# Spatial distribution of Arctic bacterioplankton abundance is linked to distinct water masses and summertime phytoplankton bloom dynamics (Fram Strait, 79°N)

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15   **Abstract**

16   The Arctic is impacted by climate warming faster than any other oceanic region on Earth. Assessing
17   the baseline of microbial communities in this rapidly changing ecosystem is vital for understanding
18   the implications of ocean warming and sea ice retreat on ecosystem functioning. Using CARD-FISH
19   and semi-automated counting, we quantified 14 ecologically relevant taxonomic groups of
20   bacterioplankton (*Bacteria* and *Archaea*) from surface (0-30 m) down to deep waters (2500 m) in
21   summerly ice-covered and ice-free regions of the Fram Strait, the main gateway for Atlantic inflow
22   into the Arctic Ocean. Cell abundances of the bacterioplankton communities in surface waters varied
23   from $10^5$ cells $mL^{-1}$ in ice-covered regions to $10^6$ cells $mL^{-1}$ in the ice-free regions, and were overall
24   driven by variations in phytoplankton bloom conditions across the Strait. The bacterial classes
25   *Bacteroidia* and *Gammaproteobacteria* showed several-fold higher cell abundances under late
26   phytoplankton bloom conditions of the ice-free regions. Other taxonomic groups, such as the
27   *Rhodobacteraceae*, revealed a distinct association of cell abundances with the surface Atlantic
28   waters. With increasing depth (>500 m), the total cell abundances of the bacterioplankton
29   communities decreased by up to two orders of magnitude, while largely unknown taxonomic groups
30   (e.g., SAR324 and SAR202 clades) maintained constant cell abundances throughout the entire water
31   column (ca. $10^3$ cells $mL^{-1}$). This suggests that these enigmatic groups may occupy a specific
32   ecological niche in the entire water column. Our results provide the first quantitative spatial
33   variations assessment of bacterioplankton in the summerly ice-covered and ice-free Arctic water
34   column, and suggest that further shift towards ice-free Arctic summers with longer phytoplankton
35   blooms can lead to major changes in the associated standing stock of the bacterioplankton
36   communities.

## 1     Introduction

37

38   Atmospheric and oceanic warming has a substantial impact on the Arctic Ocean already today
39   (Dobricic et al., 2016; Sun et al., 2016; Dai et al., 2019). The strong decline in sea ice coverage (Peng
40   and Meier, 2018; Dai et al., 2019) and heat transfer by the Atlantic water inflow (Beszczynska-
41   Möller et al., 2012; Rudels et al., 2012; Walczowski et al., 2017) will affect stratification of the water
42   column and can lead to an increase in upward mixing of the Atlantic core water, a process also
43   termed "Atlantification" (Polyakov et al., 2017). The main inflow of Atlantic water into the Arctic
44   Ocean occurs through the Fram Strait (Beszczynska-Möller et al., 2011), making it a sentinel region
45   for observing the ongoing changes in the Arctic marine ecosystem (Soltwedel et al., 2005, 2016). The
46   Fram Strait is also the main deep-water gateway between the Atlantic and the Arctic Ocean. It hosts
47   two distinct hydrographic regimes; the West Spitsbergen Current (WSC) that carries relatively warm
48   and saline Atlantic water northwards along the Svalbard shelf (Beszczynska-Möller et al., 2012; von
49   Appen et al., 2015), and the East Greenland Current (EGC) that transports cold polar water and sea
50   ice southwards from the Arctic Ocean along the ice-covered Greenland shelf (de Steur et al., 2009;
51   Wekerle et al., 2017).

52   Sea ice conditions have a strong impact on the seasonal ecological dynamics in Fram Strait and the
53   whole Arctic Ocean (Wassmann and Reigstad, 2011), affecting light availability and stratification in
54   the water column. The presence of sea ice and snow cover can repress the seasonal phytoplankton
55   bloom in the water column through light limitation (Mundy et al., 2005; Leu et al., 2011), or change
56   its timing, e.g. by increasing stratification of the surface waters once the ice melts (Korhonen et al.,
57   2013). Also, sea-ice algae can make up a significant proportion of the annual productivity (Leu et al.,
58   2011; Boetius et al., 2013; Fernández-Méndez et al., 2014). Previous summer observations in the
59   Fram Strait already suggested that total cell abundances and productivity of bacterioplankton
60   communities in surface waters are driven by environmental parameters associated with
61   phytoplankton bloom dynamics (Fadeev et al., 2018), such as the availability and composition of
62   organic matter (Piontek et al., 2015; Engel et al., 2019), with differences between ice-covered and
63   ice-free regions (Piontek et al., 2014; Fadeev et al., 2018).

64   Long-term summer observations in the region, conducted in the framework of the Long-Term
65   Ecological Research (LTER) site HAUSGARTEN, revealed strong ecological variations associated
66   with the Atlantic Meridional Overturning Circulation (AMOC; Soltwedel et al., 2016). Warming
67   events during the past decades influenced seasonal phytoplankton blooms by causing a slow but
68   continuous increase in biomass, and a shift from diatom- to flagellate-dominated communities
69   (Nöthig et al., 2015; Engel et al., 2017; Basedow et al., 2018). It has been recently observed that
70   phytoplankton blooms show an increasing partitioning of the produced organic carbon into the
71   dissolved phase (Engel et al., 2019), which may result in a more active microbial loop in the upper
72   ocean and less export of particulate matter (Vernet et al., 2017; Fadeev et al., 2020). In times of a
73   rapidly changing Arctic ecosystem, investigating structure and dynamics of bacterioplankton
74   communities remains a key component to the understanding of current changes in this environment.
75   However, so far, an assessment of associated responses of the key bacterial taxa responsible for an
76   increased recycling is missing, especially with regard to shifts in standing stocks.

77   To date, the majority of Arctic bacterioplankton studies are performed using high-throughput
78   sequencing of the 16S rRNA gene, which cannot be directly converted to absolute standing stock
79   abundances of specific taxonomic groups due to PCR and other quantitative biases (Gloor et al.,
80   2017; Kumar et al., 2017; Piwosz et al., 2020). Here we used semi-automatic CAtalyzed Reporter
81   Deposition-Fluorescence In Situ Hybridization (CARD-FISH; Pernthaler et al., 2002). The power of

82  this technique lies in the ability to acquire absolute abundance of the targeted taxonomic groups free
83  of compositional effect (Amann et al., 1990). Besides the ability to target and quantify specific
84  taxonomic groups, the retrieval of a positive hybridization signal furthermore indicates that the
85  analyzed cell was alive and active before fixation (Amann et al., 1990; DeLong et al., 1999).
86  Automatization of the microscopic examination and counting procedure can reach a high-throughput
87  standard (Schattenhofer et al., 2009; Teeling et al., 2012; Bižić-Ionescu et al., 2015; Bennke et al.,
88  2016). Using CARD-FISH and semi-automated cell counting, we quantified cell abundances of 14
89  taxonomic groups in 44 samples, collected at 4 different water layers from surface (15-30 m) to the
90  deep ocean (2500 m) in both, ice-free and ice-covered regions of the Fram Strait. The main objective
91  of this study was to assess the standing stocks of key taxonomic groups in summerly Arctic
92  bacterioplankton across the Strait. Using high-throughput data of bacterioplankton cell abundances
93  we tested the following hypotheses: 1) in surface waters, the abundances of different
94  bacterioplankton taxonomic groups are associated with phytoplankton bloom conditions, and are
95  linked to the abundances of specific phytoplankton populations; 2) water depth structures the
96  bacterioplankton communities, and 3) differences between communities in ice-covered and ice-free
97  regions decrease with increasing water depth.

## 2    Results and Discussion

99   We investigated a total of 44 water samples from 11 stations that represented different hydrographic
100  and biogeochemical conditions across the Fram Strait (Figure 1; Table S1). At each station, 4
101  different water layers were targeted: the surface mixed layer (0-30 m), epipelagic waters (100 m),
102  deep mesopelagic waters (500-1000 m), and bathypelagic waters (1200-2500 m). Based on the
103  known hydrography of the Strait (Rudels et al., 2012), and observed sea-ice conditions, the sampled
104  stations were grouped into three distinct regions (Figure 1): the eastern ice-free region associated
105  with the WSC (Beszczynska-Möller et al., 2012), the western ice-covered region associated with the
106  EGC (de Steur et al., 2009), and the partially ice-covered region in the north-east that is associated
107  with the highly productive ice-margin zone (further addressed as North- "N") (Hebbeln and Wefer,
108  1991; Perrette et al., 2011). At the time of sampling in June-July 2016, microscopy counts of
109  phytoplankton communities and chlorophyll *a* concentration, showed a late phytoplankton bloom
110  across the Strait (Table S1; described in detail by Fadeev et al. 2020). The phytoplankton
111  communities of the ice-covered EG and the ice-margin N stations were dominated by diatoms, in
112  contrast to the ice-free HG stations that were dominated by *Phaeocystis* spp. These locally defined
113  conditions correspond to an interannual trend of distinct phytoplankton bloom conditions observed in
114  the western ice-covered EGC and the eastern ice-free WSC (Nöthig et al., 2015; Fadeev et al., 2018).

### 2.1   Surface water bacterioplankton communities are affected by distinct phytoplankton bloom conditions

117  Phytoplankton blooms in surface waters generally lead to an increased cell abundance of
118  heterotrophic bacteria that are specialized on degradation of organic matter from algal exudates and
119  phytodetritus (Buchan et al., 2014; Teeling et al., 2016). Previous observations in the Fram Strait,
120  acquired using high-throughput sequencing of the 16S rRNA gene, revealed a strong influence of the
121  summerly phytoplankton bloom conditions on the bacterioplankton communities (Wilson et al.,
122  2017; Müller et al., 2018b), differing between the ice-covered and ice-free regions of the Strait
123  (Fadeev et al., 2018). During our sampling period, distinct phytoplankton bloom communities in
124  surface waters across the Strait were observed, with a *Phaeocystis*-dominated bloom in the ice-free
125  HG stations, a diatom-dominated bloom in the ice-covered EG stations, and mixed diatoms and
126  *Phaeocystis* populations bloom in the ice-margin N stations (Fadeev et al., 2020). Along with this,

127    we observed significantly higher cell abundances in the surface water total bacterioplankton
128    communities of the HG and N stations (13-21×$10^5$ cells mL$^{-1}$), as compared to the EG stations (0.5-
129    2×$10^5$ cells mL$^{-1}$; Kruskal-Wallis test; Chi square=81.85, df=2, *p*-value<0.01). The communities
130    were dominated by bacterial cells that comprised 8-11×$10^5$ cells mL$^{-1}$ in the HG and N stations, and
131    2×$10^5$ cells mL$^{-1}$ in the EG stations. Within the bacterial communities, a combination of classes that
132    are functionally associated with phytoplankton blooms in the region (*Bacteroidia*,
133    *Gammaproteobacteria*, and the phylum *Verrucomicrobia*) (Fadeev et al., 2018) showed several-fold
134    higher cell abundances in the HG and N stations (2.3-10×$10^5$ cells mL$^{-1}$), compared to the EG
135    stations (0.5-1.5×$10^5$ cells mL$^{-1}$). Jointly, these classes comprised up to 50% of the analyzed
136    bacterioplankton communities (Table 1). Other taxonomic groups, which were previously associated
137    with the Arctic water masses and winter communities in the Fram Strait (e.g., the class
138    *Deltaproteobacteria* and the *Thaumarchaeota*) (Wilson et al., 2017; Fadeev et al., 2018, 2020;
139    Müller et al., 2018b), showed higher cell abundances in the ice-covered EG stations, as compared to
140    the ice-free HG and ice-margin N stations (Table 1). Hence, the spatial variability in cell abundances
141    of different taxonomic groups was apparently associated with different stages of the phytoplankton
142    bloom and different water masses.

143    To further test the link with distinct bloom conditions or distinct physical conditions in Atlantic vs.
144    Arctic water masses, we conducted specific correlation tests between the cell abundances of different
145    taxonomic groups, temperature and salinity (Table S2), which define the distinct water masses in the
146    Fram Strait. We identified that cell abundances of *Verrucomicrobia* and its order *Opitutales*, as well
147    as the SAR11 clade and the *Rhodobacteraceae* family (both members of the class
148    *Alphaproteobacteria*), showed significant positive correlations to water temperature (Pearson's
149    correlation; *r*>0.5, *p*-value<0.05; Table S2), suggesting an association with the warmer Atlantic
150    waters of the eastern Fram Strait. The *Verrucomicrobia* has been previously shown to be a major
151    polysaccharide-degrading bacterial taxonomic group in Svalbard fjords (Cardman et al., 2014), and
152    therefore may also be associated with the outflow from the Svalbard fjords into the Atlantic waters of
153    the WSC (Cottier et al., 2005). The SAR11 clade and the *Rhodobacteraceae* have both been
154    previously shown to correlate with temperature at high latitudes (Giebel et al., 2011; Tada et al.,
155    2013), and are known to have distinct phylotypes in water masses with different temperatures (Selje
156    et al., 2004; Sperling et al., 2012; Giovannoni, 2017). However, the *Rhodobacteraceae* are also
157    known for their broad abilities in utilizing organic compounds (Buchan et al., 2014; Luo and Moran,
158    2014). Thus, one cannot rule out that their higher cell abundances in warmer waters of the HG and N
159    stations are associated with the late stage of the phytoplankton bloom and their exudates. In addition,
160    the SAR324 clade (*Deltaproteobacteria*) showed strong positive correlation with statistical
161    significance to salinity (Pearson's correlation; *r*>0.5, *p*-value<0.05; Table S2). During the summer,
162    with increased melting of sea ice, a low-salinity water layer is formed in surface waters, and the
163    strong stratification of this water layer enhances the development of the phytoplankton bloom
164    (Fadeev et al., 2018). Consequently, the correlation of SAR324 with higher salinity suggests that
165    their cell abundances are lower in surface waters where, in turn, we observe a strong phytoplankton
166    bloom (e.g., in WSC).

167    The distinct surface water masses in the region differ not only in their physical but also in their
168    biogeochemical characteristics (Wilson and Wallace, 1990; Fadeev et al., 2018), with higher
169    concentrations of inorganic nitrogen and phosphate in the Atlantic, compared to the Arctic water
170    masses. At the time of sampling, the typical Redfield ratio between inorganic nitrogen (mainly nitrate
171    $NO_3$) and inorganic phosphate ($PO_4$) was below 16 (Redfield, 1963; Goldman et al., 1979). This
172    suggests that the water masses were nitrogen limited across all three regions (Table S1) during
173    summer due to phytoplankton dynamics. In order to disentangle the effect of biological consumption

174   of nutrients from water mass-specific nutrient signatures, we calculated the seasonal net consumption
175   of inorganic nutrients, as the proxy for phytoplankton bloom conditions (Table S1). Consumed
176   nitrate ($\Delta NO_3$) and phosphate ($\Delta PO_4$) revealed a very strong positive correlation with statistical
177   significance (Pearson's correlation; $r=0.86$, $p$-value<0.05; Table S2). The consumed silica ($\Delta SiO_3$),
178   used by diatoms, did not show a significant correlation to $\Delta PO_4$ and $\Delta NO_3$. This further supports the
179   impact of different phytoplankton populations across the Strait (i.e., diatoms vs. *Phaeocystis*; Fadeev
180   et al., 2020). Phytoplankton bloom-associated environmental parameters (chlorophyll *a* concentration
181   and the consumed inorganic nutrients) revealed weaker relationships with cell abundances of
182   different taxonomic groups (Table S2). Furthermore, we did not observe significant positive
183   correlations of the cell abundances of diatoms or *Phaeocystis* spp., with the quantified
184   bacterioplankton taxa. This might be explained by time lags and local differences in the dynamic
185   development of phytoplankton blooms across the entire Strait (Wilson et al., 2017; Fadeev et al.,
186   2018).

187   The complexity of Fram Strait surface waters with different ice-coverages, a dynamic ice-melt water
188   layer and mesoscale mixing events of Atlantic and Polar water masses by eddies (Wekerle et al.,
189   2017), challenges the identification of specific associations between microbial cell abundances and
190   environmental parameters. While a mixture of all these environmental variables is likely shaping the
191   bacterioplankton communities, our results showed that elevated cell abundances of some taxonomic
192   groups (e.g., *Gammaproteobacteria*) had stronger association with phytoplankton bloom conditions
193   observed at the site (e.g., through a link with algal exudates and nutrients as main source for growth)
194   (Tada et al., 2011; Teeling et al., 2012). On the other hand, other taxonomic groups (e.g., SAR11
195   clade) were potentially more influenced by physical processes such as the presence of ice and distinct
196   Arctic water masses (Kraemer et al., 2020).

## 2.2   Bacterioplankton communities strongly change in cell abundance and composition with depth

199   We found that in all three regions, total cell abundances of the entire bacterioplankton community
200   were highest at surface with $10^5$-$10^6$ cells $mL^{-1}$, and significantly decreased with depth down to $10^4$
201   cells $mL^{-1}$ at meso- and bathypelagic depths (Figure 2a; Table S3; Kruskal-Wallis test; Chi
202   square=554.39, df=3, $p$-value<0.01). Members of the domain *Bacteria* dominated the communities
203   throughout the entire water column, with highest cell abundances in surface waters ($10^5$-$10^6$ cells $mL^{-1}$
204   ), and significantly lower $10^4$ cells $mL^{-1}$ at depth (Figure 2b; Kruskal-Wallis test; Chi square=35.27,
205   df=3, $p$-value<0.01). Archaeal cells had an overall lower abundance than bacterial cells by an order
206   of magnitude throughout the entire water column, ranging from $10^4$ cells $mL^{-1}$ at surface down to $10^3$
207   cells $mL^{-1}$ in bathypelagic waters (Figure 2c). However, unlike *Bacteria*, archaeal communities
208   doubled their absolute cell abundances from ca. $3\times10^4$ cells $mL^{-1}$ at surface to ca. $6\times10^4$ cells $mL^{-1}$ at
209   100 m depth, followed by a significant decrease in cell abundance at meso- and bathypelagic depths
210   (Kruskal-Wallis test; Chi square=29.04, df=3, $p$-value<0.01). Compared to the stronger decline in
211   bacterial cell numbers, this pattern mirrors the known global trend of relative archaeal enrichment in
212   epipelagic waters (Karner et al., 2001; Herndl et al., 2005; Kirchman et al., 2007; Varela et al., 2008;
213   Schattenhofer et al., 2009), and was also observed in other regions of the Arctic Ocean (Amano-Sato
214   et al., 2013). Altogether, observed here bacterioplankton cell abundances in surface waters were well
215   within the range of previous observations in the Fram Strait waters, conducted using flow cytometry
216   (Piontek et al., 2014; Fadeev et al., 2018; Engel et al., 2019). However, compared to recent CARD-
217   FISH based observations in eastern Fram Strait (Quero et al., 2020), cell abundances were
218   consistently one order of magnitude lower along the entire water column. The discrepancy might be
219   associated with methodological differences, such as shorter staining times and the usage of an

220 automated over a manual counting approach in our study. Nevertheless, both studies showed a
221 similar pattern of a strong decrease in bacterioplankton cell abundances with depth, which also
222 matches observations in other oceanic regions (Karner et al., 2001; Church et al., 2003; Teira et al.,
223 2004; Schattenhofer et al., 2009; Dobal-Amador et al., 2016).

224 In surface waters of all stations, ca. 60% of DAPI-stained total bacterioplankton community was
225 covered by the *Bacteria*-specific probes (EUB388 I-III; Table S3). At depth (>100 m), the coverage
226 of total cells by the *Bacteria*-specific probes strongly decreased to 16-40% of DAPI-stained cells
227 (ANOVA; $F_3$=15.39, $p$<0.01; Table S3). A similar decrease in detectability of the domain-specific
228 probes was previously observed in other bacterioplankton microscopy studies (Karner et al., 2001;
229 Herndl et al., 2005; Varela et al., 2008), and reasons may lie in a ribosomal nucleic acid
230 concentration decrease within the bacterial cells (i.e., lower activity) towards the oligotrophic depths.
231 In addition, there is a potential increase with greater water depths of microbial phylogenetic groups
232 that are not captured by the currently existing probes (Hewson et al., 2006; Galand et al., 2009a;
233 Agogué et al., 2011; Welch and Huse, 2011; Salazar et al., 2016).

234 Interestingly, the *Archaea*-specific probe (ARCH915) showed a different trend. In surface waters, the
235 coverage of the probe was higher in the ice-covered EG stations (8% of DAPI-stained cells),
236 compared to ice-free HG and ice-margin N stations (1-2% of DAPI-stained cells; Table S3). With
237 depth (>100 m), in EG stations the coverage of the probe increased ca. twofold, while in HG and N
238 stations the coverage of the probe increased ca. tenfold. Overall, across all three regions, coverage of
239 the *Archaea*-specific probe was significantly higher at depth (ANOVA; $F_3$=34.31, $p$<0.01), reaching
240 13-17% of DAPI-stained cells (Table S3). This trend implies an increase in relative abundance of
241 *Archaea* with depth (Müller et al., 2018a; Fadeev et al., 2020). Taken together, our findings confirm
242 previously observed higher abundances of *Archaea* in bacterioplankton communities of ice-covered
243 waters (Wilson et al., 2017; Müller et al., 2018b; Fadeev et al., 2020), and correspond to the globally
244 observed trend of an increasing archaeal importance at depth (Herndl et al., 2005; Teira et al., 2006;
245 Galand et al., 2009b).

## 2.3 Enigmatic microbial lineages increase in cell abundance towards the deep ocean

247 The deep waters of the Fram Strait basin (>500 m) have a rather homogeneous hydrography (von
248 Appen et al., 2015), and are less affected by the seasonal dynamics that govern the surface layers
249 (Wilson et al., 2017). Previous molecular observations of the deep water bacterioplankton
250 communities showed high sequence abundances of largely unknown taxonomic groups, such as the
251 SAR202 (class *Dehalococcoidia*), SAR324 (*Deltaproteobacteria*), and SAR406 (phylum
252 *Marinimicrobia*) (Wilson et al., 2017; Fadeev et al., 2020; Quero et al., 2020). There was also higher
253 archaeal sequence abundance at depth, with the class *Nitrososphaeria* reaching up to 15% of the
254 sequences in mesopelagic waters (> 200 m) (Wilson et al., 2017; Müller et al., 2018b; Fadeev et al.,
255 2020). However, it has also been recently shown that in ice-covered regions of the Strait surface-
256 dominant taxonomic groups, such as *Gammaproteobacteria* and *Nitrososphaeria*, are exported via
257 fast-sinking aggregates from surface to the deep ocean (>1000 m), where they may realize an
258 ecological niche (Fadeev et al., 2020). We observed that in all meso- and bathypelagic waters across
259 all analyzed regions the total cell abundances of the bacterioplankton communities were in the range
260 of $10^4$ cells mL$^{-1}$ (Figure 2), reflecting observations made in other regions of the Arctic Ocean (Wells
261 and Deming, 2003; Wells et al., 2006). Bacterial taxonomic groups that dominated the surface water
262 communities (e.g., *Bacteroidetes*, *Gammaproteobacteria* and *Verrucomicrobia*), in both ice-free and
263 ice-covered regions of the Strait, decreased by two orders of magnitude in their cell abundances at
264 meso- and bathypelagic depths (Kruskal-Wallis test; $p$-value<0.01; Table 2). This trend strongly

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265 correlated with the total bacterioplankton cell abundances along the general water column (Pearson's
266 correlation; $r>0.8$, $p$-value$<0.05$; Figure S1). In contrast, other bacterial groups, such as the SAR202
267 and SAR324 clades, proportionally increased in cell abundances with depth, and maintained overall
268 constant cell abundances of ca. $0.5\times10^4$ cells mL$^{-1}$ until the deep basin (Table 2). Previous molecular
269 studies of bacterioplankton communities in the Fram Strait suggested a proportional increase of these
270 largely understudied bacterial lineages in the deep ocean, which were previously found to be
271 associated with winterly (surface) bacterioplankton (Wilson et al., 2017; Fadeev et al., 2020). The
272 cell abundances presented here indicate that their increasing proportional abundance at depth is due
273 to stronger decrease in the cell abundances of other groups (Table 2; Table S4). Very little is
274 currently known about these two taxonomic groups, but previous genetic observations suggest that
275 they possess distinct metabolic capabilities, and may be involved in the degradation of recalcitrant
276 organic matter (SAR202 clade; Landry et al., 2017; Colatriano et al., 2018; Saw et al., 2019), or, in
277 sulfur oxidation (SAR324 clade; Swan et al., 2011; Sheik et al., 2014). Their homogeneous
278 distribution from the stratified surface to the homogenous deep ocean of the Fram Strait suggests that
279 these enigmatic bacterial groups fulfil an ecological niche that exists in the entire water column, and
280 thus may have unique roles in oceanic nutrient cycling.

281 The proportional decrease of archaeal cell abundances with depth was less than that of members of
282 the domain *Bacteria* (Table S4), meaning that members of the *Archaea* were proportionally
283 increasing in the total microbial deep-water communities. The *Thaumarchaeota* strongly correlated
284 with the pattern of the archaeal cell abundances (Pearson's correlation; $r=0.76$, $p$-value$<0.05$; Figure
285 S1), showing a two-fold increase in cell abundance from surface to epipelagic depth (100 m),
286 followed by a substantial decrease towards meso- and bathypelagic waters (Table S4). This two-fold
287 increase towards the epipelagic depths corresponds to previous observations of *Thaumarchaeota* in
288 the north Atlantic (Müller et al., 2018b) and further increase in cell abundances at higher depths
289 (>1000 m) was also observed in other oceanic regions (Karner et al., 2001; Church et al., 2003;
290 Herndl et al., 2005). It has been shown in molecular studies that *Thaumarchaeota* comprise a large
291 proportion of the bacterioplankton communities in the Fram Strait, especially in the epipelagic waters
292 (Wilson et al., 2017; Müller et al., 2018b; Fadeev et al., 2020). In our study, the *Thaumarchaeota*
293 exhibited their highest cell abundances at 100 m in the ice-free HG, and at the ice-margin N stations
294 ($3\times10^4$ cells mL$^{-1}$), where they comprised half of the total archaeal community (Table S4). The
295 strong absolute decrease of *Thaumarchaeota* cell abundances towards the meso- and bathypelagic
296 waters suggests a decrease in activity with depth (Herndl et al., 2005; Kirchman et al., 2007; Alonso-
297 Sáez et al., 2012), and thus lower cell detectability. In deeper water layers, other pelagic archaeal
298 groups, such as the phylum *Euryarchaeota* that was not quantified in this study, may increase in
299 abundance and form the bulk of total archaeal cells here (Galand et al., 2010; Fadeev et al., 2020).

## 3    Conclusions

301 Using state-of-the-art semi-automatic microscopy cell counting, we quantified the absolute cell
302 abundance of 14 key taxonomic groups in summer bacterioplankton communities of the Fram Strait.
303 Our observations covered both the ice-free and ice-covered regions of the Strait, which at the time of
304 sampling were characterized by different phytoplankton bloom stages. Our results showed that in
305 surface waters, abundance of some taxonomic groups was related to the Atlantic waters (e.g.,
306 *Rhodobacteraceae*). The abundance of different taxonomic groups was strongly positively (e.g.,
307 *Gammaproteobacteria*) and negatively (e.g., SAR324 clade) associated with the states of the
308 seasonal phytoplankton bloom across the Strait. Based on previous studies in the region, it is
309 conceivable that there were also specific associations between the of blooming phytoplankton and
310 different bacterioplankton taxa, however these were not observed in our analysis. This suggests that

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311 currently predicted longer seasonal phytoplankton blooms, as well as the increasing Atlantic
312 influence on the Arctic Ocean (i.e., 'Atlantification'), may have a strong impact on the composition
313 and biogeographical distribution of certain bacterioplankton taxonomic groups in the surface Arctic
314 waters.

315 This study also provides the first extensive quantification of bacterioplankton communities in the
316 deep Arctic water column (> 500 m). We showed that with depth, some taxonomic groups, such as
317 the SAR202 clade, maintained similar abundances throughout the entire water column (2500 m
318 depth), where other taxa decline by several-fold. This observation suggests that despite their low
319 abundance, some taxonomic groups may potentially realize a unique ecological niche throughout the
320 entire water column.

321 Altogether, our quantitative data on cell abundances of ecologically relevant taxonomic
322 bacterioplankton groups provide insight into factors structuring pelagic bacterioplankton
323 communities from surface to the deep waters of the Arctic Ocean and a baseline to better assess
324 future changes in a rapidly warming region.

## 4    Materials and Methods

### 4.1    Sampling and environmental data collection

327 Sampling was carried out during the RV Polarstern expedition PS99.2 to the Long-Term Ecological
328 Research (LTER) site HAUSGARTEN in Fram Strait (June 24th – July 16th, 2016). Sampling was
329 carried out with 12 L Niskin bottles mounted on a CTD rosette (Sea-Bird Electronics Inc. SBE 911
330 plus probe) equipped with temperature and conductivity sensors, a pressure sensor, altimeter, and a
331 chlorophyll fluorometer. On board, the samples were fixed with formalin in a final concentration of
332 2% for 10 – 12 hours, then filtered onto 0.2 µm polycarbonate Nucleopore Track-Etched filters
333 (Whatman, Buckinghamshire, UK), and stored at -20°C for further analysis.

334 Hydrographic data of the seawater including temperature and salinity were retrieved from
335 PANGAEA (Schröder and Wisotzki, 2014), along with measured chlorophyll *a* concentration
336 (Nöthig et al., 2018; Fadeev et al., 2020) (Table S1).

### 4.2    Catalyzed reporter deposition-fluorescence in situ hybridization (CARD-FISH)

338 We quantified absolute cell abundances of 14 key bacterioplankton groups (Table S5), based on their
339 relatively high sequence abundance and recurrences in previous molecular studies of Arctic waters
340 (Bowman et al., 2012; Wilson et al., 2017; Müller et al., 2018b; Fadeev et al., 2020). CARD-FISH
341 was applied based on the protocol established by (Pernthaler et al., 2002), using horseradish-
342 peroxidase (HRP)–labelled oligonucleotide probes (Biomers.net, Ulm, Germany). All probes were
343 checked for specificity and coverage of their target groups against the SILVA database release 132
344 (Quast et al., 2013). All filters were embedded in 0.2% low-gelling-point agarose, and treated with 10
345 mg mL$^{-1}$ lysozyme solution (Sigma-Aldrich Chemie GmbH, Hamburg, Germany) for 1 h at 37°C.
346 Filters for enumerating *Archaea* and *Thaumarchaeota* were treated for an additional 30 min in 36 U
347 mL$^{-1}$ achromopeptidase (Sigma-Aldrich Chemie GmbH, Hamburg, Germany) and 15 µg mL$^{-1}$
348 proteinase K at 37°C. Subsequently, endogenous peroxidases were inactivated by submerging the
349 filter pieces in 0.15% $H_2O_2$ in methanol for 30 min before rinsing in Milli-Q water and dehydration
350 in 96% ethanol. Then, the filters were covered in hybridization buffer and a probe concentration of
351 0.2 ng µL$^{-1}$. Hybridization was performed at 46°C for 2.5 h, followed by washing in pre-warmed
352 washing buffer at 48°C for 10 min, and 15 min in 1x PBS. Signal amplification was carried out for

8

353 45 min at 46°C with amplification buffer containing either tyramide-bound Alexa 488 (1 µg/mL) or
354 Alexa 594 (0.33 µg mL$^{-1}$). Afterwards, the cells were counterstained in 1 µg/mL DAPI (4′,6-
355 diamidino-2-phenylindole; Thermo Fisher Scientific GmbH, Bremen, Germany) for 10 min at 46°C.
356 After rinsing with Milli-Q water and 96% ethanol, the filter pieces were embedded in a 4:1 mix of
357 Citifluor (Citifluor Ltd, London, United Kingdom) and Vectashield (Vector Laboratories, Inc.,
358 Burlingame, United States), and stored overnight at -20°C for later microscopy evaluation.

### 4.3 Automated image acquisition and cell counting

360 The filters were evaluated microscopically under a Zeiss Axio Imager.Z2 stand (Carl Zeiss
361 MicroImaging GmbH, Jena, Germany), equipped with a multipurpose fully automated microscope
362 imaging system (MPISYS), a Colibri LED light source illumination system, and a multi-filter set
363 62HE (Carl Zeiss MicroImaging GmbH, Jena, Germany). Pictures were taken via a cooled charged-
364 coupled-device (CCD) camera (AxioCam MRm; Carl Zeiss AG, Oberkochen, Germany) with a 63×
365 oil objective, a numerical aperture of 1.4, and a pixel size of 0.1016 µm/pixel, coupled to the
366 AxioVision SE64 Rel.4.9.1 software (Carl Zeiss AG, Oberkochen, Germany) as described by
367 (Bennke et al., 2016). Exposure times were adjusted after manual inspection with the AxioVision
368 Rel.4.8 software coupled to the SamLoc 1.7 software (Zeder et al., 2011), which was also used to
369 define the coordinates of the filters on the slides. For image acquisition, channels were defined with
370 the MPISYS software, and a minimum of 55 fields of view with a minimum distance of 0.25 mm
371 were acquired of each filter piece by recoding a z-stack of 7 images in autofocus.

372 Cell enumeration was performed with the software Automated Cell Measuring and Enumeration Tool
373 (ACMETool3, 2018-11-09; M. Zeder, Technobiology GmbH, Buchrain, Switzerland). Cells were
374 counted as objects according to manually defined parameters separately for the DAPI and FISH
375 channels.

### 4.4 Calculation of consumed inorganic nutrients

377 Following (Fadeev et al., 2018) the nutrient consumption (Δ) at each station was calculated by
378 subtracting the mean value of all collected measurements above 50 m from the mean value of all
379 collected measurements between 50 and 100 m (below the seasonal pycnocline).

### 4.5 Statistical analyses

381 All statistical analyses and calculations in this study were performed using R (v4.0.2) (www.r-
382 project.org) in RStudio (v1.3.1056), *i.e.* statistical tests for normality, ANOVA and Kruskal-Wallis.
383 Post-hoc Wilcoxon test and Pearson's rank correlation coefficient were conducted with the R package
384 "rstatix" (v0.6.0) (Kassambara, 2020). Plots were generated using the R package "ggplot2" (v3.3.2)
385 (Wickham, 2016) and "tidyverse" (v1.3.0) (Wickham et al., 2019).

### 4.6 Data availability

387 All data is accessible via the Data Publisher for Earth & Environmental Science PANGAEA
388 (www.pangaea.de): cell abundances under doi:10.1594/PANGAEA.905212, and inorganic nutrient
389 measurements under doi:10.1594/PANGAEA.906132. Scripts for processing the data can be
390 accessed at https://github.com/edfadeev/FramStrait-counts.

### 4.7 Conflict of Interest

392  *The authors declare that the research was conducted in the absence of any commercial or financial*
393  *relationships that could be construed as a potential conflict of interest.*

## 5  Author contributions

395  MC-M, EF and VS-C designed and conducted the study. MC-M, EF and VS-C wrote the manuscript
396  with guidance from AB. All authors critically revised the manuscript and gave their approval of the
397  submitted version.

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687 **9     Figures and Tables**

688   **Figure 1**. Oceanographic overview of the Fram Strait, including the monthly mean of sea-ice cover
689   and sea surface temperature during July 2016. The sea ice concentration is represented by inverted
690   grayscale (gray=low, white=high). Arrows represent general directions of the WSC (in red) and the
691   EGC (in blue). Stations of water column sampling are indicated and colored according to their sea-
692   ice conditions: ice-covered EGC stations - blue, ice-margin N stations - gray, ice-free WSC stations -
693   red. The map was modified from (Fadeev et al., 2020).

694   **Figure 2.** Bacterioplankton cell abundances in the different regions of the Fram Strait: Total
695   bacterioplankton (A); *Bacteria* (B); and *Archaea* (C). Box plots were calculated based on cell
696   abundance. Note the different scale of the cell abundances for *Archaea*. The different regions are
697   indicated by color: ice-covered EGC- blue, ice-margin N - gray, ice-free WSC - red. The asterisks
698   represent levels of statistical significance of difference between all three regions per depth and
699   domain: * < 0.05, ** < 0.01, *** < 0.001.

700 **Table 1**. Average cell abundances and proportions (% of DAPI stained cells) of selected taxonomic groups in surface (0-30 m) and
701 epipelagic (100 m) depths of different regions across the Fram Strait. The proportions (%) were calculated based on the total
702 bacterioplankton cell abundances, 'n' represents the number of counted fields of view. All values are represented in $10^5$ cells mL$^{-1}$. SAR11
703 clade (SAR11), *Gammaproteobacteria* (GAM), *Alteromonadaceae/Colwelliaceae/Pseudoalteromonadaceae* (ATL), *Bacteroidetes* (BACT),
704 *Polaribacter* (POL), *Verrucomicrobiales* (VER), *Opitutales* (OPI), *Rhodobacteraceae* (ROS), *Deltaproteobacteria* (DELTA), and
705 *Thaumarchaeota* (THA).

| Region | Water layer | SAR11 | % | n | GAM | % | n | ALT | % | n | BACT | % | n | POL | % | n |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EGC | Surface | 1.9 ± 0.7 | 50 | 53 | 0.3 ± 0.2 | 13 | 67 | 0.2 ± 0.1 | 7 | 64 | 0.6 ± 0.4 | 18 | 66 | 0.4 ± 0.3 | 11 | 62 |
| EGC | Epipelagic | 1.0 ± 0.6 | 26 | 50 | 0.2 ± 0.1 | 5 | 77 | 0.1 ± 0.0 | 2 | 61 | 0.3 ± 0.2 | 8 | 93 | 0.1 ± 0.0 | 2 | 52 |
| N | Surface | 4.2 ± 1.0 | 24 | 81 | 2.1 ± 0.6 | 13 | 78 | 0.1 ± 0.0 | 1 | 68 | 2.1 ± 0.8 | 12 | 85 | 1.3 ± 0.6 | 8 | 85 |
| N | Epipelagic | 2.2 ± 0.3 | 29 | 73 | 0.4 ± 0.1 | 5 | 109 | 0.2 ± 0.1 | 2 | 87 | 0.4 ± 0.1 | 6 | 102 | 0.1 ± 0.0 | 2 | 98 |
| WSC | Surface | 6.1 ± 2.0 | 38 | 150 | 1.6 ± 0.3 | 14 | 189 | 0.3 ± 0.1 | 2 | 186 | 2.1 ± 1.0 | 16 | 163 | 0.8 ± 0.2 | 7 | 162 |
| WSC | Epipelagic | 1.9 ± 0.2 | 32 | 175 | 0.2 ± 0.0 | 3 | 214 | 0.1 ± 0.0 | 1 | 186 | 0.2 ± 0.0 | 4 | 195 | 0.1 ± 0.0 | 1 | 176 |

| Region | Water layer | VER | % | n | OPI | % | n | ROS | % | n | DELTA | % | n | THA | % | n |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EGC | Surface | 0.1 ± 0.0 | 3 | 41 | 0.1 ± 0.0 | 2 | 53 | 0.2 ± 0.1 | 7 | 44 | 0.2 ± 0.1 | 7 | 57 | 0.1 ± 0.0 | 3 | 34 |
| EGC | Epipelagic | 0.1 ± 0.0 | 2 | 63 | 0.1 ± 0.0 | 2 | 70 | 0.3 ± 0.2 | 9 | 60 | 0.1 ± 0.0 | 4 | 67 | 0.1 ± 0.02 | 4 | 75 |
| N | Surface | 0.9 ± 0. 1 | 5 | 91 | 0.9 ± 0.01 | 5 | 91 | 0.6 ± 0.0 | 3 | 92 | 0.2 ± 0.1 | 1 | 86 | 0.1 ± 0.0 | 1 | 65 |
| N | Epipelagic | 0.2 ± 0.1 | 2 | 98 | 0.2 ± 0.1 | 2 | 107 | 0.2 ± 0.0 | 3 | 108 | 0.2 ± 0.0 | 3 | 94 | 0.3 ± 0.0 | 4 | 122 |

| WSC | Surface | 1.1 ± 0.0 | 5 | 171 | 0.8 ± 0.3 | 5 | 172 | 0.7 ± 0.3 | 4 | 165 | 0.1 ± 0.0 | 1 | 121 | 0.1 ± 0.0 | 1 | 178 |
| WSC | Epipelagic | 0.1 ± 0.0 | 2 | 219 | 0.1 ± 0.0 | 2 | 238 | 0.1 ± 0.0 | 2 | 223 | 0.2 ± 0.1 | 4 | 196 | 0.3 ± 0.1 | 5 | 246 |

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708 **Table 2**. Average cell abundances and proportions (% of DAPI stained cells) of selected taxonomic groups in deep water layers of the
709 different regions across the Fram Strait. The proportions (%) were calculated based on the total bacterioplankton cell abundances, 'n'
710 represents the number of counted fields of view. Standard error was not calculated for samples of the EGC located in the bathypelagic zone
711 due to one station located at this depth in the region. All values are represented in $10^5$ cells $mL^{-1}$. *Chloroflexi* (CFX), *Deltaproteobacteria*
712 (DELTA)*, Thaumarchaeota* (THA), *Rhodobacteraceae* (ROS), SAR202, SAR324, SAR406 and SAR11 clades.

| Region | Water layer | CFX | % | n | DELTA | % | n | THA | % | n | ROS | % | n |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| EGC | Mesopelagic | 0.02 ± 0.0 | 5 | 57 | 0.03 ± 0.01 | 5 | 45 | 0.01 ± 0.0 | 2 | 27 | 0.1 ± 0.0 | 11 | 75 |
| EGC | Bathypelagic | 0.02 ± NA | 4 | 18 | 0.02 ± NA | 3 | 33 | 0.01 ± NA | 2 | 14 | 0.03 ± NA | 5 | 14 |
| N | Mesopelagic | 0.03 ± 0.0 | 3 | 116 | 0.04 ± 0.0 | 5 | 99 | 0.01 ± 0.0 | 1 | 28 | 0.1 ± 0.01 | 13 | 128 |
| N | Bathypelagic | 0.02 ± 0.0 | 6 | 115 | 0.03 ± 0.0 | 8 | 123 | 0.01 ± 0.0 | 4 | 39 | 0.1 ± 0.0 | 20 | 122 |
| WSC | Mesopelagic | 0.03 ± 0.0 | 3 | 217 | 0.1 ± 0.01 | 6 | 139 | 0.02 ± 0.0 | 3 | 86 | 0.1 ± 0.01 | 7 | 195 |
| WSC | Bathypelagic | 0.02 ± 0.0 | 4 | 199 | 0.1 ± 0.02 | 9 | 130 | 0.02 ± 0.0 | 4 | 54 | 0.04 ± 0.01 | 14 | 197 |
| **Region** | **Water layer** | **SAR202** | **%** | **n** | **SAR324** | **%** | **n** | **SAR406** | **%** | **n** | **SAR11** | **%** | **n** |
| EGC | Mesopelagic | 0.02 ± 0.0 | 4 | 55 | 0.05 ± 0.0 | 6 | 60 | 0.01 ± 0.0 | 1 | 11 | 0.15 ± 0.1 | 22 | 49 |
| EGC | Bathypelagic | 0.02 ± NA | 5 | 26 | 0.03 ± NA | 5 | 35 | 0.01 ± NA | 3 | 6 | 0.07 ± NA | 14 | 32 |
| N | Mesopelagic | 0.03 ± 0.0 | 3 | 107 | 0.06 ± 0.0 | 6 | 66 | 0.01 ± 0.0 | 1 | 18 | 0.17 ± 0.0 | 20 | 101 |
| N | Bathypelagic | 0.03 ± 0.0 | 8 | 120 | 0.03 ± 0.0 | 8 | 54 | 0.01 ± 0.0 | 3 | 37 | 0.09 ± 0.0 | 27 | 85 |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| WSC | Mesopelagic | 0.03 ± 0.0 | 5 | 215 | 0.05 ± 0.0 | 5 | 168 | 0.01 ± 0.0 | 2 | 37 | 0.16 ± 0.0 | 19 | 166 |
| WSC | Bathypelagic | 0.03 ± 0.0 | 7 | 210 | 0.05 ± 0.0 | 6 | 138 | 0.01 ± 0.0 | 3 | 45 | 0.09 ± 0.0 | 21 | 201 |

Figure showing cell abundance (cells mL$^{-1}$) across regions (WSC, N, EGC) and depth zones (surface 15-30 m, epipelagic 100 m, mesopelagic 500-1000 m, bathypelagic >1200 m) in panels A, B, and C.