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## **Marine bacterial enrichment in the sea surface microlayer, and surface taxa aerosolization potential in the Western Mediterranean Sea**

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1 **Abstract**

2  
3 The sea surface microlayer (SSML) is critical to air-sea exchanges of gases and primary  
4 aerosols. However, despite the extent of this boundary layer, little is known about its specific  
5 bacterial community (bacterioneuston) and how it may affect ocean-atmosphere exchanges.  
6 Here, we studied the bacterial community composition in the surface waters of three different  
7 basins of the Western Mediterranean Sea and assessed the selective air-sea transfer of marine  
8 bacteria through experimental nascent sea spray aerosol production in a 10 L tank with plunging  
9 jets. In situ, the bacterioneuston harbored basin-specific enriched taxa and followed a similar  
10 spatial pattern as the underlying bacterioplankton community. Aerosolization potential showed  
11 that sea spray taxa might be recruited from both the underlying water and the SSML, and that  
12 taxa enriched in the bacterioneuston were not always aerosolized. Our results suggest that the  
13 Mediterranean nutrient gradient, as well as pulse events such as dust deposition, affect the  
14 distribution of the bacterial community at the ocean-atmosphere interface, which may impact  
15 biogeochemical processes, climate regulation and bacterial dispersal through aerosolization.

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## 30           **Introduction**

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32           The sea surface microlayer (SSML) is a thin (1-1000  $\mu\text{m}$ ) gel-like matrix at the surface of the  
33 ocean (Engel *et al.*, 2017 and reference therein). This ocean skin harbors a specific ecology and  
34 chemistry in comparison to the underlying water (ULW). The biogeochemical and physical  
35 processes there, are critical to air-sea exchanges of energy, gases and primary aerosols which  
36 affect climate (Engel *et al.*, 2017, Barthelmeß *et al.*, 2021, Hendrickson *et al.*, 2021).  
37 Atmospheric deposition can also accumulate at the SSML, influencing biogeochemical processes  
38 (Astrahan *et al.*, 2016) before being exported to deeper waters. However, despite the geographic  
39 extent of the SSML, the biogeographic distribution of the bacterial community living there (the  
40 bacterioneuston) and its potential role in ocean-atmosphere connectivity is still poorly  
41 understood.

42           The bacterioneuston is a key player in the SSML biogeochemical cycles and in air-sea  
43 processes. Its activities affect organic matter composition and concentration, gas fluxes, physical  
44 properties of the SSML through gel formation, and thus, aerosol composition and numbers (e.g.  
45 Upstill-Goddard *et al.*, 2003, Reinthaler *et al.*, 2008, Kurata *et al.*, 2016, Engel *et al.*, 2018,  
46 Freney *et al.*, 2020, Sun *et al.*, 2020, Sellegri *et al.*, 2021). The bacterioneuston composition  
47 appears to be tightly linked to the ULW bacterial community. Nevertheless, while some studies  
48 found that the bacterioneuston was enriched in specific taxa compared to the ULW (Franklin *et*  
49 *al.*, 2005, Zäncker *et al.*, 2018), others report no significant differences between the two layers  
50 (Agogue *et al.*, 2005, Obernosterer *et al.*, 2008). These discrepancies might be the results of  
51 spatiotemporal variations, winds, and SSML chemical properties but also be the results of the  
52 SSML collection method (Stolle *et al.*, 2010, Cunliffe *et al.*, 2011, Rahlff *et al.*, 2017, Wong *et*  
53 *al.*, 2021).

54 Sea spray aerosols (SSA) represents one of the most abundant sources of natural aerosol  
55 particles in the atmosphere and contribute significantly to global aerosol fluxes (McNeill, 2017).  
56 SSA are produced mainly by rising bubbles bursting at the air-sea interface. As bubbles rise  
57 through the water column they scavenge inorganic and biological material, which play a  
58 significant role in the SSML formation (Engel *et al.*, 2017). Thus, bacterial accumulation at the  
59 SSML might be a precursor to their aerosolization; and SSML properties might affect the  
60 selective transfer of bacteria to SSA (Aller *et al.*, 2005, Michaud *et al.*, 2018). Indeed, nascent  
61 SSA have been shown to contain a large diversity of bacteria which appear to be a subset of the  
62 community present in the surface water (Fahlgren *et al.*, 2015, Rastelli *et al.*, 2017, Michaud *et*  
63 *al.*, 2018, Freitas *et al.*, 2022). These studies suggest that bacterial aerosolization is selective,  
64 which might be influenced by cellular properties and environmental conditions (Rastelli *et al.*,  
65 2017, Michaud *et al.*, 2018). Some of these airborne bacteria can directly influence atmospheric  
66 processes, cloud formation and climate through their activities and icenucleating capacities  
67 (Amato *et al.*, 2017, Failor *et al.*, 2017, Beall *et al.*, 2021, Trueblood *et al.*, 2021, Šantl-Temkiv  
68 *et al.*, 2022). Moreover, as SSA travel long distance (Bondy *et al.*, 2017, Mayol *et al.*, 2017,  
69 Šantl-Temkiv *et al.*, 2018, Johansson *et al.*, 2019), they are a potential vector of microbial  
70 dispersal, influencing bacterial biogeography.

71 Here, we studied the bacterial community composition in the surface waters of three different  
72 basins of the oligotrophic Western Mediterranean Sea. We compared the spatial distribution of  
73 the bacterioneuston with the bacterioplankton in the ULW, and evaluated the taxa enriched in the  
74 SSML between the studied basins. We further assessed the aerosolization potential of surface  
75 taxa through onboard experimental nascent SSA production.

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## 78 **Material and Methods**

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### Sea water sampling

81 Seawater was collected during the ‘ProcEss studies at the Air-sEa Interface after dust  
82 deposition in the MEditerranean sea’ cruise (PEACETIME), onboard the R/V “Pourquoi Pas ?”  
83 in May/June 2017 (Guieu *et al.*, 2020). Stations were sampled in the Ionian Sea (ION),  
84 Tyrrhenian Sea (TYRR), and in the Algerian basin (WEST) from a zodiac (Fig. S1). Water  
85 collection is described in detail in Zäncker *et al.* (2021). Briefly, at each station sea surface  
86 microlayer (SSML) water was sampled using the glass plate method, and uUnderlying water  
87 (ULW) was sampled 20 cm below the SSML with two acid-cleaned bottles that were opened ca.  
88 20 cm below the surface. At station FAST (the western most station), we sampled surface water  
89 before a wet dust deposition event, and then 2h, 24h and 48h after the rain (SSML was not  
90 sampled before the rain).

### 91 Nascent sea spray aerosols

92 Nascent sea spray aerosols (nSSA) were produced onboard, as described in Trueblood *et al.*  
93 (2021). Briefly, nSSA were generated in a 10 L glass tank with a plunging jet system linked to a  
94 continuous flow of surface water (5 m) from the ship underway system. nSSA filters were  
95 collected for bacterial community composition at two stations in the Ionian Sea, and three  
96 stations in the Algerian basin (Fig. S1),. and at station FAST 2h and 24h after the wet dust  
97 deposition event. nSSA were filtered onto glass fiber filters over 24h at 16.5 LPM and  
98 immediately stored at -20°C. Samples for bacterial abundance in nSSA were collected from 28  
99 stations using a PILS sampler. 0.5 mL samples were fixed with glutaraldehyde (0.5% final), flash  
100 frozen and stored at -80°C.

101 Bacterial abundance

102 2mL samples were fixed with glutaraldehyde (1% final concentration) for bacterial abundance in  
103 the SSML and the ULW. Samples were stored immediately at -20°C. Abundance was measured  
104 by flow-cytometry as described in Zäncker *et al.* (2021).

105 For bacterial abundance in the nSSA, the samples were stained with Sybr Green and measured  
106 by flow cytometry (BD-FACS Calibur). True count beads and 2µm beads were used as  
107 reference. Potential autofluorescent particles were subtracted from the counts.

108 DNA sampling, sequencing and sequence analysis

109 400 mL water for SSML and ULW were filtered through a 0.2µm filter (Durapore) after a pre-  
110 filtration through a 100 µm mesh, and immediately stored at -80°C. DNA was extracted as  
111 described in Zäncker *et al.* (2021). DNA extracts were quantified and normalized and used as  
112 templates for PCR amplification of the V4-V5 region of the 16S rRNA gene (Parada *et al.*,  
113 2016), as described in Dinasquet *et al.* (2022). The nSSA filters were extracted with a Zymo  
114 quick Fungal/Bacterial DNA miniprep as described in Dadaglio *et al.* (2018). DNA extracts were  
115 quantified and normalized and used as templates for PCR amplification of the V4 region of the  
116 16S rRNA gene (Apprill *et al.*, 2015).

117 All reads were processed using the Quantitative Insight Into Microbial Ecology 2 pipeline  
118 (QIIME2 v2020.2, Bolyen *et al.*, 2019). Reads were truncated to 250bp to cover the V4 region,  
119 based on sequencing quality, denoised, merged and chimera-checked using DADA2 (Callahan *et al.*  
120 *et al.*, 2016). A total of 953 amplicon sequence variants (ASVs) were obtained. Taxonomy  
121 assignments were made against the database SILVA 132 (Quast *et al.*, 2013). All sequences  
122 associated with this study have been deposited under the BioProject ID: PRJNA693966.

123            Statistics

124            Alpha and beta-diversity indices for community composition were estimated after  
125 randomized subsampling to 7888 reads for the analysis with nSSA samples and to 24728 for the  
126 analysis with only the surface water samples 16S rDNA. Analyses were run in QIIME 2 and in  
127 Primer v.6 software package (Clarke & Warwick, 2001). Differences between the samples  
128 richness and diversity were assessed using Kruskal-Wallis pairwise test. Beta diversities were  
129 run on Bray Curtis dissimilarity. Differences between samples' beta diversity were tested using  
130 PERMANOVA (Permutational Multivariate Analysis of Variance) with pairwise test and 999  
131 permutations. The sequences contributing most to the dissimilarity between layers were  
132 identified using the ANalysis of Composition of Microbiomes (ANCOM)(Mandal *et al.*, 2015).

133

134



## 135                    **Results and discussion**

136            The Mediterranean Sea is the largest semi-enclosed ocean basin. It is also a large Low-  
137 Nutrient-Low-Chlorophyll (LNLC) region, characterized by a long summer stratification period  
138 and a west-to-east gradient of increasing oligotrophy, where microbial growth is generally  
139 limited by phosphorus availability (Durrieu de Madron *et al.*, 2011). The Mediterranean bacterial  
140 biogeography was shown to reflect the oligotrophy gradient and physical barriers from surface to  
141 deep waters (Mapelli *et al.*, 2013, Sebastián *et al.*, 2021). Here, we further describe, for the first  
142 time to our knowledge, the spatial distribution of the Mediterranean bacterial community at the  
143 air-sea interface and the aerosolization potential of surface taxa.

### 144            *Spatial distribution of bacteria community composition in the SSML and ULW*

145            The biogeochemical context of the SSML sampled during this cruise is described in Tovar-  
146 Sanchez *et al.* (2020) and Zäncker *et al.* (2021). Briefly, these studies show that trace metal and  
147 TEP were consistently enriched in the SSML. DOC was also enriched in the SSML (as shown  
148 here, Fig.S2). Picophytoplankton were generally more abundant in the SSML, but no significant  
149 difference was observed in the eukaryotic community composition and diversity (Zäncker *et al.*,  
150 2021). The bacterial abundance decreased from west to east in both the SSML and ULW but  
151 showed no significant enrichment in the SSML (Table 1, Tovar-Sánchez *et al.*, 2020, Zäncker *et*  
152 *al.*, 2021). The bacterioplankton community, however, showed significant differences between  
153 layers. Evenness was significantly lower in the SSML compared to the ULW (Fig.S3, Kruskal  
154 Wallis  $p=0.006$ ).

155            The bacterioneuston has been shown to be tightly linked to the bacterial community in the  
156 ULW just below (Cunliffe *et al.*, 2013). Overall, reflecting previous studies from surface mixed

157 layer communities, the spatial distribution of the bacterial community in the first micrometers of  
158 the SSML followed the Mediterranean Sea oligotrophic gradient and physical barriers. The  
159 overall surface bacterioplankton (combined SSML and ULW) was significantly different  
160 between basins (Fig.1, Permanova  $p < 0.01$ ). Similar spatial distribution of the main taxa reported  
161 for surface mixed layers (Mapelli *et al.*, 2013, Sebastián *et al.*, 2021) were also observed here.  
162 Indeed, the relative abundance of the Gamma-Proteobacteria, Oceanospirillales,  
163 Alteromonadales and Pseudoalteromonadales increased from West-to-East in both the SSML and  
164 ULW, while the relative abundance of cyanobacteria (*Synechococcus*, but especially  
165 *Prochlorococcus*) decreased (Fig.2, S4).

166 Nevertheless, due to the weak cloud coverage, the Mediterranean bacterioneuston is subject  
167 to strong solar radiation that may influence its composition compared to lower surface layers.  
168 The bacterioneuston has only been studied at a few coastal stations of the North-west  
169 Mediterranean Sea (Agogue *et al.*, 2005, Joux *et al.*, 2006), and despite strong potential stressors  
170 no significant differences were observed between the ULW and the SSML. Here, closely  
171 comparing the ULW and SSML communities showed that the bacterioneuston in the Ionian and  
172 Tyrrhenian Seas were significantly different between the two layers (Fig.1,  $p < 0.05$ ). Generalist  
173 Gamma-Proteobacteria (Oceanospirillales, Alteromonadales and Pseudoalteromonadales) were  
174 particularly enriched in the SSML compared to the ULW (Fig.2, S4), which may be due to  
175 different physico-chemical properties of the SSML.

176 No significant differences were observed between SSML and ULW communities in the  
177 Western basin. However, at station FAST (Fig.S1) which was influenced by a wet dust  
178 deposition event (Tovar-Sánchez *et al.*, 2020, Van Wambeke *et al.*, 2020, Desboeufs *et al.*,  
179 2022), the SSML and ULW clustered separately with specific taxa changing in response to dust

180 compared to other Western stations (Fig.1, S4). This might be due to the Mediterranean  
181 bacteria's capacity to rapidly respond to dust input (Tsiola *et al.*, 2017, Dinasquet *et al.*, 2022),  
182 especially in the SSML (Astrahan *et al.*, 2016) or to the direct deposition of dust attached  
183 bacteria (Rahav *et al.*, 2016, Mescioglu *et al.*, 2019, Aalismail *et al.*, 2020) to the SSML.

184

### 185 *Aerosolization potential of surface taxa to sea spray aerosols*

186 It is challenging to disentangle the role of marine bacteria on the atmospheric microbiome  
187 due to the large influence of bacteria attached to anthropogenic, terrestrial and mineral aerosols  
188 (e.g.Lang-Yona *et al.*, 2022), in particular in the semi-enclosed and dust impacted Mediterranean  
189 Sea (Rahav *et al.*, 2016, Gat *et al.*, 2017, Mescioglu *et al.*, 2019). To isolate the aerosolization  
190 potential of marine bacteria, complex experimental procedures with nSSA production are  
191 necessary. But only few studies have investigated the selective transfer of marine taxa from  
192 surface waters into nSSA (Fahlgren *et al.*, 2015, Rastelli *et al.*, 2017, Michaud *et al.*, 2018,  
193 Freitas *et al.*, 2022).

194 Sea spray aerosols are formed by bubbles rising through the water column and potentially  
195 scavenging material from the surface and SSML. Hence, bacterial accumulation at the SSML  
196 might be a precursor to their aerosolization (Aller *et al.*, 2005).In order to better understand the  
197 aerosolization potential of bacteria in the surface Mediterranean Sea, we compared the sequential  
198 enrichment of bacterial taxa from the ULW to the SSML, to onboard experimentally produced  
199 nSSA with surface water from the same stations. Concentration of bacteria in the nSSA likely  
200 followed the same west-to-east gradient of decreasing abundance as the ULW and SSML (Table  
201 1) and were in line with previous observations in marine aerosols in situ, in the Mediterranean

202 Sea (from 7 to 25x10<sup>3</sup> cells m<sup>-3</sup>)(Mescioglu *et al.*, 2019) and in the North Atlantic (~8.02x10<sup>3</sup>  
203 cells m<sup>-3</sup>)(Mayol *et al.*, 2014). The nSSA bacterial community showed significantly lower  
204 diversity but higher evenness than the surface communities (Fig. S3, Kruskal-Wallis p <0.001).  
205 The community structure also appeared to be basin specific with the Ionian and Western nSSA  
206 communities clustered separately from ULW and SSML water communities (Fig. S5),  
207 suggesting selective transfers of bacterial taxa, as observed in previous studies (Fahlgren *et al.*,  
208 2015, Rastelli *et al.*, 2017, Michaud *et al.*, 2018, Freitas *et al.*, 2022). Interestingly the  
209 transferred cyanobacteria followed a similar spatial gradient as in surface layers, with  
210 *Prochlorococcus* better aerosolized in the Western basin where it is more abundant and  
211 *Synechococcus* in the Ionian Sea. Sequential enrichment of some taxa (e.g. Rhizobiales,  
212 *Sphingobium*, *Pseudomonas*, *Vibrio* and *Staphylococcus*) was observed from ULW, SSML to  
213 nSSA but generally aerosolized taxa appeared to be present but not abundant throughout the  
214 surface waters. Some taxa that were enriched in the SSML had a low aerosolization potential,  
215 which suggests that not all bacterioneuston taxa are scavenged into the aerosols, and this might  
216 be specific to cellular properties or environmental factors especially the physical properties of  
217 the SSML.

218 Most of the aerosolized taxa observed here (Table 2, Fig 2, 3, S4) are commonly observed in  
219 marine aerosols in other oceanic regions (e.g. Cho & Hwang, 2011, Fahlgren *et al.*, 2015,  
220 Michaud *et al.*, 2018, Mescioglu *et al.*, 2019, Lang-Yona *et al.*, 2022), suggesting that cellular  
221 properties consistent within these groups independent from environmental factors, influence their  
222 sea-to-air transfer. A few of these taxa (Table 2, Fig 2, 3, S4) are related to known opportunistic  
223 pathogens (e.g. *Vibrio*, *Pseudomonas*, *Staphylococcus*, *Streptococcus*) for marine organisms.  
224 Others are associated to known phototrophs or have specific sulfur requirements (e.g. SAR11,

225 SAR86, *Ectothiorhodobacterales*, *Coralimargarita*), which may be an advantage to survive  
226 harsh atmospheric conditions. Some of the taxa with high aerosolization potentials have also  
227 been shown to increase in response to higher temperature or to dust deposition (e.g. Westrich *et*  
228 *al.*, 2016, Sato-Takabe *et al.*, 2019, Dinasquet *et al.*, 2022), which suggests that their dispersal  
229 may have a greater impact on marine biogeochemical cycles and ecosystem health in the future  
230 Mediterranean Sea.

231

### 232 Conclusion

233 The biogeographic distribution of the bacterial community in the very first centimeters of the  
234 water column – the sea-air interface, is influenced by similar horizontal and vertical gradients, as  
235 previously described for lower depths. This surface community appears to follow the  
236 oligotrophic gradient but may also be influenced by pulse events like dust deposition that  
237 stimulate the growth of specific opportunistic taxa. The bacterioneuston plays a crucial role in  
238 the ocean and the atmosphere connectivity, where they are critical to air-sea exchange affecting  
239 climate. Here, we show through onboard experiments that surface Mediterranean taxa have a  
240 range of aerosolization potential. As described in other oceanic regions, these taxa can be  
241 sequentially enriched through the surface layers and selectively transferred into the aerosols.  
242 Sequential enrichment in the SSML and aerosolization of bacteria may be affected by future  
243 climate conditions and aerosol deposition in the Mediterranean Sea. This could have a large  
244 impact on climate, microbial biogeography and ecosystem services.

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## 260 **Conflict of interest statement**

261 The authors declare that the research was conducted in the absence of any conflict of interest.

262

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## **Tables and figures**

**Table 1:** Bacterial abundance in the three sampled basins, in the nascent sea spray aerosols (cells  $m^{-3}$ ) and in the surface water (SSML and ULW, cells  $mL^{-1}$ ).

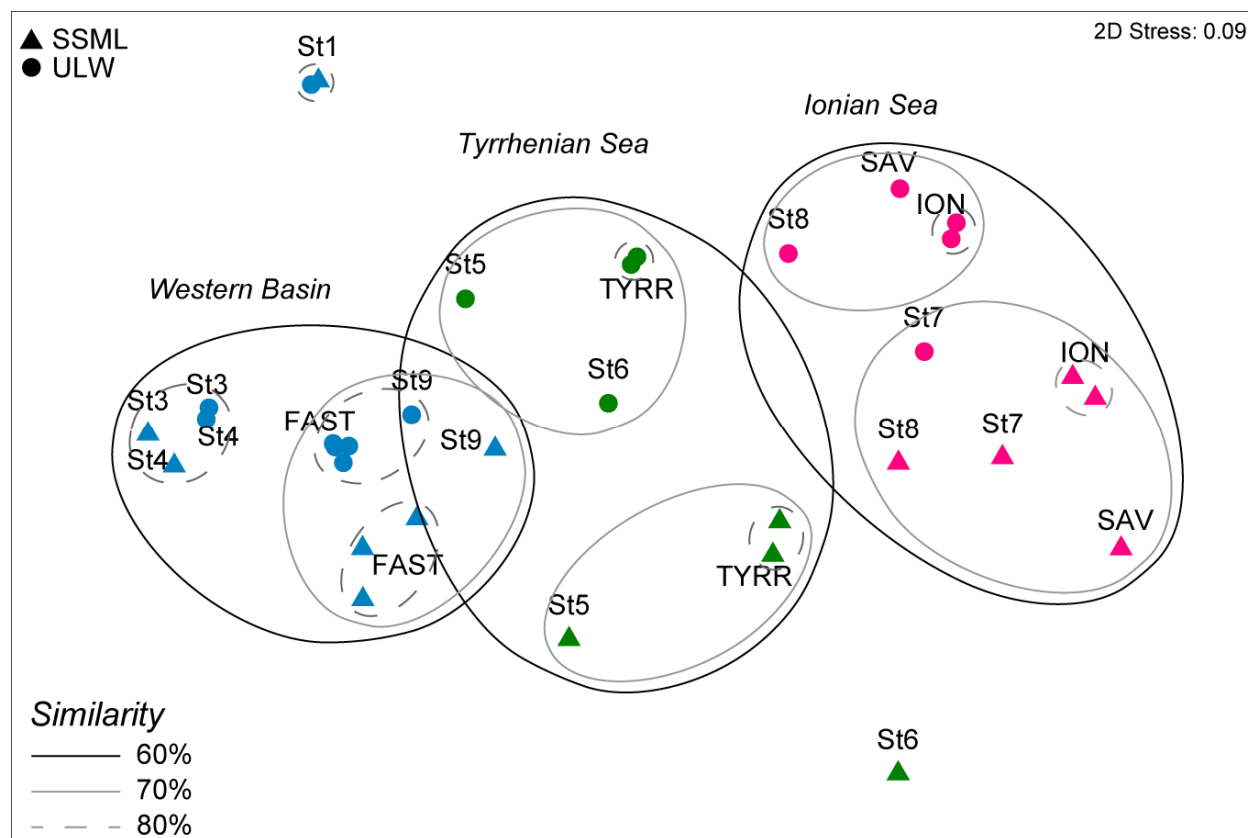
	WEST	TYRR	ION	Total
SSML*	$6.62 \times 10^5 \pm 2.04 \times 10^5$ (n=8)	$4.96 \times 10^5 \pm 5.37 \times 10^4$ (n=4)	$2.92 \times 10^5 \pm 8.08 \times 10^4$ (n= 5)	$5.14 \times 10^5 \pm 2.17 \times 10^5$ (n=17)
ULW*	$5.87 \times 10^5 \pm 1.24 \times 10^5$ (n=8)	$4.83 \times 10^5 \pm 2.62 \times 10^4$ (n=4)	$2.85 \times 10^5 \pm 6.39 \times 10^4$ (n=5)	$4.74 \times 10^5 \pm 1.59 \times 10^5$ (n=17)
nSSA	$5.68 \times 10^3 \pm 3.49 \times 10^3$ (n=4)	$4.03 \times 10^3 \pm 3.62 \times 10^2$ (n=2)	$1.92 \times 10^3$ (n=1)	$4.67 \times 10^3 \pm 2.86 \times 10^3$ (n=7)

\*Bacterial abundance data in the SSML and ULW are also presented between Basin in Zäncker *et al.*, 2021 and details per station are presented in in Tovar-Sanchez *et al.*, 2020.

**Table 2:** Enrichment in the SSML and aerosolization potential in the nSSA and of the most abundant genus responsible for the difference between the communities in the ULW, SSML and nSSA based on Analysis of composition of microbiome (ANCOM).

Class	Order	Genus	SSML enrichment	Aerosolization potential	
			From ULW	from SSML	from ULW
Alpha-proteobacteria	Pelagibacterales	SAR11 clade	52%	189%	98%
Alpha-proteobacteria	Puniceispirillales	SAR116 clade	108%	31%	33%
Alpha-proteobacteria	Rhizobiales	<i>Bradyrhizobium</i>	111%	53300%	59012%
Alpha-proteobacteria	Rhizobiales	<i>Methylobacterium</i>	260%	1662%	4320%
Alpha-proteobacteria	Rhodobacterales	<i>Ascidiaceihabitans</i>	61%	47%	29%
Alpha-proteobacteria	Rhodospirillales	AEGEAN-169	60%	182%	110%
Alpha-proteobacteria	Sphingomonadales	<i>Sphingobium</i>	720%	639%	4598%
Beta-proteobacteria	Burkholderiales	<i>Delftia</i>	63%	1924%	1216%
Delta-proteobacteria	Bdellovibrionales	OM27 clade	448%	91%	407%
Gamma-proteobacteria	Alteromonadales	<i>Pseudoalteromonas</i>	542%	12%	67%
Gamma-proteobacteria	Alteromonadales	<i>Alteromonas</i>	246%	17%	41%
Gamma-proteobacteria	Cellvibrionales	OM60 clade	88%	18%	16%
Gamma-proteobacteria	Oceanospirillales	<i>Halomonas</i>	363%	1%	3%
Gamma-proteobacteria	Oceanospirillales	<i>Litoricola</i>	79%	4%	3%
Gamma-proteobacteria	Oceanospirillales	<i>Marinomonas</i>	81%	25029%	20154%
Gamma-proteobacteria	Pseudomonadales	<i>Acinetobacter</i>	152%	9%	13%
Gamma-proteobacteria	Pseudomonadales	<i>Pseudomonas</i>	197%	181%	356%
Gamma-proteobacteria	Vibrionales	<i>Vibrio</i>	173%	2739%	4732%
Gamma-proteobacteria	SAR86 clade		72%	491%	352%
Gamma-proteobacteria	Xanthomonadales	<i>Stenotrophomonas</i>	233%	0%	0%
Bacilli	Bacillales	<i>Staphylococcus</i>	146%	8975%	13140%
Bacteroidetes	Balneolales	<i>Balneola</i>	76%	74%	56%
Bacteroidetes	Flavobacteriales	NS4	64%	23%	14%
Bacteroidetes	Flavobacteriales	NS9	92%	91%	84%
Bacteroidetes	Flavobacteriales	NS5	85%	51%	43%
Cyanophyceae	Synechococcales	<i>Prochlorococcus</i>	71%	202%	142%
Cyanophyceae	Synechococcales	<i>Synechococcus</i>	77%	19%	14%
Verrucomicrobia	Opitutales	<i>Coraliomargarita</i>	69%	354%	252%
Verrucomicrobia	Opitutales	<i>Lentimonas</i>	79%	181%	147%

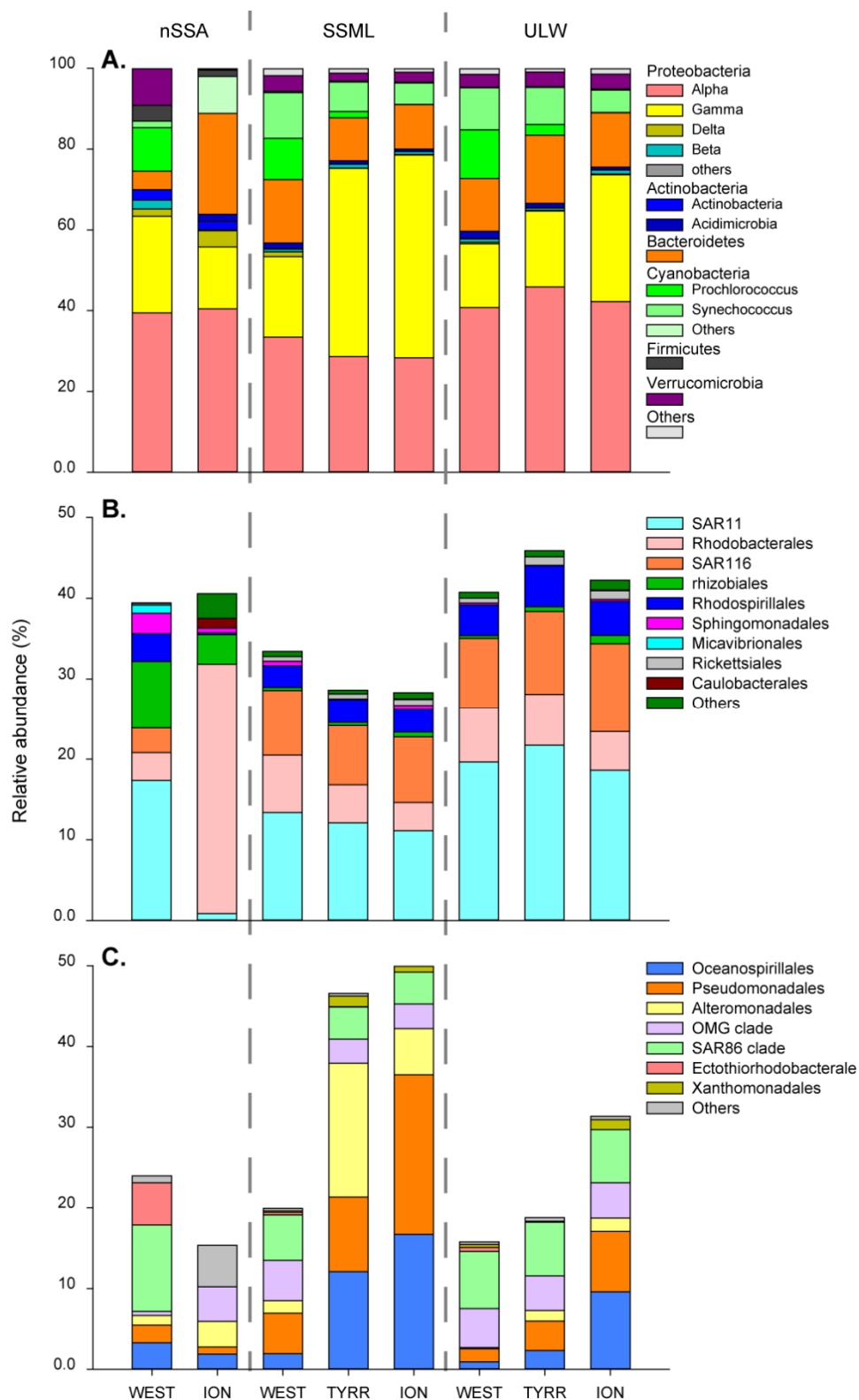
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**Figure 1:** nMDS plot of bacterial community composition in the SSML and ULW at each station based on Bray-Curtis dissimilarities of the 16S rDNA sequences. Samples clustering at different level of similarity are circled together, basin groups are significantly different from each other ( $p < 0.01$ ) based on a PERMANOVA test.

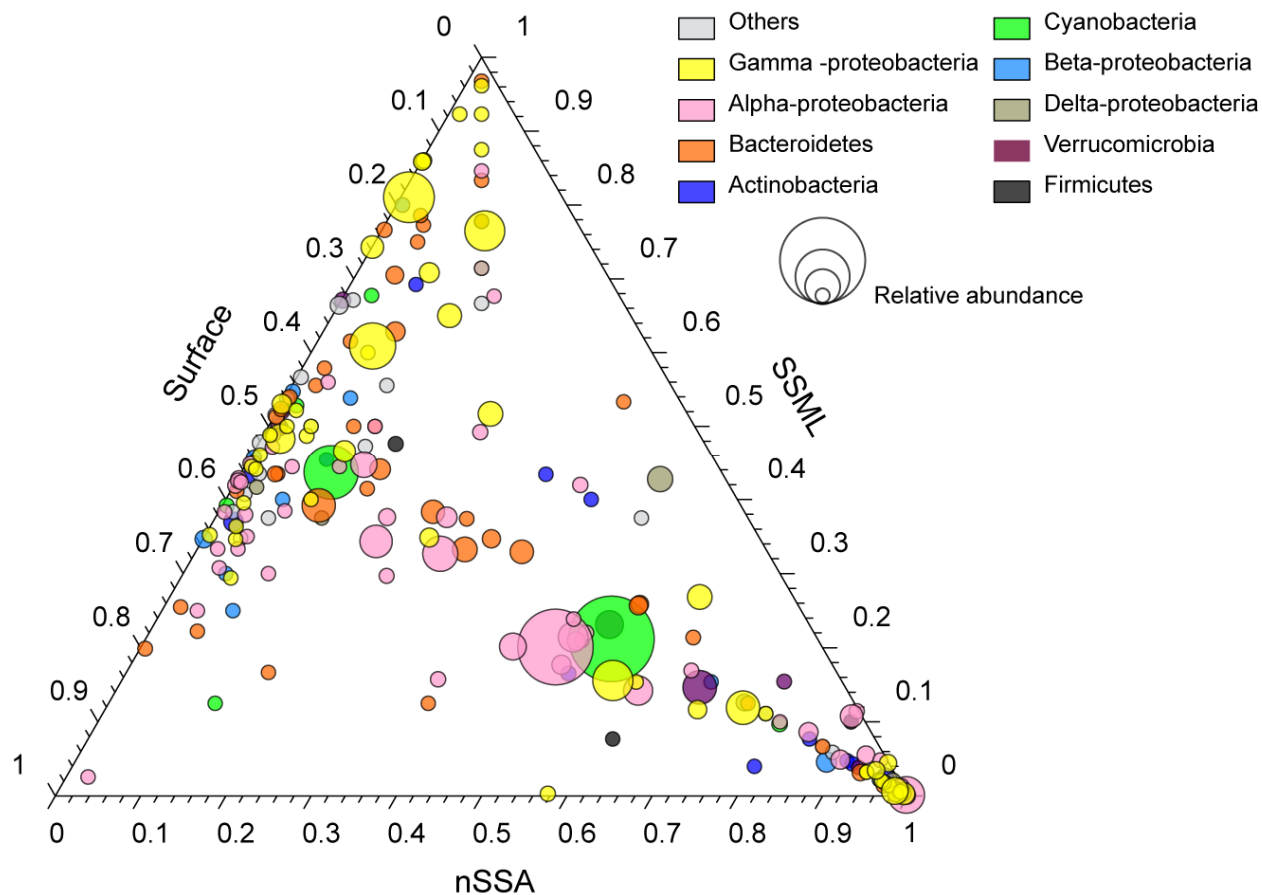


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**Figure 2:** Average community composition at the phylum level (A), Alpha-proteobacteria family level (B) and Gamma-proteobacteria family level (C) distribution in the different basins in the nSSA, SML and ULW.

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**Figure 3:** Ternary plot bacterial taxa enriched across the three fractions: surface water, sea surface microlayer (SSML) and nascent sea spray aerosol (nSSA). Each bubble represents one major bacterial group (collapsed at the genus level colored per phylum), the size of the bubble represents the overall relative abundance of the group in the three fractions. “Others” is an average of low abundance phyla.