

1 **Decadal trend of plankton community change and habitat shoaling in the Arctic gateway recorded**
2 **by planktonic foraminifera**

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17 **Abstract**

18 The Fram Strait plays a crucial role in regulating the heat and sea-ice dynamics in the Arctic. In response
19 to the ongoing global warming, the marine biota of this Arctic gateway is experiencing significant
20 changes with increasing advection of Atlantic species. The footprint of this “Atlantification” has been
21 identified in isolated observations across the plankton community, but a systematic, multi-decadal
22 perspective on how regional climate change facilitates the invasion of Atlantic species and affects the
23 ecology of the resident species is lacking. Here we evaluate a series of 51 depth-resolved plankton
24 profiles collected in the Fram Strait during seven surveys between 1985 and 2015, using planktonic
25 foraminifera as a proxy for changes in both the pelagic community composition and species vertical
26 habitat depth. The time series reveals a progressive shift towards more Atlantic species, occurring
27 independently of changes in local environmental conditions. We conclude that this trend is reflecting
28 higher production of the Atlantic species in the “source” region, from where they are advected into the
29 Fram Strait. At the same time, we observe that the ongoing extensive sea-ice export from the Arctic and
30 associated cooling-induced decline in density and habitat shoaling of the subpolar *Turborotalita*
31 *quinqueloba*, whereas the resident *Neogloboquadrina pachyderma* persists. As a result, the planktonic
32 foraminiferal community and vertical structure in the Fram Strait shifts to a new state, driven by both
33 remote forcing of the Atlantic invaders and local climatic changes acting on the resident species. The
34 strong summer export of Arctic sea ice has so far buffered larger plankton transformation. We predict
35 that if the sea-ice export will decrease, the Arctic gateway will experience rapid restructuring of the
36 pelagic community, even in the absence of further warming. Such a large change in the gateway region
37 will likely propagate into the Arctic proper.

38

39 **Introduction**

40 Over the last decades, the Arctic has experienced warming and sea ice decline of “unprecedented”
41 extent, shifting to a climatic state not experienced throughout the 20th Century (Box et al., 2019). A key
42 region for the heat budget and sea-ice dynamics of the Arctic is the Fram Strait. This narrow passage
43 constitutes the only deep-water connection with the Atlantic Ocean, facilitating the inflow of a large
44 portion of the warm and saline Atlantic Water, the export of sea ice from the Arctic (Beszczynska-
45 Möller et al., 2012), and exchange of marine biota between the polar Arctic Mediterranean and the
46 subarctic North Atlantic (Bluhm et al., 2015; Kosobokova & Hirche, 2009; Wassmann et al., 2015). The
47 Atlantic Water (AW) is transported through the eastern part of the strait by the West Spitsbergen Current
48 (WSC), while in the western part, the East Greenland Current (EGC) carries polar water and sea ice
49 from the Arctic Ocean and Nordic Seas to the south (Fig.1). The AW inflow to the Arctic has warmed
50 over the last decades (Beszczynska-Möller et al., 2012; Polyakov et al., 2012; Wassmann et al., 2015)
51 and is regarded as one of the main drivers of the current changes in the Arctic marine environment
52 (Onarheim et al., 2014).

53 The apparent increase in the advection of AW and the resulting changes in the Arctic Ocean are reflected
54 in the “Atlantification” of the marine community in the Fram Strait (Andrews et al., 2018; Gluchowska
55 et al., 2016; Kraft et al., 2013; Schröter et al., 2019). A long-term record of planktonic foraminiferal
56 shells in a marine sediment core from the Fram Strait indicates that the recent changes are unparalleled
57 over the last two millennia (Spielhagen et al., 2011). The ongoing Atlantification of the Arctic gateway
58 contrasts with the changes in the physical environment of the upper ocean in the region. Unlike the rest
59 of the Arctic realm, in the summers between 1985 and 2015, the Fram Strait has been cooling at the
60 surface (~ 0.5 °C), and sea ice has expanded along the east coast of Greenland and Svalbard (Fig. 1).
61 This seemingly counterintuitive trend is a reflection of the increasing reduction in summer sea ice in the
62 Arctic and the associated increased export of Arctic sea ice into the Greenland Sea (Wang et al., 2019).
63 Net changes in sea surface temperatures (SST) in the Fram Strait are therefore the result of the combined
64 effect of increasing advection and warming of northward-flowing AW and increased sea-ice export in
65 the EGC flowing southward. The higher export of Arctic sea ice and its melting in the Greenland Sea
66 also contribute to a large-scale surface freshening, which suppresses oceanic mixing and facilitates
67 cooling of the surface waters (Kwok et al., 2005) that are overlying the warm Atlantic inflow in the
68 subsurface.

69 Thus, the environmental conditions in the Fram Strait, taken alone, should not facilitate Atlantification
70 of the marine biota. Indeed, the observed increase in abundance of subpolar species and associated
71 community changes have been interpreted as a consequence of warming in the North Atlantic “source”
72 region and intensification of the AW inflow carrying the subpolar biota into the Fram Strait (Wassmann
73 et al., 2015). In this scenario, the increasing proportion of Atlantic biota should occur independently of
74 the local conditions in the Fram Strait and the Atlantification process should be associated with a re-
75 arrangement of the vertical structure of the pelagic communities.

76 Accurate investigation of these dynamics are missing due to the lack of long-term time series on
77 plankton distribution patterns available from the region (Dornelas et al., 2018). Furthermore, research
78 on zooplankton response to climate change, and foraminifera in particular, rarely include an assessment
79 of the effects on the vertical distribution of the marine species community (Jonkers et al., 2021; Jorda et
80 al., 2020). Here, we analyse three decades of changes in population structure and vertical distribution of
81 planktonic foraminifera, a distinctive group of Arctic unicellular calcareous zooplankton, in the Fram
82 Strait recorded by 51 species-resolved vertical profiles of standing stocks sampled between 1985 and
83 2015. Planktonic foraminifera species distribution is controlled by temperature (Bé & Tolderlund, 1971;
84 Fenton et al., 2016; Morey et al., 2005), and they show distinct depth habitats, which vary with changing
85 environmental conditions (Greco et al., 2019; Rebotim et al., 2017) and the sedimentary record indicates
86 that foraminifera are sensitive indicators of climate change since the preindustrial era (Spielhagen et al.,
87 2011; Jonkers et al., 2019), making them ideal sentinels of Fram Strait Atlantification and changes in
88 vertical habitat structure. To this end, we combined data from repeated foraminiferal surveys in the Fram
89 Strait with in-situ and regional environmental descriptors to assess the extent and environmental

90 determinants of recent changes in (i) planktonic foraminiferal community composition, (ii) species
91 standing stocks and (iii) shifts in vertical distribution of species.

92 **Material and Methods**

93 *Biological data*

94 Over the last four decades, the plankton community of the Fram Strait has been sampled regularly with
95 replicate vertical profiles available for most sampling years. Among the collected zooplankton,
96 planktonic foraminifera have been the most frequently quantified and reported at species level, allowing
97 us to compile a dataset of five surveys of planktonic foraminifera repeated at virtually the same location
98 and same time of year in the Fram Strait between 1985 and 2011 containing a total of 45 vertical profiles.
99 In order to extend the length of the time series, we generated new data from one profile taken in July
100 2014 and a survey with five profiles sampled in July 2015. In 2014, planktonic foraminifera were
101 sampled from three different depth intervals in the upper water column (0–50 m, 50–200 m, and 200–
102 600 m) by the means of a WP2 net with aperture 0.25 m² and mesh size of 90 µm during an
103 oceanographic cruise with *R/V Helmer Hanssen*. The following year, sampling was carried out on the
104 *R/V Polarstern* using a multiple closing plankton net (Hydro-Bios, Kiel) with an opening of 0.25 m² and
105 equipped with 5 nets each with a mesh size of 55 µm.

106 Samples from both expeditions were wet-sieved through 250 and 63 µm sieves and stained with Rose
107 Bengal/ethanol mixture after collection to facilitate the distinction between cytoplasm-bearing and
108 empty shells. The samples were processed at the University of Bremen and at UiT the Arctic University
109 of Norway in Tromsø, where planktonic foraminifera were picked under a binocular microscope and
110 air-dried. All specimens in the fraction above 63 µm were counted and identified to species level
111 following the taxonomy of Brummer and Kroon (1988) and Hemleben (1989). Concentrations of the
112 resident species (*Neogloboquadrina pachyderma* and *Turborotalita quinqueloba*) and of the Atlantic
113 species (*Globigerina glutinata*, *Globigerina bulloides*, *Neogloboquadrina incompta*, *Globigerinita*
114 *uvula*, and *Orcadia ridelii*) were derived from counts by using the volume of filtered water determined
115 from the product of towed interval height and the net opening.

116 The new data and the literature data had to be first harmonised to the same taxonomy. As a result, counts
117 of *N. pachyderma* and the Atlantic species from the ARK III/3 cruise could not be used in the analyses
118 due to the different taxonomical resolution of the original study (Carstens et al., 1997). In their paper,
119 the authors did not distinguish between *N. pachyderma* and *N. incompta*, previously considered
120 ecophenotypic variants of the same species, but now known to be genetically distinct forms (Darling et
121 al., 2006). Only data on the polar species *T. quinqueloba* collected during the same expedition could be
122 included in the analyses. Because of their consistently low density and variable species composition, the
123 concentrations of all non-resident (Atlantic) species were lumped into one category for the downstream
124 analyses. For samples collected in 2008, the proportion of the Atlantic species was assumed to be 2%
125 of the total assemblage as stated by the authors of the original study (Manno & Pavlov, 2014). Because

126 of the taxonomic lumping, the vertical habitat of the Atlantic species could not be evaluated. Since the
127 distinction between cytoplasm-bearing and empty shells has not been done consistently, the analysis is
128 based on the concentration of all shells. Greco et al. (2019) have shown that this treatment causes a
129 slight but consistent overestimation of the vertical habitat depth, but since the vast majority of the
130 collected specimens in the plankton are cytoplasm-bearing, the effect on standing stock estimates is
131 likely negligible. Further, the different surveys have used different vertical sampling schemes and
132 resolutions. Therefore, the individual vertical density profiles were converted to a common vertical
133 scheme resolving standing stock at three depths (0–50 m, 50–100 m, 100–200 m) using a custom script
134 in R (R Core Team, 2017). This scheme was chosen to avoid extrapolation and reflects the most shared
135 position of depth-interval boundaries among the sampling schemes. We derived total species abundance
136 as the sum of the concentrations within the different intervals. For the two polar species, *N. pachyderma*
137 and *T. quinqueloba*, the depth habitat was calculated as in Greco et al. (2019).

138 *Environmental parameters*

139 The habitat of planktonic foraminifera reflects the vertical structure of physical and biological properties
140 of the surface ocean layer. Therefore, next to the consideration of the temporal trends, to understand
141 why population densities, species composition and vertical habitat have been shifting, we have tested
142 models explaining the observed variability with physical properties of the environment. In Arctic polar
143 waters, the main parameter affecting planktonic foraminiferal species composition appears to be
144 temperature (Jonkers et al., 2019; Morey et al., 2005) in combination with sea-ice concentration
145 (Carstens et al., 1997; Pados & Spielhagen, 2014). Additionally, in the Fram Strait an important
146 parameter is also the depth of the Atlantic layer (Pados et al., 2015; Simstich et al., 2003). In contrast,
147 salinity, within the range of typical open marine conditions, has been shown not to affect planktonic
148 foraminifera (Greco et al., 2019).

149 In-situ temperature profiles were retrieved from CTD data from the respective expeditions. Data
150 deposited in PANGAEA were accessed using the R package “pangaeR” (version 08.2) (Simpson &
151 Chamberlain, 2018). For nine stations from the iAOOS and HH14 cruises, CTD data were obtained from
152 the original investigators. The CTD temperature profiles were used to extract Sea Surface Temperature
153 (SST), here defined as the average temperature in the uppermost 6 meters from the sea surface, and the
154 minimum depth of the Atlantic Water layer (AWz), defined as the depth where temperature rises above
155 2 °C (Beszczynska-Möller et al., 2012). As no CTD data were collected during the ARK III/3 cruise
156 (Carstens et al., 1997), for these stations we extracted the SST and AWz from the NOAA Optimum
157 Interpolation Sea Surface Temperature V2 [weekly resolution] (Reynolds et al., 2002) and the Hadley
158 Centre EN4 dataset (Good et al., 2013), respectively. For all stations, in situ sea-ice concentration and
159 the distance from the ice margin at the time of sampling were extracted from 25 km×25 km resolution
160 passive microwave satellite raster imagery obtained from the Sea Ice Index Version 3.0 product of the
161 National Snow and Ice Data Centre (Fetterer et al., 2017) using a custom script in R.

162 The foraminiferal assemblage captured in the net is the result of growth over several weeks (Carstens
163 & Wefer, 1992). To a certain degree, the observed composition thus reflects processes acting
164 throughout the habitat traversed by the plankton before being intercepted by the net. To account for the
165 effect of these processes, next to the in-situ parameters, we also analyse two descriptors of the overall
166 oceanographic state of the sampling area (spatial polygon including all the sampling locations present
167 in our compilation) at the time of sampling. These include the average SST of the sampling area
168 derived from the NOAA Optimum Interpolation Sea Surface Temperature V2 (Reynolds et al., 2002)
169 and the average sea-ice extent of the sampling area extracted from the Sea Ice Index Version 3.0
170 (Fetterer et al., 2017). Data on the projected Arctic sea-ice extent between 2010 and 2090 relative to
171 the month of August under two climate scenarios (RCP 4.5 and RCP 8.5) were obtained from the
172 Climate data store (<https://cds.climate.copernicus.eu/>). The projected Arctic sea ice coverage is
173 derived from model simulations presented in Khon et al. (2017).

174 In addition to the physical environment, the foraminiferal population also likely reflects the trophic
175 structure of their habitat. This is often highly correlated with the physical parameters of the environment
176 (sea ice extent, distance from sea-ice edge), but could also act independently. Unfortunately, neither in-
177 situ observations, nor satellite image data are available throughout the sampling period to generate
178 representative and robust estimates of productivity.

179 *Statistical analyses*

180 We used the obtained dataset to investigate the effect of the environmental parameters and time (i.e.,
181 sampling year, since all years the sampling took place in summer) on the composition, total abundance,
182 density, and depth habitat of planktonic foraminiferal species in the Fram Strait. First, we had to rule
183 out the potential influence of the longitudinal gradient of physical properties in the Fram Strait (Fig. 1)
184 on the monitored parameters. Since in most years, the geographical extent of the sampling straddled this
185 gradient, the presence of different hydrographic regimes in the east and in the west Fram Strait (WSC
186 and EGC respectively) could potentially be the dominant factor influencing the planktonic foraminifera
187 community. To test the effect of the longitudinal gradient, we performed a hierarchical cluster analysis
188 using the unweighted pair group method with arithmetic mean (UPGMA) based on the Bray–Curtis
189 dissimilarity index on species density data using the *hclust* function in the package “vegan” (version
190 2.5-6) (Oksanen et al., 2018) in R and observed the clustering of sample sites assigned to the two
191 hydrographic regimes in the region defined as in Fadeev et al. (2018). This analysis revealed no
192 preferential clustering of samples according to the region (Fig. 1b), indicating that the observed
193 variability is due to factors other than the sampling location.

194 Changes in the community structure of planktonic foraminifera were then analysed using a multivariate
195 approach. We used nonmetric multidimensional scaling (NMDS) to visualize the similarities of
196 assemblages observed across the stations using the *metaMDS* function from the R package “vegan”
197 (version 2.5-6) (Oksanen et al., 2018). For the NMDS, data by Carstens (1997) were not included in

198 order to eliminate potential biases due to the taxonomic ambiguity in the counts (*N. pachyderma* and *N.*
199 *incompta* not distinguished, see above). The obtained ordination was used to assess the individual
200 effects of the tested environmental variables on the foraminiferal community by performing BIOENV
201 analysis (Clarke & Ainsworth, 1993). This test allows the identification of variables that best explain
202 the variance in the biological community by calculating a correlation coefficient that is then subjected
203 to a permutation test to determine its significance. Prior to this step, we checked for the presence of
204 collinearity between the environmental variables using the variance inflation factor (VIF) with the
205 *vifstep* function from the R package “usdm” (version 1.1-18). The function calculates the VIF for a set
206 of variables and excludes the highly correlated variables (VIF > 5) (Fenton et al., 2016) from the set
207 through a stepwise procedure. The remaining environmental variables were included in the BIOENV
208 analysis using the *envfit* function from the R package “vegan” with 999 permutations.

209 Next, generalized linear models (GLM) were applied to assess the effects of time and environmental
210 drivers on the individual density of *N. pachyderma*, *T. quinqueloba* and of the Atlantic species. As we
211 analysed count data, we used the *floor* function in R to derive discrete values from the total
212 concentrations of the three taxonomic groups as a prior step (Zuur et al., 2007) and explored the
213 relationship with the potential predictors with bivariate GLM using the *glm* function in R indicating a
214 quasi-poisson error distribution with log as link function. For the three groups, *N. pachyderma*, *T.*
215 *quinqueloba* and Atlantic species, the total concentration (dependent variable) was regressed against the
216 sampling year (time), longitude (as a proxy for the two hydrographic regimes), SST, average SST of the
217 sampling area, ice-concentration, distance from ice-margin, AWz, and average sea-ice extent of the
218 sampling area as independent variables. Trait variance explained by individual parameters was
219 calculated using pseudo-R² for Poisson GLMs as 100*(model null deviance- model deviance)/model
220 null deviance (Dobson, 2002). Where more than one predictor displayed a significant effect on the
221 density, VIF was calculated among the variable, variables identified as causing variance inflation were
222 dropped, and the GLMs were re-applied allowing for interactions among the remaining variables.

223 The relationship between environmental and temporal controllers on the depth habitat (DH) of the
224 resident species *N. pachyderma* and *T. quinqueloba* were investigated through bivariate correlation
225 (Pearson *r*). Square root transformation was performed on *T. quinqueloba* data to obtain symmetric
226 distribution. Multiple linear models were applied to species depth habitat and variables that displayed a
227 significant correlation. The normality of the residuals was checked after the linear model was applied
228 (Zuur et al., 2009). As for the density, in case of more than one predictor displayed a significant
229 correlation with DH, we proceeded to calculate the VIF between the concurrent variables and re-applied
230 the linear model for the remaining variables allowing interactions. Results from models that explained
231 most of the variance (higher pseudo-R² and R²) are presented and discussed.

232 **5.3 Results**

233 *Species composition*

234 All samples contained an assemblage typical for the polar environment of the Fram Strait, dominated
235 by *N. pachyderma*, which represented 56% of the total assemblage in our compilation. Not all the
236 stations presented the same species proportions: *T. quinqueloba* was the most abundant species in 17
237 stations. The abundance of the Atlantic species also varied greatly in our compilation ranging from total
238 absence to 27 % of the total assemblage in the samples taken in 2014. The BIOENV analysis revealed
239 that three of the tested variables correlate significantly with the obtained ordination without variance
240 inflation: Year ($R^2 = 0.46$, p-value = 0.001), SST of the sampling area ($R^2 = 0.36$, p-value = 0.008), and
241 distance from the sea-ice margin ($R^2 = 0.23$, p-value = 0.023) (Fig. 3 and Fig. 4b). This indicates that
242 the assemblage composition has changed through time and that at least part of the change can be
243 attributed to changes in the physical environment.

244 *Species density*

245 The time series of population density reveal a considerable amount of variance within each sampling
246 period, with years with unusually high density for some species, and an apparent trend of increasing
247 density of Atlantic species (Fig. 2a). Potential predictors of the observed trends in population density of
248 the three taxonomic groups were thus investigated using generalised linear model and the results are
249 summarised in Table 1 and in Figure 4. The two best predictors of the density of *N. pachyderma* were
250 longitude (Pseudo- $R^2 = 0.18$, p-value = 0.01) and the SST of the sampling area (Pseudo- $R^2 = 0.14$, p-
251 value = 0.002), both showing a negative relationship with the concentration of *N. pachyderma* (Fig 4a).
252 The final model including the summing effects of the two predictors explained 38% of the total variance.
253 The SST of the sampling area was also negatively associated with the density of *T. quinqueloba* (Pseudo-
254 $R^2 = 0.14$, p-value = 0.002), but the variable was removed due to high collinearity (VIF > 5). The
255 remaining two predictors, year of sampling and sea-ice extent had a VIF < 2 and were included in the
256 final model along with their interactions explaining 51% of the observed variance. Only the year of
257 sampling alone was identified as a significant predictor of the total density of the Atlantic species
258 (Pseudo- $R^2 = 0.17$, p-value = 0.02).

259 *Depth habitat*

260 The two species *N. pachyderma* and *T. quinqueloba* displayed a similar vertical distribution in the water
261 column with average living depths 37–140 m and 44–142 m, respectively (Fig.2b). Factors controlling
262 the variability in the observed depth habitat of the two species were investigated by a linear model. This
263 revealed that sea-ice extent in the sampling area alone was the only significant predictor of the depth
264 habitat of *N. pachyderma* (Adj. $R^2 = 0.091$, p-value = 0.03). In contrast, all the variables investigated
265 showed a significant correlation with the variability of the depth habitat of *T. quinqueloba* (Table 1) and
266 only the overall SST in the area had to be excluded because of variance inflation. A combined linear
267 model with interactions still identified three variables as significantly and independently affecting the
268 depth habitat of the species. Longitude, sea-ice extent and sampling year explain together 47 % of the
269 observed variance in the depth habitat of *T. quinqueloba*.

270 Discussion

271 The results of the BIOENV analysis indicate a steady rise in the concentration of Atlantic species
272 throughout the observational period (Fig. 3). The same pattern emerged from the GLM (Table 1, Fig. 4)
273 with the year of sampling significantly correlated with population density of the Atlantic species and
274 explaining 18% of the variance in our observations. The declining trend in SST in the Fram Strait
275 suggests that the observed increase in the abundance of Atlantic species in the region cannot be the result
276 of habitat tracking. Since none of the tested environmental factors was a significant predictor of the
277 density of Atlantic species in the region either, their rising abundance must reflect changes in the
278 “source” region in the Nordic Seas from where the species are advected northward with the AW. An
279 increase in density or a change in phenology of these species in the Nordic Seas would result in higher
280 density in the Fram Strait region even without changes in the intensity of AW inflow. Indeed, evidence
281 from moorings has shown that the variability observed in the advection of “Atlantic” copepods in the
282 Fram Strait reflects their phenology and not the intensity of the AW inflow (Basedow et al., 2018). The
283 invoked changes in Atlantic species population dynamics in the “source” region is consistent with the
284 increasing abundance of planktonic foraminifera in the North Atlantic recorded in Continuous Plankton
285 Recorder (CPR) observations (Beaugrand et al., 2013). Importantly, a recent investigation based on
286 satellite-derived altimetry observations showed that an increase in surface velocity of the North Atlantic
287 Current from 1993 to 2016, resulted in a northward shift in the spatial distribution of the coccolithophore
288 *Emiliana huxleyi* (Oziel et al., 2020).

289 In contrast to the rising abundance of the Atlantic expatriates, the subpolar resident species *T.*
290 *quinqueloba* shows decreasing population density through time (Figures 2, 3 and 4) leading to lower
291 proportions in the planktonic foraminiferal community (Fig. 3). Contrary to the non-resident, advected
292 Atlantic species, the Fram Strait region is the primary habitat of *T. quinqueloba* (Schiebel et al., 2017)
293 and its abundance in the Fram Strait is not reflecting AW inflow. However, this species is known to
294 prefer warmer, subpolar, waters and is largely absent from the Arctic proper (Carstens et al., 1997;
295 Manno & Pavlov, 2014; Pados & Spielhagen, 2014; Volkmann, 2000). Therefore, the increasing sea-
296 ice export and decreasing SST in the Fram Strait make the region less suitable for this species. Indeed,
297 next to time, a significant component of the variability in the abundance of this species can be explained
298 by local properties in the Fram Strait, in a direction consistent with the above hypothesis: the species is
299 less abundant where/when sea-ice cover is more extensive (Table 1, Fig. 4). Since the local conditions
300 in the Fram Strait are highly variable, a single observation like that by Manno & Pavlov (2014), would
301 easily appear to indicate an opposing trend, highlighting the necessity and merit of the long-term
302 replicated data series presented in this study.

303 Thus, the changing abundance of *T. quinqueloba* appears to be consistent with habitat tracking,
304 responding to the temporal evolution of local conditions in the Fram Strait. This conclusion is further
305 supported by the observed concomitant shallowing of the vertical habitat of this species through time
306 (Fig. 4), which is reflecting the shallower habitat of the species in the presence of sea ice (Table 1).

307 Previous observations on *T. quinqueloba* in the Fram Strait also showed shallower habitat in the presence
308 of sea ice (Carstens et al., 1997; Volkmann, 2000). The current increase in sea ice in the Fram Strait
309 thus acts to reduce the population density of this species and shoal its vertical habitat, both occurring in
310 the direction consistent with habitat tracking.

311 Consistently with the increasing sea-ice extent and decreasing temperature, the habitat of the Fram Strait
312 remains suitable for the polar species *N. pachyderma*, which shows no significant temporal trend in its
313 density or vertical habitat (Fig. 2). Instead, the variability in these parameters can be explained by local
314 parameters with higher density and shallower habitat occurring when and where the sea-ice cover is
315 more extensive (Table 1, Fig. 4). Peaks in *N. pachyderma* density in cold polar waters were observed in
316 previous studies (Manno & Pavlov, 2014; Volkmann, 2000) as well as its high occurrence along the sea-
317 ice margin considered, where higher primary production by diatoms represents a major food source for
318 this species (Greco et al., 2021). The habitat shoaling towards sea ice is entirely consistent with a recent
319 analysis of factors affecting the vertical habitat of this species (Greco et al., 2019).

320 Our in-situ, vertically, resolved observations of three decades of plankton change in the Fram Strait
321 provide direct evidence that trends in population density are associated with significant shifts in the
322 vertical position of the involved species. This observation is significant, as it could not have been derived
323 from CPR or sediment trap devices or remote sensing of the ocean surface. The existence of systematic
324 vertical shifts in plankton populations has significant consequences for biogeochemical cycling in the
325 upper ocean (Bianchi et al., 2013). In addition, the changes in plankton vertical habitat in the Fram Strait
326 may affect species interactions with other resident or immigrant Atlantic species, as vertical niche
327 partitioning among closely related species of zooplankton is an important mechanism of adaptation to
328 the Arctic environment (Kosobokova et al., 2011). In light of these observations, we postulate that the
329 assessment of future changes in the marine biota in the Arctic gateway must also consider the vertical
330 dimension of the pelagic habitat (Gluchowska et al., 2017; Jorda et al., 2020; Knutsen et al., 2017;
331 Kosobokova et al., 2011).

332 Overall, we thus show that plankton in the Arctic gateway is assuming an unusual composition, with the
333 resident species shifting towards more polar taxa and shallower habitat, tracking local environmental
334 change, being confronted with increasing abundance of Atlantic expatriates, rising due to processes
335 favouring their growth in the Nordic Seas. Since there is no reason to believe that this observation based
336 on planktonic foraminifera should not apply to other plankton groups, this shift in community
337 composition likely alters the diversity of planktonic communities, in turn affecting the established food
338 webs of the involved species (Griffith et al., 2019; Kortsch et al., 2015). At present, the increased sea-
339 ice export in the Fram Strait compensates the overall regional warming in the Arctic, muting the changes
340 in plankton communities in the region. Indeed, in the adjacent Barents Sea, in absence of sea-ice export,
341 the Atlantification of the foraminiferal community appears stronger (Ofstad et al., 2020), likely further
342 enhanced by import of nutrients that promotes phytoplankton production (Lewis et al., 2020). This

343 means that once the ice export in the Fram Strait ceases to be fuelled by the increasing Arctic sea ice
344 reduction (Årthun et al., 2021; Guarino et al., 2020), the planktonic community will likely abruptly shift
345 to a completely different state with more Atlantic and more non-sea-ice species, possibly impacting the
346 carbon export of the region (Anglada-Ortiz et al., 2021). Observational data of sea-ice extent and future
347 predictions plotted in Figure 1d show that, in the Fram Strait, the trend towards an increase in sea-ice
348 export seems to have already reached its maximum. The projections point at a further reduction showing
349 that by the year 2050, the sea-ice extent in the area will attain values below the variability of the
350 observational era in the last four decades (Fig. 1d). Thus, this would be the time when we can expect
351 the regime shift to occur. Acting as the gateway to the Arctic, this rapid shift in the Fram Strait will
352 likely propagate into the Arctic proper.

353 **Data availability**

354

355 All new data on which this study is based will be deposited on the public repository PANGAEA. The
356 data as used in this study, including the environmental data and biological data sources, are available
357 on Zenodo (<https://doi.org/10.5281/zenodo.5266464>).

358

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360

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371

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373 **References**

374

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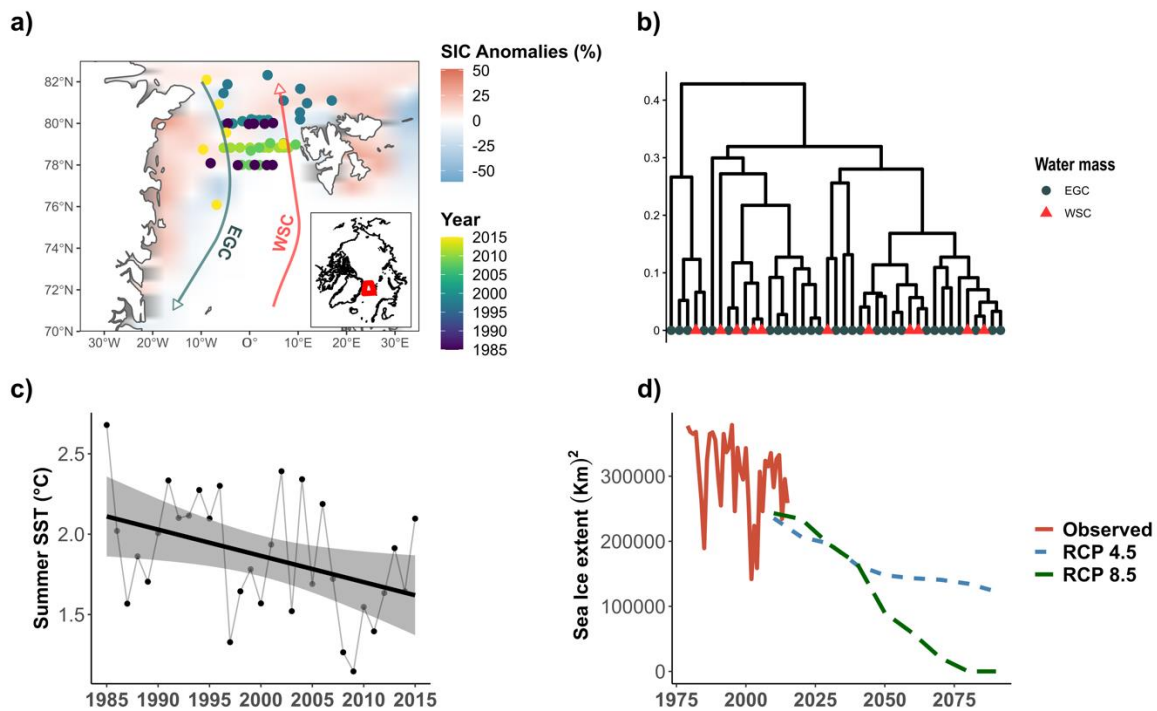


Figure 1 a) Plankton net stations with vertically resolved planktonic foraminifera counts used in this study color-coded by year of sampling. Background colour indicates Sea Ice Anomalies (SIC) in the Fram Strait calculated for the period 1985-2015. Data from Sea Ice Index Version 3.0 (Fetterer et al., 2017). Arrows indicate the two main water masses present in the Fram Strait (East Greenland Current -EGC- and the West Spitzbergen Current -WSC-). b) Hierarchical cluster analysis showing the similarity of foraminiferal assemblages, symbols show the water mass identified with the position of the station. c) Summer SST in the sampling area in the period 1985-2015. Data from NOAA Optimum Interpolation Sea Surface Temperature V2 [weekly resolution] (Reynolds et al., 2002). d) Observational and predicted Sea-ice extent in the sampling area for the month of August from 1979 to 2090. Observational data (red line) from Sea Ice Index Version 3.0 (Fetterer et al., 2017). Model prediction for Representative concentration pathways 4.5 and 8.5 (green and blue lines respectively) based on results of Khon et al. (2017).

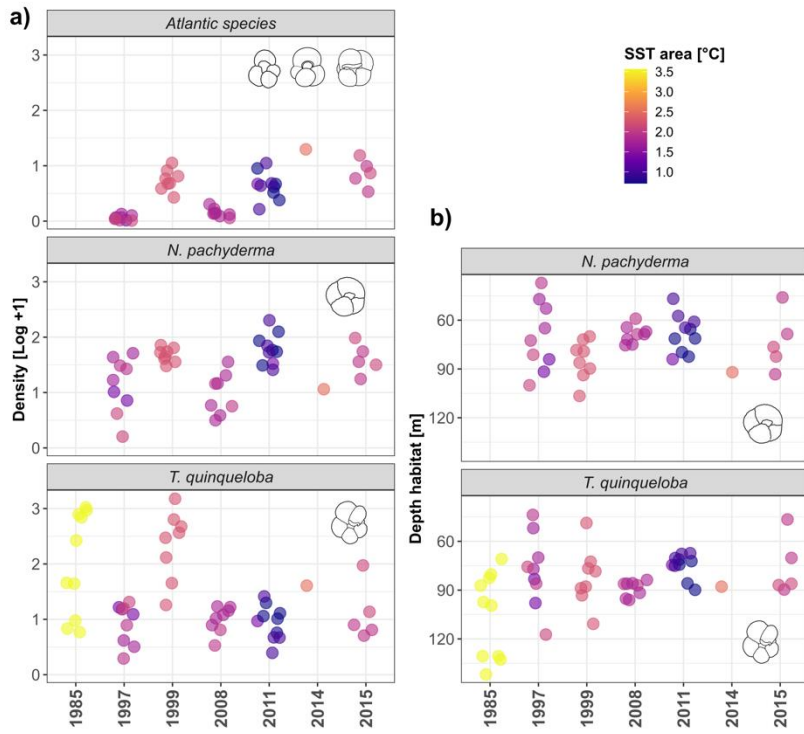


Figure 2 a) Density and Depth habitat (b) of planktonic foraminifera species plotted against year. Colour indicates temperature of the area at the time of sampling.

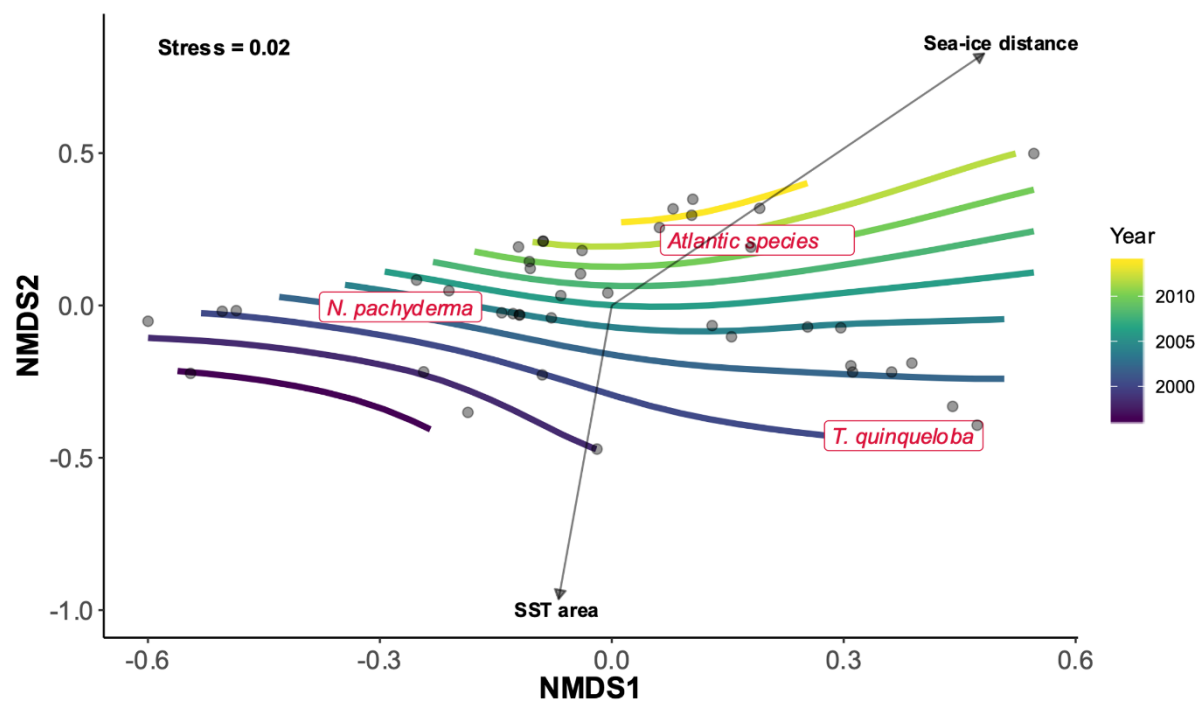


Figure 3 NMDS ordination based on Bray-Curtis similarities Index of planktonic foraminifera abundances with fitted environmental vectors. Contour lines were derived from surface fitting (GAM) of the variable sampling year.

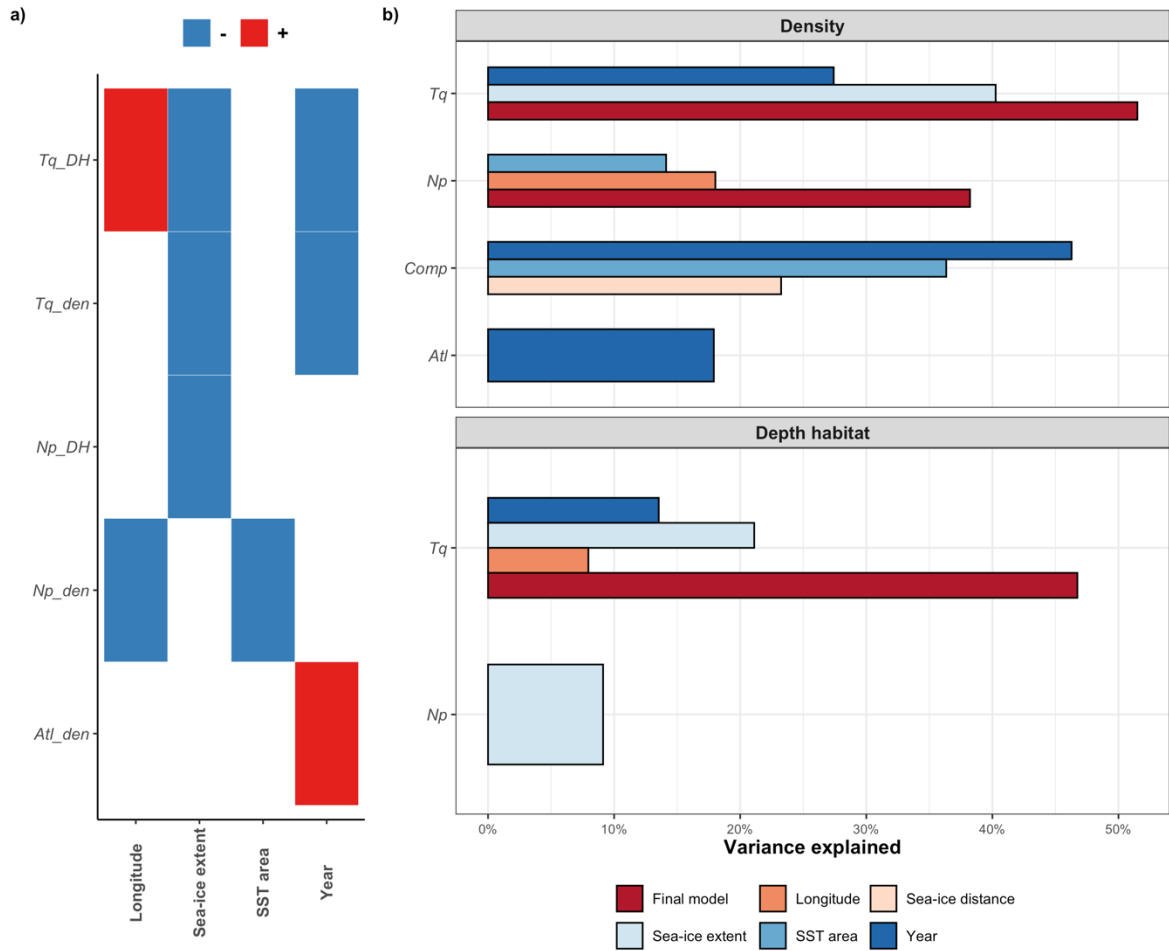


Figure 4 a) Heat-map showing the direction of the relationship with tested environmental variables and modelled responses. b) Bar plot showing amount of variance explained by the singular predictor and the final model. (Abbreviations: Np= *Neogloboquadrina pachyderma*, Tq= *Turborotalita quinqueloba*, Atl= Atlantic species, DH= depth habitat, den= density, Comp= species composition).

	<i>p</i> - value	Pseudo / Adj. R ²
<i>N. pachyderma</i> Density		
Longitude	0.01	18.03
SST area	0.02	14.12
SST area + Longitude		38.23
<i>T. quinqueloba</i> Density		
Year	0	27.42
SST area	0	29.06
Sea-ice extent	0	40.26
Year * Sea-ice extent		51.5
Atlantic species Density		
Year	0.02	17.91
<i>N. pachyderma</i> Depth habitat		
Sea-ice extent	0.03	9.13
<i>T. quinqueloba</i> Depth habitat		
Longitude	0.03	7.96
Latitude	0.02	8.53
Year	0	13.54
SST	0.02	8.4
SST area	0	19.14
Sea-ice concentration	0.01	12.5
Sea-ice distance	0	13.54
Sea-ice extent	0	21.11
Longitude * Sea-ice extent * Year	0	46.74

Table 1 Results of the Generalised linear models and mixed linear models.