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1 **Fish gut and skin microbiota dysbiosis induced by exposure to commercial**
2 **sunscreen formulations**

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5

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11

12 **Abstract**

13 UV filters (organic or mineral) present in sunscreen products are emerging contaminants of
14 coastal aquatic environments. There is an urgent need to understand marine organisms
15 responses to these compounds. In this study, we investigated the effect of exposure to dilutions
16 of commercial sunscreen formulations on bacterial communities of mullet (*Chelon* sp.). The
17 gut and skin mucus microbial communities were characterized using a metabarcoding approach
18 targeting the 16S rRNA gene. Our results revealed that mullets had its own bacterial
19 communities that differ from their surrounding habitats and specific to tissue. The dilutions of
20 commercial sunscreens modified the relative abundance of *Actinobacteriota*, *Bacteriodota* and
21 *Proteobacteria* for both gut and skin microbiota. They also allowed to bacteria affiliated to
22 *Mycobacterium*, *Nocardia* and *Tenacibaculum* genera, known to house pathogenic species, to
23 colonize the epithelium which may have implications for fish host health.

24

25 **Keyword:** Sunscreen, microbiota, bacterial shifting, fish, UV filters

26 INTRODUCTION

27 Shorelines are areas of high biodiversity but are also repositories for several contaminants
28 (Worm et al., 2006). Consequently, a large number of studies have been conducted in order to
29 highlight the effect of contaminants upon the living biota in these zones. Besides historical
30 contaminants, recent research in ecotoxicology aims at investigating the biological impact of
31 emerging contaminants. UV filters (UVFs) are part of these emerging contaminants. These
32 compounds are presents in sunscreen products and are transferred from the human skin into the
33 aquatic environment during recreational activities (bathing) or through waste water effluents.
34 Certain coastal areas showed concentration of UVFs from few ng L^{-1} (Labille et al., 2020) to
35 several $\mu\text{g L}^{-1}$ (Bratkovics et al., 2015; Rodríguez et al., 2015). The impact of these chemicals
36 upon neurological function, reproduction or development has already been demonstrated in
37 aquatic organisms (Christen et al., 2011; Paredes et al., 2014; Tao et al., 2020). Be that as it
38 may, further research are still needed in order to understand the toxicological effects of UVFs.
39 Indeed, experimental approaches until now mainly focus on the acute toxicity of single UVFs
40 molecule while sunscreen exposures are long term, seasonal and include a combination of
41 several UVFs and excipients (Cuccaro et al., 2022). Moreover, several research are needed
42 since ecotoxicological studies have been conducted taking into account the impact of these
43 contaminants upon a restricted number of biological function (with an important focus on
44 endocrine disruption and reproduction). Finally, marine species, and particularly marine teleost,
45 have been few considered in this research field (Carve et al., 2021; Grimmelpont et al., 2023).
46 Regarding this state-of-the-art background, the present work aims at understanding the effect
47 of a long term and realistic UV filters contamination upon the microbiota of marine teleost fish.
48 Grey mullets (*Chelon* sp.) has been chosen as a genus of interest regarding its abundance in
49 littoral habitats (coasts, estuaries) (Laffaille et al., 1998), i.e., where sunscreens products are

50 the more concentrated, and because of its role as an ecosystem engineers, enhancing the transfer
51 of organic matter between habitats of the shoreline (Lebreton et al., 2011).

52 The microbiota, is unique to an organism and specific to a system. Research on teleost
53 microbiota is still scarce compared to studies in humans or mammal models, but it is commonly
54 accepted that the microbiota is essential in maintaining fish health and that water quality is an
55 important environmental factor that could influence the diversity of bacterial communities.
56 Currently, the most studied microbiota in fish are the gut or the gastrointestinal ones that plays
57 a critical role in nutrition, development, immunity and resistance to pathogens (Egerton et al.,
58 2018; Tarnecki et al., 2017; Wang et al., 2018). Certain other mucosal tissues, such as the skin,
59 could be major entry pathways for pathogens or pollutants, and their microbiota probably plays
60 a major role as a defense barrier (Merrifield and Rodiles, 2015).

61 In the present study, we aimed to improve the current knowledge on a potential link between
62 UVFs in seawater and teleost microbiota. Two categories of UVFs products were used, organic
63 and mineral. After experimental exposure to these pollutants, we investigated the impact on the
64 microbiota of fish (*Chelon* sp.) and on the surrounding environment (i.e., water). More
65 precisely, using metabarcoding approaches, we investigated whether the bacterial communities
66 of mullet differ from their surrounding habitats (seawater in tanks). Then, we assessed the
67 structure, diversity and taxonomic composition of two bacterial microbiota (gut and skin) and
68 possible interactions. Finally, we examined whether UVFs exposure could affect these
69 microbial communities, which may suggest a possible dysbiosis.

70

71 **MATERIALS AND METHODS**

72 *Fish maintenance*

73 Mulletts (*Chelon* sp.) were fished, during summer 2020, in salt marshes of l'Houmeau
74 (46°12'14" N 1°11'42" W) using fyke net. Then, fish were transferred in 400 L acclimatization

75 tanks filled with aerated natural seawater. Tanks were equipped with an external filter (Eheim
76 professional 3 2080, Eheim, Deizisau, Germany) ensuring the quality of the seawater which
77 was renewed at 30% every week. Acclimation period started two months before
78 experimentations and temperature in acclimatization tanks was set at $20^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ (hysteresis)
79 with a TECO[®] Refrigeration technologies thermoregulator (Ravenna, Italy). Fish were fed at
80 last three times per week with commercial food pellets (Neo Repro II, Le Gouessant, France)
81 and exposed to a 12h :12h light/dark. Nitrites were daily controlled and always below 0.1 mg.
82 L⁻¹. Oxygen was always above 90 percent of air saturation. At this moment, fish were juveniles
83 in their second year and were sexually immature (determination of the sex was impossible).
84 Experiments were carried out respecting regulations of the Animal Care Committee of France
85 (ACCF) (APAFIS#25159-2019102913067306 v7; UMR7266 LIENSs approval number:
86 173002).

87

88 *Sunscreen exposure media*

89 Two solutions of exposure were produced: one based on organic UVFs and one on mineral
90 UVFs.

91 The organic exposure media was made using two commercial sunscreens. The two sunscreens
92 were chosen since they contained the three majors organic UVFs (i.e., Octocrylene; 2-ethyl-
93 hexyl-4-trimethoxycinnamate; Ethylhexyl Salicylate) used by bathers on a beach of the French
94 Atlantic coast (Minimes, La Rochelle) - according to a survey conducted in the ANR CUTE
95 project during summer 2019. Neither of these sunscreens contains mineral UVFs. The
96 ingredients of the two commercial sunscreens used are listed in **Supplementary Table S1**. The
97 organic sunscreen exposure media was made in the dark to avoid photodegradation of the UVFs
98 compounds. During 24 hours, a magnetic-stirrer was used to mix 4.8 g of both sunscreens (i.e.,
99 9.6 g in total) with 1.2 L of natural seawater in a glass beaker (2L). After this, a 2 hours period

100 of decanting was respected and the solution was finally filtered through glass microfiber filters
101 (0.47 μm , Whatman, UK) thanks to a vacuum pump. The organic sunscreen exposure media
102 was stored at 4°C in the dark before use.

103 The mineral exposure media was made with a commercial sunscreen containing Titanium
104 dioxide as the active ingredient which is the most used mineral UVF in personal care product.
105 The list of ingredients of this commercial sunscreen is also provided (**Supplementary Table**
106 **S1**) and this sunscreen does not contain organic UVFs. The mineral sunscreen exposure media
107 was obtained using the same protocol than previously described for the organic exposure media
108 excepted that 9.6 g of a single sunscreen was used.

109

110 *Experimental design*

111 Thirty-four fish were transferred from acclimatization tanks to three different aquaria of 100 L
112 to form the control group (mean weight \pm SD: 37.2 g \pm 9.4 g; n=12,), organic UVF group (mean
113 weight \pm SD: 30.9 g \pm 4.0 g; n=11) and mineral UVF group (mean weight \pm SD: 34.0 g \pm 3.6
114 g; n=11). During the whole experimental period, fish were fed daily with the same food than
115 during the acclimatization period (Neo Repro II, Le Gouessant, France) at 1.5% of their
116 biomass. The three tanks were placed in a thermoregulated room allowing to stabilize
117 temperature at 19.91°C \pm 0.05°C for Control group; 20.14°C \pm 0.06°C for Organic UVF group
118 and 20°C \pm 0.43°C for Mineral UVF group. Oxygen level was maintained with an air-pump.
119 Seawater of each aquarium was renewed every day with 200 L (see below), thanks to an
120 overflowing system. Aquaria were not cleaned during the total duration of the experiment in
121 order to avoid any potential contamination with solvent or detergent. Twice a day, temperature,
122 nitrites (< 0.20 mg. L⁻¹ \pm 0.02 mg. L⁻¹) and oxygen levels (> 80% of air saturation) were
123 monitored.

124

125 *Experimental protocol and Sampling*

126 During 35 days, 50 mL of organic exposure media, mineral exposure media or seawater were
127 daily injected within the water column of the Organic UVFs, the Mineral UVFs and the control
128 tanks (100 L), respectively. *In fine*, the nominal concentrations of sunscreen in organic and
129 mineral UVF tanks were the same (i.e., 4mg/L of sunscreen) in order to allow comparison of
130 toxicity between them. A previous article (Grimmelpont et al., 2023), exposed the
131 concentration of three organic UV filters (octocrylene, ethylhexyl salicylate, 2-ethyl-hexyl-4-
132 trimethoxycinnamate) measured for this experiment. Briefly, during the six hours following the
133 injection of the exposure media, concentrations were environmentally relevant i.e., few $\mu\text{g L}^{-1}$
134 (Bratkovics et al., 2015; Grimmelpont et al., 2023). Six hours after the injection, the renewal of
135 the aquaria was conducted by adding 200 L of clean seawater. This leads to a decrease of the
136 organic UV filters concentrations: octocrylene concentrations were approximatively divided by
137 three due to water renewal and it was the only organic UV filter detected (Grimmelpont et al.,
138 2023). Due to this water renewal and probably also due to UV filters degradation, no increasing
139 residual concentration was observed (Grimmelpont et al., 2023). UVFs injection and the
140 consecutive renewal of seawater 6 hours after permitted to simulate the daily increase and the
141 consecutive decrease of UV filters due to bathing time slot in touristic beaches (Picot-Groz et
142 al., 2018). After the 35 days of exposure, all samples were collected on the same day (4 June
143 2021) under a laminar flow hood and using sterile materials. First, water (1L) from each tank
144 was collected in sterile jars and immediately filtered on 0.22 μm sterile membranes in triplicate,
145 using a sterile filtration unit connected to a manual pump. Filters were frozen at -80°C until
146 DNA extraction. Secondly, each fish was taken out of tank alive with a sterile landing net and
147 a skin sample was immediately collected on an area of 2-3 square centimeters located on the
148 right side of the back above the lateral line using a sterile swab and frozen at -80°C until DNA
149 extraction. Thirdly, after euthanasia, with tricaine methane sulphonate (MS-222; 0.1 g L^{-1} ,

150 Sigma-Aldrich, St Quentin-Fallavier, France), 3 cm of digestive tract tissue were cut and
151 sampled from the mid- and hindgut (no anatomical cues allowing a clear distinction between
152 them), approximately at 5 cm above the anal sphincter under the laminar flow hood and frozen
153 at -80°C until DNA extraction. All details of samples were given in **Supplementary Table 2**.

154

155 *16S rRNA bacterial diversity analyses*

156 DNA from the different tissues (gut and skin), and from the water were used for amplification
157 of prokaryotic diversity based on the 16S rRNA gene and sent to the Bordeaux Transcriptome
158 Genome Platform (www.pgtb.cgfb.u-bordeaux.fr; Cestas, France). Total DNA was extracted
159 from each tissue (around 250 mg) using a Qiagen® Power Fecal Pro DNA kit, and for water,
160 using a Qiagen® DNeasy PowerWater kit, following the manufacturer's instructions. Negative
161 controls (blank samples from each extraction kit) were also used for amplification. Sequencing
162 was performed on a 450 bp fragment of the 16S rRNA gene (V3-V4 variable region) frequently
163 used for analyses the microbial diversity (Fadrosh et al., 2014; Klindworth et al., 2013) on the
164 Illumina MiSeq platform, using 2 x 250 bp chemistry.

165

166 *Bioinformatics data processing*

167 Prokaryotic 16S rRNA paired-end reads were depleted from their primers with Cutadapt version
168 3.4. All individual fastq files forward and reverse were processed using the DADA2 version
169 1.24 pipeline, that describes microbial communities using amplicon sequence variants (ASVs)
170 (Callahan et al., 2016). In brief, reads were filtered and trimmed with the filterAndtrim function
171 based on sequence quality profiles, so that Q-scores remains above 30, (truncLen at (228, 219),
172 max EE at 2, maxN at 0, and truncQ at 2). The error model was calculated for forward and
173 reverse reads with learnErrors function, then filtered reads were dereplicated with default
174 parameters and merged with a minimum overlap of 12 nucleotides, allowing no mismatches.

175 The amplicons were then filtered by size (390 - 435 bp). Chimeras were removed with
176 removeBimeraDenovo function and ASVs were taxonomically assigned with IdTaxa function
177 using the Genome Taxonomy Database Silva SSU r138 (Parks et al., 2018).

178

179 *Statistical analysis and Visualizations*

180 All statistical analyses and data visualizations were carried out in R (R version 4.2.0 (Team,
181 2013) using R studio v 2022.02.1). Alpha diversity was computed using the Phyloseq R package
182 version 1.40.0 (McMurdie and Holmes, 2013) and R vegan package version 2.6-2 (Oksanen et
183 al., 2008). Differences in the alpha diversity indexes among conditions were tested using a
184 Kruskal–Wallis test. Beta diversity analyses were performed on Bray-Curtis distances on a
185 normalized dataset using the rarefaction method and were visualized using non-metric
186 multidimensional scaling (NMDS). The normalization for Beta diversity analyses was made
187 with rarefy_even_depth function. Sample groups were compared by a permutational
188 multivariable analysis of variance (999 permutations) with the adonis2 function of the Vegan
189 package and the beta dispersion analysis was performed with the betadisper function. Multilevel
190 comparisons for the conditions were also performed with the pairwise adonis function
191 (Martinez Arbizu, 2017). Differences in taxon abundances associated with tissues and
192 treatments were studied using a model based on negative binomial distribution, as implemented
193 by the DESeq function in the DESeq2 package version 1.36., $p < 0.01$ was considered
194 significant. Boxplots and barplots were produced with ggplot2 version 3.3.6. Ven diagrams
195 were generated using Venny version 2.1 software (Oliveros, 2007)
196 (<https://bioinfogp.cnb.csic.es/tools/venny/index.html>).

197

198 *Co-occurrence network analysis*

199 Microbial co-occurrence networks for gut and skin, all treatments together, were generated
200 using SPIEC-EASI (Sparse inverse covariance estimation for ecological association inference)
201 version 1.1.2 (Kurtz et al., 2015). The SPIEC-EASI statistical method combines data
202 transformations, developed for compositional data, with a sparse graphical model inference
203 framework, and inverse covariance selection algorithms (Kurtz et al., 2015). Pre-filtering of
204 ASVs was performed, retaining only ASVs with a proportion at least 0.01% of total abundance.
205 Network properties such as modularity, node degree, mean path distance, clustering coefficient
206 and hub score are detailed in Layeghifard, Hwang and Guttman 2017. Network modules were
207 calculated by the Louvain algorithm and microbial co-occurrence networks were visualized
208 with the R package igraph version 1.3.4 (Csardi and Nepusz, 2006).

209

210 *Data availability*

211 The data supporting the results presented in this article are available from the NCBI SRA
212 repository (BioProject PRJNA1003672).

213

214 **RESULTS**

215 *Bacterial diversity analysis*

216 Negative controls (six) analysis of metabarcoding was performed and represented 1.66% of
217 total reads after the affiliation process (97,397) (**Supplementary Table S3**). We obtained
218 49,394 reads with the extraction kit for Gut and only 6,082 with the PCR amplification blank.
219 We discarded ASVs from blanks and chloroplast with the Decontam R package version 1.16
220 (Davis et al., 2018), producing a final abundance table of 11,827 ASVs assigned with the Silva
221 SSU r138 database.

222 The metabarcoding approach (region V3-V4 of the 16S rRNA gene) used to characterize 60
223 bacterial communities associated with two environments (Fish and Water), two tissues (Gut

224 and Skin), and three treatments (Control, mineral UVF and organic UVF) produced 5,055,118
225 reads after the bioinformatics processing (**Supplementary Table S3**).

226 Alpha diversity are shown in **Supplementary Figure S1** and index values details for all
227 samples in **Supplementary Table S4**. We observed that richness (number of observed ASVs)
228 from the two environments was significantly different ($p = 0.03$), and the comparison of the
229 Shannon and InvSimpson indexes between treatments for the skin tissue showed significant
230 differences (**Supplementary Table S5**). The average richness was for the Water (804 ± 121)
231 in comparison with Gut (643 ± 327), and Skin (575 ± 205). At the tissue level, comparison
232 between the different conditions of exposure showed high intra-variability with mean richness
233 values for Gut were: Control (610 ± 352), oUVF (584 ± 337), and mUVF (798 ± 268) whereas
234 Skin were: Control (606 ± 220), oUVF (594 ± 176), and mUVF (485 ± 183).

235 Community structure analyses were performed with Beta diversity indexes that allowed a better
236 understood of relationships between bacterial communities. Permutational multivariate analysis
237 of variance (PERMANOVA) analyses indicated significant difference among the two
238 environments (Water and Fish), between both tissue for fish (Gut and Skin), and between
239 treatment (oUVF vs mUVF) for both tissues (**Supplementary Table S6**). NMDS plots were
240 2D representation of bacterial communities from Gut or Skin tissue samples (**Figure 1**). The
241 NMDS plot of Gut did not show an obvious separation between treatment samples (**Figure 1A**).

242 However, PERMANOVA analysis indicated significant difference for the pairwise comparison
243 between oUVF and mUVF (**Supplementary Table S6**). The NMDS plot of Skin showed a
244 clear separation between treatment samples (**Figure 1B**), and all pairwise comparison analyses
245 (i.e., Control vs oUVF; Control vs mUVF; oUVF vs mUVF) were significant suggesting that
246 the factor 'treatment' could explain 30% of the total bacterial variation in skin (**Supplementary**
247 **Table S6**). PERMANOVA analyse for Water samples indicated significant difference but not
248 for all pairwise comparison (Supplementary Table S6). Analyses of the Beta dispersion (i.e.,

249 distance to centroid) showed that microbial community dispersion were the same in Control,
250 oUVF and mUVF for Water, Gut and Skin samples (**Supplementary Table S6**).

251

252 *Microbial taxonomic composition and co-occurrence network*

253 Bacterial community composition of Water, Gut and Skin had almost the same taxonomic
254 pattern with three major phyla, but relative abundance was specific to each environment or
255 tissue (**Figure 2**): the water microbiota was dominated by *Proteobacteria* (54%), *Bacteriodota*
256 (18%) and *Verrucomicrobiota* (14%); the gut was dominated by *Proteobacteria* (63%),
257 *Planctomycetota* (12%) and *Verrucomicrobiota* (7%); and the skin microbial community by
258 *Proteobacteria* (62%), *Bacteriodota* (24%) and *Verrucomicrobiota* (5%). The *Proteobacteria*
259 phylum was composed of two classes: *Alphaproteobacteria* and *Gammaproteobacteria* for all
260 sample groups. Bacterial community composition at the phylum level was the same between
261 treatments (i.e., control and both UVFs), but the relative abundance of each phylum was
262 different. For example, for Gut, *Fusobacteriota* was higher for the mUVF condition or,
263 conversely, *Bacteroidota*, was prevalent in the oUVF treatment for Gut, Skin, and Water.

264

265 To determine the core microbiota (i.e., microbial taxa shared among multiple samples from a
266 particular tissue), we identified core taxa for each treatment by tissue with a combined approach
267 (Neu et al., 2021) with an occurrence of 90% and a relative abundance (> 0.1%). Then, we
268 compared and identified the core taxa with a Venn diagram (**Figure 3**). The core microbiota
269 included six and seven ASVs for Gut and Skin, respectively. The taxonomic composition of
270 each core microbiota was identified at the phylum and family or genus levels (**Figure 3**). The
271 core microbiota of Gut was composed of three families or genera (in brackets in **Figure 3**). The
272 core microbiota of Skin was more diverse, with four families or six genera. The core microbiota
273 of each fish tissues appeared to be specific, indeed no ASVs was shared between the gut and

274 skin core microbiota. We identified some of these ASVs present in all Water samples; only one
275 (*Rhodobacteraceae*) in the core microbiota of Gut and four (Clade Ia, *Glaciacola*,
276 *Neptuniibacter*, *Roseibacillus*) in the core microbiota of Skin.

277 Venn diagrams revealed ASVs common to treatments (oUVF or mUVF). For Gut, 10 microbial
278 taxa were shared between the two treatments (1 *Actinobacteriota*, 4 *Alphaproteobacteria*, 1
279 *Gammaproteobacteria*, 3 *Planctomycetota* and 1 *Verrucomicrobiota*) whereas for Skin none.
280 Finally, Venn diagrams also exposed ASVs specific to each UVFs treatment by tissue
281 (**Supplementary Table S7**). We could observe different genus specific to oUVF or mUVF for
282 Gut and Skin. The family *Rhodobacteraceae* seems to be present in both tissues or treatments
283 but in fact it is different ASVs.

284

285 Co-occurrence network analysis using SPIEC-EASI was carried out to explore Gut and Skin
286 microbial interactions. Overall topological features of Gut and Skin networks were performed
287 (**Supplementary Table S8**). They were both relatively poorly dense (0.02), showed
288 comparable clustering coefficients (0.08 and 0.06) and mean path distance (2.9 and 2.72). The
289 numbers of nodes and edges (i.e., links between each pair of nodes) were different, with 566
290 nodes and 3472 edges for the Gut and more 792 nodes and 6818 edges for the Skin network,
291 suggesting that bacterial interactions could be more numerous in Skin microbial community
292 than in the Gut (**Figure 4**). The Network community algorithm (Louvain) showed that the Gut
293 network could be divided into 11 modules (i.e., a group of ASVs nodes that were interconnected
294 more frequently among themselves than with nodes in other modules), while the Skin network
295 could be divided into 13 modules (**Figure 4**). However, four modules from the Gut network
296 accounted for 52 % (module 1, 2, 9 and 10) and also four modules from the Skin network
297 accounted for 48 % (module 4, 5, 7 and 10). The size of the modules ranged from 26 to 95
298 nodes for the Gut and from 30 to 103 nodes for the Skin network. The taxonomic compositions

299 of the modules for both networks were investigated and represented in a heat map (**Figure 4**).
300 For the Gut network, 14 phyla or classes were observed: five of them were represented inside
301 each of the 11 modules (*Alphaproteobacteria*, *Bacteroidota*, *Gammaproteobacteria*,
302 *Planctomycetota*, and *Verrucomicrobiota*) but three of them were presented in only one module
303 (*Campilobacterota* (M11), *Dependentia* (M9), and *Myxococcota* (M9)). For the Skin network,
304 15 phyla/classes were observed and four phyla were inside each module (*Alphaproteobacteria*,
305 *Bacteroidota*, *Gammaproteobacteria* and *Planctomycetota*).

306

307 *Differential abundance analyses of bacterial communities*

308 For the Gut bacterial community analysis, we used one dataset between oUVF *versus* mUVF,
309 the only significant comparison (see the bacterial diversity analysis above). A differential
310 abundance analysis at the genus level showed that 34 ASVs were significantly different
311 between oUVF and mUVF samples but only 15 were affiliated at the genus level and
312 represented in **Figure 5**. The Log₂ Fold Change is the effect size estimate: Log₂ Fold Change >
313 0 shows how much the genus abundance seems to be different due to oUVF in comparison to
314 mUVF, and inversely. These differential abundances were mainly related to various genera
315 whereas mUVF different were related to 3 genera (*Paraoerskovia*, *Propionigenium* and
316 *Thaumasiovibrio*).

317 For Skin bacterial communities analyses, we performed three different comparisons (oUVF
318 *versus* mUVF, mUVF *versus* Control and oUVF *versus* Control) (**Figure 6**). A differential
319 abundance analysis at the genus level showed that 89 ASVs were significantly different
320 between oUVF and mUVF samples, 77 ASVs significant between mUVF and Control samples
321 and 28 AVSs significant between oUVF and Control samples. Remarkably, some genus showed
322 differential abundances in both tissue for oUVF: *Lewinella*, *Maribacter* and *Rubritalea* and for
323 mUVF: *Thaumasiovibrio*. For the mUVF treatment, almost all ASVs significantly found in

324 analysis against oUVF were also significant against Control samples (**Figure 6**). For oUVF, ten
325 ASVs were found significant for both analyses against mUVF and Control (*Bdellovibrio*,
326 *Cohaesibacter*, *Leucothrix*, *Lewinella*, *Pseudofulvibacter*, *Pseudohongiella*, *Rubritalea*,
327 *Tenacibaculum*, *Tropicibacter*, *Yoonia-Loktanella*). For Control samples, only two ASVs were
328 observed significant for both analyses (against oUVF and mUVF): *Malaciobacter* and
329 *Terasakiella* (**Figure 6**).

330

331 **DISCUSSION**

332 **Mullets - associated microbiota**

333 In this study, we show that mullet harbored bacterial communities distinct from their
334 surrounding environment and according to the tissue considered (gut or skin), suggesting
335 specific microbiota. Our results reveal a gut microbiota with a taxonomic composition
336 dominated by *Proteobacteria* and a core microbiota composed by *Proteobacteria* (*Alpha*- and
337 *Gammaproteobacteria*) and *Actinobacteriota*. These finding are consistent with a recent
338 publication with the same method (metabarcoding of the V3-V4 region of 16S rRNA using
339 Illumina technology) on gut microbiota in wild thick-lipped grey mullets (*Chelon labrosus*),
340 caught near Malaga (Spain) that also detected no statistical differences among anterior and
341 posterior section of intestinal sections (García-Márquez et al., 2022). Their analyses revealed a
342 taxonomic composition dominated by the phylum *Proteobacteria* (> 81%) with a huge part of
343 *Gammaproteobacteria*. A previous study, evaluated the structure and taxonomical composition
344 of the gut microbial communities in three cryptic wild flathead grey mullets (*Mugil cephalus*),
345 from adults and juvenile samples, under potential migratory effects, in the Taiwan Strait, using
346 Illumina technology (metabarcoding of the V1-V2 region of 16S rRNA) (Le and Wang, 2020).
347 Despite distinct adult and juvenile structure of gut microbiota, fish still share a core microbiota
348 dominated by *Proteobacteria*, *Firmicutes* and *Actinobacteriota*. Gut microbiota from different

349 grey mullets (*Chelon labrosus*, *C. ramada*, *C. saliens* and *M. cephalus*) in a Western
350 Mediterranean coastal lagoon (Sardinia, Italy) were investigated with a simple PCR approach
351 of the 16S rRNA gene. Intestinal bacterial sequences were identified as *Alpha*-,
352 *Gammaproteobacteria* and *Actinobacteriota*, and the dominant genus was *Pseudomonas* (Floris
353 et al., 2021). All these results from wild mullets reveal the same dominant phylum
354 (*Proteobacteria*) and a specific core gut microbiota despite external factors as pollutant (UV
355 filters), distinct geographical locations or migratory effects suggesting that mullets gut
356 microbiota is more driven by species-specific factor. This is consistent with recent observations
357 in three fish species (the flag cichlid, the pacu and the black piranha) in the Brazilian Amazon
358 basin with a metabarcoding approach targeting the V3-V4 region of the 16S rRNA gene
359 (Sylvain et al., 2020). These authors had shown that the factor “host species” modulated gut
360 microbiota and suggested that intestinal microbiota was more appropriated to study long-term
361 host-microbe interactions (coevolution).

362

363 Skin bacterial communities have not been widely studied compared to gut microbiota despite
364 their direct contact with seawater. The skin microbiota is expected to play roles as a physical
365 barrier, since the mucous layer of the epithelium, is the first line of immune or anti-oxidant
366 defense against pathogens and pollutants (Llewellyn et al., 2014; Merrifield and Rodiles, 2015).
367 The skin bacterial community of fish appear to be affected by dietary, environmental and
368 genetics factors (Merrifield and Rodiles, 2015). Our analyses disclose a skin microbiota with
369 many interactions dominated by *Proteobacteria*, *Bacteriodota* and *Verrucomicrobiota* with a
370 core microbiota composed of seven ASVs from these phyla.

371 A study had characterized gills and skin microbiota of Thinlip mullet (*C. ramada*) co-cultured
372 with Nile tilapia (*Oreochromis niloticus*) in semi-intense pond systems targeting V3-V4 region
373 of 16S rRNA gene using Illumina technique (Elsheshtawy et al., 2021). Their analyses had

374 shown that external microbiota was organ specific (i.e., gill or skin specific) and the skin
375 microbiota of both species was similar (no species specific). The core microbiota of the mullet
376 skin consisted of 14 genera with a higher abundance of *Proteobacteria*. On the contrary, a study
377 of skin microbiota on six species (including *Mugil cephalus*) of Gulf of Mexico provided
378 evidence for host species specific (Larsen et al., 2013). Investigations on three fish from the
379 Brazilian Amazon basin (Sylvain et al., 2020) showed that the skin mucus microbiota was
380 mainly associated with environmental physiochemistry and bacterioplankton community
381 structure. These authors suggested that skin microbiota should be used for the development of
382 bacterial biomarkers of environmental status.

383

384 **UV filters exposure**

385 In marine organisms, only scarce studies were available on the significant effects of organic or
386 mineral UV filters on bacteria species. We showed that both dilutions of commercial sunscreen
387 changed the diversity and the taxonomic composition of mullets microbiota, especially the skin
388 one. The organic UV filters used here was predominantly composed by Octocrylene (OC),
389 Ethylhexyl methoxycinnamate (EHMC) and Ethylhexyl Salicylate (ES) (see **Supplementary**
390 **Table S1** for complete list of components). The impact of five organic UV filters (including
391 OC and EHMC) on 27 relevant marine bacteria was investigated (Lozano et al., 2020). EHMC
392 was the most toxic compound affecting five bacteria among *Actinobacteriota* and *Firmicutes*
393 (gram negative and positive bacteria) whereas OC was toxic to one species (*Actinobacteriota*).
394 Effects of organic UV filters on microbiota of aquatic organism was almost unknown despite
395 that environmental factors were recognized to change gut and severely skin microbiota. A study
396 on benzophenone-3 (BP3), another common compound of organic UV filters, showed that
397 exposure on Goldfish (*Carassius auratus*) had significant effects on the gut microbiota (Zhang
398 et al., 2020). The core gut microbiota was composed by four phyla: *Proteobacteria*,

399 *Actinobacteriota*, *Fusobacteria* and *Verrucomicrobiota* but their abundances were changed
400 under BP3 exposure. Indeed, *Proteobacteria* phylum decreased and *Bacteriodota* phylum
401 raised as the *Mycobacterium* genus (*Actinobacteriota*). In this study, organic UV filters
402 exposure increased *Bacteriodota* relative abundance especially *Lewinella*, *Maribacter*,
403 *Pseudofulvibacter*, *Tenacibaculum* genera for both gut and skin microbiota. *Tenacibaculum*
404 genus included many pathogens for multiple marine fish species worldwide but ecological data
405 and naturel reservoir are still unclear (Avendaño-Herrera et al., 2006; Mabrok et al., 2023).
406 Studies on Atlantic salmon (*Salmo salar*), showed that *Tenacibaculum* species dominated the
407 cutaneous skin and ulcer mucus surface of fish (Karlsen et al., 2017) and was perhaps the
408 dominant genus on skin microbiota infected by a parasite copepod (Llewellyn et al., 2017).
409 Experiment with a *Neoparamoeba perusans* (parasite agent), *Tenacibaculum dicentrarchi* had
410 a significantly higher abundance inside amoebic gill disease -affected tissue than unaffected
411 tissues (Slinger et al., 2020).
412 The metabarcoding results showed that among *Actinobacteriota*, the *Nocardia* genus relative
413 abundance raised in gut microbiota and was a specific ASV for the skin one. This genus is
414 known to contain pathogen of fish (Kim et al., 2018) and investigations on response of the
415 Medaka (*Oryzias latipes*) fish gut microbiota to cyanobacteria blooms was an obvious increase
416 in relative abundance of *Nocardia* (Duperron et al., 2019).
417 Furthermore, the *Bdellovibrio* genus was detected only with organic UV filters exposure. These
418 bacteria are obligate bacterial predators of other gram-negative bacteria, widespread in marine
419 environment but characterized by low abundances except in polluted areas (Ezzedine et al.,
420 2022). Despite, an obvious potential as probiotic for aquaculture industry, few research were
421 conducted on fish microbiota (Bonfiglio et al., 2020). A recent study, investigated the effects
422 of introducing *Bdellovibrio* into the water of Goldfish (*Carassius auratus*) tanks and showed

423 an improvement of the survival rates and change of the bacterial distribution of gill microbiota
424 (Zhang et al., 2023).

425 The mineral UV filter used in this study was mainly composed by Titanium Dioxide (TiO₂).
426 TiO₂ nanoparticles are commonly used in human cosmetics industry as sunscreens and are one
427 of the main food additives (Egerton and Tooley, 2012). Food TiO₂ exposure is recognized as
428 safe for Human but concern about its genotoxicity begin to raise since observations of variation
429 in specific phyla and genera abundances were made in gut microbiota of rodent models
430 (Rinninella et al., 2021). In sunscreens, TiO₂ is used as physical sun blockers to protect human
431 skin and *a priori* considered safe but its impact on aquatic environment is not so clear (Sharma
432 et al., 2019). Studies on TiO₂ exposure using Zebrafish (*Danio rerio*) as model showed that
433 infected gills had an increase of bacterial load (Huang et al., 2021) and with a chronic co-
434 exposure to bisphenol A the composition of the gut microbiota shifted (Chen et al., 2018). Both
435 studies suggested that titanium dioxide exposure perturbs the dynamic of fish microbiota and
436 could have toxicological implications for host health. Another study on juvenile hybrid grouper
437 revealed modifications of the diversity and composition of the intestinal microbiota, with an
438 increased of the relative abundance of *Actinobacteriota* and *Bacteriodota*, after 14 days of nano-
439 TiO₂ exposure (Duan et al., 2023).

440 In the present study, mineral UV filters exposure altered relative abundances of bacterial lineage
441 of both gut and skin microbiota as the *Thaumasiovibrio* (*Gammaproteobacteria*) genus. Other
442 *Gammaproteobacteria* genera (*Glaciacola*, *Nepttuniibacter*, *Vibrio*) seem specific or important
443 under mineral UVF exposure.

444 *Thaumasiovibrio* is a novel genus within the family *Vibrionaceae* isolated from the reef
445 seawater off Ishigaki, Japan (Amin et al., 2017) and has not yet been reported to associated fish
446 microbiota. Instead of *Vibrio* spp. that are well-known as serious opportunistic pathogens of
447 fish (Colwell and Grimes, 1984), and reported to change skin microbiota of European Seabass

448 (Cámara-Ruiz et al., 2021). Other bacteria seem specific to the gut microbiota as
449 *Mycobacterium* (*Actinobacteriota*), a genus known as pathogens of fish (Kim et al., 2018). The
450 increase of abundance of this genus was also induced by BP3 exposure on the gut microbiota
451 of Goldfish (Zhang et al., 2020) and by cyanobacterial bloom on the gut microbiota of Medaka
452 (Duperron et al., 2019).

453

454 **CONCLUSIONS**

455 For the first time, the present study detailed an important shift in the bacterial composition of
456 gut and skin microbiota induced by commercial sunscreens exposure. Indeed, the relative
457 abundances of *Bacteroidota*, *Actinobacteroidota* or *Proteobacteria* phylum were deeply
458 modified. Additionally, proliferation of some genera as *Mycobacterium*, *Tenacibaculum*,
459 *Nocardia* were observed in the skin microbiota. Thus, sunscreens could potentially disturb the
460 first biological barrier against bacterial infections, the skin microbiota, allowing opportunistic
461 pathogens bacteria to colonize the mucous layer of the fish epithelium. These results bring
462 information for study on marine pollutant as the sunscreen products and open news perspectives
463 as the use of skin mucus microbiota seem better suitable rather than the gut microbiota.

464

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476

477 **Declaration of competing interests**

478 The authors declare no competing interests.

479

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672 **Figures**

673 **Figure 1**

674 NMDS-plot based on Bray-Curtis distances illustrating the similarities and differences in the
675 composition of bacterial communities from the three treatments of the gut microbiota (**A**) and
676 of the skin microbiota (**B**).

677 **Figure 2**

678 Bacterial community composition at the phylum of Water and two subsamples (Gut and Skin)
679 of *Chelon* sp. for each treatment (Control, mineral UVF and organic UVF). Relative abundance
680 is represented in terms of percentage of the total effective bacterial sequences per sample.

681 **Figure 3**

682 Venn diagrams between the three treatments (Control, mineral UVF and organic UVF) for the
683 Gut samples (**A**) and Skin samples (**B**). Only ASVs with an occurrence of 90% and a relative
684 abundance > 0.1% (relative abundance of total reads) were used.

685 **Figure 4**

686 Network analysis showing co-occurrence patterns of bacterial communities among Gut (**A**) and
687 Skin (**B**), respectively. The nodes are colored according to modularity classes. Components of
688 taxonomical diversity in each module of the co-occurrence network are given at the
689 phylum/class level.

690 **Figure 5**

691 Differentially abundant features of Gut samples between two treatments. Analysis was
692 performed for organic UVF versus mineral UVF samples. Each circles represents an ASV at
693 the genus level and each color a phylum. Log2FoldChange indicates an under or overabundance
694 (Log2FoldChange < 0 or > 0) of the specified ASVs.

695 **Figure 6**

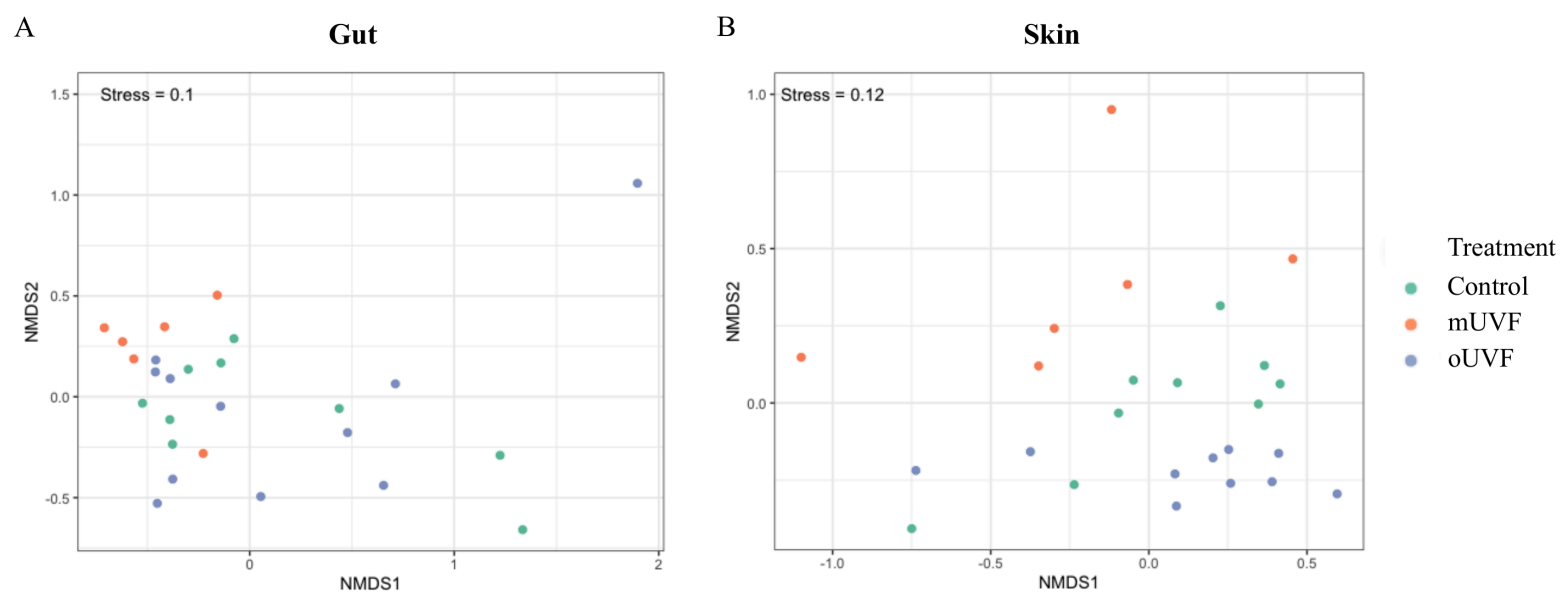
696 Differentially abundant features of Skin samples between three treatments (Control, mineral
697 UVF and organic UVF). Each circles represents an ASV at the genus level and each color a
698 phylum. Log2FoldChange indicates an under or overabundance (Log2FoldChange < 0 or > 0)
699 of the specified ASVs.

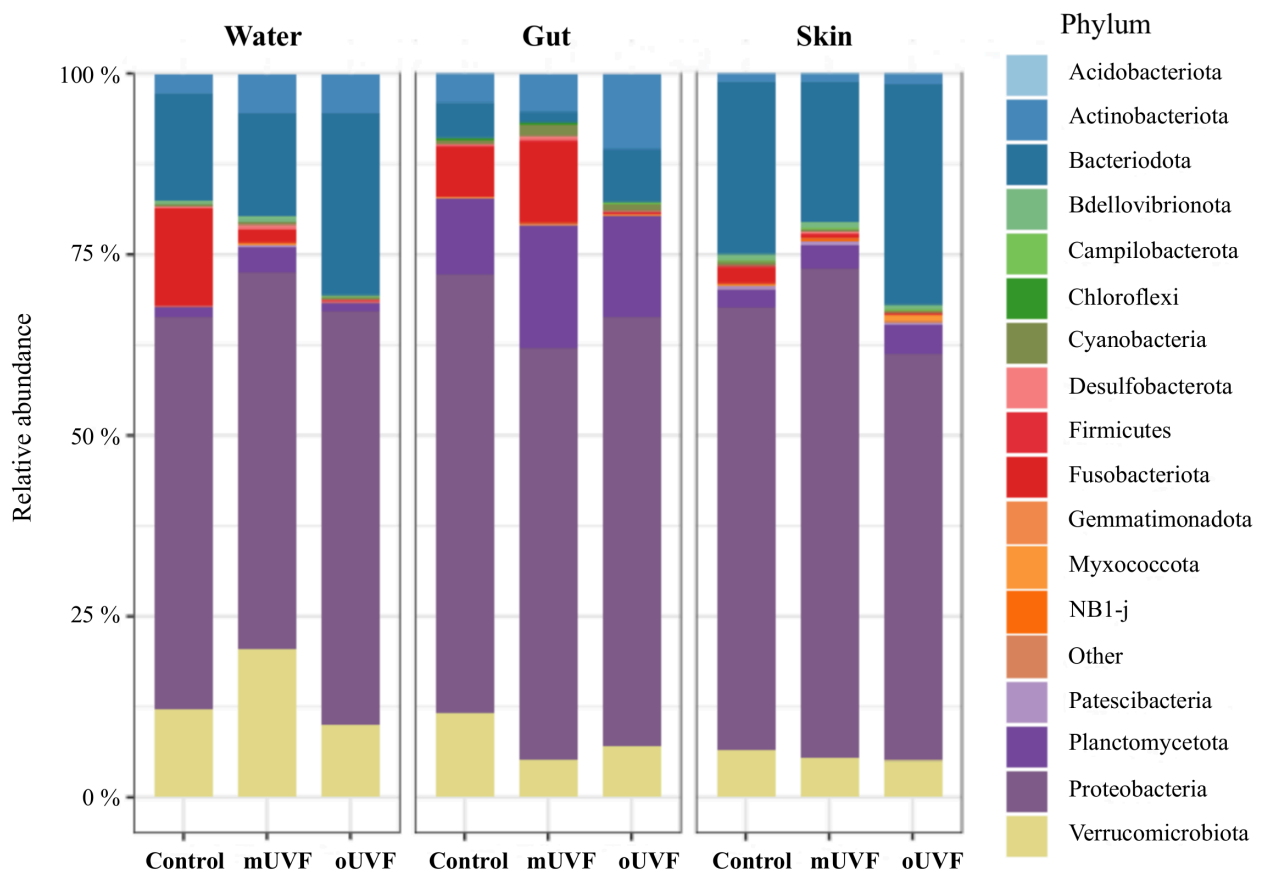
Declaration of interests

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

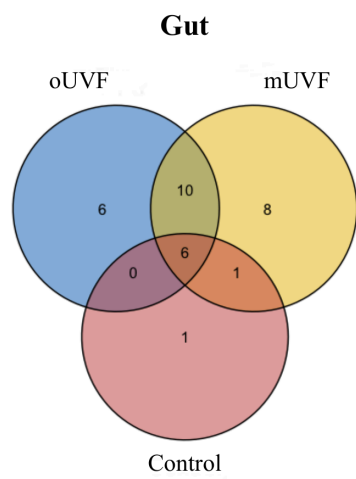
The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Christel Lefrancois reports financial support was provided by French National Research Agency. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



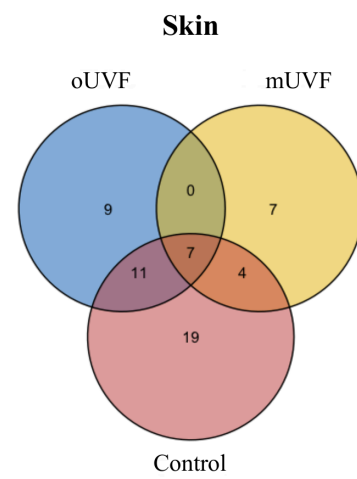


A

**Core:**

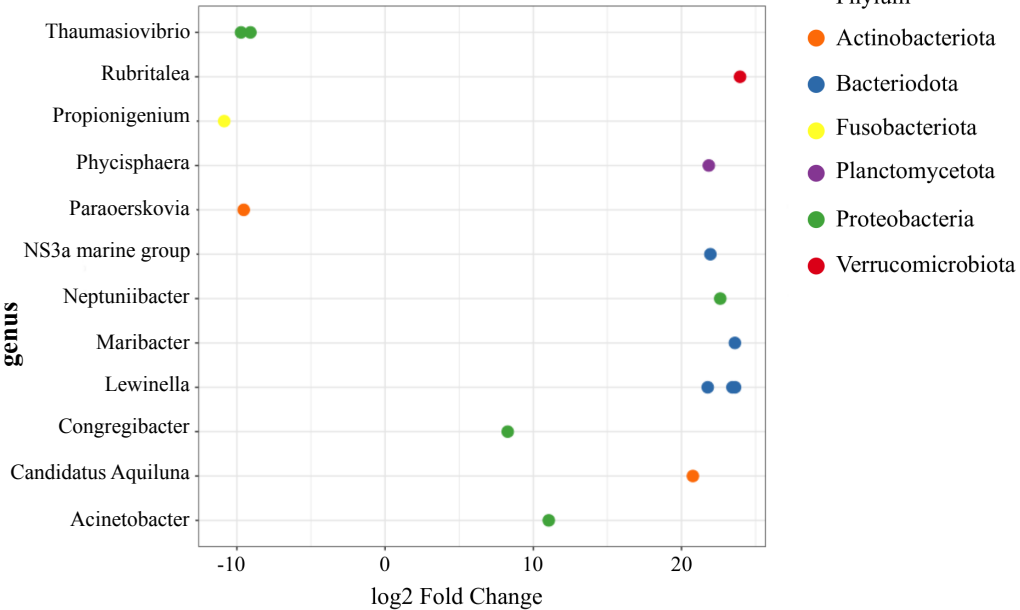
- 1 *Actinobacteriota* (*Nocardia*)
- 4 *Alphaproteobacteria* (*Rhodobacteraceae*)
- 1 *Gammaproteobacteria* (*Vibrio*)

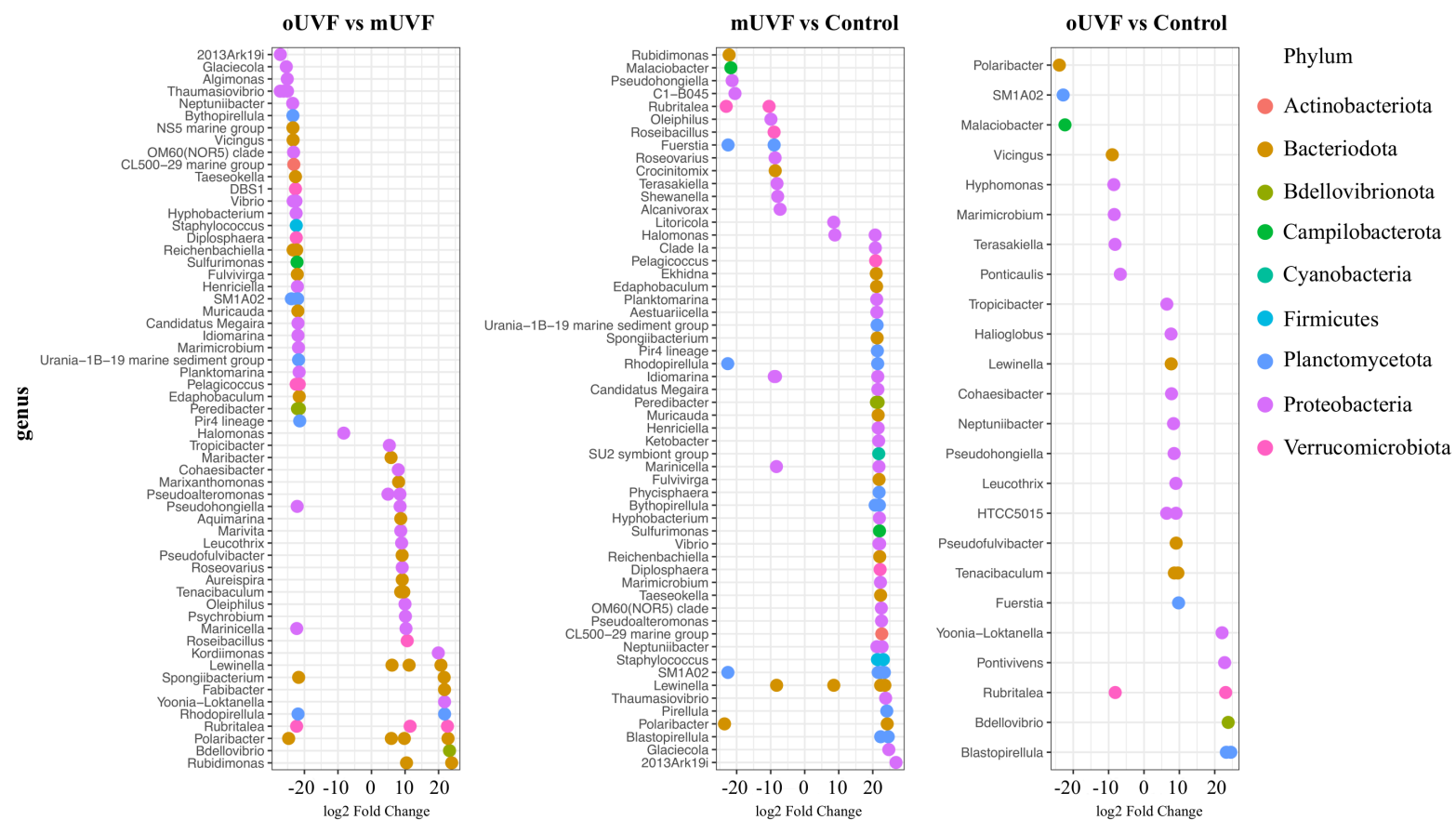
B

**Core:**

- 1 *Alphaproteobacteria* (*Clade Ia*)
- 3 *Bacteroidota* (*Pseudofulvibacter*, *Winogradskyella*)
- 2 *Gammaproteobacteria* (*Glaciecola*, *Neptuniibacter*)
- 1 *Verrucomicrobiota* (*Roseibacillus*)

oUVF vs mUVF





Author Statement

Laure Bellec: formal analysis, writing – review & editing

Thomas Milinkovitch: Resources, methodology

Emmanuel Dubillot: Resources, methodology

Eric Pante: Resources

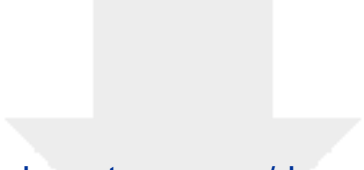
Damien Tran: Resources

Christel Lefrancois: Funding acquisition, project administration

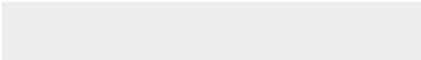



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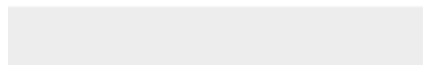


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