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

Bellec Laure [1, *], Milinkovitch Thomas [2], Dubillot Emmanuel [2], Pante Éric [3], Tran Damien [1], Lefrancois Christel [2]

[1] Univ. Bordeaux, CNRS, Bordeaux INP, EPOC, UMR 5805, F-33600 Pessac, France
[2] La Rochelle Univ., CNRS, LIENSs, UMR 7266, F-17000 La Rochelle, France
[3] Bretagne occidentale Univ., CNRS, IRD, Ifremer, IUEM, UMR 6539, F-29280 Plouzané, France

* Corresponding author : Laure Bellec, email address : laure.bellec@u-bordeaux.fr

Abstract :

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

Highlights

► UV filters (organic and mineral) disturbed skin and gut microbiome of grey mullets. ► The skin microbiota was severely modified by UV filters exposure. ► UV filters exposure allowed to pathogens bacteria to colonize the skin mucus of fish. ► The skin microbiota of fish is better suitable for study environmental factor.

Keywords : Sunscreen, microbiota, bacterial shifting, fish, UV filters

INTRODUCTION

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

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

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

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

MATERIALS AND METHODS

Fish maintenance

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

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

Sunscreen exposure media

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

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

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

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

Experimental design

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

Experimental protocol and Sampling

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

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

16S rRNA bacterial diversity analyses

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

Bioinformatics data processing

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

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

Statistical analysis and Visualizations

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

Co-occurrence network analysis

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

Data availability

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

RESULTS

Bacterial diversity analysis

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

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

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

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

Community structure analyses were performed with Beta diversity indexes that allowed a better understood of relationships between bacterial communities. Permutational multivariate analysis of variance (PERMANOVA) analyses indicated significant difference among the two environments (Water and Fish), between both tissue for fish (Gut and Skin), and between treatment (oUVF vs mUVF) for both tissues (**Supplementary Table S6)**. NMDS plots were 2D representation of bacterial communities from Gut or Skin tissue samples (**Figure 1**). The NMDS plot of Gut did not show an obvious separation between treatment samples (**Figure 1A**). However, PERMANOVA analysis indicated significant difference for the pairwise comparison between oUVF and mUVF (**Supplementary Table S6**). The NMDS plot of Skin showed a clear separation between treatment samples (**Figure 1B**), and all pairwise comparison analyses (i.e., Control vs oUVF; Control vs mUVF; oUVF vs mUVF) were significant suggesting that the factor 'treatment' could explain 30% of the total bacterial variation in skin (**Supplementary Table S6**). PERMANOVA analyse for Water samples indicated significant difference but not for all pairwise comparison (Supplementary Table S6). Analyses of the Beta dispersion (i.e.,

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

Microbial taxonomic composition and co-occurrence network

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

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

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

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

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

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

Differential abundance analyses of bacterial communities

For the Gut bacterial community analysis, we used one dataset between oUVF *versus* mUVF, the only significant comparison (see the bacterial diversity analysis above). A differential abundance analysis at the genus level showed that 34 ASVs were significantly different between oUVF and mUVF samples but only 15 were affiliated at the genus level and represented in **Figure 5.** The Log_2 Fold Change is the effect size estimate: Log_2 Fold Change > 0 shows how much the genus abundance seems to be different due to oUVF in comparison to mUVF, and inversely. These differential abundances were mainly related to various genera whereas mUVF different were related to 3 genera (*Paraoerskovia, Propionigenium* and *Thaumasiovibrio*).

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

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

DISCUSSION

Mullets - associated microbiota

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

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

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

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

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

UV filters exposure

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

Actinobacteriota, *Fusobacteria* and *Verrumicomicrobiota* but their abundances were changed under BP3 exposure. Indeed, *Proteobacteria* phylum decreased and *Bacteriodota* phylum raised as the *Mycobacterium* genus (*Actinobacteriota*). In this study, organic UV filters exposure increased *Bacteriodota* relative abundance especially *Lewinella*, *Maribacter*, *Pseudofulvibacter*, *Tenacibaculum* genera for both gut and skin microbiota. *Tenacibaculum* genus included many pathogens for multiple marine fish species worldwide but ecological data and naturel reservoir are still unclear (Avendaño-Herrera et al., 2006; Mabrok et al., 2023). Studies on Atlantic salmon (*Salmo salar*), showed that *Tenacibaculum* species dominated the cutaneous skin and ulcer mucus surface of fish (Karlsen et al., 2017) and was perhaps the dominant genus on skin microbiota infected by a parasite copepod (Llewellyn et al., 2017). Experiment with a *Neoparamoeba perusans* (parasite agent), *Tenacibaculum dicentrarchi* had a significantly higher abundance inside amoebic gill disease -affected tissue than unaffected tissues (Slinger et al., 2020).

The metabarcoding results showed that among *Actinobacteriota*, the *Nocardia* genus relative abundance raised in gut microbiota and was a specific ASV for the skin one. This genus is known to contain pathogen of fish (Kim et al., 2018) and investigations on response of the Medaka (*Oryzias latipes*) fish gut microbiota to cyanobacteria blooms was an obvious increase in relative abundance of *Nocardia* (Duperron et al., 2019).

Furthermore, the *Bdellovibrio* genus was detected only with organic UV filters exposure. These bacteria are obligate bacterial predators of other gram-negative bacteria, widespread in marine environment but characterized by low abundances except in polluted areas (Ezzedine et al., 2022). Despite, an obvious potential as probiotic for aquaculture industry, few research were conducted on fish microbiota (Bonfiglio et al., 2020). A recent study, investigated the effects of introducing *Bdellovibrio* into the water of Goldfish (*Carassius auratus*) tanks and showed

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

The mineral UV filter used in this study was mainly composed by Titanium Dioxide (TiO_2). TiO_2 nanoparticles are commonly used in human cosmetics industry as sunscreens and are one of the main food additives (Egerton and Tooley, 2012). Food TiO_2 exposure is recognized as safe for Human but concern about its genotoxicity begin to raise since observations of variation in specific phyla and genera abundances were made in gut microbiota of rodent models (Rinninella et al., 2021). In sunscreens, TiO_2 is used as physical sun blockers to protect human skin and *a priori* considered safe but its impact on aquatic environment is not so clear (Sharma et al., 2019). Studies on TiO_2 exposure using Zebrafish (*Danio rerio*) as model showed that infected gills had an increase of bacterial load (Huang et al., 2021) and with a chronic co-exposure to bisphenol A the composition of the gut microbiota shifted (Chen et al., 2018). Both studies suggested that titanium dioxide exposure perturbs the dynamic of fish microbiota and could have toxicological implications for host health. Another study on juvenile hybrid grouper revealed modifications of the diversity and composition of the intestinal microbiota, with an increased of the relative abundance of *Actinobacteriota* and *Bacteriodota*, after 14 days of nano-TiO_2 exposure (Duan et al., 2023).

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

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

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

CONCLUSIONS

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

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Declaration of competing interests

The authors declare no competing interests.

References

Amin, A.R., Tanaka, M., Al-Saari, N., Feng, G., Mino, S., Ogura, Y., Hayashi, T., Meirelles, P.M., Thompson, F.L., Gomez-Gil, B., 2017. Thaumasiovibrio occultus gen. nov. sp. nov. and Thaumasiovibrio subtropicus sp. nov. within the family Vibrionaceae, isolated from coral reef seawater off Ishigaki Island, Japan. Systematic and applied microbiology 40, 290–296.

Avendaño-Herrera, R., Toranzo, A.E., Magariños, B., 2006. Tenacibaculosis infection in marine fish caused by Tenacibaculum maritimum: a review. Diseases of aquatic organisms 71, 255–266.

Bonfiglio, G., Neroni, B., Radocchia, G., Marazzato, M., Pantanella, F., Schippa, S., 2020. Insight into the Possible Use of the Predator Bdellovibrio bacteriovorus as a Probiotic. Nutrients 12, 2252.

Bratkovics, S., Wirth, E., Sapozhnikova, Y., Pennington, P., Sanger, D., 2015. Baseline monitoring of organic sunscreen compounds along South Carolina's coastal marine environment. Marine Pollution Bulletin 101, 370–377.

Callahan, B.J., McMurdie, P.J., Rosen, M.J., Han, A.W., Johnson, A.J.A., Holmes, S.P., 2016. DADA2: High-resolution sample inference from Illumina amplicon data. Nature Methods 13, 581–583. https://doi.org/10.1038/nmeth.3869

Cámara-Ruiz, M., Cerezo, I.M., Guardiola, F.A., García-Beltrán, J.M., Balebona, M.C., Moriñigo, M.Á., Esteban, M.Á., 2021. Alteration of the Immune Response and the Microbiota of the Skin during a Natural Infection by Vibrio harveyi in European Seabass (Dicentrarchus labrax). Microorganisms 9, 964.

Carve, M., Nugegoda, D., Allinson, G., Shimeta, J., 2021. A systematic review and ecological risk assessment for organic ultraviolet filters in aquatic environments. Environmental Pollution 268, 115894.

Chen, L., Guo, Y., Hu, C., Lam, P.K.S., Lam, J.C.W., Zhou, B., 2018. Dysbiosis of gut microbiota by chronic coexposure to titanium dioxide nanoparticles and bisphenol A: Implications for host health in zebrafish. Environmental Pollution 234, 307–317. https://doi.org/10.1016/j.envpol.2017.11.074

Christen, V., Zucchi, S., Fent, K., 2011. Effects of the UV-filter 2-ethyl-hexyl-4-trimethoxycinnamate (EHMC) on expression of genes involved in hormonal pathways

in fathead minnows (Pimephales promelas) and link to vitellogenin induction and histology. Aquatic toxicology 102, 167–176.

Colwell, R.R., Grimes, D.J., 1984. Vibrio diseases of marine fish populations. Helgoländer Meeresuntersuchungen 37, 265–287. https://doi.org/10.1007/BF01989311

Csardi, G., Nepusz, T., 2006. The igraph software package for complex network research. InterJournal, complex systems 1695, 1–9.

Cuccaro, A., Freitas, R., De Marchi, L., Oliva, M., Pretti, C., 2022. UV-filters in marine environments: a review of research trends, meta-analysis, and ecotoxicological impacts of 4-methylbenzylidene-camphor and benzophenone-3 on marine invertebrate communities. Environmental Science and Pollution Research 1–22.

Davis, N.M., Proctor, D.M., Holmes, S.P., Relman, D.A., Callahan, B.J., 2018. Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data. bioRxiv 221499. https://doi.org/10.1101/221499

Duan, Y., Yang, Y., Zhang, Z., Xing, Y., Li, H., 2023. Toxicity of titanium dioxide nanoparticles on the histology, liver physiological and metabolism, and intestinal microbiota of grouper. Marine Pollution Bulletin 187, 114600.

Duperron, S., Halary, S., Habiballah, M., Gallet, A., Huet, H., Duval, C., Bernard, C., Marie, B., 2019. Response of fish gut microbiota to toxin-containing cyanobacterial extracts: a microcosm study on the medaka (Oryzias latipes). Environmental Science & Technology Letters 6, 341–347.

Egerton, S., Culloty, S., Whooley, J., Stanton, C., Ross, R.P., 2018. The Gut Microbiota of Marine Fish. Front. Microbiol. 9, 873. https://doi.org/10.3389/fmicb.2018.00873

Egerton, T.A., Tooley, I.R., 2012. UV absorption and scattering properties of inorganic-based sunscreens. Int J Cosmet Sci 34, 117–122. https://doi.org/10.1111/j.1468-2494.2011.00689.x

Elsheshtawy, A., Clokie, B.G.J., Albalat, A., Beveridge, A., Hamza, A., Ibrahim, A., MacKenzie, S., 2021. Characterization of external mucosal microbiomes of nile tilapia and grey mullet co-cultured in semi-intensive pond systems. Frontiers in Microbiology 12, 773860.

Ezzedine, J.A., Desdevises, Y., Jacquet, S., 2022. Bdellovibrio and like organisms: current understanding and knowledge gaps of the smallest cellular hunters of the microbial world. Critical Reviews in Microbiology 48, 428–449.

Fadrosh, D.W., Ma, B., Gajer, P., Sengamalay, N., Ott, S., Brotman, R.M., Ravel, J., 2014. An improved dual-indexing approach for multiplexed 16S rRNA gene sequencing on the Illumina MiSeq platform. Microbiome 2, 6. https://doi.org/10.1186/2049-2618-2-6

Floris, R., Sanna, G., Mura, L., Fiori, M., Culurgioni, J., Diciotti, R., Rizzo, C., Lo Giudice, A., Laganà, P., Fois, N., 2021. Isolation and identification of bacteria with surface and antibacterial activity from the gut of Mediterranean grey mullets. Microorganisms 9, 2555.

García-Márquez, J., Cerezo, I.M., Figueroa, F.L., Abdala-Díaz, R.T., Arijo, S., 2022. First evaluation of associated gut microbiota in wild thick-lipped grey mullets (chelon labrosus, risso 1827). Fishes 7, 209.

Grimmelpont, M., Lefrançois, C., Panisset, Y., Jourdon, G., Receveur, J., Le Floch, S., Boudenne, J.-L., Labille, J., Milinkovitch, T., 2023. Avoidance behaviour and toxicological impact of sunscreens in the teleost Chelon auratus. Marine Pollution Bulletin 194, 115245.

Huang, C.-Y., Yu, W.-S., Liu, G.-C., Hung, S.-C., Chang, J.-H., Chang, J.-C., Cheng, C.-L., Sun, D.-S., Lin, M.-D., Lin, W.-Y., 2021. Opportunistic gill infection is associated with TiO2 nanoparticle-induced mortality in zebrafish. PloS One 16, e0247859.

Karlsen, C., Ottem, K., Brevik, Ø.J., Davey, M., Sørum, H., Winther-Larsen, H., 2017. The environmental and host-associated bacterial microbiota of Arctic seawater-farmed Atlantic salmon with ulcerative disorders. Journal of Fish Diseases 40, 1645–1663.

Kim, B.S., Park, J.W., Kang, G.S., Jin, J.H., Roh, H.J., Kim, D.H., Lee, M.K., Do Huh, M., 2018. First report of nocardia infection in cultured Japanese eel, Anguilla japonica. Journal of fish diseases 41, 1921–1927.

Klindworth, A., Pruesse, E., Schweer, T., Peplies, J., Quast, C., Horn, M., Glöckner, F.O., 2013. Evaluation of general 16S ribosomal RNA gene PCR primers for classical and next-generation sequencing-based diversity studies. Nucleic Acids Res 41, e1–e1. https://doi.org/10.1093/nar/gks808

Kurtz, Z.D., Müller, C.L., Miraldi, E.R., Littman, D.R., Blaser, M.J., Bonneau, R.A., 2015. Sparse and Compositionally Robust Inference of Microbial Ecological Networks. PLOS Computational Biology 11, 1–25. https://doi.org/10.1371/journal.pcbi.1004226

Labille, J., Slomberg, D., Catalano, R., Robert, S., Apers-Tremelo, M.-L., Boudenne, J.-L., Manasfi, T., Radakovitch, O., 2020. Assessing UV filter inputs into beach waters during recreational activity: A field study of three French Mediterranean beaches from consumer survey to water analysis. Science of the Total Environment 706, 136010.

Laffaille, P., Brosse, S., Feunteun, E., Baisez, A., Lefeuvre, J.-C., 1998. Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel Bay, in: Amiard, J.-C., Le Rouzic, B., Berthet, B., Bertru, G. (Eds.), Oceans, Rivers and Lakes: Energy and Substance Transfers at Interfaces, Developments in Hydrobiology. Springer Netherlands, Dordrecht, pp. 121–133. https://doi.org/10.1007/978-94-011-5266-2_10

Larsen, A., Tao, Z., Bullard, S.A., Arias, C.R., 2013. Diversity of the skin microbiota of fishes: evidence for host species specificity. FEMS microbiology ecology 85, 483–494.

Layeghifard, M., Hwang, D.M., Guttman, D.S., 2017. Disentangling interactions in the microbiome: a network perspective. Trends in microbiology 25, 217–228.

Le, M.H., Wang, D., 2020. Structure and membership of gut microbial communities in multiple fish cryptic species under potential migratory effects. Scientific reports 10, 7547.

Lebreton, B., Richard, P., Parlier, E.P., Guillou, G., Blanchard, G.F., 2011. Trophic ecology of mullets during their spring migration in a European saltmarsh: A stable isotope study. Estuarine, Coastal and Shelf Science 91, 502–510. https://doi.org/10.1016/j.ecss.2010.12.001

Llewellyn, M., Leadbeater, S., Garcia, C., Sylvain, F.-E., Custodio, M., Ang, K., Powell, F., Carvalho, G., Creer, S., Elliot, J., 2017. Parasitism perturbs the mucosal microbiome of Atlantic Salmon. Scientific reports 7, 43465.

Llewellyn, M.S., Boutin, S., Hoseinifar, S.H., Derome, N., 2014. Teleost microbiomes: the state of the art in their characterization, manipulation and importance in aquaculture and fisheries. Front. Microbiol. 5. https://doi.org/10.3389/fmicb.2014.00207

Lozano, C., Matallana-Surget, S., Givens, J., Nouet, S., Arbuckle, L., Lambert, Z., Lebaron, P., 2020. Toxicity of UV filters on marine bacteria: Combined effects with damaging solar radiation. Science of the Total Environment 722, 137803.

Mabrok, M., Algammal, A.M., Sivaramasamy, E., Hetta, H.F., Atwah, B., Alghamdi, S., Fawzy, A., Avendaño-Herrera, R., Rodkhum, C., 2023. Tenacibaculosis caused by Tenacibaculum maritimum: Updated knowledge of this marine bacterial fish pathogen. Frontiers in cellular and infection microbiology 12, 1068000.

Martinez Arbizu, P., 2017. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.0 1.

McMurdie, P.J., Holmes, S., 2013. phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. PLOS ONE 8, e61217. https://doi.org/10.1371/journal.pone.0061217

Merrifield, D.L., Rodiles, A., 2015. The fish microbiome and its interactions with mucosal tissues, in: Mucosal Health in Aquaculture. Elsevier, pp. 273–295. https://doi.org/10.1016/B978-0-12-417186-2.00010-8

Neu, A.T., Allen, E.E., Roy, K., 2021. Defining and quantifying the core microbiome: challenges and prospects. Proceedings of the National Academy of Sciences 118, e2104429118.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H., Wagner, H., 2008. The vegan package: community ecology package, version 1.13-1. URL: http://vegan. r-forge. r-project. org.

Oliveros, J.C., 2007. Venny. An interactive tool for comparing lists with Venn's diagrams [WWW Document]. URL https://bioinfogp.cnb.csic.es/tools/venny/index.html

Paredes, E., Pérez, S., Rodil, R., Quintana, J.B., Beiras, R., 2014. Ecotoxicological evaluation of four UV filters using marine organisms from different trophic levels Isochrysis galbana, Mytilus galloprovincialis, Paracentrotus lividus, and Siriella armata. Chemosphere 104, 44–50.

Parks, D.H., Chuvochina, M., Waite, D.W., Rinke, C., Skarshewski, A., Chaumeil, P.-A., Hugenholtz, P., 2018. A standardized bacterial taxonomy based on genome phylogeny substantially revises the tree of life. Nature Biotechnology 36, 996–1004. https://doi.org/10.1038/nbt.4229

Picot-Groz, M., Fenet, H., Martinez Bueno, M.J., Rosain, D., Gomez, E., 2018. Diurnal variations in personal care products in seawater and mussels at three Mediterranean coastal sites. Environmental Science and Pollution Research 25, 9051–9059.

Rinninella, E., Cintoni, M., Raoul, P., Mora, V., Gasbarrini, A., Mele, M.C., 2021. Impact of food additive titanium dioxide on gut microbiota composition, microbiota-associated functions, and gut barrier: a systematic review of in vivo animal studies. International Journal of Environmental Research and Public Health 18, 2008.

Rodríguez, A., Sanz, M., Rodríguez, J., 2015. Chemosphere Occurrence of eight UV filters in beaches of Gran Canaria (Canary Islands). An approach to environmental risk assessment 131, 85–90.

Sharma, S., Sharma, R.K., Gaur, K., Cátala Torres, J.F., Loza-Rosas, S.A., Torres, A., Saxena, M., Julin, M., Tinoco, A.D., 2019. Fueling a hot debate on the application of TiO2 nanoparticles in sunscreen. Materials 12, 2317.

Slinger, J., Adams, M.B., Wynne, J.W., 2020. Bacteriomic profiling of branchial lesions induced by Neoparamoeba perurans challenge reveals commensal dysbiosis and an association with Tenacibaculum dicentrarchi in AGD-affected Atlantic salmon (Salmo salar L.). Microorganisms 8, 1189.

Sylvain, F.-É., Holland, A., Bouslama, S., Audet-Gilbert, É., Lavoie, C., Val, A.L., Derome, N., 2020. Fish skin and gut microbiomes show contrasting signatures of host species and habitat. Applied and environmental microbiology 86, e00789-20.

Tao, J., Bai, C., Chen, Y., Zhou, H., Liu, Y., Shi, Q., Pan, W., Dong, H., Li, L., Xu, H., 2020. Environmental relevant concentrations of benzophenone-3 induced developmental neurotoxicity in zebrafish. Science of the Total Environment 721, 137686.

Tarnecki, A.M., Burgos, F.A., Ray, C.L., Arias, C.R., 2017. Fish intestinal microbiome: diversity and symbiosis unravelled by metagenomics. J Appl Microbiol 123, 2–17. https://doi.org/10.1111/jam.13415

Team, R.C., 2013. R: A language and environment for statistical computing.

Wang, A.R., Ran, C., Ringø, E., Zhou, Z.G., 2018. Progress in fish gastrointestinal microbiota research. Rev Aquacult 10, 626–640. https://doi.org/10.1111/raq.12191

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B., Lotze, H.K., Micheli, F., Palumbi, S.R., 2006. Impacts of biodiversity loss on ocean ecosystem services. science 314, 787–790.

Zhang, P., Lu, G., Liu, J., Yan, Z., Wang, Y., 2020. Toxicological responses of Carassius auratus induced by benzophenone-3 exposure and the association with alteration of gut microbiota. Science of The Total Environment 747, 141255.

Zhang, Y., Zhu, Z., Jiang, Y., Ji, T., Bai, H., Zhao, H., Yang, H., 2023. Addition of Bdellovibrio to aquaculture water can significantly alter the distribution of microbial community on the gills and enhance the survival rate of Carassius auratus gibelio. Aquaculture 739820.

Figures

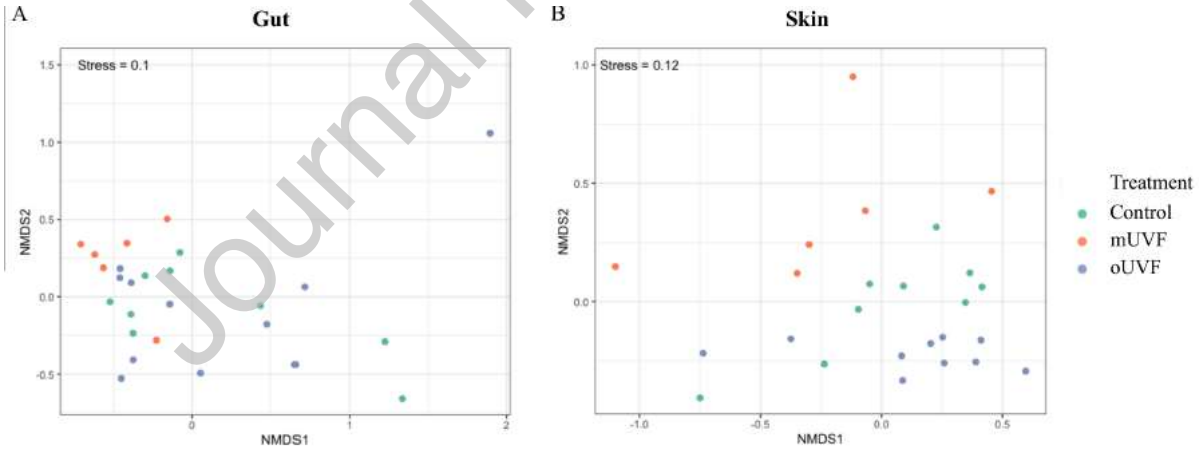

Figure 1

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

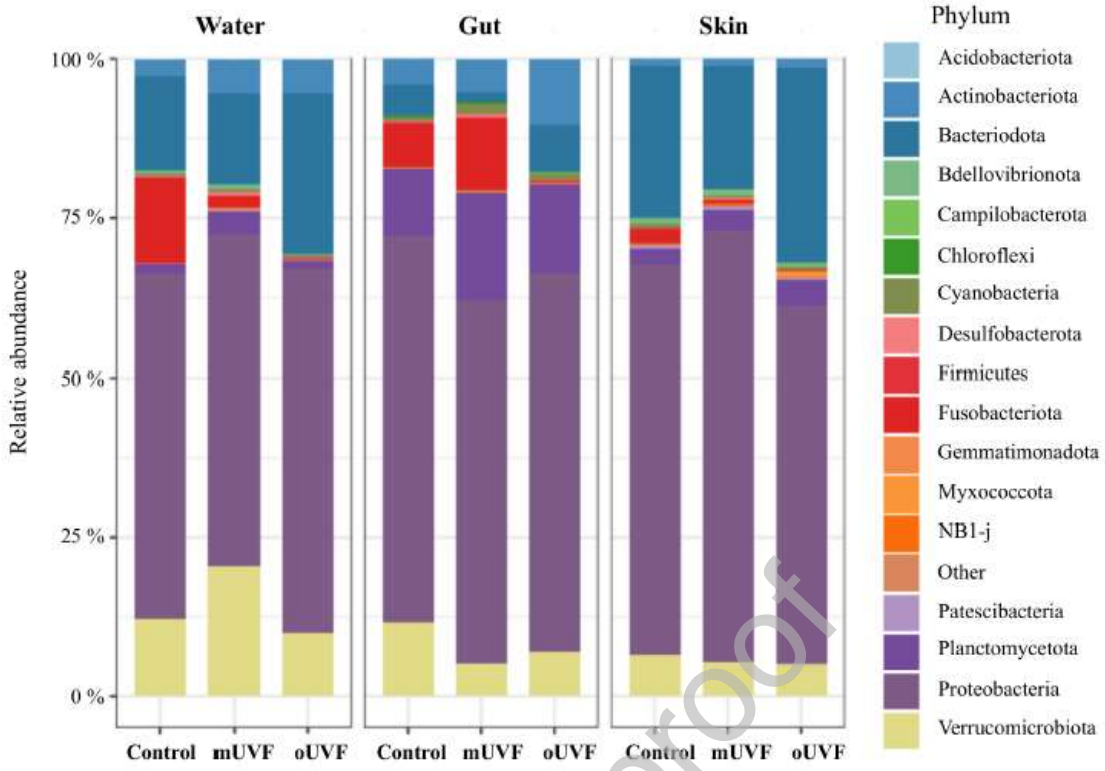

Figure 2

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

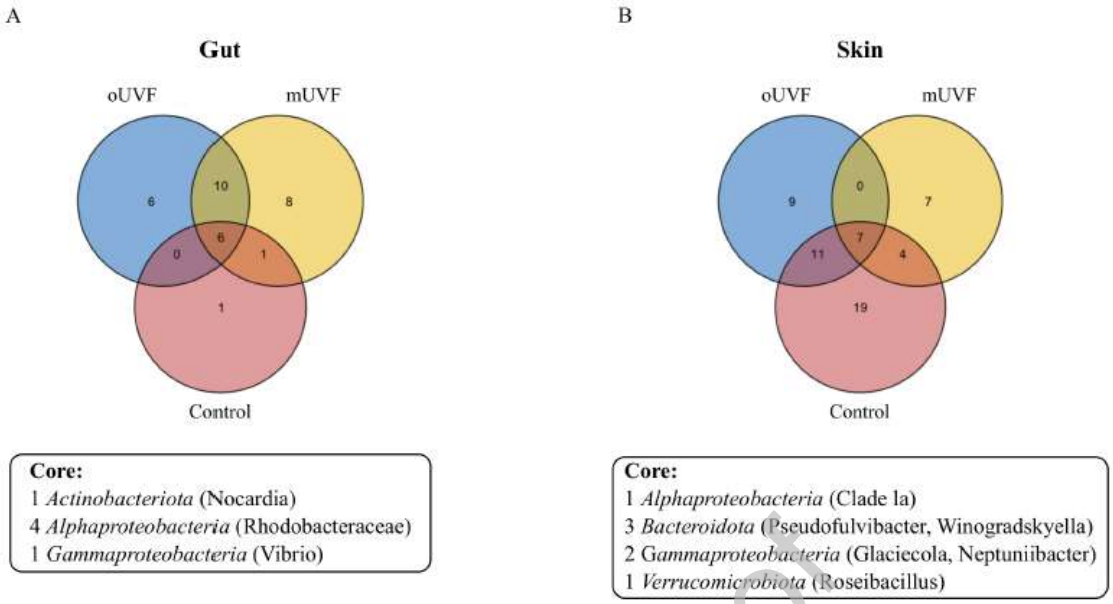

Figure 3

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

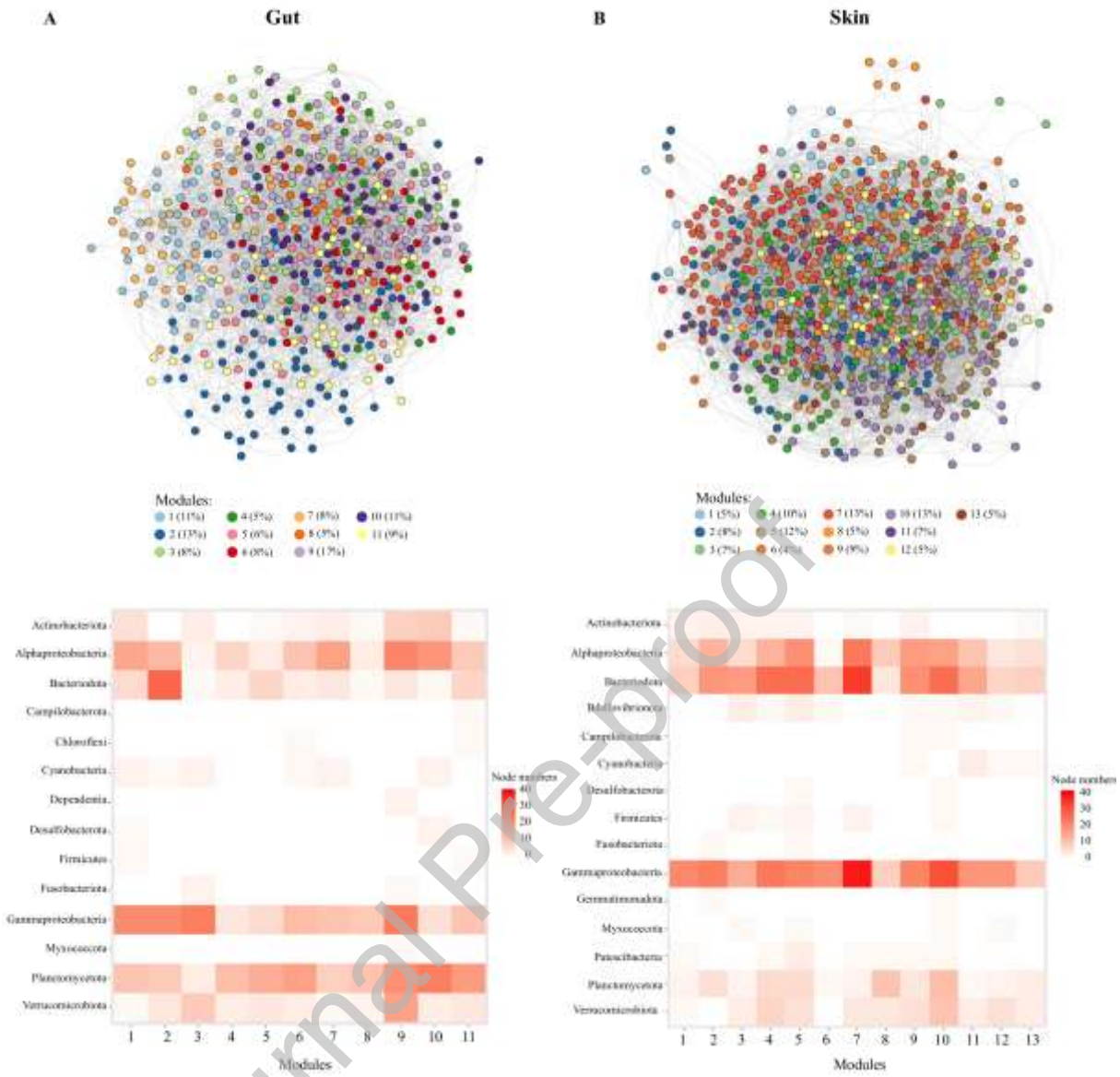

Figure 4

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

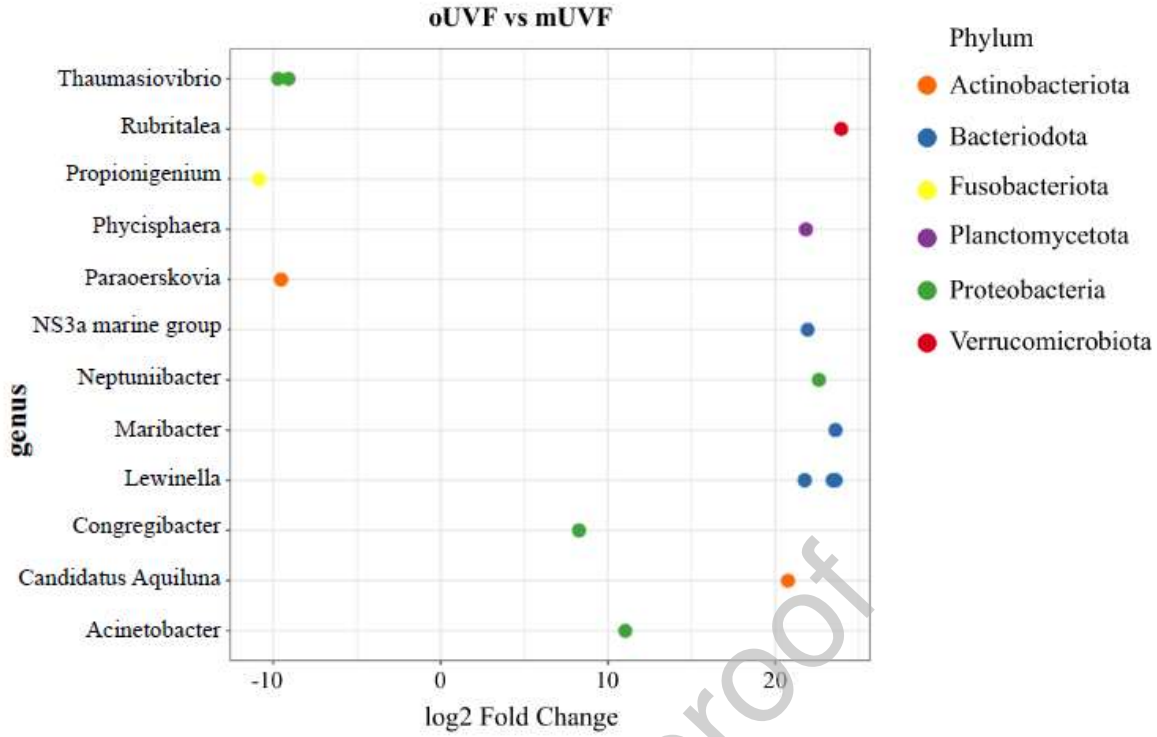

Figure 5

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

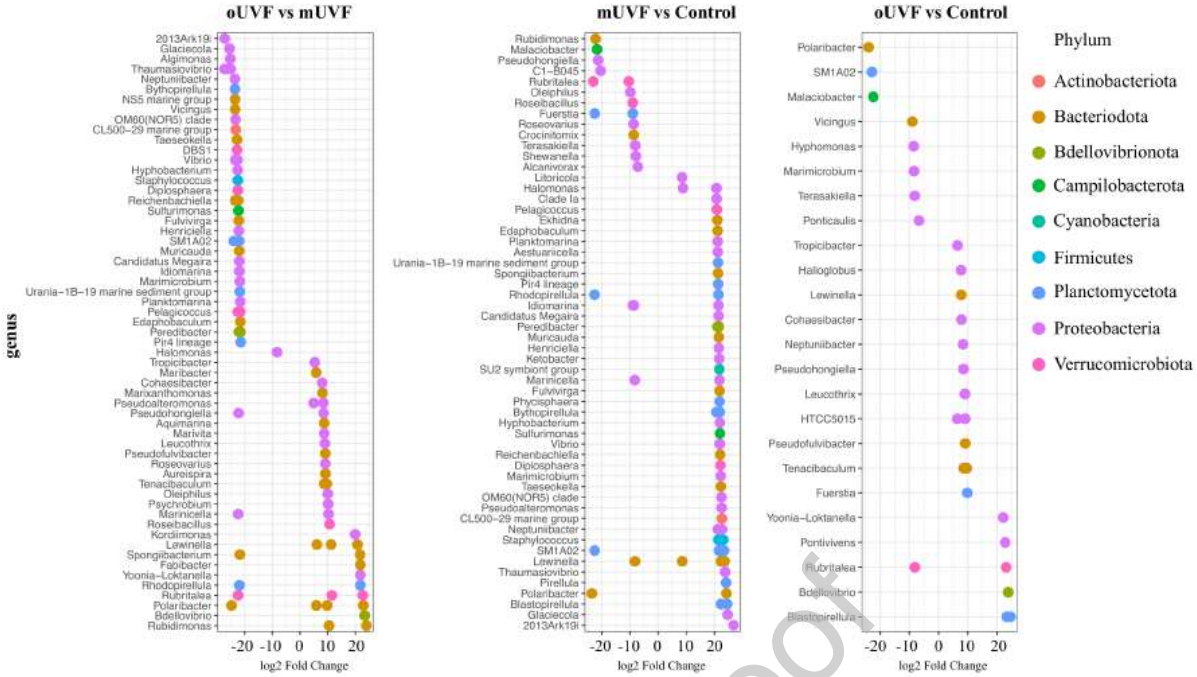

Figure 6

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

Autour 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

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.