of 32 vertical casts were deployed ≈ 20 km apart from each other (Figure 1), from 0 to 600 m water depth. Temperature and salinity were measured using a CTD SBE 9 plus. The fluorescence data were obtained using a CHELSEA (©) fluorimeter mounted on the CTD frame and converted into Chl-*a* concentrations (mg/m$^3$) on the basis of a calibration curve constructed after High Pressure Liquid Chromatography (HPLC) analyses of more than 2 water samples per station. All data were thereafter spatially interpolated and plotted according to the DIVA application (Troupin et al., 2012) of the Ocean Data View program (Schlitzer, 2014). At 7 of the 32 CTD stations (every ≈100 km, Figure 1), both surface (2 m) and sub-surface (20 m) water samples were collected by way of Niskin bottles (rosette holding the CTD devices) for phytoplankton analysis. Details on water sample treatments (sampling and filtration), pigment analyses (through HPLC; van Heukelem et Thomas, 2001) and determination of phytoplankton composition (following the CHEMTAX method; Makey et al., 1996) are given in Giraudeau et al., (2016).

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

Living PF were collected at 7 of the 32 CTD stations (#3 to #9), plus 2 stations (#1 and #2) located ≈ 20 km apart from the central point of the main South-to-North CTD transect (Figure 1; Table 1), using a stratified plankton tow (MultiNet Hydro-Bios type Midi, opening of 0.25 m2) equipped with five nets (mesh size 100 µm). At each station, one single vertical haul sampled five successive water layers from the sea surface to 100 m depth. For each of the five depth intervals (0–20 m, 20–40 m, 40–60 m, 60–80 m, 80–100 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 individually picked, stored in counting cells and identified at the species level, following the SCOR WG138 taxonomy as implemented in Siccha and Kucera (2017). 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 abundances, the latitude of the station and parameters of the ambient waters (temperature, salinity, Chl-*a* concentration). Empty tests, considered as dead individuals were separately numbered. Results are given in relative abundances (% of the total, live or dead fauna) or in absolute abundances in number of individuals per m$^3$ of filtered water (ind.m$^{-3}$).

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### 3.3. Protein biomass and test size measurements

Immediately after sampling (on board), few living individuals (≈60) were picked out of the shallowest water samples (0 – 20 m) of the 7 stations sampled along the main CDT transect (stations 3 to 9) for protein extraction and measurement. Each foraminifer picked for protein measurement was carefully selected under the strict condition of its shell to be fully filled with cytoplasm. After picking, individuals were immediately cleaned to remove all particles stuck to the test including organic matter. Individual were stored in a 1.5 mL Eppendorf cup 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 $\mu m^2$ (pixel size). Images were analysed for their two dimensional (silhouette) morphometry (Beer et al., 2010), including foraminiferal test minimum diameter being the shortest distance wall to wall passing 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 and handling. 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).

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

At 5 sites of the main CTD transect, an interface corer (Multitube type Oktopus GmbH, INSU[1] division of Brest, France) was implemented 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 horizontal and undisturbed water-sediment interface was selected. The core-top sediment (0-0.5 cm slice) was sampled and fixed with 95 % ethanol and Rose Bengal. This organic stain reacting with both live and dead cytoplasm was used here to distinguish PF still bearing a coloured cytoplasm thus very recently deposited from empty tests of fossil PF. The last study on Rose Bengal-stained individuals of Foraminifera, focussing only on benthic ones did not remove the uncertainty about the exact duration of complete cytoplasm degradation in the tests (Schönfeld et al., 2013), thus we cannot be precise on the time-scale pointed out by Rose Bengal-stained specimens.

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.

## 4. Results

### 4.1. Environmental parameters

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Temperature, salinity and fluorescence-derived Chl-*a* data from the 32 CTD casts were compiled to display the upper 100 meters of the S-N vertical section across the Barents Sea Opening (Figure 2). In the southern first half 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 more stratification was observed in the water column. According to Loeng (1991), encountered surface water masses are characterised by their temperature and salinity values. From South to North of the CTD cast transect: i) high temperatures and low salinities reflected the Norwegian Coastal Water (NwCW), 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 Spitsbergen Banken; ii) at the northern end of the transect, the NwAW penetrated the Barents Sea through the Storfjordrenna trough with temperatures from 6 to 8° and an open marine salinity of 35.1. The same CTD data set allowed Giraudeau et al., (2016) to highlight the signature of Barents Sea bottom water (<2°C and ≈35.0) below 450 m water depth, all across the BSO (not shown in Figure 2).

The Chl-*a* content followed the hydrological pattern above described (Figure 2 c). Relatively high concentrations (mean ≈ 0.8 mg/m$^3$) were located in the surface mixed layer composed of NwCW. The highest values around 1.25 mg/m$^3$ were recorded off the Norwegian coast. Chl-*a* content decreased northwards (north of 74.5°N) to reach ≈ 0.4 mg/m$^3$ 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 (Giraudeau at al., 2016): Fuco-flagelattes (25 to 43%; major component *Phaeocystis pouchetii*), Prasinophytes (15 to 30%; major components *Micromonas pusilla* and *Bathycoccus pusilla*) and Prymnesiophytes (13 to 24%; major component *Emiliana huxleyi*). Three other features are noteworthy (Figure 2 d): i) the dominance of dinoflagelattes (24%) at the southernmost station of the transect (close to the Norwegian coast) contrasted with its 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.

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

Data from the 7 stations of the South-to-North CDT transect with 5 values per station, were compiled to display the repartition of PF absolute abundances (total assemblage and species-specific) in the upper 100 meters of the vertical section across the BSO. 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.

Total absolute abundances of living PF fauna varied between 0 and 400 ind.m$^{-3}$ (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. in NwCW. The two stations located at the south and north extremities of the transect (# 3, off Norwegian coast, and #9, off the Spitsbergen coast) displayed low densities (10 to 50 ind.m$^{-3}$). At station 1, located above

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the Barents Sea margin slope, the maximal abundance of 220 ind.m$^{-3}$ was recorded in a deeper habitat (20-40 m, Figure 3). Station 2, located relatively inside the Barents Sea, was very poor in PF (<10 ind.m$^{-3}$). In total, 10 species were observed. The studied area was characterised by the large occurrence of subpolar to polar species (Figure 4), listed in descending order: *Globigerinita uvula* (45%), *Turborotalita quinqueloba* (26.2%), *Neogloboquadrina incompta* (15%) and *Neogloboquadrina pachyderma* (8.9%). There was a noticeable presence of the temperate water species *Globigerina bulloides* (2.7%), 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 major species, *T. quinqueloba* dominated the PF fauna only at station 9, with 45 % of the total assemblage and 26 ind.m$^{-3}$. 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$^{-3}$, respectively) and at station 5 and 7 for *T. quinqueloba* (53 and 80 ind.m$^{-3}$, respectively). The northernmost 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$^{-3}$ for *G. uvula*, and 30 ind.m$^{-3}$ for *T. quinqueloba*). The two other major species *N. pachyderma* and *N. incompta* presented similar low relative abundances (4 to 22%, and 8 to 25%, respectively). For both species, maximum absolute abundance of about 40-45 ind.m$^{-3}$ occurred in the central part of the transect between [72-74°N].

The NMDS analyse 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 whereas *T. quinqueloba* and *G. uvula* plot separately from each other but also from the *N. pachyderma* / *N. incompta* area.

### 4.3. Planktonic foraminifera protein biomass

Individual protein content (BCA method) and associated test minimum diameter (i.e. the shortest distance wall to wall passing through the centre of the proloculus) were measured for a total of 272 specimens of the 4 major species encountered along the South-North transect, including 32 specimens of *Neogloboquadrina pachyderma*, 58 *Neogloboquadrina incompta*, 72 *Globigerinita uvula* and 110 *Turborotalita quinqueloba*. A minimum of 5 individuals per species (until a max of 25) was selected at each sampled depth-interval of the 7 stations along the S-N transect, paying careful attention to sample the whole range of size variation observed in the population present in a net sample. For 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.

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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* represent the biggest species with a median of 200 µm, and *G. uvula* the smallest one with a median of 110 µm (Table 2). For each studied species, the mean size is equal to the median size indicating 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 µm of protein per µm of foraminiferal shell diameter. It varies depending on species from 0.0004 (*G. uvula*) to 0.0426 µg (*T. quinqueloba*). The 4 studied species display similar trends in their SNP per station, characterized by a northward 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*.

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

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.

Concentrations of planktonic foraminifera with colourless empty tests (Figure 7 a) varied from a maximum of 6200 ind.cm$^{-3}$ at station 4 (71.3°N) to a minimum of 200 ind.cm$^{-3}$ at the septentrional station 9. All along the S-N transect, the fossil assemblages were dominated by *Neogloboquadrina pachyderma* (31 to 59%). Assemblages were more balanced at the two ends of the transect where *N. pachyderma* showed off at its lowest occurrence. At the southernmost point, station 3 presents a co-occurrence with *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$^{-3}$. All along the transect, the relative abundance of *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 largely dominated by *G. uvula* (38%). North of 74°, the fauna was balanced between *N. incompta* (33 and 9 %) and *G. uvula* (8 and 34%).

## 5. Discussion

*Distribution pattern of living planktonic foraminifera at the Barents Sea Opening*

In late summer 2014 the hydrology at the BSO was characterised, from the South to 74.5°N, by a strong water stratification with a 30 m thick Chl-*a* enriched lens of NwCW overlapping northwards the NwAW (saltier and colder). Further North, a well-mixed water column with characteristics of the NwAW occupied the Storfjordrenna trough where a coccolithophore bloom (Giraudeau et al., 2016) and the highest concentration of cyanobacteria were recorded in the upper water column.

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Despite these marked features the global 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 such as temperature, salinity and primary production on PF density (Schiebel et al., 2017). In accordance to Retailleau et al., (2018) conclusions, multiples indices however highlight the possible importance of water turbidity in PF abundance distribution. The highest densities of planktonic foraminifera occurred in the 0-20m upper water layer between 70.5 and 74.5°N, and very low abundances were recorded nearby the Norwegian and Spitzbergen coasts. The low abundances at the two ends of the studied transect 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* in the high-latitude (> 70°N) waters at the BSO. This species, described as a temperate to polar species (Schiebel and Hemleben, 2017), is known to occupy 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 as the dominant species in polar regions, making up more than 90% of the total planktonic foraminifera assemblages (e.g. Schiebel et al., 2017). The high densities of *G. uvula* recorded at the BSO in 2014 seem to be inconsistent with 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 to these observations could be linked to global climate changes and particularly to the Arctic amplification. In this context, the western Barents Sea faced both a warming (SST anomalies ≈ +2°C) and an increase in salinity (SSS anomalies ≈ +0.3) during the last decades (Dobrynin and Pohlmann, 2015). These hydrological changes clearly impact the plankton dynamics and biogeography, with a northwards shift of the natural range of biological communities (Barton et al., 2016). Thus the species distribution of planktonic foraminifera would best probably 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 confirm the shift of planktonic foraminifera assemblages to warmer conditions already asserted from North Atlantic (Jonkers et al., 2019) and from southern Indian Ocean data (Meilland et al., 2017).

A second hypothesis for the dominance of *G. uvula* in our sampling area is 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

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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).

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 supposed to follow food availability and primary production (Volkmann 2000, Schiebel and Hemleben 2017), but we did not observe any 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 8, located at the cross road 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). For this particular location, the concentration of phytoplankton was relatively low and the phytoplankton community showed singular characteristics, in comparison to the southern part of the studied 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 thus is that *G. uvula* and *T. quinqueloba* high densities reflect more food composition (quality) than food concentrations (quantity). This also implies that satellite-derived chlorophyll concentrations, considered as indices for algal bloom, may not always be good indicators to perceive neither lateral extension nor intensity of foraminiferal production.

*Planktonic foraminifera protein concentration, potential marker of their metabolism*

Based on previous studies, the protein concentration of planktonic foraminifera can be used as a proxy of its biomass ($C_{org}$) and foraminiferal biomass should remain the same for a given size (Schiebel and Movellan, 2012). However, in our study, the SNP (size normalized protein content) of planktonic foraminifera appears to decrease with higher latitude and with related decrease in Chl-*a* concentration and temperature, whereas the sizes of individuals picked for these analyses remain constant. If proteins are the main component of zooplankton biomass ($C_{org}$) in all oceanographic regions, from the tropics to polar areas, they are closely followed by lipids (e.g., Percy and Fife 1981; Donnelly et al., 1994; Kumar et al., 2013; Yun et al., 2015). 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, but also seasonal features, with higher percentages 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

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of energy (biomass / $C_{org}$) of the planktonic foraminifera 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 are supposed to 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 his life (Mayzaud, 1976). This suggests that individuals from a same species can display more or less proteins for a same biomass in different locations.

*Discrepancy between upper water column and interface sediment samples*

The PF species compositions recorded during the late summer 2014 in the water column and in surficial 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, co-dominated by *T. quinqueloba* and *N. pachyderma* (Figure 7 a). Affected by differential settling velocities (200 and 500 $m.day^{-1}$ in normal conditions) 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 smear 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 superposed water masses (Kuhnt at al. 2013). The BSO present a complex hydrography with the buoyant NwCW flowing northwards above the NwAW that is entering eastwards the Barents Sea when cold BSAW is creeping westwards. In such area, the PF settling velocities and extension of lateral advection are completely unknown. 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, aware of the eventual lateral advection of shells, Pados and Spielhagen, (2014) concluded 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 ± 0.6 $mm.yr^{-1}$ has been recently measured in the Storfjordrenna outlet [76°N-17°E], close to our station 9 (Fossile et al., submitted), the upper core-top sediments (0-0.5 cm slice) may have recorded less than a decade. Staying aware about the eventual variability of the sedimentation rate along the studied transect,

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we hypothesise that the sea surface-bottom differences in the foraminiferal assemblages along the South-to-North transect at the BSO might have detected a real community change within a short period of time (about a decade).

Furthermore, the analysis of sediment from the 5 core-tops collected during the MOCOSED cruise demonstrated strong differences between the assemblages of fossil fauna, i.e. empty tests of individuals dead for a while, and recently settled tests, 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 higher than the ones observed for the fossil faunas (Figure 7). At 72.9°N in the surficial sediment, *G. uvula* reaches up to 38% of the coloured assemblages (Figure 7 b) whereas it never exceeds 25% in the non-coloured ones (Figure 7 a). The large representation 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 present a strong seasonal character with a production period focussed in late summer as a response to their favourite 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 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 surficial sediment and plankton tow sampled in late summer 2014 suggests that this species may demonstrate a more sustainable behaviour with a regular production throughout the year. This hypothesis is supported by a recent study showing that abundances and distribution of the species *N. pachyderma* are not significantly perturbed by seasonal seawater temperature, productivity or salinity variations occurring in the Arctic (Greco et al., 2019). Thus it makes sense that *N. pachyderma* production appears to be yearly sustained and constant in the area whereas other species clearly respond to a local seasonal signal.

## 6. Conclusion

Our sampling and analytic approaches combining the use of plankton net, core-top and Niskin bottle samples, CTD probes, molecular biology (protein measurement) 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 main results of the present study can be synthetized as follows:

a) The PF species composition observed at the BSO during the MOCOSED14 cruise is diverse, with more than 10 different species including: *Globigerinita uvula* (45%), *Turborotalita quinqueloba* (26.2%), *Neogloboquadrina incompta* (15%), *Neogloboquadrina pachyderma* (8.9%), *Globigerina bulloides* (2.7%) and *Globigerinita glutinata*, *Neogloboquadrina dutertrei*, *Globigerinoides ruber*, *Globigerinoides sacculifer* and *Orcadia riedeli* (<1%).

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b) The two species *G. uvula* and *T. quinqueloba* clearly dominate the living (water sample) population and display high patchy abundances suggesting they occur in late summer in response to physico-chemical conditions and related specific primary productivity. The species *N. pachyderma* and *N. incompta* show low densities but a continuous distribution pattern in the water samples. The core-top assemblages, very largely dominated by *N. pachyderma* with a co-occurrence of *N. incompta* suggest that both species present a more consistent production over the course of the year.

c) The dominance of *G. uvula* in water samples likely reflect a summer signal and potentially the temperature increase experienced over the last decades by the Barents Sea and the North Atlantic Ocean under global climate change.

d) PF abundances observed in the studied area are high, ranging from 0 to 400 ind.m$^{-3}$ (LPF, surface waters) in the plankton tow and from 200 to 8000 ind.cm$^{-3}$ in surface sediments (empty tests). The lower abundances were recorded nearby the Norwegian and Spitzbergen coasts. These observations highlight the fact that waters under continental influences (nutrient-enriched, more turbid) are rather inhospitable for PF production.

e) The discrepancy between species distribution (patchy for *T. quinqueloba*, *G. uvula* and continuous for *N. pachyderma* and *N. incompta*) is not reflected in their size-normalized protein concentration profile, suggesting a decoupling between PF dynamics and their metabolism.

f) Size-normalized protein concentrations of the four major species described at the BSO decrease with the increasing latitude (and a decrease in temperature and Chl-*a* concentration). This observation leads us to hypothesise that foraminifera of different species or within the same species have the potential to balance the ratio between their protein and lipid concentrations (known to be a major component of zooplankton $C_{org}$) in order to adapt to their environmental conditions (e.g. temperature change). Further analyses on planktonic foraminifera lipid concentration and composition are thus needed and would help us to better understand the metabolism of these organisms.

**Data availability**

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

**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 | | |
|---|---|---|---|---|---|---|---|
| Station | Latitude (°N) | Longitude (°E) | Date | Depth of sampling site (m) | Multinet | Phytoplankton | Multitube |
| 3 | 69.845 | 13.879 | 22.08.14 | 2675 | x | x | x |
| 4 | 71.308 | 13.942 | 23.08.14 | 1940 | x | x | x |
| 5 | 72.138 | 14.098 | 23.08.14 | 1253 | x | x | |
| 1 | 72.893 | 11.762 | 16.08.14 | 1839 | x | | |
| 6 | 72.897 | 14.207 | 24.08.14 | 990 | x | x | x |
| 2 | 72.912 | 19.487 | 17.08.14 | 430 | x | | |
| 7 | 73.736 | 14.376 | 24.08.14 | 1320 | x | x | |
| 8 | 74.537 | 14.508 | 25.08.14 | 1978 | 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 µm] of the minimum (i.e. the shortest) diameter of all the 272 BCA measured specimens, per species.

| | Test size distribution parameters in µm | | | |
|---|---|---|---|---|
| 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 |

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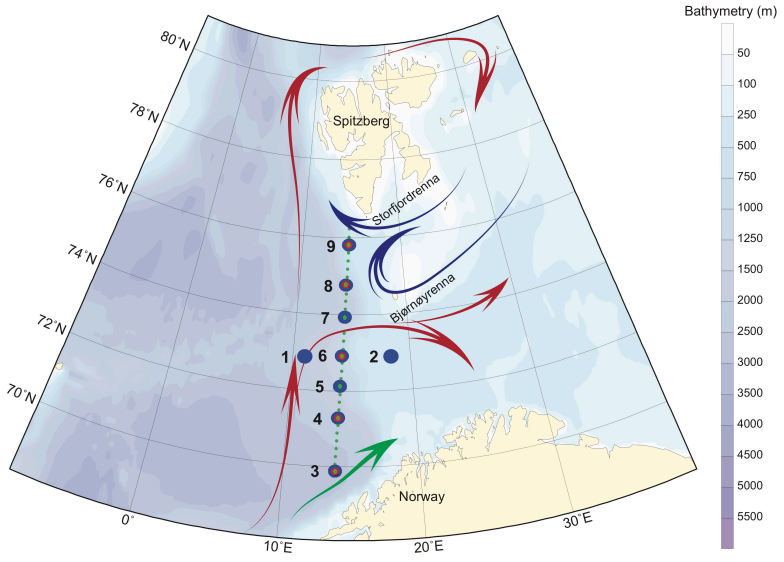


**Figure 1:** Sampling map of the MOCOSED cruise in the western Barents Sea with schematic surface circulation (red arrows = Atlantic Water; blue arrows = Arctic Water; green arrow = Norwegian Coastal Current; adapted from Oziel et al., 2017). Little green dots display the 32 CTD/Niskin stations along the South-to-North transect; large blue circles show the location of the 9 MultiNet stations; medium red circles underline the 5 multicore stations.

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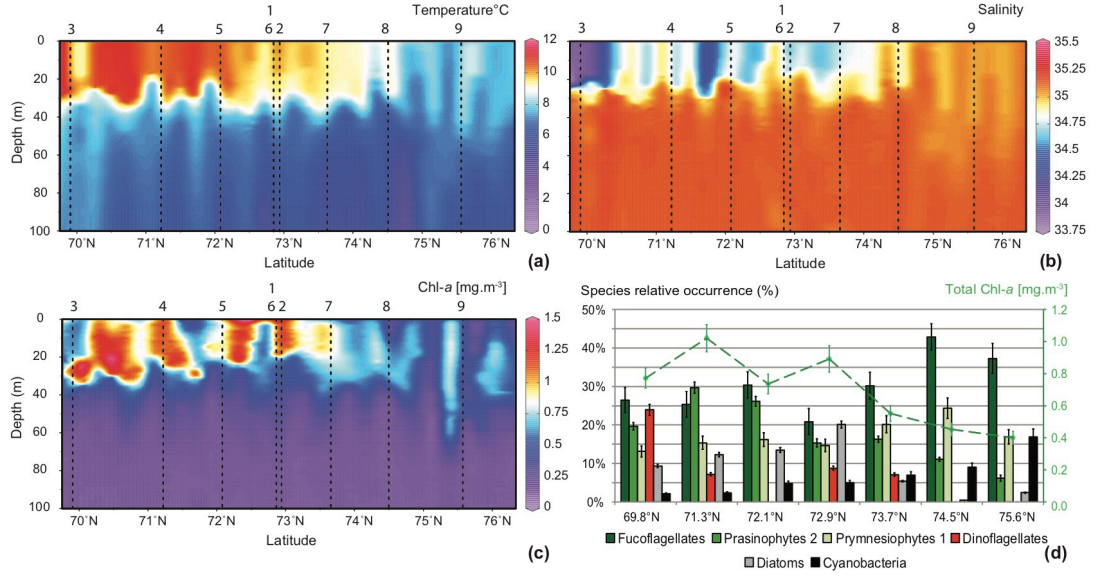


590 **Figure 2:** South-North, 0-100 m deep sections across the Barents Sea Opening, compiled from data of the 32 CTD casts: (a) Temperature (°C); (b) Salinity; and (c) Chl-*a* concentrations (mg.m$^{-3}$). Vertical dashed lines and associated numbers correspond to the location of the MultiNet hauls. 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).

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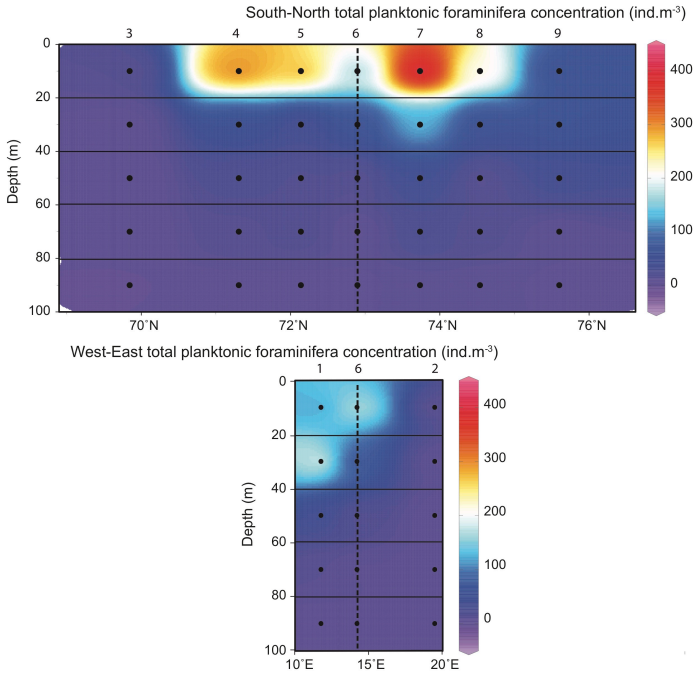


595 **Figure 3:** Distribution of planktonic foraminifera total abundances (ind.m$^{-3}$) in the 0-100 m depth section across the Barents Sea Opening (upper panel) and in the West-East transect (stations 1, 6 and 2; lower panel). Station names are indicated above vertical alignments of 5 dots representing the middle points of the 5 net sampling intervals.

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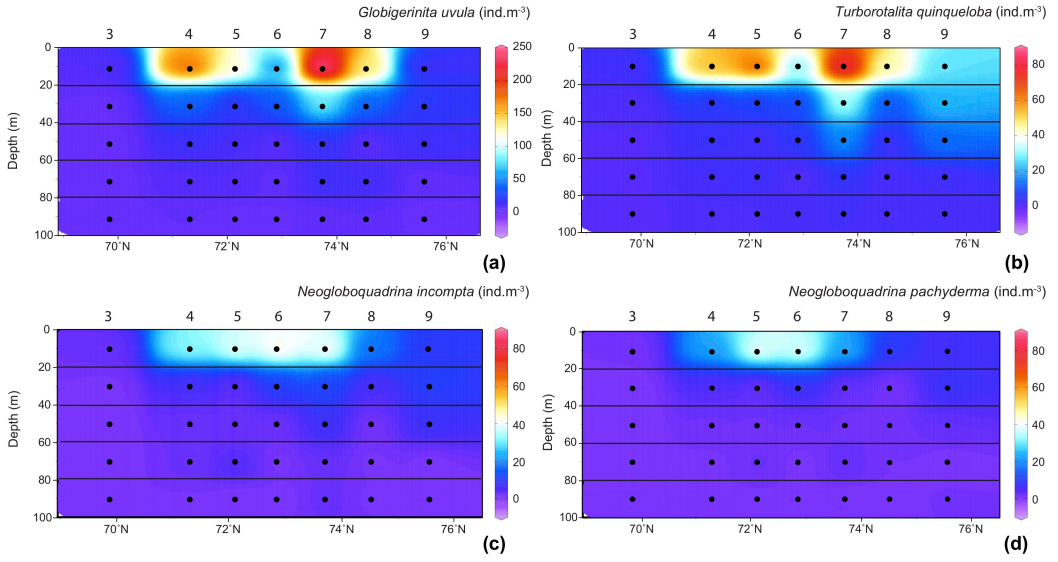


**Figure 4:** Distribution of the four major species abundances (ind.m$^{-3}$) in the 0-100 m depth section across the Barents Sea Opening. (a) For *Globigerinita uvula* with species abundances (z-axes) going from 0 to 250 ind.m$^{-3}$; (b) for *Turborotalita quinqueloba* (c) *Neogloboquadrina incompta*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

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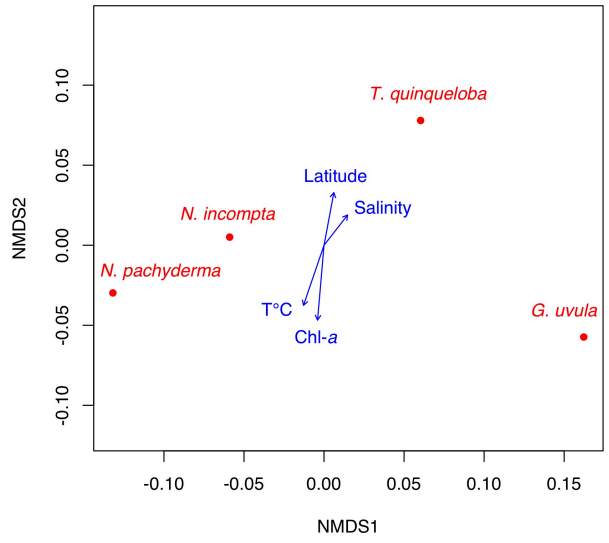


**Figure 5:** Standard nonmetric multidimensional scaling ordination analysis (NMDS) of planktonic foraminifera species distribution (red dots) with temperature, salinity, Chl-*a* and station location as factor (blue arrows).

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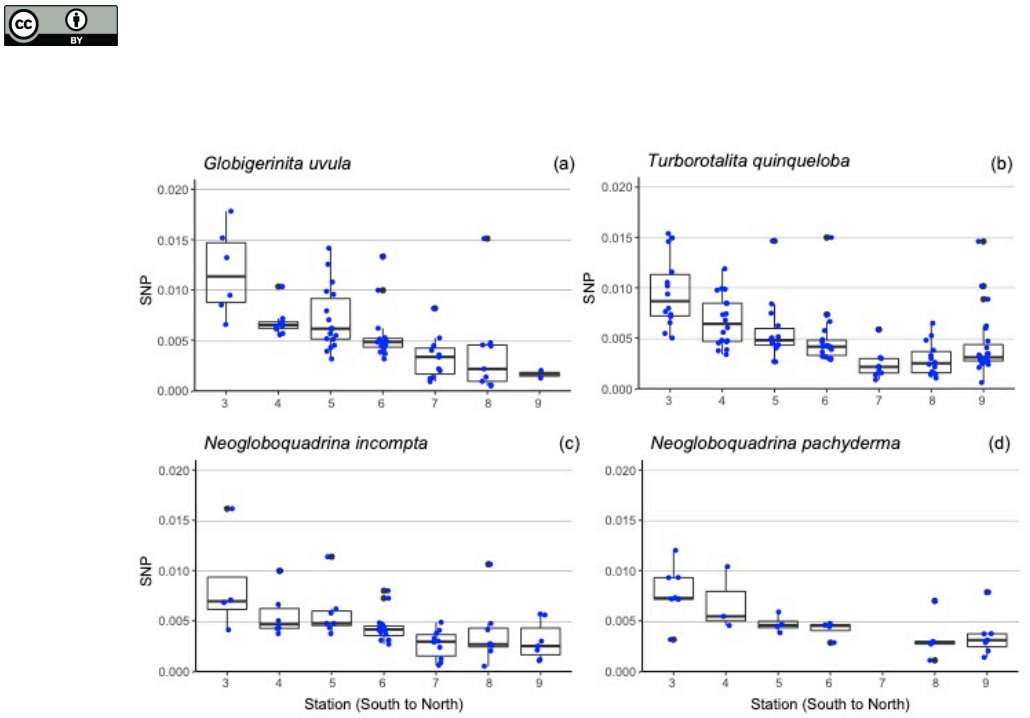


610 **Figure 6:** Boxplot of the size normalized protein biomass (SNP, µg.µm$^{-1}$), along the South-to-North transect (from station 3 = 69.8°N to station 9 = 75.6°N) (a) for *Globigerinita uvula* (b), *Turborotalita quinqueloba* (c), *Neogloboquadrina incompta* (d) and *Neogloboquadrina pachyderma*. 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*IQR.

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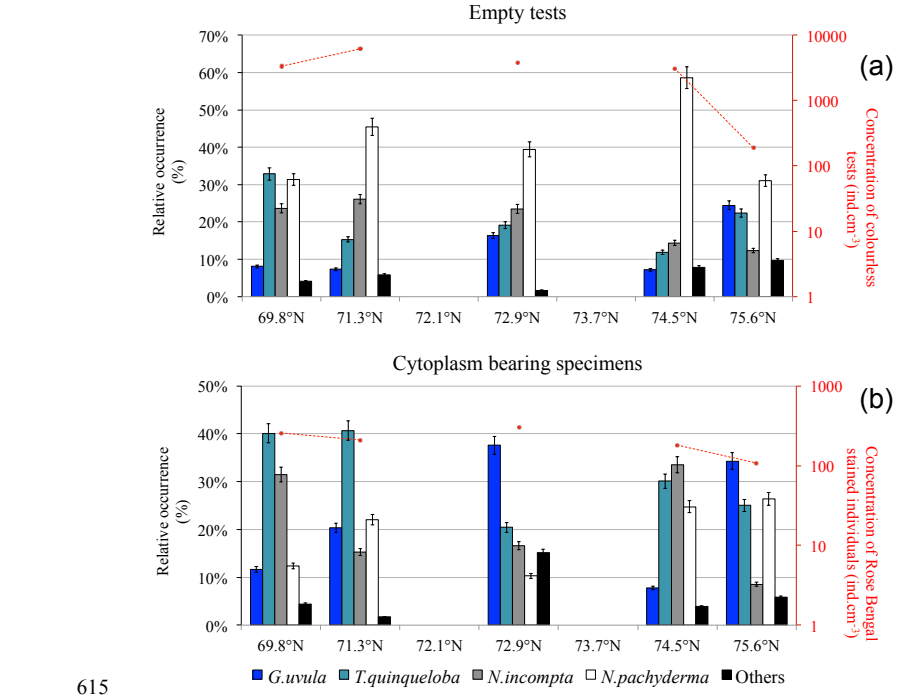


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**Figure 7:** Relative species occurrence (% of the total fauna) of planktonic foraminifera found in the upper 0.5 cm core-top sediment (histograms) and total concentration of individuals per $cm^3$ of dry sediment (logarithmic Y axis on the right):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