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Impact of extreme weather events on pelagic cyanobacterial communities: an in situ mesocosm study in the Gulf of Finland

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ABSTRACT

Cyanobacteria play a critical role in regulating carbon, nitrogen, and phosphorus cycles in the Baltic Sea, seasonally forming extensive blooms under nitrogen-limited conditions in summer. Understanding their responses to environmental disturbances is crucial in the Baltic Sea where increasing and persistent surface water temperature anomalies were observed over the past two decades. During a 17-day mesocosm experiment in the southwestern Finnish archipelago (Gulf of Finland) designed to investigate microbial community dynamics under varying nutrient conditions, the unexpected occurrence of a natural disturbance event created a unique opportunity to assess the effects of pronounced physical changes on cyanobacterial dynamics. The natural disturbance overshadowed the expected effects of the nutrient treatments, which was especially evident for cyanobacteria. The picocyanobacterium *Cyanobium* spp. emerged as the dominant species throughout the study, particularly following the occurrence of the near gale wind-driven rainfall, likely due to its adaptability to rapid environmental changes. Conversely, the filamentous cyanobacteria *Aphanizomenon* spp. and *Pseudoanabaena* spp. thrived under stable conditions. These findings highlight the resilience of picocyanobacteria to environmental fluctuations and their primary role in driving cyanobacterial community dynamics during summer in the Baltic Sea, where natural perturbations are expected to occur with increasing frequency due to climate change.

1. Introduction

The Baltic Sea is a semi-enclosed, shallow, brackish body of water with interconnected deeper basins. To the north, it is bordered by the Gulf of Bothnia, which is separated from the central Baltic (Baltic Proper) by the Åland Sea. Approximately ~85 million people live within the Baltic Sea's drainage basin (HELCOM, 2023), exerting a significant pressure on the ecosystem through agriculture, urbanization and industrialization (Hannerz and Destouni, 2006; Unger et al., 2013). Influx of anthropogenic nutrients into the Baltic Sea via rivers and atmospheric deposition has led to accelerated eutrophication and decreased water transparency due to increased phytoplankton biomass and organic particles (Andersen et al., 2011; Fleming-Lehtinen and Laamanen, 2012; Carstensen et al., 2014).

One of the most significant ecological concerns in the Baltic Sea is the proliferation of toxic cyanobacterial blooms (Vahtera et al., 2007). Decomposition of these blooms cause near-bottom hypoxia, leading to the death of fish and benthic invertebrates (Luckas et al., 2005; Mazur-Marzec et al., 2006; Karjalainen et al., 2007; Sivonen et al., 2007; Uronen, 2007; Paerl and Otten, 2013). Factors that create favourable

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environmental conditions for bloom formation include rising temperatures (Paerl and Huisman, 2008; Kosten et al., 2012; Reinl et al., 2022), increased water column stability (Visser et al., 2016), high nutrient inputs (Smith, 2003; Smith and Schindler, 2009; Paerl and Otten, 2013), changes in the concentrations of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) (Smith, 1983; Orihel et al., 2012; Harris et al., 2024), shifts in food web structure (Elser, 1999), the presence of persistent organic pollutants and organic nutrient forms (Harris and Smith, 2016; Reinl et al., 2022), and alterations in light availability and carbon dioxide levels, e.g. elevated CO_2, can enhance the competitive advantage of bloom-forming cyanobacteria under eutrophic conditions (Van de Waal et al., 2011; Lyche Solheim et al., 2024).

The Gulf of Finland, situated in the northeastern part of the Baltic Sea, is a stratified and expansive estuary characterized by substantial freshwater inflow at its eastern end and a relatively open exchange with the Baltic Proper through its western boundary. A seasonal thermocline typically develops in April–May, leading to strong stratification that persists until September–October. The upper mixed layer typically extends to a depth of 10–20 m, with temperatures decreasing from around 15–20 °C at the top of the thermocline to about 2–4 °C in the colder intermediate layer.

Wind driven upwelling events play a critical role in vertical nutrient transport in the Baltic Sea during summer (Zhurbas et al., 2008; Lips et al., 2009) and can support the proliferation of small unicellular picocyanobacteria (cell size <2 μm). They are abundant and significant primary producers globally, with the genera *Prochlorococcus* and *Synechococcus* being particularly dominant (Flombaum et al., 2013; Díez et al., 2016; Celepli et al., 2017; Cabello-Yeves et al., 2022). While picocyanobacteria are also major contributors to primary production in the Baltic Sea, their communities are dominated by the genus *Cyanobium* (Stal et al., 2003; Celepli et al., 2017), whereas *Prochlorococcus* is not present in the Baltic Sea (Celepli et al., 2017). Additionally, vertical mixing can enhance cyanobacterial growth by keeping the phosphacline, typically located in the upper part of the seasonal thermocline, within the mixed layer (Laanemets et al., 2004). Upwelling helps to suspend cells of non-buoyant cyanobacterial taxa, potentially increasing the competition for nutrients and light. This process can also promote cell sedimentation strategies, such as programmed cell death or resting stages, as observed in taxa that develop akinetes (Wasmund et al., 2012). Conversely, in a stratified system, such as the Gulf of Finland during the summer season, favourable conditions (e.g. low DIN:DIP ratio) for the growth of filamentous cyanobacteria, including *Aphanizomenon flos-aquae*, *Dolichospermum* spp., *Nodularia spumigena*, and *Pseudoanabaena* spp., exist. Bloom initiation of key species such as *N. spumigena* and *A. flos-aquae* occurs in the Baltic Sea during summer after the excess phosphate pool has been depleted, although growth rates remain low when water temperatures drop below 15 °C. Specifically, *A. flos-aquae* exhibits a greater tolerance to colder water compared to *N. spumigena* (Wasmund, 1997).

Decline in water temperature determined by heavy weather events can have different impacts on cyanobacterial species, with pelagic and benthic life stages responding distinctively (Cottingham et al., 2021). For example, wind-driven turbulence has been shown to negatively impact filamentous cyanobacteria (Visser et al., 2016; Moe et al., 2019). However, certain species, such as *Planktothrix agardhii*, developed adaptations such as efficient use of low light, buoyancy regulation, and tolerance to high turbidity, enabling them to dominate particularly in shallow lakes (Scheffer et al., 1997). Upwelling events caused by severe weather/wind conditions can lead to a premature decline in actively growing pelagic cyanobacteria when causing a collapse of gas vesicles. During turbulent mixing combined turgor and hydrostatic pressure changes occur, which prevent cells from actively controlling their buoyancy via gas vesicles, causing them to sink to the sediment where growth conditions are unfavourable (Kinsman et al., 1991; Walsby, 1994; Visser et al., 1996; Huisman et al., 2004). Conversely, cyanobacterial benthic stages can benefit from upwelling by enabling their return to the water column through germination and active recruitment or passively through physical resuspension from the sediment or ebullition (Cottingham et al., 2021; Slavin et al., 2022).

The productivity of the Gulf of Finland, like other regions of the Baltic Sea, is significantly influenced by anthropogenic inputs of nitrogen and phosphorus that disrupt the natural nitrogen cycle. When bottom waters become oxygen-depleted, sediments release phosphorus, and to some extent nitrogen (mainly as ammonium and organic N), back into the water column – a process often termed 'internal loading' - which sustains hypoxic zones and eutrophication despite reductions in external phosphorus inputs (Conley et al., 2002). Changes in the DIN:DIP ratio can induce shifts in phytoplankton community composition. The dynamics of these nutrients are further altered by the intensification of natural weather events in the Baltic Sea coastal regions, whose frequency and intensity are linked to climate change (Rutgersson et al., 2022; Meier et al., 2022). Weather events also increase riverine nitrogen and phosphorus discharges from anthropogenic sources (e.g., urban runoff), exacerbating eutrophication (Ikeda et al., 2009), and disrupting water circulation, resuspending sediments, and upwelling nutrient-rich waters (Wasmund et al., 2012). Their impact on nutrient dynamics is further influenced by their timing; occurrences in late summer or early autumn can result in large pulses from agricultural fields that can promote the development of cyanobacterial blooms (Ouillon, 2018).

This work was conducted as part of a larger study replicating nutrient conditions characterized by a decreasing DIN:DIP ratio. These conditions, typically observed between late spring and early summer before cyanobacterial bloom onset in the Gulf of Finland, were simulated in an offshore semi-open experimental setup. We primarily aimed to study the response of microbial communities to distinct nutrient limitations described in Vanharanta et al. (2024) and Spilling et al. (2025). During the experiment, an unexpected intense weather event occurred, providing an unforeseen opportunity to test the hypothesis that different taxonomic groups of cyanobacteria adapt and thrive differently under fluctuating environmental conditions in this Baltic Sea region. Here, we focus on the often neglected picocyanobacteria and their role in the microbial community compared to the larger filamentous cyanobacteria following the drop in temperature associated with the intense weather event.

2. Material and methods

2.1. Experimental setup

A mesocosm experiment was conducted at Tvärminne Zoological Station, Finland (59.843 N; 23.259E), in June 2021 for 17 days. Twelve translucent plastic bags (0.9 m diameter, 2 m depth) were arranged in a linear array on a floating platform (Spilling et al., 2022). Each was filled with 1.2 m^3 of surface water, while two additional bags were used to ensure equal light exposure but not sampled. Dissolved inorganic phosphate (DIP) was measured before the experiment, and phosphate (KH_2PO_4) was added to all mesocosms to reach a concentration of 0.66 μmol L^{-1} to reproduce the typical inorganic N:P ratio, typically observed after the spring bloom in the Gulf of Finland and the Baltic Proper. Four treatments were adopted: i) three mesocosms received inorganic nitrogen ($NaNO_3^-$) at a concentration of 3.66 μmol L^{-1} (N-treatments); ii) three received organic carbon (glucose) at a concentration of 25 μmol L^{-1} (C-treatments); iii) three received both additions (NC-treatments); iv) three served as unamended controls (Control treatments). Mesocosms were covered with plastic lids to avoid external organic contamination but allowed for gas exchange (SI_1). Water samples were collected from 0.5 m depth with a Limnos sampler (HYDRO-BIOS Apparatebau GmbH, Altenholz, Germany) and transported to the laboratory. Water temperature, salinity and dissolved oxygen were measured outside (via ProSolo handheld, ODO/T and ODO/CT probes) and inside the mesocosms via loggers (HOBO U26; Onset Inc., USA), as reported in

Vanharanta et al. (2025). Moreover, samples for concentrations of dissolved inorganic nutrients ($NO_3^- + NO_2^-$, PO_4^{3-}, NH_4^+) were taken from the experimental bags and determined using standard colorimetric methods (Grasshoff et al., 2009).

2.2. Weather measurements

For the duration of the experiment, data on wind speed and precipitation intensity were sourced from the Finnish Meteorological Institute's website (https://en.ilmatieteenlaitos.fi/download-observations , accessed June 10, 2023). Precipitation intensity measurements were obtained from the Hanko Tvärminne station and wind speed measurements from the Hanko Tulliniemi weather station, the nearest station equipped with an anemometer. Although located approximately 20 km from the experimental site, it reliably represents the local wind conditions. Daily mean values for wind speed, water temperature, and precipitation intensity were calculated using observations (point measurements recorded at 10-min intervals; SI_2) from the 24 h preceding each sampling time point (SI_3). This approach ensured alignment with the number of samples from which we generated 16S rRNA gene sequence data ($n = 96$) and facilitated hypothesis testing.

2.3. Biological parameters

2.3.1. Cyanobacterial pigments measurements

Optical measurements of photosynthetic cyanobacterial pigments phycocyanin and phycoerythrin were carried out in situ with a lightweight, hand-held Pulse Amplitude Modulation fluorometer (Aquapen, Photon Systems Instruments, Czech Republic) to provide estimates of cyanobacterial biomass. Relative phycocyanin / phycoerythrin concentrations were measured using 630 nm excitation light. The FixArea, representing the total area above the fast chlorophyll-*a* fluorescence induction (OJIP) transient between F40μs and F1s, was used to capture the relative fluorescence signal of these pigments.

2.3.2. Picocyanobacteria abundance

Subsamples of 2.5 mL were collected and fixed with 1 % paraformaldehyde for 15 min in darkness before flash-freezing in liquid nitrogen and storage at −80 °C until processing. This method was used to detect and count heterotrophic and autotrophic bacteria via flow cytometry (LSR II, BD flow cytometer BD Biosciences, USA) equipped with lasers emitting at 488 nm and 633 nm. Staining of the samples was performed with SYBRGreen I (Molecular Probes, Eugene, Oregon, USA) at a 10^{-4} (*v*/v) concentration prior to the enumeration, as reported by Gasol and Del Giorgio (2000). CountBright beads (Molecular Probes, Thermo Fischer Scientific) were added to each sample to estimate the counting volume. For the detection of picocyanobacteria, red fluorescence (Chlorophyll-*a*) and green fluorescence were used according to Gasol and Del Giorgio (2000) with the FACSDiva Software (BD Biosciences). Cell counts were obtained with the Flowing Software version 2.5.1 (https://bioscience.fi/services/cell-imaging/flowing-software/).

2.3.3. Filamentous Cyanobacteria abundance

Subsamples of 10 mL were collected, formaldehyde-fixed and stained with 4′,6-diamidino-2-phenylindole (DAPI) solution (1 mg mL^{-1}, Thermo Fischer Scientific, Langenselbold, Germany). The staining was performed in darkness at room temperature for 10 min. This process involved filtering the dye off and washing each filter with Phosphate Buffered Saline (PBS) before allowing it to dry at room temperature. Detection and counts of filamentous cyanobacteria were conducted according to Andersen and Throndsen (2003), using a fluorescence microscope equipped with DAPI and chlorophyll filter sets (Axioskop 2 mot PLUS, equipped with a Zeiss AxioCam 712 colour camera, Carl Zeiss, Jena, Germany). Accumulated polyphosphate granules composed of chains longer than 15 P-subunits could be visualized due to the formed complex with the dye that increased their fluorescence and shifted their absorption spectrum from 456 nm to 526 nm via bright yellow fluorescence (Tijssen et al., 1985; Ohtomo et al., 2008; Diaz and Ingall, 2010).

2.4. 16S rRNA gene sequence data processing

Subsamples of 400–500 mL were filtered onto sterile polycarbonate filters in duplicates (Whatman® Nucleopore™ Track-Etched Membranes, diam. 47 mm, pore size 0.2 μm). The filters were placed in cryogenic vials, immediately flash-frozen in liquid nitrogen, and then stored at −80 °C until DNA extraction as described in Nercessian et al. (2005). Library preparation was performed by LGC Genomics GmbH (Berlin, Germany) with the amplification of the hypervariable V3–V4 region of the 16S rRNA gene using the primer set 341F–785R (Herlemann et al., 2011; Klindworth et al., 2013) for high-throughput sequencing on the Illumina MiSeq platform (Illumina Inc., San Diego, California, USA) using a V3 kit for 2 × 300 bp paired-end reads with a total sequencing amount of ~20 million reads. Demultiplexed raw sequences without Illumina adapters were provided by LGC Genomics GmbH (Berlin, Germany). Amplicon sequence variants (ASVs) were generated and taxonomically classified using a tailored workflow (Hassenrück, 2022) written in snakemake pipeline (Martin, 2011; Köster and Rahmann, 2012). DADA2 (Callahan et al., 2016) was used for denoising, merging paired-end reads, and for removing chimeras. The resulting ASVs were taxonomically assigned using SILVA 138.1 (Quast et al., 2012) and PR2 (Guillou et al., 2013). The workflow further included also the use of blastn (Camacho et al., 2009) and GNU parallel (Tange, 2011). Copy number correction was performed using PICRUSt2 v2.2.5.1 (Douglas et al., 2020) excluding ASVs with an NSTI (nearest sequenced taxon index) > 1 from further analysis.

2.5. Statistical data analysis

All statistical data analyses and visualization were performed in R 4.1.3 (R Core Team, 2022) using the packages tidyverse 1.3.1 (Wickham et al., 2019), vegan 2.5–7 (Oksanen et al., 2013), car 3.0–12 (Fox et al., 2012), dplyr 1.0.8 (Wickham et al., 2022), reshape 0.8.9 (Wickham, 2007), scales 1.2.0 (Wickham et al., 2023), partR2 0.9.1 (Stoffel et al., 2021), multcomp 1.4–19 (Hothorn et al., 2008), multcompView 0.1–8 (Graves et al., 2019), lmerTest 3.1–3 (Kuznetsova et al., 2017), RColorBrewer 1.1–3 (Neuwirth, 2014), broom 1.0.9 (Robinson et al., 2025), sandwich (Zeileis et al., 2020), readr 2.1.5 (Wickham et al., 2024), and Writexl (Ooms, 2023). Post-processing of the figures was performed using Inkscape 1.0.2–2 (Inkscape project).

Beta-diversity was evaluated by calculating Bray-Curtis dissimilarity and visualized using non-metric multidimensional scaling (NMDS) to identify potential clustering of samples over the course of the experiment. To examine the effects of time (experimental day) and mesocosm treatment on the bacterial communities, a Permutational Multivariate Analysis of Variance (PERMANOVA) was conducted. Furthermore, a pairwise Analysis of Similarities (ANOSIM) with Bonferroni correction was performed to assess their temporal development. Beta-diversity dispersion analysis was carried out to assess multivariate homogeneity. Given the occurrence of the wind-driven rainfall between experimental days 4 and 6, a separate PERMANOVA was performed to evaluate the effects of water temperature and wind speed on bacterial community composition, as well as on the rescaled cyanobacterial subset of the community, where only ASVs with a relative abundance of at least 0.1 % in one or more samples were retained. To estimate absolute taxon abundances, the total sequence proportion of non-cyanobacterial ASVs was related to the quantified heterotrophic bacterial cell counts, using this relation as reference for the estimation of the absolute abundance of all ASVs. This way the linear and monotonic relationships between the class Cyanobacteriia and the other eight most abundant bacterial classes in the dataset were calculated via Pearson, Spearman, and Kendall coefficients with Bonferroni-adjusted *p*-values.

To test the hypothesis that picocyanobacteria respond more rapidly to perturbations due to faster growth, net growth rates (μ d^{-1}) were estimated from the slope of ln-transformed abundance vs. experimental day. Abundances were expressed as cells L^{-1} for picocyanobacteria and as filaments L^{-1} for filamentous cyanobacteria (*Aphanizomenon* spp. + *Dolichospermum* spp.). Thus, μ reflects net population change per unit (cells for picocyanobacteria; filaments for filamentous taxa), rather than per-cell physiology. Positive values indicate net increases, while negative values indicate net declines. For filamentous taxa, μ was reported on a per-filament basis; however, we note that changes in filament counts may also arise from processes such as filament fragmentation, which could decouple filament numbers from actual biomass production. For each mesocosm and cyanobacterial taxonomic group, a linear regression of ln-abundance against experimental day (0–15) was fitted, with the slope taken as μ. Mean μ values and standard errors were summarized across mesocosms. For positive μ, doubling times (T_e) were calculated as: 1) $\mu = \ln Nt2 - \ln Nt1/t2 - t1; 2)\ T_e = ln2/\mu$, where N is abundance and t is experimental day. These estimates represent realized net population change (growth minus losses and physical transport), rather than intrinsic physiological growth rates.

3. Results and discussion

3.1. Development of inorganic nutrients throughout the experiment

Inorganic phosphorus concentration was initially equal across all mesocosms. The highest rate of phosphate (PO_4^{3-}) uptake occurred within the first three days, and it was higher in the N- and NC-treatments compared to the C-treatments and controls (Vanharanta et al., 2024). Despite this rapid uptake, phosphate was never fully depleted in any mesocosm throughout the entire experiment, unlike nitrate, which became depleted in all. This is in line with findings by Granéli et al. (1990) confirming that nitrate is often consumed more rapidly due to its preferential uptake by phytoplankton for growth. Ammonium (NH_4^+) concentrations decreased by nearly half in all mesocosms within one day, from approximately 0.32 ± 0.02 μmol L^{-1} to around 0.17 ± 0.05 μmol L^{-1}, given its rapid uptake.

3.2. Occurrence of a natural perturbation event during the experiment

A natural perturbation event occurred between days 4 and 6 of the experiment and was characterized by high precipitation intensity and wind speed, as well as lower water temperature (SI_2). Wind speed began to rapidly increase at the end of day 3 from 4.8 m s^{-1} to the peak of 16.4 m s^{-1} halfway through day 4, before decreasing to 7.5 m s^{-1} by the start of day 5, and then quickly rising again to 11.5 m s^{-1} during the same day (Fig. 1). These near gale force peaks in wind speed (Beaufort scale Force 7; sustained winds of 28–33 knots, 13.9–17.1 m s^{-1}) occurred along with two consecutive precipitation events between the middle of day 4 and the beginning of day 5, with rainfall intensities strongly increasing from 6.3 to 31.3 mm h^{-1}. A small roof prevented the rainwater from entering the mesocosms, but the strong wind and rain were accompanied by a decline in water temperature, both outside and inside the mesocosms, decreasing from 20.8 °C at the beginning of day 4 to 13.2 °C on days 8 and 9 (Vanharanta et al., 2025). The weather perturbation introduced significant shifts in environmental conditions that likely altered nutrient distribution, light penetrations and community dynamics as consequence of the unexpected environmental fluctuation. These changes highlight the dominance of stochastic environmental factors in line with findings on the impact of the episodic disturbances in coastal ecosystems (Cloern, 1996).

3.3. Bacterial community development

The number of sequence reads per sample varied from 14,241 to 130,485, representing 3587 bacterial ASVs, 126 of which were identified as cyanobacterial taxa. Of these, 18 ASVs classified as *Cyanobium* sp. PCC-6307, two ASVs classified as *Aphanizomenon* sp. MDT14a, one classified as *Aphanizomenon* sp. NIES81, and two classified as *Pseudoanabaena* sp. PCC-7429 were retained (SI_4). The NMDS ordination indicated that the temporal development of the bacterial communities across the experimental days overshadowed the treatment effect (Fig. 2). The Permutational Multivariate Analysis of Variance (PERMANOVA) conducted to assess whether changes in the total bacterial community composition could be attributed to experimental days, treatments, or

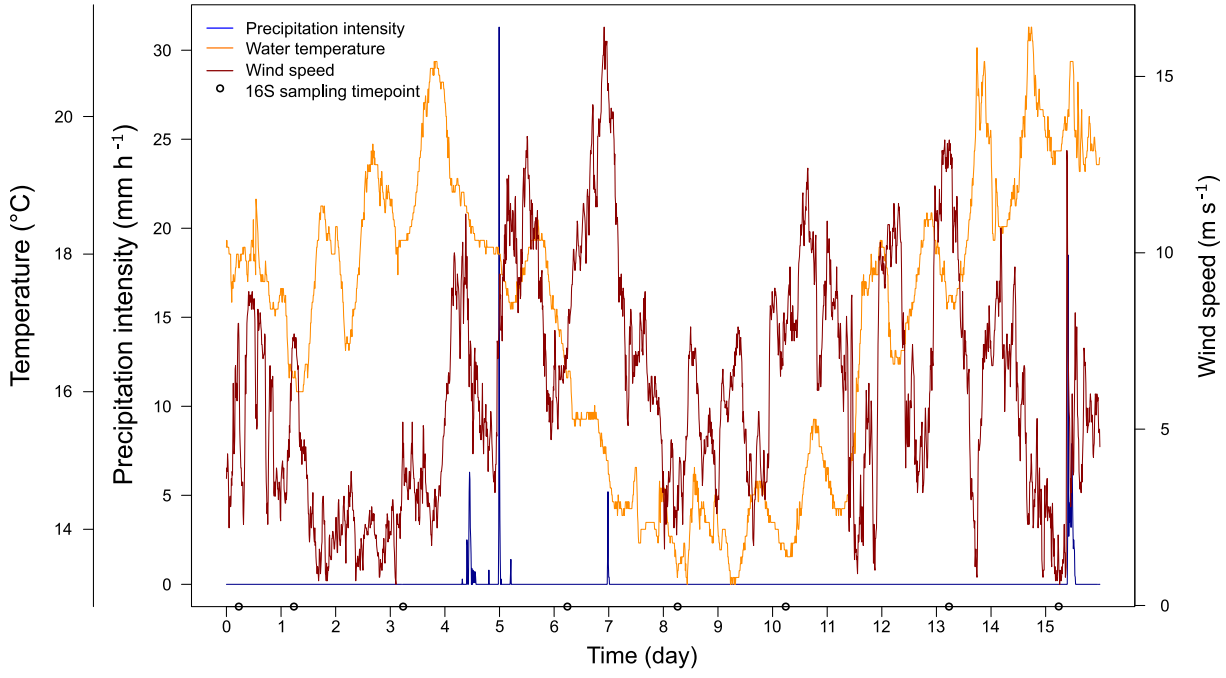

Fig. 1. Weather data. The blue line indicates the precipitation intensity (first left y axis). The orange line indicates the water temperature outside the mesocosms (second left y axis). The dark red line indicates the wind speed (right y axis). Open circles on the x-axis indicate the sampling time points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

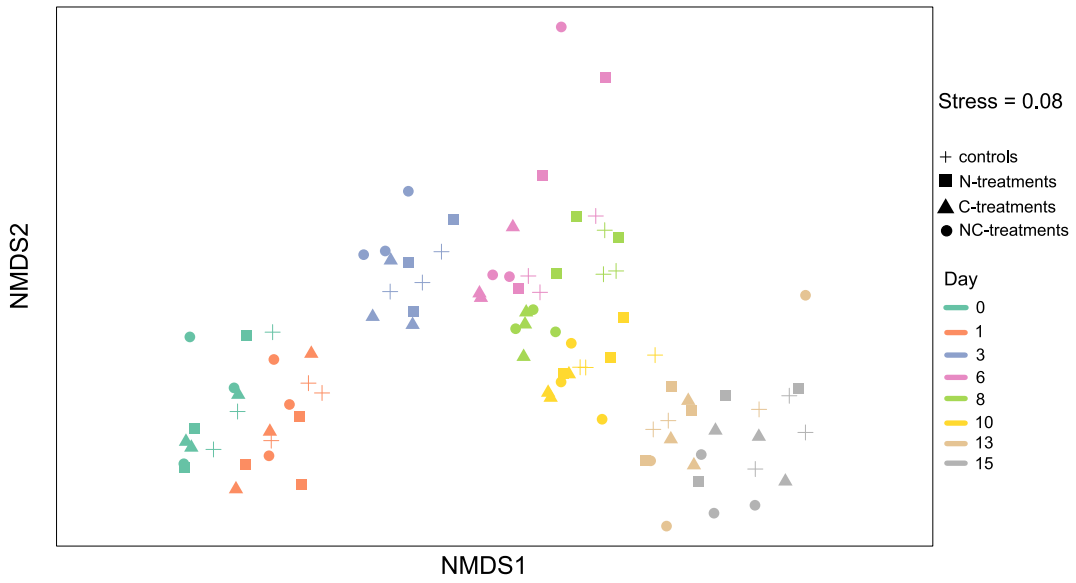

Fig. 2. Non-metric multidimensional scaling (NMDS) plot showing variation in microbial community composition throughout the experiment. Experiment days are indicated by different colours. Treatments are indicated by different symbols.

their interaction revealed a highly significant effect of experimental day ($F = 15.59$, $p = 0.001$), explaining 49.87 % of the observed variation. The treatment effect was also significant but only accounted for 5.00 % of total variability ($F = 3.14$, $p = 0.001$). Residual variability amounted to 45.13 %, reflecting the influence of unmeasured factors and inherent stochasticity in community dynamics, consistent with previous studies (Shade et al., 2012), which emphasize resilience and adaptability in fluctuating environments. The dominant influence of experimental day as a key driver of changes in community structure across the experiment, with a comparatively minor contribution of treatment effects, was observed also in other works where the complexity of bacterial ecosystem responses was demonstrated (Le et al., 2022). This emphasizes the need to account for temporal dynamics alongside treatments when investigating structural changes in a bacterial community.

Pairwise ANOSIM tests confirmed the significance of temporal development of the bacterial community throughout the experiment. The ANOSIM R ranged from 0.12 to 1.0, indicating varying degrees of separation between communities at different time points. Strong dissimilarity was observed between earlier and later time points, particularly between days 0 and 15 ($R = 1.0$, $p \leq 0.001$) and between days 0 and 13 ($R = 1.0$, $p < 0.001$), reflecting significant shifts in community structure over time. Notably, the comparison of days 3 (before the perturbation) and 6 (after the perturbation) yielded an ANOSIM R-value of 0.616, with $p \leq 0.001$, highlighting the impact of the weather event on community dynamics. In contrast, comparisons between proximate time points, such as days 6 and 8 ($R = 0.243$, $p = 0.009$) and days 13 and 15 ($R = 0.281$, $p < 0.001$), exhibited lower R-values, indicating minimal changes in composition between these days. Overall, the analysis confirms a clear temporal progression in community structure, with significant shifts between most time points. While ANOSIM results indicated greater similarity among communities in the later stages of the experiment, the beta-diversity dispersion analysis revealed additional insights into within-group heterogeneity. A boxplot of distances to group centroids by day (SI_1) showed that communities at the very beginning (days 0 and 1) had lower dispersion, indicating reduced heterogeneity. During the perturbation (e.g., between days 3 and 8), dispersion increased, suggesting greater heterogeneity, whereas later stages showed more compositional similarity across time points. Although this pattern cannot be conclusively attributed to the weather event or nutrient treatments due to the limited number of replicates per mesocosm, it underscores the role of temporal dynamics in shaping bacterial community variability (Fuhrman et al., 2015) and highlights the importance of multiple environmental drivers in ecological dynamics.

3.4. *Effects of a disruptive weather event on (cyano)bacterial community*

PERMANOVA analyses conducted to assess the influence of the natural perturbation event described above on the composition of the bacterial and cyanobacterial community indicated significant influences of water temperature and wind speed. Water temperature accounted for 4.80 % of the variation in bacterial community structure ($F = 4.88$, $p = 0.001$), and wind speed explained 2.59 % of the variation ($F = 2.63$, $p = 0.011$). Similarly, water temperature exhibited a significant impact on the cyanobacterial subset of bacterial community ($F = 4.312$, $p = 0.003$), accounting for 4.23 % of the variation, while wind speed had a smaller but still statistically significant, effect ($F = 2.659$, $p = 0.019$), explaining 2.6 % of the variation. Precipitation intensity data were not tested in the PERMANOVA analysis, as precipitation events occurred during the experimental time in between sampling events, when no samples for 16S rRNA gene data generation were collected. Consequently, while water temperature and wind speed explained small but significant fractions of the variation, temporal dynamics themselves accounted for a substantial proportion of community turnover. The remaining variability is likely attributable to other unmeasured abiotic and biotic drivers (e.g., light availability, mixing regime, grazing, competition, viral lysis) that also fluctuate over time, as well as to the limitations of sampling resolution that may have decoupled short-term environmental changes from community responses. This interpretation is consistent with other mesocosm studies reporting considerable residual variation (Richardson et al., 2019; Harris et al., 2024) and highlights the importance of integrating temporal dynamics with multiple environmental and biological factors to better understand mechanisms of microbial community change. Although the perturbation coincided with near-gale wind speeds, the mesocosms were covered and therefore did not transmit wind-driven vertical mixing. This limits our interpretation to the biological and chemical consequences of the rapid temperature decline and excludes the physical turbulence component that typically accompanies storms in the Gulf of Finland. As vertical mixing can deepen the mixed layer, disrupt stratification, and accelerate loss processes in filamentous cyanobacteria, our results likely represent conservative estimates of natural storm-driven impacts.

A consistent decrease in the median relative abundance of the class Cyanobacteriia was observed across all mesocosms prior to the wind-driven rainfall event (from 10.2 % on day 0 to 2.5 % on day 3), followed by a notable recovery and a steady increase afterward (peaking at 19.3 % by day 15). This general trend was mirrored in the taxon *Cyanobium* sp. PCC-6307, which exhibited a decline before the near gale event occurred (from 9.8 % on day 0 to 1.6 % on day 3 before rising steadily to reach a peak of 18.8 % of the total bacterial community by day 15). This taxon consistently dominated among cyanobacterial taxa throughout the experiment, with its relative abundance peaking after the perturbation (Fig. 3). In contrast, other cyanobacterial taxa such as *Aphanizomenon* and *Pseudanabaena* were present at much lower relative abundances (1–5 % of the total bacterial community) and followed distinct temporal patterns (the first one more dominant on day 1 and 3, the latter one on day 10, 13, 15) constituting minor components in terms of contributions to the overall bacterial community. The steep post-perturbation increase in the relative abundance of *Cyanobium* sp. PCC-6307 may have been related to the rise in water temperature that occurred after the wind-driven rainfall. Similar conditions observed in freshwater systems have shown to also favour other cyanobacterial species, such as *Microcystis* (Briddon et al., 2022). The fluctuations in cyanobacterial populations before and after heavy rainfalls observed in this study reflect findings from other studies where enhanced cyanobacterial growth and an altered community structure coincide with heavy weather events (Richardson et al., 2019; Harris et al., 2024).

3.5. Unicellular and filamentous cyanobacterial biomass

The fluorescence levels of phycocyanin/phycoerythrin peaked before the wind-driven rainfall event, indicating an abundant cyanobacterial community prior to its occurrence. Specifically, relative fluorescence units were recorded at 1.91×10^5, 1.70×10^5, and 1.54×10^5 during the first three days, followed by a significant drop to around 0.35×10^5 units immediately after the perturbation (Fig. 4A). The pattern in fluorescence data further supported the results of the sequence-based analysis that the weather perturbation and the drop in water temperature had a detrimental effect on the cyanobacterial community. For instance, Paerl et al. (2020) reported that strong weather events can lead to significant shifts in picophytoplankton community structure, affecting both biomass and species composition. Notably, contrasting responses of picocyanobacteria and filamentous cyanobacteria were highlighted in our study. Picocyanobacteria showed a marked increase in cell abundance post-perturbation, rising nearly tenfold from 4.99×10^4 cells mL^{-1} to 4.86×10^5 cells mL^{-1} by day 13 (Fig. 4B). In contrast, filamentous cyanobacteria from the genus *Aphanizomenon* peaked before the perturbation, followed by a sharp decline during it. Although this genus showed a resurgence in the subsequent days, it did not return to pre-perturbation levels. The genus *Pseudoanabaena* displayed a different trend, peaking on day 15 at 4.20×10^3 and 4.67×10^3 filaments L^{-1}. During the perturbation itself, filaments of both genera were nearly undetectable, underscoring the contrasting dynamics of these taxa compared to the rapid and substantial recovery observed for picocyanobacteria (Fig. 4C and D).

The increase in abundance of pico-sized cyanobacteria suggests that they are more resilient and benefit from natural disturbances, while filamentous species exhibit delayed recovery. Specifically, *Aphanizomenon* spp. showed a marked decline during the perturbation, potentially due to its greater reliance on stable conditions for growth (even in colder water) and its slower cell division rates. Following the stabilization of environmental conditions post-perturbation, *Pseudoanabaena* spp. emerged in the succession, mirroring a pattern observed in other filamentous taxa that rely on sediment germination for reestablishment (e.g. *Dolichospermum* spp.; Wasmund, 2017). Studies by Huisman and colleagues(2004) highlighted how environmental disturbances, such as wind events, can shift competitive dynamics within phytoplankton communities, favouring smaller, faster-growing species like picocyanobacteria. In the context of the larger project, Spilling et al. (2025) demonstrated that also eukaryotic members of the phytoplanktonic community as small chlorophytes (e.g., *Monoraphidium* sp.) and diatoms could thrive under these nutrient and environmental conditions likely due to comparable physiological traits. Over the whole experiment, picocyanobacteria exhibited modest but positive net growth ($\mu \approx 0.05 \pm 0.015$ d^{-1}; doubling time = 13.7 days), whereas combined filamentous cyanobacteria showed no net increase ($\mu \approx -0.005 \pm 0.019$ d^{-1}), although interval-based estimates indicated short-lived growth bursts (both at the beginning and at the end of the experiment), which, however, did not translate into cumulative net gains (Table S1.1 and Fig. S1.2 in SI_1). The differential responses of picocyanobacteria and filamentous cyanobacteria have important ecological implications. Picocyanobacteria, which recovered rapidly, contribute significantly to primary production and nutrient cycling in aquatic ecosystems. Their resilience suggests that they may benefit under increasing weather variability due to climate change. Filamentous taxa, on the other hand, play crucial roles in nitrogen fixation and carbon sequestration, and

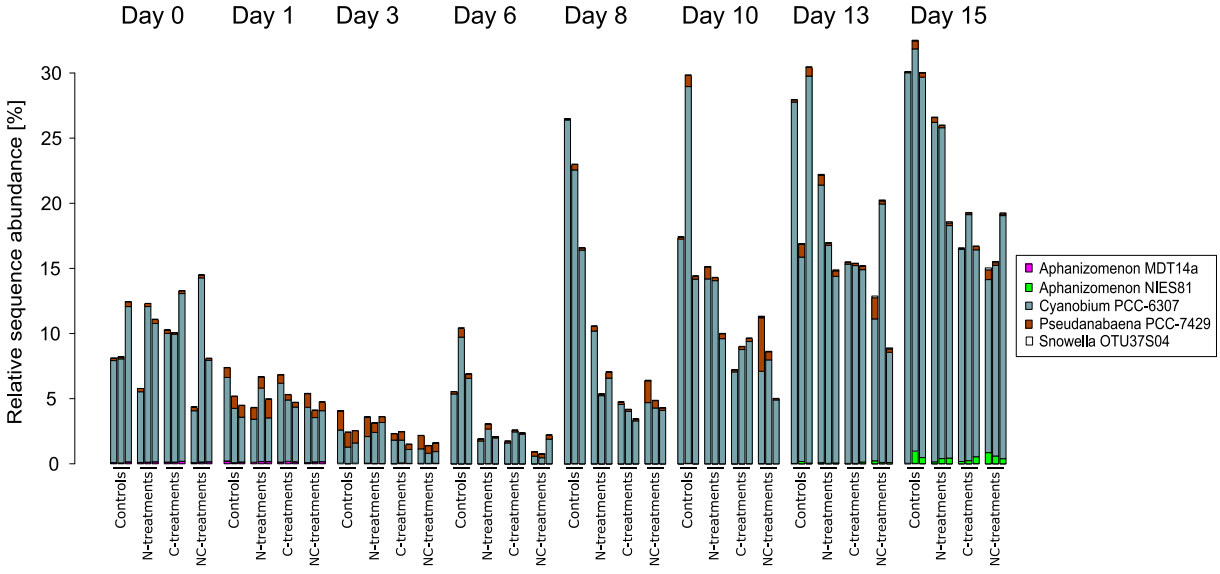

Fig. 3. Temporal development of the cyanobacterial community composition throughout the experiment identified by 16S rRNA gene sequences. Each taxon is indicated by a different colour.

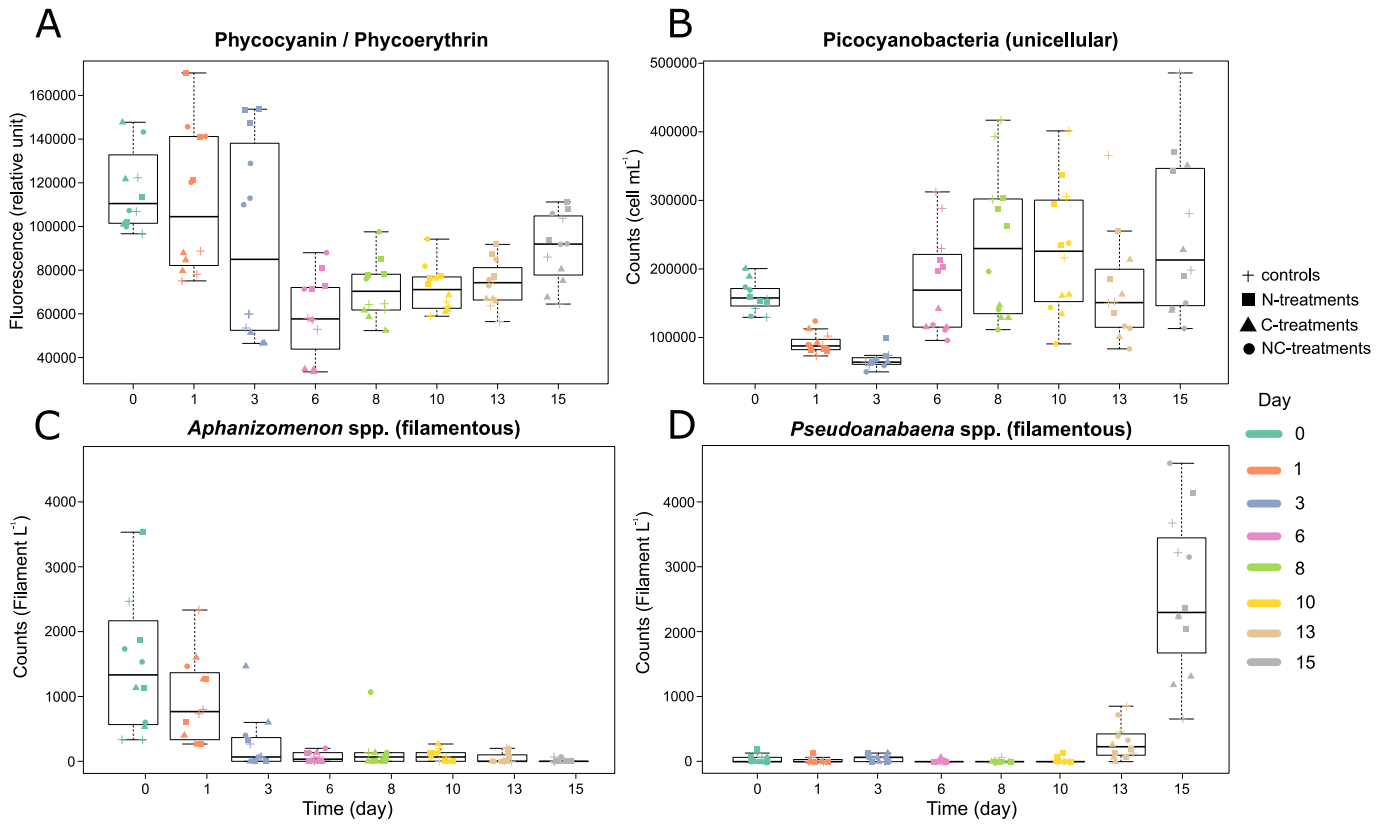

Fig. 4. Biological parameters measurements. **A.** Fluorescence signal measurements of Phycocyanin / Phycoerythrin. **B.** Cell counts of Picocyanobacteria. **C.** Filament counts of *Aphanizomenon*. **D.** Filament counts of *Pseudoanabaena*.

their delayed recovery could have cascading effects on ecosystems with limited nutrients availability.

The results from sequence data, fluorescence measurements, flow cytometry and microscopy counts reveal congruent patterns for different cyanobacterial taxonomic groups responding to the perturbation event. The sharp decrease in the relative sequence abundance of *Cyanobium* sp. PCC-6307 during the wind-driven rainfall, followed by a recovery to peak by day 15 aligned with the fluorescence data, where phycocyanin / phycoerythrin levels also dropped sharply after the perturbation but showed substantial recovery in subsequent days. Sequence data displayed a strong increase in relative abundance of *Cyanobium* sp. PCC-6307, while fluorescence and cell count data corroborate this pattern, demonstrating a marked rise in picocyanobacterial cell density post perturbation. Similarly, filamentous taxa like *Aphanizomenon* spp. and *Pseudoanabaena* spp. exhibited declines during the disturbance, with *Pseudoanabaena* peaking later, as noted in both sequence data and filament counts. These complementary findings suggest that the dynamics of the cyanobacterial community in response to heavy weather events are potentially shaped by the morpho-physiological traits and ecological strategies of the different cyanobacterial groups that comprise it. For instance, the rapid recovery of *Cyanobium* sp. reflects its resilience. In contrast, filamentous taxa like *Aphanizomenon* spp. showed a lagged recovery, consistent with their slower growth strategies. Furthermore, the variability in community composition accounted for by environmental factors, such as water temperature and wind speed, agrees with the fluorescence-based detection of cyanobacterial biomass decline indicating perturbation-driven community restructuring. Since turbulence-induced gas vesicle collapse and enhanced sinking are important loss pathways for filamentous cyanobacteria during storm events (Visser et al., 1996; Huisman et al., 2004), the absence of direct wind-driven mixing in our covered mesocosms likely muted these physical processes. Thus, the steep decline of *Aphanizomenon* spp. during the perturbation reflects primarily the biological response to thermal deterioration, whereas in natural conditions, mixing-driven sinking would be expected to intensify this decline. Conversely, the strong post-perturbation rebound of picocyanobacteria may represent only a partial expression of their competitive advantage under fluctuating, mixed-layer conditions in situ, where mixing also enhances nutrient entrainment.

3.6. Correlation between cyanobacteria and other bacteria

Cyanobacteriia were among the nine most dominant bacterial classes identified in the experiment (SI_5). The correlation analysis between Cyanobacteriia and the other eight dominant bacterial classes identified throughout the experiment highlighted associations with Verrucomicrobiae and Planctomycetes, which demonstrated highly significant positive correlations (SI_1). Previous studies have explored interspecific relationships within microbial communities, indicating that Cyanobacteriia can influence and be influenced by the abundance of other bacterial groups through competitive or cooperative interactions (Eiler et al., 2012; Pestana et al., 2022; Harris et al., 2024).

Verrucomicrobiae displayed the strongest association with Cyanobacteriia (Pearson: $r = 0.790$, $p < 0.01$; Spearman: $\rho = 0.858$, $p < 0.01$; Kendall: $\tau = 0.664$, $p < 0.01$), possibly related to polysaccharide metabolism, as previously reported (Kahru et al., 2018). Such a strong positive correlation suggests an ecological interaction that warrants further investigation. This correlation was previously observed in a study on "*Spartobacteria baltica*" (Herlemann et al., 2013), where the most highly correlated organism identified was a picocyanobacterium with a 16S rRNA gene sequence identical to *Synechococcus/Cyanobium* sequences from freshwater (Crosbie et al., 2003) and from the Baltic Sea (Sjöstedt et al., 2012). Moreover, Herlemann et al. (2013) explored the genetic potential of "*Spartobacteria baltica*" to utilize various

polysaccharides during its abundance peak in late July, when blooms of filamentous cyanobacteria are more likely to occur (Kahru et al., 2018). Hence, the existence of a dynamic interplay between these groups in nutrient cycling and energy flow was indicated. Cyanobacteria are likely to be the main source of polysaccharide substrates degraded by Verrucomicrobiae, which is equipped with genes encoding glycoside hydrolases. Planctomycetia (Pearson: $r = 0.671$, $p < 0.01$; Spearman: $\rho = 0.744$, $p < 0.01$; Kendall: $\tau = 0.533$, $p < 0.01$) and Gammaproteobacteria (Pearson: $r = 0.362$, $p < 0.01$; Spearman: $\rho = 0.438$, $p < 0.01$; Kendall: $\tau = 0.272$, $p < 0.01$) also showed significant correlations with Cyanobacteriia, suggesting a close functional or ecological association (Harris et al., 2024). Interestingly, Bdellovibrionia presented significant associations in the nonparametric tests (Spearman: $\rho = 0.502$, $p < 0.01$; Kendall: $\tau = 0.327$, $p < 0.01$), suggesting a potential ecological interaction with Cyanobacteriia. Previous studies have identified Bdellovibrionia as predators of cyanobacteria, employing a stepwise process involving attachment, cell wall degradation (using enzymes like glycanases) and subsequent lysis of internal component of cyanobacterial cells (Li et al., 2021; Bauer and Forchhammer, 2021). In contrast, Actinobacteria and Alphaproteobacteria exhibited weak and not statistically significant correlations with Cyanobacteriia (Actinobacteria, Pearson: $p = 0.61$; Spearman: $p = 0.054$; Kendall: $p = 0.08$; Alphaproteobacteria, Pearson and Spearman: $p = 1.0$). These findings highlight the potential ecological significance of associations of cyanobacteria with Verrucomicrobiae, Planctomycetes, and Gammaproteobacteria, suggesting their involvement in key microbial interactions related to nutrient cycling, polysaccharide degradation, and community structuring.

4. Conclusions

The development of the cyanobacterial community in this study was primarily influenced by a natural perturbation event characterized by a significant drop in water temperature. This disruption overshadowed the effects of nutrient treatments and revealed distinct adaptive strategies among different cyanobacterial taxa. Notably, the picocyanobacterium *Cyanobium* spp. emerged as the dominant taxon, taking advantage of strong environmental fluctuations. Its small size, unicellular structure, and low surface-to-volume ratio likely conferred a competitive advantage under rapidly changing conditions. In contrast, filamentous cyanobacteria, such as *Aphanizomenon* spp. and *Pseudoanabaena* spp., showed a preference for stable environments and exhibited delayed recovery following the perturbation. These findings underscore the critical role of environmental variability in shaping community dynamics. Picocyanobacteria's resilience highlights their potential to dominate under scenarios of increased weather variability anticipated with climate change. This has significant ecological implications, as these taxa contribute substantially to primary production and nutrient cycling in marine systems. Conversely, the slower recovery of filamentous cyanobacteria – key contributors to nitrogen fixation - suggests that increasing frequency and intensity of perturbations could disrupt their ecological roles, with cascading effects on nutrient availability and carbon cycling in the Baltic Sea. Future studies should extend the duration of mesocosm experiments to better capture the dynamics of slow-growing filamentous cyanobacteria and explore additional environmental factors such as light availability and induced mixing. Investigating the interplay between cyanobacteria and other microbial taxa in the context of climate-induced disturbances could also provide deeper insights into the resilience and adaptability of marine microbial ecosystems. Overall, this study demonstrates that short-term natural perturbations can have profound effects on cyanobacterial community composition, favouring more resilient picocyanobacteria over filamentous taxa. As the lack of wind-driven mixing showed that the physical component of storm forcing could not be captured in our setup, future mesocosm studies that account for water temperature variability in open natural mixing conditions will be essential to disentangle the relative contributions of physical turbulence and biological mechanisms in shaping cyanobacterial succession during extreme weather events. Hence, these findings highlight the need to consider environmental variability in ecosystem management and climate change models, as shifts in microbial community structure could alter primary production, nutrient cycling, and food web dynamics in marine ecosystems.

CRediT authorship contribution statement

Mariano Santoro: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Mari Vanharanta:** Writing – review & editing, Methodology, Investigation. **Cristian Villena-Alemany:** Writing – review & editing, Methodology, Investigation. **Christiane Hassenrück:** Writing – review & editing, Software, Formal analysis, Data curation. **Martin Hagemann:** Writing – review & editing, Supervision. **Hans-Peter Grossart:** Writing – review & editing, Methodology, Investigation. **Kasia Piwosz:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Kristian Spilling:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Matthias Labrenz:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.

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Data availability

The original contributions presented in this study are included in the article and the associated supplementary material. The sequences generated in this study have been deposited in the European Nucleotide Archive (ENA) at EMBL-EBI under Bioproject PRJEB72147 (https://www.ebi.ac.uk/ena/browser/view/PRJEB72147) using the data brokerage service of the German Federation for Biological Data (Diepenbroek et al., 2014Data from all other measured physical, chemical and biological parameters are available on PANGAEA (Vanharanta et al., 2025). Custom code for the bioinformatics processing, and data analysis used in this study is available at https://git.io-warnemuende.de/bio_inf/IOWseq000041_AQUACOSM_exp.

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