

# Long-term measurements reveal a 100-day lag between peaks in phytoplankton chlorophyll and benthic bacterial abundance in the Fram Strait

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## Abstract

Repeated measurements of benthic and pelagic parameters in the rapidly changing Arctic Ocean provide a unique insight into spatial and interannual trends and changes in the ecosystem. Here, we compiled biogenic and biogeochemical measurements collected from sediment cores at the Long-Term Ecological Research Observatory HAUSGARTEN located in the Fram Strait. A total of 21 stations were visited yearly over a period of 18 years (2002–2019). The time series highlighted an increase in bacterial numbers for samples collected 50 days after the peak phytoplankton bloom. Although bacterial abundances were not bathymetric depth-dependent when viewed across all years, we observed a seasonal trend in benthic microbial abundance closely related to the timing of the phytoplankton bloom with a time-lag of 100 days between the surface phytoplankton peak and the peak in bacterial abundance in the sediment. Considering the residence time of phytoplankton in the upper ocean and the water depth, we estimated an average settling velocity for phytodetritus of 30 m.d<sup>-1</sup>, which is similar to previous observations from Fram Strait. This suggests that settling organic matter promotes vertical microbial connectivity and benthic bacterial abundance in the deep ocean, shaping the microbial biogeography, diversity, and biogeochemical processes.

**Keywords:** vertical microbial connectivity; bacteria; phytoplankton sedimentation and deposition; long-term observations; LTER HAUSGARTEN

## Introduction

While global warming has already caused drastic changes in high-latitude ecosystems during the past decades, we are still only beginning to understand what consequences such changes have on pelagic and benthic biogeochemical processes. Since the 2000s, the Arctic sea-ice extent has decreased by ~12.8% per decade (Meredith et al. 2019), implying strong physical (e.g. stratification, light availability) and ecosystemic perturbations (e.g. shifts in species composition, carbon export; Ramondenc et al. 2022).

The marine Arctic biogeochemical cycles are shaped by Pacific and Atlantic inflows, as well as the influence of large Arctic rivers, which carry heat, nutrients, and planktonic organisms to the Central Arctic Ocean (CAO). The Fram Strait is the only deepwater gateway to the CAO that is affected by marine heatwaves, often referred to as the “Warm Water Anomaly” (Beszczynska-Möller et al. 2012). Still, the difficulties in accessing the region during winter limit our ability to study the consequences and predict the repercussions of environmental changes on Arctic and subarctic ecosystems. To compensate for the poor accessibility, polar ocean observatories have been established (Soltwedel et al. 2005) and have improved our understanding of interannual changes in pelagic (Nöthig et al. 2015, Schröter et al. 2019, Nöthig et al. 2020) and benthic species composition (Taylor et al. 2017; Soltwedel et al. 2020, Górska et al. 2022). Moreover, the development of autonomous instruments mounted on mooring lines, i.e.

sediment traps, helps to describe both the interannual and seasonal patterns of planktonic composition in the water column with environmental factors. For instance, Ramondenc et al. (2022) used swimmer abundances from sediment traps as a proxy for monthly and yearly zooplankton distribution. While pelagic sampling is possible using autonomous systems, sampling of benthic ecosystems generally requires access with a research vessel, which limits sampling to the summer period.

Originally, the ocean seafloor was considered to be a stable environment without seasonal variability (Sanders 1968), suggesting that the time of sampling does not impact the scientific results. However, today we know that polar marine ecosystems exhibit extreme seasonality with a robust and tight pelagic-benthic coupling (Carmack and Wassmann 2006, Wassmann et al. 2006), which is driven by organic matter deposition on the seafloor. Phytoplankton blooms at high latitudes reach a maximum between May and July (Mayot et al. 2018) and display different timing, duration, and magnitude according to the sea-ice conditions and water stratification (Carmack and Wassmann 2006, Mayot et al. 2018). After being produced in the euphotic zone and before reaching the ocean floor, the organic matter undergoes multiple transformations, such as heterotrophic bacteria remineralization (Kwon et al. 2009), zooplankton grazing, and fecal pellet production (Van der Jagt et al. 2020), while being exported as aggregates and marine particles through the water column (Iversen 2023). Hence, beyond the supply of food to the deep

sea and seafloor, sinking aggregates connect and disperse pro- and eukaryotic organisms from the surface to the deep ocean (Preston *et al.* 2020, Fadeev *et al.* 2021). Owing to the sampling strategy and restricted access to the Fram Strait throughout the year, benthic researches focused on studying the spatial and interannual variabilities of benthic organisms across all size classes, from bacteria (Jacob *et al.* 2013) to epi/megafauna (Bergmann *et al.* 2011, Vedenin *et al.* 2019, Soltwedel *et al.* 2020). However, further insights into how the seasonal input of organic matter, as well as pro- and eukaryotes to the Arctic and Subarctic seafloor, impacts the benthic microbial dynamics are essential. This understanding is critical for unraveling the complexities of biogeochemical cycling and nutrient production in the deep sea.

The question therefore arises: Is the abundance of Arctic benthic bacteria on the seafloor stable over time, or have we overlooked temporal patterns due to limited sampling periods? To answer this question, we combined annually collected data from a time series spanning from 2002 to 2019 at the HAUSGARTEN observatory. The main objectives of this study were to (i) characterize the spatiotemporal changes of bacterial abundance in the surface layer of the deep seafloor, (ii) determine bacterial dynamics in relation to environmental conditions, and (iii) identify potential factors that impact seasonal variations in benthic bacterial communities in the Fram Strait.

## Materials and methods

### Study area

The Fram Strait is located between Greenland and the Svalbard archipelago, acting as a passage between the northward-flowing, salty, and warm West Spitsbergen Current (WSC) and the southward-flowing, cold, and fresher East Greenland Current (EGC) (Fig. 1). Besides the general water flow that creates a strong longitudinal gradient, a part of the WSC recirculates in the central Fram Strait (Fig. 1). Faced with the high ecological interest of this area, the Alfred Wegener Institute Helmholtz Center for Polar and Marine Research (AWI) established the Long-Term Ecological Research (LTER) observatory HAUSGARTEN in 1999. Currently, the observatory is composed of 21 permanent stations covering the entire water column (a water depth range of 250–5500 m) and the uppermost sediment layers of the sea floor (Soltwedel *et al.* 2016) (Fig. 1, Table S1). The LTER site is visited yearly during the Arctic summer to conduct repeat sampling (e.g. water samples, sediment cores) and deploy moorings that are equipped with autonomous instruments performing year-round measurements and sampling (e.g. temperature and oxygen sensors, autonomous water samplers, sediment traps). In this context, the HAUSGARTEN observatory represents a unique sampling site allowing synchronous multidisciplinary research activities to study the pelagic-benthic coupling in a region strongly exposed to climate change.

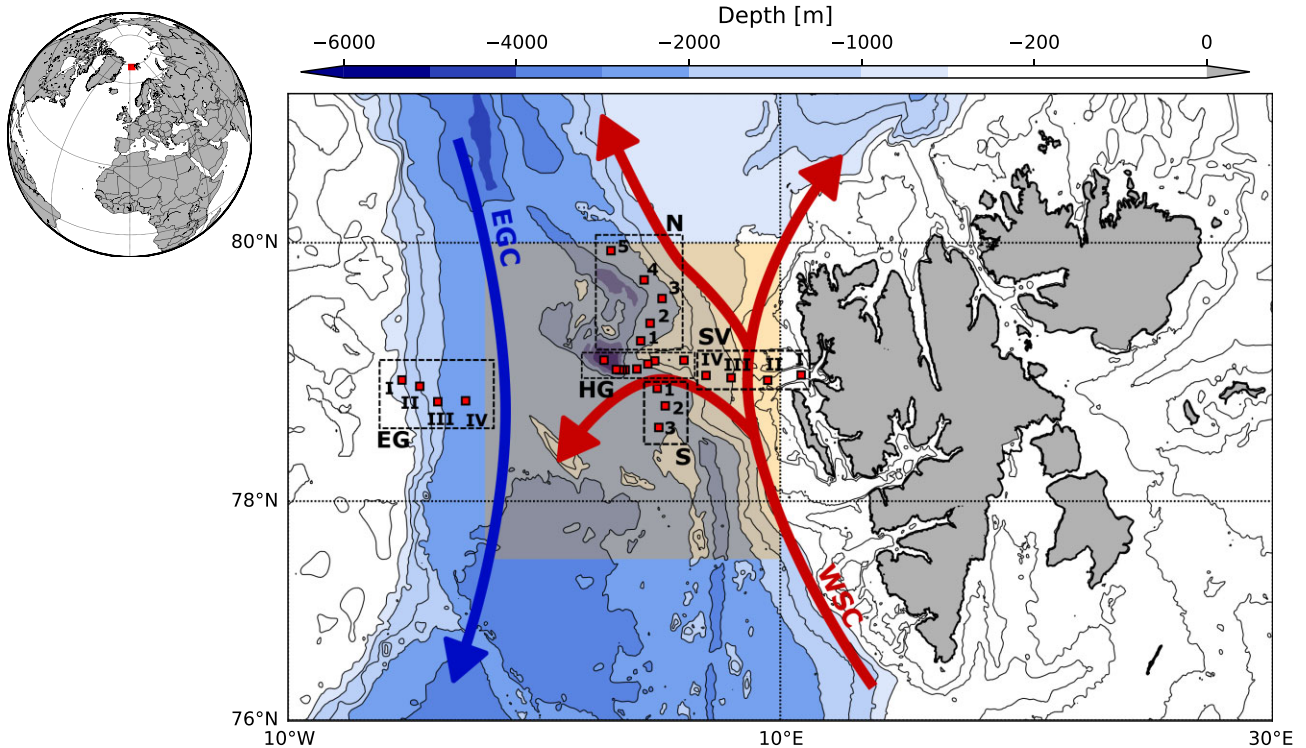
### Sediment collection and treatment

During the polar expeditions operated by the Alfred Wegener Institute from 2002 to 2019, a Multiple Corer (MUC) was used to sample the uppermost sediment layers at each of the 21 HAUSGARTEN sampling sites (Table S1; Fig. 1 *red squares*). At each station, three sediment samples were taken from three different cores collected by the same multicorer

deployment. The upper five centimeters of the MUC cores were then subsampled using disposable plastic syringes with the anterior ends cut off ( $\varnothing$  1.2 and 2 cm). Sediments were analyzed for various biogenic compounds, bacterial numbers, and biomass as well as bacterial exo-enzymatic activity (see below). Samples for biogeochemical measurements were preserved on board and stored at  $-20^{\circ}\text{C}$  for later analyses in the home laboratory, always directly after the cruise. Bacterial exo-enzymatic activity measurements were conducted on board immediately after sampling, while sediment for bacterial counts was preserved in 2% formalin right after sampling to stop metabolic processes, cell division and to ensure cell integrity during storage. Water content, indicating the porosity of the sediments, was determined by measuring the weight loss of wet sediment samples dried at  $60^{\circ}\text{C}$ . Total organic matter content was determined as ash-free dry weight after combustion of the dried sediment (2 h at  $500^{\circ}\text{C}$ ; Greiser and Faubel 1988). The total of available organic hydrocarbons in the sediment was assessed by measuring the organic carbon content via gas chromatography using a CNS element analyzer (Kirsten 1979). The availability of phytodetritus, which represents the prime food source for benthic organisms, was assessed from measurements of sediment-bound chlorophyll-*a* and its degradation products (phaeopigments). Chloroplastic pigments were extracted in 90% acetone and measured on a Turner fluorometer (Shuman and Lorenzen 1975). The bulk pigments (chlorophyll-*a* plus phaeopigments) were termed chloroplastic pigment equivalents (CPE; Thiel 1978). Particulate proteins, operationally defined as  $\gamma$ -globulin equivalents, were measured according to the Bradford method as described in Greiser and Faubel (1988). Phospholipid concentrations were used as a proxy for the total microbial biomass in the sediments. Lipids were determined following a method provided by Findlay *et al.* (1989), with slight modifications as described in Boetius and Lochte (1994). Bacterial abundance was counted manually by epifluorescence microscopy after staining with acridine orange, according to Meyer-Reil (1983). Volumetric determinations to estimate the mean bacterial biomass per cell were conducted with the Porton grid as described by Grossmann and Reichardt (1991). Bacterial biomass was estimated using a conversion factor of  $3.0 \cdot 10^{-13} \text{ g C } \mu\text{m}^{-3}$  (Børsheim *et al.* 1990). Bacterial enzymatic activities (esterase turnover rates) were estimated using the fluorogenic substrate fluorescein-di-acetate (FDA). FDA measurements, assessing the potential hydrolytic activity of bacteria, were carried out according to Köster *et al.* (1991). All raw data used in this study are provided in the Supplementary data (Table S1).

### Chlorophyll-*a* concentration and analyses

Merged sensor (MERIS, MODIS aqua, SeaWiFS, VIIRS, OLCI) products of the ESA Ocean Color CCI Climate Change Initiative are used to compute surface chlorophyll-*a* concentration (Version 4.0, European Space Agency, available online at <http://www.esa-oceancolour-cci.org>). Monthly average chlorophyll-*a* data with a 4 km spatial resolution were extracted from 1998 to 2019 for the region of the HAUSGARTEN observatory [area between  $77.5^{\circ}\text{N}$  and  $80^{\circ}\text{N}$  and  $2^{\circ}\text{W}$  and  $10^{\circ}\text{E}$  in Fram Strait] (Fig. 1 *large orange rectangle*). Annual surface phytoplankton phenology was plotted as Julian days and then smoothed by applying a locally weighted



**Figure 1.** Sampling sites of the LTER observatory HAUSGARTEN and major currents in the Fram Strait (WSC: West Spitsbergen Current; EGC: Eastern Greenland Current). The orange-shaded area represents data taken for long-term analyses of monthly chlorophyll-a recorded by satellite from 1998 to 2019. The abbreviations SV, S, N, EG, and HG refer to the Svalbard, South, North, East Greenland, and HAUSGARTEN sampling areas, respectively.

smoothing. The day of chlorophyll peak for each year was defined as the maximum of the smoothed trends.

### Statistical analyses

We used a principal component analysis (PCA) to identify key environmental variables driving bacterial abundance and activity in the multidimensional data set. To avoid statistical bias, samples where some parameters were missing were not included in the multivariate analysis, and the data were standardized to unit variance before PCA application. The number of interpretable components in the PCA was considered significant according to the broken stick model (Frontier 1976). Thus, a component is considered or excluded if the PCA-associated eigenvalue is respectively greater or lower than the value given by the broken stick distribution. Additionally, we conducted local polynomial regressions (R function “loess”) to depict the temporal trends of surface chlorophyll and benthic bacterial abundance.

All statistical analyses and illustrations presented in this manuscript were conducted and created using Python and R computer programs. The packages *vegan* (Oksanen et al. 2007) and *FactoMineR* (Lê et al. 2008) were used for multivariate analysis, and the *ggplot2* package (Wickham 2011) was used for illustration.

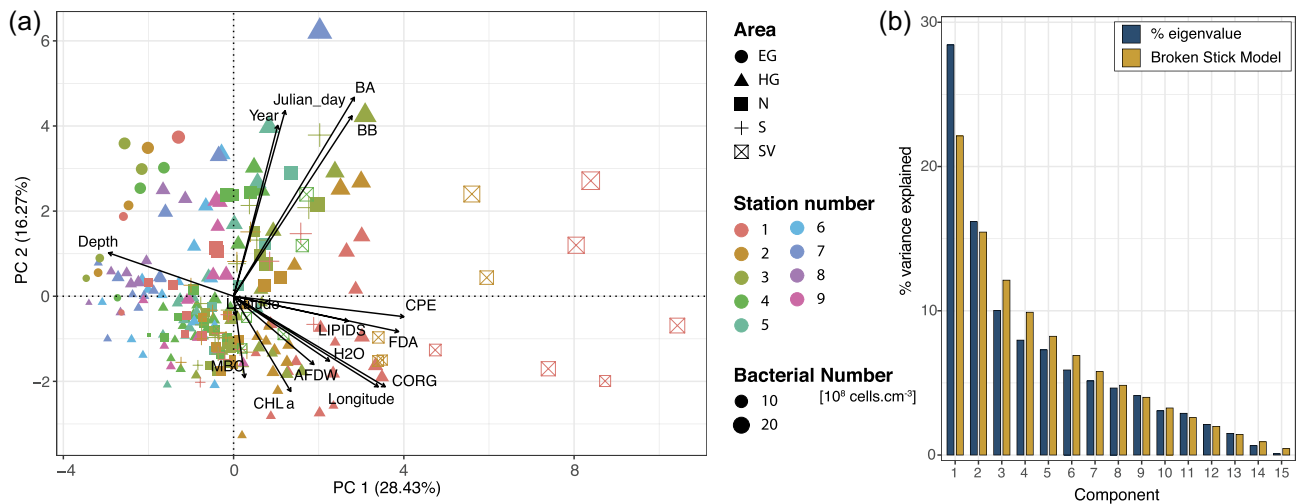
## Results and discussion

### Environmental gradients and temporal changes

The broken stick model suggested that only the first two PCA axes had non-random variability (Fig. 2). The first axis (PC1) and the second axis (PC2) explained 28.4% and 16.3% of

the variability in the data set, respectively. PC1 was driven by large opposing contributions such as the bathymetric (depth) and longitudinal gradient (Fig. 2). Organic carbon, water content, bacterial activities, as well as ash-free dry weights were positively correlated to the longitude of the sampling site, suggesting that sites in the eastern Fram Strait had higher biogenic compounds than the western side. This confirms previous observations where biogenic compounds and bacterial activities decreased in sediments collected further eastward (Soltwedel et al. 2016, Hoffmann et al. 2018). While several studies have reported that bacterial numbers are bathymetric depth-dependent, i.e. less bacterial abundance with increasing depth (Kröncke et al. 1994, Tholosan et al. 1999, Turley and Stutt 2000, Davey et al. 2001, Quéric et al. 2004, Rowe and Deming 2011), our study could not confirm that observation. Indeed, even if some years showed decreasing microbial abundance with increasing depth (i.e. 2008, 2009, 2010, 2012; data not shown), this trend was lost when viewed across the entire time series due to strong interannual variations in bacterial numbers.

PC2 was driven by four positively correlated variables, i.e. Julian day, year, bacterial abundance, and bacterial biomass (Fig. 2). The correlation observed is likely influenced by the shift in sampling periods towards the end of the year, coinciding with an increase in bacterial number/biomass. This contradicts the suggestions of the seafloor as a stable environment (Sanders 1968) but aligns with more recent benthopelagic studies (Turley and Mackie 1995, Rapp et al. 2018, Fadeev et al. 2021). Hence, our findings suggest that the deep ecosystem in the Fram Strait varies temporally, which can be caused by (i) a significant increase in bacterial numbers in the



**Figure 2.** (a) PCA biplot of the sediment variables recorded at the LTER observatory HAUSGARTEN and (b) comparison of eigenvalues from the broken-stick method. Shape, color, and dot size indicate, respectively, the sampling site, station number, and bacterial abundances. The abbreviations SV, S, N, EG, and HG refer to the Svalbard, South, North, East Greenland, and HAUSGARTEN sampling areas, respectively. Acronyms for biogeochemical measurements performed on sediment cores include: BA for bacterial abundance, BB for bacterial biomass, MBC for mean bacterial biomass per cell, CPE for chloroplast pigments equivalents, LIPIDS for phospholipid concentrations, CORG for organic carbon content, CHL a for sediment-bound chlorophyll-a, AFDW for ash-free dry weight, H2O for water content, and FDA for fluorescein-di-acetate.

uppermost sediment layers in more recent years or (ii) that benthic bacterial numbers follow the seasonality observed in the euphotic zone, however, with an offset due to the sedimentation time from the ocean surface to the seafloor.

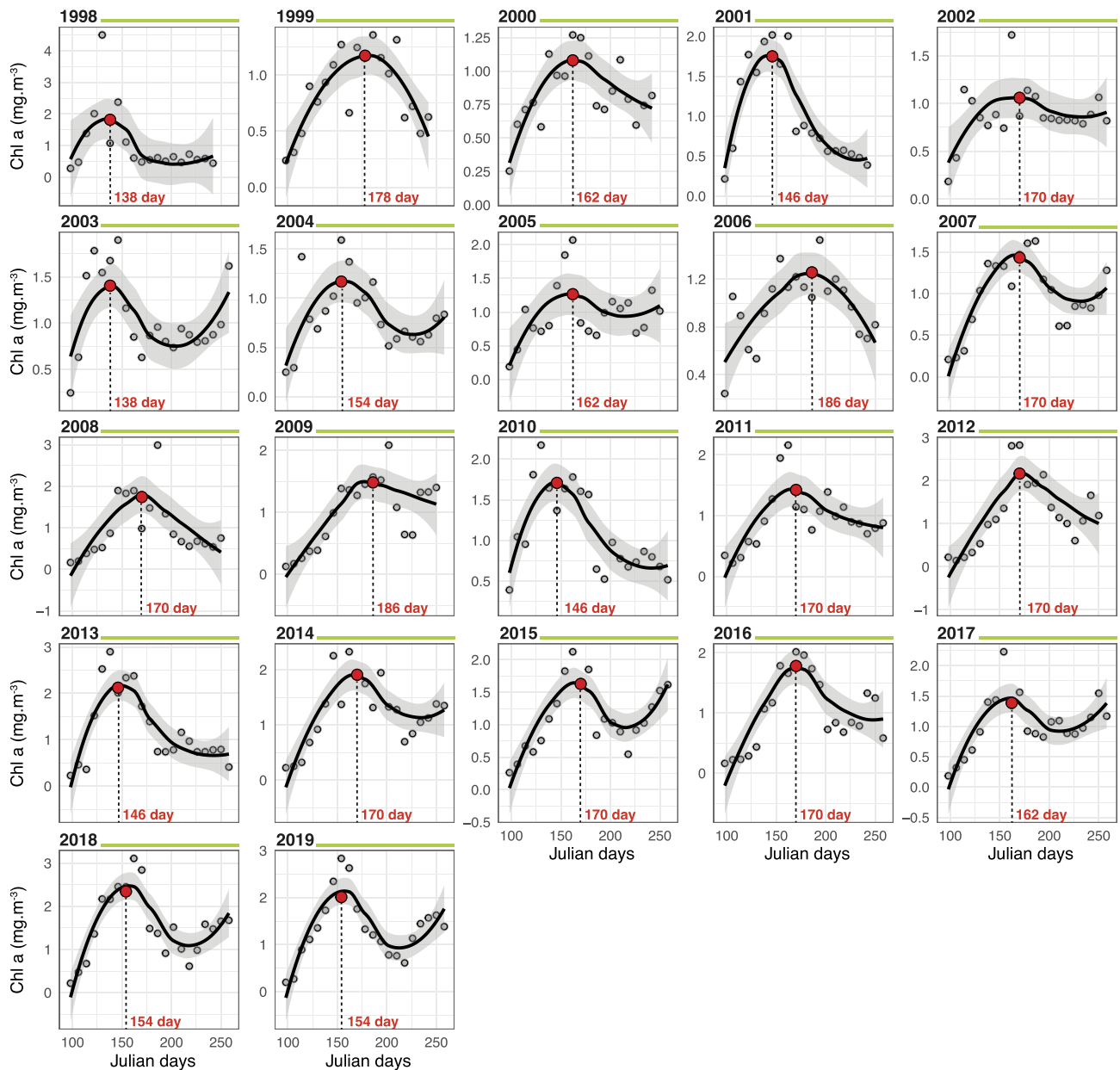
The monthly spatial averaged chlorophyll-a concentrations estimated *via* satellites in the Fram Strait region over a period of 22 years showed typical seasonal variations with large temporal (timing, duration) and magnitude changes (Fig. 3). Throughout the time series, the peak in the chlorophyll-a concentration, i.e. the peak of phytoplankton bloom, occurred between the 138th and 186th days of the year and ranged from  $1.3 \text{ mg}\cdot\text{m}^{-3}$  in 2000 to  $4.5 \text{ mg}\cdot\text{m}^{-3}$  in 1998. Sea ice and stratification of the water column were identified as the key factors affecting and controlling the timing of summer phytoplankton bloom (Wassmann and Reigstad 2011, Mayot et al. 2018, Nöthig et al. 2020). We compared local regressions fitted on bacterial abundances from the surface sediment as a function of Julian day of the sediment sampling and as the time-lag in days between sediment sampling and chlorophyll-a peak in the surface water (Fig. 4). A stronger correlation was observed when the bacterial numbers in the sediment were plotted as a function of the time-lag between chlorophyll-a and sampling time ( $R^2 = 0.51$ ) compared to a function of sampling time of the year ( $R^2 = 0.34$ , Fig. 4). This suggests that variations in benthic microbial abundances in the Fram Strait are linked to the sedimentation and deposition of organic matter on the seafloor through the settling of phytoplankton. A time-lag of 100 days between the chlorophyll-a peak in the euphotic zone and the peak of bacterial abundances in the uppermost sediment layers of the HAUSGARTEN observatory occurred, suggesting that deposition of phytoplankton-derived organic matter on the seafloor occurs roughly 100 days after the peak in phytoplankton bloom.

#### Vertical connectivity or benthic microbial response?

Although microbial communities from the upper ocean and deep sea show minimal overlap (Walsh et al. 2016), it has

been shown that there is a vertical microbial connectivity where a large amount of bacteria attached to settling organic aggregates can be transported to the seafloor (Turley and Mackie 1995, Rapp et al. 2018, Fadeev et al. 2021). Hence, it is possible that the increase in benthic bacterial abundance was (i) due to arrival of additional bacteria with the settling aggregates or (ii) that the deposition of organic matter from the aggregates stimulated growth of the benthic resident bacteria.

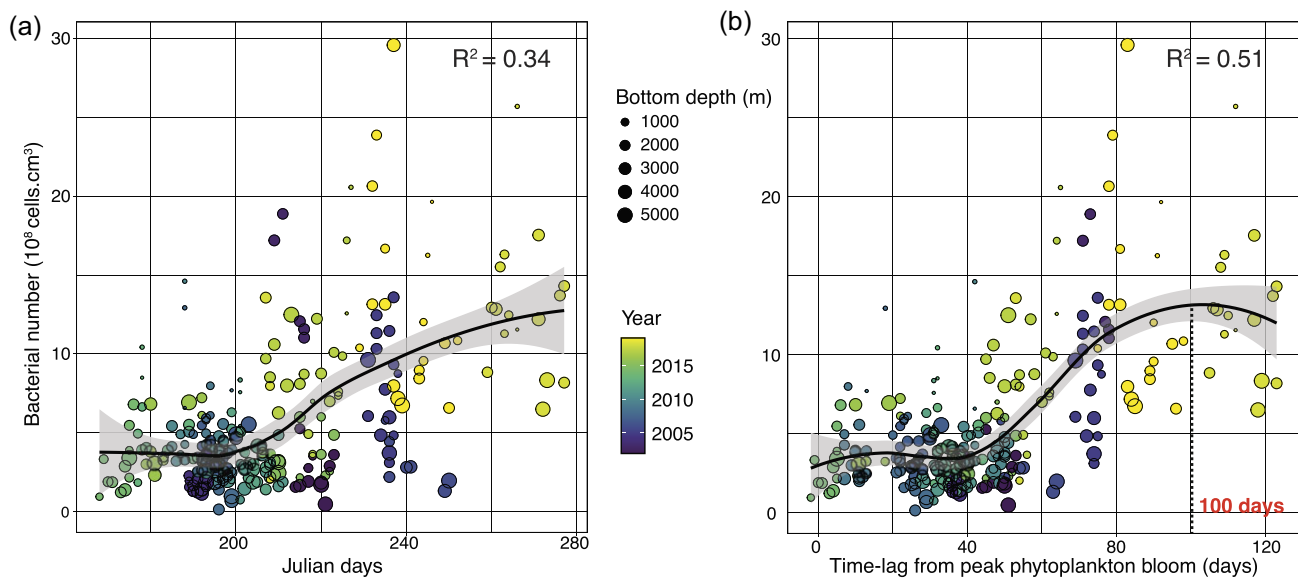
In the central Arctic ocean, ice-algae aggregates transport large numbers of microbial cells from surface ocean to the seafloor, thereby altering the composition of the benthic microbial community (Rapp et al. 2018). Fadeev et al. (2021) estimated that 10%–20% of the benthic bacteria may have been deposited with settling aggregates in both ice-free and ice-covered regions of the Fram Strait. This shows that there is a microbial vertical connectivity between the surface ocean and the deep seafloor in the Fram Strait and that organic matter arrives with their associated microbial communities. A similar pattern is also observed in eukaryotic diversity at global scale, where the proportion of pelagic DNA in the sediment increases with latitude and correlates with particulate organic carbon export (Cordier et al. 2022). Such seeding of the seafloor may help the efficiency of biogeochemical cycling by stimulating substrate availability and growth of the benthic resident bacteria and, hence, explain a substantial increase of 3.5-fold in numbers of bacteria on the seafloor after the sedimentation of detritic material from the surface ocean. The time-lag of  $\sim 100$  days between the peak in phytoplankton bloom and the peak in bacterial abundance can be used to estimate the average settling velocity of the organic material during its journey through the water column. The HAUSGARTEN observatory has an average water depth of 3000 m. Assuming that the increase in benthic microbial abundance is directly related to the deposition of settling phytoplankton aggregates, this suggests that the aggregates sank  $\sim 30 \text{ m}\cdot\text{d}^{-1}$ . This is similar to observations by Wekerle et al. (2018), who measured the sinking velocities of *in situ* collected



**Figure 3.** Spatial average of remotely sensed chlorophyll-a for the entire Fram Strait study region (see Fig. 1) from 1998 to 2019. Red dots, vertical dashed lines, and red numbers indicate the Julian day of the chlorophyll peak defined in this study for each year.

aggregates and found average settling velocities of  $30 \text{ m.d}^{-1}$  ( $n = 22$ ) and  $77 \text{ m.d}^{-1}$  ( $n = 7$  with two aggregates sinking faster than  $125 \text{ m.d}^{-1}$ ) at the stations HG-IX and N4, respectively. The authors concluded that settling velocities between 20 and  $60 \text{ m.d}^{-1}$  were more realistic than the case with  $120 \text{ m.d}^{-1}$ . Ramondenc et al. (submitted) investigated eDNA sequences extracted from sediment cores and captured a specific community mainly composed of pelagic ciliates (Strombidinopsidae family) and pelagic diatoms (Bacillariophyta order) correlating to Julian day. It is well known that microzooplankton protists such as ciliates can feed on chain-forming diatom (Banse 1982) and bacteria (Sherr and Sherr 1987), and inhabit settling aggregates (Allredge and Silver 1988, Silver et al. 1998). Hence, we suggest that the increasing benthic bacterial abundance is directly linked to the deposition of settling phytoplankton aggregates.

While sinking aggregates can transport bacteria to the deep sea, their long-term presence in sediments is limited (Rapp et al. 2018). Resident deep-sea bacteria are likely to be better adapted to *in situ* conditions (i.e. cold temperature and high pressure) of the deep-sea environment than surface-derived bacteria (Tamburini et al. 2006, Tamburini et al. 2013). According to Teske et al. (2011), resident benthic bacteria have a wider range of enzymatic capabilities and are able to hydrolyze diverse organic matter inputs compared to the bacteria found in the water column. Hence, while the immediate increase in bacterial abundance in the surface sediment is likely via aggregate-associated bacteria that arrive with settling organic matter, the environment-adapted benthic bacteria may be more efficient in utilizing the newly sedimented organic matter and also subsequently contribute to the rapid response in bacterial abundance to the organic



**Figure 4.** Bacterial number measured in the uppermost sediment layer at the HAUSGARTEN observatory according to (a) the Julian day of the sediment sampling ( $R^2 = 0.34$ ) and (b) the time-lag of chlorophyll peak in the euphotic zone ( $R^2 = 0.51$ ). Dot color represents the year of the polar expeditions. The thick lines and shaded area represent, respectively, the local regression and the confidence interval.

matter deposition on the seafloor. This is supported by previous observations of an immediate increase in benthic microbial respiration rates and activities following organic matter deposition to the seafloor (Boetius and Lochte 1996, Kanzog *et al.* 2009). However, the multivariate analysis performed in this study did not show any correlation between bacterial abundance and bacterial activity, benthic energy availability, or benthic carbon content. It therefore seems to be a more complex system where linear response between benthic microbial communities and substrate input does not exist, which could be linked to the type of planktonic community that comprises the settling aggregates (Braeckman *et al.* 2018).

## Conclusion

To conclude, this study reveals a distinct seasonal fluctuation in bacterial abundances within surface sediment driven by organic matter export from the surface ocean. The findings highlight that changes in benthic bacterial dynamics are more closely tied to the time-lag following surface ocean productivity rather than water depth, underscoring the critical role of temporal factors in shaping seafloor microbial communities. The observed benthic bacterial dynamics could result from (i) the physical transport of aggregate-associated bacteria and/or (ii) the stimulation of sediment bacterial growth. However, further *in situ* investigations are needed to determine bacterial abundances based entirely on particle deposition. This requires estimating aggregate concentration and the bacterial numbers associated with specific aggregate sizes and/or carbon content. Another approach could involve determining benthic bacterial abundances based on the benthic bacterial growth rate within the timeframe of aggregate deposition versus sampling time.

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## Author contributions

S.R., M.H.I., and T.S. designed the study. T.S. provided background and data for the sediment cores. S.R. analyzed the data and wrote the manuscript with guidance from M.H.I. and T.S. All authors critically revised the manuscript and gave their approval of the submitted version.

## Supplementary data

[Supplementary data](#) is available at ICESJMS online version of the manuscript.

*Conflict of interest:* The authors declare no competing interests.

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## Data availability

The data supporting the findings of this study are available in the supplementary file.

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