Can Bacillus-based bioaugmentation alter the structure of the bacterioplankton community in a freshwater pond?

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Abstract. Freshwater ecosystems are increasingly exposed to anthropogenic pressures, which may lead to disturbances in microbial processes essential for their proper functioning. Bioaugmentation using microorganisms with potentially beneficial properties is being considered as a method to support the functioning and protection of aquatic ecosystems. The aim of this study was to assess the effect of pond bioaugmentation with a commercial Bacillus-based biopreparation on the taxonomic structure and physiological condition of bacterioplankton. The study was conducted in a pond located in the Botanical Garden of Kazimierz Wielki University in Bydgoszcz, Poland, with sampling carried out during selected months from April to June 2024 and from April to October 2025. Bacterioplankton abundance and cell membrane integrity were determined using cytological methods and the LIVE/DEAD® BacLight™ assay, while taxonomic structure was analyzed based on sequencing of the V1–V9 regions of the 16S rRNA gene using Oxford Nanopore Technology. Following application of the biopreparation, a transient increase in bacterioplankton abundance and in the proportion of cells with intact cytoplasmic membranes was observed. The taxonomic structure of bacterioplankton remained stable throughout the study period, with Betaproteobacteria, Flavobacteria, Cyanophyceae, Cytophagia, and Gammaproteobacteria remaining the dominant groups. The proportion of bacteria of the genus *Bacillus* in the overall bacterioplankton community was low and increased only transiently following application of the biopreparation. The absence of persistent changes in community structure and the low and transient proportion of *Bacillus* suggest that the introduced bacteria did not gain a sustained competitive advantage. The observed changes in bacterioplankton abundance and physiological condition may instead indicate an indirect effect of the biopreparation on the indigenous bacterial community, through temporary modification of environmental conditions or substrate availability that may have promoted bacterial growth and maintenance of cell membrane integrity.

Keywords: bacterioplankton, microbial activity, microbial diversity, biopreparations, restoration, *Bacillus*

1. Introduction

Aquatic ecosystems play a key role in the functioning of the biosphere by providing drinking water resources, regulating the cycling of matter and energy, and serving as habitats

for numerous organisms (Tan et al., 2015). As an integral component of the infrastructure of large cities, they also perform important ecological and recreational functions (Kubera and Małecka-Adamowicz, 2017). In recent decades, however, increasing anthropogenic pressure and the effects of climate change have contributed to the progressive degradation of aquatic environments. Deteriorating water quality poses a serious threat not only to ecosystem functioning but also to public health and the stability of ecosystem services (Rojas et al., 2022).

The diversity and abundance of microorganisms inhabiting aquatic ecosystems are among the key factors determining their ecological stability (Jeffries et al., 2016). Microorganisms play an essential role in the decomposition of organic matter and in the cycling of elements through biogeochemical cycles (Newton et al., 2011). Disruptions of these processes may result in the gradual shallowing and even disappearance of water bodies. This is particularly important in the case of small water bodies, which constitute a numerous and valuable component of the natural environment (Kubera and Donderski, 2017). The efficiency of these processes largely depends on the metabolic activity of indigenous bacterial populations. Since only a small proportion of bacteria can be detected using traditional cultivation methods (Amann et al., 1995), culture-independent techniques have become essential for assessing bacterial abundance and physiological condition in aquatic environments. Among these, flow cytometry and epifluorescence microscopy are widely used methods that enable the rapid quantification and characterization of bacterial communities (Gong et al., 2016). Meanwhile, advances in microbial ecology and the study of microbial diversity have been facilitated by metagenomics, which provides information on the structure of entire microbial communities (Thomas et al., 2012; Escobar-Zepeda et al., 2015). Analysis of the qualitative and quantitative structure of aquatic bacterial populations is of key importance for understanding the functions performed by microorganisms in aquatic ecosystems (Senjarini et al., 2013). Research on microbial ecology also has practical implications, as knowledge of the factors shaping microbial community structure may support efforts to respond to changes in the functioning of aquatic ecosystems (Mansour et al., 2018). For these reasons, further research is needed to deepen our understanding of the taxonomic and functional diversity of bacterial populations that contribute to the stability of aquatic ecosystems. At the same time, biomonitoring and the development of new methods for the protection of aquatic environments should remain priority areas of scientific research.

The aim of the study was to assess the effect of pond bioaugmentation with a commercial Bacillus-based biopreparation on the taxonomic diversity and cell membrane integrity of bacterioplankton. The novelty of this study lies in the integrated assessment of

bacterioplankton responses to the application of a commercial Bacillus-based biopreparation, combining changes in bacterial abundance and cell membrane integrity with taxonomic profiling based on full-length 16S rRNA gene sequencing. This approach provides insight into both the short-term physiological responses of bacterioplankton and the persistence of introduced Bacillus bacteria within the indigenous bacterial community, contributing to a better understanding of the ecological implications of bioaugmentation in freshwater ecosystems.

2. Materials and methods

2.1 Study area and sampling

The study was conducted in a pond located in the Botanical Garden of Kazimierz Wielki University in Bydgoszcz, Poland (Fig. 1). The pond is an artificial water body with a surface area of 669 m², a volume of approximately 650 m³, and a maximum depth of approximately 1 m (Habel et al., 2025). Bacterioplankton was sampled using a dipper from a depth of approximately 0.5 m below the water surface. At each sampling occasion, three parallel water samples were collected and analyzed separately. The results obtained from the three replicates were averaged to obtain a single mean value for each sampling occasion. Consequently, a total of 10 sampling occasions were represented in the final dataset. Water sampling was conducted on 10 sampling occasions during selected months from April to June 2024 and from April to October 2025. All samples were analyzed immediately after collection.

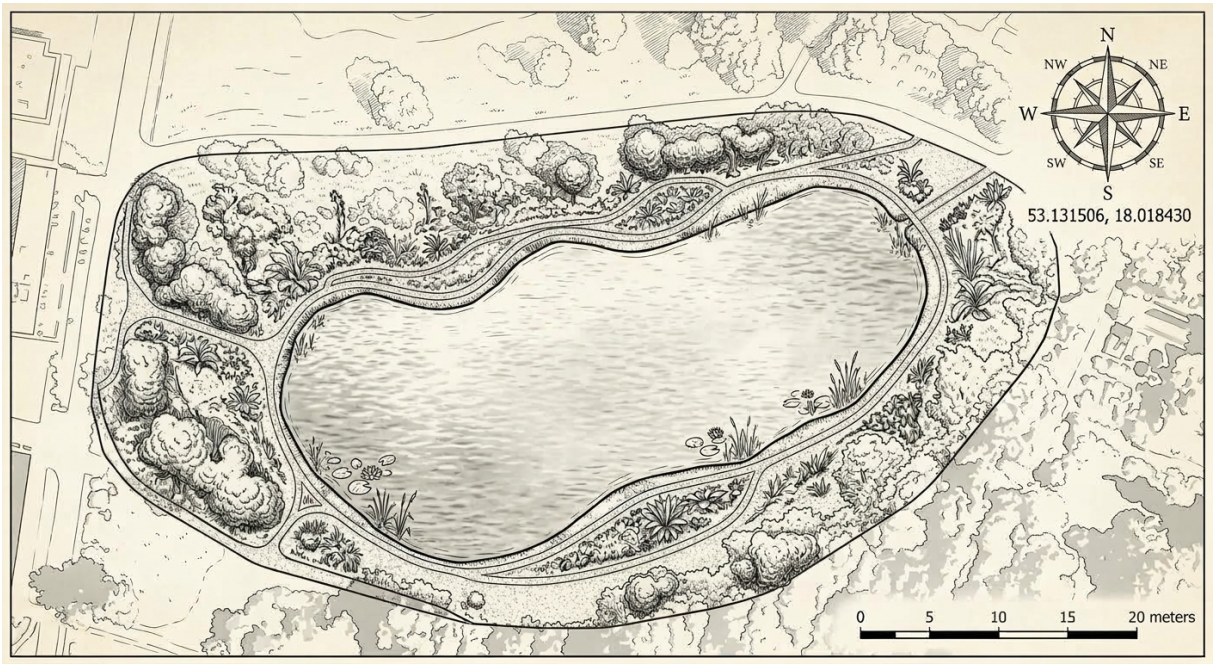

Fig. 1 General characteristics of the study pond, including its location and dimensions

The pond was bioaugmented with a commercially available, environmentally friendly biopreparation intended to accelerate the decomposition of organic matter in soil, including crop residues, manure, and catch crops. According to the manufacturer's specifications, the preparation contained a mixture of five bacterial strains belonging to the genus *Bacillus*, at a concentration of $\geq 5 \times 10^9$ CFU mL^{-1}. Bioaugmentation was carried out in April, May, August, and September 2025. During the first application, 20 L of the preparation was applied, whereas 5 L was applied during each of the subsequent applications.

2.2 Cytoplasmatic membrane integrity of bacterial cells

Cell membrane integrity, representing one aspect of the physiological condition of bacterial populations, was assessed using cytological methods based on fluorescence staining. The LIVE/DEAD® BacLight™ Bacterial Viability Kit was used to simultaneously determine bacterial abundance and assess cell membrane integrity. To ensure optimal visualization of bacterial cells, separate filters were used for propidium iodide (Ex 540/Em 605) and SYTO®9 (Ex 480/Em 535). Samples were prepared using black membrane filters with a pore size of 0.2 µm. For each sample, at least 20 randomly selected microscopic fields of view were examined to determine bacterial abundance and assess cell membrane integrity. Bacterial cells were visualized and enumerated using Motic Images Advanced 3.2 software.

2.3 Samples preparation and bacterial DNA extraction

To obtain sufficient quantities of environmental DNA (eDNA), water samples were subjected to membrane filtration immediately after arrival at the laboratory. The samples were first pre-filtered through cellulose filters with a nominal pore size of approximately 30 µm. The resulting prefiltrate was then passed through 0.22 µm membrane filters. The filters were placed in sterile Falcon tubes and stored at −86 °C until DNA extraction.

Bacterial DNA was extracted from the filters using the DNeasy® PowerWater® Kit (Qiagen), following the manufacturer's instructions and previously validated protocols (Reynoso et al., 2019). The extracted genetic material was subsequently subjected to sequencing using Oxford Nanopore Technology (ONT) by an external sequencing provider.

2.4 PCR Amplification and Sequencing

To characterize the taxonomic structure of the bacterial community, the V1–V9 region of the 16S rRNA gene was amplified using Q5 HiFi 2× Master Mix (NEB) and the universal primer pair 27F (5′-AGAGTTTGATCMTGGCTCAG-3′) and 1492R (5′-

TACGGYTACCTTGTTACGACTT-3′). The resulting amplicons were sequenced using Oxford Nanopore Technology with the Native Barcoding 1D protocol. Sequencing was performed using the default instrument settings and MinKNOW software version 6.5.14. Taxonomic classification of the obtained reads was performed using the UBLAST algorithm against the NCBI database.

2.5 Statistical analysis

Statistical analyses of the obtained data were performed using Statistica 13.3 software. The assumption of normality of the data distribution within the analyzed groups was assessed using the Shapiro–Wilk test. Differences between groups were subsequently evaluated using one-way analysis of variance (ANOVA) or the non-parametric Kruskal–Wallis rank-sum test, as appropriate. Statistical significance was set at $p \leq 0.05$.

3. Results

Bacterial abundance in the studied water body exhibited pronounced seasonal variability throughout the study period (Fig. 2). In 2024, a gradual increase in bacterial abundance was observed during the spring–summer period, from 4.80×10^5 cells/mL in April to 6.72×10^5 cells/mL in June. In 2025, following the initiation of biopreparation application in April and May, a marked but short-lived increase in bacterial abundance was recorded. Bacterial abundance increased from 6.36×10^5 cells/mL in April to a maximum of 31.32×10^5 cells/mL in June, followed by a pronounced decline in the subsequent months. Following further applications of the biopreparation in August and September, bacterial abundance increased again; however, the values reached (approximately 17×10^5 cells/mL) were lower than the maximum recorded during the first half of the year.

Periods of increased bacterial abundance were followed by a decline to levels comparable to those observed before application or within the typical range of seasonal variability.

Statistical analysis confirmed significant differences in bacterioplankton abundance among the sampling periods ($p < 0.05$). However, post-hoc tests did not reveal statistically significant differences between individual groups.

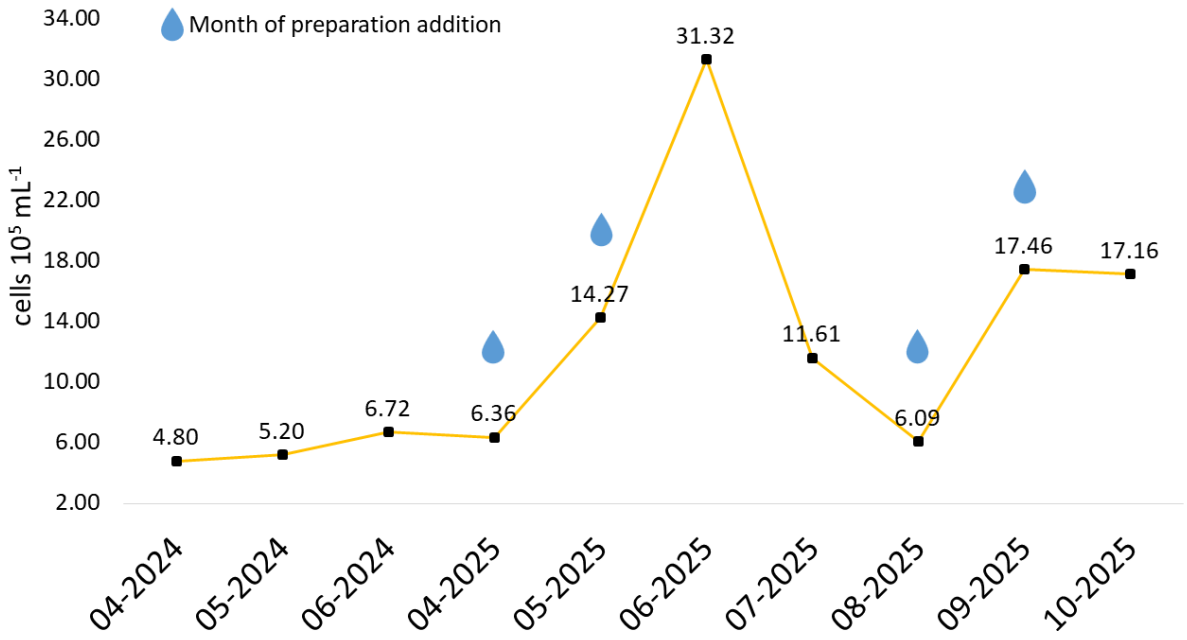

Fig.2 Dynamics of changes in bacterioplankton abundance during the two study periods: from April to June 2024 and from April to October 2025.

As shown in Fig. 3, the bacterioplankton community also exhibited temporal variability in the proportions of cells with intact cell membranes (MEM[+]) and cells with damaged membranes (MEM[−]). In 2024, cells with damaged membranes predominated, accounting for approximately 70% of the population, whereas cells with intact membranes represented only about 30%. At the beginning of the 2025 sampling season (April), the proportion of MEM[+] cells was the lowest recorded throughout the study period (14.96%). Following the first cycle of biopreparation application (April–May), the proportion of MEM[+] cells increased markedly, exceeding 69–78%. However, in the subsequent months, the proportion of cells with intact membranes declined again, reaching a minimum in August (18.26%). Following the second cycle of biopreparation application (August–September), a further increase in the proportion of MEM[+] cells was observed, reaching 63.57% in September and 78.31% in October. As observed for bacterial abundance, statistical analysis revealed significant differences in the physiological structure of the bacterioplankton among the sampling periods ($p < 0.05$), although no statistically significant differences were detected between individual

months.

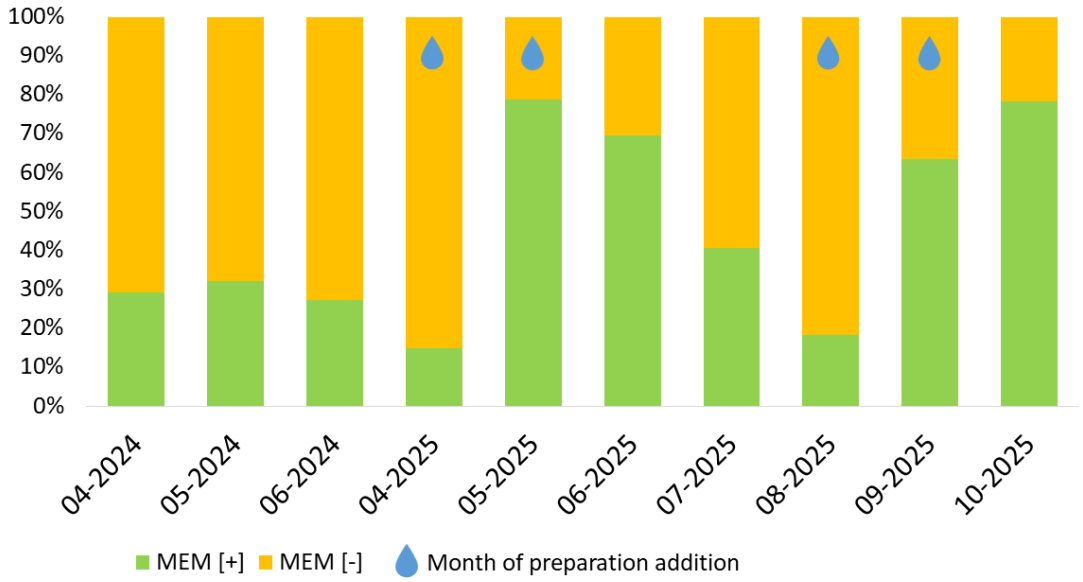

Fig.3 Dynamics of changes in the abundance of planktonic bacterial cells with intact and damaged cell membranes during the two study periods: from April to June 2024 and from April to October 2025.

Analysis of the bacterioplankton taxonomic profile based on the V1–V9 regions of the 16S rRNA gene revealed a relatively stable community composition throughout the study period. Regardless of the sampling date, the dominant groups were the classes Betaproteobacteria, Flavobacteria, Cyanophyceae, Cytophagia, and Gammaproteobacteria (Fig. 4). The relative abundance of these taxa remained at comparable levels both before and after application of the biopreparation, indicating no pronounced changes in the composition of the dominant microbial groups. Only minor fluctuations in the relative abundance of individual classes were observed during the study period.

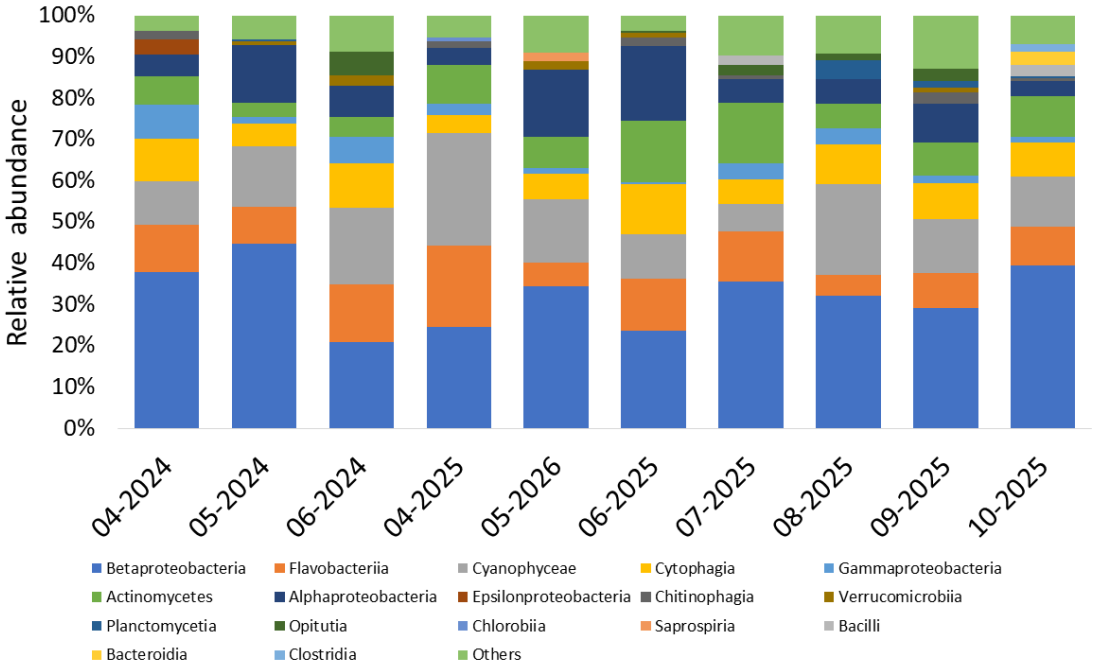

Fig. 4 Taxonomic structure of the bacterioplankton community at the class level during the two study periods: from April to June 2024 and from April to October 2025.

Analysis of the relative abundance of bacteria belonging to the genus *Bacillus* showed that this taxon represented only a minor fraction of the total bacterioplankton community in the studied pond. A short-term increase in the relative abundance of *Bacillus* was observed during periods following application of the biopreparation; however, these changes were transient and did not result in the sustained dominance of this genus within the microbial community of the pond (Fig. 5). Despite repeated applications of the preparation, *Bacillus* bacteria accounted for only a fraction of one percent of the total bacterial community.

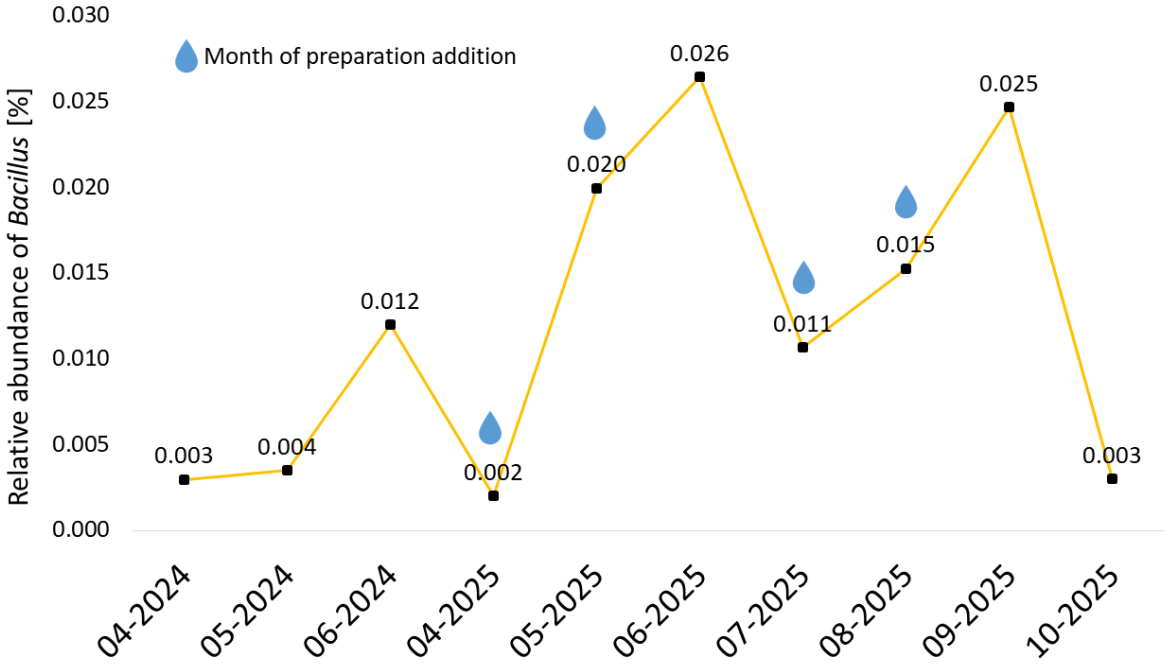

Fig. 5 Relative abundance of bacteria belonging to the genus *Bacillus* in the bacterioplankton community during the two study periods: from April to June 2024 and from April to October 2025.

4. Discusstion

Bioaugmentation is increasingly being considered as a strategy to support the functioning of aquatic ecosystems through the introduction of microorganisms with potentially beneficial metabolic properties. However, its effectiveness under natural conditions may be constrained by the complexity of established microbial communities, substrate availability, and fluctuations in environmental conditions. In the present study, application of a commercial biopreparation containing bacteria of the genus *Bacillus* was associated with short-term changes in bacterioplankton abundance and physiological condition, whereas the overall taxonomic structure of the community remained relatively stable.

The results presented in Fig. 2 indicate temporal changes in bacterioplankton abundance following application of the biopreparation. The observed increase in bacterial abundance may have been associated with a transient improvement in conditions conducive to microbial growth, potentially resulting from the supply of readily available organic substrates or other components contained in the preparation. However, the observed changes cannot be unequivocally attributed solely to bioaugmentation. Variations in bacterioplankton abundance are a natural feature of freshwater ecosystem functioning. Planktonic bacterial communities undergo seasonal fluctuations driven by, among other factors, temperature, nutrient availability, organic matter content, oxygen conditions, and the development of autotrophic organisms.

Studies conducted in freshwater ecosystems have shown that temperature and parameters related to nutrient availability are among the important factors shaping the temporal dynamics of bacterial communities (Paruch et al., 2020).

The most pronounced response potentially associated with biopreparation application was observed in the proportion of cells with intact cell membranes. In April 2025, MEM[+] cells accounted for 14.96% of the bacterial population, whereas following the first application cycle, their proportion increased to values exceeding 69–78%. After declining again during the summer period, the second application cycle was followed by another increase in the proportion of MEM[+] cells, reaching 63.57% in September and 78.31% in October. At the same time, statistical analysis revealed significant differences among the study periods; however, post-hoc tests did not identify unambiguous differences between individual months.

It should be emphasized, however, that cell membrane integrity does not necessarily indicate full metabolic activity or the ability of a cell to proliferate. Therefore, LIVE/DEAD-based staining methods should primarily be interpreted as indicators of membrane status and potential cell viability rather than as direct measures of metabolic activity. Berney et al. (2007) highlighted the possibility of intermediate physiological states associated with different degrees of membrane damage. Consequently, the increase in the proportion of cells with intact membranes observed in the studied pond should not be directly equated with an increase in metabolic activity.

Similar relationships have also been observed in lake ecosystems. Salmaso et al. (2018), who investigated bacterioplankton communities over two complete annual cycles, demonstrated recurrent seasonal dynamics of bacterial assemblages associated primarily with changes in temperature, thermal stratification, and seasonal nutrient availability. Thus, in the studied pond, at least some of the observed changes in bacterial abundance and physiological condition may have resulted from natural seasonal variability, with the effects of biopreparation application potentially superimposed on these underlying seasonal patterns.

Analysis of the V1–V9 regions of the 16S rRNA gene revealed a relatively stable taxonomic structure of the bacterioplankton community. Throughout the study period, the same major bacterial groups remained dominant, and their relative abundances were comparable before and after application of the biopreparation. This taxonomic stability may be associated with the inherent resistance of established microbial communities to short-term disturbances. Existing microbial assemblages may limit the establishment of newly introduced microorganisms through competition for resources and niche space, as well as through direct interactions among populations (Shade et al., 2012). Experimental studies on the introduction

of non-native microorganisms have indicated that communities with greater diversity and more complex structures may exhibit greater resistance to colonization by exogenous microorganisms (Tao et al., 2018). A similar phenomenon may have occurred in the studied pond. The bacterioplankton community was already established before the onset of bioaugmentation, and the introduction of *Bacillus* bacteria represented a short-term disturbance to the existing ecological system. The results concerning the relative abundance of *Bacillus* (Fig. 5) provide further support for this interpretation. Despite a transient increase in their relative abundance following application of the preparation, these bacteria accounted for only a minor fraction of the total community and did not achieve sustained dominance. The low and transient contribution of *Bacillus* to the bacterioplankton community may indicate limited persistence of the introduced inoculum. As emphasized by Cycoń (2026), assessment of bioaugmentation effectiveness should consider not only the presence of introduced microorganisms but also the persistence of their functional effects over time and under competitive environmental conditions. Importantly, however, the lack of sustained *Bacillus* colonization did not indicate a complete absence of an ecosystem response to biopreparation application. In the studied pond, application of the preparation was followed by increases in bacterioplankton abundance and in the proportion of cells with intact membranes, while no substantial restructuring of the overall taxonomic composition was observed. This may indicate that the potential effects of bioaugmentation do not necessarily depend on the permanent replacement of a fraction of the indigenous community by microorganisms introduced with the preparation. Instead, components of the biopreparation may have temporarily increased the availability of readily assimilable substrates or other compounds capable of stimulating the activity of indigenous microorganisms. A similar phenomenon has been reported in studies investigating the application of *Bacillus* bacterial mixtures in aquaculture systems. Li et al. (2022) demonstrated that the addition of *Bacillus* bacteria could modify microbial community composition and improve water quality parameters, with the observed response being associated, among other factors, with changes in the relative abundance of specific functional bacterial groups. These findings suggest that the effects of *Bacillus* bacteria may be expressed not only through their sustained establishment and dominance within the microbial community, but also through indirect effects on the functioning and composition of the pre-existing microbial assemblage.

5. Conclusions

Despite the absence of significant changes in the taxonomic structure of the bacterioplankton community, application of the biopreparation was followed by a transient increase in bacterial abundance and a higher proportion of cells with intact cell membranes. The observed changes may have been associated with indirect effects of the biopreparation, potentially related to the introduction of organic compounds, enzymes, or bacterial metabolites, although the mechanisms underlying these responses remain unclear. Such effects may have influenced bacterial growth and cell membrane integrity without necessarily altering the overall taxonomic structure of the community. The absence of persistent changes in the taxonomic structure of the bacterioplankton community, together with the low and transient relative abundance of bacteria assigned to the genus Bacillus, provides no clear evidence of sustained establishment of the introduced bacteria within the community. However, the methods used in this study do not allow the persistence of the specific strains introduced with the biopreparation to be conclusively determined. These potential effects may also have been associated with localized changes in environmental conditions, such as substrate availability or oxygen microgradients, which could have temporarily influenced the functioning of the microbial community.

Several limitations should be considered when interpreting the results. First, the study was conducted in a single pond, which limits the generalizability of the findings to other freshwater ecosystems. In addition, the 16S rRNA gene-based analysis provides information on the taxonomic structure of the microbial community but, by itself, does not allow direct inferences about the metabolic activity of individual taxa. Therefore, future studies should integrate analyses of microbial community structure with concurrent monitoring of physicochemical parameters, substrate availability, and indicators of microbial metabolic and functional activity. Such an integrated approach would provide a more comprehensive assessment of the mechanisms underlying the effects of bioaugmentation and help distinguish the direct effects of the introduced microorganisms from those associated with changes in environmental conditions.

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Conflicts of Interest: The authors declare no conflicts of interest in this research.

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