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**Long distance runners in the marine realm:
New insights into genetic diversity, kin relationships and social fidelity
of Indian Ocean male sperm whales**

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37

38 **Abstract**

39

40 Adult male sperm whales (*Physeter macrocephalus*) are long distance runners of the marine realm,
41 feeding in high latitudes and mating in tropical and subtropical waters where stable social groups of
42 females and immatures live. Several areas of uncertainty still limit our understanding of their social and
43 breeding behaviour, in particular concerning the potential existence of geographical and/or social
44 fidelities.

45 In this study, using underwater observation and sloughed-skin sampling, we looked for male social
46 fidelity to a specific matrilineal sperm whale group near Mauritius. In addition, we captured a wider
47 picture of kin relationships and genetic diversity of male sperm whales in the Indian Ocean thanks to
48 biopsies of eight unique individuals taken in a feeding ground near the Kerguelen and Crozet
49 Archipelagos (Southern Indian Ocean).

50 Twenty-six adult male sperm whales, of which 13 were sampled, were identified when socializing with
51 adult females and immatures off Mauritius. Long-term underwater observation recorded several
52 noteworthy social interactions between adult males and adult females and/or immatures. We identified
53 seven possible male recaptures over different years (three by direct observation, and four at the gametic
54 level), which supports a certain level of male social fidelity. Several first- and second-degree kin
55 relationships were highlighted between members of the social unit and adult males, confirming that
56 some of the adult males observed in Mauritian waters are reproductive. Male social philopatry to their
57 natal group can be excluded, as none of the males sampled shared the haplotype characteristic of the
58 matrilineal social group. Mitochondrial DNA control region haplotype and nucleotide diversities
59 calculated over the 21 total male sperm whales sampled were similar to values found by others in the
60 Indian Ocean.

61 Our study strongly supports the existence of some levels of male sperm whale social fidelity, not directed
62 to their social group of birth, in the Indian Ocean. Males sampled in breeding and feeding grounds are
63 linked by kin relationships. Our results support a model of male mediated gene flow occurring at the
64 level of the whole Indian Ocean, likely interconnected with large-scale geographical fidelity to ocean
65 basin, and a small-scale social fidelity to matrilineal social groups.

66

67 **Introduction**

68

69 Sexual dimorphism, defined as differences in external appearance or other characteristics between the
70 two sexes of a species (Mesnick and Ralls, 2018), is widespread among animals, and especially in
71 vertebrates (Shine, 1989). Sexual dimorphism can be behavioural, morphological and/or concern life
72 history. Marked sexual dimorphism is present in several marine mammal species (Mesnick and Ralls,
73 2018). Morphological differences are obvious, for example, in elephant seals (*Mirounga angustirostris*
74 and *M. leonina*), males being up to ten times larger than females (Le Boeuf and Laws, 1994) and in
75 narwhals (*Monodon monoceros*) where males possess a tusk (Gerson and Hickie, 1985). Other species
76 display marked sexual segregation in geographical distribution, such as the Indo-Pacific bottlenose
77 dolphins (*Tursiops aduncus*, Smolker et al., 1992; Galezo et al., 2017), or exhibit differences in their
78 feeding ecology such as the resident fish-eating population of killer whales of the northeastern Pacific
79 Ocean (*Orcinus orca*, Beerman et al., 2016).

80 Sperm whales certainly display some of the most striking sexual dimorphism among cetaceans, both in
81 terms of body size with adult males growing up to 18m long and a weight of 45t, while females usually
82 remain around 11m long for 13t (Best, 1979; Cantor et al., 2019); but also in terms of feeding ecology,
83 geographical distribution and social organization (Rice, 1989; Whitehead and Kahn, 1992; Teloni et al.,
84 2008; Kobayashi et al., 2020). Male and female sperm whales live in societies that are strongly
85 geographically segregated post-maturity (e.g. Christal, 1998; Gordon et al., 1998; Christal and
86 Whitehead, 1999; Lyrholm et al., 1999; Whitehead et al., 2008; Labadie et al., 2018). Adult females
87 form social units with immatures, stable over time and found all year round in warm waters at low
88 latitudes (Whitehead and Kahn, 1992; Konrad et al., 2018; Sarano et al., 2021a). In contrast, males
89 disperse from their natal group after 6-8 years old, before their sexual maturity, and move poleward to
90 areas abundant in food (Rice, 1989). After their twenties, they make periodic forays to warmer waters
91 for mating, with no known clear frequency, seasonal agendas nor migration routes (Best, 1979).
92 Although we know that adult male sperm whales can travel thousands of kilometres across ocean basins
93 (Engelhaupt et al., 2009; Mizroch and Rice, 2012), no recurrent migration routes between feeding and
94 breeding areas have so far been identified (Cantor et al., 2019).

95 In cold waters, non-breeding adult males can be encountered alone or in small groups called “bachelor
96 groups”, groups of tens individuals of about the same age (e.g. Christal and Whitehead, 1997; Jaquet et
97 al., 2000; Lettevall et al., 2002). They may become more and more solitary as they age (Best, 1979). In
98 northern Norway, Nova Scotia (Canada) and Kaikoura (New Zealand) feeding grounds, no noticeable
99 social interaction between adult males were observed when foraging (Lettevall et al., 2002; Madsen et
100 al., 2002). Yet, some recent studies show that males can form long-term associations (Kobayashi et al.,
101 2020) and have fluid and unstructured social interactions that allow the social transmission of
102 depredation techniques in the Gulf of Alaska (Schakner et al., 2014) or permit coordinated anti-predator

103 responses (Curé et al., 2013). Long-term photo-identification studies around Crozet and Kerguelen
104 archipelagos (Crozet/Kerguelen, Southern Indian Ocean), in the Bleik Canyon (northern Norway) and
105 in the Nemuro Strait (northern Japan) indicate that adult males exhibit site fidelity at local scales
106 (Rødland and Bjørge, 2015; Labadie et al., 2018; Kobayashi and Amano, 2020).

107 In the low latitudes, the social interactions of adult male sperm whales with stable social groups of
108 females and immatures and adult male movement patterns in breeding grounds remain poorly known.
109 Adult males may temporarily join social units to breed and stay in the same area for periods estimated
110 from a few hours to a few days off the Galapagos Islands (Coakes and Whitehead, 2004) to few weeks
111 in the West Indies (Gero et al., 2014). During this period, large males roam around, apparently avoiding
112 one another while visiting groups of females (Cantor et al., 2019) and having limited social interactions
113 with members of the social units (adult females and/or immatures, Gero et al., 2014). The existence of
114 geographical and/or social fidelity is questioned in males, however fidelity of adult males to the ocean
115 of their birth (i.e. a large geographical scale natal philopatry) has been suggested by whaling reports
116 (Best, 1979). Using genetic assignment, Mesnick et al. (2011) highlighted that, in the North Pacific, a
117 higher-than-randomly-expected proportion of males returned to their population of origin to mate. Males
118 sharing first order kinships (mostly full siblings) have also been identified in the Azores and in the
119 Chagos Archipelago (Pinela et al., 2009; Alexander et al., 2016). Photo-identification recaptures of a
120 same male over several years in the same study area occurred in different breeding grounds of the
121 Atlantic (in the Azores and the West Indies, Gero et al., 2014; Van der Linde and Eriksson, 2020) and
122 of the Pacific (The Galapagos, Christal, 1998), where they may socialise with different social groups of
123 the same vocal clan (Rendell et al., 2005). Gero et al. (2014) suggested that male fidelity to breeding
124 sites might occur, based on the identification of the same male spanning a period of ten years and the
125 observation of a gathering of dozens of females and immatures around a male.

126 Altogether, these results suggest that some levels of geographical and social fidelity could exist in male
127 sperm whales. This hypothesis requires more evidence to be confirmed, however long-term monitoring
128 of adult male sperm whales is difficult. Few studies have included males in analyses when studying
129 female social groups (e.g. Coakes and Whitehead, 2004; Rendell et al., 2005; Pinela et al., 2009; Gero
130 et al., 2014), and this scarcity of data prevents clear conclusions concerning male sperm whale
131 movement patterns and social fidelity being drawn.

132

133 In the Indian Ocean breeding grounds, sperm whales have been less studied than in the Pacific and the
134 Atlantic. Several social groups have been observed (Gordon, 1987; Whitehead and Kahn, 1992; Sarano
135 et al., 2021b), and photoidentification campaigns and satellite tracks confirmed that sperm whales are
136 common near the Mauritius and La Reunion Islands (Huijser et al., 2020; Chambault et al., 2021; Sarano
137 et al., 2021b). The predominant matrilineality of a particular social group, the “Irène’s group” has been
138 recently demonstrated near Mauritius (Sarano et al., 2021a). But except for some photo-identified
139 individuals (Sarano et al., 2021b), male sperm whales encountered within the breeding grounds of the

140 Indian Ocean are very poorly known. More knowledge comes from the feeding grounds of the Indian
141 Ocean, and in particular from Crozet/Kerguelen (Janc et al., 2018; Labadie et al., 2018; Richard et al.,
142 2020), however the movement patterns between feeding and breeding grounds are not known.

143 In this study, we investigated the spatial and social fidelity of adult male sperm whales in the Indian
144 Ocean. Using nine years of monitoring sperm whale social groups off Mauritius paired with genetic
145 information collected on individuals from both this area and the Crozet/Kerguelen region, our aims were
146 to: i) assess the association patterns and genetic relatedness of adult males with the members of a resident
147 social group they associate with; ii) determine the extent of genetic relatedness across adult males, and,
148 iii) analyse possible social and geographical fidelity of adult male sperm whales, including whether they
149 show fidelity to their natal social group.

150

151

152 **Material and methods**

153

154 *Field work off Mauritius and skin sample collection*

155 Field work took place off the western coast of Mauritius (Mascarenes Islands, Indian Ocean) between
156 latitudes 20.465°S 57.334°E and 19.986°S 57.605°E, up to 15 km off the coast (Sarano et al., 2021a).
157 Sea surface and underwater observations have been carried out since 2011, under the auspices of a
158 project called *Maubydick* led by the MMCO (Marine Megafauna Conservation Organization, Sarano et
159 al., 2021a, 2021b). Since 2015, fieldwork has been conducted almost daily between February and May,
160 and some sporadic observations made during the rest of the year, except in January.

161 Sperm whales were identified based on specific morphological characteristics (e.g., marks on caudal
162 and pectoral fins and body marks, described in detail in Sarano et al. (2021b). An “Identity card” was
163 established for each individual and these used to construct a catalogue of individuals (Sarano et al.,
164 2021b). During underwater observation non-invasive samples from individually identified sperm whales
165 were collected from sloughed skin fragments as described by Sarano et al. (2021a).

166

167 *Collection of sperm whale biopsies off the Crozet and Kerguelen Archipelagos*

168 The Crozet and Kerguelen archipelagos (Crozet/Kerguelen), located in the subantarctic waters of the
169 south Indian Ocean (respectively 46°S and 49°S), are part of the French TAAF (*Terres Australes et*
170 *Antarctiques Françaises*). One sperm whale sample came from a stranded male found on the shore of
171 Kerguelen in 2007. The other samples (n=8) were collected between 2011 and 2018 from fishing vessels
172 targeting Patagonian toothfish (*Dissostichus eleginoides*), a fish species targeted by sperm whales,
173 (Roche and Guinet, 2007; Tixier et al., 2010; Richard et al., 2020). One sample was taken from a dead
174 individual entangled on a longline (Richard et al., 2020) and the others were biopsies collected with a
175 crossbow (Barnett Rhino or Barnett Wildcat), which fired a hollow-tipped biopsy dart with a floatable

176 head (Lambersten, 1987; Tixier et al., 2019). All samples were conserved in absolute ethanol. The
177 sampling of sperm whales at Crozet/Kerguelen was approved by the *Comité de l'Environnement Polaire*
178 and the French Ministry of Research (04040.03).

179

180 *Molecular methods and analysis*

181 All molecular analysis followed the same methodology as previously described (Alfonsi et al., 2012;
182 Decker et al., 2017; Sarano et al., 2021a). Briefly, genomic DNA was extracted from the skin and biopsy
183 samples using the NucleoSpin DNA RapidLyse® kit (Macherey-Nagel, Düren, Germany). DNA
184 concentrations were standardized to 10ng/ μ L. Several molecular analyses were performed for each
185 sample including molecular sexing (Richard et al., 1994), sequencing of a 638bp fragment of the mtDNA
186 control region (MCR: amplified with the primers DLP1.5 and DLP8G, Garrigue et al., 2004) and
187 genotyping of 18 microsatellites loci (Table S1).

188 mtDNA sequences were manually edited and aligned with Geneious Pro v.7.1 (Biomatters Ltd,
189 Auckland, New Zealand). The 638bp long MCR fragment used is the same region used in Sarano et al.,
190 (2021a). This fragment overlapped fully with the data from Morin et al. (2018) and partially (602bp in
191 common) with the sequences determined by Alexander et al. (2016). It also overlapped fully with the
192 283bp fragment and partially with the 563bp fragment (514bp in common) determined by Day et al.
193 (2021). A new dataset that included all these sequences was constructed to allow a large-scale
194 comparison between mitochondrial haplotypes. The numbers of haplotypes, the haplotype diversity (H)
195 and the nucleotide diversity (π) were calculated using the program DnaSP, V.5.10.01 (Librado and
196 Rozas, 2009). The software Arlequin, V3.5.1.2 (Excoffier et al., 2005), was used to calculate F_{ST} and
197 Φ_{ST} , fixation index estimators for mitochondrial genomes.

198 Fragment sizes were determined using the “Microsatellite Plugin” of Geneious Pro v.7.1 (Biomatters
199 Ltd, Auckland, New Zealand). All the molecular analyses were performed in at least two independent
200 experiments, from different samples of a same individual when available, or twice from the same sample
201 following Sarano et al. (2021a). Twenty-two individuals sampled at least three times between 2017 and
202 2020 (Table S2) allowed us to estimate the microsatellite-genotyping errors linked to possible poor-
203 quality DNA extracts. We calculated an overall error rate of 2.1% per allele (52 alleles incorrect among
204 the 2432 scored) with this error rate then used in kinship analyses.

205

206 *Definition of individual specific genotypes*

207 The procedure of anonymization of the samples described in Sarano et al. (2021a) was also applied to
208 all the samples of this new study to confirm the correspondence between field-identification of
209 individuals (here 13 adult males and an immature female, Chesna sampled only in 2020) and genetic
210 individuals, identified by matching genotypes in the laboratory. Briefly, when collected in the field, each
211 skin sample was assigned to one of the individuals identified and then anonymized with an alphanumeric
212 code. To confirm the validity of the field identifications of skin samples, all the steps of the genetic

213 analyses were performed with anonymized skin samples: samples taken from the same individual were
214 confirmed based on similar genotypes using the Identity Analysis function in CERVUS (Kalinowski et
215 al., 2007) as described in Sarano et al. (2021a). Genetic individuals and their corresponding samples are
216 listed in Table S2.

217

218 *Kinship analysis*

219 Kinship analyses were performed on the complete dataset (with duplicate samples removed), that is
220 adult females and immatures previously analysed (Sarano et al., 2021a) with the newly sampled Chesna
221 (sampled in 2020, Table S2), and all the males sampled in Mauritian waters (n=13) and in
222 Crozet/Kerguelen (n=8). Kinship analysis followed the same methodology as described in Sarano et al.
223 (2021a). Briefly, we first used different estimators to calculate the relatedness coefficient r between all
224 the genotyped individuals using the R package *Related* (Pew et al., 2014) and the software ML relate
225 (Kalinowski et al., 2006). *Related* was used to determine that the r estimators W (Wang, 2002) and L&L
226 (Li et al., 1993) had the highest correlation between observed and expected relatedness values and were
227 thus selected to calculate the relatedness coefficients. ML relate (Kalinowski et al., 2006) was used to
228 calculate a relatedness coefficient based on the probabilities of sharing alleles identical by descent, and
229 to assign the most probable familial relationships (among parent–offspring (PO), full sibling (FS), half-
230 sibling (HS), unrelated (U)) to each dyad.

231 The software Cervus 3.0.7 (Kalinowski et al., 2007) was also used to assign likely kinships. Based on
232 the combined results of these analysis, all probable first- and second-degree kin relationships (Blouin,
233 2003) were listed. The consistency between familial relationships hypothesized by ML relate and r
234 coefficient calculations was analysed for each dyad (see also Sarano et al., 2021a for a more detailed
235 explanation about this procedure).

236

237

238 **Results**

239

240 *2011-2020 assessment of adult male sperm whale observations off Mauritius*

241 A total of 26 adult males were identified based on their body length by underwater observations between
242 2011 and 2020 off Mauritius (Table S3). Males were observed in 2011, 2013 and yearly since 2015
243 when the observation effort significantly increased (Sarano et al., 2021b). Since then, adult male sperm
244 whales were sighted each year with a maximum of 10 different individuals observed in 2019. Adult
245 males were observed during a total of 59d over the 2015-2020 period with a maximum of 29d in 2019
246 (Table S3). Observations of adult males occurred most of the year with at least one male seen each
247 month from February to December. Over the 2015-2020 period of observations, April was the month
248 with the highest rate of identification (seven males). Almost half of the males were identified on at least

249 two different days within or between years (n=11), 15 were seen only once. When multiple sightings of
250 the same male occurred during a given year, the longest span between the first and the last sightings was
251 47d (Léonard and Jason in 2019), with a mean of 8.25d (range = 1d-47d) (Table S3). Three males were
252 positively identified over multiple years: Jonas, sighted in 2018 and 2019; Navin, sighted in 2015 and
253 in 2018; and Hugues, sighted in 2013 and again 6 years later in 2019 (Table S3).

254

255 *Observation of particular social interactions between adult male sperm whales and members of the*
256 *Irène's group*

257 Different socializing behaviours were observed between adult females and/or immatures of the Irene's
258 group. Figure 1 shows an example of an adult male (Reza) surrounded by an adult female and seven
259 immatures (five males and two females) of the Irène's group. This kind of socializing behaviour between
260 an adult male and several immatures is not uncommon since it was observed and filmed 16 times in
261 2019, and involved 5 different adult males: Daniel, Reza, Léonard, Jason, Jonas.

262



263

264 **Figure 1.** Social interactions between an adult male (Reza, **Re**), an adult female (Germine, **G**) and different immatures of the
265 Irène's group: Eliot (**E**) 8yrs-old; Arthur (**A**) and Roméo (**Ro**) 6yrs-old; Ali (**Al**) Daren (**D**) and Chesna (**C**) 1yr-old, and Miss
266 Toutou (**M**) 3yrs-old.

267

268 The arrival of Jonas and Aman in July 2018 was also a particularly interesting event: this arrival initiated
269 a large gathering of females and immatures of different social units. At least 60 females and immatures
270 were observed at this time (MMCO, Field report of the July 18, 2018). Social interactions (e.g.,
271 *swimming together*) were also observed between adult males present in Mauritian waters at the same
272 time. The most striking example of these social interactions was that of Jason and Léonard. Throughout
273 their presence, from April 23, 2019 to June 8, 2019, they were observed together at each observation
274 (n=11) (Table S3).

275

276 *Genetic analysis*

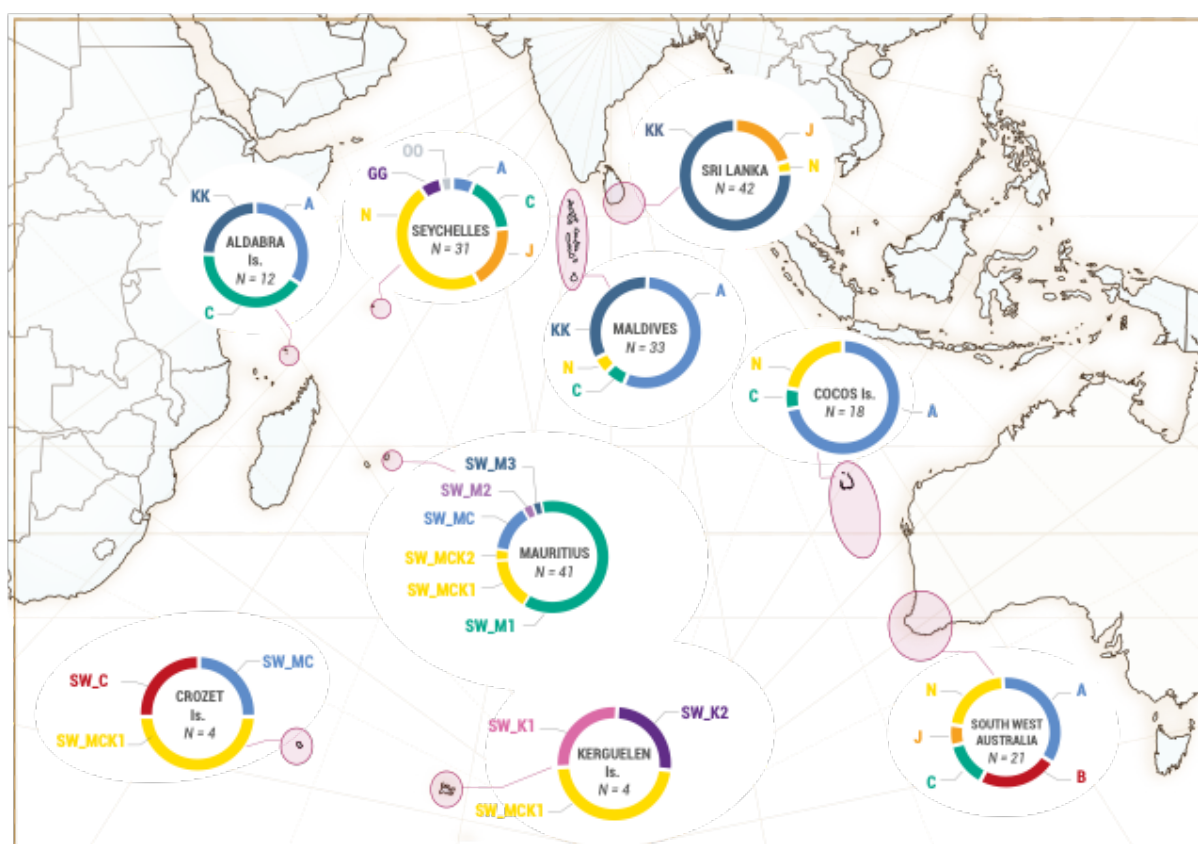
277 A total of 132 sloughed skin samples were collected between 2017 and 2020 (Table S2). They were
278 assigned in the field to 41 different sperm whales, i.e. to 18 adult females and 10 immatures (Table S2
279 and Sarano F. et al. 2021) and to 13 adult males (Table S2). Mitochondrial and nuclear loci were
280 amplified, allowing an analysis of variation over 638 bp of the MCR (Genbank references: MK907146-
281 MK907148, MK907159, MK907163, MK907172, MW854724-MW854731 and MW929445-
282 MW929452) and at 16 polymorphic microsatellite loci (Table S1). The Identity Analysis based on
283 microsatellite polymorphisms performed in CERVUS identified thirteen genetically distinct individuals
284 from Mauritius corresponding to the 13 adult males identified in the field (all pID <2.45e⁻¹²). All
285 genotypes assigned to the same individual had between 87.5% and 100% identity, and the differences
286 were all consistent with allelic drop out. Mitochondrial haplotypes were all 100% identical between
287 samples of the same individual. Only three skin samples had to be reassigned to another sperm whale
288 than the one identified in the field after a *posteriori* careful examination of video recordings (see Table
289 S2 and Sarano et al. 2021 for more explanation). Nine samples were taken off Crozet/Kerguelen, among
290 which 8 genetic individuals were identified, Bio_Cro_2011_1 and Bio_Cro_2017 corresponding to the
291 same individual (pID = 2.6e⁻²³). Six MCR haplotypes were detected among the thirteen adult male sperm
292 whales sampled off Mauritius ($H=0.72$, $\pi=0.00265$). Five different MCR haplotypes were identified in
293 the eight male sperm whales sampled in Crozet/Kerguelen ($H=0.78$, $\pi=0.00274$). Mitochondrial Φ_{ST}
294 calculated between males sampled near Mauritius and those sampled in Crozet/Kerguelen was
295 significant ($\Phi_{ST}=0.136$, $p=0.037$), and the F_{ST} value was just above the significant value fixed to 5%
296 ($F_{ST}=0.125$, $p=0.055$).

297

298 *Genetic relationships between Irène's social unit members and adult males sampled off Mauritius*

299 In this study, the mitochondrial haplotype names correspond to the geographical places they came from
300 (M: Mauritius, C: Crozet, K: Kerguelen). The correspondence with the haplotypes defined by Alexander
301 et al. (2016) is presented in Table S4 and Figure 2. One adult male harboured the SW_M1 haplotype,
302 corresponding to haplotype C of Alexander et al. (2016), characteristic of the Irène's group (Sarano et

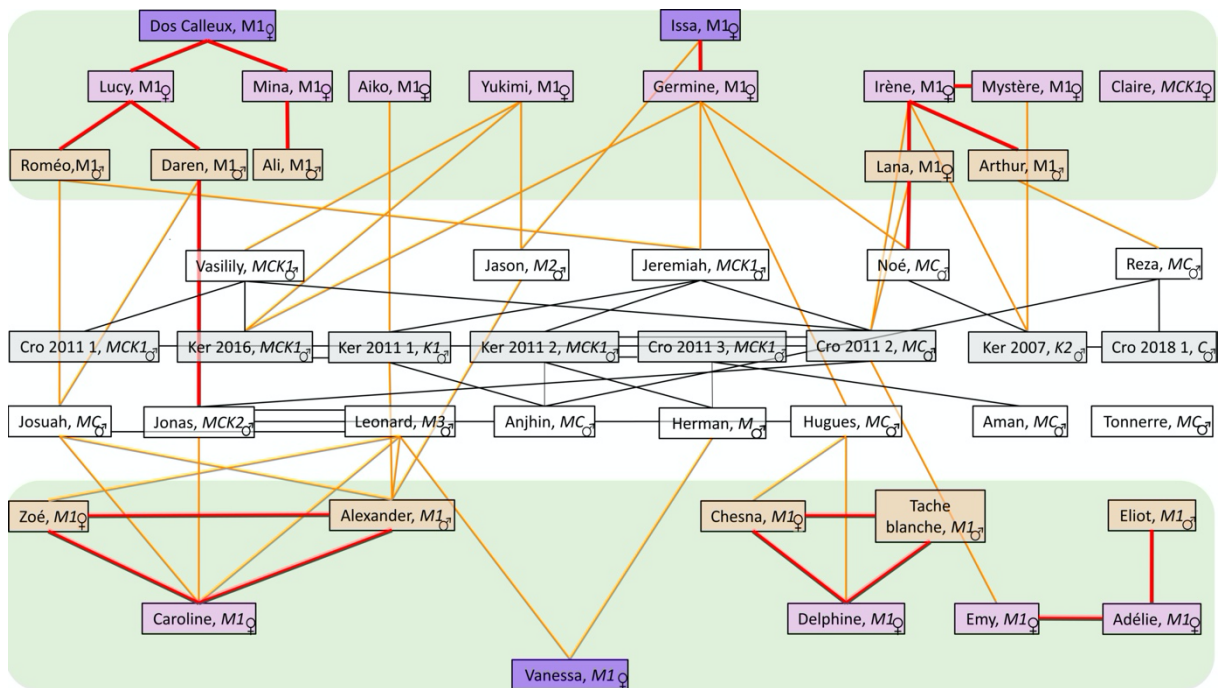
303 al., 2021a). Two others had the same haplotype (SW_MCK1) as Claire, the sole adult female of the
304 Irene's social group with a different MCR haplotype (Sarano et al., 2021a), corresponding to the
305 haplotype N.001.001 mainly found in the Seychelles, in the Coco Islands and in the south west Australia
306 by Alexander et al. (2016). Another adult male had the haplotype MCK2 (differing from SW_MCK1 at
307 position 609, table S4), one had the haplotype SW_M3 corresponding to the haplotype KK found almost
308 exclusively in the Indian Ocean off Sri Lanka (Alexander et al., 2016) and off Albany in Australia (Day
309 et al., 2021). Seven males shared the haplotype SW_MC, identical to the haplotype A.001.001, common
310 in the Indian Ocean (Figure 2). The last male possessed a new haplotype, SW_M2, not found previously
311 anywhere else.
312



313
314 **Figure 2. Geographical repartition of the mitochondrial haplotypes in the Indian Ocean** determined by Alexander et al.
315 2016 (haplotypes named with one or two letters) and haplotypes determined during this study (haplotypes names starting by
316 SW). A same colour indicates corresponding haplotypes (602bp in common).
317 N: number of sperm whales for each diagram.
318

319 Kinship analysis revealed two first- and 20 second-degree kin relationships (11 with adult females, 9
320 with immatures) between the 13 adult males sampled in Mauritius and members of the Irène's group
321 (Figure 3 and Table S5). One adult male, Jonas, was identified as the father of Daren, a young male born
322 in 2018; and a second adult male, Noé, was identified as the father of Lana, a young female born in 2019
323 (Figure 3, Table S5). All but three adult males presented at least one second-degree relationship with
324 members of the Irène's group with a maximum of four (Josuah and Léonard) (Figure 3).

325 Four possible full sibling relationships (same mother and father) have also been discovered in the Irène's
 326 group (two between immatures and two between adult females).
 327



328
 329 **Figure 3: Schematic representation of the kin relationships between all the members of the Irène's group and the adult**
 330 **males sampled off Mauritius (n=13) and in the Sub-Antarctic waters of the South of the Indian Ocean (n=8).**

331 First-degree (red lines) and second-degree (black lines between two adult males and orange lines between an adult male and a
 332 member of Irène's group) relationships between the different sperm whales are represented (second degree between members
 333 of the Irène's social group are not represented for the sake of clarity, see Sarano et al. (2021a) for these relationships). The
 334 name, sex, and mitochondrial haplotypes (listed in Table S4) are indicated for each individual. Adult females are represented
 335 in purple (dark for older individuals, as estimated in the field, and light purple for the others), young sperm whales within the
 336 Irène's social group in orange, and adult males are in white (males from Mauritius) and in light grey (males from
 337 Crozet/Kerguelen – sampling locations designated by “Cro” and “Ker”, respectively). The two green boxes represent two social
 338 subgroups identified within the Irène's social group (Sarano et al. 2021). As stated in Sarano et al. (2021), this diagram
 339 was constructed to be consistent with the analyses conducted. Although we performed different analyses that produced similar
 340 results, uncertainty exists in the relatedness estimate calculations, which might influence some of these relationships.

341
 342 *Large geographic scale kin relationships in the Indian Ocean*

343 Two haplotypes (SW_MCK1 and SW_MC) were found both in Crozet/Kerguelen and in Mauritian
 344 males. SW_MCK1, shared by four sub-Antarctic sperm whales (two sampled in Crozet and two in
 345 Kerguelen) was the most frequent. The haplotype SW_MC was found in one sperm whale from Crozet
 346 (Figure 2). Three other haplotypes were found in the Crozet/Kerguelen samples that were not observed
 347 among males sampled off Mauritius: SW_K1 and SW_K2, found in two sperm whales sampled in the
 348 Kerguelen and SW_C, found in one sperm whale in Crozet. SW_K1 matched the haplotype 10 defined
 349 by Day et al. (2021) found off South Australia and Victoria, and SW_K2 corresponded to the haplotype
 350 GG (Alexander et al., 2016), exclusively found in the Indian Ocean in the Seychelles. SW_C
 351 corresponds to haplotype B (Alexander et al., 2016; Day et al., 2021), found in Australia (Figure 2).

352 Males from Kerguelen/Crozet shared no first-degree relations with the Irène’s group and had fewer
 353 second-degree relationships ($n=9$, among which only two are found with immatures of the Irène’s group)
 354 than Mauritian males (Figure 3). However, some of these males shared strong second-degree
 355 relationships with members of the Irène’s group (for example *Mystère* and *Ker 2007*, $r=0.38$). Among
 356 all adult males sampled off Mauritius or in the south of the Indian Ocean, 24 second-degree relationships
 357 were identified (Figure 3, Table S5).

358

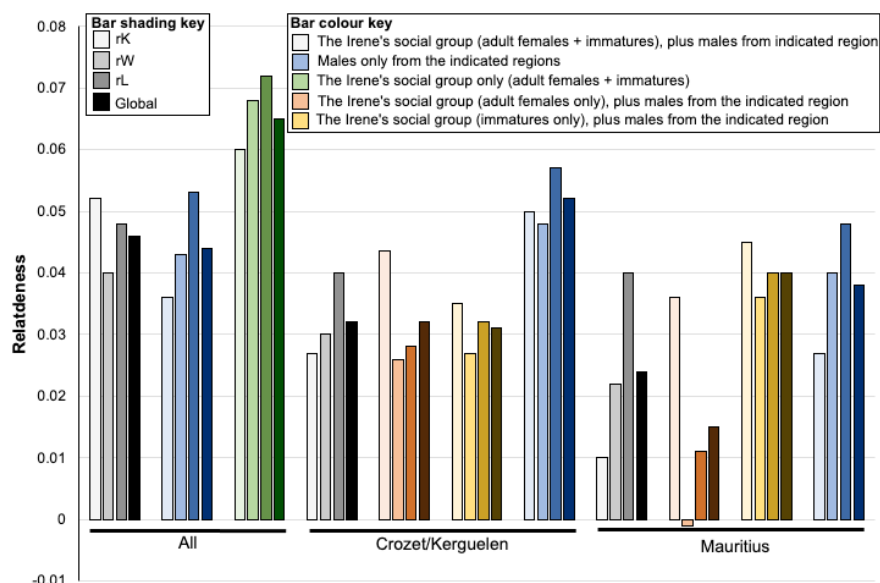
359 *Average relationship coefficients*

360 During this study, 22 sperm whales (21 adult males and 1 immature female) were added to the 27 already
 361 analysed in Sarano et al. (2021a). The 49 sperm whales in total included in this study were the 25
 362 members of the Irène’s social group, 2 members of another social group, “the Reshna group”, one
 363 unidentified female, 13 adult males sampled off Mauritius, and the 8 adult males sampled in
 364 Crozet/Kerguelen (the complete list is given in Table S2). The mean relatedness of these different
 365 samples and of different combinations were calculated (Figure 4, Table S6). Across all the included
 366 individuals (in Mauritius and in Crozet/Kerguelen), we calculated an average $r=0.046$, similar to that
 367 calculated between all adult males ($r=0.044$; Table S6). As expected, members of the mostly matrilineal
 368 Irène’s group had a higher average pairwise r ($r=0.065$, Figure 4).

369 Average relatedness values were higher among males sampled in Crozet/Kerguelen ($r = 0.052$) than
 370 between these males and members of the Irène’s group, whether the Irène group was partitioned into
 371 adult females only, immatures only, or the entire group ($r = 0.031-0.032$, Figure 4 and Table S6)

372 In contrast, the partitioning of the Irène group had an impact on the relatedness values in comparison to
 373 males sampled in Mauritius. The average relatedness of the Mauritius males to adult females only from
 374 the Irène group was lower ($r = 0.015$) than the relatedness between the immatures and the males ($r =$
 375 0.040 , Figure 4 and Table S6).

376



377

378 **Figure 4: Differences of average relatedness coefficients in groups and subgroups**

379 Relatedness coefficients r_K (Kalinowski *et al.* 2006), r_W (Wang 2002) and r_L (Li *et al.* 1993) were calculated through *ML*
380 *Relate* and through *Relate*. r_{Global} is the average value of the three coefficients (r_K , r_W and r_L). The four relatedness estimators
381 are first represented for all individuals, for all adult males and for all members of the Irène's group. Note that the values of
382 the Irène's group are higher (shown in green).
383 Different combinations of individuals were then formed, and the relatedness coefficients calculated. The partitioning of the
384 Irène's group between adult females and immatures had a strong impact of the r calculated with adult males sampled off
385 Mauritius, but not with those from Crozet/Kerguelen.

387

388 **Discussion**

389

390 Currently, our knowledge of behaviour, ecology and genetic diversity of emblematic marine megafauna
391 still suffers from holes. An outstanding example concerns male sperm whales, the “largest toothed
392 creature on Earth” (Cantor *et al.*, 2019). Sperm whales are steeped in our culture, from the star of one
393 of the most-read novels (Melville, 1851) to the use of their spermaceti oil during the industrial revolution
394 (e.g. Whitehead, 2002). But social and breeding behaviours of male sperm whales remain largely
395 unclear, especially in terms of geographical and social fidelity. Here, we studied sperm whales off
396 Mauritius under the auspices of the Maubydick project (Sarano *et al.*, 2021a, 2021b) and off
397 Crozet/Kerguelen (Janc *et al.*, 2018; Labadie *et al.*, 2018; Richard *et al.*, 2020). This allowed us to
398 document the presence of different males visiting the focal mostly matrilineal sperm whale social unit,
399 the Irène group, to identify several recaptures of males with the Irène group over years, to decipher some
400 paternal kinships as well as to capture a diagram of kin relationships at a larger geographic scale. Based
401 on this, we infer that adult males can show social and geographical fidelities to breeding and feeding
402 areas within the Indian Ocean.

403

404 *Our study evidenced no natal philopatry of the male sperm whales for the Irène social group*

405 Natal philopatry can be defined as fidelity to birthplace and has been evidenced in different species of
406 marine mammals (e.g. Baker *et al.*, 2013; Rendell *et al.*, 2019). Among the 13 adult males sampled in
407 Mauritian waters, 12 did not share the SW_M1 haplotype characteristic of the Irène social group (Sarano
408 *et al.*, 2021a), and can therefore not have been born in this group. Only one, Herman, had the SW_M1
409 MCR haplotype, but mitogenome sequencing revealed seven mutations between Hermann's and the
410 predominant Irène's group mitogenome (Justine Girardet, Agnès Dettai & Jean-Luc Jung, unpublished).
411 Nuclear DNA analysis is consistent with this statement: the lowest average r calculated for any
412 combination of individuals in our study, was between the adult female members of the Irène's group
413 and males sampled off Mauritius (Figure 4, Table S6).

414

415

416

417 *Over-years recaptures of different males in the Irène group and estimation of male social fidelity*

418 In contrast to the lack of natal philopatry of adult males demonstrated by our analyses, our study
419 highlights seven examples (three confirmed by resightings over multiple years, and four correlated to
420 gametic recaptures) of males coming back several times to the same area and to the same social unit to
421 breed. These are strong indications that adult male sperm whales may show social fidelity to particular
422 female-dominated social groups, not based on kin relationships with adult females in the group, and
423 that, in turn, they must be well known by the members of these female-dominated social groups.

424 Nuclear DNA analysis revealed two father-offspring relationships between adult males sampled off
425 Mauritius and immature members of the Irène's group. One paternity has been attributed to Jonas (father
426 of Daren born in 2018), and one to Noé (father of Lana born in 2019), both sampled in 2018 (figure 4
427 and Table S4). These "gametic" recaptures (Garrigue et al., 2004) proved that some of the males
428 observed in Mauritian waters are reproductive. This reproductive status is supported by the value of the
429 average r calculated between males from Mauritius and members of the Irène group, which is nearly
430 tripled if immatures of the Irène's group alone are considered as compared to adult females of the group
431 (Figure 4, Table S6). The presence of Jonas in the Irène's group was highlighted over at least three
432 different years (1 year, in 2017, for mating as proved by the "gametic" recapture, and two years of
433 observation, in 2018 and 2019).

434 In addition, nuclear DNA analysis revealed 4 potential full sibling relations. Two are detected between
435 immatures (Alexander and Zoé born in 2019 and 2013, Chesna and Tache Blanche born in 2018 and
436 2011). The other two are between adult females (Adélie and Emy, Mystère and Irène) whose years of
437 birth are unknown. As twins in sperm whale are very rare (Best et al., 1984), it can be assumed that they
438 were not born the same year. Thus, the fathers of each of these four pairs came back at least in two
439 different years to the same group – and to the same specific receptive female – to mate. The father of
440 Chesna and Tache blanche could in addition be the father of Eliot, supposed half-brother of Tache
441 Blanche (Figure 3). Despite these gametic recaptures being based on relatedness estimate calculations,
442 and therefore subject to uncertainties, these findings provide powerful evidence in support of enduring
443 relationships between adult males and specific female-dominated social groups.

444 It is of note that the three males recaptured between years were seen at the same period of the year
445 (Hugues in October 2013 and October-November 2019, Navin in July 2015 and June 2018, Jonas in
446 July 2018 and May-June 2019). This could indicate either a certain degree of seasonality specific to
447 each individual, or, if they are visiting different female-dominated social groups, a difference in the
448 order that each social group is visited between males. The case of Jonas stands out: Jonas was observed
449 in 2018 and 2019, he is the likely father of Daren, born in 2018, and maybe triggered the gathering of
450 tens of females and immatures in 2018. Jonas has therefore a marked and repeated social fidelity for the
451 Irène's group, and is in turn well known to the group members. As suggested by Gero et al. (2014),
452 spectacular gatherings could also support the hypothesis that females play a role in mating choice.

453

454 *Social interactions between adult males and Irène's group members*

455 Male sperm whales were present in the Irène's social group most of the year with a peak of occurrence
456 in April and May during the austral autumn, which could represent the breeding season. Labadie et al.
457 (2018) and Janc et al. (2018) highlighted a seasonality in occurrence of sperm whales in the high latitude
458 feeding area of the Indian Ocean, with increased sightings in spring and summer. However, observations
459 in Mauritius are only conducted daily from February to May, thus the number of males identified in
460 each month could be biased in other months by lower observation effort, therefore reproduction
461 throughout the year cannot be excluded. Residency of males off Mauritius appears to be on the scale of
462 a few days to few weeks with an average stay (8.25d), twice as high as that previously reported off
463 Dominica, for example (3.76d) (Gero et al., 2014). Recurrent interactions between adult males and
464 members of the social unit have been observed, confirming previous observations (e.g. Gordon et al.,
465 1998; Gero et al., 2014). Limited interactions between adult males and adult females and/or immatures
466 have already been reported, for example in Northern Chile and off Dominica (Coakes and Whitehead,
467 2004; Gero et al., 2014). Here, the males identified were often observed in proximity (i.e. less than
468 100m) of members of the Irène's social group and several types of interactions (e.g., physical contacts,
469 vocal interactions) were recorded with both adult females and immatures. The exceptional gathering of
470 tens of individuals, - which probably represent a substantial proportion of the local population -, after
471 the arrival of two adult males in the Mauritian waters (MMCO, Field report of July 18 2018) seems to
472 not be restricted to the Indian Ocean: Gero et al. (2014) observed a similar aggregation of several tens
473 of individuals near an adult male in the Atlantic. Some males appear therefore to be well known to
474 particular stable social groups. This assumption is reinforced by the numerous interactions observed
475 between adult males and females, and by the several full sibling relationships identified.

476

477 *Population genetics and geographical philopatry of male sperm whales in the Indian Ocean*

478 While all members of the Irène's group except one harboured the same MCR haplotype (Sarano et al.
479 2021), adult male sperm whales showed a mtDNA diversity in the same range of what was calculated
480 by Alexander et al. (Alexander et al., 2016) for the broader Indian Ocean (Haplotype diversities around
481 $H=0.8$, nucleotide diversities around $\pi=0.0028$). The haplotypes identified in this study near Mauritius
482 and matching to Alexander et al. (2016) haplotypes all corresponded to minor and major haplotypes of
483 the Indian Ocean. In Crozet/Kerguelen, mtDNA haplotypes suggest a widespread geographic origin of
484 adult male sperm whales: they match to North Indian Ocean haplotypes identified from the west to the
485 east of the Ocean (Figure 2). Even though we sampled only limited numbers of male sperm whales, tests
486 of differentiation based on mtDNA detected some levels of genetic differentiation between Mauritius
487 and Crozet/Kerguelen (Φ_{ST} and F_{ST} significant or nearly so), which reflect divergent distribution of
488 mtDNA haplotypes between the two sites, although a high number of second- and third-degree
489 relationships were found between males sampled in the two areas.

490 While the mtDNA results likely reflect the widespread origin of males at specific geographic locations,
491 nuDNA polymorphisms support male-mediated gene flow at large scales, and highlight the reproductive
492 status of males sampled off Mauritius. Adult males of both areas (Crozet/Kerguelen vs Mauritius) show
493 equivalent numbers of second-degree relations with adult females of the Irène group (seven second-
494 degree relations for the eight males sampled in Crozet/Kerguelen and 11 second-degree relation for the
495 13 males sampled in Mauritius (Figure 3, Table 1). But many more second-degree relations are found
496 between immatures of the Irène Group and males of Mauritius (n=9) than with those sampled in
497 Crozet/Kerguelen (only two second-degree relations).

498 The average relatedness r calculation revealed similar patterns: between males sampled in
499 Crozet/Kerguelen and members of the Irène's group, the average r is similar when subsetting to adults
500 or immatures of the Irène's group. Therefore, males sampled in Crozet/Kerguelen do not appear to breed
501 preferentially with the Irène social group. This situation is strongly contrasting with the pattern observed
502 for males sampled in Mauritius, where their role of as paternal relatives was demonstrated by a three
503 times higher average relatedness with immatures than with adult females (Figure 4).

504

505 *New insights into adult male sperm whale diversity in the Indian Ocean*

506 Male recaptures and social interactions between males and members of social groups have already been
507 observed and suggest some levels of male social fidelity in breeding areas in the Pacific (Rendell et al.,
508 2005) and in the West Indies (Gero et al., 2014). Here, we confirm and extend these observations in the
509 Indian Ocean. The level of this male social fidelity (e.g., for social units, for vocal clans, defined in
510 Konrad et al., 2018) is still to be evaluated.

511 Our results suggest that this fidelity is not due to natal social philopatry, i.e. fidelity for the social group
512 of birth. It appears this behaviour is exclusive to female sperm whales. Therefore, males must acquire
513 their fidelity for places and groups other than that of their birth and based on the diversity of mtDNA
514 haplotypes observed in males, this might occur across large geographical scales.

515 The high mtDNA diversity found in male sperm whales (as compared to the almost complete absence
516 of diversity found in the group of Irène) is likely to reflect disparities in their respective birth places.
517 Alexander et al. (2016) found that, in the Indian Ocean, 44.4% of the variance in mtDNA frequencies
518 was explained by regions, and 12.3% by social groups. If the mostly matrilineal nature of the Irène's
519 group (Sarano et al., 2021a) is a more or less general rule for sperm whale social units in the Indian
520 Ocean, the geographical patterns of mtDNA distributions found by Alexander et al. (2016) may well
521 correspond to discrete regional partitions of social units, more than to different proportions of mtDNA
522 haplotypes in different populations, found for instance in humpback whales (e.g. Baker et al., 2013;
523 Richard et al., 2018). This would be explained by the strong natal social philopatry of females (more
524 than by a natal geographical philopatry). Interestingly, the situation could well be different in the Pacific,
525 where sperm whale social groups could be of larger size and aggregate more often (Whitehead and

526 Kahn, 1992), and where partitioning of variance in mtDNA has been explained by social groups and not
527 by regional differences (Alexander et al., 2016).

528 The number of adult male sperm whales sampled off Mauritius is relatively low (n=13), but it is
529 nevertheless notable that their mtDNA haplotypes are frequent in different regions of the Indian Ocean
530 neighbouring Mauritius. In contrast, sperm whales sampled in the Crozet/Kerguelen (n=8) have
531 haplotypes found in a much broader area covering all the north of the Indian Ocean, from west to east
532 (this study, Alexander et al., 2016; Day et al., 2021). This is reflected by significant or near so Φ_{ST} and
533 F_{ST} values between Mauritian and Crozet/Kerguelen males. Mesnick et al. (2011) suggested that, in the
534 North Pacific, male sperm whales from different region mix in feeding grounds and exhibit some degree
535 of geographical philopatry for the region of their birth when breeding. Our results highlight a lack of
536 natal philopatry of male sperm whales at the social unit scale but they could well fit into the Mesnick et
537 al. (2011) hypothesis, with a certain degree of philopatry at a larger geographic scale (here, an area
538 corresponding more or less to the north west of the Indian Ocean). As in the North Pacific (Mesnick et
539 al., 2011), and still remaining cautious because of the low number of samples in our study, the high
540 latitude feeding areas in the Southern Indian Ocean could host mixed groups of male sperm whales with
541 a widespread geographic origin, larger than in the breeding areas. These observations are in perfect
542 agreement with previous population genetic studies, highlighting a strong female philopatry and male-
543 mediated gene flow (Lyrholm et al., 1999; Engelhaupt et al., 2009; Alexander et al., 2016).

544
545 It is of note that a double fidelity of adult male sperm whales for breeding and feeding grounds exists in
546 the Indian Ocean: (i) a certain level of male fidelity has been detected in feeding grounds of the Indian
547 Ocean (Labadie et al., 2018); our results, a same male has been sampled in 2011 and 2017 off Crozet),
548 and (ii) our study highlights the existence of a social and geographical fidelity in a sperm whale breeding
549 area of the south west of the Indian Ocean.

550 Until now, sperm whales were not believed to follow defined migration routes (Cantor et al., 2019), but,
551 at least in the Indian Ocean, as some degree of fidelity is now proved both for breeding and feeding
552 areas, male sperm whales could well take similar routes to migrate on successive years, also supported
553 by the similar time of year distinct males were observed when resighted between years. Estimating the
554 strength of both fidelities as well as long-term satellite tags could help to confirm this hypothesis.

555

556

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558

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571

572

573 **Ethics**

574

575 Permission to conduct the Maubydick project, including the taking of sloughed skin fragments, was
576 granted by the Department for Continental Shelf, Maritime Zones Administration and Exploration of
577 the Mauritius Prime Minister Office, on the 21 February 2017. Skin samples were sent to Brest (France)
578 under the CITES agreement FR1702900025-I.

579

580

581 **Authors' contribution**

582

583 Both FS and JLJ designed the study. FS, JG, GR, PT, CG, AA and JLJ contributed variously to the
584 conception of the project. FS, VSS, RH, AP, GR, PT, CG and HV performed the field experiments and
585 identification of individual sperm whales. JG, JLJ, and AMGS conducted the genetic analysis
586 (laboratory procedures). JG and JLJ analysed and interpreted the genetic data
587 JLJ and JG wrote the manuscript. PT, AA, FS, VSS, BM AMGC, GR, CG, HV and OA critically revised
588 the manuscript.

589

590

591 **Competing interests**

592

593 The authors declare no competing interest

594

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