Molecular Ecology

SPECIAL ISSUE Evolutionary Genomics: Understanding and Adapting to Climate Change

WILEY

MOLECULAR ECOLOGY

ORIGINAL ARTICLE OPEN ACCESS

Temperature and Ultraviolet Radiation Influence the Skin Microbiome of Humpback Whales

Aída I. Murillo-Herrera[1,2,3] | Luis E. Eguiarte[1] | Eliana Paola Acuña Gómez[2] | Cristina Castro[4] | Jorge Acevedo[2] | Juliana Castrillon[4] | Lautaro Oyarzún-Galaz[2] | Pedro Valenzuela[2] | Anelio Aguayo-Lobo[2,5] | Luis A. Pastene[6] | Valeria Souza[1,2]

[1]Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad de México, México | [2]Centro de Estudios del Cuaternario de Fuego, Patagonia y Antártica (CEQUA), Punta Arenas, Chile | [3]Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Unidad de Posgrado, Ciudad de México, México | [4]Pacific Whale Foundation, Ecuador, Puerto López, Manabí, Ecuador | [5]Departamento Científico, Instituto Antártico Chileno, Punta Arenas, Chile | [6]Institute of Cetacean Research, Tokyo, Japan

Correspondence: Valeria Souza (souza@unam.mx)

Received: 2 December 2025 | **Revised:** 7 July 2026 | **Accepted:** 23 July 2026

Keywords: *Megaptera novaeangliae* | *Psychrobacter* | skin microbiome | *Tenacibaculum* | thermal stress | UVB radiation

ABSTRACT

The skin microbiome of humpback whales harbours diverse microbial communities that play a crucial role in host skin protection and environmental interaction. However, studies on cetacean skin microbiomes in the Southern Hemisphere focus on feeding grounds, with limited information on microbiome dynamics at breeding grounds and during migration across contrasting habitats. We characterised the skin microbiome of 46 humpback whales from two seasonal habitats: the Magellan Strait feeding ground and the Ecuadorian coast breeding ground, comparing age, sex, environmental conditions, and seawater. Amplicon sequencing of the 16S rRNA gene revealed no differences in alpha diversity, but habitat-specific compositional shifts were found. *Psychrobacter* was detected in both regions, with higher abundance in the feeding ground, while *Tenacibaculum* remained abundant across sites. Additional taxa exhibited habitat-specific patterns, including bacteria associated with thermal sensitivity and ultraviolet radiation-tolerance in the Magellan Strait, and lactic acid bacteria in Ecuador. Skin microbiomes were similar between age classes and sexes, but distinct from seawater. Our findings show that geographic and environmental factors, such as superficial seawater temperature and maximum ultraviolet B radiation, shape the skin microbiome of humpback whales, with certain taxa reflecting migratory behaviour across seasonal habitats.

1 | Introduction

The skin of mammals represents a particular ecological niche, colonized by numerous microorganisms that compose their microbiome, and functions as an interface between the host tissues and the environment (Ghosh and Panda 2023; Prescott et al. 2017). Given the potential fast adaptive response of bacteria to environmental change, derived from their short generation times and genetic plasticity, the skin microbiome serves as a bioindicator of environmental perturbation (Karimi et al. 2017). Microbial communities have complex mutualistic and commensal interactions with the host that influence the skin homeostasis. This prevents the colonization and invasion of pathogenic and opportunistic microbes through indirect interspecies interactions—such as competitive exclusion—or by direct mechanisms, including the production of antimicrobial peptides (AMPs), short-chain fatty acids (SCFA), cytokines and other microbial compounds (Ghosh and Panda 2023; Lunjani et al. 2021; Swaney and Kalan 2021), as well as compounds from the host (Nakatsuji et al. 2023).

Understanding how microbial communities are structured and the origin of the skin colonization is relevant. Marine animals are uniquely immersed in waters populated by free-living microorganisms (Apprill 2017), and during migration, they traverse diverse oceanic habitats that harbour distinct bacterial communities (Rusch et al. 2007). For this reason, the microbial colonization of the skin in marine mammals has often been assumed to be strongly influenced by the surrounding seawater. However, several studies have demonstrated that the microbial composition of seawater differs from the skin microbiome (Apprill et al. 2011; Hooper et al. 2019; Robles-Malagamba et al. 2020) and other body parts (Bik et al. 2016).

Among cetaceans, skin microbiomes have shown a species-specific pattern (Chiarello et al. 2017; Toro et al. 2021). This is consistent with family-level differences that correlate with host phylogeny, suggesting a coevolutionary pattern in the assembly of marine mammal microbiomes (Apprill et al. 2020). Similar patterns have been observed in other marine vertebrates, in particular in fish (Minich et al. 2022).

Among marine mammals, skin microbiome studies have been conducted on cetaceans, mainly in humpback whale (*Megaptera novaeangliae*; hereafter referred to as HW), a highly migratory species of baleen whale. In this species, Apprill et al. (2011) were the first to describe the resident bacteria on their skin, and subsequent studies described a core bacterial community of HWs inhabiting the North Pacific and Atlantic Oceans (Apprill et al. 2014) and the culturable diversity (Keller et al. 2021). In the Southern Hemisphere, the skin microbial composition has been reported only in two previous studies, both focused on the eastern South Pacific HWs feeding grounds in high and medium latitudes (Bierlich et al. 2018; Toro et al. 2021; see review in Ochoa-Sánchez et al. 2023).

The eastern South Pacific HW population, also named Breeding Stock G (BSG) by the International Whaling Commission (IWC), inhabits the western coast of South America and breeds from northern Peru (Pacheco et al. 2009) to southern Nicaragua (De Weerdt et al. 2020). This HW population primarily migrates to feed off the western Antarctic Peninsula in the Antarctic IWC management Area I (Acevedo et al. 2017; Mackintosh 1965; Stevick et al. 2004; Stone et al. 1990), the South Orkney Islands (Dalla Rosa et al. 2012) and the South Sandwich Islands (Castro et al. 2023). A fraction of this HW population utilizes as feeding grounds the inland waters of the Magellan Strait, southern Chile, during the austral summer and fall (Acevedo et al. 2006, 2013; Gibbons et al. 2003).

Skin microbiome on HW and other cetacean species can vary according to body site, foraging season, sampling year, and geographic area (Bierlich et al. 2018; Chiarello et al. 2017; Toro et al. 2021; Van Cise et al. 2020). Also, latitudinal differences in northern HWs between feeding and breeding grounds have been identified, with environmental conditions and host metabolic state potentially related (Apprill et al. 2014). Additionally, ecotypes, philopatry behaviour, life history and horizontal transfer through social interaction also seem relevant in shaping skin microbial communities (Hooper et al. 2019).

Despite the notable advances in understanding cetacean skin microbial composition, a significant knowledge gap remains. In particular, the BSG of HW has not been examined in its breeding grounds, limiting our understanding of how the microbiome varies across contrasting habitats that whales occupy during their annual migration. Moreover, little is known about how these microbial patterns are influenced by host intrinsic factors such as age class, sex, and environmental conditions. Addressing these gaps is essential not only for understanding the ecological and physiological drivers of the skin microbiome on humpback whales but also for developing baseline frameworks for future research and conservation strategies.

In this study, we focused on the skin microbial composition and structure of BSG of HWs across two seasonal habitats associated with two migratory destinations in the eastern South Pacific Ocean, the Magellan Strait feeding ground in Chile and the breeding ground on the coasts of Ecuador. Our objectives were to: (1) characterize the microbial diversity and composition of the skin in HWs from the BSG, (2) contrast if microbial patterns are affected by seasonal habitats (feeding and breeding grounds) geographic characteristics, (3) identify local environmental drivers of skin microbial composition along with key taxa associated, (4) assess the influence of host intrinsic factors such as age class (adults and calves) and sex on the skin microbial structure, (5) compare the skin microbiome of HWs with that of the surrounding seawater and to identify a shared core microbiome.

2 | Materials and Methods

2.1 | Study Area

The study area includes two important regions for marine mammals' conservation on the Pacific coasts of South America, where part of the feeding and breeding grounds of HWs of the BSG are located (Figure 1).

2.1.1 | Feeding Ground

Situated in the central-western portion of the Magellan Strait in the Francisco Coloane-Marine Coastal Protected Area (FCMCPA), at 180 km NW from Punta Arenas city (53°43′S, 71°52′W; Figure 1). This protected area of 67,197 ha was created in 2003 to conserve the region's ecosystems and natural habitats, and includes the Francisco Coloane Marine Park of 1500 ha as the core zone, which focuses on preserving a part of the feeding ground for HWs, and other species (Aguayo-Lobo et al. 2011; Ministerio del Medio Ambiente 2018). Here, HWs have a mixed diet that includes subantarctic krill, squat lobsters and Fuegian sprats (Acevedo et al. 2011; Haro et al. 2016).

This feeding ground is characterised by a cold-temperate coastal climate, with annual precipitation ranging from 2000 to 3000 mm and an average air temperature of 6.5°C, along with a summer thermal amplitude of approximately 4.5°C (Comas 1984; Zamora and Santana 1979).

Oceanographically, this area is a highly productive fjord system that forms part of the Patagonian Cold Estuarine System,

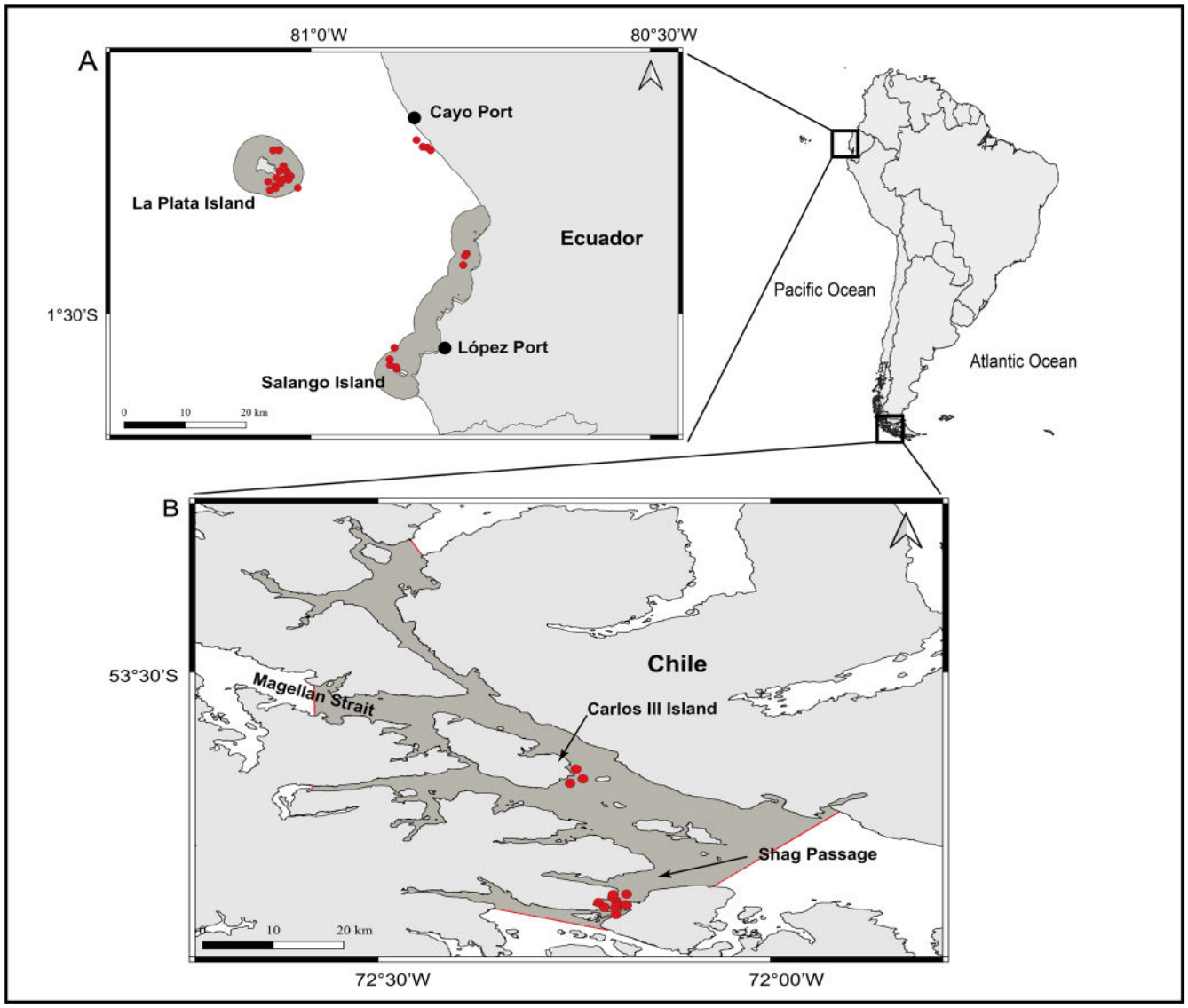

FIGURE 1 | Study area and biopsy sampling locations (red circles) of humpback whales in the Ecuadorian breeding ground (A) and the Magellan Strait feeding ground in Chile (B). The dark grey polygon represents the Marine Protected Area.

which is influenced by multiple cold-water masses that originate from the Pacific, Atlantic and Southern Oceans that converge and are mixed with freshwater inputs from rivers and glaciers (Panella et al. 1991; Valdenegro and Silva 2003). These water masses, with average temperatures of 7.1°C–8.6°C and salinities between 27 and 30 PSU during summer and autumn, are strongly driven by tidal currents and intense winds, leading to complex circulation patterns and localized upwelling (Valle-Levinson et al. 2006).

2.1.2 | Breeding Ground

Located in the southern Manabí province in Ecuador (01°28′ S; 80°46′ W), along the coastal marine strip, between Puerto Cayo and Machalilla National Park (MNP), including Salango and La Plata Islands, on the continental shelf of Ecuador and along the border of the Cantagallo Marine Reserve (Castro et al. 2022). The protected marine area of the MNP expands up to 144.3 km^2, where Puerto López is one of the most important areas in Ecuador for whale-watching since 1980 (Castro et al. 2022). The MNP is characterized by predominantly shallow waters (10–30 m), with a maximum depth of 200 m, where HWs are regularly sighted from mid-May to mid-October, including mother-calf pairs along with competitive groups of males engaged in breeding activities (Scheidat et al. 2000).

The Manabí province has a tropical savanna climate (INOCAR 2015), which is partly influenced by a system of ocean currents of different origins and temperatures that flow through the MNP (Flacher et al. 1997). During the austral winter (June to November), the region is influenced by the eastward-flowing Equatorial countercurrent and the cold Humboldt Current from the south, leading to a strong seasonal oceanographic regime characterized by a pronounced Equatorial Front, with warm waters (19°C–24.5°C) and salinities of 33.5 to 35.0 PSU (Chinacalle-Martínez et al. 2021; Cucalón 1986, 1989; Glynn 2003). Furthermore, the vertical structure of the water column exhibits strong thermohaline gradients between 30 and 50 m depth, beneath a well-defined surface mixed layer (Cucalón 1986, 1989).

TABLE 1 | Sample distribution of humpback whales by seasonal habitat, age class and sex.

Season	Habitat	Location	Age class		Sex		Year	
			Adult	Calf	Female	Male	2022	2023
Austral	Magellan Strait, Chile	Carlos III Island	3	0	2	1	0	3
Summer–Fall		Paso Shag	11	2	5	8	4	9
Austral Winter–Spring	Coasts of Ecuador	Puerto Cayo	6	1	6	1	7	
		La Plata Island	15	3	9	9	8	10
		Salango Island	5	0	3	2	0	5
		Total	40	6	25	21	19	27

2.2 | Humpback Whale Samples

Skin biopsies were collected during 2022 and 2023 in the Magellan Strait feeding ground ($n = 16$) between February and April, and from the Ecuadorian breeding ground ($n = 30$) between August and October. Sampling effort was uneven across years, with fewer samples collected in the Magellan Strait in 2022 (Figure 1; Table 1).

Each sample was subdivided for different purposes, with the outermost epidermal layer preserved specifically for microbiome analyses. A total of 46 biopsy skin samples were obtained from adults and calves, using a non-lethal 7 mm diameter dart tip made of surgical steel (Ceta-dart), targeting the upper flank near the dorsal fin, propelled by a crossbow of 150 and 175 lb., and shot from a small vessel. Biopsies were obtained opportunistically during surveys, depending on whale sightings and were restricted to animals that showed no visible signs of illness. Individual's sex (Table 1) determination was performed by the amplification of the chromosome Y genetic marker (Gilson et al. 1998).

Other complementary metadata associated with each biopsy, including date, geographic location, group size and composition, sea state and photo-identification code, were recorded.

2.3 | Animal Care Considerations

Following the 3R's principle (Replacement, Reduction and Refinement), the number of individuals sampled was minimized by using photo-identification to avoid resampling. The remote sampling method involves a brief and minor intervention with negligible risk of pain, suffering or distress, and was chosen because it is considered minimally invasive, non-lethal, and does not cause permanent tissue damage, as reviewed by Noren and Mocklin (2012) allowing all whales to resume normal behaviour immediately after sampling, with no adverse events recorded.

2.4 | Seawater Samples

Surface seawater associated with sampling areas of HWs ($n = 8$) was collected using a 5 L Niskin bottle, pre-washed with seawater by submersion 1 or 2 times at the sampling site before final samples were taken. Immediately, seawater samples were filtered using a vacuum pump through a polycarbonate membrane filter (Advantec, MFS Inc.) with a pore size of 0.2 μm and a 47 mm diameter.

2.5 | Sample Preservation

Samples collected in Ecuador were immediately stored in 2 mL cryotubes and placed on dry ice aboard the vessel. Within 2–3 h from collection, samples were transferred to a −20°C freezer at the laboratory of the Pacific Whale Foundation.

Samples collected in the Magellan Strait were stored in liquid nitrogen after collection due to the long distances that prevented returning to the city on the same sampling day.

Samples from both study areas were later transferred to an ultralow-temperature freezer at −80°C in the Molecular Genetics Laboratory of CEQUA, Punta Arenas, Chile, until processing.

2.6 | Environmental Conditions

Parameters such as seawater surface temperature (SST, °C), salinity (PSU), dissolved oxygen ($mg\,L^{-1}$), chlorophyll ($mg\,L^{-1}$) and maximum UVA and UVB radiation ($W\,m^{-2}$) were recorded in the Magellan Strait feeding ground immediately after biopsy and/or seawater sampling (Table 2) using a WIMO NKE multiparameter probe at depths ranging from 2 to 3 m. Daily maximum UVA and UVB radiation values for each sampling date were provided by the Laboratory for Atmospheric Research (LIA) at the University of Magallanes, using a UVA-1/UVB-1 ultraviolet pyranometer YES (Yankee Environmental Systems).

In the Ecuadorian breeding ground, in situ measurements were not available due to logistical constraints and the lack of UV radiation monitoring stations. Therefore, oceanographic environmental variables were obtained from satellite-derived products provided by the Marine Data Viewer of Copernicus Marine Service (https://data.marine.copernicus.eu/viewer/), and maximum UVA and UVB radiation values were retrieved from the Clouds and the Earth's Radiant Energy System (CERES; https://ceres-tool.larc.nasa.gov) database. All satellite-derived variables were matched to the corresponding sampling dates using daily values and the location of the biopsies.

TABLE 2 | Environmental conditions associated with humpback whale skin samples from the Magellan Strait feeding ground and the Ecuador breeding ground (mean ± standard deviation).

Study area	SST (°C)	Salinity (PSU)	Dissolved oxygen ($mg\,L^{-1}$)	Chlorophyll ($mg\,L^{-1}$)	UVA max ($W\,m^{-2}$)	UVB max ($W\,m^{-2}$)
Magellan Strait, Chile	8.7 ± 0.6	29.5 ± 0.5	8.8 ± 0.8	5.8 ± 5.6	28.8 ± 13.5	0.9 ± 0.8
Coasts of Ecuador	24.9 ± 1.3	33.9 ± 0.1	7.2 ± 0.1	1.3 ± 0.2	12.2 ± 2.4	0.3 ± 0.1

Satellite products and in situ measurements provided spatially and temporally consistent estimates with reduced differences, suitable for comparative purposes. In open ocean conditions such as near Isla de la Plata, differences are typically within ~0°C–0.4°C for SST under mixed conditions, up to ~1°C under stratification, ~15%–20% for chlorophyll-a, ~0.1–0.2 PSU for salinity, ~0.5 $mg\,L^{-1}$ for dissolved oxygen (Cerdeira Estrada et al. 2015; Donlon et al. 2002; López-Ramírez et al. 2024; O'Reilly et al. 1998; Stramska et al. 2021) and up to 20% for UV radiation within the same physical units (Arola et al. 2002; Kazantzidis et al. 2006).

2.7 | DNA Extraction and Sequencing

DNA was extracted from an average sample of 0.030 mg of epidermal tissue and from seawater filters using the FastDNA Spin kit for Soil (MP Biomedical, Santa Ana, CA, USA) following a modified extraction protocol. Before DNA extraction, samples were incubated in sterile phosphate-buffered saline (PBS) with agitation at 1500 rpm and 56°C for 2 h in a MultiTherm heat shake (Benchmark Scientific Inc., Edison, N.J., USA) to promote microbial detachment from the skin and seawater filters, thereby enriching microbial cells in suspension relative to host material. Following incubation, the suspension was transferred to another tube and mixed with lysis solution, and homogenized using a FastPrep-24 5G bead beating device (MP Biomedicals, Irvine, California, USA) at 4 m/s for two 30 s cycles, with a 1 min ice bath between cycles, followed by centrifugation at 14,000 g for 15 min. For the protein precipitate step, samples were incubated at −20°C for 5 min, followed by 10 min centrifugation. To remove residual wash solution, tubes were air-dried in a PCR cabinet for 30 min. To enhance DNA concentration, the binding matrix was resuspended in 25 μL of Ambion Nuclease-Free Water (Invitrogen, Thermo Fisher Scientific) followed by a 5 min incubation step at 56°C in the MultiTherm heat shake (Benchmark Scientific Inc., Edison, N.J., USA).

To assess for possible microbial contamination of kit reagents, four distilled water blanks were processed for DNA extraction. In addition, to further determine the reliability of the sequence processing and taxonomic assignments, two positive controls were included, consisting of a mock microbial community comprising seven known species of *Bacillus and Domibacillus*, isolated from the Cuatro Ciénegas basin in Coahuila State, Mexico, that were sequenced alongside humpback whale and seawater samples. The first mock community consisted of a pooled sample of DNA extracts from each of the seven species grown individually. The second mock community consisted of a single DNA extraction from a consortium of the same seven species, grown together for 48 h in marine agar.

DNA extracts were sent to Macrogen Inc. (Seoul, South Korea) for 16S rRNA gene amplification of the V3-V4 hypervariable region using primers 341F/805R (Klindworth et al. 2013). Library preparation was carried out using the Herculase II Fusion DNA Polymerase Nextera XT index V2 Kit (Illumina, San Diego, CA, USA) and paired-end sequencing (2 × 300 pb) was performed on the MiSeq platform (Illumina, San Diego, CA, USA). Negative controls (distilled water blanks) did not yield any detectable PCR-enriched products during library preparation, as confirmed by fragment size analysis with a 2100 Bioanalyzer instrument (Agilent Technologies) and qPCR quantification; therefore, we were not able to obtain sequencing libraries for the negative controls.

2.8 | Sequence Processing

DNA sequences were processed using R v4.4.1 (R Core Team 2024), and amplicon sequence variants (ASVs) were inferred with DADA2 v1.28.0 (Callahan et al. 2016). Primer length nucleotides were removed at the start of each read, forward and reverse reads were quality trimmed and truncated at 270 and 210 nt, respectively. Ambiguous bases were not allowed, and expected errors higher than two were discarded. Error rate learning, denoising and sample composition inference were performed, followed by merging of forward and reverse reads. Only sequences between 400 and 480 nt were kept for chimera removal using the 'consensus' method. The taxonomic assignment of ASVs was performed using the SILVA rRNA database v138.1 (Quast et al. 2013), and further imported into phyloseq (McMurdie and Holmes 2013). To validate the accuracy of the DADA2 pipeline and ASV taxonomic classification, the ASVs identified in each of the two kinds of positive controls were compared with the original mock community composition. This resulted in the correct recovery of the expected taxa (i.e., *Bacillus* and *Domibacillus*), indicating a reliable sequence processing and a correct taxonomic assignment. As the positive controls served solely as quality-control samples, they were excluded from downstream analyses.

Further possible contaminant ASV identification and removal were conducted using the decontam package with the 'frequency' method (Davis et al. 2018), which flags ASVs whose frequency varies inversely with sample DNA concentration. The values of extracted DNA concentrations provided to decontam were obtained prior to library preparation using the

QuantiFluor dsDNA System and measured on a Victor Nivo Multimode Microplate Reader at Macrogen Inc. (Seoul, Korea). In addition, sequences assigned to chloroplasts, mitochondria, eukaryotes and phyla represented by a single ASV, detected in only one sample, were removed to exclude extremely low prevalence and poorly supported taxonomic assignments.

Before the statistical analysis, rarefaction curves were constructed using the rarecurve function of the vegan package to assess sequencing depth (Oksanen et al. 2025), with all samples reaching a plateau. To remove potential biases and variations associated with sampling and sequencing depth (Weiss et al. 2017), rarifying without replacement to 65,000 reads was used as a normalization technique, following guidance from rarefaction curves and was used for downstream analysis, except for differential abundance analysis.

2.9 | Statistical Analysis

Relative abundance composition of microbial taxa in all samples was calculated and plotted with the microViz package (Barnett et al. 2021). Additionally, unique phyla in HWs' skin to each seasonal habitat were identified (present in at least one sample) and subsequently compared between habitats.

Alpha diversity was estimated through the Shannon index (Shannon 1948), which was selected for being less sensitive to singleton removal by the DADA2 algorithm (Kleine Bardenhorst et al. 2022). This index was calculated for each seasonal habitat (Magellan Strait and Ecuadorian coasts), age class (adults and calves), sex, sample types (whale and seawater) and compared using a non-parametric Wilcoxon rank sum test (as normality assumptions were not met based on the Shapiro–Wilk test) and visualized as boxplots using the microbiome package (Lahti and Shetty 2019).

The core microbiome analysis was calculated with the amp_venn function from the package ampvis2 (Andersen et al. 2018) and consisted of a three-way comparison of HWs from the Magellan Strait, HWs from Ecuador and pooled seawater samples across sites due to the limited seawater sample size. Set parameters included no minimum abundance threshold and ASVs occurring within a read frequency threshold of 50%, 75% and 90%. Also, separate comparisons between whales from each seasonal habitat and their associated seawater were calculated.

To identify patterns in community composition on the skin and seawater microbiome, a Principal Coordinate Analysis (PCoA) was performed using a Bray–Curtis dissimilarity matrix on log-transformed data (Anderson et al. 2006) to reduce differences in scale and limit the influence of highly abundant taxa (Anderson and Willis 2003; Borcard et al. 2011). The PCoA results were plotted using the microViz package (Barnett et al. 2021).

Permutational multivariate analysis of variance (PERMANOVA) was then conducted using the adonis2 function (Oksanen et al. 2025) to evaluate differences in the skin microbiomes of HWs across seasonal habitats (including sampling year as a covariate to account for interannual variation via marginal effects), age class and sexes. To assess differences between the host and the marine environment, we conducted an overall comparison between seawater and HWs' skin microbiomes. The PERMANOVA results were complemented with a multivariate homogeneity of groups dispersion analysis (PERMDISP), including a bias adjustment for unequal sample sizes using the betadisper function (Oksanen et al. 2025).

To explore the relationship between the microbial community composition and the environmental conditions (SST, salinity, chlorophyll, maximum UVA and UVB radiation), a distance-based Redundancy Analysis (dbRDA) was performed on the same log-transformed data as PCoA. Environmental variables were standardized using the decostand function (Oksanen et al. 2025) and assessed for collinearity before model fitting, via correlation analysis ($r > 0.7$). Non-collinear variables were then used in a forward selection model to maximize explained variance with ordiR2step function (Oksanen et al. 2025) and further evaluated with the Variance Inflation Factor (VIF) < 10 (Signorell 2025). The final dbRDA model included maximum UVB radiation and SST as significant variables, evaluated via an ANOVA-like permutation test with anova.cca function (Oksanen et al. 2025).

For the identification of differentially abundant taxa between HWs' skin microbiomes from the Magellan Strait and Ecuador, an analysis of the composition of microbiomes with bias correction (ANCOM-BC2) (Lin and Peddada 2024) was performed on non-rarified data with the ancombc2 function, using Holm-adjusted *p*-values (q) and structural zeros detection. A sensitivity analysis was also conducted to evaluate the sensitivity of the results to pseudo-count addition for taxa with zero counts, which can otherwise inflate the false positive rate. This analysis identifies if taxa *p*-values remain consistent with and without the addition of different pseudo-counts. Taxa showing consistent significance were considered robust.

To identify the HWs' microbial taxa response to environmental conditions detected by dbRDA, an analysis of microbiome multivariable association with a linear model (MaAsLin 2) (Mallick et al. 2021) was conducted at the genus level on the rarefied dataset. Within MaAslin2, total sum scaling (TSS) was applied to normalize microbial counts into relative abundances, followed by arcsine square-root transformation to stabilize variance for proportional data. The model included SST and maximum UVB radiation as fixed effects and seasonal habitat as a random effect; *p*-values were adjusted for multiple testing using the Benjamini-Hochberg method.

3 | Results

A total of 54 samples (HW = 46, seawater = 8) were analysed, yielding 6,708,809 total reads (mean ± SD: 121,978 ± 39,729 reads) distributed in 6945 ASVs after taxonomic and contaminant filtering. From each sample type, seawater contained 4425 ASVs (84,889 ± 16,673 reads), whereas HW skin contained 2760 ASVs (12,9134 ± 38,932 reads). The assessment of potential contaminants identified 53 ASVs (37,443 total reads) spanning several taxa (Table S1), which were then removed from downstream analyses, along with non-target and low-prevalent features that included 423 ASVs (62,877 total reads). After rarefying

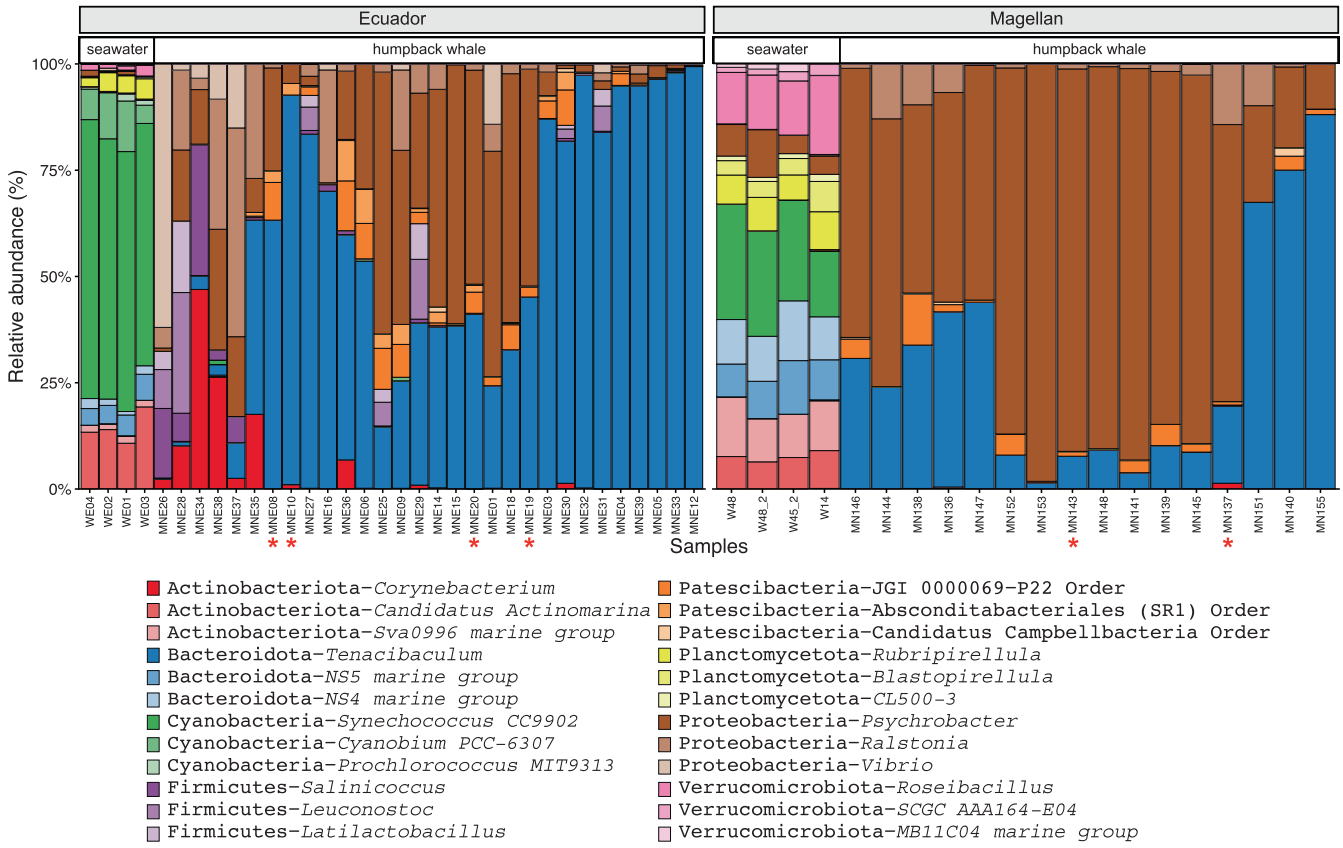

FIGURE 2 | Microbiome of the humpback whale skin and the surrounding seawater. Stacked bar plot showing the eight bacterial phyla with the highest mean relative abundance and the three most abundant genera within each phylum. Colours represent distinct phyla, while different shades indicate genera within the same phylum. For the phylum Patescibacteria, the lowest resolved taxonomic rank corresponded to the order level. Samples are grouped by host (MN; $n = 46$), including calves (red asterisks), and by seawater (W; $n = 8$) from seasonal habitats at the breeding ground off the Ecuadorian coast and the feeding ground in the Magellan Strait in Chile.

to even sequencing depth, 84% of ASVs were kept (6299 ASVs) and 52% of total reads (3,510,000 reads) from the filtered dataset. In HW samples, 98% of ASVs were retained (2708 ASVs; 130 ± 70 ASVs), 771 ASVs were from HWs of the Magellan Strait (84 ± 42 ASVs) and 2137 ASVs were from HWs of Ecuador (155 ± 67 ASVs). In seawater samples, 86% of total ASVs were retained (3824 ASVs; 815 ± 280 ASVs), 1381 ASVs from Ecuador and 2480 ASVs from the Magellan Strait.

Thirty-three microbial phyla were identified, with 26 detected in HW skin and 33 in seawater. All phyla belonged to bacteria, except for Thermoplasmatota, an archaeal phylum exclusively detected in seawater samples. The most abundant phyla identified on HW skin and seawater samples were Proteobacteria, Bacteroidota, Cyanobacteria, Actinobacteria, Firmicutes, Patescibacteria, Planctomycetota and Verrucomicrobiota.

3.1 | Humpback Whale Skin Microbiome From Seasonal Habitats

The relative abundance of the microbial composition on HW skin (Figure 2) was dominated by the phylum Proteobacteria (mean ± SD; 49% ± 24%) and Bacteroidota (43% ± 29%). Members of Proteobacteria were more abundant in the Magellan Strait feeding ground (61% ± 21%) than in the breeding ground of Ecuador (42% ± 24%). In contrast, members of Bacteroidota were more abundant in Ecuador (47% ± 31%) than in the Magellan Strait (35% ± 20%). In addition, we found phyla exclusively detected in Ecuador skin samples, including Campylobacterota, Dependentiae, Marinimicrobia (SAR406 clade), SAR324 clade (Marine Group B), Spirochaetota, WPS-2 and Nitrospirota, whereas no unique phyla were identified in skin samples from the Magellan Strait.

At the genus level, *Psychrobacter* (Moraxellaceae) and *Tenacibaculum* (Flavobacteriaceae) were the taxa with the highest relative abundance found on HW skin across both seasonal habitats (Figure 2). In the Magellan Strait, *Psychrobacter* dominated the skin of HWs (mean ± SD; 39% ± 26%), followed by *Tenacibaculum* (19% ± 24%). In contrast, in Ecuador, *Tenacibaculum* (33% ± 30%) had a higher relative abundance compared to *Psychrobacter* (11% ± 13%) (Figure S1).

Skin microbiomes of HWs had similar alpha diversity (Shannon index; Figure 3) between seasonal habitats ($W = 302$, p-value = 0.157), sexes ($W = 299$, $p = 0.431$) and age classes ($W = 82$, $p = 0.327$). However, differences in the skin microbial community composition (beta diversity) were detected across HWs' seasonal habitats (Table 3). These differences remained after accounting for interannual variation, which explained a smaller proportion of the variance than seasonal habitat. Other factors,

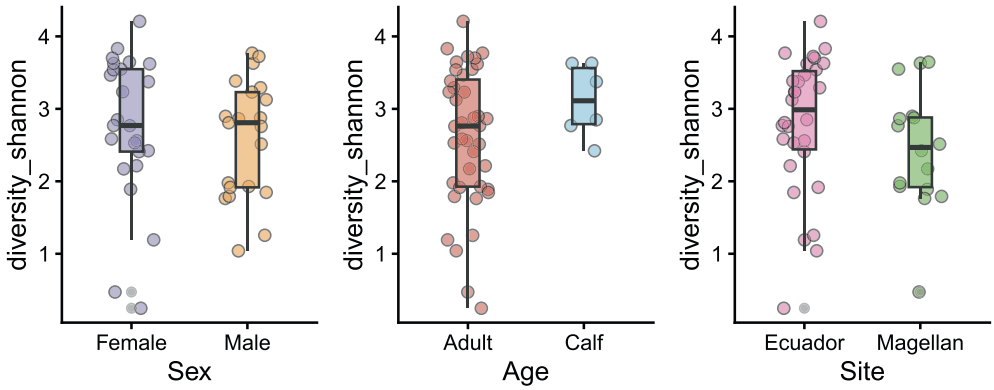

FIGURE 3 | Alpha diversity of the microbial communities associated with humpback whale skin. Boxplot of Shannon index comparison across seasonal habitats (Magellan Strait and Ecuador), sex and age classes (adults and calves). No differences were detected among any of the evaluated factors (Wilcoxon rank-sum test, $p > 0.05$).

TABLE 3 | Ecological variables and host intrinsic factors associated with beta diversity of the humpback whale skin microbiome.

		PERMANOVA			PERMDISP	
Model	**Factor**	***F***	***R^2***	***p***	***F***	***p***
Single-factor	Age (Calves vs. Adults)	1.081	0.024	0.322	0.005	0.937
	Sex	1.027	0.023	0.378	0.769	0.381
	Host vs. seawater	7.487	0.126	0.001	2.56	0.13
	Seasonal habitat	5.465	0.11	0.001	0.446	0.485
Multifactor	Year + Seasonal habitat					
	Year	2.2	0.043	0.002	4.818	0.009
	Seasonal habitat	5.858	0.115	0.001		

such as sex or age classes, showed no differences in bacterial community composition. No differences in dispersion were found between seasonal habitats, sex or age classes, in contrast to site-year combinations, which indicated non-uniform dispersion. Due to uneven sample sizes across age classes and sampling years among seasonal habitats, inferences about how these factors affect the skin microbiomes of HWs are limited.

Differences in the microbial composition of HWs between seasonal habitats were further supported by the PCoA, which showed a partial overlap in the microbial structure between the two study areas along PCo1, with calves clustering within adult samples. The first two coordinates (i.e., PCo1 and PCo2) together explained 22.8% of the variance (Figure 4A).

HW skin microbiome structure according to environmental conditions was analysed, and a dbRDA model was obtained ($F = 3.78$, $p = 0.001$) (Figure 4B) based on a forward selection test. The model identified SST ($F = 5.77$, $p = 0.001$) and maximum UVB radiation ($F = 1.70$, $p = 0.016$) as the primary environmental drivers of microbial community composition on HW skin, explaining 9.56% and 2.5% of the variance (adj. R^2), respectively. No collinearity between variables was detected (VIF < 1.3), and the two constrained axes accounted for up to 13.2% of the total variation, with a substantial portion of the variation remaining unexplained by the measured environmental factors.

The differential microbiome composition analysis using ANCOM-BC2 on HW skin from the Magellan Strait and Ecuador (Figure 5A) identified 107 taxa across both study areas, including core and low-prevalence taxa detected in at least 10% of samples. Of these, 23 taxa were considered to be differentially abundant (Holm adj. $q \leq 0.05$), and only a subset passed the sensitivity analysis, revealing distinct microbial patterns associated with each seasonal habitat.

For example, in the Ecuadorian breeding ground, some key genera in HWs' skin microbiome included lactic acid bacteria (*Latilactobacillus*), halophiles (*Halomonas, Idiomarina*), common animal skin bacteria (*Corynebacterium*), facultative anaerobes (*Vibrio*), cyanobacteria (*Synechococcus*) and other less characterized taxa (Figure 5A).

In contrast, HWs' microbiomes in the Magellan Strait feeding ground at genus level showed a higher relative abundance of psychrophilic bacteria (*Psychrobacter*; *Colwellia*), and other key marine genera (*Aliivibrio*), common gut-associated bacteria (*Clostridium sensu stricto*, *Escherichia-Shigella*), UV-resistant bacteria (*Deinococcus*) (Figure 5A), and poorly characterized marine bacteria (genera *Dyella, Lawsonella, Obscuribacteraceae, Rubripirellula*), along with chitinolytic bacteria (order *Chitinophagales*), that exhibited the highest LFC and were considered of biological relevance, despite not reaching

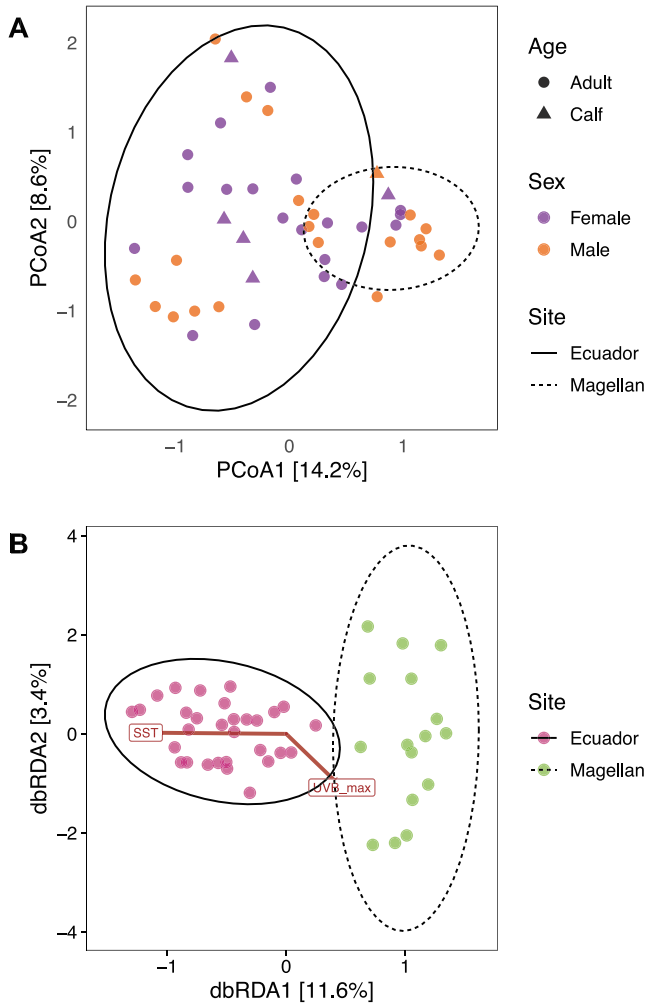

FIGURE 4 | Beta diversity of humpback whales' skin microbiome. (A) Ordination diagram of Principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity of the skin microbiome of humpback whales from two seasonal habitats (the Magellan Strait feeding ground and the Ecuadorian breeding ground). (B) Distance-based redundancy analysis (dbRDA) illustrating the influence of environmental variables, including sea surface temperature (SST) and maximum UVB radiation (UVB max), on humpback whale microbial community composition.

statistical significance (Figure S2). A complete list of all differentially abundant taxa is provided in Table S2.

To further examine whether environmental conditions such as SST and maximum UVB radiation were related to microbial key taxa across seasonal habitats, an additional multivariate associations analysis using MaAsLin2 identified a total of 26 key taxa (Figure 5B) at the genus level as environmentally responsive ($q < 0.05$). *Psychrobacter* and *Pseudomonas* were negatively associated with higher SST, whereas lactic acid bacteria such as *Lactilactobacillus, Lactococcus* and *Leuconostoc*, halophilic taxa such as *Salinicoccus*, and mammalian skin-associated bacteria such as *Corynebacterium* were positively associated with higher SST. In contrast, genera such as *Deinococcus*, along with *Pseudomonas, Cutibacterium* and *Lacuniphaera*, as well as other lesser-known genera, were found to be positively associated with maximum UVB radiation (Figure 5B). *Tenacibaculum* was not associated with SST or maximum UVB radiation. A full list of microbial taxa associations can be found in Table S3.

3.2 | The Marine Environment

Seawater and HW skin microbiomes differed in community composition (Figure 2), showing no differences in multivariate dispersion within each environment (seawater vs. HW skin; Table 3). The PCoA (Figure 6A) further illustrated that the microbial structure of the two environments (host skin and seawater) is unique, but still similar within the study areas. In this case, the first two coordinates (PCo1 and PCo2) explain 24.3% of the variance, and along PCo1, a clear clustering of each environment (host skin and seawater) is observed (Figure 6A). Alpha diversity estimates also showed differences between HWs and seawater from the Magellan Strait ($W = 64$, $p = 0.0004$; Figure 6B).

Seawater microbial composition associated with the Magellan Strait feeding ground had a different structure from HWs' skin (Figure 2), although Proteobacteria remained the dominant phylum (53%), followed by Bacteroidota (17%). However, at the genus level, other marine taxa were represented in seawater samples, such as SAR11 *Clade Ia* (7.8%), *Amylibacter* (4.5%), *Synechococcus* (4.7%), *Planktomarina* (3%), *Roseibacillus* (3%). In contrast, seawater from the Ecuador breeding ground was mainly composed of phylum Cyanobacteria (52%) and Bacteroidota (17%), with a clear dominance of genus *Synechococcus* (45%), *candidatus Actinomarina* (10.5%), *Cyanobium* PCC-6306, *Rubripirellula* (2.8%), SAR11 *Clade Ia* (4.6%) and NS5 marine group of class Flavobacteriia (3.5%) (Figure S3).

3.3 | Shared Taxa Between HWs and Seawater

To assess the potential contribution of environmental microbial communities to the whale skin microbiome, we performed a three-way comparison (Figure 7), which consistently identified (75% and 50% threshold) the ASV4 classified as genus *Ralstonia* (Burckholderiaceae), being shared by HWs' skin samples from each seasonal habitat with combined seawater samples, whereas no shared ASVs under a more stringent threshold (90%) were found (Table S4).

Host skin samples between seasonal habitats only shared two additional ASVs (75% threshold), also identified as *Ralstonia (ASV18, ASV25)*. At the lower frequency threshold (50%), 16 ASVs were identified, including *Pelomonas saccharophila, Aquabacterium commune*, the genera *Tenacibaculum, Pseudomonas, Psychrobacter, Celeribacter* and *Sphingobium*, besides other ASVs classified as family Moraxellaceae and Flavobacteriaceae.

In whales from the Magellan Strait, the core microbiome (75% threshold) included five ASVs identified as *Pelomonas saccharophila*, genera *Pseudomonas, Burckholderia-Caballeronia-Paraburkholderia* and the families Moraxellaceae and Flavobacteriaceae. However, with a lower threshold (50%), 15 ASVs were identified, including the genus *Psychrobacter* and

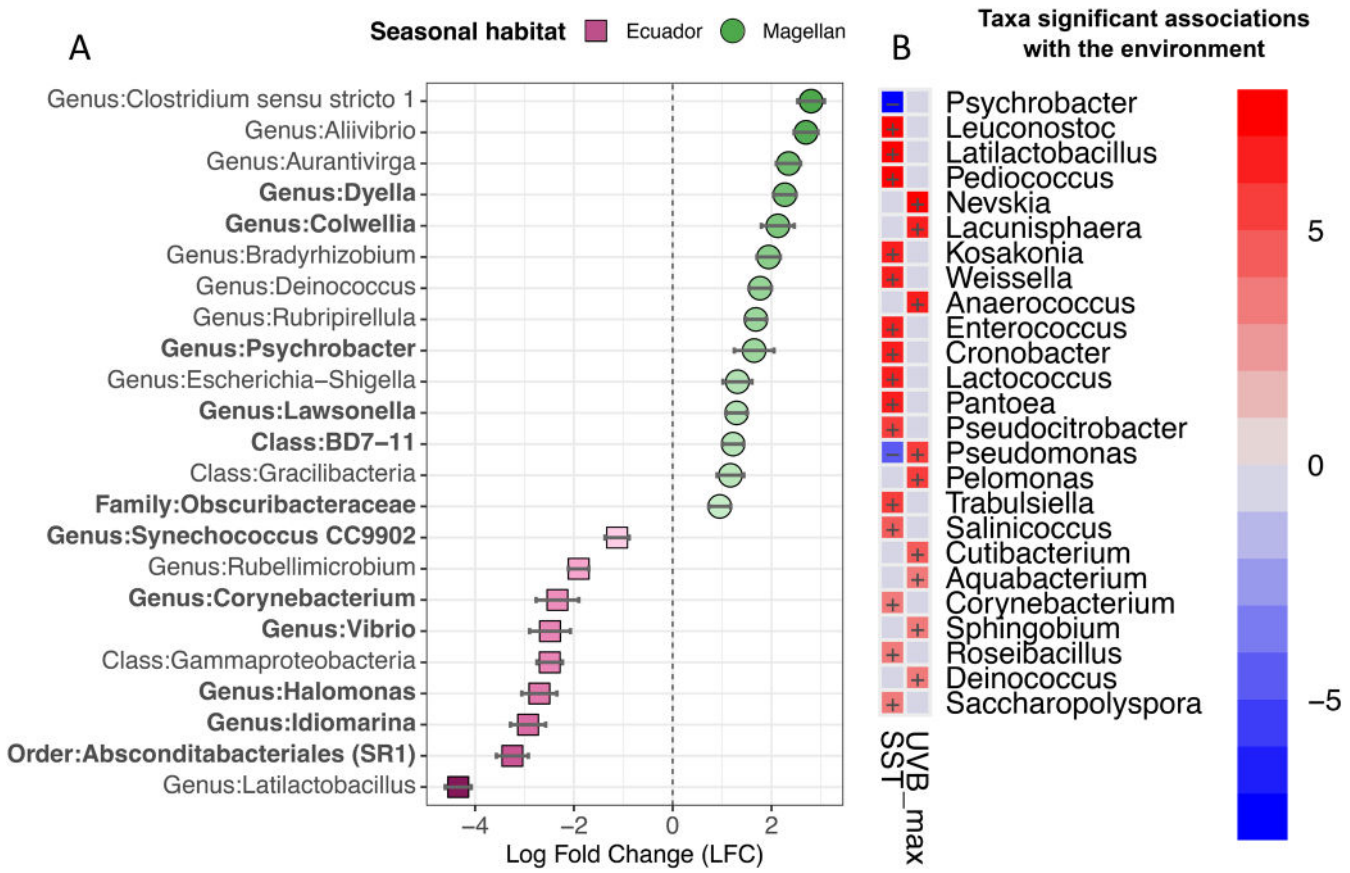

FIGURE 5 | Differential abundance analysis of the humpback whale skin microbiome. (A) Seasonal habitats differential composition analysis by ANCOM BC2, showing the log fold change (LFC) in relative abundance of bacterial taxa between seasonal habitats (Magellan Strait feeding ground and Ecuador breeding ground). Only significant taxa after Holm-adjusted p-value (q) ≤ 0.05 and prevalence in at least 10% of samples are shown with standard error bars, and taxa that passed the sensitivity analysis are shown in bold. (B) Heatmap showing MaAsLin2 multivariable associations ($q < 0.05$) of key bacteria at the genus level with environmental conditions (SST and maximum UVB radiation), including seasonal habitat as a random effect.

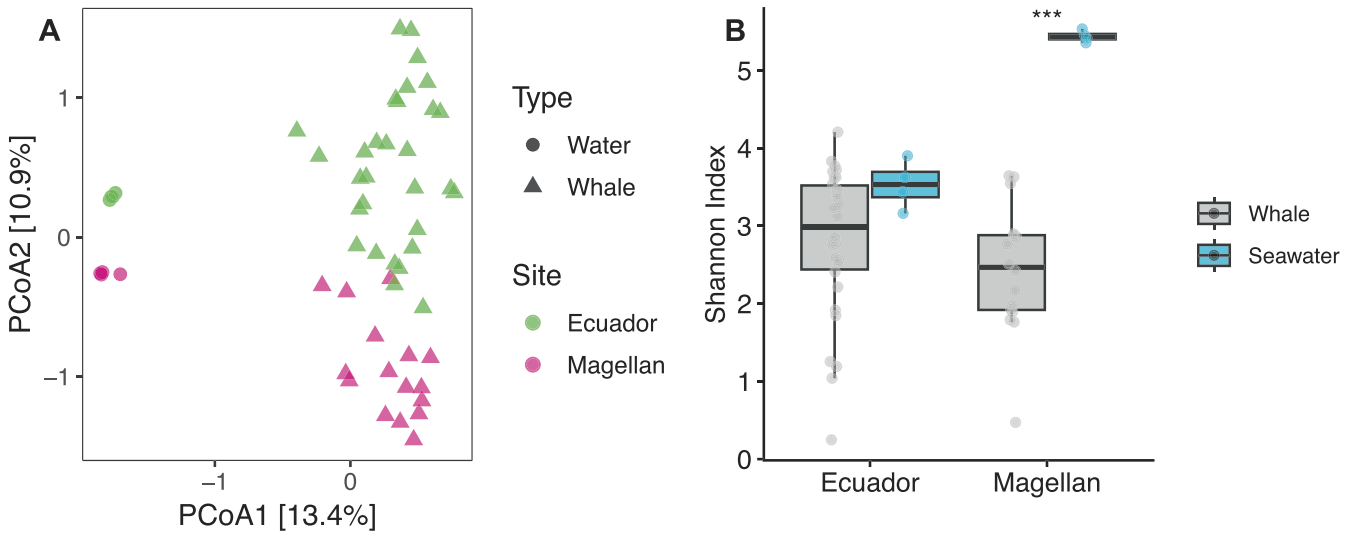

FIGURE 6 | Diversity of host and seawater microbiome comparison. (A) Principal coordinate analysis (PCoA) based on Bray–Curtis dissimilarity illustrating the beta diversity of humpback whale skin and seawater microbiome from the Magellan Strait in Chile and the coasts of Ecuador. (B) Boxplots comparison of alpha diversity (Shannon index) for host and seawater samples (Wilcoxon rank-sum test, ***$p < 0.001$).

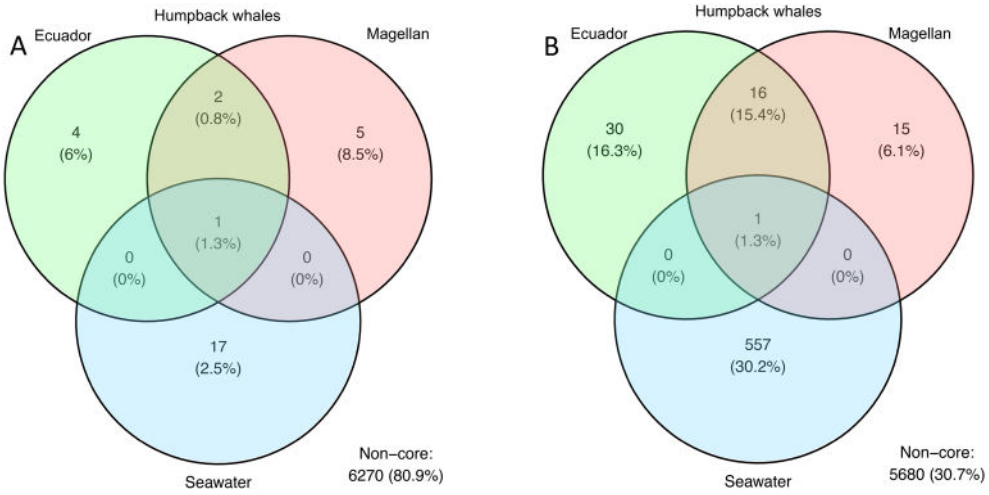

FIGURE 7 | Core microbiome analysis of humpback whale skin and seawater. Venn diagram intersections show the number of ASVs that represent the shared core microbiome according to a frequency threshold of 75% (A) and 50% (B). Numbers in parentheses within each circle indicate the relative abundance that core ASVs represent.

Tenacibaculum, families Moraxellaceae, Flavobacteriaceae, Cardiobacteriaceae and order JGI 0000069-P22 (class Gracilibacteria).

In whales from Ecuador, the core microbiome (75% threshold) comprised four ASVs, classified as genera *Cutibacterium*, *Tenacibaculum* and *Psychrobacter*. With a lower threshold (50%), the number of shared ASVs increased to 30, incorporating *Salinicoccus carnicancri*, the genera *Enterobacter, Escherichia-Shigella, Halomonas, Burckholderia-Caballeronia-Paraburkholderia* and ASVs of families Moraxellaceae, Sedimenticolaceae, Cardiobacteriaceae and Saccharospirillaceae.

In joint seawater samples, the core microbiome included 17 ASVs (75% threshold), mainly comprised of SAR11 (class Alphaproteobacteria) from Clade Ia, Clade Ib, Clade II, besides other taxa such as genera *Pseudoalteromonas, Psychrobacter, Alteromonas*, families Cryomorphaceae and AEGEAN-169 marine group (order Rhodospirillales). Using a lower threshold (50%), 557 core ASVs were identified from several other taxa (Table S4).

To further disentangle habitat-specific patterns, a separate two-way comparison between whale skin and associated seawater within each habitat (Magellan Strait and Ecuador) was performed. These analyses yielded consistent patterns with the three-way comparison, showing limited overlap of ASVs between seawater and skin microbiomes, and even within whale individuals from each site (Table S4). Notably, some of the core ASVs within seawater samples at varying thresholds of the three and two-way comparisons were also classified as the genera *Psychrobacter* and *Tenacibaculum*, although not the same ASVs found within HWs' skin, indicating some taxonomic overlap at higher ranks, but not at the ASV level.

4 | Discussion

In this study, we characterised the skin microbiome of humpback whales from the eastern South Pacific, Breeding Stock G (BSG), across two key migratory habitats. Overall, the microbial alpha diversity remained consistent across habitats and host intrinsic factors, while differences in community composition were detected between feeding and breeding grounds, possibly influenced by environmental conditions associated with each habitat.

One of the main findings of our study indicates that the skin microbial composition of the eastern South Pacific HW population changes across migratory destinations between feeding and breeding grounds, while maintaining a similar alpha diversity, suggesting that individuals harbour a comparable richness and relative abundance structure across habitats. Previous studies on northern HWs' population have suggested that host metabolic state –feeding in high latitudes and fasting in low-latitude breeding grounds—is the main driver of variation in the skin microbiomes alongside geographic location (Apprill et al. 2014). The nutritional status may affect the skin microbiome through the skin renewal process, promoted by temperate seawater (Pitman et al. 2020), which may impose a higher energetic cost (Thometz et al. 2021). In cetaceans, the skin renewal may modulate the bacterial load, as happens in amphibian skin (Weitzman et al. 2025). which can change the biochemical environment of the skin—including the lipidic components (Bierlich et al. 2018), like SCFA—that in turn can regulate the host's immune response (Chen et al. 2022).

This skin renewal process in temperate seawater has been proposed as an important factor in whale migration between feeding and breeding grounds, rather than metabolic state alone (Lefort et al. 2025; Pitman et al. 2020). This is supported by reports of opportunistic feeding behaviour along the Pacific coasts of South America (Millien et al. 2025) and in other HW populations in highly productive temperate areas (Findlay et al. 2017; Gill et al. 1999), suggesting that the nutritional status is unlikely to be the primary determinant of skin microbial structure. Instead, the skin microbiomes of the eastern South Pacific population appear to reflect a geographic structuring (Bierlich et al. 2018; Toro et al. 2021). Based on this, our study provides the first direct evidence of microbial differences between feeding and breeding grounds in the eastern

South Pacific HW population, extending the central role of geography in shaping the skin microbiome across migratory habitats and latitudinal gradients.

Environmental conditions such as SST and, to a lesser extent, maximum UVB radiation were identified as key drivers of the skin microbial composition. This could be explained by the strong thermal gradient between the Magellan Strait's colder subantarctic waters and the markedly warmer conditions in Ecuador. Meanwhile, UVB radiation effects may reflect the recent record in depletion levels of atmospheric ozone in Antarctica (2019–2023), particularly during the austral summer (Robinson et al. 2024)—when HWs occupy the feeding grounds–, mainly driven by atmospheric dynamics such as the polar vortex (Bernhard et al. 2023; Casiccia et al. 2008; Cordero et al. 2022; Robinson et al. 2024). In Chilean Patagonia fjords, UV radiation penetration can reach depths of 2–27 m during summer (Huovinen et al. 2016), potentially affecting the microbial communities on exposed skin. However, a substantial portion of the observed microbial variability on HW skin remained unexplained, suggesting that additional factors, such as local oceanographic conditions, ecological context and population-level structure linked to migratory behaviour, could play a substantial role in driving the microbiome composition across habitats.

Within this context of biogeographic variation across seasonal habitats associated with different environmental conditions, two highly prevalent taxa and part of the core microbiome were identified on the skin of HWs in both seasonal habitats: the genera *Psychrobacter* and *Tenacibaculum*. Both bacterial groups have been broadly found in cetacean skin, including humpback whales (Apprill et al. 2014; Bierlich et al. 2018; Chiarello et al. 2017; Dominguez-Sanchez et al. 2024; Hansen et al. 2026; Hooper et al. 2019; Robles-Malagamba et al. 2020; Toro et al. 2021; Van Cise et al. 2020). Due to their high prevalence, these genera have been suggested as commensal-symbiotic bacteria of HWs' skin (see Apprill et al. 2014). As important components of cetacean skin microbiomes, changes in their proportions or prevalence may indicate skin dysbiosis (Dominguez-Sanchez et al. 2024) or skin disease (Van Cise et al. 2020). Thus, the relationship of *Psychrobacter* and *Tenacibaculum* with host health is likely dependent on every species context, and within our study, their high abundance supports the idea of these taxa as potential indicators of host health condition, rather than direct markers of disease.

In the Magellan Strait feeding ground, a high abundance of genus *Psychrobacter* was expected by previous descriptions from the eastern South Pacific HW population (Bierlich et al. 2018; Toro et al. 2021). In our study, *Psychrobacter* was not only differentially abundant in the Magellan Strait, but also exhibited a strong negative association with increasing SST, supporting the idea of thermal variation sensitivity (Bierlich et al. 2018). While *Psychrobacter* is a cold-adapted bacterium, flexible ecotypes retain the ability to grow at mammalian body temperatures (~37°C) (Welter et al. 2021), a dual nature that may facilitate host colonization while providing a competitive advantage in polar waters.

This pattern contrasts with a lower abundance of *Psychrobacter* in the northern population of HWs at high-latitude feeding grounds such as Alaska (Apprill et al. 2014), suggesting regional differences in host-microbe-environmental interactions. Altogether, these results provide evidence of shifts in skin microbial dominance across the BSG migratory range and that *Psychrobacter*'s distribution on HW's skin follows a thermal gradient, possibly associated with specific water masses in the southern hemisphere, highlighting its dynamic and environmentally responsive role within the HW skin microbiome.

The genus *Tenacibaculum*, despite exhibiting higher mean relative abundance on HWs from Ecuador, was not identified as differentially abundant between seasonal habitats or associated with environmental conditions. Although a higher abundance in Ecuador is consistent with whales sampled in a low-latitude area in American Samoa (Apprill et al. 2014), the lack of significance due to interindividual variability may be driven by other factors not considered in this study.

Tenacibaculum appears to be a prevalent resident of whale skin, linked to its ability to thrive at mesophilic temperatures (15°C–34°C) (Avendaño-Herrera et al. 2006)—near mammalian body temperature—and its enhanced surface adherence via adhesins (Pérez-Pascual et al. 2017). Such traits likely facilitate successful host colonization, as in species within this genus (i.e., *Tenacibaculum maritimum*) in fish (Mabrok et al. 2023). *Tenacibaculum* high prevalence across both habitats possibly reflects the selection of microbial taxa that can persist through contrasting environments during long-distance migration, potentially reducing microbial turnover (Pearman et al. 2024). This indicates a relevant ecological role on HW skin that may respond instead to a microbial biogeographic distribution, likely shaped by migratory factors, which constitutes novel observations for a low-latitude breeding ground for the eastern South Pacific HW population.

In the Magellan Strait feeding ground, we additionally detected a differential abundance of the genus *Colwellia* (Alteromonadaceae), a psychrophilic bacterium that produces trehalose, an extracellular polysaccharide with anti-freezing properties (Techtmann et al. 2016), cold-active enzymes, polyunsaturated fatty acids that enhance membrane fluidity, antioxidants and osmo-protectants. Some species also tolerate high-pressure conditions (Kusube et al. 2017; Methé et al. 2005), a trait that may be advantageous during HW's deep dives in cold waters. These traits suggest that *Colwellia* may inadvertently contribute to the host's ability to cope with low-temperature stress.

Some bacteria in HW from the Magellan Strait were positively associated with maximum UVB radiation levels, including the genus *Deinococcus*, a bacterium highly resistant to radiation and oxidizing agents that possesses highly efficient DNA repair mechanisms (Burrell et al. 1971; Daly et al. 1994; Gerber et al. 2015; Slade and Radman 2011). Similarly, the genus *Sphingobium* (Sphingomonadaceae) may tolerate UV stress through antioxidant production that neutralizes reactive oxygen species (ROS), as reported in related taxa (Harel et al. 2023). Also, genus *Cutibacterium* counteracts UV radiation through anti-inflammatory compounds and free fatty acid production (Ma et al. 2026). These bacteria, beyond their cellular tolerance to UVB radiation effects, share the ability to form biofilms (Coenye et al. 2022; Guo et al. 2023; Zhong et al. 2018), a trait that decreases UV transmission to the cell by

providing a protective matrix (Elasri and Miller 1999), improving cell survival as reported in *Deinococcus* (Guo et al. 2023).

Bacterial exopolymers have demonstrated photoprotective properties on mammalian keratinocytes by reducing UVB damage through collagen recovery and antioxidant enzymes (Xu et al. 2024), besides modulating host skin signalling to improve the skin barrier integrity (Mercer et al. 2026) or reduce pro-inflammatory cytokines (Keshari et al. 2019). Based on this, and given the proximity of the Magellan Strait to Antarctica and the influence of the Antarctic Ozone Hole in the southern area of South America (Casiccia et al. 2008), UV-tolerant bacteria could be expected, as they may reflect environmental selection. They could also modulate HWs' skin response to UV radiation stress exposure and ROS production through host–microbe interactions, and may represent a biochemical shield (biofilms) for whales under high UV conditions.

Chitinolytic bacteria also displayed a higher abundance in the Magellan Strait, including the genus *Aliivibrio* (Skåne et al. 2022), identified in fish and cephalopods (Dunlap 2009) and the order Chitinophagales, commonly found on HW skin that feed in the Antarctic Peninsula (Bierlich et al. 2018). Chitinolytic bacteria may contribute as a defence mechanism against fungal infections (Rebollar et al. 2019). However, chitin is also a structural component of the exoskeleton of whale crustaceans' epibionts, which can cause skin lesions (Ten et al. 2022; Zhang et al. 2021), as well as of diatoms (Durkin et al. 2009), that are highly abundant towards the poles (Pierella Karlusich et al. 2025), and can adhere to HW skin (Apprill et al. 2014) and other cetaceans inhabiting cold Antarctic water (Hooper et al. 2019). Although Chitinophagales did not reach statistical significance in the Magellan Strait, possibly due to intra-group variability, its presence along with *Aliivibrio* highlights the potential role of chitinolytic bacteria on HW skin, likely reflecting interactions with fungi, epibiotic diatoms and other chitin-containing organisms that may accumulate on the host surface due to reduced skin turnover in colder waters.

In whales from Ecuador, the genus *Halomonas* was identified as differentially abundant. This halotolerant bacterium produces ectoine—to maintain osmotic balance (Feng et al. 2024)—and the polysaccharide levan, which is involved in biofilm formation (Dogsa et al. 2013), a key function that provides protection against a hostile environment and mediates host-microbe communication (Brandwein et al. 2016). Levan is also known to promote fibroblasts and keratinocytes' proliferation, thereby improving the integrity of the skin barrier (Erginer et al. 2023).

Lactic acid bacteria (LAB) also possess the ability to produce levan, such as the genus *Latilactobacillus* (Dinić et al. 2024) and higher SST-associated bacteria *Lactococcus* (Nehal et al. 2019) and *Leuconostoc* (Shi et al. 2018). LAB promotes an acidic skin pH and prevents the proliferation of pathogens through bacteriocins (Brandi et al. 2020; Suzuki and Suzuki 2021), modulates the anti-inflammatory response (Dinić et al. 2024) and exhibits antioxidant activity (Bisson et al. 2025). LAB also facilitates skin renewal and protection, as lactate plays an important role in wound healing and tissue regeneration by promoting collagen synthesis through fibroblast stimulation (Ruan et al. 2025).

Therefore, the activity of *Halomonas* and LAB, together with the physiological response of the skin to warmer waters (increased peripheral blood flow and accelerated skin turnover)—which reflects a trade-off between thermoregulation and circulation (Pitman et al. 2020)—, may help with skin renewal, facilitating the removal of diatoms and other epibionts acquired in higher latitude feeding grounds, while simultaneously supporting the skin homeostasis.

Regarding host intrinsic factors like age class, HWs' calves—which are born in low latitudes like Ecuador and subsequently migrate to the feeding ground alongside their mothers—showed a similar alpha diversity and community structure as adult whales. However, given the limited number of calf samples and data dispersion, this finding should be interpreted with caution. Still, our results are consistent with previous observations in the northern HW population (Apprill et al. 2014) and bottlenose dolphins in Florida (Robles-Malagamba et al. 2020), where age did not appear to influence the host skin microbiome. Calves and mothers maintain frequent physical contact during nursing and surface interactions, as well as through social associations for cooperative purposes (Franklin et al. 2021). Such interactions could facilitate microbial transference, leading to a relatively homogeneous skin microbiome between calves and adults. This suggests that during the early stages of whale life, maternal influence may play a crucial role in the microbial colonization of the skin.

We found no effect of host sex on HWs' skin microbiome in terms of alpha diversity or composition. Although sex-related differences have been reported in other cetacean species (Van Cise et al. 2020), HW populations appear to maintain a consistent skin microbiome between sexes (Apprill et al. 2014; Bierlich et al. 2018), possibly due to social behaviours. For example, in the breeding grounds, competitive groups formed by multiple male escorts surrounding a single female with the aim of reproducing, engage in a range of interactions of varying intensities, including bubble blowing, collisions, tail lashes and body thrashes, among others (Cusano et al. 2021). Whereas in feeding grounds, coordinated group foraging behaviours such as bubble-net feeding can also promote close physical interactions (Mastick et al. 2022). During these social activities, some direct or indirect microbial transmission could take place, as observed in cohabitant human couples (Ross et al. 2017), which may lead to similar microbial signatures between sexes in HW populations.

Seawater and HW skin shared some dominant taxa at higher taxonomical ranks, but had an overall different microbial composition at genus and family level, supporting the idea that they represent distinct ecological niches shaped by host-associated and environmental pressures (Apprill et al. 2014; Bik et al. 2016; Chiarello et al. 2017; Hansen et al. 2026; Hooper et al. 2019; Robles-Malagamba et al. 2020; Toro et al. 2021), and instead, the seawater likely acts as a reservoir of microbial diversity (Sehnal et al. 2021). This limited overlap is consistent within marine mammal studies (Bik et al. 2016; Chiarello et al. 2017), and may be partly explained by the fine-scale resolution of ASVs,

which can underestimate a true ecological overlap when analyses are conducted at the ASV level rather than at higher taxonomic ranks, particularly within broadly distributed species like whales and among large spatial sampling areas.

Within this context, the detection of genus *Ralstonia* (Burkholderiaceae) as part of the core microbiome stands out, given the small number of seawater samples analysed. This genus has been reported only in cetacean oral (Soares-Castro et al. 2019) and blow microbiomes (Wan et al. 2022), while the family Burkholderiaceae has been found on beluga whale skin (Van Cise et al. 2020), and in Patagonian fjords has been proposed as an indicator of freshwater inputs (Tamayo-Leiva et al. 2021). *Ralstonia* is widely distributed across environments (Liu et al. 2025), can act as an opportunistic human pathogen (Rajni et al. 2023), and persists in pure water systems (Adley et al. 2005; McAlister et al. 2002) through biofilm formation (Kenzaka et al. 2026). At the same time, related taxa are capable of colonizing epithelial surfaces through adhesins (David et al. 2015), supporting *Ralstonia*'s potential to associate with host skin. However, the limited number of shared ASVs between seawater and host microbiomes suggests that, despite continuous environmental exposure, only a subset of microbes successfully colonize and persist on the host. Overall, these findings may reflect a broad ecological distribution and a potential terrestrial influence on host-marine microbiomes.

5 | Conclusions

Our results show that the skin microbiome of HWs is primarily structured by geographic and environmental factors, rather than individual host-specific traits. Despite similar alpha diversity across all individuals, compositional differences were found across migratory habitats (breeding vs. feeding grounds), reflecting taxon-specific responses to latitudinal environmental gradients, suggesting microbial shifts linked to temperature and UV exposure. These patterns indicate that whale skin microbiomes may serve as sensitive indicators of ecological variability across habitats.

Author Contributions

A.I.M.-H. conceptualization, data curation, formal analysis, investigation, visualization, writing, review and editing of the original draft. L.E.E. conceptualization, fieldwork, writing, review and editing of the original draft. E.P.A.G. conceptualization, project administration, resources, supervision, review and editing of the original draft. C.C. resources, fieldwork, review and editing of the original draft. J.A. fieldwork, data curation, investigation, visualization, writing, review and editing original draft. J.C. fieldwork, review and editing of the original draft. L.O.-G. fieldwork and review the original draft. P.V. lab work, review of the original draft. A.A.-L. review and editing of the original draft. L.A.P. conceptualization, fieldwork and review of the original draft. V.S. conceptualization, fieldwork, project administration, resources, supervision, writing, review and editing of the original draft.

Acknowledgements

We want to thank Centro de Estudios del Cuaternario de Fuego-Patagonia y Antártica (CEQUA) for making possible the development of this research as part of the science strengthening project 'Microbiome of external surface of keystone species of ecological and economic importance in the Magallanes region and the Chilean Antarctic: microbes as bioindicators of the aquatic ecosystem health in a global warming scenario' (ANID project number R20F0009). We are also grateful to all CEQUA's team members for their valuable work during field campaigns to the Francisco Coloane Marine and Coastal Protected Area at the Magellan Strait, Chile and Machalilla National Park in Ecuador. From Ecuador, we are grateful to the Pacific Whale Foundation, in addition to Luna, Hernán and May, for their support during field campaigns in Machalilla National Park, as well as the volunteers from the Central University, the Pontifical Catholic University of Ecuador, the team and the tourism company Palo Santo Travel, in Puerto López. We also want to thank Fernando Félix from El Museo de Ballenas in Salinas, Ecuador and Universidad Católica del Ecuador, Quito, Ecuador, for his assistance with whale sampling permits. We also thank the Laboratory for Atmospheric Research (LIA) at the University of Magallanes for providing daily UVA and UVB values from the Magellan Strait. We thank Dr. Rosalinda Tapia López for her laboratory assistance in sample processing and Dr. Erika Aguirre-Planter for logistic support, both from the Instituto de Ecología, Universidad Nacional Autónoma de México. This manuscript was prepared during the sabbatical leave 2024-25 of L.E.E. and V.S., who acknowledge their institution, Universidad Nacional Autónoma de México for the support provided. We also acknowledge the support received from the Consejo Nacional de Humanidades, Ciencia y Tecnología (CONAHCyT) of México that transitioned to Secretaría de Ciencia, Humanidades, Tecnología e Innovación (SECIHTI) through a graduate scholarship (CVU827448) to A.I.M.-H. This study is part of the requirements for obtaining a Doctoral degree at the Posgrado en Ciencias Biológicas of the Universidad Nacional Autónoma de México (UNAM).

Funding

This work was financed by the Agencia Nacional de Investigación y Desarrollo de Chile (ANID) project number R20F0009. The field campaign in Ecuador was supported by Palo Santo Travel and the Pacific Whale Foundation. Funders had no role in study design, analysis or study report.

Ethics Statement

Samples of HWs were obtained by experienced researchers following the bioethical guidelines of the Comité de Ética, Bioética y Bioseguridad from Universidad de Concepción (protocol number CEBB 1081–2021). The protocol and number of samples were performed according to a research permit N°E-2021-531 of the Subsecretaría de Pesca y Acuicultura of Chile, and by the Ministerio del Ambiente, Agua y Transición Ecológica N°2323 from Ecuador. This study was conducted in accordance with the local Animal Protection Law from Chile and the local Forestry and Conservancy of Natural Protected Areas and Wildlife Law from Ecuador. In addition, the guidelines from the general regulation for watching mammals, reptiles and hydrobiological birds and cetacean sighting registry from the Subsecretaría de Pesca y Acuicultura of Chile and the Interministerial agreement no. 20140004 from Ecuador were followed.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The raw 16S rRNA sequences used in this study are available via SRA BioProject accession number PRJNA1230204. https://dataview.ncbi.nlm.nih.gov/object/PRJNA1230204?reviewer=fdf954spsvkt17oq6i111d6gn6

References

Acevedo, J., A. Aguayo-Lobo, J. Allen, et al. 2017. "Migratory Preferences of Humpback Whales Between Feeding and Breeding Grounds in the Eastern South Pacific." *Marine Mammal Science* 33, no. 4: 1035–1052. https://doi.org/10.1111/mms.12423.

Acevedo, J., A. Aguayo-Lobo, and L. A. Pastene. 2006. "Filopatría de la ballena jorobada (*Megaptera novaeangliae* Borowski, 1781), al área de alimentación del estrecho de Magallanes." *Revista de Biología Marina y Oceanografía* 41, no. 1: 11–19. https://doi.org/10.4067/S0718-19572006000100004.

Acevedo, J., D. Haro, L. Dalla Rosa, et al. 2013. "Evidence of Spatial Structuring of Eastern South Pacific Humpback Whale Feeding Grounds." *Endangered Species Research* 22, no. 1: 33–38. https://doi.org/10.3354/esr00536.

Acevedo, J., J. Plana, A. Aguayo-Lobo, and L. Pastene. 2011. "Surface Feeding Behavior of Humpback Whales in the Magellan Strait." *Revista de Biología Marina y Oceanografía* 46, no. 3: 483–490.

Adley, C. C., M. P. Ryan, J. T. Pembroke, and F. M. Saieb. 2005. "Ralstonia Picketii: Biofilm Formation in High Purity Water." In *Biofilms: Persistence and Ubiquity*, edited by A. J. McBain, D. G. Allison, J. Pratten, D. A. Spratt, M. Upton, and J. Verran, 151–162. Biofilm Club.

Aguayo-Lobo, A., J. Acevedo, and S. Cornejo. 2011. *La ballena jorobada, conservación en el Parque Marino Francisco Coloane*. Ocho Libros.

Andersen, K. S., R. H. Kirkegaard, S. M. Karst, and M. Albertsen. 2018. "ampvis2: An R Package to Analyse and Visualise 16S rRNA Amplicon Data." *BioRxiv: The Preprint Server for Biology*: 299537. https://doi.org/10.1101/299537.

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. "Multivariate Dispersion as a Measure of Beta Diversity." *Ecology Letters* 9, no. 6: 683–693. https://doi.org/10.1111/j.1461-0248.2006.00926.x.

Anderson, M. J., and T. J. Willis. 2003. "Canonical Analysis of Principal Coordinates: A Useful Method of Constrained Ordination for Ecology." *Ecology* 84, no. 2: 511–525. https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2.

Apprill, A. 2017. "Marine Animal Microbiomes: Toward Understanding Host-Microbiome Interactions in a Changing Ocean." *Frontiers in Marine Science* 4, no. 222: 1–9. https://doi.org/10.3389/fmars.2017.00222.

Apprill, A., C. A. Miller, A. M. van Cise, et al. 2020. "Marine Mammal Skin Microbiotas Are Influenced by Host Phylogeny." *Royal Society Open Science* 7, no. 5: 192046. https://doi.org/10.1098/rsos.192046.

Apprill, A., T. A. Mooney, E. Lyman, A. K. Stimpert, and M. S. Rappé. 2011. "Humpback Whales Harbour a Combination of Specific and Variable Skin Bacteria." *Environmental Microbiology Reports* 3, no. 2: 223–232. https://doi.org/10.1111/j.1758-2229.2010.00213.x.

Apprill, A., J. Robbins, A. M. Eren, et al. 2014. "Humpback Whale Populations Share a Core Skin Bacterial Community: Towards a Health Index for Marine Mammals?" *PLoS One* 9, no. 3: e90785. https://doi.org/10.1371/journal.pone.0090785.

Arola, A., S. Kalliskota, P. N. Den Outer, et al. 2002. "Assessment of Four Methods to Estimate Surface UV Radiation Using Satellite Data, by Comparison With Ground Measurements From Four Stations in Europe." *Journal of Geophysical Research: Atmospheres* 107, no. D16: ACL-11. https://doi.org/10.1029/2001JD000462.

Avendaño-Herrera, R., A. E. Toranzo, and B. Magariños. 2006. "Tenacibaculosis Infection in Marine Fish Caused by *Tenacibaculum maritimum*: A Review." *Diseases of Aquatic Organisms* 71, no. 3: 255–266. https://doi.org/10.3354/DAO071255.

Barnett, D. J. M., I. C. W. Arts, and J. Penders. 2021. "microViz: An R Package for Microbiome Data Visualization and Statistics." *Journal of Open Source Software* 6, no. 63: 3201. https://doi.org/10.21105/joss.03201.

Bernhard, G. H., A. F. Bais, P. J. Aucamp, A. R. Klekociuk, J. B. Liley, and R. L. McKenzie. 2023. "Stratospheric Ozone, UV Radiation, and Climate Interactions." *Photochemical & Photobiological Sciences* 22: 1–53. https://doi.org/10.1007/s43630-023-00371-y.

Bierlich, K. C., C. Miller, E. DeForce, A. S. Friedlaender, D. W. Johnston, and A. Apprill. 2018. "Temporal and Regional Variability in the Skin Microbiome of Humpback Whales Along the Western Antarctic Peninsula." *Applied and Environmental Microbiology* 84, no. 5: 1–15. https://doi.org/10.1128/AEM.02574-17.

Bik, E. M., E. K. Costello, A. D. Switzer, et al. 2016. "Marine Mammals Harbor Unique Microbiotas Shaped by and Yet Distinct From the Sea." *Nature Communications* 7, no. 1: 10516. https://doi.org/10.1038/ncomms10516.

Bisson, G., C. Comuzzi, L. G. Gómez-Mascaraque, et al. 2025. "Investigating the Bioactivities of a Dextran and Levan Mixture Produced by the Sourdough-Derived *Leuconostoc mesenteroides* Strain DSA_F." *Food and Bioprocess Technology* 18, no. 4: 3918–3932. https://doi.org/10.1007/s11947-024-03711-7.

Borcard, D., F. Gillet, and P. Legendre. 2011. "Numerical Ecology With R." In *Use R!* edited by R. Gentleman, K. Hornik, and G. G. Parmigiani. Springer. https://doi.org/10.1007/978-1-4419-7976-6.

Brandi, J., S. Cheri, M. Manfredi, et al. 2020. "Exploring the Wound Healing, Anti-Inflammatory, Anti-Pathogenic and Proteomic Effects of Lactic Acid Bacteria on Keratinocytes." *Scientific Reports* 10, no. 1: 11572. https://doi.org/10.1038/s41598-020-68483-4.

Brandwein, M., D. Steinberg, and S. Meshner. 2016. "Microbial Biofilms and the Human Skin Microbiome." *npj Biofilms and Microbiomes* 2, no. 1: 1–6. https://doi.org/10.1038/s41522-016-0004-z.

Burrell, A. D., P. Feldschreiber, and C. J. Dean. 1971. "DNA-Membrane Association and the Repair of Double Breaks in X-Irradiated *Micrococcus radiodurans*." *Biochimica et Biophysica Acta (BBA)—Nucleic Acids and Protein Synthesis* 247, no. 1: 38–53. https://doi.org/10.1016/0005-2787(71)90805-7.

Callahan, B. J., P. J. McMurdie, M. J. Rosen, A. W. Han, A. J. A. Johnson, and S. P. Holmes. 2016. "DADA2: High-Resolution Sample Inference From Illumina Amplicon Data." *Nature Methods* 13, no. 7: 581–583. https://doi.org/10.1038/nmeth.3869.

Casiccia, C., F. Zamorano, and A. Hernández. 2008. "Erythemal Irradiance at the Magellan's Region and Antarctic Ozone Hole 1999-2005." *Atmosfera* 21, no. 1: 1–12.

Castro, C., J. Castrillon, and W. Gómez. 2022. "Whale-Watching Tourism as a Driving Force for Socioeconomic Development in Puerto López, Machalilla National Park, Manabí, Ecuador." *Mammalia Aequatorialis* 4: 67–80. https://doi.org/10.59763/mam.aeq.v4i.51.

Castro, C., M. H. Engel, and A. R. Martin. 2023. "First Humpback Whale Movement Between Ecuador and the South Sandwich Islands: Redefines the Easternmost Migration Point of Breeding Stock G." *Aquatic Mammals* 49, no. 4: 382–387. https://doi.org/10.1578/AM.49.4.2023.382.

Cerdeira Estrada, S., N. M. González, F. E. Müller Karger, and R. Pérez de los Reyes. 2015. "Estudio comparativo de la temperatura superficial del mar detectada vía satelite y por mediciones *in situ* al norte de Cuba y NE de la península de Yucatán." *Mapping* 60: 66–72.

Chen, H., Q. Zhao, Q. Zhong, et al. 2022. "Skin Microbiome, Metabolome and Skin Phenome, From the Perspectives of Skin as an Ecosystem." *Phenomics* 2, no. 6: 363–382. https://doi.org/10.1007/s43657-022-00073-y.

Chiarello, M., S. Villéger, C. Bouvier, J. C. Auguet, and T. Bouvier. 2017. "Captive Bottlenose Dolphins and Killer Whales Harbor a Species-Specific Skin Microbiota That Varies Among Individuals." *Scientific Reports* 7, no. 1: 1–12. https://doi.org/10.1038/s41598-017-15220-z.

Chinacalle-Martínez, N., E. García-Rada, J. López-Macías, et al. 2021. "Oceanic Primary Production Trend Patterns Along Coast of Ecuador." *Neotropical Biodiversity* 7, no. 1: 379–391. https://doi.org/10.1080/23766808.2021.1964915.

Coenye, T., K.-J. Spittaels, and Y. Achermann. 2022. "The Role of Biofilm Formation in the Pathogenesis and Antimicrobial Susceptibility of *Cutibacterium acnes*." *Biofilm* 4: 100063. https://doi.org/10.1016/j.biofilm.2021.100063.

Comas, A. X. 1984. "Notas sobre el clima de Magallanes (Chile)." *Revista de Geografía* 18: 95–110.

Cordero, R. R., S. Feron, A. Damiani, et al. 2022. "Persistent Extreme Ultraviolet Irradiance in Antarctica Despite the Ozone Recovery Onset." *Scientific Reports* 12, no. 1: 1266. https://doi.org/10.1038/s41598-022-05449-8.

Cucalón, E. 1986. "Sinopsis de la oceanografía de la región frente a las costas de Ecuador." In *Bases biológicas y marco conceptual para el manejo de los recursos pelagicos en el Pacifico Suroriental*, 30–33. Oldepesca.

Cucalón, E. 1989. "Oceanographic Characteristics Off the Coast of Ecuador." In *A Sustainable Shrimp Mariculture Industry for Ecuador*, edited by S. Olsen and L. Arriaga, 185–194. Coastal Resources Center, University of Rhode Island.

Cusano, D. A., D. Paton, M. J. Noad, and R. A. Dunlop. 2021. "Socially Complex Breeding Interactions in Humpback Whales Are Mediated Using a Complex Acoustic Repertoire." *Frontiers in Marine Science* 8: 665186. https://doi.org/10.3389/fmars.2021.665186.

Dalla Rosa, L., F. Félix, P. T. Stevick, et al. 2012. "Feeding Grounds of the Eastern South Pacific Humpback Whale Population Include the South Orkney Islands." *Polar Research* 31, no. 1: 17324. https://doi.org/10.3402/polar.v31i0.17324.

Daly, M. J., O. Ling, and K. W. Minton. 1994. "Interplasmidic Recombination Following Irradiation of the Radioresistant Bacterium *Deinococcus radiodurans*." *Journal of Bacteriology* 176, no. 24: 7506–7515. https://doi.org/10.1128/jb.176.24.7506-7515.1994.

David, J., R. E. Bell, and G. C. Clark. 2015. "Mechanisms of Disease: Host-Pathogen Interactions Between Burkholderia Species and Lung Epithelial Cells." *Frontiers in Cellular and Infection Microbiology* 5: 80. https://doi.org/10.3389/fcimb.2015.00080.

Davis, N. M., D. M. Proctor, S. P. Holmes, D. A. Relman, and B. J. Callahan. 2018. "Simple Statistical Identification and Removal of Contaminant Sequences in Marker-Gene and Metagenomics Data." *Microbiome* 6, no. 1: 226. https://doi.org/10.1186/s40168-018-0605-2.

De Weerdt, J., E. A. Ramos, and T. Cheeseman. 2020. "Northernmost Records of Southern Hemisphere Humpback Whales (*Megaptera novaeangliae*) Migrating From the Antarctic Peninsula to the Pacific Coast of Nicaragua." *Marine Mammal Science* 36, no. 3: 1015–1021. https://doi.org/10.1111/mms.12677.

Dinić, M., J. L. Burgess, J. Lukić, et al. 2024. "Postbiotic Lactobacilli Induce Cutaneous Antimicrobial Response and Restore the Barrier to Inhibit the Intracellular Invasion of *Staphylococcus aureus* In Vitro and Ex Vivo." *FASEB Journal* 38, no. 14: e23801. https://doi.org/10.1096/fj.202400054RR.

Dogsa, I., M. Brloznik, D. Stopar, and I. Mandic-Mulec. 2013. "Exopolymer Diversity and the Role of Levan in *Bacillus subtilis* Biofilms." *PLoS One* 8, no. 4: e62044. https://doi.org/10.1371/journal.pone.0062044.

Dominguez-Sanchez, C. A., S. H. Ferguson, T. Edkins, B. G. Young, and J. Kringorn. 2024. "Pilot Study: Decoding the Skin Microbiome of Bowhead (*Balaena mysticetus*) and Killer Whales (*Orcinus orca*) in Nunavut, Canada." *Arctic Science* 10, no. 1: 169–188. https://doi.org/10.1139/as-2023-0028.

Donlon, C. J., P. J. Minnett, C. Gentemann, et al. 2002. "Toward Improved Validation of Satellite Sea Surface Skin Temperature Measurements for Climate Research." *Journal of Climate* 15, no. 4: 353–369. https://doi.org/10.1175/1520-0442(2002)015%3C0353:TIVOSS%3E2.0.CO;2.

Dunlap, P. V. 2009. "Bioluminescence, Microbial." In *Encyclopedia of Microbiology, Third Edition*, 45–61. Elsevier. https://doi.org/10.1016/B978-012373944-5.00066-3.

Durkin, C. A., T. Mock, and E. V. Armbrust. 2009. "Chitin in Diatoms and Its Association With the Cell Wall." *Eukaryotic Cell* 8, no. 7: 1038–1050. https://doi.org/10.1128/EC.00079-09.

Elasri, M. O., and R. V. Miller. 1999. "Study of the Response of a Biofilm Bacterial Community to UV Radiation." *Applied and Environmental Microbiology* 65, no. 5: 2025–2031. https://doi.org/10.1128/AEM.65.5.2025-2031.1999.

Erginer, M., B. Gökalsin, S. Tornaci, C. Sesal, and E. Toksoy Öner. 2023. "Exploring the Potential of Halomonas Levan and Its Derivatives as Active Ingredients in Cosmeceutical and Skin Regenerating Formulations." *International Journal of Biological Macromolecules* 240: 124418. https://doi.org/10.1016/J.IJBIOMAC.2023.124418.

Feng, Y., M. Qiu, L. Shao, et al. 2024. "Strategies for the Biological Production of Ectoine by Using Different Chassis Strains." *Biotechnology Advances* 70: 108306. https://doi.org/10.1016/j.biotechadv.2023.108306.

Findlay, K. P., S. M. Seakamela, M. A. Meÿer, et al. 2017. "Humpback Whale 'Super-Groups'—A Novel Low-Latitude Feeding Behaviour of Southern Hemisphere Humpback Whales (*Megaptera novaeangliae*) in the Benguela Upwelling System." *PLoS One* 12, no. 3: e0172002. https://doi.org/10.1371/journal.pone.0172002.

Flacher, A., J. Sonnenholzner, D. Pérez, L. Jaramillo, E. Espinoza, and Ecociencia. 1997. "Diagnóstico ecológico y socieconónomico del área marino-costera del Parque Nacional Machalilla." In *Evaluación del área marina del Parque Nacional Machalilla: Parte I*. Instituto Ecuatoriano Forestal y de Areas Naturales y Vida Silvestre, Dirección Nacional de Areas Naturales y Vida Silvestre.

Franklin, T., W. Franklin, L. Brooks, P. Harrison, A. A. Pack, and P. J. Clapham. 2021. "Social Behaviour of Humpback Whales (*Megaptera novaeangliae*) in Hervey Bay, Eastern Australia, a Preferential Female Stopover During the Southern Migration." *Frontiers in Marine Science* 8: 652147. https://doi.org/10.3389/fmars.2021.652147.

Gerber, E., R. Bernard, S. Castang, et al. 2015. "*Deinococcus* as New Chassis for Industrial Biotechnology: Biology, Physiology and Tools." *Journal of Applied Microbiology* 119, no. 1: 1–10. https://doi.org/10.1111/jam.12808.

Ghosh, A., and S. Panda. 2023. "Cutaneous Dysbiosis and Dermatophytosis: The Unexplored Link." *Indian Journal of Dermatology* 68, no. 5: 508–514. https://doi.org/10.4103/IJD.IJD_828_23.

Gibbons, J., J. J. Capella, and C. Valladares. 2003. "Rediscovery of a Humpback Whale (*Megaptera novaeangliae*) Feeding Ground in the Straits of Magellan, Chile." *Journal of Cetacean Research and Management* 5, no. 2: 203–208.

Gill, P., K. Evans, and H. Wapstra. 1999. "Feeding by Humpback Whales in Tasmanian Waters." *Records of the Queen Victoria Museum* 107: 1–5.

Gilson, A., M. Syvanen, K. Levine, and J. Banks. 1998. "Deer Gender Determination by Polymerase Chain Reaction: Validation Study and Application to Tissues, Bloodstains, and Hair Forensic Samples From California." *California Fish & Game* 84, no. 4: 159–169.

Glynn, P. W. 2003. "Latin American Coral Reefs." In *Coral Communities and Coral Reefs of Ecuador*, edited by J. Cortés. Elsevier Science. https://doi.org/10.1016/B978-044451388-5/50020-5.

Guo, Q., Y. Zhan, W. Zhang, et al. 2023. "Development and Regulation of the Extreme Biofilm Formation of *Deinococcus radiodurans* R1 Under Extreme Environmental Conditions." *International Journal of Molecular Sciences* 25, no. 1: 421. https://doi.org/10.3390/ijms25010421.

Hansen, J. J., J. C. G. Bloodgood, B. K. Reese, et al. 2026. "Novel Method for Collecting Skin Microbiome Samples From Free-Ranging Bottlenose Dolphin." *Marine Mammal Science* 42, no. 1: e70104. https://doi.org/10.1111/mms.70104.

Harel, N., N. Ogen-Shtern, L. Reshef, D. Biran, E. Z. Ron, and U. Gophna. 2023. "Skin Microbiome Bacteria Enriched Following Long Sun Exposure Can Reduce Oxidative Damage." *Research in Microbiology* 174, no. 8: 104138. https://doi.org/10.1016/j.resmic.2023.104138.

Haro, D., L. Riccialdelli, J. Acevedo, A. Aguayo-Lobo, and A. Montiel. 2016. "Trophic Ecology of Humpback Whales (*Megaptera novaeangliae*) in the Magellan Strait as Indicated by Carbon and Nitrogen Stable Isotopes." *Aquatic Mammals* 42, no. 2: 233–243. https://doi.org/10.1578/AM.42.2.2016.233.

Hooper, R., J. C. Brealey, T. van der Valk, et al. 2019. "Host-Derived Population Genomics Data Provides Insights Into Bacterial and Diatom Composition of the Killer Whale Skin." *Molecular Ecology* 28, no. 2: 484–502. https://doi.org/10.1111/mec.14860.

Huovinen, P., J. Ramírez, and I. Gómez. 2016. "Underwater Optics in Sub-Antarctic and Antarctic Coastal Ecosystems." *PLoS One* 11, no. 5: e0154887. https://doi.org/10.1371/journal.pone.0154887.

INOCAR. 2015. *Atlas marino costero del Ecuador*. Ministerio de Defensa Nacional.

Karimi, B., P. A. Maron, N. Chemidlin-Prevost Boure, N. Bernard, D. Gilbert, and L. Ranjard. 2017. "Microbial Diversity and Ecological Networks as Indicators of Environmental Quality." *Environmental Chemistry Letters* 15, no. 2: 265–281. https://doi.org/10.1007/s10311-017-0614-6.

Kazantzidis, A., A. F. Bais, J. Gröbner, et al. 2006. "Comparison of Satellite-Derived UV Irradiances With Ground-Based Measurements at Four European Stations." *Journal of Geophysical Research: Atmospheres* 111, no. D13207: 2005JD006672. https://doi.org/10.1029/2005JD006672.

Keller, A. G., A. Apprill, P. Lebaron, et al. 2021. "Characterizing the Culturable Surface Microbiomes of Diverse Marine Animals." *FEMS Microbiology Ecology* 97, no. 4: 1–14. https://doi.org/10.1093/femsec/fiab040.

Kenzaka, T., T. Ichijo, and T. Yamazaki. 2026. "High Extracellular Polymeric Substance Production and Biofilm-Forming Capacity of *Ralstonia pickettii* Isolates From ISS Potable Water." *Microbiology Spectrum* 14, no. 3: e02913-25. https://doi.org/10.1128/spectrum.02913-25.

Keshari, S., A. Balasubramaniam, B. Myagmardoloonjin, D. R. Herr, I. P. Negari, and C.-M. Huang. 2019. "Butyric Acid From Probiotic *Staphylococcus epidermidis* in the Skin Microbiome Down-Regulates the Ultraviolet-Induced Pro-Inflammatory IL-6 Cytokine via Short-Chain Fatty Acid Receptor." *International Journal of Molecular Sciences* 20, no. 18: 4477. https://doi.org/10.3390/ijms20184477.

Kleine Bardenhorst, S., M. Vital, A. Karch, and N. Rübsamen. 2022. "Richness Estimation in Microbiome Data Obtained From Denoising Pipelines." *Computational and Structural Biotechnology Journal* 20: 508–520. https://doi.org/10.1016/J.CSBJ.2021.12.036.

Klindworth, A., E. Pruesse, T. Schweer, et al. 2013. "Evaluation of General 16S Ribosomal RNA Gene PCR Primers for Classical and Next-Generation Sequencing-Based Diversity Studies." *Nucleic Acids Research* 41, no. 1: e1. https://doi.org/10.1093/nar/gks808.

Kusube, M., T. S. Kyaw, K. Tanikawa, et al. 2017. "*Colwellia marinimaniae* sp. Nov., a Hyperpiezophilic Species Isolated From an Amphipod Within the Challenger Deep, Mariana Trench." *International Journal of Systematic and Evolutionary Microbiology* 67, no. 4: 824–831. https://doi.org/10.1099/ijsem.0.001671.

Lahti, L., and S. Shetty. 2019. "Tools for Microbiome Analysis in R. Microbiome Package v.1.32.0. (Version 1.32.0) [Computer Software]."

Lefort, K. J., L. Storrie, N. E. Hussey, and S. H. Ferguson. 2025. "Aseasonal Migration of a Northern Bottlenose Whale Provides Support for the Skin Molt Migration Hypothesis." *Ecology and Evolution* 15, no. 2: e70921. https://doi.org/10.1002/ece3.70921.

Lin, H., and S. D. Peddada. 2024. "Multigroup Analysis of Compositions of Microbiomes With Covariate Adjustments and Repeated Measures." *Nature Methods* 21, no. 1: 83–91. https://doi.org/10.1038/S41592-023-02092-7.

Liu, G., C. Mao, Q. Li, D. Huo, and T. Li. 2025. "Comparative Genomic Analysis Reveals the Adaptive Traits of *Ralstonia* spp. in Aquatic Environments." *Frontiers in Microbiology* 16: 1625651. https://doi.org/10.3389/fmicb.2025.1625651.

López-Ramírez, J. A., M. V. Morales-Zárate, U. Rubio-Rodríguez, C. A. Salinas-Zavala, and F. Chávez-Juárez. 2024. "Sea Surface Temperature Differences Between in Situ and GHRSST (L4) Records in a Socio-Ecological Critical Area of the Northeastern Pacific Ocean May 2015 to July 2016." *Latin American Journal of Aquatic Research* 52, no. 4: 637–645. https://doi.org/10.3856/vol52-issue4-fulltext-3169.

Lunjani, N., S. Ahearn-Ford, F. S. Dube, C. Hlela, and L. O'Mahony. 2021. "Mechanisms of Microbe-Immune System Dialogue Within the Skin." *Genes and Immunity* 22, no. 5–6: 276. https://doi.org/10.1038/S41435-021-00133-9.

Ma, Y., Z. Ni, L. Zhu, et al. 2026. "Skin Commensal *Cutibacterium acnes* Alleviates UVB-Induced Solar Dermatitis via Ceramide-Mediated TLR4–MyD88–NF-κB." *Free Radical Biology and Medicine* 249: 76–88. https://doi.org/10.1016/j.freeradbiomed.2026.02.074.

Mabrok, M., A. M. Algammal, E. Sivaramasamy, et al. 2023. "Tenacibaculosis Caused by *Tenacibaculum maritimum*: Updated Knowledge of This Marine Bacterial Fish Pathogen." *Frontiers in Cellular and Infection Microbiology* 12: 1068000. https://doi.org/10.3389/fcimb.2022.1068000.

Mackintosh, N. A. 1965. *The Stocks of Whales*. Fishing News (Books) Ltd.

Mallick, H., A. Rahnavard, L. J. McIver, et al. 2021. "Multivariable Association Discovery in Population-Scale Meta-Omics Studies." *PLoS Computational Biology* 17, no. 11: e1009442. https://doi.org/10.1371/journal.pcbi.1009442.

Mastick, N. C., D. Wiley, D. E. Cade, C. Ware, S. E. Parks, and A. S. Friedlaender. 2022. "The Effect of Group Size on Individual Behavior of Bubble-Net Feeding Humpback Whales in the Southern Gulf of Maine." *Marine Mammal Science* 38, no. 3: 959–974. https://doi.org/10.1111/mms.12905.

McAlister, M., L. Kulakov, J. O'Hanlon, M. Larkin, and K. Ogden. 2002. "Survival and Nutritional Requirements of Three Bacteria Isolated From Ultrapure Water." *Journal of Industrial Microbiology and Biotechnology* 29, no. 2: 75–82. https://doi.org/10.1038/sj.jim.7000273.

McMurdie, P. J., and S. Holmes. 2013. "Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data." *PLoS One* 8, no. 4: e61217. https://doi.org/10.1371/journal.pone.0061217.

Mercer, S. D., A. Elias, G. Taylor, et al. 2026. "Ultraviolet Radiation Reshapes the Metabolome of Skin Commensal Bacteria, Influencing AhR Signaling and Barrier Function." *Applied and Environmental Microbiology* 92, no. 4: e0238525. https://doi.org/10.1128/aem.02385-25.

Methé, B. A., K. E. Nelson, J. W. Deming, et al. 2005. "The Psychrophilic Lifestyle as Revealed by the Genome Sequence of *Colwellia psychrerythraea* 34H Through Genomic and Proteomic Analyses." *Proceedings of the National Academy of Sciences* 102, no. 31: 10913–10918. https://doi.org/10.1073/pnas.0504766102.

Millien, V., N. Stafiej, F. Félix, and H. M. Guzman. 2025. "Migratory Behaviour of Humpback Whales in the Southeastern Pacific Under Climate Change." *Scientific Reports* 15, no. 1: 3989. https://doi.org/10.1038/s41598-025-87489-4.

Minich, J. J., A. Härer, J. Vechinski, et al. 2022. "Host Biology, Ecology and the Environment Influence Microbial Biomass and Diversity in 101 Marine Fish Species." *Nature Communications* 13, no. 1: 6978. https://doi.org/10.1038/s41467-022-34557-2.

Ministerio del Medio Ambiente. 2018. *Área Marina Costera Protegida de Múltiples Usos y Parque Marino Francisco Coloane. Plan estratégico para el manejo de conservación y desarrollo de actividades sostenibles 2018–2027*, 56. Secretaría Regional Ministerial del Medio Ambiente de

Magallanes y Antárctica Chilena, Comité Operativo del Área Marina Costera Protegina de Múltiples Usos Francisco Coloane,Wildlife Conservation Society.

Nakatsuji, T., S. L. Brinton, K. J. Cavagnero, et al. 2023. "Competition Between Skin Antimicrobial Peptides and Commensal Bacteria in Type 2 Inflammation Enables Survival of *S. aureus*." *Cell Reports* 42, no. 5: 112494. https://doi.org/10.1016/j.celrep.2023.112494.

Nehal, F., M. Sahnoun, S. Smaoui, B. Jaouadi, S. Bejar, and S. Mohammed. 2019. "Characterization, High Production and Antimicrobial Activity of Exopolysaccharides From *Lactococcus lactis* F-Mou." *Microbial Pathogenesis* 132: 10–19. https://doi.org/10.1016/j.micpath.2019.04.018.

Noren, D. P., and J. A. Mocklin. 2012. "Review of Cetacean Biopsy Techniques: Factors Contributing to Successful Sample Collection and Physiological and Behavioral Impacts." *Marine Mammal Science* 28, no. 1: 154–199. https://doi.org/10.1111/j.1748-7692.2011.00469.x.

Ochoa-Sánchez, M., E. P. Acuña Gomez, L. Ramírez-Fenández, L. E. Eguiarte, and V. Souza. 2023. "Current Knowledge of the Southern Hemisphere Marine Microbiome in Eukaryotic Hosts and the Strait of Magellan Surface Microbiome Project." *PeerJ* 11: 2–44. https://doi.org/10.7717/peerj.15978.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2025. "Vegan: Community Ecology Package [Computer Software]." https://CRAN.R-project.org/package=vegan.

O'Reilly, J. E., S. Maritorena, G. Mitchell, et al. 1998. "Ocean Color Chlorophyll Algorithms for SeaWiFS." *Journal of Geophysical Research* 103, no. C11: 24937–24953. https://doi.org/10.1029/98JC02160.

Pacheco, A. S., S. Silva, and B. Alcorta. 2009. "Winter Distribution and Group Composition of Humpback Whales (*Megaptera novaeangliae*) Off Northern Peru." *Latin American Journal of Aquatic Mammals* 7, no. 1–2: 33–38. https://doi.org/10.5597/lajam00131.

Panella, S., A. Michellato, R. Perdicaro, G. Magazzu, F. Decembrini, and P. Scarazzato. 1991. "A Preliminary Contribution to Understanding the Hydrological Characteristics of the Strait of Magellan: Austral Spring 1989." *Bollettino di Oceanologia Teorica Ed Applicata* 9, no. 2–3: 107–126.

Pearman, W. S., G. A. Duffy, N. J. Gemmell, S. E. Morales, and C. I. Fraser. 2024. "Long-Distance Movement Dynamics Shape Host Microbiome Richness and Turnover." *FEMS Microbiology Ecology* 100, no. 7: fiae089. https://doi.org/10.1093/femsec/fiae089.

Pérez-Pascual, D., A. Lunazzi, G. Magdelenat, et al. 2017. "The Complete Genome Sequence of the Fish Pathogen *Tenacibaculum maritimum* Provides Insights Into Virulence Mechanisms." *Frontiers in Microbiology* 8: 1542. https://doi.org/10.3389/fmicb.2017.01542.

Pierella Karlusich, J. J., K. Cosnier, L. Zinger, et al. 2025. "Patterns and Drivers of Diatom Diversity and Abundance in the Global Ocean." *Nature Communications* 16, no. 1: 3452. https://doi.org/10.1101/2024.06.08.598090.

Pitman, R. L., J. W. Durban, T. Joyce, H. Fearnbach, S. Panigada, and G. Lauriano. 2020. "Skin in the Game: Epidermal Molt as a Driver of Long-Distance Migration in Whales." *Marine Mammal Science* 36, no. 2: 565–594. https://doi.org/10.1111/mms.12661.

Prescott, S. L., D. L. Larcombe, A. C. Logan, et al. 2017. "The Skin Microbiome: Impact of Modern Environments on Skin Ecology, Barrier Integrity, and Systemic Immune Programming." *World Allergy Organization Journal* 10, no. 1: 29. https://doi.org/10.1186/S40413-017-0160-5.

Quast, C., E. Pruesse, P. Yilmaz, et al. 2013. "The SILVA Ribosomal RNA Gene Database Project: Improved Data Processing and Web-Based Tools." *Nucleic Acids Research* 41, no. D1: D590–D596. https://doi.org/10.1093/NAR/GKS1219.

R Core Team. 2024. *R: A Language and Environment for Statistical Computing, (Version 4.4.1) [Computer Software]*. R Foundation for Statistical Computing. https://www.R-project.org/.

Rajni, E., P. Goel, M. K. Sarna, A. Jorwal, C. Sharma, and P. Rijhwani. 2023. "The Genus *Ralstonia*: The New Kid on the Block." *Journal of the Royal College of Physicians of Edinburgh* 53, no. 1: 44–52. https://doi.org/10.1177/14782715221145579.

Rebollar, E. A., T. Bridges, M. C. Hughey, D. Medina, L. K. Belden, and R. N. Harris. 2019. "Integrating the Role of Antifungal Bacteria Into Skin Symbiotic Communities of Three Neotropical Frog Species." *ISME Journal* 13, no. 7: 1763–1775. https://doi.org/10.1038/S41396-019-0388-X.

Robinson, S. A., L. E. Revell, R. Mackenzie, and R. Ossola. 2024. "Extended Ozone Depletion and Reduced Snow and Ice Cover—Consequences for Antarctic Biota." *Global Change Biology* 30, no. 4: 1–10. https://doi.org/10.1111/gcb.17283.

Robles-Malagamba, M. J., M. T. Walsh, M. S. Ahasan, et al. 2020. "Characterization of the Bacterial Microbiome Among Free-Ranging Bottlenose Dolphins (*Tursiops truncatus*)." *Heliyon* 6, no. 6: e03944. https://doi.org/10.1016/J.HELIYON.2020.E03944.

Ross, A. A., A. C. Doxey, and J. D. Neufeld. 2017. "The Skin Microbiome of Cohabiting Couples." *MSystems* 2, no. 4: e00043-17. https://doi.org/10.1128/msystems.00043-17.

Ruan, D., T. Hu, X. Yang, X. Mo, and Q. Ju. 2025. "Lactate in Skin Homeostasis: Metabolism, Skin Barrier, and Immunomodulation." *Frontiers in Immunology* 16: 1510559. https://doi.org/10.3389/fimmu.2025.1510559.

Rusch, D. B., A. L. Halpern, G. Sutton, et al. 2007. "The Sorcerer II Global Ocean Sampling Expedition: Northwest Atlantic Through Eastern Tropical Pacific." *PLoS Biology* 5, no. 3: e77. https://doi.org/10.1371/journal.pbio.0050077.

Scheidat, M., C. Castro, J. Denkinger, J. Gonz, and D. Adelung. 2000. "A Breeding Area for Humpback Whales (*Megaptera novaeangliae*) of Ecuador." *Journal of Cetacean Research and Management* 2: 165–171. https://doi.org/10.47536/jcrm.v2i3.501.

Sehnal, L., E. Brammer-Robbins, A. M. Wormington, et al. 2021. "Microbiome Composition and Function in Aquatic Vertebrates: Small Organisms Making Big Impacts on Aquatic Animal Health." *Frontiers in Microbiology* 12: 567408. https://doi.org/10.3389/fmicb.2021.567408.

Shannon, C. E. 1948. "A Mathematical Theory of Communication." *Bell System Technical Journal* 27: 379–423.

Shi, Q., Y. Hou, Y. Xu, K. Krogh, and M. Tenkanen. 2018. "Enzymatic Analysis of Levan Produced by Lactic Acid Bacteria in Fermented Doughs." *Carbohydrate Polymers* 208: 285–293. https://doi.org/10.1016/j.carbpol.2018.12.044.

Signorell, A. 2025. "DescTools: Tools for Descriptive Statistics, [Computer Software]." https://andrisignorell.github.io/DescTools.

Skåne, A., P. K. Edvardsen, G. Cordara, et al. 2022. "Chitinolytic Enzymes Contribute to the Pathogenicity of *Aliivibrio salmonicida* LFI1238 in the Invasive Phase of Cold-Water Vibriosis." *BMC Microbiology* 22, no. 1: 1–16. https://doi.org/10.1186/s12866-022-02590-2.

Slade, D., and M. Radman. 2011. "Oxidative Stress Resistance in *Deinococcus radiodurans*." *Microbiology and Molecular Biology Reviews* 75, no. 1: 133–191. https://doi.org/10.1128/MMBR.00015-10.

Soares-Castro, P., H. Araújo-Rodrigues, F. Godoy-Vitorino, et al. 2019. "Microbiota Fingerprints Within the Oral Cavity of Cetaceans as Indicators for Population Biomonitoring." *Scientific Reports* 9, no. 1: 1–15. https://doi.org/10.1038/s41598-019-50139-7.

Stevick, P. T., A. Aguayo, J. Allen, et al. 2004. "Migrations of Individually Identified Humpback Whales Between the Antarctic Peninsula and South America." *Journal of Cetacean Research and Management* 6, no. 2: 109–113. https://doi.org/10.47536/jcrm.v6i2.773.

Stone, G. S., L. Flórez-González, and S. Katona. 1990. "Whale Migration Record." *Nature* 346: 705. https://doi.org/10.1038/346705a0.

Stramska, M., M. Konik, P. Aniskiewicz, J. Jakacki, and M. Darecki. 2021. "Comparisons of Satellite and Modeled Surface Temperature and Chlorophyll Concentrations in the Baltic Sea With in Situ Data." *Remote Sensing* 13: 3049. https://doi.org/10.3390/rs13153049.

Suzuki, A., and M. Suzuki. 2021. "Antimicrobial Activity of *Lactococcus lactis* Subsp. Lactis Isolated From a Stranded Cuvier's Beaked Whale (*Ziphius cavirostris*) Against Gram-Positive and -Negative Bacteria." *Microorganisms* 9, no. 2: 1–14. https://doi.org/10.3390/microorganisms9020243.

Swaney, M. H., and L. R. Kalan. 2021. "Living in Your Skin: Microbes, Molecules, and Mechanisms." *Infection and Immunity* 89, no. 4: 1–18. https://doi.org/10.1128/iai.00695-20.

Tamayo-Leiva, J., J. Cifuentes-Anticevic, P. Aparicio-Rizzo, J. I. Arroyo, I. Masotti, and B. Díez. 2021. "Influence of Estuarine Water on the Microbial Community Structure of Patagonian Fjords." *Frontiers in Marine Science* 8: 611981. https://doi.org/10.3389/fmars.2021.611981.

Techtmann, S. M., K. S. Fitzgerald, S. C. Stelling, et al. 2016. "*Colwellia psychrerythraea* Strains From Distant Deep Sea Basins Show Adaptation to Local Conditions." *Frontiers in Environmental Science* 4: 33. https://doi.org/10.3389/fenvs.2016.00033.

Ten, S., J. A. Raga, and F. J. Aznar. 2022. "Epibiotic Fauna on Cetaceans Worldwide: A Systematic Review of Records and Indicator Potential." *Frontiers in Marine Science* 9: 846558. https://doi.org/10.3389/fmars.2022.846558.

Thometz, N. M., H. Hermann-Sorensen, B. Russell, D. A. S. Rosen, and C. Reichmuth. 2021. "Molting Strategies of Arctic Seals Drive Annual Patterns in Metabolism." *Conservation Physiology* 9, no. 1: coaa112. https://doi.org/10.1093/conphys/coaa112.

Toro, F., J. Alarcón, S. Márquez, et al. 2021. "Composition and Structure of the Skin Microbiota of Rorquals Off the Eastern South Pacific." *FEMS Microbiology Ecology* 97, no. 5: 1–10. https://doi.org/10.1093/femsec/fiab050.

Valdenegro, A., and N. Silva. 2003. "Caracterización oceanográfica física y química de la zona de canales y fiordos Australes de Chile entre el Estrecho de Magallanes y Cabo de Hornos (CIMAR 3 FIORDOS)." *Ciencia y Tecnología del Mar* 26, no. 2: 19–60.

Valle-Levinson, A., J. L. Blanco, and M. Frangópulos. 2006. "Hydrography and Frontogenesis in a Glacial Fjord Off the Strait of Magellan." *Ocean Dynamics* 56, no. 3–4: 217–227. https://doi.org/10.1007/s10236-005-0048-8.

Van Cise, A. M., P. R. Wade, C. E. C. Goertz, et al. 2020. "Skin Microbiome of Beluga Whales: Spatial, Temporal, and Health-Related Dynamics." *Animal Microbiome* 2, no. 1: 1–16. https://doi.org/10.1186/s42523-020-00057-1.

Wan, X., J. Li, R. Tian, et al. 2022. "The Effects of Human Care on the Blowhole and Gut Microbiotas of Two Cohabiting Dolphin Species Based on a Year-Round Surveillance." *Frontiers in Marine Science* 9: 1024117. https://doi.org/10.3389/fmars.2022.1024117.

Weiss, S., Z. Z. Xu, S. Peddada, et al. 2017. "Normalization and Microbial Differential Abundance Strategies Depend Upon Data Characteristics." *Microbiome* 5, no. 1: 27. https://doi.org/10.1186/S40168-017-0237-Y.

Weitzman, C. L., G. P. Brown, K. Gibb, and K. Christian. 2025. "Cutaneous Shedding in Amphibians Causes Shifts in Bacterial Microbiomes." *Integrative Zoology* 20, no. 4: 807–816. https://doi.org/10.1111/1749-4877.12858.

Welter, D. K., A. Ruaud, Z. M. Henseler, et al. 2021. "Free-Living, Psychrotrophic Bacteria of the Genus *Psychrobacter* Are Descendants of Pathobionts." *MSystems* 6, no. 2: e00258-21. https://doi.org/10.1128/msystems.00258-21.

Xu, X., Z. Ding, C. Pu, et al. 2024. "The Structural Characterization and UV-Protective Properties of an Exopolysaccharide From a *Paenibacillus* Isolate." *Frontiers in Pharmacology* 15: 1434136. https://doi.org/10.3389/fphar.2024.1434136.

Zamora, E., and A. Santana. 1979. "Características climáticas de la costa occidental de la Patagonia entre las latitudes 46° 40′y 56° 30′S." *Anales del Instituto de la Patagonia* 10: 109–144.

Zhang, X., J. Yuan, F. Li, and J. Xiang. 2021. "Chitin Synthesis and Degradation in Crustaceans: A Genomic View and Application." *Marine Drugs* 19, no. 3: 153. https://doi.org/10.3390/MD19030153.

Zhong, D., W. Ma, X. Jiang, Y. Yuan, H. Li, and Y. Li. 2018. "Biofilm Microbial Diversity Under Conditions of Different Pipe Materials and Chlorine Residual Levels." *Desalination and Water Treatment* 133: 191–198. https://doi.org/10.5004/dwt.2018.23042.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Microbiome of humpback whale skin across seasonal habitats. Heatmap of the top 20 bacterial taxa based on relative abundances (%) within major taxonomical rank from humpback whale skin according to seasonal habitats (breeding and feeding grounds in Ecuador and the Magellan Strait in Chile, respectively). **Figure S2:** Humpback whales skin microbiome differential composition analysis between seasonal habitats by ANCOM BC2. The top 30 bacterial taxa exhibiting log fold changes (LFC) in relative abundance between humpback whales sampled in the Magellan Strait feeding ground in Chile and the breeding ground in Ecuador are shown. Only taxa with 10% prevalence are included; those that passed the sensitivity analysis are highlighted in bold, and standard error bars are shown. Significance is indicated by Holm adj. *p*-value (*q*) 0.001***, 0.01**, 0.05. **Figure S3:** Microbiome of seawater associated with humpback whales across seasonal habitats. Heatmap of the top 20 bacterial taxa based on relative abundances (%) within major taxonomical rank from seawater samples associated with humpback whales from breeding and feeding grounds in Ecuador and the Magellan Strait, Chile, respectively. **Table S1:** ASVs identified as contaminants by decontam package. **Table S2:** Bacterial taxa of humpback whale skin microbiomes that are differentially abundant between seasonal habitats identified by ANCOM-BC2. **Table S3:** Bacterial genera associated with environmental conditions (SST and maximum UV-b) identified by MaAsLin2 at the genus level. **Table S4:** Core microbiome analysis across humpback whale skin and seawater samples under different frequency thresholds and group comparisons, including Venn diagrams showing the number of shared ASVs among groups and relative abundance in parenthesis. ASVs are reported at the lowest available taxonomic level and annotated as genus (g), family (f), order (o), class (c) or phylum (p).