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Fine-scale bacterioplankton turnover across a narrow low-salinity estuarine gradient in northern Vietnam

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Abstract

Estuarine bacterioplankton communities often vary along broad freshwater-to-marine gradients, whereas community turnover within the low-salinity end of these gradients remains less well resolved. Here, we examined bacterioplankton communities at four stations along a low-salinity estuarine transect in Hai Phong, northern Vietnam, spanning only 0.10–2.53‰ salinity, using 16S rRNA gene amplicon sequencing. Despite this narrow range, community composition changed markedly along the transect. E1 and E2, both at 0.10‰, were the most similar, whereas community dissimilarity increased toward E3 (1.30‰) and E4 (2.53‰). Alpha diversity showed a non-monotonic pattern and peaked at E3. Taxonomic composition also shifted, with *Limnohabitans*, *Malikia*, and *Vogesella* more prominent at E1–E2, whereas the CL500-29 marine group and *Cyanobium* PCC-6307 increased at E3 and/or E4. Nevertheless, 216 ASVs were detected across all four libraries, indicating that community differentiation occurred within a substantially shared bacterial assemblage. These observations provide evidence of fine-scale bacterioplankton turnover within a compressed low-salinity interval and highlight the potential ecological heterogeneity of the freshwater–oligohaline transition. Given the limited number of stations and single sampling campaign, broader spatial and temporal replication will be required to determine the generality and persistence of this pattern.

1. Introduction

Estuaries are dynamic transition zones where freshwater and seawater mix over relatively short distances, generating pronounced gradients in salinity, nutrients, suspended matter, and organic matter. Bacterioplankton respond rapidly to these environmental changes and play central roles in carbon and nutrient cycling in the water column (Gasol and Kirchman 2018). Salinity is a well-established correlate of estuarine bacterial biogeography (Bouvier and del Giorgio 2002; Crump et al. 2004; Campbell and Kirchman 2013), although its influence is embedded within broader hydrodynamic and biogeochemical variation. Recent studies across contrasting estuarine and coastal systems illustrate this environmental coupling. In the tropical Gulf of Nicoya, river discharge and tidal exchange reorganize microbial assemblages together with salinity, dissolved organic carbon, and nutrients (Marín-Vindas et al. 2023; Soria-Píriz et al. 2024). Environmental variation also structures bacterioplankton communities across near- and offshore waters of the Yangtze Estuary and northern Chinese coastal waters (Xian et al. 2024; Li et al. 2025). High-resolution studies in the Warnow and Elbe further demonstrate substantial spatial and temporal variation in bacterial communities across freshwater–brackish systems in association with salinity, discharge, nutrients, temperature, and season (Sperlea et al. 2025; Russnak et al. 2026). Collectively, these studies emphasize that estuarine bacterioplankton patterns emerge from interacting environmental gradients rather than from salinity acting in isolation.

Most estuarine surveys encompass a substantial portion of the freshwater-to-marine continuum, an approach well suited to identifying broad biogeographic patterns but potentially providing less resolution near the freshwater end. This low-salinity interval may nevertheless contain substantial ecological heterogeneity. Earlier work suggested that salinity-related effects on bacterial diversity may become more pronounced below approximately 5‰ (Kan et al. 2007). More recent studies have documented pronounced microbial turnover across freshwater and oligohaline reaches (Amadei Martínez et al. 2025), while bacterial alpha diversity in the Elbe Estuary was highest in oligohaline samples (Russnak et al. 2026). These observations suggest that the freshwater–oligohaline transition should not necessarily be treated as a single, relatively homogeneous compartment and that finer spatial resolution within this interval may reveal ecologically relevant community variation.

Northern Vietnamese estuaries experience strong riverine and tidal forcing, yet bacterioplankton variation at such fine low-salinity scales remains poorly documented. Here, we characterized bacterioplankton communities at four stations along a low-salinity estuarine transect in Hai Phong, northern Vietnam, spanning only 0.10–2.53‰. Rather than attempting to characterize the full freshwater-to-marine continuum, we focused specifically on this compressed low-salinity interval. We asked whether bacterioplankton community composition changes detectably across this interval, whether community dissimilarity increases along the transect, and which bacterial groups contribute most clearly to the observed turnover. By resolving community variation within a portion of the estuarine continuum that may be represented at relatively coarse spatial resolution in broader surveys, this study provides a focused assessment of fine-scale bacterioplankton heterogeneity near the freshwater–oligohaline transition.

2. Materials and Methods

Surface water was sampled at 0.5 m depth between 09:00 and 11:00 on 4 July 2026 during a rising tide along a low-salinity estuarine transect in Hai Phong City, northern Vietnam. Four stations (E1–E4) were sampled along the estuarine transect, spanning salinities of 0.10, 0.10, 1.30, and 2.53‰, respectively (Fig. 1). Water was collected aseptically in sterile polypropylene bottles and transported to the laboratory within 2 h in dark, ice-cooled containers. Temperature, salinity, and dissolved oxygen (DO) were measured in situ using a calibrated multiparameter probe. Dissolved inorganic nutrients, including ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), orthophosphate (PO_4^{3-}), and dissolved silicate (SiO_2), were determined spectrophotometrically following standard methods for water analysis (APHA 2023). For

microbiome analysis, water was filtered through sterile 0.2-µm polycarbonate membrane filters; filters were flash-frozen and stored at −80°C until DNA extraction.

Bacterial DNA was extracted from membrane filters using the DNeasy PowerSoil Pro Kit (QIAGEN, Hilden, Germany) according to the manufacturer's instructions, with blank extractions processed as negative controls. DNA quality and quantity were assessed by spectrophotometry (NanoDrop, Wilmington, DE, USA). The V3–V4 region of the bacterial 16S rRNA gene was amplified using primers 341F (5'-CCTACGGGNGGCWGCAG-3') and 805R (5'-GACTACHVGGGTATCTAATCC-3'), modified for Illumina sequencing (Klindworth et al. 2013). Successfully amplified samples and negative controls were sequenced on an Illumina MiSeq platform using paired-end 2 × 250-bp reads. For the four sequencing libraries analyzed here, 204,388 raw reads were obtained, of which 155,629 non-chimeric reads remained after quality filtering, denoising, merging, and chimera removal (Table S1).

Demultiplexed paired-end reads were processed using DADA2 (Callahan et al. 2016). Forward and reverse reads were truncated according to their quality profiles, then filtered, denoised, merged, and screened for chimeras. ASVs assigned to Eukaryota, Archaea, chloroplasts, or mitochondria were removed. Negative controls were included in the sequencing workflow, and potential contaminants were assessed using decontam (Davis et al. 2018). Taxonomy was assigned against SILVA release 138 (Quast et al. 2013). Community data were organized and analyzed using phyloseq (McMurdie and Holmes 2013), with multivariate analyses performed using vegan (Oksanen et al. 2022). To standardize sequencing depth among libraries, the four libraries were rarefied to 10,968 reads per library. Observed ASV richness, Chao1 richness, Shannon diversity, and Simpson diversity were calculated from the rarefied dataset, and rarefaction curves were used to assess sequencing coverage. For community-composition analyses, the rarefied ASV counts were converted to relative abundances, and Bray–Curtis dissimilarities were calculated from these relative-abundance profiles. The resulting Bray–Curtis distance matrix was used for principal coordinates analysis (PCoA), salinity-constrained distance-based redundancy analysis (dbRDA), and the Mantel analysis. For descriptive visualization, salinity was fitted onto the PCoA ordination using the envfit function in vegan. The salinity-constrained dbRDA was fitted using capscale. A Mantel test using Spearman rank correlation was used to assess the correspondence between Bray–Curtis community dissimilarities and pairwise Euclidean distances in salinity. Because only four independent stations were available, the salinity–community analyses were treated as exploratory rather than confirmatory. Permutation-based tests were requested with 999 permutations; where the number of unique permutations was constrained by the four-station design, all available permutations were enumerated. Statistical results were therefore interpreted jointly with effect sizes, ordination patterns, and pairwise community dissimilarities rather than on statistical significance alone. Core ASVs were operationally defined for this study as ASVs detected in all four environmental libraries (100% prevalence), without an additional relative-abundance threshold. The 25 most abundant shared ASVs presented in Table S2 were ranked by total read abundance across the four rarefied libraries. Hierarchical clustering of the 30 most abundant bacterial taxa was based on log1p-transformed relative abundances, followed by row-wise Z-score standardization, Euclidean distance, and average-linkage clustering.

3. Results and Discussion

3.1. Low-salinity gradient and sequencing saturation

The four stations represented a compact freshwater-to-low-salinity transition, with salinity increasing from 0.10‰ at E1 and E2 to 1.30‰ at E3 and 2.53‰ at E4 (Table 1; Fig. 1). Dissolved oxygen increased toward E4, whereas nutrient concentrations showed less consistent spatial patterns. For example, NO_3^- reached its highest concentration at E2 rather than increasing or decreasing monotonically along the transect (Table 1; Fig. S3). Such covariation is characteristic of estuarine systems, where freshwater–marine mixing interacts with discharge, local nutrient inputs, biological uptake, organic matter dynamics, and residence time (Crump et al. 2004; Marín-Vindas et al. 2023; Soria-Píriz et al. 2024). Accordingly, salinity is treated here primarily as a spatially structured environmental correlate of community variation rather than as an independently manipulated driver.

Table 1
Physicochemical characteristics and bacterioplankton alpha-diversity indices at the four sampling stations along the low-salinity estuarine transect.

Station	Temp (°C)	Salinity (‰)	DO (mg/L)	NO_2^- (µg/L)	NH_4^+ (µg/L)	PO_4^{3-} (µg/L)	NO_3^- (µg/L)	SiO_2 (mg/L)	Observed ASVs	Chao1 Index	Shannon Index	Simpson Index
E1	29.1	0.10	3.68	183.56	109.54	32.82	111.87	4.07	478	494	5.03	0.98
E2	29.0	0.10	3.18	211.65	147.39	35.17	724.84	4.07	749	790	5.46	0.99
E3	29.0	1.30	4.65	195.20	55.99	39.20	86.10	3.89	1,062	1,159	6.03	0.99
E4	30.2	2.53	5.10	168.39	110.15	30.97	435.01	4.33	712	759	5.60	0.99

Abbreviations: DO, dissolved oxygen; Temp, water temperature. Alpha-diversity indices were calculated after rarefaction to 10,968 reads per library.

Rarefaction curves approached asymptotes for all four libraries (Fig. S1). At the standardized depth of 10,968 reads per library, the curves indicated that a substantial proportion of the detectable ASV richness was represented, supporting descriptive comparisons of alpha diversity among stations.

3.2. Non-monotonic alpha-diversity pattern

Alpha diversity varied substantially among the four stations but did not follow a monotonic pattern along the low-salinity transect (Fig. 2; Table 1). Observed richness increased from 478 ASVs at E1 to 749 at E2 and reached a maximum of 1,062 at E3 (1.30‰), before declining to 712 at E4 (2.53‰). Chao1 and Shannon diversity showed the same broad pattern, identifying E3 as the station with the highest local bacterial diversity.

The occurrence of the diversity maximum at an intermediate position along the transect is consistent with the possibility that low-salinity transition zones contain overlapping bacterial populations associated with different water masses, together with taxa responding to local environmental conditions. Previous work has shown that estuarine communities can contain freshwater and marine populations transported into the estuary as well as populations developing within the estuarine environment itself (Crump et al. 2004). More recently, Russnak et al. (2026) reported maximum bacterial alpha diversity in oligohaline samples from the Elbe Estuary, while high-resolution sampling in the Warnow revealed substantial short-range variation in microbial richness and composition (Sperlea et al. 2025). The E3 maximum should nevertheless be interpreted as a station-level observation rather than evidence for a general intermediate-salinity diversity maximum. With one library per station and a single sampling campaign, the present dataset cannot distinguish a reproducible salinity-related pattern from spatial or temporal heterogeneity specific to the sampling event. The result instead highlights that pronounced local variation in bacterial alpha diversity can occur within a compressed low-salinity interval.

3.3. Fine-scale community turnover across the low-salinity gradient

Community composition showed a clearer directional pattern than alpha diversity. E1 and E2, both characterized by a measured salinity of 0.10‰, formed the most similar pair (Bray–Curtis dissimilarity = 0.234), whereas dissimilarity between E1 and the progressively more saline stations increased to 0.520 at E3 (1.30‰) and 0.678 at E4 (2.53‰) (Fig. 3). Thus, appreciable compositional differentiation was observed across an absolute salinity range of only 2.43‰. The PCoA was consistent with this spatial pattern, with the first two axes accounting for 94.4% of the ordination variation (PCoA1 = 68.0%; PCoA2 = 26.4%). The fitted salinity vector was aligned with the main direction of community differentiation (Fig. 3). The salinity-only dbRDA accounted for 67.76% of the fitted community variation (adjusted R^2 = 51.64%), and the Mantel analysis yielded a positive rank correlation between community and salinity distances (Spearman r = 0.971). However, neither permutation test reached the conventional significance threshold (P = 0.0833 for both analyses; Table 2). Given the four-station design, these results are interpreted as descriptive evidence of a directional association rather than statistical confirmation of a salinity effect.

Table 2
Exploratory associations between salinity and bacterioplankton community composition across the four sampling stations.

Method	Metric	Value	Interpretation
dbRDA (Salinity)	R^2	67.76%	Proportion of fitted community variation associated with salinity
	Adjusted R^2	51.64%	Adjusted model effect size
dbRDA (Salinity)	F-statistic	4.204	Model test statistic
dbRDA (Salinity)	P-value	0.0833	Not statistically significant at α = 0.05; exploratory inference limited by n = 4 stations
Mantel Test (Salinity vs Bray-Curtis)	Mantel r (Spearman)	0.971	Positive rank association between community and salinity distances
	P-value	0.0833	Not statistically significant at α = 0.05; exploratory inference limited by n = 4 stations

Comparable bacterioplankton turnover has been documented across broader estuarine gradients, where salinity varies together with freshwater discharge, tidal exchange, nutrients, organic matter, and other environmental factors (Marín-Vindas et al. 2023; Soria-Píriz et al. 2024; Amadei Martínez et al. 2025; Sperlea et al. 2025; Russnak et al. 2026). The distinctive feature of the Hai Phong observations is the spatial scale over which differentiation was detected: measurable community reorganization occurred within the 0.10–2.53‰ interval rather than across a full freshwater-to-marine continuum. At the same time, E1 and E2 differed despite having the same recorded salinity, demonstrating that salinity alone cannot account for all of the observed variation. This contrast indicates appreciable local heterogeneity even at the freshwater end of the transect. Taken together, the station-to-station dissimilarities support a pattern of fine-scale community turnover associated with the low-salinity transition, while the limited spatial replication precludes separating the contribution of salinity from other covarying environmental and local factors.

3.4. Taxonomic turnover and shared ASVs

The community-level pattern was accompanied by changes in the relative abundance of major bacterial lineages. Pseudomonadota decreased from 61.2% at E1 to 35.5% at E4, Actinomycetota reached their highest relative abundance (37.9%) at E3, and Bacteroidota and Cyanobacteriota became more prominent at E3–E4 (Fig. S2). At finer taxonomic resolution, *Polynucleobacter*, *Limnohabitans*, *Malikia*, and *Vogesella* were more prominent at E1–E2, whereas the CL500-29 marine group and *Cyanobium* PCC-6307 increased at E3 and/or E4 (Fig. 4; Fig. S5). These taxonomic shifts were consistent with the community-level differentiation represented by Bray–Curtis dissimilarities and the PCoA.

Similar freshwater-to-brackish transitions in dominant bacterial groups have been reported in other estuarine systems. Actinomycetota were prominent in upstream reaches of the Schelde, whereas the relative contribution of marine-associated bacteria increased downstream (Amadei Martínez et al. 2025). In the Warnow, Actinobacteria were more characteristic of freshwater samples, whereas Bacteroidia and Cyanobacteria contributed more toward the brackish Baltic end (Sperlea et al. 2025). The Hai Phong observations are broadly consistent with this ecological transition, although the present dataset captures only its low-salinity portion and does not establish salinity-specific responses for individual taxa.

Despite these compositional shifts, a substantial component of the assemblage was shared among stations. A total of 216 ASVs were detected in all four libraries (Fig. S4), including members of the hgcI clade, *Polynucleobacter*, and the CL500-29 marine group among the most abundant shared ASVs (Table S2). The coexistence of these shared ASVs with increasing Bray–Curtis dissimilarity and changes in dominant taxa indicates that fine-scale differentiation involved substantial redistribution of relative abundance within a shared bacterial assemblage, together with differences in ASV occurrence, rather than complete replacement of the community. This combination of shared membership and compositional turnover provides a useful perspective on the low-salinity transition. Community differentiation across short estuarine distances need not require wholesale taxonomic replacement; instead, changes in the relative contribution of broadly distributed and locally varying populations may generate pronounced differences in community structure. Because the present observations represent a single sampling campaign, determining whether these patterns reflect persistent spatial organization will require replicated sampling across seasons, tidal conditions, and additional low-salinity stations.

4. Conclusions

Bacterioplankton communities showed appreciable compositional differentiation across the narrow 0.10–2.53‰ low-salinity interval examined in Hai Phong, northern Vietnam. Alpha diversity varied non-monotonically and reached its maximum at the intermediate station,

while major bacterial lineages and dominant taxa changed in relative abundance along the transect. At the same time, 216 ASVs were shared among all four libraries, indicating that fine-scale community differentiation occurred within a substantially shared bacterial assemblage rather than through wholesale taxonomic replacement. Together, these observations highlight the ecological heterogeneity that can occur within the freshwater–oligohaline portion of an estuarine continuum, a zone that may be represented at relatively coarse resolution in broader estuarine surveys. Because the present study was based on four stations sampled during a single campaign, the observed associations should be considered spatially focused and exploratory. Replicated sampling across seasons, tidal conditions, and additional low-salinity stations will be necessary to determine the temporal persistence and broader generality of these patterns.

Declarations

Author contributions

Pham The Thu: Conceptualization, Project administration, Visualization, Writing – original draft, Writing – review & editing. Le Ba Hoang Hiep: Investigation. Mathilde Vigneron: Data curation, Formal analysis, Investigation, Writing – review & editing. Yvan Bettarel: Formal analysis, Writing – review & editing. Dao Huong Ly: Investigation. Pham Tien Tai: Investigation. Dinh Van Nhan: Writing – review & editing. Dao Thi Anh Tuyet: Writing – review & editing. Tran Manh Ha: Writing – review & editing. All authors reviewed and approved the final manuscript.

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Ethics approval

Not applicable. This study analyzed environmental water samples and did not involve human participants or experimental animals.

Competing interests

The authors declare no competing interests.

Data availability

The raw 16S rRNA gene amplicon sequencing reads generated in this study are available in the NCBI Sequence Read Archive (SRA) under BioProject accession PRJNA1529955.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this manuscript, the authors used ChatGPT (OpenAI) to assist with language editing and readability. The authors reviewed and edited the manuscript and take full responsibility for its content.

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Figures

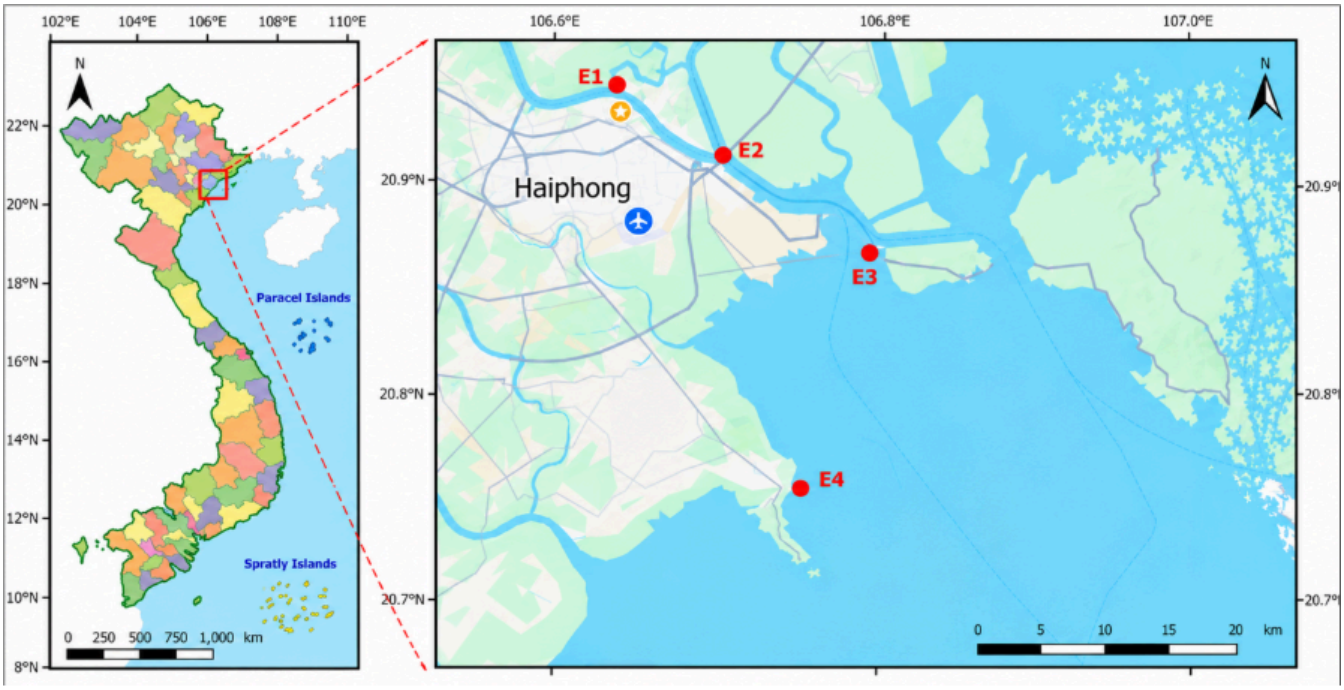


Figure 1

Location of the study area in northern Vietnam and distribution of the four sampling stations (E1–E4) along the low-salinity estuarine transect in Hai Phong

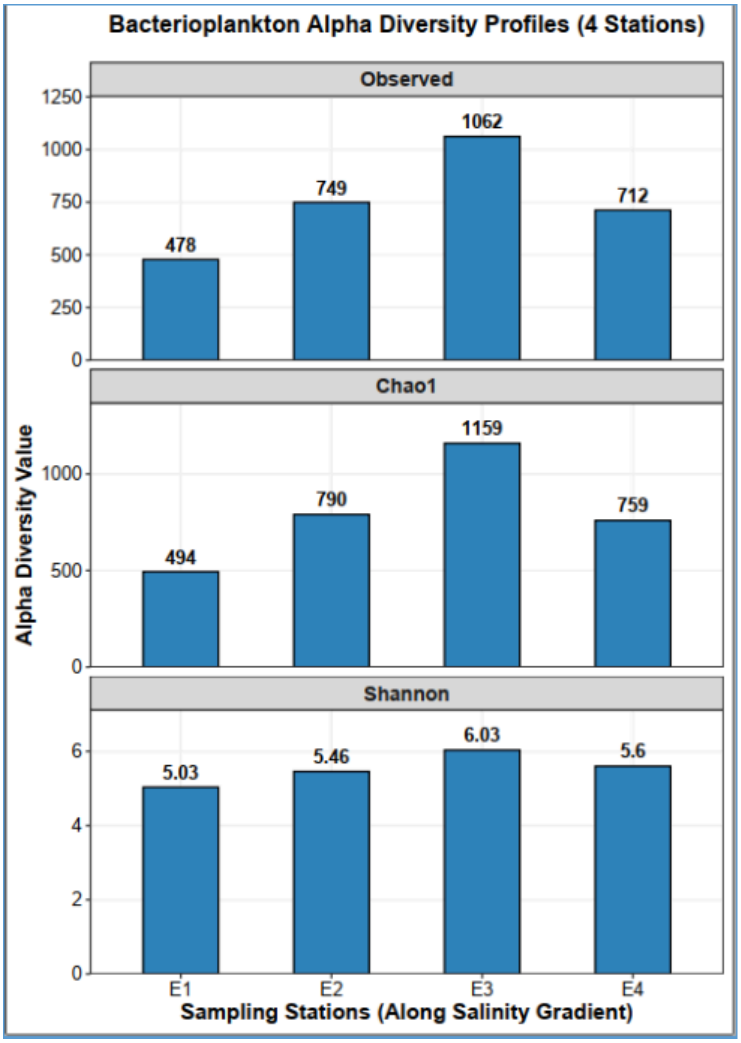


Figure 2

Bacterioplankton alpha-diversity profiles across the four sampling stations. Observed ASV richness, Chao1 richness, and Shannon diversity were calculated after rarefaction to 10,968 reads per library. Each station is represented by one biological library

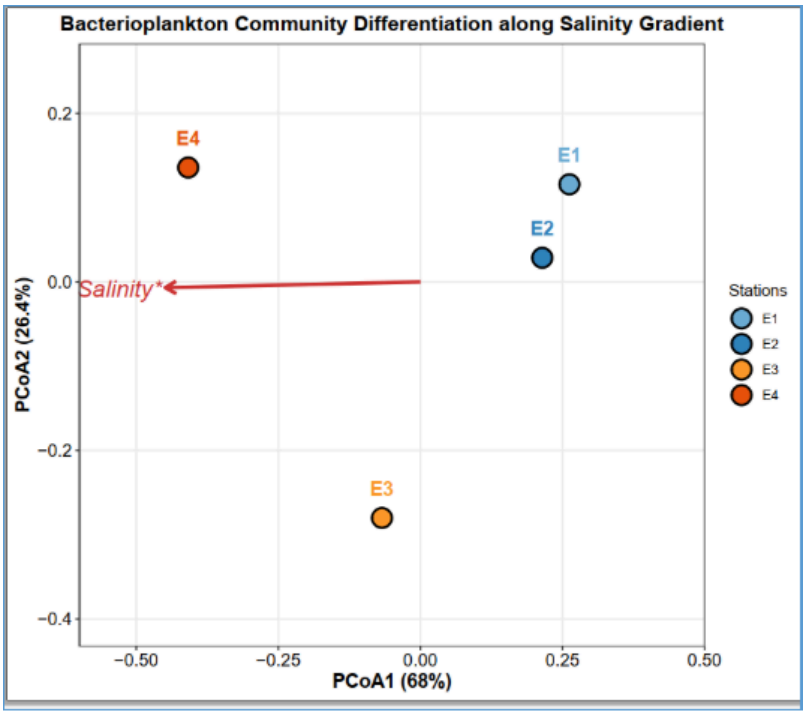


Figure 3

Principal coordinates analysis (PCoA) of Bray–Curtis dissimilarities among the four bacterioplankton communities. Bray–Curtis dissimilarities were calculated from relative abundances derived from the rarefied ASV dataset. PCoA1 and PCoA2 accounted for 68.0% and 26.4% of the ordination variation, respectively (94.4% combined). The fitted salinity vector (envfit) is shown descriptively to indicate the direction of the salinity gradient in ordination space

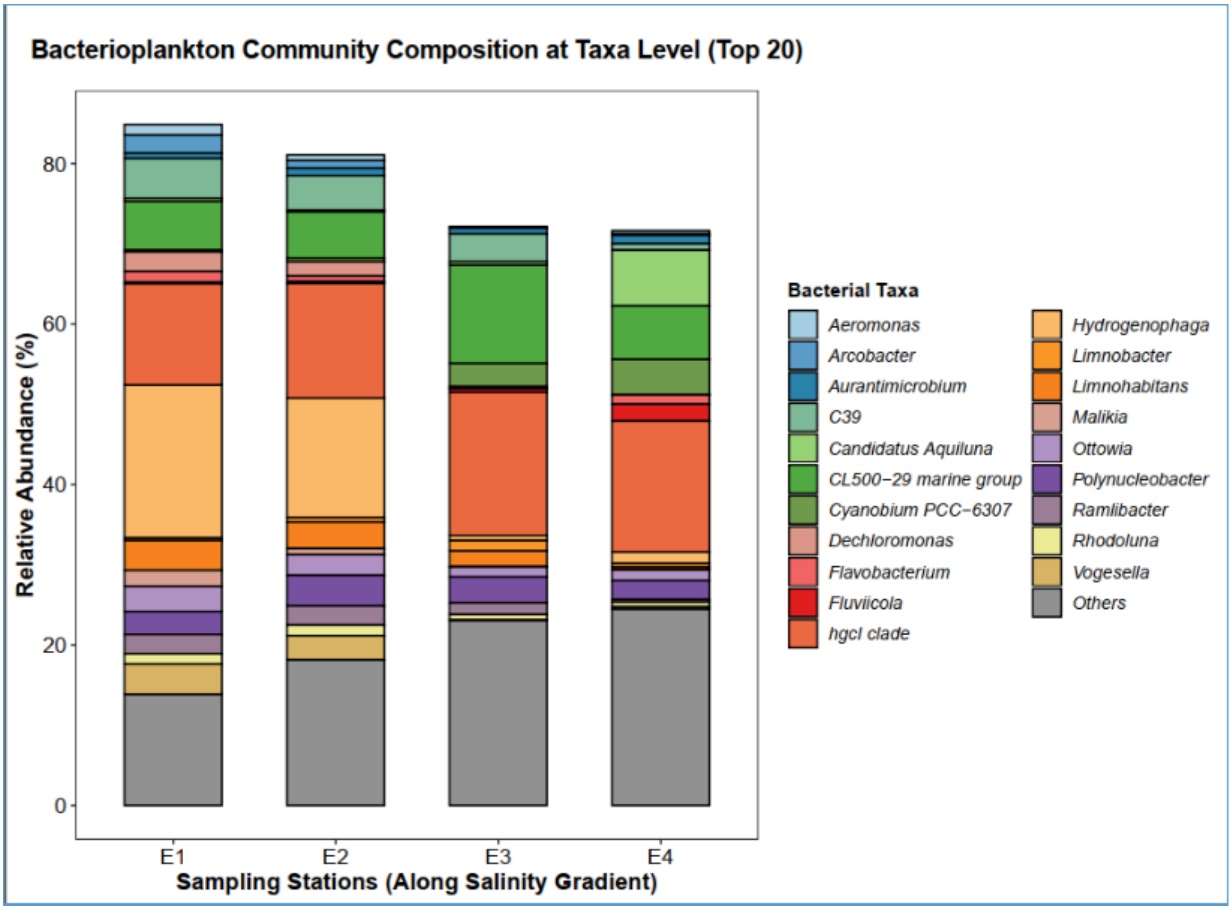


Figure 4

Relative abundance of the 20 most abundant bacterial taxa across the four sampling stations (E1–E4) along the low-salinity estuarine transect

Supplementary Files

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