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1 Protecting marine biodiversity beyond national jurisdiction: a penguins’ perspective

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22

23

24 *“Perspectives articles should not exceed 8000 words. Word counts include text, references, figures and tables. Each
25 figure or table should be considered equal to 300 words.”*

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5 **ABSTRACT**

6 The expansion of human activities in offshore maritime regions has outpaced the development of scientific
7 knowledge and cooperative governance across these areas beyond national jurisdiction (ABNJ). In this context,
8 current negotiations by the United Nations aim for an international legally-binding instrument to improve
9 governance and sustainable use of biodiversity in ABNJ. Penguins are among the most threatened seabird groups
10 today, notably at sea from fisheries and oiling. Here, we examine the available information on penguin movements
11 and evaluate their use of ABNJ to reveal ecologically significant areas. We highlight that in most of the 18 extant
12 penguin species, the birds may undertake spectacular migrations, seasonally or throughout life-cycle stages. Long-
13 range movements were reported in 16 species, with trans-jurisdictional distribution in 14 species, including 13 in
14 ABNJ. Species richness in ABNJ varied extensively according to oceanic region, but less according to season. We
15 propose that the new treaty may overcome some of the current challenges to penguin conservation, notably by
16 creating an authority able to designate large protected areas in ABNJ, by further promoting the precautionary
17 approach to extraction activities, and by developing technology transfer to effectively monitor ocean uses.
18 Underlining the penguins’ remarkable connectivity to the high seas may further strengthen the development of this
19 instrument aiming to preserve a common heritage of mankind.

20

21 **Introduction**

22

23 Animals with long-range movements are exposed to contrasting degrees of protection and threats as they travel
24 across geographic regions and countries' jurisdictions [1]. Such transboundary movements may thus challenge, or
25 promote, the implementation of adequate strategies for biodiversity conservation [2].

26 In the marine environment, political boundaries exist in the form of Exclusive Economic Zones (EEZs), which
27 include waters out to generally 200 nautical miles (370.4 km) from a State's shoreline. As legally defined by the
28 1982 United Nations Convention on the Law of the Sea (UNCLOS), EEZs provide exclusive rights to the coastal
29 State for the exploitation and management of local marine resources. Importantly, further offshore from EEZs are
30 the areas beyond national jurisdiction (ABNJ, the 'high seas'), which are recognized as global commons under the
31 UNCLOS. These vast areas represent 64% of the ocean's surface and 95% of its volume, and opposite to the EEZs
32 they lack a comprehensive governance structure [3, 4]. This deficiency is especially concerning as the recent
33 expansion of anthropic activities in ABNJ has outpaced the development of scientific research and cooperative
34 governance in these areas [5, 6].

35

36 Area-based management tools (ABMTs), including marine protected areas (MPAs), are widely recognized as key
37 instruments to help conserving and restoring biodiversity. Studies highlighted the need to design and implement a
38 network of such protected areas, including in the high seas, to adequately preserve marine migratory species
39 currently threatened with extinction [7]. Yet States face legal challenges to create and manage such ABMTs in
40 ABNJ [8, 9]. In this context, the UN General Assembly decided to develop an international legally-binding
41 instrument (ILBI) under the UNCLOS, on the conservation and sustainable use of marine biological diversity of
42 ABNJ (UN resolution 69/292 of 19 June 2015). Intergovernmental Conferences were convened to elaborate the text
43 of a treaty (UN resolution 72/249 of 24 December 2017), with the aim of developing the instrument as soon as
44 possible.

45

46 Progress in environmental negotiations can be hindered by several aspects of scientific uncertainty including gaps in
47 knowledge, as shown by social sciences [10, 11]. Therefore, gathering available information on transboundary
48 movements may improve the relevance of adopted measures, by highlighting specific needs in conservation policy
49 to address in this treaty [2]. Over the past decades, substantial advances have been made in our understanding of
50 marine wildlife movements in the high seas thanks to the development of electronic tracking devices. A variety of
51 marine vertebrates encompassing fishes, sharks and cetaceans were documented migrating across very large scales
52 beyond EEZs; even more remarkably, this was also the case for marine animals constrained to return ashore for
53 breeding, such as sea turtles, seals and seabirds [1, 7, 12]. Penguins (Sphenisciformes) are, with albatrosses and
54 petrels (Procellariiformes), the most threatened seabird group [13], facing a number of cumulative perils to their
55 conservation both on land and at sea. The most documented at-sea threats encompass pollution (notably oiling),
56 fishing (through both bycatch and resource competition), and climate change, all of which may affect penguins in
57 their nearshore and/or offshore habitats [14, 15].

58 One could expect the movement range of penguins to be reduced compared to other marine vertebrates, for three
59 reasons. First, penguins are constrained in the extent of their at-sea provisioning trips by frequent returns to their
60 nest during the breeding season, unlike fishes, sharks, cetaceans and sea turtles. Second, unlike flying seabirds
61 which may sustain high speeds aloft and accordingly distribute over considerable ranges (e.g., [1]), penguins’
62 locomotion by swimming may minimize their movement radius. And third, penguins are unique among seabirds in
63 that they remain out of water when moulting, which potentially constrains their at-sea range after breeding. Yet, case
64 studies showed that penguins may, at least seasonally, migrate over unexpectedly large scales, across maritime
65 boundaries of the southern hemisphere (e.g., [16, 17, 18]). Such observations question the overall extent to which
66 penguins may exploit the high seas, where they currently lack effective protection from human activities.

67

68 Three decades of at-sea tracking studies on penguins across nearly all species, now provide a relevant body of
69 knowledge to address this question in the context of conservation policy [19]. The objectives of this paper are thus
70 to examine, for each of the 18 extant penguin species, whether the birds are known to perform transboundary
71 movements across EEZs and/or to the ABNJ; and if yes, in which region(s) and season(s). These results aim to
72 inform stakeholders on the extent to which penguins (1) may reveal ecologically significant areas in the high seas,
73 and (2) may promote and in turn benefit from the development of an ILBI for the conservation of marine
74 biodiversity in ABNJ.

75

76 **Methods**

77

78 *Literature search*

79 For each penguin species, publications were searched in Google Scholar between December 2019 and July 2020
80 using the combined keywords “at-sea”, “distribution”, and the species names. Papers referenced in the accessed
81 publications were also examined. Importantly, while this paper could not provide an exhaustive review of penguin
82 movement studies, we were particularly interested in examining those showing large-scale movements, in each
83 species. Studies mostly relied on telemetry techniques to track the penguins’ at-sea distribution, but direct
84 observations from ship-based surveys were also included. Records of vagrant or dead birds ashore were not
85 considered relevant here, as these may indicate aberrant, non-viable movements for the populations, with uncertain
86 path. For example, juvenile northern rockhopper penguins *Eudyptes moseleyi* banded on Amsterdam Is. (southern
87 Indian Ocean) were found dead on Australian coasts [20], but as the birds might have died before crossing
88 jurisdictions this did not constitute adequate evidence for trans-EEZ movements here.

89

90 *Distribution versus jurisdictions*

91 Georeferenced contours of EEZs (version 11: 2019-11-18) were downloaded from the Marine Regions portal:
92 <http://www.marineregions.org/downloads.php>. The penguin distributions’ outermost coordinates were read from the
93 mapped locations, or as indicated in the text. These coordinates were then overlaid on the EEZ contours. For each
94 species, publications were listed showing cases of (1) distribution range greater than the maximal width of an EEZ

95 (370.4 km), mirroring the capacity for the birds to potentially reach the high seas; (2) movements reaching other
96 EEZ(s); and (3) evidence for use of ABNJ by the studied animals. However, since it was not always possible to
97 accurately examine the birds' individual distribution from the literature, only the clear-cut cases were used here. It is
98 thus acknowledged that other studies may exist that would bring further evidence for transboundary movements in
99 each species, including cases when the borders were crossed by only a small geographical extent.

100 Besides, disputes exist between countries regarding the sovereignty of islands, and this paper does not take any party
101 in these disputes. To recognize that such cases may translate into distinct biodiversity management regimes between
102 regions, the EEZ around any disputed territory was considered as that of a third-party nation. Finally, under the
103 Antarctic Treaty System, no national claim is recognized on Antarctic waters; the EEZ surrounding the Antarctic
104 continent was hence considered as a single, continuous and distinct one in this study.

105 106 *Penguins' life-cycle stages*

107 During breeding, penguins regularly return ashore to feed their offspring and/or switch duties with their mate
108 (reviewed in [21]). Accordingly, breeding penguins undertake typically short foraging trips lasting from less than a
109 day (notably during chick-rearing) to a few weeks. In contrast, outside the breeding period penguins generally
110 remain at sea for months (hence potentially ranging further offshore), and particularly during two phases of their life
111 cycle. First, when juvenile birds disperse after fledging and until their first return, often the following year. Second,
112 between breeding seasons, when adult penguins generally make a long seasonal retreat to sea, typically spanning
113 winter across species and revolving around the moult. In some species however, adult penguins regularly return
114 ashore throughout their non-breeding period. In this paper we separated penguin movements according to three life-
115 cycle stages: juvenile dispersal, and adults' breeding (comprising incubation, brood-guard and chick-rearing phases)
116 and non-breeding (comprising pre- and post-moult phases) periods.

117 118 *Unavoidable biases*

119 It was unavoidable that depending on the regional coastline layout, penguins from one study site had uneven
120 chances to cross jurisdictions compared to others. Cases include (1) whether there was one or several EEZs along
121 the regional coastline (e.g., single EEZ around Australia versus several contiguous EEZs around southern Africa);
122 (2) uneven distances from each study site to the closest border along that coast (e.g., birds from northern Argentina
123 are closer to Uruguay's EEZ, than those from central localities); (3) EEZs extending further offshore due to
124 neighbouring domestic islands, potentially containing even long-ranging distributions (e.g., New Zealand's
125 subantarctic islands stretching out southward); and (4) a reduced EEZ width, due to the presence of a foreign
126 coastline less than 400 nm from the study site (e.g., Kerguelen and Heard Is. in the southern Indian Ocean show
127 compressed EEZ widths at their opposing sides), putting shorter-range penguins across EEZs. All these special cases
128 nevertheless reflect the reality of current political biogeography.

129 Besides, some species breed at more sites than others, thus providing more opportunities to cross jurisdictions.
130 Similarly, at-sea movements have been studied more (or at all) for certain species, life-cycle stages and sites, than
131 others: nevertheless, this aligned well with the objective of this study to reflect the current state of knowledge.

132

133 **Penguins' long-range movements across genera**

134 We examined a total of 131 documents, providing information on penguins' at-sea distribution for a combination of
135 254 populations/stages, across all 18 species (Table S1). Long-range movements were documented in 16 species
136 (89% of penguin species; Table 1), spread across all extant genera except *Megadyptes* (Fig. S1). Such movements
137 lead the penguins across different marine regions, or even oceans (Fig. 1).

138 In brush-tailed penguins (genus *Pygoscelis*), remarkably large-scale movements were observed across all three life-
139 cycle stages, with a record of 4,124 km reached from the nest by a wintering chinstrap penguin (*P. antarctica*, [31]).
140 Some Adélie penguin *P. adeliae* populations appeared rather sedentary however throughout the non-breeding period
141 [54], and so were most of the non-breeding adult gentoo penguins *P. papua*, which only partially migrate otherwise
142 [30].

143 In contrast, all adult crested penguins (genus *Eudyptes*) that have been studied during non-breeding phases have
144 consistently shown spectacular migrations. For example, pre-moulting Fiordland penguins *E. pachyrhynchus* show
145 return trips extending up to 2,288 km [44], and southern rockhopper penguins *E. chrysocome* may move >3,500 km
146 from their colony after moult, to the open ocean [37]. However, juvenile dispersal in crested penguins remains
147 virtually unknown.

148 In this respect, the greatest juvenile dispersals have been observed in the large-sized emperor and king penguins
149 (*Aptenodytes forsteri* and *A. patagonicus*, respectively): satellite tracking showed juveniles reaching at least 3,503
150 and 4,783 km away from their nest, with minimum distances travelled totalling 7,794 and 11,712 km in each
151 species, respectively [23, 26].

152 The banded penguins (genus *Spheniscus*) undertake more modest-range migrations (reaching 1000–2000 km in post-
153 moulting Humboldt *S. humboldti*, Magellanic *S. magellanicus* and juvenile African *S. demersus* penguins [47, 48,
154 51]). As in the little penguin *Eudyptula minor* (ranging up to >500 km; [53]), these long-range movements generally
155 remained closer to the shore than in other genera.

156

157 **Evidence of transboundary movements**

158

159 The penguins' long-range movements were largely transboundary: among the 16 long-ranging species, there was
160 evidence for individuals reaching beyond their initial EEZ in 14 of them (Fig. S1). Transboundary movements have
161 thus been documented in the majority of penguin species (78%), and despite the fact that in two species (the royal *E.*
162 *schlegeli* and erect-crested *E. sclateri* penguins), little data is available yet on the birds' at-sea distribution.

163

164 *Species account*

165 In 12 species, birds moved across contiguous countries' EEZs. For example, juvenile African penguins moved from
166 the South African to the Namibian EEZs [51]. Similarly, juvenile gentoo penguins *P. papua* may move from the
167 French to the Australian EEZs in the southern Indian Ocean [35].

168 Most importantly, the literature provided at least 120 cases of penguins using ABNJ, across 13 species. For example,
169 macaroni *E. chrysolophus* and Fiordland penguins undertake remarkable migrations reaching oceanic habitats in
170 ABNJ, during both pre- and post-moult phases [37, 45]. More penguin species were found to reach the ABNJ than
171 to move across EEZs: this may be because some species (e.g., *E. moseleyi*) breed exclusively on remote oceanic
172 islands surrounded by ABNJ and where no other EEZ extends nearby.

173 Besides, in 11 species (among *Aptenodytes*, *Pygoscelis*, *Eudyptes* and *Spheniscus* genera) we found evidence of both
174 types of transboundary movements, across EEZs and to ABNJ.

175 176 *Species richness across ABNJ*

177 Across their long-range movements, penguins distributed in most oceanic areas south of 37°S (Fig. 2). Each ABNJ
178 sector harboured 2–10 species (predominantly 6–7), and 0–5 species per year quarter (predominantly 4; Table S2).
179 The highest annual diversity (10 species) was found in ABNJ sector 2: north of the Polar Front, from the Eastern
180 Indian Ocean to New Zealand (Fig. S2), with 3–4 species in each quarter. Also, ABNJ bordering South America
181 (sector 4) held notably high diversity year-round (8 species; predominantly 5 during each quarter). Opposite, the
182 lowest number of species known to exploit ABNJ was found in sector 3 (Pacific region: 2 species), with only 0–1
183 species depending on the season. Species richness in any ABNJ sector remained 0–5 across seasons (predominantly
184 4–5 species); cases with nil known richness occurred only in quarters 1 and 4, matching most species' breeding
185 season.

186 187 *ABNJ use across stages*

188 Adult non-breeding phases consistently provided the most cases of long-range movements (n=13 species), multi-
189 EEZ (n=7) or ABNJ (n=10) use (Fig. S3). Less species (n=6) were documented reaching ABNJ during juvenile
190 dispersal, however this possibly reflects a lower number of studies focusing on this life-cycle stage. Importantly, in
191 eight species, the birds moved extensively even during the breeding season. This included seven species reaching
192 ABNJ while breeding. For example, in king penguins foraging trips can last several weeks during chick-rearing, and
193 coherently, the birds can repeatedly reach the high seas (and other EEZs) throughout the breeding season [16, 25], in
194 addition to non-breeding phases [26, 27]. The king penguin is thus a clear example of species using ABNJ year-
195 round. More surprisingly, use of ABNJ during the breeding season was also documented in smaller-sized species.
196 Adélie and Magellanic penguins reach the high seas while breeding [30, 49], and among eudyptids so do the
197 macaroni, royal and both species of rockhopper penguins [35, 39, 41]. It is thus remarkable that at least these seven
198 species are known to reach ABNJ when their movement range is highly constrained.

199 200 **Challenges and opportunities for penguin conservation in ABNJ**

201
202 In this paper we highlight that most penguin species have remarkable capacities of long-range movements to ABNJ,
203 across regions and seasons: penguins are thus potentially at risk from human activities developing there.
204 Accordingly, the development of an ILBI to preserve marine biodiversity in the high seas is greatly relevant to

205 penguins. In particular, better coordinating the regulation of potentially harmful human activities at sea, and
206 facilitating the creation of protected areas in southern ABNJ would likely benefit to penguin conservation.

207

208 *Current challenges to implement ABMTs in the high seas*

209 Experience shows that MPAs and other ABMTs may effectively benefit to marine wildlife, including penguins (e.g.,
210 [55]). Implementing such protective measures has long been requested in ABNJ as well, to protect a variety of
211 mobile species such as penguins [7, 14, 56]. However, the current international legal framework does not fully
212 provide for the creation of ABMTs in the high seas [57], and consequently the few MPAs existing in ABNJ are
213 implemented under different institutional regimes [8]. Therefore a very first challenge, from a governance
214 perspective, is dealing with legal fragmentation [8, 58]. Indeed, the UNCLOS addresses the conservation of living
215 resources within EEZs (Article 61) but lacks mechanisms for establishing MPAs in the high seas (Part VII, Section
216 2). The 1992 UN Convention on Biological Diversity also provides a mechanism to implement ABMTs, but it is
217 generally not applicable beyond national jurisdiction. Consequently, the main legal levers currently available for
218 restricting access to certain areas of the high seas are regionally-based [8]: Regional Fisheries Management
219 Organizations (RFMOs), regional environmental protection conventions with authority in ABNJ (e.g., in Antarctic
220 waters the Convention on the Conservation of Antarctic Marine Living Resources – CCAMLR); or global, across
221 ABNJ: e.g. the International Seabed Authority and the International Maritime Organization through the International
222 Convention for the Prevention of Pollution from Ships (MARPOL).

223 The fact that the existing framework for the management of ABNJ is fragmented, uneven and uncoordinated,
224 currently results in a sub-optimal management regime, with the above organisations having overlapping mandates
225 but showing little cooperation or coherence between them [57]. Notably, fragmented governance may prevent or
226 impede collaboration between organizations to monitor and enforce the designated areas in the high seas (e.g., boat
227 or plane patrols); it may also be the cause for RFMOs to often be slow or reluctant to follow the advice of their
228 science advisory bodies on ABMTs [8]. An overarching authority coordinating a precautionary approach to
229 managing anthropic activities in ABNJ would hence likely result in better preserving biodiversity in the high seas.

230

231 Second, the legitimacy of prioritizing nature conservation over human use, when designating large protection areas,
232 can be questionable, notably if people's subsistence depends on activities in that area [59]. These social justice
233 implications are less prevalent in the high seas, however coexistence of humans and living species is at the centre of
234 the ecosystemic approach, a key avenue for a successful marine governance [60] and one of the principles included
235 in article 5 of the draft Treaty. This tension is reflected in part VII of UNCLOS, dedicated to the high seas. In fact
236 "freedom of the high seas" (art. 87 of UNCLOS), which includes freedom of navigation, overflight, to lay submarine
237 cables and pipelines, to construct artificial islands, fishing and scientific research, is the objective of most of its
238 provisions, whereas the conservation and management of the living resources of the high seas, comes only as a
239 second section and starts with the right to fish (art. 116). In sum, designating ABMTs should not undermine the
240 mandate of the UNCLOS, establishing undeniable freedom-of-navigation rights in ABNJ.

241

242 Last, there is the scientific challenge to identify the key utilized areas across time and taxa, within immense
243 distribution ranges of mobile marine species [7, 9]. Current research on migratory connectivity in the oceans,
244 identifying nodes of distribution aggregation and biological corridors between nodes, aims to promote the inclusion
245 of such connectivity in the design of ocean conservation and management measures (e.g., [2]). Yet, information for
246 many migratory taxa is currently insufficient or lacking.

247

248 *Expected progresses from the treaty*

249 Negotiations over an ILBI to preserve marine biodiversity in ABNJ cover a ‘Package Deal’ of four issues: marine
250 genetic resources; ABMTs; conducting environmental impact assessments (EIAs); and capacity-building and the
251 transfer of marine technology. The stakes are high, and the treaty thus brings “high hopes for the high seas” [61]:
252 international cooperation is expected in order to adopt an ambitious, effective and equitable treaty with strong global
253 oversight. Most importantly, negotiations for the ILBI provide an opportunity to fill the legal gap for implementing
254 high sea ABMTs, notably by providing an authority and/or a framework for coordinating the needed scientific
255 research in ABNJ [57].

256

257 The current draft (reviewed in [62]) includes in its general provisions (Part I) the precautionary approach to the
258 exploitation of biodiversity in the high seas (draft Article 5), and the principle of common heritage of mankind to
259 protect. These principles seem crucial to reach the long-term conservation objective stated in draft Article 2 and, if
260 applied, would clearly improve the management of human activities in ABNJ.

261 Regarding ABMTs (Part III), draft Article 15 further requires State Parties to promote coherence and
262 complementarity in establishing ABMTs, which may help tackling the challenges associated with the current
263 fragmented governance framework. Importantly, with the aim to centralize information and discussions, draft
264 Article 19 gives the Conference of Parties (COP) responsibility for the decision-making process. In some cases the
265 COP could recommend that State Parties promote the adoption of management measures; and the COP itself could
266 take decisions on the adoption of such measures where there are no relevant legal instruments, frameworks or bodies
267 [62]. In this regard, the governance structure foreseen in the draft treaty is much alike the UNFCCC (United Nations
268 Framework Convention on Climate Change) one.

269

270 Another important progress may be achieved thanks to cooperation and technology transfer (Part IV). Remote
271 surveillance of fisheries, from satellites [63] and other technological advances (e.g., [64]), is developing quickly and
272 may become a key to monitoring and enforcing MPAs in ABNJ. Promoting capacity-building and technology
273 transfer may thus facilitate effective, global monitoring of designated ABNJ through new technologies [8].

274 Regarding Institutional arrangements (Part VI), it is detailed that a scientific and technical body will provide advice
275 on the four elements of the Package Deal (draft Article 49): this would also help to implement new ABMTs.
276 However, some elements in the current draft treaty may not be sufficiently ambitious to deliver an optimal, effective
277 governance framework [62]. For example, in Part IV (EIAs), the draft treaty may require to all activities that have an
278 impact in ABNJ, to conduct an EIA; but without detailing whether this would be only advisory, or whether States

279 Parties or the COP would ultimately decide or provide authorizations for such activities. Also up to now, the COP
280 has not been awarded the general power to take binding decisions.

281

282 *A giant leap for penguin conservation?*

283 Considering the prevalence of their long-range movements emphasized in this study, penguins are remarkably little
284 represented in the 1979 Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention;
285 CMS): only Humboldt (Appendix I) and African (Appendix II) penguins are included. This early intergovernmental
286 treaty, under the aegis of the United Nations Environmental Programme, aimed to preserve migratory wildlife and
287 their habitats worldwide; however, it is of little help for threatened penguins migrating across ABNJ (Table 1). The
288 new treaty on ABNJ may better benefit to penguins and facilitate their conservation against an array of threats at
289 sea. We identify below a few elements directly applicable to penguins in the context of one threat: fisheries.

290

291 First, the treaty may provide authority to develop ABMTs in areas with fragmented governance. For example,
292 hotspots of trawl fishing effort were highlighted in ABNJ off southeast Argentina, an ocean sector devoid of specific
293 RFMO or fisheries management body [63], but with high penguin species richness (Fig. 2). Among the penguin
294 species using this area, at least four (*A. patagonicus*, *E. chrysolophus*, *E. chrysocome* and *S. magellanicus*) are
295 known bycatch in the neighbouring domestic fisheries [15]. Importantly, these four species are found as bycatch in
296 all four fishing gear types examined in the region (trawl, gillnet, purse seine, longline; [15]), which closely match
297 the four most operated ones in the ABNJ (longline, purse seine, squid jigging, and trawl; [65]). It is thus very likely
298 that at least these four species are bycaught by high sea fisheries, at least in this area. The new ILBI may empower
299 the COP to manage fisheries in this area, and the COP could in turn propose to implement ABMTs in such areas
300 where unclear governance and high fishing effort correlate with severe mortality risk for several penguin species.

301

302 Second, even in areas where governance for environmental management is clearer, the treaty may bring overarching
303 authority to take decisions on ABMTs in the high seas when science-based evidence is available. For example, in
304 2011 CCAMLR adopted a legally-binding Conservation Measure on establishing MPAs. Since then, several MPA
305 proposals have been submitted (e.g., in East Antarctica), but most have been unsuccessful due to political and
306 fishing interests in the Southern Ocean [8]. In such cases when fisheries' interests impede the development of
307 ABMTs against science-based evidence, the new ILBI seems likely to help abiding to scientific recommendations.
308 Outside the CCAMLR application area, important areas used by endangered penguins were also highlighted, that do
309 not overlap any existing MPA [9]; however the designation of a large MPA in this region is not achievable by single
310 neighbouring States. In this case again, the overarching authority of the COP could directly recommend the RFMO
311 to adjust fisheries management to implement a new ABMT in the region.

312

313 And third, the core principles set in this treaty are an opportunity to implement a more precautionary approach for
314 the exploitation of ABNJ [8]. Currently, fisheries are one of the major threats to penguin conservation at sea (albeit
315 possibly not for all species), through indirect effects such as resource competition, and direct mortality reported

316 notably from domestic gillnet fisheries [14, 15, 66]. In contrast, penguins moving to ABNJ may seem to exploit
317 oceanic deserts devoid of human activity [44], but the severity of the impacts that high seas fisheries have or will
318 have on penguins is largely unknown. Precautionary measures to protect penguins in ABNJ seem particularly valid,
319 for several reasons. First, penguins are long-lived animals with low reproductive rates, which makes their
320 populations particularly vulnerable to chronic impacts on their survival or reproductive success, with long
321 recovering processes [56]. Second, penguins are marine predators, and thus protecting the main areas they use has
322 top-down effects translating into preserving the resource and food webs they depend on [7]. Third, industrial
323 fisheries are expanding and intensifying in ABNJ [6, 63]. Fourth, there are significant levels of illegal fishing
324 detected in the high seas [64]. And fifth, studies [67, 68] show that the RFMOs have somewhat failed to (1) prevent
325 stocks' overexploitation, (2) assess compliance to regulations, (3) produce transparent data on fishing effort and
326 bycatch in ABNJ and (4) achieve sufficient coverage of fisheries by onboard observers to assess the efficacy of
327 bycatch mitigation measures. Therefore, in line with the precautionary approach underlined in its general provisions,
328 the new treaty is an opportunity to implement in ABNJ a network of areas with preventively restricted human use,
329 aiming to preserve the feeding habitats used by mobile species such as penguins, before impacts on their populations
330 would appear or aggravate.

331 Our study supports that protected areas designated in ABNJ south of 35°S would predominantly be used by a
332 diversity of penguins regardless of season (with the exception of the Pacific sector north of the Polar Front, during
333 summer). Studies showed the disproportionate value of very large-scale MPAs to global marine conservation
334 targets, despite potential social justice concerns [59, 69]. Our results based on ecological indicator species may
335 hence guide the designation of such large-scale protection areas in ABNJ, following a precautionary approach in a
336 context of growing human footprint [6].

337

338 **Conclusions**

339 The expansion of ocean uses, especially in the high seas, has rapidly outpaced the development of scientific
340 knowledge on marine wildlife distribution and ecosystem resilience capacities [5, 6]. Yet, knowledge on marine
341 animals' at-sea movements is crucial to improve the management of biodiversity at the national and international
342 levels [19]. In this work we highlight that transboundary movements, notably to the high seas, are remarkably
343 prevalent among penguin species, for which human activities conducted in ABNJ can be major threats. Therefore,
344 penguin conservation seems deeply intertwined with the development of the new ILBI to protect biodiversity in
345 ABNJ.

346 This ambitious treaty is notably expected to strengthen existing governance frameworks, and to place cooperation
347 and science at the core of the management regime for this vast global commons [61]. Taking advantage of
348 technological advances allowing to adequately monitor vast regions in ABNJ [6, 63, 64], new policies developed
349 under this treaty could hence be extremely effective for the conservation of penguins and their habitats at sea, with
350 less potential socio-economic harm than in domestic waters.

351 Applied to penguin conservation, the treaty and its envisioned ecosystemic and precautionary approaches may
352 provide the needed structure to implement a network of large ABMTs in the most used ABNJ across species [2, 7].

353 Further analyses will be required to identify which sectors exactly are a priority [9], and expanding tracking studies
354 is also needed to fully grasp the extent to which penguin may use ABNJ across species, sites and life-cycle stages.
355 Public outreach has proven to be a key dimension of the UNFCCC COPs [70] and may also be crucial to the success
356 of this new treaty [8]. Highlighting oceanic migrations through charismatic animals such as penguins may represent
357 a unique way to harness public concern for the conservation of this common heritage of mankind.
358 Finally, the negotiations over this treaty will serve as a new opportunity to attempt and effectively preserve marine
359 biodiversity in ABNJ, knowing that one remaining alternative could be the total closure of high seas to activities of
360 extraction. Modelling studies [71] showed that closing high seas to fishing would induce cooperation among
361 countries in the exploitation of migratory resource stocks and provide a refuge sufficiently large to recover stock
362 levels, thereby greatly increasing fisheries profit, fisheries yields, and fish stock conservation. Reduced impacts on
363 non-target species, including penguins, would likely follow from such restrictions. It is thus crucial to keep in mind
364 that the success or failure of the new treaty in the long-term will be measured against such alternatives: this should
365 allow stakeholders to re-evaluate whether the exploitation of global commons through industrial, not always
366 economically viable activities [65], is ecologically sustainable.

367

368 **Acknowledgements**

369 The authors declare they have no conflict of interest.

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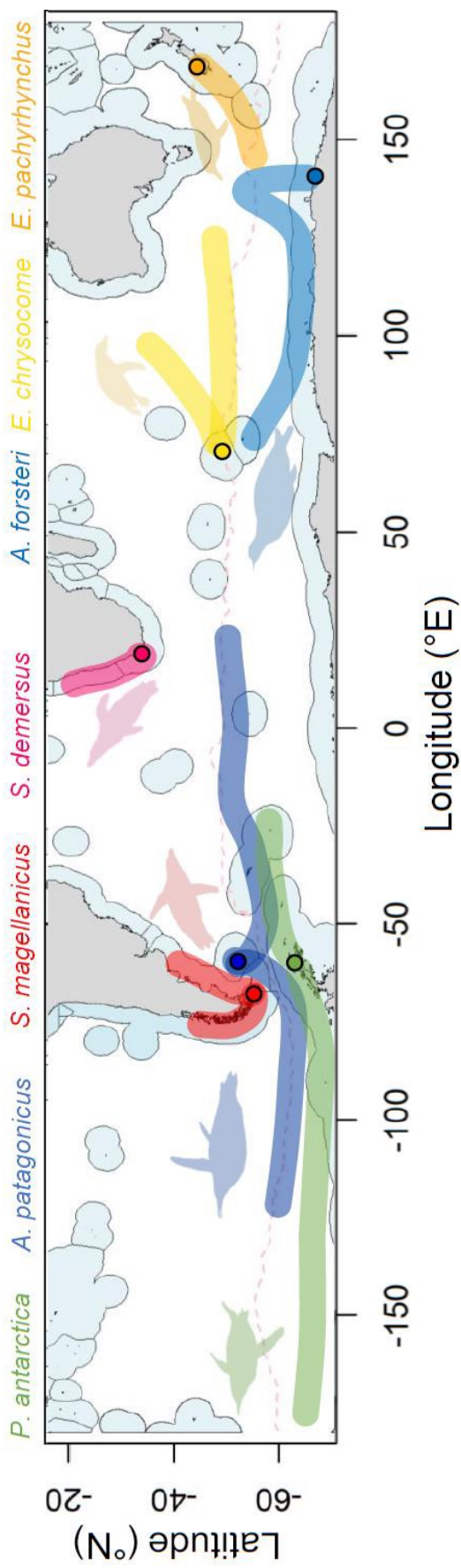
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520 **Figure 1.** EEZs of the Southern Hemisphere (blue shadings), and examples of transboundary movements observed in seven penguin species: juveniles of African

521 (*Spheniscus demersus*, pink, [51]), King (*Aptenodytes patagonicus*, dark blue, [26]) and Emperor (*A. forsteri*, blue, [23]) penguins; pre-moulting Fiordland

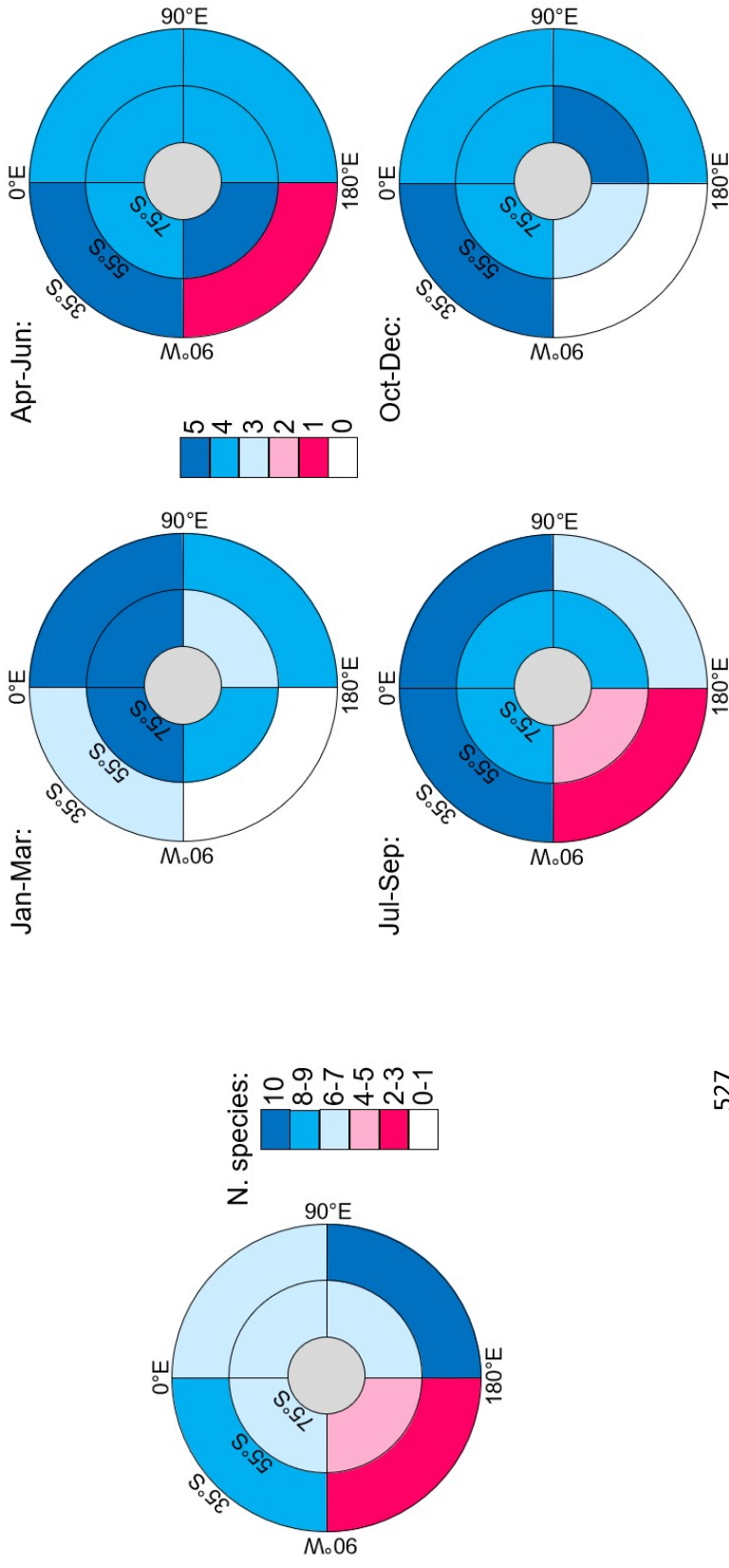
522 penguins (*Eudyptes pachyrhynchus*, orange, [44]); and post-moulting Chinstrap (*Pygoscelis antarctica*, green, [31]), Magellanic (*S. magellanicus*, red, [50]) and

523 Southern Rockhopper (*E. chrysosome*, yellow, [37]) penguins. Circles indicate the originating locality. The pink dashed line symbolizes the location of the

524 Antarctic Polar Front.

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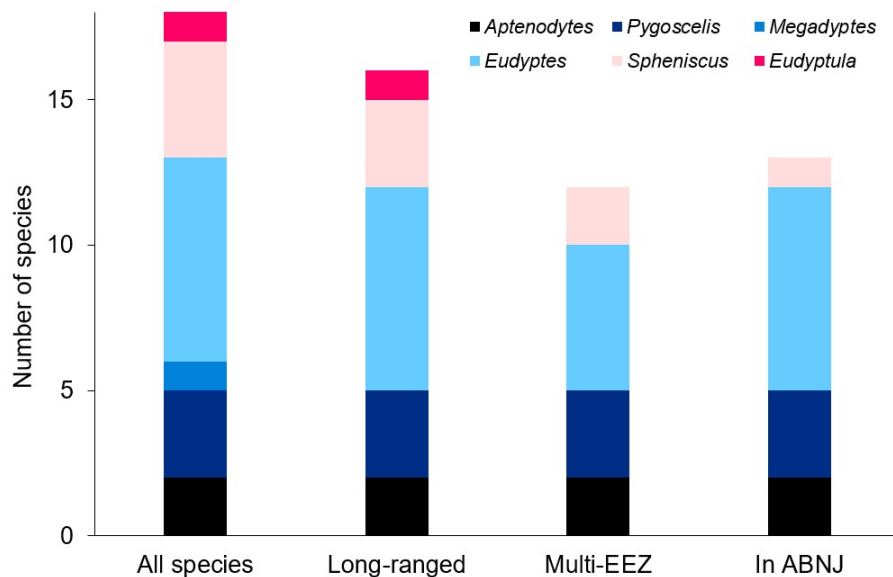
529 **Figure 2.** Number of penguin species documented to use ABNJ per geographic sector (left) and year quarter (right).

530

531 **Table 1.** Overview of at-sea movements documented in the 18 penguin species: long-ranged (extending >370.4 km), crossing multiple EEZs, and/or reaching
 532 ABNJ. The life-cycle stage(s) during which a given movement type was documented is indicated (Ju: juvenile dispersal; Br and Nb: adult breeding and non-
 533 breeding stages, respectively; Un for unknown). More references are detailed in Suppl. Table 1.

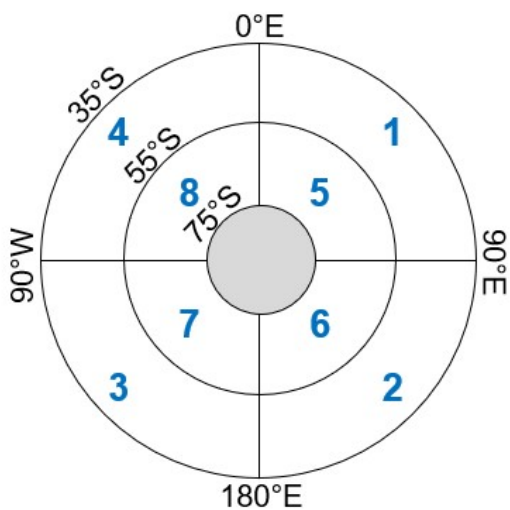
Species	IUCN status	Long-range	Multi-EEZ	In ABNJ	Examples
Emperor penguin <i>Aptenodytes forsteri</i>	NT	Ju, Br, Nb, Un	Ju	Ju, Nb, Un	[17, 22, 23, 24]
King penguin <i>Aptenodytes patagonicus</i>	LC	Ju, Br, Nb, Un	Ju, Br	Ju, Br, Nb, Un	[16, 25, 26, 27]
Adélie penguin <i>Pygoscelis adeliae</i>	LC	Ju, Br, Nb, Un	Nb	Ju, Br, Nb, Un	[28, 29, 30]
Chinstrap penguin <i>Pygoscelis antarctica</i>	LC	Ju, Nb, Un	Ju, Nb	Ju, Nb, Un	[18, 31, 32]
Gentoo penguin <i>Pygoscelis papua</i>	LC	Ju, Un	Ju, Br	Un	[33, 34, 35, 36]
Yellow-eyed penguin <i>Megadyptes antipodes</i>	EN	No evidence	No evidence	No evidence	
Macaroni penguin <i>Eudyptes chrysolophus</i>	VU	Ju, Br, Nb, Un	Br, Nb	Ju, Br, Nb, Un	[34, 35, 37, 38]
Royal penguin <i>Eudyptes schlegeli</i>	NT	Br, Un	Br	Br, Un	[34, 39]
Southern Rockhopper penguin <i>Eudyptes chrysocome</i> (including "Eastern" <i>E. filholi</i>)	VU	Br, Nb, Un	Br, Nb	Br, Nb, Un	[37, 38, 39, 40]
Northern Rockhopper <i>Eudyptes moseleyi</i>	EN	Br, Nb	No evidence	Br, Nb	[9, 37, 41]
Snares penguin <i>Eudyptes robustus</i>	VU	Nb, Un	Nb	Nb, Un	[34, 42]
Erect-crested penguin <i>Eudyptes sclateri</i>	EN	Ju	Unknown	Ju	[43]
Fiordland penguin <i>Eudyptes pachyrhynchus</i>	VU	Nb, Un	Nb	Nb, Un	[34, 44, 45]
Humboldt penguin <i>Spheniscus humboldti</i>	VU	Nb	No evidence	No evidence	[46, 47]
Magellanic penguin <i>Spheniscus magellanicus</i>	NT	Br, Nb	Br, Nb	Br, Nb	[36, 48, 49, 50]
African penguin <i>Spheniscus demersus</i>	EN	Ju, Nb	Ju	No evidence	[51, 52]
Galápagos penguin <i>Spheniscus mendiculus</i>	EN	No evidence	No evidence	No evidence	
Little penguin <i>Eudyptula minor</i>	LC	Nb	No evidence	No evidence	[53]

536 **Supplementary material**



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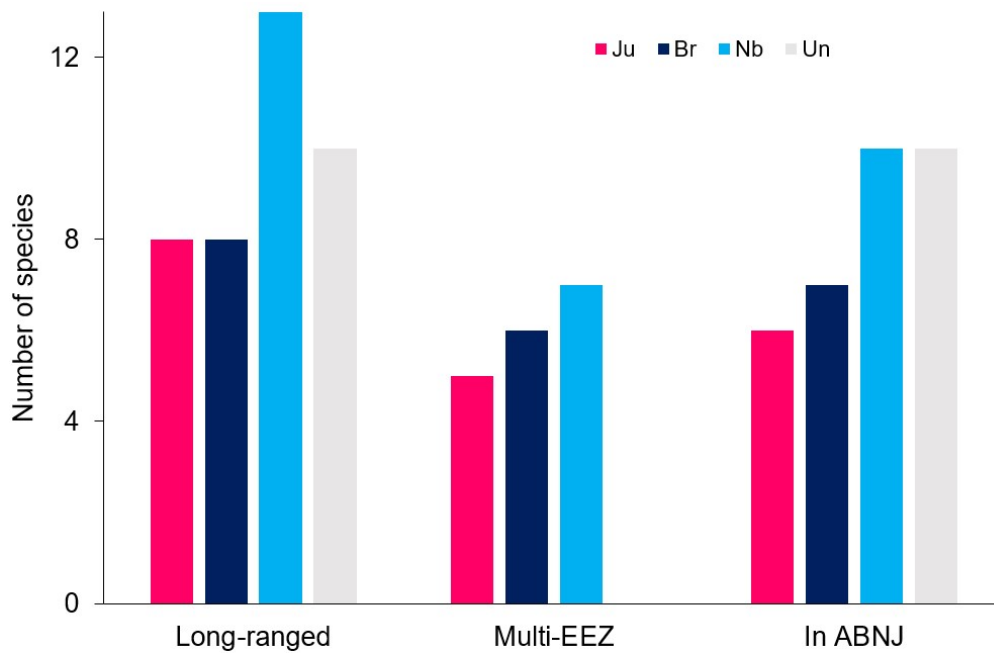
Supplementary Figure S1. Number of penguin species within each genus (n=18 species), in which cases have been documented for movements of long range, crossing multiple EEZs and reaching ABNJ. Note that at-sea movements are little known in some species.



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Supplementary Figure S2. Description of the geographic sectors used in Supplementary Tables 1 & 2. Sectors are numbered from 1 to 8 (blue digits), and cover the circumpolar area between 35°S and 75°S. These latitudinal boundaries match the northernmost extent of penguin distribution in this study and the southernmost extent of ABNJ, respectively. The average latitude of the Antarctic Polar Front (c. 55°S) further separates sectors 1–4 to the north, from sectors 5–8 to the south.

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553 **Supplementary Figure S3.** Number of penguin species within each life-cycle stage (Ju: juvenile dispersal; Br and
554 Nb: adult breeding and non-breeding stages, respectively; Un for unknown), in which cases have been documented
555 for movements: of long range, crossing multiple EEZs and reaching ABNJ. Note that at-sea movements are little
556 known in some species.

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558

559 **Supplementary Table S1.** (Excel file). Detailed results on penguins' at-sea movements, from all examined
560 references (n=131). Geographic sectors (S1 to S8) are spatially organized as shown on Fig. S2, and year quarters are
561 as follow: January–March (Q1), April–June (Q2), July–September (Q3), and October–December (Q4).

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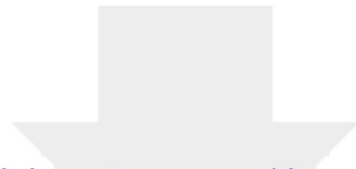
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564 **Supplementary Table S2.** (Excel file). Summary of Table S1 with species account per sector (S1 to S8) and year
565 quarter (Q1 to Q4).

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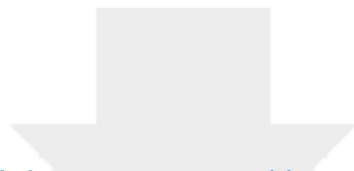
Conflict of Interest

- 1 The authors declare they have no conflict of interest.



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Supplementary Material
Supplementary Table S1.xlsx





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