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Identifying biological sources and indicators of surfactants in the sea surface microlayer and subsurface waters using fluorescence and microbial community profiling

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Abstract

Marine surfactants accumulate in the sea surface microlayer (SML) where they influence gas transfer velocities and air-sea exchange of climate relevant gases. Despite their importance, the biological sources and reliable proxies of marine surfactants remain poorly constrained. This study paired measurements of surfactant concentrations and fluorescent dissolved organic matter (FDOM) composition with bacterial and protist community profiles in the SML and subsurface waters (SSW) across three hydrographic regions and two seasons in the northwestern Atlantic Ocean. Surfactant concentrations were significantly enriched in the SML relative to the SSW, and temporal differences are a major driver of variability in surfactant concentrations, as demonstrated by the highest values recorded during a fall picoeukaryotic bloom. Surfactant concentrations showed a positive correlation with tryptophan-like FDOM, supporting a biogenic source of marine surfactants. Microbial community composition differed between the SML and SSW, with the SML enriched in small, resource-efficient taxa adapted to high-light and low-nutrient conditions. Significant correlations were observed between surfactant concentrations and diverse microbial taxa, including picoeukaryotic phytoplankton such as *Ostreococcus, Bathycoccus,* and *Micromonas*; heterotrophic bacteria such as the NS5 marine group*, Pseudoalteromonas*, SAR86, and *Candidatus Actinomarina*; as well as phagotrophic protists such as MAST-7B and Cercozoa, and parasitic dinoflagellates from the Dino-Group-I and Dino-Group-II clades. The diversity of surfactant associated microbial candidates suggests that surfactant production reflects a broader range of microbial processes than phytoplankton activity alone, with tryptophan-like FDOM capturing this integrated biological process more effectively than chlorophyll-a concentrations. These findings establish tryptophan-like FDOM as a promising proxy for predicting marine

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surfactant concentrations and highlight the need for an in-depth understanding of the diverse microbial sources of surfactants.

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1 Introduction

Surfactants are amphiphilic organic compounds composed of a hydrophilic moeity and a hydrophobic moeity. They are typically characterized by lower oxygen-to-carbon and higher hydrogen-to-carbon ratios relative to bulk dissolved organic matter (DOM) (Burdette et al., 2022; Coffey et al., 2025) and include a wide range of compounds such as phospholipids, amino acids, fatty acids, alkyl sulfates and linear alkylbenzene sulfonates (Frew et al., 2006; Cochran et al., 2016; Barthelmeß and Engel, 2022). Due to their amphiphilic nature, they tend to adsorb at air-water interfaces like bubbles and the sea surface microlayer (SML). The SML is the topmost 10s to 100s µm thick layer of the ocean with distinct physicochemical and biological characteristics compared to underlying subsurface waters (SSW) (Zhang et al., 2003; Cunliffe et al., 2013; Ebling and Landing, 2015; Wurl et al., 2018; Burdette et al., 2022; Coffey et al., 2025). Surfactants in the SML influence gas transfer velocities, aerosol particle emissions and subsequent cloud droplet formation, and trace gas uptake at the ocean surface (Hoffman and Duce, 1976; Wilson et al., 2015). These surfactant effects may be a source of inaccuracies in existing global climate models, creating a need for effective proxies for estimating the spatiotemporal variability of surfactants and their impact on air-sea processes (Pereira et al., 2018).

In the ocean, surfactants are primarily derived from biological sources, including bacterial and phytoplankton exudates (Zutic et al., 1981; Hardy, 1982; Liu et al., 2023). Several studies have linked increases in surfactant concentrations to high primary productivity, particularly during phytoplankton bloom seasons (Gašparović and Ćosović, 2003; Gašparović et al., 2007; Frka et al., 2009; Wurl et al., 2011). Surface slicks have also been associated with the presence of specific groups of surfactant-producing bacteria (Kurata et al., 2016). These bacteria are thought to be primarily hydrocarbon degrading groups such as *Bacillus*, *Paracoccus*, and *Pseudoalteromonas*,

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which synthesize biosurfactants that facilitate the solubilization and uptake of hydrophobic substrates (Maneerat et al., 2006; Antoniou et al., 2015; Morales-Guzmán et al., 2021). Additional biological contributions may arise from processes such as protist grazing, parasitism, and viral lysis, although these pathways remain relatively unexplored. Surfactants can also originate from terrestrial and anthropogenic sources, including plant-derived compounds (e.g., saponins) (Rai et al., 2021), microbial biosurfactants transported from sediments (Morales-Guzmán et al., 2021), and anthropogenic inputs such as linear alkylbenzene sulfonates and per- and polyfluoroalkyl substances (PFAS) (Jardak et al., 2016). Despite these diverse sources, their relative contributions to surfactant concentrations and composition, and their impact on air-sea processes, are not well understood. In addition, there remain gaps in the specific microbial communities contributing to surfactant concentrations. Identifying these diverse microbial sources is important because their spatiotemporal abundance can be linked to surfactant concentrations and composition, which are known to influence the magnitude of surfactant effects on air-sea processes (Frossard et al., 2019; Burdette et al., 2022; El Haber et al., 2024).

Fluorescent dissolved organic matter (FDOM) constitutes a subset of DOM that fluoresces under ultraviolet (UV) light (Stedmon and Bro, 2008). The study of FDOM using spectrofluorometry provides a relatively fast and cost-effective approach for tracking organic matter sources and transformations in aquatic ecosystems (Huguet et al., 2009). FDOM spans a range of biological and terrestrial origins and is broadly categorized into humic-like and protein-like components. Humic-like components are typically associated with terrestrially derived and degraded organic matter, whereas protein-like components are linked to both photosynthetic and heterotrophic microbial activity and are considered indicators of recently produced autochthonous organic matter (Coble, 1996; Stedmon and Markager, 2005; Yamashita et al., 2015; Devresse et

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al., 2023). Establishing relationships between FDOM composition and surfactant concentrations may therefore help infer the relative contributions of biological versus terrestrial sources of surfactants. In addition, tryptophan-like FDOM has been positively correlated with surfactant-like DOM, including unsaturated aliphatics, peptide-like compounds, and sulfur-rich compounds (Coffey et al., 2025), suggesting that it may serve as a proxy for surfactant abundance in marine systems.

Amplicon sequencing of marker genes, including the 16S rRNA gene for bacteria and the 18S rRNA gene for protists, enables high-resolution characterization of microbial community composition across diverse environments. Such approaches have identified dominant SML taxa, including bacterial groups such as Proteobacteria, Cyanobacteria, Actinobacteria, and Bacteroidetes (Cunliffe et al., 2011; Rahlff et al., 2021; Tastassa et al., 2025), as well as protists including Alveolata, Chrysophyceae, and Stramenopiles (Taylor and Cunliffe, 2014; Zäncker et al., 2021). Seasonal and spatial variations in these communities have also been reported (Čanković et al., 2022; Liu et al., 2023); however, studies that simultaneously measure microbial community structure alongside surfactant concentrations are limited. Linking microbial community structure with surfactant concentrations across contrasting hydrographic regions and seasons will help identify key biological indicators and potential surfactant producing taxa, providing new insight into the microbial processes that regulate surfactant variability in the ocean.

In this study, we characterize the bacterial and protist communities through 16S rRNA and 18S rRNA gene amplicon sequencing, respectively, in the SML and SSW at three sites in the Northwestern Atlantic during the summer and fall of 2022, and we assess their temporal and spatial variations. Concurrent measurements of surfactant concentrations and FDOM composition were paired with the microbial community data to identify biogenic and terrestrial contributions to

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surfactant pools and to detect potential microbial biomarkers and candidate surfactant producing taxa.

2 Methods

2.1 Sampling Locations

Two research cruises were conducted in summer (August 24 – September 2) and fall (November 10 – 11) 2022 to collect SML and SSW samples from the northwestern Atlantic Ocean aboard the *R/V Hugh R. Sharp*. Details about the project and sampling sites are outlined by Agblemanyo et al. (2026) and briefly described here. During the summer cruise, three sites were sampled, including a Delaware Coast station (38.72, -74.75), a Virginia Coast station (37.81, -75.42), and a Continental Slope station (37.83, -73.72). In the fall, only the Delaware Coast station was sampled because the cruise was cut short, as it coincided with Hurricane Ian. These sampling sites were chosen to span a range of terrestrial/marine influences and biological productivities. The Virginia Coast station is the closest to land and is impacted by the Chincoteague Bay, while the Continental Slope station is the farthest offshore. The Delaware Coast station is farther from land than the Virginia Coast station and is also directly impacted by the Delaware Bay. The two coastal stations represent sites with higher terrestrial influence, whereas the Continental Slope station represents marine conditions.

2.2 SML and SSW Sample Collection

SML samples were collected using the rosette-based glass plate (RGP) sampler. The RGP sampler was made up of three large glass plates (66 x 76 cm) attached to the metal frame of a 24-bottle rosette sampler and was controlled using the A-frame and mechanical winch system of the

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R/V Hugh R. Sharp. A detailed description of the RGP sampler, which enables safe, ship-based deployment of the sampler for the collection of high volume (~1 L h^{-1}) samples, is provided by Agblemanyo et al. (2026). SSW samples were collected from ~0.5 m depth using a modified pump profiler system (Hudson et al., 2019) from the starboard side of the ship directly after sampling the SML. These paired SML and SSW samples were collected three times throughout the day at each sampling station, including afternoon (~13:00), evening (~18:30) and night (~02:30), with a small number of stations also including a morning (~10:00) sample. Only three samples were obtained from the Virginia Coast station due to storm conditions during sampling. Sample metadata and environmental parameters are provided in Table S1.

2.3 Dissolved Organic Matter Measurements

DOM characteristics, including FDOM composition, surfactant concentrations, and dissolved organic carbon (DOC) concentrations were measured for the collected SML and SSW samples. For all DOM analyses, samples were filtered immediately after collection using pre-combusted (450 ºC, 4 h) 0.7 µm pore size glass fiber filters and stored for subsequent analysis.

Anionic surfactant concentrations were determined using ~100 mL of filtered samples. Samples were solid phase extracted on the ship using ENVI-18 cartridges (C18 sorbent material, 0.5 g bed weight, Millipore Sigma). The cartridges containing the retained extracts were stored at -20 ºC until elution in the lab. Surfactant concentrations were subsequently quantified using the colorimetric method according to established protocols (Gérard et al., 2016; Frossard et al., 2019; Burdette and Frossard, 2021; Bramblett and Frossard, 2024).

Aliquots of the filtered samples (~10 mL) were stored at 4 ºC for FDOM analysis and were analyzed within two weeks of sample collection. Fluorescence excitation emission matrices

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(EEMs) of the samples were obtained using a HORIBA Aqualog® spectrofluorometer across excitation and emission wavelength ranges of 230 – 700 nm and 245 – 822 nm, respectively. Readings were acquired at intervals of 2 nm for excitation and 4.65 nm for emission. EEMs data were corrected for inner filter effects and Raman calibrated (McKnight et al., 2001; Lawaetz and Stedmon, 2009). Parallel factor analysis (PARAFAC) was then used to deconvolute fluorescent components across samples using R packages *staRdom* and *eemR* (Ohno, 2002; Pucher et al., 2019; Ouyang et al., 2024). The resulting components were validated by comparison with reference spectra in the OpenFluor database (Murphy et al., 2014) (Table S2).

For DOC analysis, ~20 mL of the filtered samples were acidified to pH 2 using 2 M HCl and then purged to remove inorganic carbon. DOC concentrations were then measured by high temperature (680 ºC) catalytic oxidation (Emery et al., 1971; Sharp et al., 1993) using a Shimadzu TOC-Vcph analyzer. Calibration curves generated from potassium hydrogen phthalate standards were used to quantify DOC mass concentrations (mg of DOC per L). A detailed description of the DOC concentrations of these samples have already been published (Agblemanyo et al., 2026). In this study, the DOC concentrations were used to normalize the FDOM and surfactant concentrations, and throughout the text, surfactant concentrations are reported as µmol surfactant per mg DOC, while FDOM concentrations are reported as Raman Units (RU) per mg DOC.

2.4 DNA Extraction, Sequencing and Analysis

The collected SML and SSW water samples (~200 mL) were also filtered right after sampling using 0.22 µm nitrocellulose membrane filters. The filters were wrapped in precombusted aluminum foil packets and stored at -80 ºC until DNA extraction. Genomic DNA was extracted from the filters using the DNeasy® PowerSoil® (QIAGEN, Georgetown, MD, USA) Pro Kit following manufacturer's instructions. The V4 regions of the 16S and 18S rRNA

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genes were amplified using the 515F (5′-GTG-CCA-GCM-GCC-GCG-GTA-A-3′) and 806R (5′-GGA-CTA-CHV-GGG-TWT-CTA-AT-3′) primers (Caporaso et al., 2012) for bacteria, and the TAReuk_F (5′-CCA-GCA-SCY-GCG-GTA-ATT-CC-3′) and TAReuk_R (5′-ACT-TTC-GTT-CTT-GAT-YRA-3′) primers (STOECK et al., 2010) for protists, respectively. The amplified products were then sequenced on the MiSeq platform (Illumina, Inc., San Diego, CA, USA) at the Microbial Analysis, Resources, and Services (MARS) facility of the University of Connecticut following their standard protocols (Chen et al., 2023).

Bioinformatics analyses were conducted using the Mothur v.1.48.0 pipeline (Kozich et al., 2013). Paired end reads were assembled into contigs, screened for chimeras, and unique sequences were assigned as amplicon sequence variants (ASVs). Taxonomic classification of the bacteria 16S rRNA gene sequences was performed using the SILVA version 138.2 database (Quast et al., 2012) for bacteria, while protist 18S rRNA gene sequences were classified using the PR^2 version 5.1.1 database (Guillou et al., 2012; González-Miguéns et al., 2025). The number of sequences were normalized by subsampling to 10,054 sequences per sample for bacteria and 1,072 sequences per sample for protists, after removing an SML and an SSW protist sample which had less than 1000 reads. Chloroplast, mitochondria, archaea and eukaryotic sequences present in the 16S rRNA gene dataset were removed, whereas metazoan and higher plant sequences were removed from the 18S rRNA gene dataset. ASVs not present in more than 5% of samples were also removed.

2.5 Additional Oceanographic Measurements

Sea surface salinity and temperature were measured and recorded continuously with shipboard instrumentation (SBE 45, Sea-Bird, at 3.7 m depth) and were averaged for the times at which samples were collected. Chlorophyll-*a* (chl-*a*) concentrations were measured continuously with the shipboard fluorometer (AU10, Turner). The shipboard fluorometer measurements were

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calibrated using the chl-*a* concentrations of discrete samples that were measured in the lab using the spectrophotometric method described by Aminot and Rey (2000).

2.6 Statistical Analyses

Statistical similarities and differences in DOM (surfactant concentrations and FDOM composition) between the SML and SSW were assessed using the Wilcoxon rank-sum test (two independent data sets) and across stations using the Kruskal-Wallis test (four independent data sets). Correlations between surfactant concentrations and FDOM components were determined using Pearson correlation analysis.

Microbial ASV sequence counts were converted to relative abundances for visualization. For statistical analyses, ASV counts were centered log-ratio (clr) transformed to account for compositionality using the *compositions* package (van den Boogaart and Tolosana-Delgado, 2008). Differences in microbial community composition were estimated using Bray-Curtis dissimilarities and visualized via principal coordinates analysis (PCoA) using the *vegan* package (Oksanen et al., 2022). Differences in microbial community structure between sample types and among stations were also tested using permutational analysis of variance (PERMANOVA). Indicator species analysis was then conducted using the *multipatt* function in the *indicspecies* package (De Cáceres and Legendre, 2009) to identify specific ASVs significantly associated ($p < 0.05$) with either the SML or SSW or with the different stations.

General relationships between DOM variables and microbial community structure were examined using distance-based redundancy analysis (dbRDA). Correlation network analysis was then used to identify significant associations between ASVs and DOM variables (surfactant concentrations and FDOM components) based on Pearson correlations ($p < 0.05$). Networks were

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constructed and visualized using the *igraph* (Csárdi and Nepusz, 2006) and *ggraph* (Pedersen, 2022) packages, where nodes represent ASVs or DOM variables, and edges represent significant correlations. Network structure was characterized by modularity (Q) and was calculated using the *bipartite* package (Dormann et al., 2009).

3 Results

3.1 Physicochemical Properties of Sampling Stations

The average salinities during summer sampling were 32.5 ± 0.03, 32.4 ± 0.20 and 33.2 ± 0.20 ppt and average chl-*a* concentrations were 2.20 ± 0.67, 0.36 ± 0.15 and 0.25 ± 0.10 µg L^{-1} for the Virginia Coast, Delaware Coast and Continental Slope stations, respectively. The Continental Slope station, which was farthest from land, had the highest salinity compared to the two coastal stations. The Virginia Coast station had the highest chl-*a* concentration in the summer, followed by the Delaware Coast with the Continental Slope station having the lowest. During the fall sampling at the Delaware Coast station, average salinity and chl-*a* concentration was 33.0 ± 0.10 ppt and 2.74 ± 0.98 µg L^{-1}, respectively. The Delaware Coast chl-*a* concentration in the fall was the highest compared to all other sites, indicating a potential bloom during the fall sampling.

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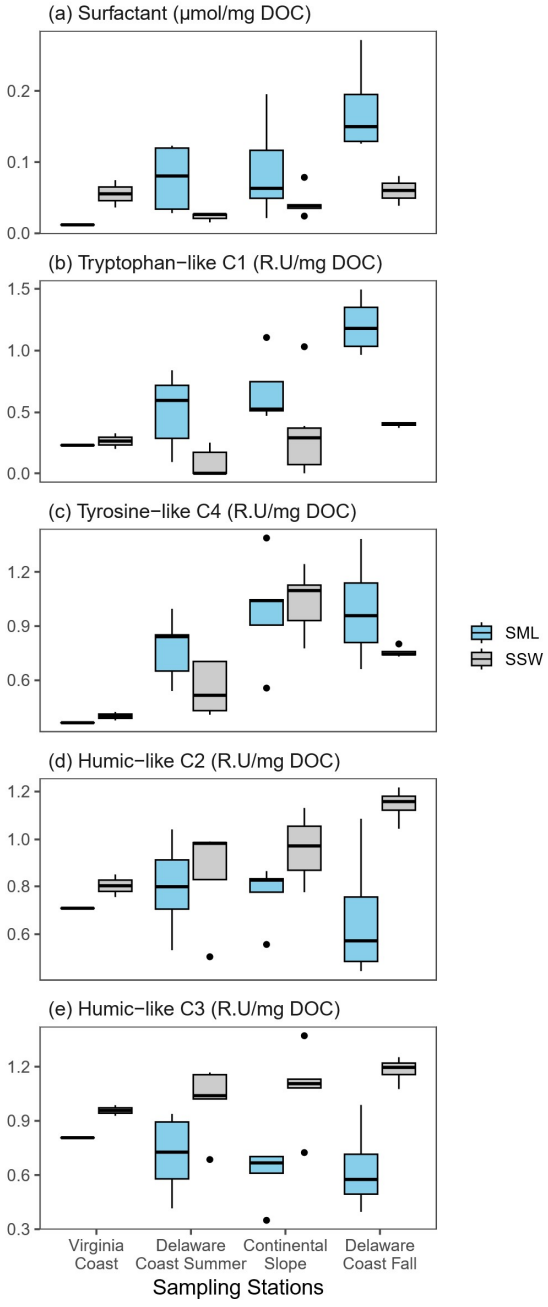

Figure 1: Different fractions of DOM normalized by DOC in SML and SSW measured at the four sampling stations, including (a) surfactant concentrations (μmol surfactant per mg DOC) and PARAFAC FDOM components (with units of RU per mg DOC) including tryptophan-like C1(b), tyrosine-like C4 (c), marine humic-like C2 (d), and terrestrial humic-like C3 (e).

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3.2 Surfactant Concentrations in SML and SSW

Surfactant concentrations (Figure 1a) were significantly higher (Wilcoxon, $p = 0.028$) in the SML (mean of 0.10 ± 0.07 µmol surfactant mg^{-1} DOC, n = 16) compared to the SSW (mean of 0.04 ± 0.02 µmol surfactant mg^{-1} DOC, n = 13) across all of the sampling locations and dates, which supports their preferential accumulation in the SML. Surfactant concentrations were not significantly different in either the SML or SSW across the summer sampling stations (Kruskal-Wallis, $p > 0.05$). However, the SML surfactant concentrations were generally higher at the Continental Slope (0.09 ± 0.07 µmol surfactant mg^{-1} DOC), followed by Delaware Coast (0.08 ± 0.05 µmol surfactant mg^{-1} DOC), and then Virginia Coast (0.01 µmol surfactant mg^{-1} DOC). In the SSW, surfactant concentrations generally declined from Virginia Coast (0.06 ± 0.03 µmol surfactant mg^{-1} DOC) to Continental Slope (0.04 ± 0.02 µmol surfactant mg^{-1} DOC) and Delaware Coast (0.02 ± 0.01 µmol surfactant mg^{-1} DOC). Additionally, there were significant seasonal differences in the surfactant concentrations of the Delaware Coast fall and summer samples (Kruskal-Wallis, $p < 0.05$). SML surfactant concentrations more than doubled from summer (0.08 ± 0.05 µmol surfactant mg^{-1} DOC) to fall (0.17 ± 0.07 µmol surfactant mg^{-1} DOC), and SSW concentrations similarly increased from summer (0.02 ± 0.01 µmol surfactant mg^{-1} DOC) to fall (0.06 ± 0.02 µmol surfactant mg^{-1} DOC). This seasonal increase indicates higher release of surfactants during the fall bloom.

3.3 FDOM composition in SML and SSW

PARAFAC analysis of the fluorescence EEMs data identified four major FDOM components (C1 to C4) across all samples, which included two protein-like and two humic-components (Table S2). The protein-like components were identified as tryptophan-like (C1, ex/em = 276/339 nm) and tyrosine-like (C4, ex/em = 276/309) FDOM, and the two humic-like

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peaks were identified as marine humic-like (C2, ex/em = 250/395) and terrestrial humic-like (C3, 259/464) FDOM (Coble, 1996, 2007). The protein-like components indicate freshly produced or autochthonous biological DOM (Coble, 1996, 2007). The marine humic-like component C2 are associated with microbial reprocessed DOM, whereas the terrestrial humic-like component C3 are associated with high aromatic and humic substances from soils and vascular plants (Coble, 1996, 2007).

The tryptophan-like C1 (Figure 1b) was significantly more abundant in the SML compared to the SSW (Kruskal-Wallis, $p < 0.05$), whereas the tyrosine-like C4 (Figure 1c) was not significantly different between the two layers. In contrast, the humic-like C2 (Figure 1d) and C3 (Figure 1e) components were significantly more abundant in the SSW (Kruskal-Wallis, $p < 0.05$), signifying higher relative quantities of aromatic and humified DOM in SSW compared to the SML. Tyrosine-like C4 was the only FDOM component that differed significantly across summer stations, showing lower abundance at the Virginia Coast than at the Continental Slope (Kruskal-Wallis, $p = 0.0006$). Similarly to surfactant concentrations, the tryptophan-like C1 displayed significantly higher abundance in fall compared to summer at the Delaware Coast station (Kruskal-Wallis, $p = 0.023$), whereas the remaining FDOM components were statistically similar across the two seasons.

3.4 Relationships between FDOM Components and Surfactant Concentrations

Surfactant concentrations were significantly, positively correlated with the tryptophan-like C1 (r = 0.68, $p<0.05$) and significantly, negatively correlated with the terrestrial humic-like C3 component (r = -0.43, $p<0.05$) (Figure S1). This suggests that the processes and conditions that produce tryptophan-like FDOM also yield enhanced surfactant concentrations. Given a presumed

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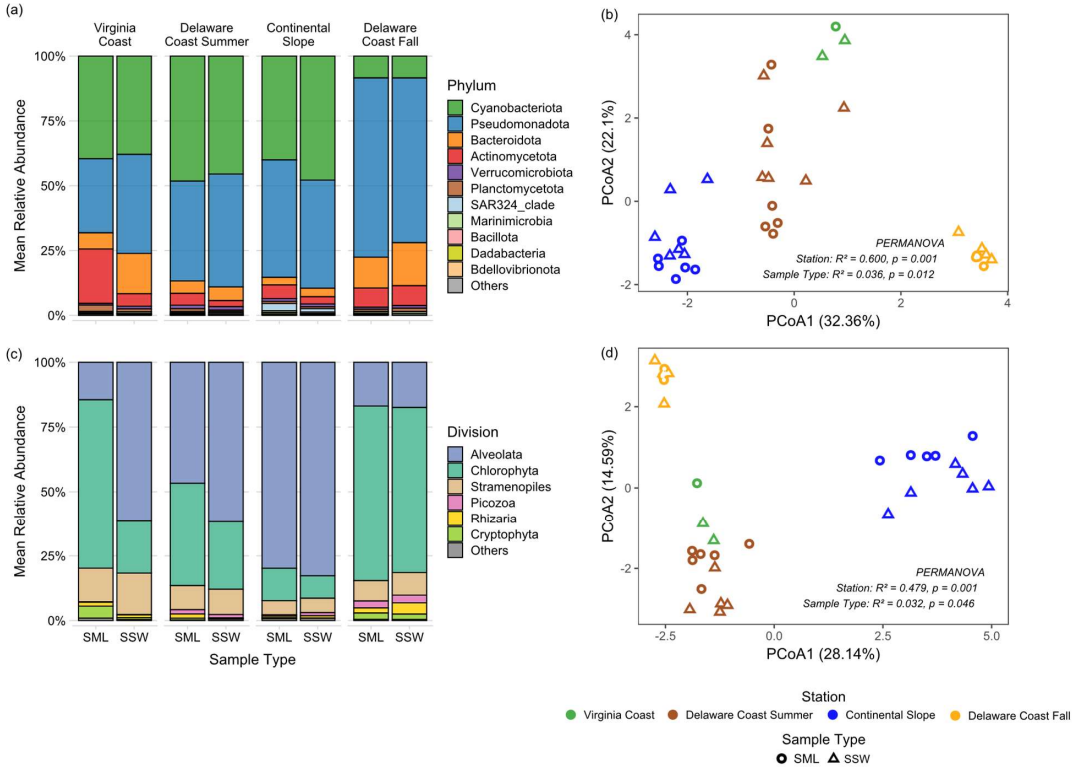
291 biological source for C1 (Coble, 1996, 2007), this observation supports the biological and marine
292 source of surfactant-like compounds in the SML.



293
294 **Figure 2:** Microbial community structure of bacteria and protists in the SML and SSW across
295 sampling stations. (a) Mean relative abundance of bacterial phyla and (c) protist divisions across
296 all samples collected at each site. PCoA based on Bray-Curtis dissimilarity of (b) bacterial and (d)
297 protist communities. PERMANOVA results are shown for the effects of station and sample type
298 on the microbial communities.

299 **3.5 General Microbial Community Structure**

300 Amplicon sequencing of the 16S and 18S rRNA genes identified 1127 bacterial ASVs and
301 481 protist ASVs across all samples, representing unique microbial lineages and suggesting higher
302 bacterial diversity relative to protist communities. The most abundant microbial groups across all
303 stations in both the SML and SSW samples included the bacterial phyla Pseudomonadota,
304 Cyanobacteriota, Bacteroidota, and Actinomycetota, as well as the protist divisions Alveolata,

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Chlorophyta, and Stramenopiles (Figures 2a & 2c). On average, Pseudomonadota (47%), Cyanobacteriota (36.3%), Bacteroidota (7%), and Actinomycetota (5%) made up more than 95% of the bacteria phyla in this study (Figure 2a), whereas Alveolata (53%), Chlorophyta (34%) and Stramenopiles (8%) together made up 92% of the protist divisions (Figure 2c).

The microbial communities varied significantly between the SML and SSW and between the different stations/seasons (PERMANOVA, $p<0.05$), as observed by the distinct clustering in the principal coordinate analysis (PCoA) (Figures 2b & 2d). For bacterial communities, the first PCoA axis (explaining 32.4% of variance) captured seasonal variation, as shown by the clustering of the Delaware Coast fall samples on the positive end of PCoA1 and summer samples clustered toward the negative end of PCoA1. The second axis (22.1%) reflected spatial differences that are related to proximity to shore and salinity, as observed by the Continental Slope samples clustering at the negative end of PCoA2 while the Delaware Coast and Virginia Coast samples clustered toward the positive end of PCoA2 (Figure 2b). In protist communities, the first axis explained 27.1% of the variation and was primarily associated with spatial differences, as can be seen by the clear separation of Continental Slope samples on the positive end of PCoA1 from the Virginia Coast and Delaware Coast samples clustering on the negative end. The second axis (14.6%) captured seasonal variation as noted by the separation of Delaware Coast fall samples on the positive PCoA2 from the summer samples which clustered toward the negative PCoA2 (Figure 2d).

These compositional variations are observed at the phylum/division level. For example, Chlorophyta was consistently more abundant in the SML across all samples (Figure 2c), and Actinomycetota was similarly enriched in the SML in the summer samples, though this pattern

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was less pronounced in the fall (Figure 2a). In contrast, the bacterial phylum Bacteroidota and the protist division Alveolata were more abundant in the SSW across all samples.

Across the summer stations, Bacteroidota was more abundant at the coastal stations (Delaware Coast and Virginia Coast) compared to the Continental Slope, whereas SAR324 (Marine Group B) was more prevalent at the Continental Slope station (Figure 2a). Among protists, Alveolata was more abundant offshore, while Chlorophyta and Stramenopiles increased at the coastal stations (Figure 2c). Seasonal patterns at the Delaware Coast station showed increases in Pseudomonadota, Actinomycetota, and Bacteroidota in the fall, while Cyanobacteriota decreased (Figure 2a). The protist groups Chlorophyta and Cryptophyta also increased in fall, while Alveolata decreased (Figure 2c). The compositional differences are explored in further detail at the ASV level in subsequent sections.

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Table 1: Phylum and genus of the top 10 most abundant bacterial lineages (ASVs) significantly associated with the SML or SSW, with mean abundance, association strength, and P value (full list of significant taxa is provided in Table S3).

Phylum	Genus	ASV	Mean Abundance (%)*	Association Strength (r.g)+	P value
SML Associated Taxa					
Actinomycetota	*Candidatus Actinomarina*	ASV010	2.51	0.35	0.015
Pseudomonadota	SAR86 clade	ASV008	2.11	0.26	0.02
Pseudomonadota	SAR86 clade	ASV013	2.06	0.30	0.006
Pseudomonadota	SAR86 clade	ASV014	1.38	0.16	0.046
Pseudomonadota	*Candidatus Puniceispirillum*	ASV031	0.92	0.36	0.001
Pseudomonadota	SAR116 clade	ASV020	0.90	0.21	0.013
Pseudomonadota	AEGEAN-169 marine group	ASV030	0.83	0.28	0.032
Pseudomonadota	*Paracoccaceae*	ASV026	0.74	0.21	0.047
Pseudomonadota	AEGEAN-169 marine group	ASV040	0.74	0.34	0.013
Pseudomonadota	SAR86 clade	ASV044	0.58	0.31	0.006
SSW Associated Taxa					
Pseudomonadota	*Caulobacter*	ASV009	4.80	0.39	0.001
Bacteroidota	NS5 marine group	ASV017	1.22	0.11	0.042
Pseudomonadota	*Alteromonas*	ASV038	0.98	0.29	0.049
Pseudomonadota	*Cupriavidus*	ASV059	0.82	0.44	0.001
Pseudomonadota	*Comamonadaceae*	ASV079	0.47	0.30	0.01
Bacteroidota	*Mesoflavibacter*	ASV130	0.33	0.29	0.002
Bacteroidota	*Cryomorphaceae*	ASV067	0.28	0.19	0.027
Pseudomonadota	*Thalassospira*	ASV207	0.21	0.39	0.002
Pseudomonadota	*Thalassolituus*	ASV290	0.21	0.31	0.014
Bacteroidota	*Fluviicola*	ASV072	0.18	0.23	0.006

*Mean relative abundance (%) of each ASV calculated within its associated sample type (SML or SSW).

+Group-equalized point-biserial correlation coefficient (r.g) showing association strength between each ASV and sample type.

3.6 SML and SSW Associated Microbial Taxa

Indicator species analysis identified specific bacterial and protist lineages that were significantly associated either with the SML or SSW. A total of 30 bacterial ASVs (2.7% of bacterial ASVs) were associated with the SML, whereas 107 ASVs (9.5% of bacterial ASVs) were associated with SSW (Table S3). At the phylum level, a majority of both the SML and SSW associated bacteria ASVs belonged to Pseudomonadota, though the SML showed a higher

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proportion of Pseudomonadota relative to SSW. The SSW associated bacteria were more diverse and were dominated by ASVs of the phyla Bacteroidota and Cyanobacteria. However, while both layers share bacteria at the phylum level, a more resolved taxonomic level reveals ecologically distinct assemblages between the SML and SSW. Some of the abundant SML associated bacteria lineages (Table 1) included those of SAR86 (ASV008, ASV013, ASV014, ASV044), *Candidatus Actinomarina* (ASV010), SAR116 clade (ASV020), *Candidatus Puniceispirillum* (ASV031), *Paracoccaceae* (ASV026), and AEGEAN-169 marine group (ASV030, ASV040), the majority of which are photoheterotrophs found to be abundant in oligotrophic waters. Notable SSW associated bacteria lineages (Table 1) included *Caulobacter* (ASV009), *Cupriavidus* (ASV059), *Alteromonas* (ASV038), *Comamonadaceae* (ASV079) and *Mesoflavibacter* (ASV130), which are typically associated with terrestrial and organic matter-rich environments.

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Table 2: Division and genus of the top 10 most abundant protist lineages (ASVs) significantly associated with the SML or SSW, with mean abundance, association strength, and P value (full list of significant taxa is provided in Table S4).

Division	Genus	ASV	Mean Abundance (%)*	Association Strength (r.g)+	P value
SML Associated Taxa					
Chlorophyta	*Ostreococcus*	ASV001	20.53	0.26	0.011
Chlorophyta	*Ostreococcus*	ASV034	2.82	0.30	0.023
Alveolata	Dino-Group-II-Clade-1_X	ASV183	0.91	0.35	0.017
Rhizaria	*Cryomonadida XX*	ASV488	0.55	0.27	0.028
Stramenopiles	*Phytophthora*	ASV1099	0.22	0.30	0.009
Alveolata	Dino-Group-II	ASV1402	0.18	0.30	0.039
Alveolata	Dino-Group-V XX	ASV184	0.16	0.36	0.005
Alveolata	Dino-Group-II-Clade-22 X	ASV850	0.14	0.31	0.04
Alveolata	*Prorocentrum*	ASV231	0.09	0.34	0.005
Alveolata	Dino-Group-II-Clade-12 X	ASV1232	0.08	0.36	0.015
SSW Associated Taxa					
Alveolata	*Gyrodinium*	ASV003	8.72	0.26	0.037
Alveolata	*Gyrodinium*	ASV021	2.62	0.42	0.003
Alveolata	*Strombidiidae X*	ASV162	1.16	0.41	0.001
Alveolata	*Laboea*	ASV043	0.65	0.38	0.001
Alveolata	*Gonyaulax*	ASV197	0.51	0.32	0.029
Alveolata	*Gyrodinium*	ASV046	0.50	0.38	0.016
Alveolata	*Strombidiidae X*	ASV073	0.31	0.36	0.039
Alveolata	*Strombidiidae X*	ASV247	0.25	0.45	0.002
Alveolata	*Spirotrichea*	ASV265	0.25	0.41	0.01
Alveolata	*Oligotrichida XX*	ASV373	0.21	0.43	0.003

*Mean relative abundance (%) of each ASV calculated within its associated sample type (SML or SSW).
+Group-equalized point-biserial correlation coefficient (r.g) showing association strength between each ASV and sample type.

For protists, 23 (4.8% of protist ASVs) and 21 (4.4% of protist ASVs) protist lineages associated with the SML and SSW, respectively (Table S4). At the division level, Alveolata dominated the indicator ASV pool in both SML and SSW, with all SSW associated protist lineages belonging to Alveolata. Unlike bacteria, the SML associated protist lineages were more diverse than those of the SSW, with the SML protists additionally dominated by Chlorophyta, Stramenopiles and Rhizaria. At a more resolved taxonomic level, some of the abundant SML

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enriched protist lineages (Table 2) were the green algae *Ostreococcus* (ASV001, ASV034), the dinoflagellates Dino-Group-II clades (ASV183, ASV1402, ASV200, ASV1232, ASV850) and Dino-Group-V (ASV184), and the heterotrophic flagellate *Cryomonadida* (ASV488). While those for the SSW were the mixotrophic dinoflagellates *Gyrodinium* (ASV003, ASV021, ASV046) and *Gonyaulax* (ASV197), the ciliates *Strombidiidae* (ASV162, ASV073, ASV247), *Spirotrichea* (ASV265), and *Laboea* (ASV043).

Table 3: Phylum and genus of the top 10 most abundant bacterial lineages (ASVs) significantly associated with each sampling station, with mean abundance, association strength, and P value (additional significant lineages are provided in Table S5).

Phylum	Genus	ASV	Mean Abundance (%)*	Association Strength (r.g)+	P value
Virginia Coast					
Cyanobacteriota	*Cyanobium* PCC-6307	ASV019	1.08	0.89	0.001
Pseudomonadota	HIMB11	ASV023	0.90	0.86	0.001
Actinomycetota	PeM15	ASV068	0.43	0.54	0.025
Cyanobacteriota	*Synechococcus* CC9902	ASV056	0.42	0.76	0.001
Actinomycetota	*Microbacteriaceae*	ASV092	0.29	0.70	0.004
Cyanobacteriota	*Synechococcus* CC9902	ASV074	0.27	0.82	0.001
Bacteroidota	*Mesoflavibacter*	ASV130	0.17	0.48	0.034
Cyanobacteriota	*Cyanobium* PCC-6307	ASV164	0.15	0.94	0.001
Bacteroidota	*Formosa*	ASV075	0.14	0.83	0.001
Cyanobacteriota	*Cyanobium* PCC-6307	ASV176	0.13	0.93	0.001
Delaware Coast Summer					
Pseudomonadota	Comamonadaceae	ASV079	0.24	0.42	0.039
Verrucomicrobiota	Roseibacillus	ASV085	0.24	0.80	0.001
Pseudomonadota	Clade III	ASV071	0.24	0.78	0.001
Pseudomonadota	SAR116 clade	ASV105	0.22	0.62	0.003
Pseudomonadota	OM60(NOR5) clade	ASV107	0.18	0.68	0.001
Pseudomonadota	Litorivicinus	ASV099	0.17	0.70	0.001
Pseudomonadota	SAR92 clade	ASV152	0.15	0.46	0.032
Bacteroidota	NS5 marine group	ASV123	0.15	0.76	0.001
Bacteroidota	NS5 marine group	ASV150	0.15	0.55	0.015
Bacteroidota	NS4 marine group	ASV086	0.13	0.66	0.003
Continental Slope					
Cyanobacteriota	*Prochlorococcus* MIT9313	ASV003	3.18	0.95	0.001
Cyanobacteriota	*Cyanobium* PCC-6307	ASV006	2.85	0.81	0.001

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SAR324 clade (Marine group B)	SAR324 clade insertae sedis	ASV024	0.86	0.79	0.001
Pseudomonadota	*Paracoccaceae*	ASV032	0.48	0.90	0.001
Pseudomonadota	SAR116 clade	ASV042	0.40	0.91	0.001
Cyanobacteriota	*Synechococcus* CC9902	ASV016	0.38	0.87	0.001
Pseudomonadota	Clade Ib	ASV007	0.35	0.76	0.001
Pseudomonadota	SAR116 clade	ASV036	0.26	0.77	0.001
Pseudomonadota	SAR86 clade	ASV043	0.25	0.90	0.001
Pseudomonadota	KI89A clade	ASV063	0.23	0.72	0.001
	Delaware Coast Fall				
Pseudomonadota	Clade Ia	ASV002	10.16	0.80	0.001
Pseudomonadota	SAR86 clade	ASV008	1.78	0.71	0.001
Actinomycetota	*Candidatus Actinomarina*	ASV011	1.42	0.93	0.001
Pseudomonadota	SAR86 clade	ASV014	1.19	0.89	0.001
Bacteroidota	NS5 marine group	ASV017	1.05	0.88	0.001
Bacteroidota	NS5 marine group	ASV025	0.67	0.99	0.001
Pseudomonadota	*Candidatus Puniceispirillum*	ASV037	0.35	0.84	0.001
Pseudomonadota	SAR86 clade	ASV048	0.28	0.92	0.001
Pseudomonadota	SUP05 cluster	ASV058	0.25	0.94	0.001
Cyanobacteriota	*Synechococcus* CC9902	ASV015	0.25	0.82	0.001

*Mean relative abundance (%) of each ASV calculated across all samples.
+Group-equalized point-biserial correlation coefficient (r.g) indicating the strength of association between each ASV and sample stations.

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Table 4: Division and genus of the top 10 most abundant protist lineages (ASVs) significantly associated with each sampling station, with mean abundance, association strength, and P value (additional significant lineages are provided in Table S6).

Division	Genus	ASV	Mean Abundance (%)*	Association Strength (r.g)+	P value
Virginia Coast					
Chlorophyta	*Chlorellales_X*	ASV117	0.30	0.85	0.001
Alveolata	*Dinophyceae*	ASV040	0.26	0.89	0.001
Chlorophyta	*Picochlorum*	ASV101	0.26	0.84	0.001
Stramenopiles	*Leptocylindrus*	ASV010	0.24	0.81	0.001
Stramenopiles	*Guinardia*	ASV065	0.23	0.84	0.001
Stramenopiles	*Thalassiosiraceae*	ASV127	0.21	0.98	0.001
Stramenopiles	*Cyclotella*	ASV121	0.20	0.90	0.001
Alveolata	Dino-Group-II-Clade-6_X	ASV160	0.18	0.74	0.002
Stramenopiles	*Minutocellus*	ASV161	0.16	0.92	0.001
Alveolata	Dino-Group-II-Clade-6_X	ASV055	0.16	0.99	0.001
Delaware Coast Summer					
Chlorophyta	*Ostreococcus*	ASV034	1.86	0.71	0.004
Stramenopiles	MAST-9D	ASV094	1.67	0.89	0.001
Alveolata	*Gyrodinium*	ASV063	0.77	0.62	0.01
Alveolata	*Dinophyceae*	ASV116	0.63	0.65	0.008
Alveolata	*Gonyaulax*	ASV148	0.59	0.63	0.006
Alveolata	*Dadayiella*	ASV392	0.48	0.87	0.001
Stramenopiles	MAST-4B	ASV141	0.31	0.53	0.025
Alveolata	Dino-Group-II-Clade-3_X	ASV235	0.27	0.53	0.034
Alveolata	*Gonyaulax*	ASV197	0.27	0.57	0.013
Alveolata	*Strombidiidae*	ASV523	0.23	0.67	0.002
Continental Slope					
Alveolata	Dino-Group-II-Clade-6_X	ASV012	3.04	0.89	0.001
Alveolata	Dino-Group-I-Clade-5_X	ASV025	2.70	0.97	0.001
Alveolata	Dino-Group-I-Clade-1_X	ASV032	1.03	0.81	0.002
Chlorophyta	*Chloropicon*	ASV045	0.82	0.91	0.001
Alveolata	Dino-Group-II-Clade-6_X	ASV039	0.81	0.87	0.001
Alveolata	*Strombidiidae_X*	ASV162	0.60	0.53	0.02
Alveolata	Dino-Group-II-Clade-10-and-11_X	ASV058	0.57	0.83	0.001
Alveolata	Dino-Group-I-Clade-1_X	ASV056	0.56	0.54	0.026
Alveolata	*Dinophyceae*	ASV064	0.55	0.65	0.006
Chlorophyta	Prasino-Clade-9_XXX	ASV136	0.53	0.86	0.003
Delaware Coast Fall					
Chlorophyta	*Ostreococcus*	ASV001	16.70	0.77	0.001
Alveolata	*Dinophyceae*	ASV011	0.91	0.97	0.001
Rhizaria	*Acanthometra*	ASV018	0.78	0.88	0.001

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Stramenopiles	*Minidiscus*	ASV017	0.60	0.98	0.001
Picozoa	*Picomonas*	ASV027	0.59	0.92	0.001
Cryptophyta	*Plagioselmis*	ASV016	0.50	0.66	0.008
Chlorophyta	*Micromonas*	ASV023	0.47	0.93	0.001
Chlorophyta	*Bathycoccus*	ASV008	0.46	0.78	0.002
Alveolata	Dino-Group-II-Clade-14_X	ASV038	0.28	0.97	0.001
Stramenopiles	Pelagomonadales_clade_B1	ASV041	0.28	0.85	0.001

*Mean relative abundance (%) of each ASV calculated across all samples.
+Group-equalized point-biserial correlation coefficient (r.g) indicating the strength of association between each ASV and sample stations.

3.7 Site and Season Associated Microbial Taxa

Indicator species analysis also revealed distinct microbial assemblages associated with the different stations across both bacterial (Table 3) and protist (Table 4) communities. The Virginia Coast station was characterized by a highly productive coastal assemblage in both communities. Bacterial indicators were dominated by Cyanobacteria, particularly *Cyanobium* PCC-6307 and *Synechococcus* CC9902 ASVs, alongside heterotrophic taxa including *Formosa*, *Mesoflavibacter*, and *Microbacteriaceae*. The protist community was dominated by diatoms including *Leptocylindrus*, *Guinardia*, *Thalassiosiraceae*, *Cyclotella*, and *Minutocellus*.

The Delaware Coast summer station had more heterotrophic and mixotrophic taxa in both the protist and bacteria communities. Bacteria groups were mainly heterotrophic and included NS4 and NS5 marine groups, SAR92 clade, *Litorivincus*, OM60(NOR5) clade, SAR116 clade, and Clade III. The protist community was dominated by dinoflagellates and ciliates, including *Gyrodinium, Dinophyceae, Dadayiella, Gonyaulax,* Dino-Group-II-Clade-3, and *Oligotrichida*, alongside heterotrophic flagellates MAST-4B and MAST-9D.

The Delaware Coast fall samples were dominated by phototrophic picoeukaryotic green algae including *Ostreococcus, Micromonas, Bathycoccus,* and *Plagioselmis*, which corresponds to their highest chlorophyll-a concentration and supports a fall bloom during our sampling. Other

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abundant protists were small flagellates including *Picomonas* and *Pelagomonadales* clade B1. Bacteria groups were a combination of both eutrophic and oligotrophic taxa, such as *Candidatus Actinomarina, Candidatus Puniceispirillum,* NS5 marine group, SUP05 cluster, and *Synechococcus* CC9902.

The Continental Slope station was distinguished by predominantly oligotrophic taxa. Bacteria groups included SAR116 clade, SAR86 clade, SAR324 clade, Clade Ib, *Paracoccaceae*, *Cyanobium* PCC-6307, and *Prochlorococcus* MIT9313. The protist community had multiple Dino-Group-I and Dino-Group-II clades alongside *Dinophyceae*, *Strombidiidae*, and the prasinophyte green algae Prasino-Clade-9 and *Chloropicon*.

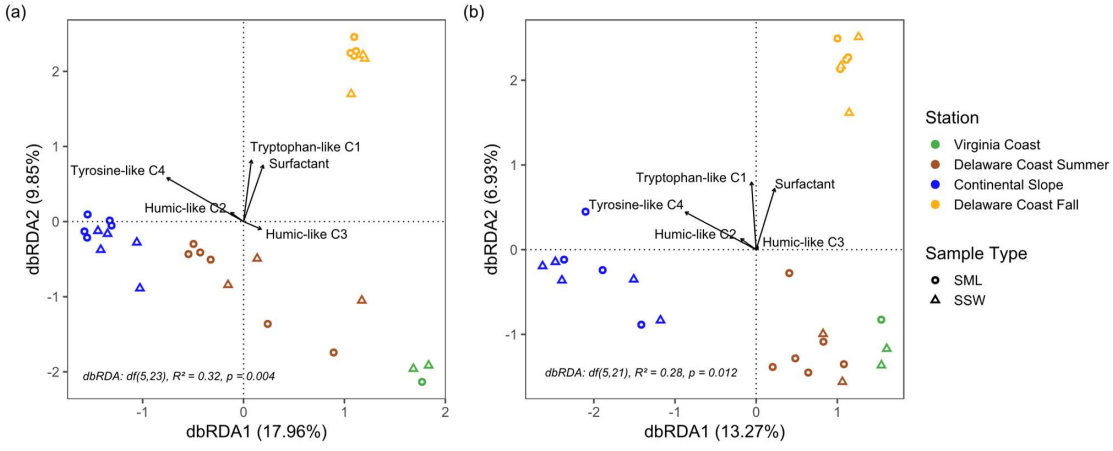

Figure 3: Distance-based redundancy analysis of (a) bacterial and (b) protist community composition, constrained by DOM variables across sampling stations. Vectors represent DOM predictors with direction and length indicating the direction and relative strength of their relationships with community composition, respectively.

3.8 Relationships between Microbial Communities and DOM Composition

Surfactant and FDOM concentrations significantly explained the variance in the microbial composition dataset for both bacteria (dbRDA: df(5,23), r^2=0.32, p=0.004) and protists (dbRDA:

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df(5,21), r^2=0.28, p=0.012), suggesting significant relationships between the DOM composition (FDOM component abundance and surfactant concentration) and microbial composition (Figure 3). For both bacteria and protists, tyrosine-like C4, tryptophan-like C1, and surfactant concentration explained most of the variations in microbial composition. Tyrosine-like C4 was more associated with the microbial communities of the Continental Slope station, while surfactant concentrations and tryptophan-like C1 were more associated with the fall Delaware Coast microbial communities (Figure 3).

The relationships between DOM and microbial communities were further explored through correlation network analysis. The abundance of 448 bacterial (Figure 4; Table S7) and 168 protist (Figure 5; Table S8) ASVs were significantly correlated either negatively or positively with FDOM components and surfactant concentrations, forming single interconnected networks (compartments = 1). In both protist and bacterial communities, the highest number of ASVs correlated with tyrosine-like C4 (bacteria: n = 225; protists: n = 92), followed by tryptophan-like C1 (bacteria: n = 183; protists: n = 48), and surfactant concentrations (bacteria: n = 98; protists: n = 39), whereas humic-like components C2 (bacteria, n = 25; protists, n = 12) and C3 (bacteria: n = 19; protists: n = 19) correlated with relatively few ASVs. The correlation networks exhibited high modularity (bacteria Q = 0.529; protists Q = 0.558), where specific groups of ASVs preferentially correlated with specific DOM components rather than interacting broadly across all DOM types.

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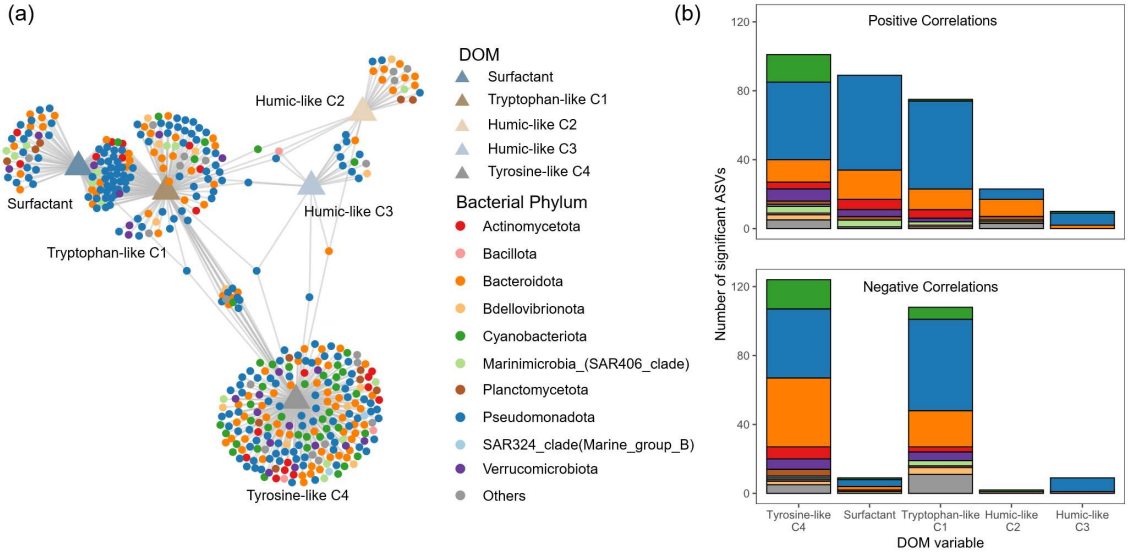

449

450 **Figure 4:** Correlations between bacterial lineages and DOM composition. (a) Bipartite
451 correlation network illustrating associations between bacterial ASVs (circles) and DOM
452 variables (triangles, with associated labels). Edges connect ASVs to the DOM variables with
453 which they are significantly correlated. (b) Number of bacterial ASVs significantly positively
454 (upper panel) or negatively (lower panel) correlated with each DOM variable.

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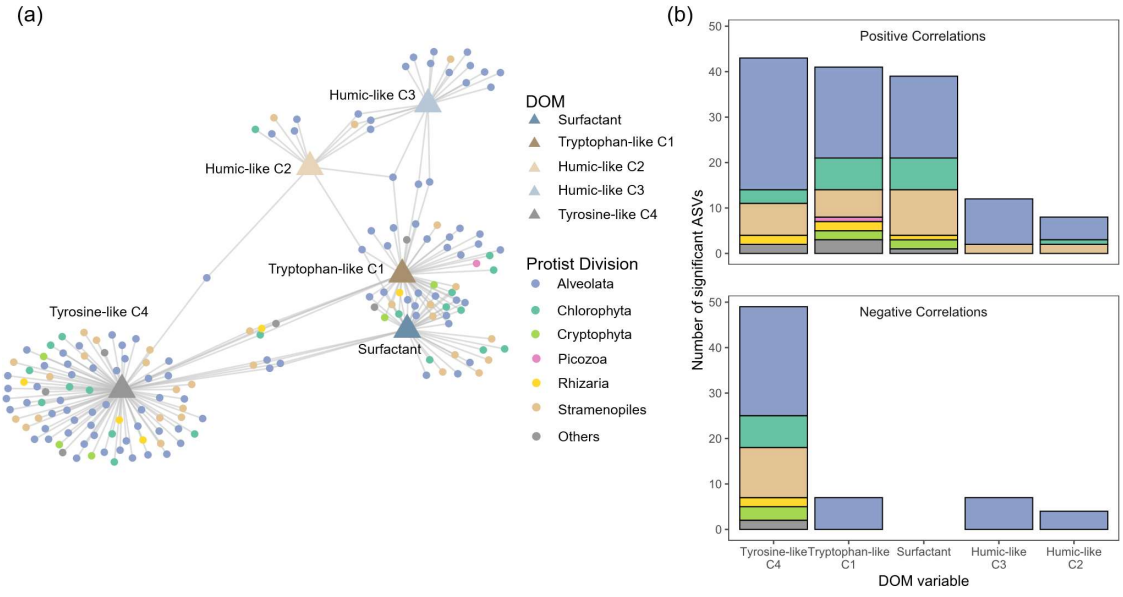

Figure 5: Correlations between protist ASVs and DOM composition. (a) Bipartite correlation network illustrating associations between protist ASVs (circles) and DOM variables (triangles). Edges connect ASVs to the DOM variables with which they are significantly correlated. (b) Number of protist ASVs significantly positively (upper panel) or negatively (lower panel) correlated with each DOM variable.

Of the 98 bacterial ASVs correlated with surfactant concentrations, the majority were positively correlated (n = 89, 91%), with only 9 ASVs (9%) showing negative correlations (Figure 4b). The phylum Pseudomonadota dominated the surfactant associated community, comprising the largest proportion of positively correlated lineages, including members of the SAR86 and SAR116 clades, *Paracoccaceae*, *Defluviicoccales*, and *Pseudoalteromonas*. Bacteroidota was the second most prominent phylum, primarily represented by the NS5 and NS9 marine groups. Additional notable lineages included *Candidatus Actinomarina* and Marinimicrobia (SAR406 clade) (Table S7).

All 39 protist ASVs positively correlated with surfactant concentrations (Figure 5b). Alveolata was the dominant phylum, driven by diverse dinoflagellate lineages, including

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unclassified *Dinophyceae*, Dino-Group-II, and Dino-Group-I Clades. Stramenopiles was the second most prominent group, comprising multiple MAST clades (MAST-3A, MAST-3F, MAST-4B, MAST-7B) and *Aureococcus*. Additional taxa included *Teleaulax* (Cryptophyta) and unclassified *Cercozoa* (Rhizaria) (Table S8).

Notably, there was high overlap in the bacterial and protist lineages correlating with the surfactant concentrations and the tryptophan-like C1 compared to the other DOM types (Figures 4a and 5a). 62 bacterial ASVs (63% of surfactant associated bacterial ASVs) and 24 protist ASVs (62% of surfactant associated protist ASVs) correlated with both surfactant concentrations and tryptophan-like C1 abundance, respectively, supporting the co-association between surfactant concentrations and tryptophan-like C1. In contrast, the overlap between surfactant concentrations and all other FDOM components, tyrosine-like C4 and humic-like C2 and C3 was markedly lower, with shared ASVs representing less than 5% of surfactant associated ASVs in both bacterial and protist networks.

The ASVs positively correlated with both surfactant and tryptophan-like C1 comprised a diverse assemblage of phototrophic, phagotrophic, and parasitic protists, along with oligotrophic and copiotrophic bacteria, most of which were abundant during the fall sampling period. Phototrophs included *Ostreococcus, Micromonas, Bathycoccus, Pseudoscourfieldia, Aureococcus*, and the diatom *Minidiscus*. Phagotrophic protists included MAST-7B*, Cercozoa*, and *Telonemia*, while parasitic lineages were dominated by multiple Dino-Group-II and Dino-Group-I clades. Oligotrophic bacteria included SAR86, *Candidatus Actinomarina*, *Candidatus Puniceispirillum, Puniceispirillales*, AEGEAN-169, and *Marinimicrobia,* whereas copiotrophic taxa included the NS5 marine group, *Pseudoalteromonas, Pseudohongiella, Porticoccus, Halieaceae, Ectothiorhodospiraceae, Paracoccaceae*, and *Defluviicoccales*. Together, these groups reflect

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complex trophic interactions associated with the accumulation of surfactants and tryptophan-like C1.

4 Discussion

4.1 FDOM Supports the Biological Source of Marine Surfactants

Surfactant concentrations showed a significant positive correlation with tryptophan-like FDOM (Peak T) (Figure S1), consistent with previous reports of positive correlations between tryptophan-like FDOM and surfactant-like DOM compositions, including the abundance of unsaturated aliphatic, peptide-like, and sulfur-rich FTICR-MS-derived molecular formulas enriched in the SML (Coffey et al., 2025). Tryptophan-like FDOM is a well-established indicator of freshly produced organic matter in marine waters (Coble, 1996, 2007). It has been shown to correlate strongly with total dissolved amino acid concentrations and serves as a more reliable tracer of recent autochthonous production than tyrosine-like FDOM (Peak B), which has a weaker correlation with total dissolved amino acids (Yamashita et al., 2015). It is produced by both photosynthetic and non-photosynthetic microorganisms and is associated with general microbial activity (Maie et al., 2007; Hudson et al., 2008; Williams et al., 2010; Fox et al., 2017; Devresse et al., 2023). Therefore, its correlation with bulk surfactant concentrations supports previous findings that biogenic processes are the primary source of marine surfactant production (Gašparović and Ćosović, 2003; Gašparović et al., 2007; Frka et al., 2009; Wurl et al., 2011) and is consistent with observations by Barthelmeß and Engel (2022), who reported elevated surfactant concentrations during periods of high lability DOM concentrations (e.g., glucose and amino acids).

In addition, surfactant concentrations were negatively correlated with terrestrial humic-like FDOM, suggesting that samples with higher contributions of terrestrially derived DOM had lower

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surfactant concentrations. This reinforces the idea that autochthonous rather than allochthonous organic matter is the dominant contributor to the marine surfactant pool.

4.2 SML Associated Taxa are Distinct from SSW

The microbial communities in both SML and SSW were generally dominated by the bacteria phyla Pseudomonadota, Cyanobacteriota, Bacteroidota, and Actinomycetota, as well as the protist divisions Alveolata, Chlorophyta, and Stramenopiles, which represent typical surface seawater communities (Li et al., 2018; Lang-Yona et al., 2022; Cohen et al., 2024) and SML communities (Cunliffe et al., 2011; Taylor and Cunliffe, 2014; Rahlff et al., 2021; Zäncker et al., 2021; Tastassa et al., 2025). The majority of microbial lineages were similarly distributed between the SML and SSW, consistent with previous studies (Zäncker et al., 2021). However, some specific lineages were significantly associated with either the SML or SSW and will provide further understanding of the factors that influence microbial enrichment and biogeochemical processes in the SML.

The SML associated bacterial lineages were primarily small-sized photoheterotrophs, including SAR86 and SAR116, which have been previously reported to be in the SML (Rahlff et al., 2021). Additionally, *Candidatus Actinomarina*, *Candidatus Puniceispirillum*, and the AEGEAN-169 marine group, which represent newly identified SML associated bacterial lineages, were observed. These bacterial lineages are generally characterized by streamlined genomes that enable efficient resource utilization and adaptation to oligotrophic conditions, as has been observed in previous work (Swan et al., 2013; Brown et al., 2014; Oggerin et al., 2024). They typically exhibit specialized light adaptations, such as the possession of proteorhodopsin (e.g., SAR86, SAR116 and *Candidatus Puniceispirillum*) and MACrhodopsin (e.g., *Candidatus Actinomarina*), which enable them to utilize sunlight for energy to sustain basal metabolism and support biomass

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synthesis or growth (Palovaara et al., 2014; Gómez-Consarnau et al., 2019; Oggerin et al., 2024). They also possess metabolic adaptations for sulfur redox cycling (Van Mooy et al., 2006; Grote et al., 2012; Ramfelt et al., 2024), which may explain the abundance of sulfur-containing compounds in the SML in previous work (Lechtenfeld et al., 2013; Liu et al., 2023; Coffey et al., 2025; Birt et al., 2026). Additionally, their small cell sizes may enhance attachment to buoyant organic aggregates, aiding their accumulation in the SML through buoyancy effects (Zäncker et al., 2018). In contrast, the SSW associated bacterial lineages included *Caulobacter*, *Cupriavidus, Alteromonas, Comamonadaceae* and *Mesoflavibacter*, which are characterized by heterotrophic lifestyles. These taxa generally lack prominent light-harvesting adaptations, such as proteorhodopsin and tend to possess larger genomes that enable the degradation of complex organic matter (Asker et al., 2007; Poehlein et al., 2011; López-Pérez et al., 2012; Wilhelm, 2018). This metabolic capability is likely advantageous in the SSW, where more aromatic and humified DOM is present compared to the SML.

Phytoplankton are known to exhibit special light adaptations, such as possession of photoprotective proteins or vertical migration in the water column to receive optimal light for photosynthesis (Lichtenberg et al., 2020; Becker et al., 2021; Salonen et al., 2024). Most phytoplankton were not significantly associated with only the SML or SSW, suggesting frequent movement between the two layers, consistent with their migratory behavior (Lichtenberg et al., 2020; Salonen et al., 2024) and the fact that samples were collected across different times of the day with different sunlight intensities. However, the green alga *Ostreococcus* was consistently enriched in the SML, which may be attributed to its efficient photosystem I antenna adjustment system that enables acclimation to high light intensities (Ishii et al., 2023). Similar to the dominant SML associated bacterial lineages, *Ostreococcus* is small in size and adapted to survive under low

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nutrient conditions (Martin et al., 2020). Other prominent SML associated protists were dinoflagellate parasites (Syndiniales), which have previously been reported to dominate both the SML and SSW taxa (Zäncker et al., 2021). The Syndiniales are intracellular parasites which infect a broad range of protist and metazoan hosts (Siano et al., 2011; Christaki et al., 2023). Their presence in the SML could be due to the enrichment of their hosts such as other protists like *Ostreococcus* and *Cryomonadida* that were enriched in the SML or zooplankton, which have also been previously observed to be enriched in the SML (Zäncker et al., 2021). Syndiniales have complex life cycles involving intracellular trophont stages that lyse hosts and release numerous short-lived dinospores (Siano et al., 2011; Christaki et al., 2023). This lytic process may also contribute to organic matter enrichment in the SML through the release of host cell contents. The SSW associated protist lineages, in contrast, were relatively large in size and typically mixotrophic dinoflagellates and ciliates that can undergo photosynthesis or switch to phagotrophy during light or nutrient stress (Li et al., 2000; Jeong et al., 2005; Stoecker et al., 2017).

4.3 Candidate Surfactant and Tryptophan-like FDOM Associated Microbial Communities

Our sampling across diverse hydrographic regions captured variations in bacterial and protist compositions along with surfactant and FDOM concentrations, which allowed us to identify biomarkers and microorganisms associated with surfactants. The microbial compositional differences across regions reflected a classic terrestrial-to-marine gradient (Cohen et al., 2024; Ruff et al., 2024). The coastal stations (Delaware Coast and Virginia Coast) were dominated by microbes typically associated with coastal and eutrophic ecosystems, whereas the Continental Slope was mainly dominated by oligotrophic microbes. A phytoplankton bloom, dominated by the picoeukaryotic green algae *Ostreococcus*, *Bathycoccus*, and *Micromonas,* was also observed during fall sampling. Surfactant and tryptophan-like FDOM concentrations were highest during

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the fall bloom, consistent with the increased production and release of freshly produced organic matter and surfactants during bloom events (Barthelmeß and Engel, 2022) and suggests a greater temporal influence on surfactant production compared to spatial influences.

Several microbial lineages (bacteria = 89; protist = 39) were positively correlated with surfactant concentrations, and a majority of these (bacteria = 63%; protist = 62%) also showed positive correlations with tryptophan-like FDOM, further supporting the co-occurrence of surfactants and tryptophan-like FDOM. These lineages represent key candidates as surfactant producers or indicators. Notable taxa include the small-sized phytoplankton *Ostreococcus*, *Micromonas*, *Bathycoccus*, *Pseudoscourfieldia*, and *Aureococcus*, as well as the diatom *Minidiscus*, which were dominant during the fall bloom. While nanophytoplankton abundance has been shown to be tightly coupled with surfactant concentrations (Barthelmeß and Engel, 2022), our data provide new insight into the specific pico- to nano-phytoplankton taxa that may drive this relationship. Small photoautotrophs such as *Ostreococcus* are known to dominate coastal waters, where they shape overall microbial community metabolic profiles (Aylward et al., 2015). With the increasing frequency and spatial extent of phytoplankton blooms documented in recent decades, particularly in coastal regions (Dai et al., 2023), their abundance is likely to increase along with surfactant production and accumulation in the SML. Previous studies using culture and bloom-induced mesocosm experiments have linked larger phytoplankton such as *Emiliania huxleyi*, *Cylindrotheca closterium*, and *Skeletonema* (Zutic et al., 1981; Bibi et al., 2025; Flores et al., 2025) to increases in surfactant concentrations. These taxa are mostly abundant during high nutrient and optimal light conditions like spring blooms, which were not captured in the present study and support a strong temporal influence on microbial composition and surfactant production.

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Heterotrophic bacterial groups, including the NS5 marine group, *Pseudoalteromonas,* *Pseudohongiella*, *Porticoccus*, *Halieaceae*, *Ectothiorhodospiraceae*, *Paracoccaceae*, and *Defluviicoccales*, were also positively correlated with surfactant and tryptophan-like FDOM concentrations. While their association with surfactants may suggest a preference for degrading surfactant-like compounds, these heterotrophic bacteria could also produce surfactants. For example, *Paracoccaceae* and *Pseudoalteromonas* are known to produce biosurfactants that enable them to metabolize hydrocarbon-rich organic matter (Antoniou et al., 2015; Morales-Guzmán et al., 2021). These bacterial groups may also contribute to surfactant production through metabolic interactions with phytoplankton, as some bacteria produce certain secondary organic compounds only in the presence of green algae (Sousoni, 2018; Chhun et al., 2021). Notably, oligotrophic-adapted bacterial groups that were more abundant in the SML, including SAR86, *Candidatus Actinomarina*, *Candidatus Puniceispirillum*, *Puniceispirillales*, and AEGEAN-169, were also positively correlated with surfactant and tryptophan-like FDOM concentrations. Their consistent association with both the SML and surfactant concentrations, combined with their ubiquity in the global ocean, suggests that these groups could represent promising candidates for tracking surfactant production across the global ocean.

Additional surfactant associated taxa were phagotrophic protists, including MAST-7B, *Cercozoa*, and *Telonemia*, as well as parasitic dinoflagellates of Dino-Group-I and Dino-Group-II clades. These associations point to additional and relatively underexplored surfactant production mechanisms. Phagotrophic protists are active grazers of bacteria and small phytoplankton, and their feeding involves cell lysis, which disrupts microbial membranes and releases intracellular material into the DOM pool. This material includes membrane lipids, amino acids, and other amphiphilic compounds with surface-active properties (Kujawinski et al., 2002). Parasitic

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dinoflagellates may contribute through similar processes, as infection and host cell lysis also release intracellular contents. These lysis-driven mechanisms of surfactant production alongside viral lysis, which likewise releases cellular contents, may play important roles in surfactant release and in predicting the timing of surfactant impacts on air-sea processes.

4.4 Implications for Understanding Surfactants in the Ocean and Future Work

Overall, our results highlight the diversity of microbial processes in the SML and the potential roles of different microbial communities in regulating surfactant composition and, by extension, air-sea interactions. In general, SML associated microbes, comprising both bacterial and protist taxa, are small in size and adapted to high-light and low-nutrient conditions compared to the SSW associated microbes, which tend to be larger and exhibit more flexible trophic strategies. These contrasting lifestyles suggest that the SML was relatively nutrient limited under our sampling conditions, or that its harsh physicochemical conditions favor microorganisms with stress tolerant and resource efficient lifestyles (Carlucci et al., 1985; Agogué et al., 2005). The smaller cell sizes of SML associated taxa may also promote their physical accumulation at the sea surface through buoyancy effects.

The composition of SML associated microbial communities has direct implications for organic matter and surfactant production at the air-sea interface. The enrichment of the green algae *Ostreococcus* in the SML points to active primary production and autochthonous synthesis of organic matter, consistent with observations of unique photosynthetic biomarker lipids in the SML (Birt et al., 2026). The enriched photoheterotrophic bacteria may further contribute to organic matter production through light-enhanced anaplerotic CO_2 fixation, whereby inorganic CO_2 is assimilated into biomass (Palovaara et al., 2014). At the same time, these bacteria may also drive biotic degradation of organic matter in the SML (Birt et al., 2026).

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The nature of nutrient limitation in the SML warrants further investigation. Nitrate plus nitrite concentrations were higher in the SML than in the SSW (Table S1), suggesting that nitrogen is not the primary limiting nutrient and instead pointing toward phosphorus limitation. Under phosphorus limitation, microorganisms are known to substitute phosphorus-containing membrane lipids with sulfolipids and betaine lipids, resulting in organic matter enriched in sulfur- and nitrogen-containing compounds (Benning et al., 1995; Van Mooy et al., 2006). This is consistent with the abundance of such compounds previously reported in the SML (Lechtenfeld et al., 2013; Coffey et al., 2025; Birt et al., 2026) and suggests that phosphorus limitation may partly shape the molecular composition of surfactants and DOM accumulating in the SML.

Our study identifies microbial groups significantly correlated with surfactant concentrations, representing candidate surfactant associated microbial communities. While correlations do not imply causation, these groups of microbes will serve as a starting point for critical screening of marine surfactant producers or biomarkers. The diversity of the surfactant associated microbial candidates, spanning both photosynthetic and non-photosynthetic lineages, suggests that surfactant concentrations in marine waters may reflect a broad range of microbial activities rather than a single dominant process. Notably, cell lysis by parasitic and phagotrophic protists appears to be an important and previously underexplored potential determinant of surfactant concentrations. If these lytic processes are indeed important sources of surfactants via the release of biological lipids and amino acids that are excellent potential surfactant compounds due to their amphiphilic properties, relationships between viral abundances and lytic processes warrant further investigation.

The biological diversity of surfactant associated microbial candidates may explain why surfactant concentrations do not correlate well with chlorophyll-a ($r = 0.09$, $df = 29$, $p = 0.62$),

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consistent with previous observations (Pereira et al., 2018; Frossard et al., 2019). In contrast, tryptophan-like FDOM showed a stronger correlation with surfactant concentrations ($r = 0.68$, $df = 30$, $p < 0.0001$) and may serve as a better proxy for estimating surfactant concentrations. Unlike chlorophyll-a, tryptophan-like FDOM is produced by both photosynthetic and non-photosynthetic microbial communities and reflects general microbial metabolic activity rather than photosynthesis alone (Maie et al., 2007; Hudson et al., 2008; Williams et al., 2010; Fox et al., 2017; Devresse et al., 2023), making it better suited to capture the diverse biological sources of marine surfactants. Additionally, while distance-based redundancy analysis revealed significant relationships among surfactant concentrations, FDOM composition, and microbial community composition, the relatively low variance explained (~30%) indicates that additional factors not captured in this study including photodegradation, vertical mixing, and bloom dynamics are also significant in determining surfactants, FDOM or microbial composition.

Targeted laboratory experiments are needed to validate the candidate surfactant producing taxa and quantify their impact on air-sea processes. We recommend combining targeted laboratory incubations with integrative omics, including metabolomics, metagenomics, and proteomics to (i) validate candidate microbial surfactant producers, (ii) identify the molecular identities of surfactants produced, and (iii) quantify their functional impacts on surface tension and gas exchange. This study did not capture all stages of the fall phytoplankton bloom cycle, which could be a future topic of study. Bloom progression from autotrophic growth through decline and into heterotrophic degradation, as well as protist and viral lysis, is likely important for understanding surfactant production dynamics (Flores et al., 2025). Characterizing surfactant concentrations and composition across a naturally occurring bloom life cycle therefore represents an important direction for future work.

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Finally, this study demonstrates that combining microbial sequencing with surfactant concentration measurements is a promising approach for identifying microbial lineages influencing surfactant concentrations. Predicting the spatiotemporal distributions of these microbial groups can improve understanding of surfactant variability and their consequences for air-sea exchange processes. Furthermore, advances in remote sensing and satellite imaging of marine microbes (IOCCG, 2014; Mouw et al., 2017), may enable the development of microbial-based proxies to improve parameterization of gas transfer velocities and enhance predictions of regional to global fluxes of climate-active gases.

Code and Data Availability

All code and datasets used in this study have been deposited on https://github.com/FEdufia/SOAPI1and2-MicrobesAndSurfactants

Supplement Link:

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Author Contributions

FE Agblemanyo: Investigation, methodology, data curation, formal analysis, validation, visualization, writing – original draft, writing – review & editing.

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JF Biddle: Investigation, methodology, validation, writing – review & editing.

AA Frossard: Conceptualization, investigation, methodology, validation, writing – review & editing, supervision, funding acquisition.

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Competing Interests

The authors declare that they have no conflict of interest.

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