Current knowledge in the Southern Hemisphere marine microbiome of eukaryotic hosts and the Strait of Magellan surface microbiome project.

Manuel Ochoa-Sánchez [1, 2, 3] , **E. Paola Acuña-Gómez** [1] , **Lía Ramírez-Fernández** [4] , **Luis E. Eguiarte** [3] , **Valeria Souza**
Corresp. [1, 3]

[1] Centro de Estudios del Cuaternario de Fuego, Patagonia y Antártica (CEQUA), Punta Arenas, Chile

[2] Universidad Nacional Autónoma de México, Posgrado en Ciencias Biológicas, Ciudad de México, México

[3] Departamento de Ecología Evolutiva, Universidad Nacional Autónoma de México, Instituto de Ecología, CDMX, México

[4] Centro de Desarrollo de Biotecnología Industrial y Bioproductos SR-245, Limache 727, Antofagasta, Chile

Corresponding Author: Valeria Souza
Email address: souza.valeria2@gmail.com

Host-microbe interactions are ubiquitous, and they play important roles in host biology, ecology, and evolution. Yet, host-microbe research has focused on inland species, whereas marine hosts and their associated microbes remain largely unexplored, especially in developing countries located in the Southern Hemisphere. Here, we review current knowledge of microbial communities associated with marine hosts in the Southern Hemisphere. There are important biases in marine host species sampled for the studies in the Southern Hemisphere, where sponges and marine mammals have received the greatest attention. Sponges associated microbes varied greatly across regions and species, nevertheless, beside taxonomic heterogeneity, the microbiome has functional consistency, whereas marine mammals' microbiome seems to be driven by geography and aging. Southern Hemisphere seabirds and macroalgae holobiont studies are also common. Seabirds associated microbes rely on amplicon studies, focused on feces. Seabird fecal microbiota is influenced by aging, sex, and species' specific factors, while macroalgae apparently actively filters the microbes that establish in its surface, in a process known as "microbial gardening". In contrast, marine invertebrates and fish microbiomes have received less attention in the Southern Hemisphere. In general, the marine holobiont in the Southern Hemisphere is characterized by few systematic and authentic holobiont studies (i.e., studies that analyze at the same time host traits [e.g., genomics, transcriptomics] and microbiome traits [e.g, 16S, metagenome]), except for some marine invertebrates and macroalgae. We believe that our project on the surface microbiome of key species in the Strait of Magellan will provide valuable information on the points listed above, which will improve the knowledge of microbial diversity in the region, as well as its current responses under the Anthropocene.

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4 Manuel Ochoa-Sánchez[1,2,3], E. Paola Acuña-Gómez [3], Lía Ramírez-Fernández[4], Luis E. Eguiarte[1],

5 Valeria Souza[1,3]

8 [1] Instituto de Ecología, Universidad Nacional Autónoma de México, AP 70-275, Ciudad

9 Universitaria, Coyoacán, 04510 CDMX, México

10 [2] Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, México

11 [3] Centro de Estudios del Cuaternario de Fuego, Patagonia y Antártica (CEQUA), Punta Arenas,

12 Chile.

13 [4] Centro de Desarrollo de Biotecnología Industrial y Bioproductos SR-245, Limache 727,

14 Antofagasta, Chile.

16 Corresponding Author:

18 Valeria Souza[1,3]

20 [1] Instituto de Ecología, Universidad Nacional Autónoma de México, AP 70-275, Ciudad

21 Universitaria, Coyoacán, 04510 CDMX, México

22 [3] Centro de Estudios del Cuaternario de Fuego, Patagonia y Antártica (CEQUA), Punta Arenas,

23 Chile.

25 Email address: souza@unam.mx

32 **Abstract**

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35 and evolution. Yet, host-microbe research has focused on inland species, whereas marine hosts

36 and their associated microbes remain largely unexplored, especially in developing countries

37 located in the Southern Hemisphere. Here, we review current knowledge of microbial

38 communities associated with marine hosts in the Southern Hemisphere. There are important

39 biases in marine host species sampled for the studies in the Southern Hemisphere, where sponges

40 and marine mammals have received the greatest attention. Sponges associated microbes varied

41 greatly across regions and species, nevertheless, beside taxonomic heterogeneity, the microbiome

42 has functional consistency, whereas marine mammals' microbiome seems to be driven by

43 geography and aging. Southern Hemisphere seabirds and macroalgae holobiont studies are also

44 common. Seabirds associated microbes rely on amplicon studies, focused on feces. Seabird fecal

45 microbiota is influenced by aging, sex, and species' specific factors, while macroalgae apparently

46 actively filters the microbes that establish in its surface, in a process known as "microbial

47 gardening". In contrast, marine invertebrates and fish microbiomes have received less attention in

48 the Southern Hemisphere. In general, the marine holobiont in the Southern Hemisphere is

49 characterized by few systematic and authentic holobiont studies (i.e., studies that analyze at the

50 same time host traits [e.g., genomics, transcriptomics] and microbiome traits [e.g, 16S,

51 metagenome]), except for some marine invertebrates and macroalgae. We believe that our project

52 on the surface microbiome of key species in the Strait of Magellan will provide valuable

53 information on the points listed above, which will improve the knowledge of microbial diversity

54 in the region, as well as its current responses under the Anthropocene.

56 **Introduction**

58 The Southern Hemisphere, and particularly the Southern Ocean and its associated ecosystems, is

59 characterized by its unique biodiversity (Rogers et al., 2020; Gutt et al., 2021). These important

60 ecosystems are facing major abiotic challenges as climate change progresses. These challenges

61 are driven primarily by ocean warming and increased UV radiation (Thompson & Salomon,

62 2002; Swart et al., 2018). Sea surface warming creates a stronger stratification in the water

63 column (Pellichero et al., 2017), as well as higher variability in the duration and extent of sea ice

64 sheet and increases in glacier melt rate in the southernmost regions (Gutt et al., 2015; Comiso et

65 al., 2017). Additionally, ocean warming increases microplancton metabolic activity, which in

66 turn accelerates oxygen depletion in the water column (Schmidtko et al., 2017), and decreases

67   ocean pH (McNeil & Matear 2008). Tragically, recent intense wildfires and volcanic eruptions in

68   the Southern Hemisphere have increased the Antarctic ozone hole size in 2020-2021, which is

69   expected to worsen ocean warming effects (Yook et al., 2022). On the other hand, atypical

70   glacier melt rate are stimulating marine primary productivity, which creates complex scenarios in

71   ice dependent species (Piñones & Fedorov 2016). For example, Antarctic krill (*Euphasia*

72   *superba*), a key species in the Antarctic trophic network, requires ice in their early stages, while

73   also forages in areas with high concentration of chlorophyll-a concentration (Kawaguchi et al.,

74   2006). Current evidence suggests that habitat quality heterogeneity along its Antarctic

75   distribution will produce contractions in its distribution (Atkinson et al., 2019; Veytia et al., 2020,

76   but see Cox et al., 2018)

77

78   However, there are also some surprising results. For example, warmer temperatures

79   coupled with low to moderate winds, increase ice melt, which in turn is expected to increase iron

80   release (Hodson et al., 2017). Iron is a primary productivity limiting factor, so its increased

81   availability triggers diatom growth, which in turn increases krill recruitment (Noble et al., 2013;

82   Bertrand et al., 2007, 2015). Ultimately, krill biomass increase provides greater resources for

83   predators, which overall increases energy transfer along the trophic network (Saba et al., 2014).

84   As climate change progresses, it is expected an intensification in seasonality, which might

85   intensify alterations in biological processes (e.g., bottom-up mechanisms).

86

87   For instance, in the Strait of Magellan – the southernmost continental region of South

88   America – climate change derived effects have been recorded since the second half of the XX

89   and early XXI century. These include, increasing sea surface temperature (Smith & Renynolds,

90   2004) and higher glacier melt rate (Aniya, 1999; Dixon and Ambinakudige, 2015). In the

91   terrestrial ecosystem, warmer seasonality is expected to increase aridity in the Patagonian region,

92   particularly in areas with herbaceous vegetation (Soto-Rogel et al., 2020). Nevertheless, the

93   region has not experienced any formal study regarding the effect of climate change in any of its

94   ecosystem properties (e.g. trophic network interactions, biogeochemical cycles, environmental

95   status). This is unfortunate since the region offers an invaluable geographic position. From the

96   marine perspective, the Strait of Magellan is uniquely influenced by the Pacific and Atlantic

97   oceans, as well as the Cape Horn current. Additionally, glacier melt seasonal input creates local

98   primary productivity bursts that have bottom-up effects that recruit species from higher trophic

99   status, which overall increases the biodiversity of the region.

100

101   Despite all the previous natural history studies and museums filled with macro-organisms'
102 diversity, eukaryotes live inside a wider microbial world. Eukaryotes' homeostasis (e.g.,
103 physiology, immunology, and metabolism) is driven or at least greatly influenced by microbes
104 (McFall-Ngai et al., 2013; Cani et al., 2019; Peixoto et al., 2021). As a result, the "hologenome
105 evolution theory" and "holobiont theory" emerged (Zilber-Rosenberg & Rosenberg, 2008;
106 Bordenstein &Theis, 2015). The holobiont term per se, is not new. It was first introduced by
107 Lynn Margulis to describe the biological unit formed between a host and a single inherited
108 endosymbiont (Margulis L. 1991). The novelty around the holobiont concept arose as a direct
109 consequence of the development and cost decrease of Next Sequencing Technologies, which spur
110 host microbial communities research. This has revealed that microbes are ubiquitous in every
111 single metazoan (Simon et al., 2019). Thus, the current holobiont concept refers to a cohesive
112 evolutionary unit formed by the host and its associated microbes (Bordenstein & Theis, 2015;
113 Rosenberg & Zilber-Rosenberg, 2018). In other words, a holobiont is a single ecological unit,
114 comprised of an intricated network of mutualistic, commensalisms, and parasitic relationships
115 between microbes and its host, that are critical for the survival of all organisms involved.
116 Nevertheless, microbial influence in the holobiont might vary among hosts (Hammer et al.,
117 2019), which has been interpreted as flaws in the holobiont concept (Moran & Sloan, 2015;
118 Douglas & Werren 2016). Holobionts could be assembled by ecological, evolutive or neutral
119 process. Hence, a first objective in holobiont research lies in determining the nature of the
120 holobiont assembly (Theis et al., 2016).

121

122   In marine hosts – which are unlikely to be studied under experimental designs – holobiont
123 research could be focused on the characterization of the host associated microbes in a relevant
124 environmental and evolutionary framework (Leray et al., 2021). Up to date, metabarcoding
125 approaches have been the most popular methods to tackle this issue. Yet, it only serves as an
126 initial step to characterize the microbial composition, as to test the holobiont hypothesis (i.e., host
127 and associated microbes evolve as a unit) further efforts encompassing host associated microbes'
128 functional characterization (e.g., metagenomic or metatranscriptomic data), coupled with host
129 molecular information (e.g., genomic or transcriptomic data), relevant environmental variables
130 measurement, as well as seasonal replicates, must be done to test the congruence of holobiont
131 response against seasonal fluctuations.

132

133   Once we have baseline information about bacterial composition associated to marine

134   hosts, we should be able to recognize hosts whose microbial communities are far from the

135   expected natural variability. Changes in the host's natural composition of microbial communities

136   are collectively termed *dysbiosis* (Zaneveld et al., 2017). Thus, the microbiome itself could be

137   used as a biosensor of host's status (Zolti et al., 2020; Inda & Lu 2020). In marine species, there

138   are several examples of the interplay between host fitness and microbial symbiosis, especially in

139   sponges (Pita et al., 2018 and references within) and algae (van der Loos et al., 2019 and

140   references within). Dysbiosis is the microbial fingerprint underlying the disruption of the host's

141   health and ecology, a highly relevant topic in the current anthropogenic climate change epoch.

142

143   Microbial communities routinely colonize metazoan internal (e.g., gut, oral) or external

144   (e.g., skin) tissues (Ross et al., 2019; Diaz et al., 2021; ANID R20F0009). However, they differ

145   in the selective pressures that influence their assemble. While internal microbial communities

146   assembly is influenced by diet and host physiology, external microbial communities assembly is

147   greatly influenced by environmental perturbations that impair host fitness (Byrd et al., 2018;

148   Kuziel & Rakoff-Nahoum 2022). Therefore, we think that surface microbial communities of

149   eukaryotes could serve as valuable tools to survey environmental status. The epidermis/outer

150   surface of eukaryotes is considered a hostile environment, yet it is frequently colonized by

151   microbes. These microbes must cope with constant shedding (in epidermis) molt (in feathers),

152   intense solar radiation exposure, low temperature, pH changes, as well as antimicrobial molecules

153   (Percival et al., 2012). Nevertheless, skin microbes play important roles in the host's health

154   (Apprill et al., 2014), since they are the first line defense against pathogens and actively

155   participate in the host's immune system maturation (Ross et al., 2019).

156

157   Marine eukaryotes vary greatly in the nature and complexity of their superficial tissue, so

158   the nature of the surface/skin is a critical issue to consider when studying the marine skin

159   microbiome of any host. For example, algae and fish both have a mucus layer in its surface/skin,

160   but their composition and function are different (Gomez et al., 2013; van der Loos et al., 2019).

161   In birds and mammals, the epidermis is covered by feathers and hair, respectively. Importantly

162   seabirds and marine mammals have developed different strategies to cope with cold water,

163   therefore their epidermis and associated elements (i.e., feathers or hair) is completely different

164   from species inhabiting tropical and temperate latitudes (Ross et al., 2019). On the other hand,

165   crustaceans' outer surface is solely its exoskeleton of chitin, so their adaptations to cold

166   temperatures are to be discovered both in their microbiome and their physiology. Even though,

167   the unique biodiversity living in the Southern Hemisphere, few holobiont studies have been

168   conducted in the region. Biodiversity studies are becoming increasingly important, as climate

169   change imposes major threats in ecosystems around the globe, especially in cold environments.

170

171   Up to date, marine holobiont studies have had spatial and phylogenetic biases; on one

172   hand, most of them have been realized in the tropics or in the Northern hemisphere (most of

173   references within Ross et al., 2019), while, on the other hand, the most studied species have been

174   sessile organisms, like sponges (Figure 1). Therefore, Southern Hemisphere marine host

175   microbiome research has received less attention across the metazoan spectrum. Moreover, there

176   are scarce microbiome studies in marine vertebrate and invertebrates. Here, we review the marine

177   host-microbiota/microbiome interactions occurring in the Southern Hemisphere. This review will

178   aid as a diagnosis of the field progress in the region, as well as to detect knowledge gaps and

179   opportunities for further research. Thus, the review is intended for scientists interested in

180   eukaryotes associated microbes, as well as anyone interested in using microbiota/microbiomes as

181   biosensors of eukaryotes' health.

182

183   In this review, our main objectives are i) review the current knowledge regarding marine

184   holobiont and microbiota/microbiome studies in the Southern Hemisphere, and ii) to describe a

185   long-term project that will improve knowledge of microbial communities associated with selected

186   taxa in the Strait of Magellan, Chile (ANID R20F00009). We start with a brief overview of the

187   surface characteristics of several taxa. Later, we review holobiont interactions in a trophic level

188   fashion, first with macroalgae, later with primary and secondary animals' consumers, and finally

189   with predators.

190

191   **Survey methodology**

192

193   We covered all marine microbe-eukaryote interaction reports in the Southern Hemisphere that we

194   were able to find. For this, we performed a comprehensive analysis of literature of the last two

195   decades in the following online databases: PubMed, Science Direct, Scopus and Google Scholar.

196   The search spanned the last two decades and was concluded at 1/February/2023. Only studies in

197   English were selected for further inspection. Several keywords were used to perform the

198   literature search, using the following key words, in combination with the terms, -holobiont-, -

199 microbiota- and -microbiome-: seaweed, sponge, invertebrate, crustacean, marine vertebrate,

200 whales, seals, seabirds. Articles found to match any of these words were examined to guarantee

201 that their sampling was done in hosts inhabiting the Southern Hemisphere.

202

203 **Results**

204

205 Overall, geographical distribution of marine host-microbial research revealed important biases.

206 Geographical biases are reflected by sampling effort across the Southern Hemisphere, since

207 research has been done predominantly in the Antarctic (above 60° S), especially in the Western

208 Antarctic, and template latitudes (between 20 – 40° S), especially in Australia, while tropical

209 (between 0 – 20° S) and cold (between 40 – 60° S) latitudes, as well as South America and Africa

210 have received less attention (Fig. 2). There are also host biases, both in terms of number of

211 studies and number of species studied. The most studied groups are marine mammals and

212 sponges (Fig. 1), which have been studied across all latitudinal regions and continents in the

213 Southern Hemisphere (Fig. 3). Nevertheless, when it comes to the number of species studied the

214 pattern has some changes, while sponges remain as the best studied group with 65 studied

215 species, the following groups are Macroalgae (24 studied species) and marine invertebrates (23

216 studied species) (Table 1). In general, the predominant molecular approach to study host-

217 associated microbial communities has been with taxonomic markers (i.e., 16S), nevertheless there

218 have been conducted some microbiome functional approaches (i.e., shotgun metagenomics),

219 especially in Australia and Antarctica hosts, whereas South American marine hosts, have had not

220 been studied with any functional approach to date (Fig. 4, Table 1).

221

222 **Macroalgae as an ecosystem**

223

224 Marine macroalgae are important ecosystem engineers that play critical roles in primary

225 production, biogeochemical cycles, and biodiversity recruitment in marine ecosystems (Tuya et

226 al., 2008. Currently, there are 11,017 species of macroalgae species with cosmopolitan

227 distribution, therefore there is a vast microbial-algae symbiotic world that remains unexplored

228 (Guiry & Guiry 2023). Macroalgae microbiome studies in the Southern Hemisphere have

229 received considerable attention with 24 studied species within 13 research articles (Table 1; Fig.

230 1). Most studies have been conducted with 16S approaches, yet there are microbiome approaches

231 with shotgun metagenomics and DNA holobiont approaches (Table 1). Macroalgae microbiome

232   sampling has been conducted worldwide, but it has been done predominantly in Australia,

233   Antarctica, and South America (Fig. 3).

234

235   Algae are an idoneous niche for aerobic and polymer degrading bacteria, since their

236   photosynthetic activity, and their rich composition in carbon and nutrients (like agar,

237   carrageenan, and cellulose), facilitate the establishment of aerobic and heterotrophic bacteria in

238   their surfaces (de Oliveira et al., 2012). Microbial macroalgal epibiotic communities (biofilms)

239   have been extensively studied in the tropics and the Northern Hemisphere (Malik et al., 2020 and

240   references within). Nevertheless, there have been conducted several macroalgae biofilm studies

241   in the Southern Hemisphere which have revealed Cyanobacteria, Proteobacteria, Firmicutes,

242   Bacteroidetes and Actinobacteria as prevalent bacterial phyla (de Oliveira et al., 2012; Albakosh

243   et al., 2016; Gaitan-Espitia & Schmid, 2020). Fungi are also important players in the macroalgae

244   biofilm composition in the Southern Hemisphere, and different species have been documented

245   from Antarctic seaweeds, being the most prevalent the filamentous fungus *Pseudogymnoascus*

246   *pannorum,* and the yeast *Metschnikowia australis* (Loque et al., 2010; Godinho et al., 2013;

247   Furbino et al., 2017; Ogaki et al., 2019).

248

249   There has been extensive research in the macroalgae holobiont that gives a rich body of

250   evidence to frame the study of macroalgae biofilms. These studies have shown that bacteria and

251   fungi inhabiting the macroalgae biofilm actively interact with its host to influence growth,

252   development, and immune function (van der Loos et al., 2019). Valuable microbes to the algal

253   host appear to be taxonomically restricted among bacteria at higher taxonomic levels, therefore,

254   biofilm composition seems to be redundant at phyla or class. Nevertheless, at lower taxonomic

255   levels (genus/ASV [Amplicon Sequence Variant]/OTU [Operational Taxonomic Unit]), there is a

256   rich spectrum of valuable microbes (Egan et al., 2013; Hollants et al., 2013). Despite taxonomic

257   variability in bacterial genera inhabiting its biofilms, traits among bacteria are shared, which

258   creates biofilms with different taxonomic composition but with apparently similar functions

259   (Egan et al., 2013).

260

261   Macroalgae seem to actively recruit its biofilm composition, a process known as

262   "microbial gardening" (Saha & Weinberger 2019). Microbial gardening allows the recruitment of

263   specific beneficial bacteria to the algae. In turn, the recruited microbes release antibiotics,

264   quorum sensing inhibitors and digestive vesicles (Wiese et al., 2009; Romero et al., 2010;

265 Richards et al., 2017) that collectively shape the biofilm composition. Although, algal biofilm

266 composition varies taxonomically, in space, time and host (Lachnit et al., 2011), it shares

267 important traits related with algae morphogenesis (Wiese et al., 2009) and nutrient

268 supplementation (Hollants et al., 2013). Overall, a "correct" microbial gardening, might confer

269 an adequate biofilm composition, able to produce a cocktail of metabolites that provide

270 protection to the algae from microbial pathogens, like bacteria or diatoms (Saha & Weinberger

271 2019), or predators like barnacle larvae or mussels (Saha et al., 2018). Interestingly, the benefit

272 conferred to algae by the surface microbiome is not taxonomically restricted, suggesting that

273 microbial traits underlying algae defense are shared by several bacterial taxa.

274

275   Besides, some bacteria of the algal biofilm produce antibiotic compounds, which act as a

276 microbial filter for the establishment of environmental microbes (Albakosh et al., 2016). For

277 example, algae's thallus produces dimethylsulfoniopropionate (Kessler et al., 2018), which

278 recruits *Roseovarius* bacteria. This bacterium releases specific morphogenetic compounds that

279 enable correct algae morphogenesis. Moreover, bacterial metabolites could enhance algal

280 performance during stress. Thallusin, a microbial derived metabolite, positively influences algal

281 growth, cell differentiation, cell wall development, and rhizoid formation during abiotic stress

282 (Alsufyani et al., 2020). Therefore, thallusin production might be an excellent example of a

283 holobiont environmental stress response.

284

285   Globally, the algal holobiont will be subject to complex scenarios under climate change.

286 Sea surface temperature, and CO_2 concentration increase, might have different outcomes in algal

287 species and also affect key microbes inhabiting macroalgae biofilms, which in turn, could impair

288 the host's health (Gaitan-Espitia & Schmid, 2020; Marzinelli et al., 2015). Moreover, it is

289 imperative to consider the effect on the interactions among microbes and microbe-algae. For

290 example, algal hosts sensible to acidification might experience lower photosynthetic rate, which

291 might hamper aerobe bacteria proliferation (Van der Loos et al., 2019). Climate change

292 environmental driven perturbations might produce common disbiotic biofilm composition in

293 stressed macroalgae (Marzinelli et al., 2015). Nevertheless, whether shifts in macroalgae biofilm

294 composition associated to environmental perturbation impairs macroalgae fitness remains

295 unexplored.

296

297   **The macroalgae holobiont in the Southern Hemisphere**

298

299   To the best of our knowledge the macroalgae microbiome has been addressed in 13 studies in the

300   Southern Hemisphere (Fig. 1). Most of these studies have been done in template latitudes,

301   particularly in Australia (Fig. 3). There are important gaps in tropical and cold latitudes, as well

302   as in selected regions, like South America, Africa and Indonesia (Fig. 3). Yet, we still ignore

303   much about South America native macroalgae microbiome, since there is only one study that

304   addressed this topic in a native species, *Macrocystis pyrifera* (Laminariales: Laminariaceae),

305   while another explored the biofilm composition of a macroalgae invasive species, *Undaria*

306   *pinnitafida* (Laminariales: Alariaceae) (Florez et al., 2019; Lozada et al., 2022). From these

307   examples, we know that macroalgae biofilm composition is different from seawater and is

308   influenced by seasonality and available nutrients. Interesting, invasive macroalgae in the

309   Southern Hemisphere, shows signs of microbial gardening, since its biofilm composition is

310   dominated by one bacterial taxon, *Leucothrix*, a gamma-proteobacteria (Florez et al., 2019;

311   Lozada et al., 2022). This could give insights about potential adaptation mechanisms of these

312   invasive species in the Southern Hemisphere, which might be relevant in the ecosystemic process

313   of the Patagonian region.

314

315   Australia is the region where the macroalgae holobiont is best understood, since it has the

316   highest number of studies (5 studies, Table 1), and diversity of molecular approximations (i.e.,

317   16S, shotgun metagenomics, DNA holobiont, Table 1). Yet, most of its research effort has

318   focused only on one species, *Ecklonia radiata* (Laminariales, Lessoniaceae), so it is unlikely that

319   their macroalgae holobiont knowledge is generalizable to all macroalgae hosts in the region

320   (Marzinelli et al., 2015, 2018; Qiu et al., 2019; Song et al., 2021; Wood et al., 2022).

321   Nevertheless, it provides valuable information that gives insight into the future that might face

322   the macroalgae holobiont. *Ecklonia radiata* biofilm composition has a dysbiotic composition

323   during environmental stress (Marzinelli et al., 2015, 2018). Yet, stress microbial signatures are

324   not consistent across individuals, which suggest that there are unexplored meaningful covariates

325   (e.g., host genetic variability) that determine the final holobiont phenotype (i.e., biofilm

326   composition) when the algae face environmental stress (Qiu et al., 2019). Besides, horizontal

327   transfer of genes related with the algae niche specific environment, and stress environmental

328   responses between biofilm bacterial members, suggest that this process might facilitate biofilm

329   adaptation to environmental stress (Song et al., 2021). Interestingly, a DNA holobiont approach

330   in the macroalgae *Phyllospora comosa* (Fucales: Seirococcaceae) revealed that host genetic

331 variability has a weak relationship with microbial composition. Moreover, its biofilm

332 composition is driven by local conditions and geography (Wood et al., 2022). Together these

333 results suggest a complex interplay in the macroalgae holobiont, where genetic variability,

334 biofilm composition, horizontal gene transfer and environmental conditions, are crucial players,

335 that create a diverse array of phenotypes. Given the unavoidable environmental changes that we

336 will face in the next decades, and the key role macroalgae play as ecosystem engineers, it is

337 imperative to detect the factors that could promote resilience in the macroalgae holobiont against

338 environmental stress, in order to keep the benefits they provide to marine biodiversity.

339

340 Although bacterial partners have received most of the attention in algae biofilm research,

341 algae biofilms harbor diverse fungal communities. Fungal biofilm composition has been explored

342 in Antarctica. Fungal epibiotic communities in Antarctic macroalgae are influenced by abiotic

343 (i.e., dissolved oxygen and organic matter) and biotic (i.e., antifungal molecules produced by the

344 host) factors (Ogaki et al., 2019). Moreover, macroalgae actively controls these communities,

345 since some fungal strains associated to algae biofilms have agarolytic and carrageenolytic

346 activity, hence, they can degrade algal biomass (Furbino et al., 2017). However, it remains

347 unknown the interactions that might take place between bacteria and fungi inhabiting the

348 macroalgae biofilm. Future studies should have more holistic approaches, where bacteria, fungi

349 and environmental covariables are simultaneously considered.

350

351 In particular, the species *Macrocystis pyrifera* is a worldwide (i.e., present both in the

352 Southern and Northern Hemisphere) distributed algae species, whose epibiotic microbial

353 communities have been addressed across several regions in the world (Florez et al., 2019; Lin et

354 al 2018; Weigel et al., 2019). These studies will be valuable to do *M. pyrifera* comparisons across

355 biogeographic regions. However, little is known from the surface biofilm of *Macrocystis pyrifera*

356 in the Strait of Magellan. In the project of the Strait of Magellan microbiome, that we will

357 describe at the end of the paper, we are attempting to characterize the bacterial and functional

358 traits/responses of *M. pyrifera*, in association with environmental factors at different dephts.

359 These data could improve our understanding in macroalgae microbiome response to climate

360 change.

361

362 **Invertebrates**

363

Sponges

Currently there are 9542 sponge species around the globe, with at least 8,864 species distributed in the Southern Hemisphere (de Voogd et al., 2023; Downey et al., 2012). Sponges are the best studied holobionts in the Southern Hemisphere, both in terms of studied species (65) and number of studies (16), most likely because sponges associated microbes produce a wide array of metabolites that have biotechnological importance (Taylor et al., 2007, Fig. 1, Table 1). The predominant approach to study the sponge holobiont is16S, nevertheless there have been conducted shotgun metagenomic approaches, which had shed light in sponges' microbiome metabolic potential (Table 1, Yang et al., 2022; Moreno-Pino et al., 2020, 2021). Sampling effort has been performed worldwide, mainly in Antarctic latitudes (tropical, template and cold latitudes) (Fig. 3).

Sponges are important ecosystem players that participate in several biogeochemical cycles, and provide stability to the benthos (Bell, 2008). Sponges are the first evolved metazoan, and therefore are the sister group to all animals (Wörheide et al., 2012). Their anatomy is unlike any other metazoan, but generally, it consists in several cell layers (Taylor et al., 2007). Most of the studies used in this revision use the outermost cell layer, nevertheless whenever a study sampled more cell layers, it is explicitly stated in the text. In a recent study in the tropical sponge holobiont conducted in the Northern Hemisphere, it was observed a high metabolic redundancy within the microbiomes that could help buffer the sponge from chemical and physical changes in their environment and from fluctuations in the population sizes of the individual microbial strains that make up the microbiome (Kelly et al., 2022). This is not surprising, since their early evolution occurred in a microbe dominated world in the late Precambrian (Renard et al., 2013). Sponge physiology seems to be microbe dependent and had reached different symbiotic-based solutions to environmental challenges (Thomas et al., 2016).

Current evidence suggests that the sponge microbiome is similar at the phylum level between species in the Southern Hemisphere and those in the Northern Hemisphere (Taylor et al., 2007). In the Southern Hemisphere the sponge microbiome is characterized by several phyla that construct a core including Proteobacteria, Bacteroidetes, Actinobacteria, Verrucomicrobia, Acidobacteria and Cyanobacteria (Rodríguez-Marconi et al., 2015; Matcher et al., 2017; Cárdenas et al., 2018; Savoca et al., 2019; Papale et al., 2020; Happel et al., 2022; Ruocco et al.,

397   2021; Yang et al., 2022). Interestingly, there is only one archaea phylum associated with sponges,

398   Thaumarchaeota, yet its association is consistent across several species (Brochier-Armanet et al.,

399   2008; Sacristán-Soriano et al., 2020; Moreno-Pino et al., 2020; Steinert et al., 2020).

400

401   Interestingly, some bacterial lineages associated to sponges are phylogenetic novelties,

402   that is, their DNA sequences are new, hence, they are unable to be identified with current

403   sequences databases knowledge. Antarctic sponges (Papale et al., 2020; Moreno-Pino 2021;

404   Happel et al., 2022), Australian sponges (Yang et al., 2022), and South African sponges (Matcher

405   et al., 2017) are the ones with more "unknown" bacterial partners. Noteworthy, phylogenetic

406   novel bacteria vary in their prevalence across sponge taxa. Sponges' genus *Sporosarcina* and

407   *Nesterenkonia* have greater phylogenetic novelty in their microbiotas (50 % or more) while

408   others, like *Cellulophaga algicola* tend to harbor fewer unknown microbes, therefore most of its

409   associated microbes is recognizable (Moreno-Pino et al., 2021). Considering metabolic evidence

410   from Northern Hemisphere tropical sponges, functional redundancy of their microbiomes might

411   allow sponges to tolerate environmental fluctuations, which allows them to distribute over wide

412   areas (Kelly et al., 2022). Hence, environmental variability could be an important driver of

413   microbiota assembly in sponges of the Southern Hemisphere, both at inter- (between different

414   species) and intraspecific (within the same species, among individuals) levels (Steinert et al.,

415   2020).

416

417   Nevertheless, besides environmental heterogeneity, phylogenetic factors (i.e.,

418   species/genera particular affinities) also play an important role in sponges' microbiota assembly.

419   For example, sponges from the genus *Mycale* display a strong bacterial core among individuals

420   and species distributed over hundreds of kilometers in the Southern Ocean (Cárdenas et al., 2018;

421   Happel et al., 2022). Similar stable associations have been found in some sponge species from

422   Antarctica (Steinert et al., 2019). *Mycale magellanica,* a common sponge living in the Strait of

423   Magellan, shares up to 74% of sequences belonging to Rhodobacteriaceae and Flavobacteriaceae

424   with individuals of *M. acerata*, a common sponge in the Western Antarctic Peninsula (Cárdenas

425   et al., 2018). Moreover, in *M. acerata*, bacterial composition is stable among individuals

426   distributed across the entire West Antarctic Peninsula (Happel et al., 2022).

427

428   Similar trends, with similar microbiota composition, are shown in Demospongiae and

429   Hexactinellida sponges from Ross Sea, Antarctica. These sponges share the bacterial genera

430   *Erwinia, Methylobacterium* and *Sphingomonas* (Papale et al., 2020). In contrast, in the same

431   region (Ross Sea), sponges' microbiotas composition has been found to be heavily influenced by

432   environmental microbes (horizontal transmission), both in the cultivable fraction and NGS-

433   microbiota (Savoca et al., 2019; Sacristán-Soriano et al., 2020). Overall, this highlights the

434   differences in bacterial composition variability among sympatric sponges, which might create

435   species or genus specific microbiota compositions.

436

437   Factors underlying microbial recruitment in sponges get more complex when we consider

438   sponges associated Archaea. For example, in Demospongiae and Hexactinellida sponges, from

439   the South Pacific Ocean, bacterial composition is species specific, while the Archaea composition

440   is individual specific (Steinert et al., 2020). Thus, Archaea composition is sparse among

441   individuals, which might suggest that Archaea are opportunistic/contingent players in the sponge

442   holobiont, or rather, their functional benefits are widely shared among several archaea taxa. This

443   pattern contrasts with the stable microbiota composition reported in Ross Sea sponges (Papale et

444   al., 2020). The differentiated trends suggest that environmental fluctuation coupled with species

445   specific filters might drive microbial composition associated with sponges.

446

447   The above examples illustrate the complex factors underlying sponge symbiotic

448   associations with bacteria, where horizontal transmission and host specific factors appear to have

449   a differential role among sponge species. Despite inconsistency among associated microbes'

450   identity, it is likely that sponges associated microbes have similar functional traits. Thus,

451   although sponges' microbiota has complex patterns, their microbiomes might have functional

452   convergence (Cristi et al., 2022).

453

454   Nevertheless, whether sponges' microbiomes taxonomy obey contingent issues (i.e.,

455   which microbe taxa arrived first or neutral process in microbiota assembly) or indeed have a

456   biological basis is an open question. Symbiotic interactions among sponge and its associated

457   bacteria dynamically shape the sponge microbiota composition. On one hand, opportunistic

458   bacteria that degrade sponge tissues, like *Bacillus, Micrococcus* and *Vibrio*, are common

459   members of the sponge holobiont. On the other hand, there are antibiotic producing bacteria that

460   regulate the former, like *Streptomyces, Aquimarina, Pseudovibrio* and *Pseudoalteromonas*

461   (Esteves et al., 2017). Variations in quorum sensing, a microbe chemical communication system,

462   also might play an important role in microbial recruitment. The genera *Pseudomonas,*

463   *Shewanella* and *Roseobacter,* common bacteria associated to sponges, produce Acyl homoseron

464   lacton, an important chemical messenger in quorum sensing (Mangano et al., 2018). The quorum

465   sensing activity by these bacteria might alter the community profile, by differential microbial

466   recruitment. Quorum sensing might be an important adaptive trait in the sponge holobiont,

467   specially under the ongoing climate derived marine changes, yet its prevalence, and more

468   important its relevance, among sponges' microbiomes has not been thoroughly studied.

469

470   Metagenomic studies have shed light on the characteristics of the functional repertoire of

471   sponges' microbiomes. Microbe metabolism differs throughout sponge tissue, highlighting a

472   tissue specific microbiome metabolism (Yang et al., 2022). Several examples pinpoint to nutrient

473   provisioning as an important trait in sponges' microbiomes. Microbial symbionts encode multiple

474   genes related to nitrogen fixation and metabolism of nitrogen compounds, sugars derived from

475   photosynthesis (Moreno-Pino et al., 2020), as well as vitamin B5 (Moreno-Pino et al., 2021). In

476   consonance with antagonistic interactions among members of the sponge microbiome, antibiotic

477   resistance, and biopolymer degradation (Moreno-Pino et al., 2021), as well as CRISPR genes,

478   transposases, detoxification genes and restriction site modifications (Moreno-Pino et al., 2020)

479   are common traits in sponges' microbiomes. The latter functions highlight the evolution of the

480   microbiome within the sponge itself, since several microbes associated with sponges degrade the

481   sponge's tissues and avoid the effect of antimicrobial compounds.

482

483   Furthermore, the high prevalence of CRISPR genes in sponges' microbiomes, suggest that

484   their bacterial members are under constant phage attack (Moreno-Pino et al., 2020), which adds

485   another complexity layer to the microbial interactions in the sponge microbiome. There is a high

486   proportion of genes in the microbial communities with unknown functions, so besides

487   phylogenetical novelty described above, there also stands out functional/metabolic microbial

488   novelty associated with sponges (Moreno-Pino et al., 2020).

489

490   Up to date, few studies have addressed the effects that marine climate change will have on

491   the sponge holobiont. An interesting exception is given by Kandler et al., (2018), which found

492   that microbial communities of the tropical sponges from New Guinea, *Coelocarteria*

493   *singaporensis* and *Stylissa* cf. *flabelliformi* might be tolerant to future marine pH conditions.

494   However, it is still an unifactorial experimental approach, that does not represent a reliable test of

495   the multifactorial climate change process. In contrast, there are other climate change driven

496   effects that might pose a major challenge to sponges in polar environments, like ice scour (seabed

497   modification caused by floating icebergs), which is predicted to increase as a direct consequence

498   of sea surface temperature rise. Ice scour damages benthic communities, specially sponges, like

499   *Isodictya kerguelenensis*. Ice scour injuries produce microbial fingerprints, that are easily

500   identified (Rondon et al., 2020). Thus, as climate change progresses and ice scour increases,

501   Antarctica sponges' integrity might be compromised in the next decades.

502

503   **Non-sponge invertebrates**

504

505   Marine invertebrates comprise between 35 - 39 recognized phyla (Valentin, JW 2006; Zhang, ZQ

506   2013). Most iconic marine invertebrates' phyla are Mollusca (118,061 species), Echinodermata

507   (20,550 species), Annelida (17, 426 species), Cnidaria (17,426 species), and Bryozoa (11,474

508   species) (Zhang, ZQ 2013). Marine invertebrates' microbiomes have received few attention, with

509   23 species within 10 research articles (Fig. 1, Table 1). However, this group has outstanding

510   examples of authentic holobiont approaches (i.e., coupled measurement of host and microbe

511   traits) (Table 1). Sampling effort has been conducted mainly in Australia, Antarctica, and Africa

512   while there are no studies addressing any marine invertebrate microbiome in South America (Fig.

513   3).

514

515   Overall, marine invertebrate microbiome is characterized by several bacterial phyla,

516   where Proteobacteria, Bacteroidetes, Verrucomicrobia, Tenericutes and Actinobacteria are the

517   most abundant (Webster & Bourne, 2007; Murray et al., 2016, 2020; Unzueta-Martínez et al.,

518   2022) Antarctic corals and snails have stable microbiotas among individuals. The Antarctic soft

519   coral, *Alcyonium antarcticum*, has a core microbiota composed by Proteobacteria, Bacteroidetes,

520   Firmicutes, Actinomycetales, Planctomycetes, Chlorobi and sulfate reductor bacteria (Webster

521   and Bourne, 2007). A similar trend is observed in the Antarctic snail *Synoicum adareanum*. This

522   invertebrate's microbiota is characterized by a high prevalence among individuals of

523   Proteobacteria, Verrucomicrobia, Actinobacteria, Nitrospirae and Bacteroidetes (Murray et al.,

524   2020). In other cases, microbes associated to invertebrates display low diversity, like the ice-

525   adhered anemone *Edwardsiella andrillae*, an endemic anemone of Ross Sea living in the sea ice-

526   water interphase, where the main phyla are Proteobacteria and Tenericutes. Interestingly, most of

527   its sequences display recent diversification branching, which suggests that its associated bacteria

528   are evolutionary recent (phylogenetically new) (Murray et al., 2016).

529

530   On the other hand, invertebrates with long and complex life cycles, also have a complex

531   pattern in their associated microbes along its life stages. In the Sydney rock oyster (*Saccostrea*

532   *glomerata*), bacterial composition is driven by life history characteristics (Unzueta-Martínez et

533   al., 2022). For example, environmental bacteria are a major source of bacterial composition in

534   swimming larvae stages, thus, the microbiota of these stages is characterized by common marine

535   free-living bacteria. On the contrary, sessile stages, like pre adult stage, adult and gametes have

536   distinct microbiota profiles. Overall, the bacterial composition across life stages in the Sydney

537   rock oyster is patchy, which suggests that the majority of oyster associated microbes are either

538   opportunistic or commensals, with few relevance to the oyster. Nevertheless, the genus *Nautella*

539   (Rhodobacterales) was consistently present across stages, increasing its abundance notably in the

540   last stages.

541

542   To the best of our knowledge, the only crustaceans in the Southern Hemisphere studied to

543   date are lobsters, krill and copepods. Overall, the bacterial microbiota of crustaceans in the

544   Southern Hemisphere is dominated by Campilobacterota, Tenericutes, Actinobacteria,

545   Firmicutes, Bacteroidetes and Proteobacteria (Clarke et al., 2019; Ooi et al., 2019; Clarke et al.,

546   2021; Oh et al., 2021; Zhang et al., 2021).

547

548   Microcrustaceans are important trophic links between primary producers (e.g., diatoms),

549   primary, and secondary predators (e.g., seabirds and fish, respectively). Antarctic krill (*Euphasia*

550   *superba*) is the trophic basis in the Southern Ocean ecosystem. Despite its inherent exposure to

551   marine bacteria, Antarctic krill hosts unique bacteria phyla in its body; furthermore, its epibiotic

552   associated bacteria differentiates as geographic distance increases. Hence, distance, rather than

553   environmental heterogeneity drives epibiotic bacteria composition in krill (Clarke et al., 2019;

554   Clarke et al., 2021). The major bacterial players in their chitin surface are Campilobacterota and

555   Tenericutes, while in the stomach and intestinal gland were Actinobacteria and Firmicutes

556   (Clarke et al., 2019). Interestingly, *Colwellia* bacteria is a prevalent member of epibiotic

557   microbiota in Antarctic krill swarms at local and regional scales (Clarke et al., 2021). Its

558   persistent association, through thousands of kilometers, might suggest an important role to krill

559   health.

560

561   Sea temperature increase might disrupt psychrophilic bacteria associated with Antarctic

562   crustaceans. In the Antarctic copepod *Tigriopus kingsejongensis*, 15 °C temperature treatment

563   has profound effects in its fecal microbiome. Temperature increase diminishes abundance of

564   psychrophilic bacteria (e.g., *Colwellia*), whereas it facilitates the increase in opportunistic

565   pathogens (e.g., *Vibrio*) and virulence genes (Oh et al., 2021). As sea surface temperature

566   increases, it is probable that the microcrustacean holobiont will face major shifts in its associated

567   bacteria, on one hand the increase of bacteria that prefer higher temperatures (e.g., *Vibrio*), and

568   on the other hand, the decrease of psychrophilic bacteria.

569

570   Natural life history events, like molting and temperature, have important effects in

571   crustacean's microbiota composition (Ooi et al., 2019; Zhang et al., 2021). Molting is a critical

572   process in crustaceans that allows them growing and sexual maturation. Evidence from the

573   chinese mud crab, *Scylla paramamosain*, suggests that molting represents a bottleneck to most of

574   its associated microbes in gills and midgut. Nevertheless, hemolymph bacteria,

575   *Halomonas* and *Shewanella*, prevail despite molting (Zhang et al., 2021). Noteworthy, the

576   abundance of this bacteria, had a high correlation with the expression of crab antimicrobial gene

577   expression. These results suggest the presence of highly adapted bacteria to the complex life

578   cycle of the mud crabs. Yet, it is uncertain to which degree, molting could alter microbiome traits

579   in the crab holobiont. Sea temperature increase might impose microbe related burdens to

580   crustaceans, as exemplified by the spiny lobster, *Panulirus ornatus*, in Australia (Ooi et al.,

581   2019). In the spiny lobster, temperature increase has a direct relationship with juvenile mortality.

582   As temperature increases, so does bacteria metabolism, which burdens the lobster immune

583   system by bacteria infiltration and subsequent uncontrolled proliferation in the hemolymph.

584

585   Interestingly, there have been conducted holobiont approaches in snails in deep

586   hydrothermal vents and several Lucanidae species (Mollusca) across the world, where host DNA

587   and microbial DNA have been simultaneously addressed (Lan et al., 2021; Osvatic et al., 2023).

588   These results have highlighted the effect of ecological niche and host-microbe metabolic

589   complementarity in microbiome assembly. Interestingly, sulfur oxidizing bacteria is present in

590   phylogenetical and geographical distant species of Lucanidae Mollusca (Lan et al., 2021; Osvatic

591   et al., 2023). The above examples highlight the relevance of coupling holobiont approaches with

592   relevant ecological data to address the meaningfulness of the interactions among hosts and its

593   associated microbes.

594

595   In the Strait of Magellan study that we will describe at the end of the article, we are

596   including two crustacean species, the centolla, *Lithodes santolla* and the channel sprawns,

597   *Munida gregaria*. The former, is an economically important species that spend most of its life in

598   the sea floor, while the latter is a key species in trophic energy transfer, since it is simultaneously

599   an important plankton consumer and is eaten by several predators (e.g., Magellanic penguin and

600   sea lion). In our holobiont study in the Magallanes region, we expect that the centolla will present

601   fewer signals related to the UV light and heat stress than any of the other species that have a more

602   ample niche in the water column or in the surface as is the case of sea lions and penguins.

603

604   **Vertebrates**

605

606   **Fish**

607

608   There are more than 20,000 species of marine fish around the globe (CML, visited 2023).

609   Fish are important links between trophic basal levels and higher ones, yet the fish holobiont is the

610   least studied in the Southern Hemisphere with 9 studied species within 4 research articles (Fig.

611   1). All fish studies have been conducted with 16S metabarcoding approaches (Table 1). Fish

612   microbiome sampling effort in the Southern Hemisphere has been predominantly done template

613   (Australia) and Antarctic latitudes (Antarctica) (Fig 2). Hence, there are important gaps in

614   tropical, template and cold latitudes, specifically in South America, Africa, and Indonesia (Fig.

615   3). Importantly, we still ignore much about native fish species microbiome, since most studies

616   have been done in commercially important species. Most fish microbiome studies have been

617   performed with the objective of testing the usefulness of microbial taxa as biosensors of the fish

618   health. Fish skin has a mucous layer over its epidermis that serves as an additional barrier

619   between the environment and the host's skin. The mucous layer consists of immunogenic

620   compounds that play important roles in innate and adaptive immunity (Gomez et al., 2013). Thus,

621   bacteria inhabiting fish skin, might be commensals in healthy individuals or

622   opportunistic/pathogenic in fish with compromised health.

623

624   Current evidence of fish bacterial microbiota in the Southern Hemisphere, has shown that

625   the most prevalent bacteria phyla associated to fish are Actinobacteria, Firmicutes,

626   Proteobacteria, Tenericutes, and Bacteroidetes (Song et al., 2016; Minich et al., 2020; Legrand et

627   al., 2018; Heindler et al., 2018). In the southern Bluefin Tuna, in Portland Australia, *Thunnus*
628   *maccoyii*, captivity and antiparasitic administration (i.e., praziquantel) have important effects in
629   fish microbiota composition. Healthy fish microbiota, without praziquantel, is dominated by
630   Mycoplasmataceae in its skin, and *Pseudomonas*, *Acinetobacter*, *Brevundimonas*, and *Delfita* in
631   its gut (Minich et al., 2020). In the Yellowtail Kingfish (*Seriola lalandi*), in temperate and
632   southern waters of Australia, early enteritis produces microbial fingerprints in its skin microbiota.
633   Early enteritis is associated with greater abundance of *Loktanella*, *Marivita,* and *Planktomarina*,
634   *Simplicispira,* and *Litoricola,* as well as decreased diversity in the microbial community (Legrand
635   et al., 2018).
636
637   Fish microbiota also has been addressed under a natural history framework. In four
638   species of wild Antarctic fish (Trematomus bernacchii (family Notothenioidei), Chionodraco
639   hamatus, (family Channichthyidae), Gymnodraco acuticeps (family Bathydraconidae), and
640   Pagothenia borchgrevinki (family Notothenioidei), gut microbiota has a stable composition
641   among several species (up to 50% sequences are shared among individuals) (Song et al., 2016).
642   This suggests the presence of a core intestinal microbiome in Antarctic fish, despite differences in
643   environment and diet, which might play important roles in fish health.
644
645   Interestingly, fish gut microbiota could serve as a biological prognosis of anthropogenic
646   impact in marine environments, when it is possible to compare historical and contemporary
647   samples. In the Antarctic fish *Trematomus* spp. historical samples (museum samples with 100
648   years old, fixed with formalin and embedded in paraffin) have revealed notable shifts in gut
649   microbiota composition. Contemporary fish gut microbiota was characterized by Chlamydia,
650   Firmicutes, Cyanobacteria and Mycoplasma. In contrast, historical fish gut microbiota was
651   dominated by Proteobacteria. Despite the richer appearance of phyla in contemporary fish, OTU
652   richness and Shannon index diversities were higher in ancient fish (Heindler et al., 2018). These
653   results attempt to elucidate the relationship between fishing practices and fish gut microbiota,
654   under a historical context. Before global fishing practices, fish were able to have a consistent diet
655   that produce redundant gut communities at the phylum level. In contrast, fishing practices
656   disrupted prey availability, which forced fish to become more opportunistic in their feeding,
657   producing gut communities with wider phylogenetic representation, albeit less diversity (Heindler
658   et al., 2018). Whether the shift from more diverse gut microbiotas enclosed in one phylum, to less

659 diverse communities with members spanning several phyla has impacts in fish (and any marine

660 host's) health, is a deep open question.

661

662   In the Strait of Magallanes project that we describe at the end of the paper, we are

663 studying two fish species, the sardine *Sprattus fuegensis* and the farm salmon, *Salmo salar*. We

664 think that the skin microbiome comparison between a wild native species (i.e., sardine) and an

665 introduced species raised in captivity (i.e., salmon) will provide important clues about local

666 marine conditions as well as the effect of captivity.

667

668 **Seabirds**

669

670   Seabirds are important components of the Southern Hemisphere (Woehler et al., 2001).

671 Currently, there are 350 species around the globe, with at least 61 species endemic to the

672 Southern Hemisphere (Croxall et al., 2012). Seabirds' microbiome has received substantial

673 attention in the Southern Hemisphere, with 22 studied species within 16 research articles (Fig. 1,

674 Table 1). Nevertheless, most of these studies are restricted to few penguin species (Table 1) and

675 in most cases have been done with fecal samples (but see Leclaire et al., 2019). However, this is a

676 global trend, since there are only two studies in the Northern Hemisphere addressing feather

677 bacterial communities, most likely because these are challenging species to sample (Pearce et al.,

678 2017; Leclaire et al., 2019). Seabird microbiome sampling effort in the Southern Hemisphere has

679 been performed in most latitudinal regions, template (Brazil & Australia), cold (Argentina and

680 Keguelen) and Antarctic latitudes (Antarctic islands and Western Antarctic Peninsula (Fig. 3).

681 Seabird microbiome has been predominantly conducted with taxonomic marker approaches (i.e.,

682 16S), hence their associated microbes have been predominantly addressed at the bacterial

683 community level. Nevertheless, these studies have been conducted with metatranscriptomics and

684 RNA viromics surveys (Marcelino et al., 2019; Wille et al., 2020).

685   Overall, the main bacterial phyla of penguins' fecal microbiota in the Southern

686 Hemisphere are Firmicutes, Proteobacteria, Actinobacteria and Bacteroidetes (Potti et al., 2002;

687 Barbosa et al., 2016; Dewar et al., 2013, 2014, 2017; Yew et al., 2017; Lee et al., 2019; Tian et

688 al., 2021a, Tian et al., 2021b). Whereas the main bacterial phyla of seabird plumage microbiota in

689 the Southern Hemisphere, is characterized by Actinobacteria, Proteobacteria, Firmicutes, and

690 Acidobacteria (Leclaire et al., 2019).

691

692   Aging is an important driver of fecal microbiota composition, both in wild and captive

693   penguins (Barbosa et al., 2016; Dewar et al., 2017; Tian et al., 2021a). In wild chinstrap penguin

694   chicks (*Pygoscelis antarctica*) fecal microbiota is dominated by Firmicutes, specially by

695   Clostridiales, *Leuconostoc* and *Fusobacterium*. In contrast, adults' fecal microbiota is dominated

696   by Proteobacteria and Bacteroidetes, specially by Neisserales, Fusobacteriales and

697   Campylobacteriales, yet there is high variability among individuals (Barbosa et al., 2016; Lee et

698   al., 2019). In contrast, in captive chinstrap penguins in the Dalian Sun Asia Aquarium, China,

699   aging only changes relative abundances of the main constituents of fecal microbiotas. Chicks'

700   fecal microbiota was dominated by *Acinetobacter*, while *Pasteurella* was the dominant bacteria

701   in senior penguins (between 22-28 years old); the fecal composition was further completed with

702   *Clostridium,* and *Fusobacterium* in chicks and adult penguins (Tian et al., 2021a). Furthermore,

703   these compositional shifts followed predicted functionality shifts. In general, predicted

704   functionality reaches its maximum diversity in adults, while it starts to decline in senior penguins

705   (after 22 years old) (Tian et al., 2021a).

706

707   Support for age of the host as an important driver of fecal microbiota composition comes

708   from the little blue penguin (*Eudyptula minor*), at the Phillip Island Nature Parks, Australia,

709   where fecal microbiota between chicks and adults differs (Dewar et al., 2017). Differences in

710   fecal microbiota composition might be explained by the kind of food that chicks and adults ate.

711   Chicks eat regurgitated food, which might not require a robust microbial metabolic repertoire to

712   aid in digestion; in contrast, adults eat raw food that might contain recalcitrant chemicals, like

713   domoic acid in fish (Lefebvre et al., 2002) or fluoride, from krill (Yoshitomi et al., 2012).

714

715   Besides community compositional comparisons, 16S surveys have been used to

716   understand changes in penguins' fecal microbiome predicted metabolic functions. For example,

717   in captive gentoo penguins (*Pygoscelis papua*) in the Dalian Sun Asia Aquarium, China, sex

718   apparently influences fecal microbiome predicted metabolism (Tian et al., 2021b). Males' fecal

719   microbiota is enriched in carbohydrate metabolism, putatively driven by Lachnospiraceae family,

720   whereas females had a fecal microbiota enriched in protein metabolism, putatively driven by

721   Fusobacteriaceae family (Tian et al., 2021b). Microbiome predicted functions from 16S data are

722   constrained by the number of available microbial genomes sequenced (Douglas et al., 2020) and

723   information on its "optimal performance" is limited to human samples, and decreases sharply in

724   environmental samples (Sun et al., 2020). Therefore, functional microbiome studies (i.e.,

725   metagenomics or metatranscriptomics) coupled with experimental/culture assays are needed to

726   validate the metabolic functions that have been attributed to penguin fecal microbiota.

727

728   Fecal microbiota comparisons between several penguin species have shed light about

729   penguin species specific factors influencing fecal microbiota composition. For example, Dewar et

730   al., (2013) compared the fecal microbiota composition of four penguin species: macaroni

731   penguins (*Eudyptes chrysolophus*), king penguins (*Aptenodytes patagonicus*) and gentoo

732   penguins from two sites, Bird Island in South Georgia and Baie du Marine, Possession Island

733   Crozet Archipelago, and little blue penguins from Phillip Island, Australia. This study revealed

734   interesting patterns in penguin fecal microbiota at phyla level, where the dominant bacterial

735   phylum of each penguin species was as follows: Firmicutes in macaroni penguins, Actinobacteria

736   in king penguins, and Proteobacteria in gentoo and little blue penguins (Dewar et al., 2013). Fecal

737   microbiota divergence among penguin species might be explained by trophic niche differences.

738   Additionally, hormone profiles might also have specific effects in gut microbiota composition.

739   However, differences could also be attributed to geographical factors. Systematic studies, where

740   multiple colonies of each species with an adequate sample size are needed to verify to what

741   extent these results reflect penguin fecal microbiota in these species.

742

743   Penguin's gastrointestinal tract has several differences along its structure. Given that fecal

744   microbiota represents the last section of the gastrointestinal tract, it is unlikely that it is a

745   representative sample of penguins' gastrointestinal microbial diversity. Indeed, stomach

746   microbiota studies conducted in Adélie (*Pygoscelis adeliae*) and chinstrap penguins in Signy

747   Island, South Orkney Islands, Antarctica have revealed bacterial community structure between

748   the stomach and fecal microbiota. Stomach microbiota of Adelie and chinstrap penguins is

749   characterized at the phyla level by Firmicutes, Proteobacteria, Fusobacteria, and Tenericutes.

750   Common genera in both species are: *Cetobacterium, Psychrobacter, Chelonobacter, Clostridium*

751   (family: Clostridiaceae), *Mycoplasma* and *Ornithobacterium* (Yew et al., 2017). These stomach

752   bacterial communities differed from those reported from the fecal microbiota of these species,

753   where Actinobacteria and Firmicutes were the dominant phyla in Adelie penguin fecal microbiota

754   (Banks et al., 2009), while chinstrap fecal microbiota is characterized by Proteobacteria and

755   Bacteroidetes (Barbosa et al., 2016; Tian et al., 2021a). Stomach bacterial differentiation might

756   be explained in part, by the presence of sphenicins, special compounds in the penguin stomach

757   that prevent bacteria from digesting food (Thouzeau et al., 2003).

758

759   Fasting is a critical event inherent to penguins' life history. Penguins experience fast when

760 they rear their chicks, and when they molt. Fasting has species-specific compositional changes in

761 the fecal microbiota of penguins (Dewar et al., 2014; Lee et al., 2019). This could be explained

762 by penguin species differences in fast length and their fecal associated microbes. In king Penguin,

763 fasting increases the relative abundance of Proteobacteria, Firmicutes, Actinobacteria,

764 *Fusobacteria* and *Bacteroidete*s. In contrast, in little blue penguin, all phyla but Proteobacteria

765 decreased its relative abundance as fasting progressed (Dewar et al., 2014). Fusobacteria is a

766 butyrate producer bacterium. Butyrate is a known anti-inflammatory agent (Canani et al., 2011).

767 Furthermore, butyrate administration in chickens has immune system functional improvement,

768 which improves health and decreases pathogen incidence (Panda et al., 2009). The enrichment of

769 *Fusobacteria* in king penguin fasting, suggest that this bacterium could play an important role in

770 metabolic homeostasis. Further evidence supporting the effect of fasting in penguins comes from

771 gentoo and chinstrap penguins in different trophic status (i.e., feeding season or fasting). In

772 feeding chinstrap and gentoo penguins, Fusobacteria and Proteobacteria were the dominant

773 bacteria, while in molting (fasting) birds, these phyla decreased while Firmicutes increased its

774 relative abundance. Nevertheless, the magnitude in the compositional changes of its fecal

775 microbiota composition differed among species. While shifts in chinstrap penguins were subtle

776 (i.e., not supported statistically), shifts in gentoo penguin were major (i.e., statistically supported)

777 (Lee et al., 2019).

778

779   It is worth mentioning, that penguin and Antarctic birds' fecal microbiota studies have shed

780 light in the widespread occurrence of genera close to known pathogens. Those genera include

781 *Campylobacter, Yersinia, Salmonella*, and *Escherichia* (Barbosa et al., 2009), yet, it is uncertain

782 to which degree they affect penguins' health, but they might have a parasitic basis. Support of

783 this, comes from Magellan penguins from Peninsula Valdez, Argentina where in penguin chicks,

784 *Corynebacterium*, a dominant bacterium in fecal samples appears to divert resources from the

785 chick, impairing its growth., but administration of a wide spectrum antibiotic, reduced

786 *Corynebacterium* abundances, reversing growth halting (Potti et al., 2002).

787

788   On the other hand, the presence of potential pathogens in Antarctic animals can be a

789 misinterpretation of what "is normal" and what is human related (Souza et al., 1999). The same

790 may occurs with virus associated with Antarctic fauna. For example, chinstrap, Adélie, and

gentoo penguins harbor a great diversity of virus in their cloaca and of their ectoparasitic mites (Wille et al., 2020). These results highlight the uniqueness fauna living in the Antarctic biome. Moreover, it calls for further microbiome research in these remote places, in order to elucidate their relationship with worldwide fauna.

Seabird plumage microbiota has been poorly studied in the Southern Hemisphere, yet, we have some insights from the blue petrel, *Halobaena caerulea,* whose plumage microbiota composition is highly variable among body sites (Leclaire et al., 2019). Furthermore, some bacteria show a positive correlation with MHC (Major histocompatibility index), which suggests that plumage bacteria are influenced by MHC allele diversity in this seabird.

Interestingly, a metatranscriptomic approach revealed a high incidence of antibiotic resistant genes in several seabirds from Australia with different trophic ecologies (Marcelino et al., 2019). Synanthropic (living near human settlement) species with filter eating habits, like several Australian ducks (*Anas* spp. and *Tadorna tadornoides*) , had the highest diversity of antibiotic resistant genes, whereas avocets (*Recurvirostra novaehollandiae*) and gentoo penguins, which live in remote areas and prey invertebrates and fish, respectively, had the fewest. However, the presence of antibiotic resistant genes is not a surprise since this seems to be a very ancient strategy in microbial communities (Souza et al., 1999). Noteworthy, although the cloacal microbiome of gentoo penguins had the less diversity of antibiotic resistant genes, it displayed resistance against unique drugs, like Macrolides, Lincosamide, and Streptogramin (Marcelino et al., 2019).

In a similar fashion, kelp gulls (*Larus dominicanus*) and Magellan penguins from Brazil were assessed by qPCR to evaluate the diversity of antibiotic genes they harbor (Ewbank et al., 2021). Ecological strategies (synanthropic / remote, migratory / non, opportunistic / specialized feeding) might have a strong association with antibiotic gene resistance transmission, with those related to anthropocentric activities having the greatest diversity in antibiotic resistance genes. As expected, kelp gull, a synanthropic species, has the greatest diversity in antibiotic resistance genes. Its antibiotic resistant gene pool has resistance against eight drugs: tetracycline, aminoglycosides, sulfonamides, chloramphenicols, macrolides, quinolones, betalactams, polymyxins. On the contrary, in the Magellan penguin, a migratory, non-synanthropic, specialized feeder (it preys mainly fish and squid) their antibiotic resistance genes diversity was

824   lower, with specific resistance against two drugs, tetracycline and quinolone (Ewbank et al.,

825   2021).

826

827   In our project on the surface microbiome of key species in the Strait of Magellan, we are

828   planning to study the feather microbiome in Magellan and King penguins. We are interested in

829   testing geographical, phenological, and developmental effects in feather microbiome of these

830   species. These works will provide original baseline knowledge regarding penguin feather

831   associated bacteria.

832

833   **Marine mammals**

834

835   Marine mammals comprise several species that collectively are considered as "marine sentinels",

836   since their population trends could give valuable insights about the status of the marine

837   ecosystem (Moore, SE, 2008). Currently, there are 115 species distributed around the globe

838   (Kaschner et al., 2011). Up to one third of them are cooccur between the template – cold latitudes

839   (i.e., 20-50) of the Southern Hemisphere. Important hotspots of marine mammals' biodiversity:

840   New Zealand, Sub-Antarctic and Southeastern Pacific islands, and offshore waters along the

841   coasts of southern South America (Kaschner et al., 2011). Marine mammals' microbiome has

842   received the greatest attention in the Southern Hemisphere, with 15 studied species within 17

843   research articles (Fig. 1, Table 1). Nevertheless, most studies have been conducted in one species

844   (humpback whale) (Table 1). In most cases, these studies have been conducted with 16S

845   approaches, but there is a pinniped shotgun metagenome (Table 1, Smith et al., 2013).

846   Interestingly, marine mammals' microbiome research has been done worldwide, with sampling

847   effort across all latitude regimes (tropical, template, cold and Antarctic), specifically in template

848   latitudes (i.e., Australia), followed by Antarctica and South America (Fig. 3).

849

850   We still lack a more comprehensive view of cetaceans' microbiome in the Southern

851   Hemisphere, since most of current studies have been done in one species over different

852   geographic locations (i.e., humpback whale) (Table 1). In contrast with cetacean microbiome

853   knowledge in the Northern Hemisphere where several species have been addressed (Sanders et

854   al., 2015; Van Cise et al., 2020; Apprill et al., 2020; Miller et al., 2020). While this gives us depth

855   in understanding humpback whale microbiome across geographic regions, it also pinpoints to the

856   great void that remains in the rest of cetaceans, like whales and dolphins. Besides humpback

857   whale, there have been conducted several studies in pinnipeds (Table 1).

858

859   In particular, marine mammals' microbiome research has been focused in whale skin and

860   blow microbiota studies. In the Southern Hemisphere skin microbiological surveys have been

861   done in rorquals (Balaenopteridae, species *Megaptera novaeangliae* [humpback whale],

862   *Balaenoptera musculus,* and *B. physalus*) as well as killer whales (*Orcinus orca*). Overall, the

863   main bacterial elements in the whale skin microbiota are Proteobacteria, Bacteroidetes,

864   Actinobacteria, and Firmicutes (Apprill et al., 2014; Pirotta et al., 2017; Bierlich et al., 2018;

865   Hooper et al., 2019; Vendl et al., 2019; Vendl et al., 2020; Toro et al., 2021).

866

867   Humpback whales are the best studied cetaceans in the Southern Hemisphere. Studies

868   from humpback whales in the South Pacific (Samoa islands), Chilean coasts and Antarctic

869   regions have allowed the detection of a skin core microbiota, characterized by *Tenacibaculum*

870   and *Psychrobacter* (Apprill et al., 2014; Bierlich et al., 2018; Toro et al., 2021). Rorquals

871   (*Megaptera novaeangliae, Balaenoptera musculus,* and *B. physalus*) skin microbiota along

872   several points in Chilean coasts have idiosyncratic and species-specific trends, that is, whales

873   have a unique skin microbial composition at the individual and the interspecific level. However,

874   their skin microbiota alpha diversity was similar in compositional terms (i.e., Shannon diversity),

875   but was slightly different in phylogenetic terms (i.e. Faith phylogenetic diversity) (Toro et al.,

876   2021).

877

878   Skin microbiota of humpback whales foraging in Antarctica and the Strait of Magellan are

879   enriched in *Psychrobacter* bacteria. Changes in sea surface temperature, as well as shifts towards

880   northern areas, are associated with decreases in *Psychrobacter* relative abundance. This pattern

881   suggests that sea temperature is an important driver in humpback whale skin microbiota assembly

882   (Bierlich et al., 2018; Toro et al., 2021).

883

884   Blow microbiota of Australian humpback whales has been surveyed to address whales'

885   health. In contrast with skin microbiota, blow microbiota is sparse among individuals, without

886   any discernable core. The most abundant microbes in the blow were *Tenacibaculum,*

887   *Pseudomonas Leptotrichia* and *Corynebacteria*. Additionally, some individuals had potential

888   respiratory pathogens in their blow microbiota, like *Balneatrix, Clostridia, Bacilli,*

889   *Staphylococcus* and *Streptococcus* (Pirotta et al., 2017; Vendl et al., 2019). Furthermore, whale

890   blow associated bacteria harbors significant phylogenetic novelty, since half sequences in some

891   individuals were only able to identify at class level (Vendl et al., 2019). Whale feeding

892   phenology is an important factor that could underlie the sparsity of blow microbiota structure.

893   While feeding blow microbiota has a core microbiota composed of *Arcobacter,*

894   *Corynebacterium, Enhydrobacter, Helcococcus* and *Tenacibaculum,* albeit in very low

895   abundance, 1.5% or less. In contrast, during migration, when whales are fasting, blow microbiota

896   among individuals becomes highly variable, with no discernible core (Vendl et al., 2020a).

897   Besides phenology or health status, whale blow microbiota is also influenced by the sociality

898   degree of the studied species. Whale species with gregarious habits (e.g., humpback whale), have

899   higher diversity and a great microbial core in their blow microbiota, in contrast with more

900   solitary whales (Vendl et al., 2020b). Likely, this could reflect the horizontal transmission of

901   blow microbes among contiguous whales, where the microbes exhaled by one individual are

902   inhaled by another, and so on. Nevertheless, more studies are needed to address if this pattern

903   emerges because of horizontal transmission or could reflect common health status among whales'

904   groups.

905

906   In the case of Killer whales, the Antarctic ecotypes have been found to harbor a distinct

907   skin microbiota from ecotypes in the northern hemisphere. Differences are driven by

908   *Tenacibaculum dicentrarchi* bacteria, diatoms, and several algae-associated bacteria (Hooper et

909   al., 2019). More systematic studies of whales associated bacteria, and ideally of an "authentic"

910   holobiont approaches (i.e., describing whale genetic traits, as well as their microbiome and

911   trancriptome) to better understand the whale holobiont.

912

913   In our project on the surface microbiome of key species in the Strait of Magellan (ANID

914   R20F0009), we are including a holobiont approach to study the humpback whales of the area. In

915   particular, we are sampling individuals that migrate to the Strait of Magellan to feed in the austral

916   summer season.

917

918   Pinnipeds are apex predators whose health might inform about marine ecosystem conditions

919   (Moore, SE 2008). Sampling pinnipeds is challenging due to the remote location of their colonies

920   and proclivity to escape from humans, hence, the most feasible samples to study them, are the

921   feces they leave in rocks. Seal fecal microbiota apparently is driven by several host factors,

922 including feeding, geographic distribution, ontogeny, trophic niche differences, anatomy, and

923 physiology, explaining, at least in part, the great fecal microbiota composition variability among

924 species, where there is no detectable fecal core microbiota. Nevertheless, it is uncertain if the

925 taxonomic differences are congruent with microbiome metabolic traits.

926

927   Overall, the main bacterial components of seal fecal microbiota are Firmicutes,

928 Fusobacteria, Bacteroidetes, Proteobacteria, and Actinobacteria (Nelson et al., 2013; Delport et

929 al., 2016; Grosser et al., 2019; Kim et al., 2020; Toro-Valdivieso et al., 2021).Nevertheless, fecal

930 microbiota from pinnipeds has been a challenging task as there seems to be a high proportion of

931 phylogenetic novelty that interferes with taxonomic identification (i.e., at the family or genus

932 level) and proper analysis of the divergence among communities (Toro-Valdivieso et al., 2021).

933 For example, across pinniped species, fecal microbiota composition at phylum level seems to be

934 identical (Nelson et al., 2013; Kim et al., 2020) but diverges at lower taxonomic levels. For

935 instance, in the southern elephant (*Mirounga leonina*) and Weddell seals (*Leptonychotes*

936 *weddelli*) at the phylum level, fecal microbiota is dominated by Firmicutes, yet at the family level

937 Ruminococcaceae and Acidaminococcaceae, respectively, drive differences in the fecal

938 microbiota composition (Kim et al., 2020). Life history characteristics create complex patterns

939 that influence fecal microbiota, as shown with the fecal microbiota of southern elephant seals and

940 leopard seals (*Hydrurga leptonyx*). In these species, fecal microbiota is shaped by the

941 simultaneous effect of species, age and sex, creating complex fecal microbiota patterns with no

942 discernable trend (Nelson et al., 2013). In the Australian fur seal (*Arctocephalus pusillus*) aging

943 from pups to adults produces a successional pattern in fecal microbiota composition. Adult fecal

944 microbiota had unique bacterial taxa, dominated by *Clostridium*, *Lactobacillus* and

945 *Enteroccoccus*. The diet shift from milk with high fat-protein in pups to a marine raw diet in

946 adults, is thought to underlie the fecal microbiota diversification (Smith et al., 2013).

947

948 A fecal microbiota survey in the Australian sea lion (*Neophoca cinerea*) showed a core fecal

949 microbiota at family level, composed of Clostridiaceae bacteria. This core arises only in wild

950 seals, which suggests that natural diet might represent a cohesive driver in fecal microbiota

951 composition. Instead, captive animals lacked Clostridiaceae bacteria in their fecal microbiota.

952 Moreover, seals from wild colonies had more fecal microbial diversity than captive colonies,

953 especially those with high densities (Delport et al., 2016). At the functional level, the Australian

954 sea lion fecal microbiome is enriched in carbohydrate metabolism, nitrogen biosynthetic and

955 nutrient transport pathways, as well as virulence genes. The fecal microbiome composition

956 appears to play an important role in fat – nutrient storage, key issues in marine mammals'

957 survival in polar ecosystems (Lavery et al., 2012). This could pinpoint to a fat storage mechanism

958 driven, or at least with high influence, of gut microbes. Nevertheless, a higher sample and more

959 phylogenetic inclusivity (i.e., more seal and sea lion's species) is needed to validate the

960 prevalence of this microbiome traits among populations and pinniped species. Interestingly,

961 Clostridiaceae bacteria has a high prevalence among Australian seal species fecal microbiota

962 (Lavery et al., 2012; Smith et al., 2013; Delport et al., 2016), which might suggest an important

963 role for these bacteria in seals digestion. Nevertheless, it is a cautionary interpretation since gut

964 microbiota composition varies along the gastrointestinal tract. Hence, fecal microbiota reflects

965 only a portion of the gut microbiome.

966

967 In the case of skin microbiota, there is one example from the Antarctic fur seal

968 (*Arctocephalus gazella*) (Grosser et al., 2019). In this fur seal, colony density drives skin

969 microbiota structure, rather than genetic similarity. High density colony had fewer alfa diversity

970 in its skin microbiota. This suggests that stress associated with overcrowding could scale to skin

971 microbiota composition, diminishing the richness and abundance of bacterial taxa. Nevertheless,

972 overcrowding, also might facilitate horizontal transmission since fur seals are in close contact.

973 This could allow fast transmission of opportunistic microbes, capable of dominating the

974 community. Most likely, the combination of both explanations might aid in illuminating the

975 pattern; stress produced by overcrowding, coupled with increased transmission of fast

976 reproducing microbes, shape the skin microbiota of colonies with high density. (Grosser et al.,

977 2019).

978 In our Strait of Magellan project (ANID R20F0009), we are studying the skin surface

979 microbiome of colonies of the South American sea lion (*Otaria byronia*), a keystone species in

980 the sub-Antarctic ecosystem.

981

982 **Discussion and perspectives**

983

984 **Microbiomes in the southern ecosystems and climate change context.**

985

986 In the southern ecosystems, including Antarctica, it has been predicted that higher temperature

987 will increase coastal ice-free areas, sea-ice loss, glacial retreat, ocean acidification and ocean

988   warming (Morley et al., 2020), affecting marine biota in all trophic level. Lower trophic levels
989   are expected to move south, depending on their tolerance of warming ocean condition and
990   productivity, meanwhile, ocean acidification will impact mainly over crustaceans and calcifying
991   organisms. Marine animals, mammals, and seabirds are expected to move to alternative locations
992   for food and breeding, for survivor and adaptation (Constable et al., 2014). However, the impact
993   of climate change over organisms and their associated microbiota as a whole—i.e., the holobiont
994   – has been poorly studied across the metazoan spectrum, with notable exceptions in some
995   invertebrates and macroalgae (Table 1). Yet, we still lack ecosystem holistic approaches (i.e.
996   including abiotic variables or ideally holobiont experimental assays where important abiotic
997   parameters, like temperature and pH are controlled), that could give us insight about marine
998   holobiont adaptability potential to the environmental changes that soon will face as a
999   consequence of anthropogenic climate change.

1000

1001   We think that the relation between the holobiont and their ecosystems is bidirectional,
1002 where the environmental changes. will affect the host and their associated microbes, meanwhile
1003 changes in the host like abundance, behavior, feeding, molting and reproduction; and their
1004 microbiome like diversity, taxonomic composition, and nutrient recycling, will impact over the
1005 environment. For example, soils impacted by penguins and pinnipeds presented high amount of
1006 nutrients such carbon, nitrogen and phosphorous (Ugolini, FC 1972; Tatur et al., 1990). Also,
1007 marine animals' impact over greenhouse gases emissions, penguins and pinniped settlement had
1008 been founded a hotspot of CO_2, methane (CH_4) and nitrous oxide (N_2O) emissions (Zhu et al.,
1009 2008; 2009). In these processes animals had a huge impact over the coastal sediments where they
1010 colonized through their feces, eggs, prey, carcasses, among others (Guo et al., 2018; Almela et
1011 al., 2022; Ramírez-Fernández et al., 2019). Feces can directly impact over soil microbiome,
1012 seeding gut microbes from marine animals, and indirectly because the high amount of nutrients
1013 that they transport from marine to terrestrial ecosystems (Guo et al., 2018). At functional level,
1014 marine animals increased soil microbial communities related with denitrification pathways
1015 (Ramírez-Fernández et al., 2021), and other nitrogen pathways involved in N_2O emissions.

1016

1017   Climate change studies should take in account the impact of environmental changes in the
1018 host and their microbiome. In our project on the surface microbiome of key species in the Strait
1019 of Magellan, we will measure environmental factors such as water temperature, UV radiation,
1020 chlorophyll content, oxygen levels, pH, salinity and nutrient content to correlates holobiont

1021   abundance, diversity, and distribution, focusing on the skin microbiome due their direct contact

1022   with the environmental parameters. The equilibrium between the holobiont and the ecosystems

1023   will allow their protection and conservation (Carthey et al., 2020).

1024

1025   **Surface microbiome of key species in the Strait of Magellan, an integrative holobiont**

1026   **project**

1027

1028   To increase the number of microbial biodiversity studies in the southern hemisphere, emerges our

1029   microbiome project of key species in the Strait of Magellan in Chile (Fig. 5). Our project will

1030   generate new baseline data for almost all the species that will be sampled (except for humpback

1031   whale skin, which has been extensively studied). Hence our project, has two stages, first baseline

1032   data generation for all considered species. Second, microbiome functional data (i.e.,

1033   metagenomics and metatranscriptomics) as well as ecosystem data integration, where host

1034   microbiome data from multiple years along environmental variables will be integrated. We think

1035   this approach will give valuable insights about host-microbiome responses to ongoing

1036   Anthropocene derived climate change. Moreover, it will generate host microbiome data framed

1037   under an ecosystemic approach, which will be valuable for further comparisons in next years,

1038   where environmental variables likely would have changed.

1039

1040   We consider that microbes are an excellent biodiversity study target, since they can show

1041   fast evolutionary responses to environmental alterations, and they have enormous metabolic and

1042   genetic diversity. We are focusing on surface microbes to test their value as biosensors of climate

1043   change effects in key hosts in the Strait of Magellan. Our project attempts to encompass trophic-

1044   level inclusivity, through sampling hosts in different (yet related) trophic levels, and an

1045   introduced species (i.e., farm salmon). We will sample a primary producer (i.e., *Macrocystis*

1046   *pyrifera*, huiro/kelp), primary consumers (i.e., two crustacean species *Lithodes santolla*, centolla

1047   and *Munida gregaria,* channel prawns), secondary predators (i.e. *Sprattus fuegensis,* Fuegian

1048   sprat*; Spheniscus magellanicus*, Magellan penguin, *Aptenodytes patagonicus,* king penguin and

1049   *Megaptera novaeangliae,* humpback whale) and an apex predator (i.e. *Otaria byronia,* South

1050   American sea lion).

1051

1052   Our project will generate original baseline knowledge of bacterial communities associated

1053   to the surface of some taxa (like penguins' feathers, sea lion fur, fish scales, or crustacea shell).

1054 Furthermore, as we plan to perform multiannual samplings, the project will bring the opportunity

1055 to dilucidate if there are microbial signatures (both at the community and genomic level)

1056 associated to seasonal variation and/or to environmental variables. Our main objective is to test if

1057 there is a core surface microbiome among marine hosts sharing the same environment (i.e., in

1058 particular in Coastal Marine Protected Area "Francisco Coloane"). Alternatively, we are

1059 interested in testing the existence of a core microbiome at different levels. For example, at host

1060 complexity (i.e., a core microbiome for invertebrates, another for mammals, etc.); trophic level

1061 (i.e., a core microbiome for primary consumers, another for primary predators, etc.); or

1062 alternatively a species-specific surface microbiome.

1063

1064   In general, the marine holobiont in the Southern Hemisphere is characterized by few

1065 systematic and authentic holobiont studies (i.e., studies that analyze at the same time host traits

1066 [e.g., genomics, transcriptomcs] and microbiome traits [e.g, 16S, metagenome], see Table 1 for

1067 holobiont studies examples). Besides there is a great bias in sampled hosts. For instance, sponges

1068 have been thoroughly sampled, but there is a great gap in marine invertebrate and vertebrate

1069 hosts. We highlight the case of marine invertebrates, which although have a relatively high

1070 number of studied species (23), it remains a tiny fraction of its huge diversity.

1071

1072   Holobiont studies are dominated by microbiota approaches, where the focus is centered in

1073 taxonomic patterns across ecological/life story conditions. These studies have highlighted the

1074 prevalence of Proteobacteria among a wide spectrum of hosts, while specific host-phyla

1075 associations complete the bacterial community. Noteworthy, microbiota approaches have been

1076 centered in the bacterial fraction, completely ignoring the potential role of fungi, virus and

1077 archeaea in the marine host holobiont. Notable exceptions where these groups have been

1078 addressed are macroalgae (fungal communities), penguins (viromics) and sponges (archaea).

1079 Nevertheless, there is no study that addresses the interactions among all these groups

1080 simultaneously, likely because technical and economic challenges (i.e., computational resources,

1081 computational skills).

1082

1083   Microbiota studies are important and economically feasible explorations, yet detailed

1084 microbiome studies including metagenomics and metatranscriptomics studies are needed to

1085 inclusively address the microbe community (fungi, eukaryotes, virus, bacteria, and archaea) as

1086 well as its functional potential along with its host. Moreover, functional holobiont data (i.e., host

1087   genomics & metagenomics/metatranscriptomics) coupled with environmental data, might provide

1088   valuable insights about the influence of ecosystemic status in host associated microbiome, which

1089   in turn could be tested for the plausibility of the microbiome to reflect host stress.

1090

1091   Microbiome studies might help in elucidating whether patchy/heterogenous distribution in

1092   microbe taxonomic profiles has different functional potential, or rather, if distinct taxonomic

1093   profiles have convergent/redundant functional profiles. Additionally, microbiome studies might

1094   help to elucidate if there is a microbiome functional profile associated with eukaryote hosts, or

1095   even among distinct hosts if there are core functions among their microbiomes. Finally, sampling

1096   must span as many individuals as possible, as well as geographic and seasonal

1097   (longitudinal/annual) representability to address whether patchy distributions among associated

1098   microbes are a natural feature of marine holobionts or a consequence of low sampling. Such a

1099   systems biology approach might bring further understanding in the complex interplay among

1100   microbes and its hosts, as well as the impact it might carry for them. We think that our project on

1101   the surface microbiome of key species in the Strait of Magellan will provide valuable information

1102   on the points mentioned above, which will contribute to the knowledge of microbial diversity in

1103   the region, as well as their current responses under Anthropocene-derived climate change.

1104

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1116

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Table 1. Summary of marine host microbiome research sampling effort in the Southern hemisphere

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Macroalgae				
Number of species sampled	Species repetitively studied (number of studies)	Predominant molecular approach	Functional microbiome/holobiont approaches	Regions repetitively sampled (number of studies)
24	*Ecklonia radiata* (4)	16S	DNA holobiont (Wood et al., 2022) Shotgun metagenomics (Song et al., 2018)	Antarctica (3) Australia (5)
Sponges				
65	*Mycale acerate* (4)	16s	Shotgun metagenomics (Moreno-Pino et al., 2020, 2021, Yang et al., 2022)	Antarctica (13)
Marine invertebrates				
23	*Euphasia superba* (2)	16S	Shotgun metagenomics (Ooh et al., 2022) DNA & RNA holobiont (Lan et al., 2021; Osvatic et al. 2023)	Antarctica (4) Australia (3)
Fish				
9	NA	16S	NA	Australia (2)
Seabirds				
22	*Aptenodytes patagonicus* (2) *Eudyptula minor* (2) *Pygoscelis adeliae* (3) *Pygoscelis antarcticus* (4) *Pygoscelis papua* (4) *Spheniscus magellanicus* (2)	16S	Metatranscriptomics (Marcelino et al., 2019)	Antarctica (5) Australia (4) Bird Island, South Georgia (2)
Marine mammals				

| 15 | *Megaptera novaeanglia* (6)
Balaenoptera musculus (2)
Neophoca cinerea (2)
Mirounga leonine (2) | 16S | Shotgun metagenomics
(Lavery et al., 2012) | Antarctica (4)
Australia (6)
Chile (2) |

Figure 1

Marine microbiome studies in the Southern Hemisphere

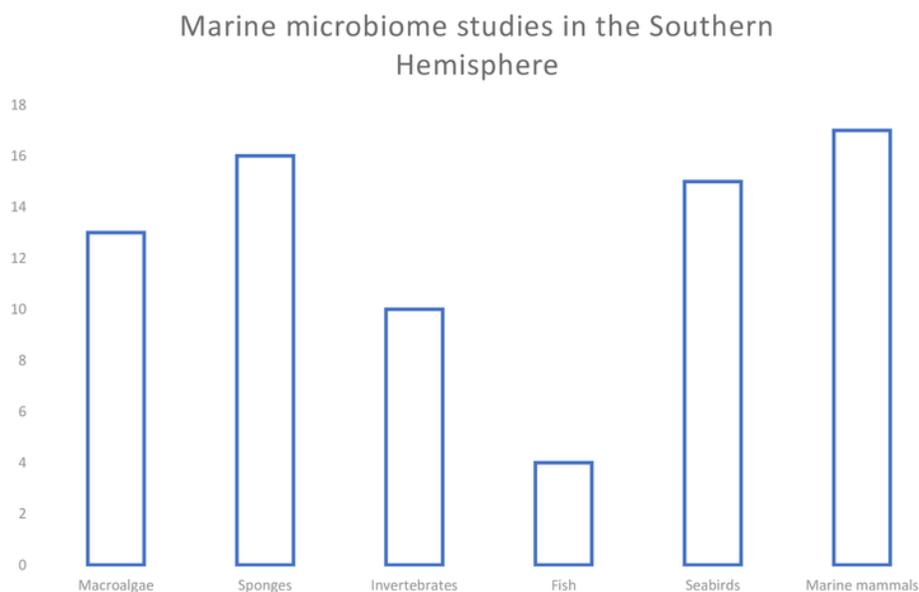
Figure 1. Total marine microbiome studies in the Southern Hemisphere reported in this review (75). The most studied groups are marine mammals (17 studies), followed by sponges (16), seabirds (15), macroalgae (13), invertebrates (10), and fish (4).

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Figure 2

Latitudinal distribution of microbiome studies in the Southern Hemisphere

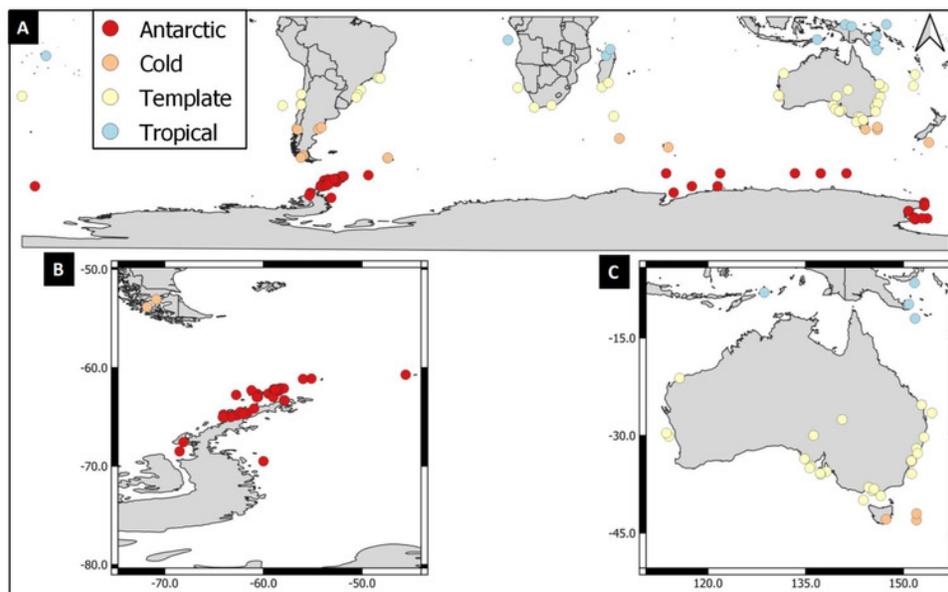
Figure 2. Southern Hemisphere map latitudinal distribution of host microbial communities sampling (A) Worldwide Southern Hemisphere. Insets with highly sampled regions. (B) Western Antarctic Peninsula. (C) Australia.

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Figure 3

Host microbiome sampling distribution in the Southern Hemisphere

Figure 3. Southern Hemisphere map of studied hosts distribution. (A) worldwide Southern Hemisphere. Insets with highly sampled regions. (B) Western Antarctic Peninsula. (C) Australia.

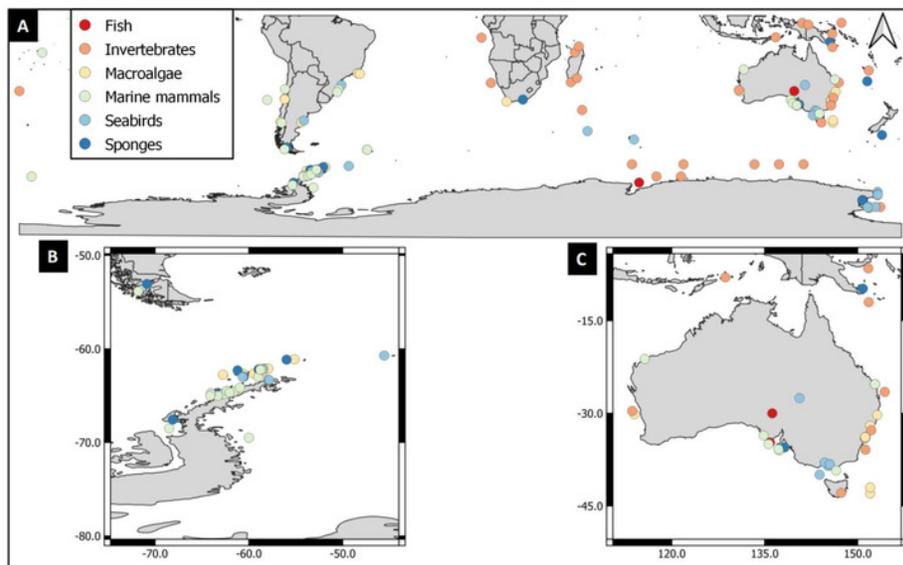
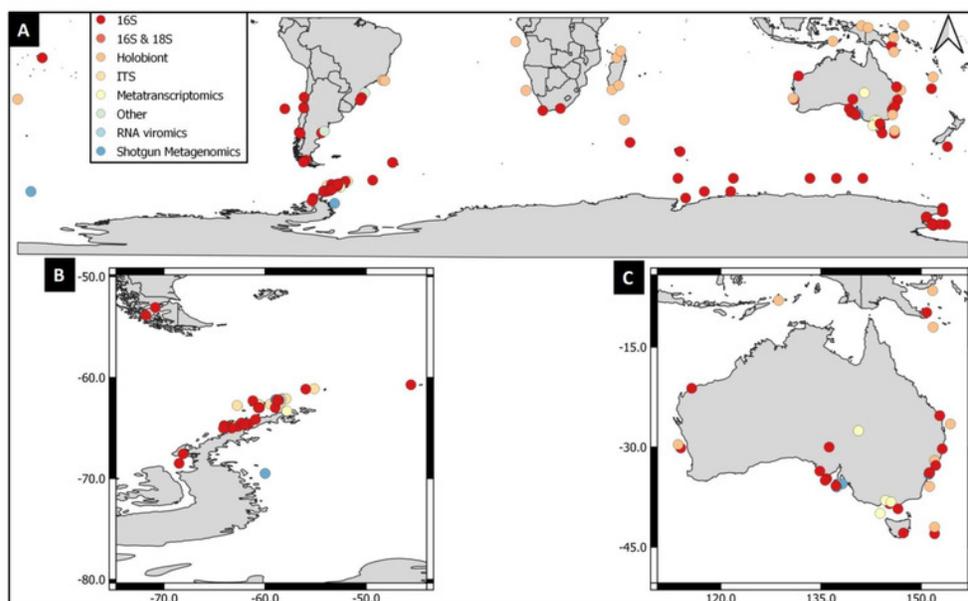



Figure 3. Southern Hemisphere map of studied hosts distribution, A) worldwide Southern Hemisphere. Insets with highly sampled regions, B) Western Antarctic Peninsula, C) Australia.

Figure 4

Southern Hemisphere distribution of molecular approaches to study marine host microbiomes

Figure 4. Southern Hemisphere map of molecular approaches used to study host microbial communities. (A) worldwide Southern Hemisphere. Insets with highly sampled regions. (B) Western Antarctic Peninsula. (C) Australia.

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Summary of the Strait of Magellan surface microbiome of key taxa project

Figure 5. Target species and main areas of field sampling of the microbiome project. (A) Target species of the microbiome project are (from top left to right): kelp / huiro (*Macrocystis pyrifera*), Fuegian sprat (*Sprattus fuegensis*), channel prawns (*Munida gregaria*), centolla (*Lithodes santolla*), Magellanic penguin (*Spheniscus magellanicus*), King penguin (*Aptenodytes patagonicus*), Humpback whale (*Megaptera novaeangliae*), South american sea lion (*Otaria byronia*), Atlantic salmon (*Salmo salar*). (B) Main areas across the Strait of Magellan that field work is taking place. The lower right side of Figures 5 (A-B) shows photographs of Carlos III Island, Contramaestre Island, King Penguin Reserve and Tuckers Islands.

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