Site fidelity and movement patterns of short-finned pilot whales within the Canary Islands: evidence for resident and transient populations

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1   **ABSTRACT**

2   1. The geographic location and oceanographic, physical and chemical water properties make the

3   Canary Islands one of the planet's biodiversity hotspots. The short-finned pilot whale (SFPW,

4   *Globicephala macrorhynchus*) is one of the archipelago's most commonly encountered species and

5   is potentially vulnerable to a range of anthropogenic pressures including habitat degradation,

6   acoustic pollution, fishing, whale-watching operations and shipping. Assessment of impact has not

7   been possible because of a lack of even basic information about occurrence and distribution.

8   2. Spatial and temporal distributions, ranging behaviour and residence patterns of short-finned pilot

9   whales were explored for the first time using survey and photo-identification data collected in the

10   Canary Islands between 1999 and 2012. In total, 1,081 pilot whale sightings were recorded during

11   70,620 km of search effort over 1,782 survey days.

12   3. Pilot whales were detected year-round and distributed non-uniformly within the archipelago, with

13   greater densities concentrated in patchy areas mainly on the leeward side of the main islands. In

14   total, 1,320 well-marked individuals were identified, which exhibited a large degree of variability in

15   site fidelity.

16   4. Different but not isolated sub-populations of pilot whales that share ranges and maintain social

17   interactions are apparently present in the Canary Islands. Strong evidence of an island-associated

18   sub-population was found, with a group of 50 "core resident" individuals associated particularly

19   with Tenerife. There are also "transient" individuals or temporary migrants, which, probably driven

20   by inter- and intraspecific competition, may travel long distances whilst using the archipelago as

21   part of a larger range.

22   5. These findings fill a major gap in the knowledge of this species occurrence, distribution,

23   movements and site fidelity in the archipelago and provide much needed data to allow the initiation

24   of informed conservation assessments and management actions.

25   **Keywords**: Archipelago, ocean, island, distribution, survey, environmental impact assessment,

26   mammals

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1. INTRODUCTION

The analysis and description of space-use patterns have been crucial in understanding the ecology of many mammalian populations (Adams & Davis, 1967; Inglis, Hood, Brown, & DeYoung, 1979), providing important insights into animals' residency (T. H. Clutton-Brock, 1989), social organization (Ostfeld, 1990), demography (T. Clutton-Brock & Albon, 1985) and distribution of animals' resources in space and time (Brown & Orians, 1970). Studies to increase our understanding of the drivers and scale of animal movement are integral components of the information needed to manage human impacts on wild cetaceans (Hastie et al., 2003; Hooker, Whitehead, & Gowans, 1999; Ingram & Rogan, 2002; Wilson, Thompson, & Hammond, 1997).

Individuals of most species are not distributed randomly and do not use all parts of their range with the same intensity. Instead, some areas are used more frequently (Adams & Davis, 1967; Dixon & Chapman, 1980) or differently (feeding, calving, etc.; Burt, 1943), forming characteristic patterns of distribution, grouping, ranging, and association (Crook, Ellis, & Goss-Custard, 1976). Intra- or inter-specific competition for the same resources in the same niche is one factor that may lead to differential space use among individuals (Milinski & Parker, 1991).

In general, an animal's range should be large enough to provide adequate food resources to satisfy energetic requirements (McNab, 1963) and there is a strong correlation between range size and the way space within range is used, and the abundance, distribution, and predictability of food resources (Davies & Houston, 1994). Where food resources are abundant and no aggressive territorial neighbours are present, animals tend to use only as much as space as they need (King, 2002), and to stay in familiar areas rather than risk moving to other areas, even if they are more productive (Switzer, 1993). If resources are uniformly spread throughout an area, animals also tend to be uniformly distributed and, if the resources are defendable, often show territoriality behaviour (Emlen & Oring, 1977). In less productive habitat and in areas characterised by patchy or limited resources, animals tend to have larger and overlapping ranges (Harestad & Bunnel, 1979) because they must travel farther to obtain enough food (T. Clutton-Brock, 1975; Schoener, 1968).

Marine mammals live in fluid, open environments with few boundaries, feed on mobile prey, and have low transport costs per unit weight (Williams, 1999). Consequently, they are highly mobile and tend to have larger ranges than terrestrial mammals of similar size (Tucker, Ord, & Rogers, 2014). Delphinids show a wide variety of site fidelity and ranging patterns; individuals may occupy large ranges or be restricted in smaller areas; some display year-round residency patterns while

59   others are seasonal or "transient" visitors (Hunt et al., 2017; McGuire & Henningsen, 2007; Parra,

60   Corkeron, & Marsh, 2006; Silva et al., 2008; Zanardo, Parra, & Möller, 2016)

61   Pilot whales (genus *Globicephala*) are highly mobile and have been described as generally

62   nomadic, without defined migrations (Olson, 2009). Some north-south and seasonal inshore-

63   offshore movements related to prey movements or incursions of warm water have been, anyhow,

64   described for long-finned pilot whales (*Globicephala melas*) (Abend & Smith, 1999; Cañadas &

65   Sagarminaga, 2000; De Stephanis, Verborgh, et al., 2008).

66   The strong genetic differentiation between short-finned pilot whales (SFPWs, *Globicephala*

67   *macrorhynchus*) found in different oceans, between populations in Japan (Oremus et al., 2009) and

68   within the Pacific Ocean, suggest regional population structure and restricted movements within

69   ocean basins (e.g. Van Cise et al., 2016). Areas of continental shelf break with steep bathymetric

70   features and submarine canyons represent important feeding habitat for coastal short-finned pilot

71   whales, which have restricted ranges in the context of the basin-wise distribution of the species

72   (Thorne et al., 2017).

73   The stable presence of this species has been described in the oceanic and volcanic archipelagos of

74   Hawaii (Mahaffy, Baird, McSweeney, Webster, & Schorr, 2015), Madeira (Alves et al., 2013) and

75   the Canary Islands (Carrillo, Pérez-Vallazza, & Álvarez-Vázquez, 2010; Heimlich-Boran, 1993). A

76   considerable variability in residency patterns has been found, with some animals showing little site

77   fidelity but others exhibiting long-term fidelity to the main islands (Alves et al., 2013; Mahaffy et

78   al., 2015).

79   Previous studies of this species have found a stable presence in southwest Tenerife (Escorza,

80   Heimlich-Boran, & Heimlich-Boran, 1992; Heimlich-Boran, 1993; Montero & Arechavaleta, 1996)

81   but there is very little information about spatial and temporal distribution patterns in that area or

82   about their occurrence in other parts of the archipelago.

83   The waters around the Canary Islands include localised areas rich in nutrients (Arístegui et al.,

84   2006; Arístegui et al., 1989; Arístegui et al., 1997), which may provide suitable habitat and

85   sufficient resources to support one or more "resident" populations of SFPWs. Such populations

86   would be expected to show high fidelity to local areas and limited ranging behaviour (Habel, Hillen,

87   Schmitt, & Fischer, 2016; King, 2002). Conversely, areas where resources are limited or available

88   intermittently may only be suitable for whales that range over greater distances utilising a wider

89   range of areas/habitats (Harestad & Bunnel, 1979; Silva et al., 2008).

90   SFPWs are subject to a range of pressures from human activities in the Canary Islands. Habitat

91   degradation, deliberate and accidental discharge of pollutants into the sea, coastal development,

92   acoustic pollution, fishing activity, whale-watching excursions, and intensification of maritime

93   traffic are all potential threats to the conservation of this species and other cetaceans that inhabit

94   these waters year-round (Carrillo & Ritter, 2010). This lack of even basic information about

95   occurrence and distribution hampers assessment of the impact of human activities on local

96   populations of this species and, therefore, conservation and management efforts.

97   In this study we use information on the distribution, occurrence patterns, individual sighting

98   frequencies, movements and area use of SFPWs over 13 years in the Canary Islands to investigate

99   whether there are coastal resident populations that can be distinguished from a more oceanic

100   population that uses the waters of the archipelago less intensively. An improved understanding of

101   spatio-temporal movements of SFPWs among the islands and the identification of any particularly

102   important areas will help to describe this species ecology in the archipelago leading to a better

103   understanding of its conservation status in the context of the multiple human pressures and

104   facilitating assessment of the need for and development of management actions.

105   **2. MATERIAL AND METHODS**

106   **Study area**

107   The study was conducted in the warm-temperate waters around the Canary Islands (area = 109,000

108   km^2), an archipelago formed by seven independent volcanic islands (Carracedo, 2001) and various

109   islets, with a total coastline of 1,500 km. The archipelago is located in subtropical latitudes 27º - 30º

110   N, on the continental rise off Cabe Juby, next to the northwest African coast, and belongs to the

111   insular arc known as Macaronesia (Figure 1).

112   **Field procedures**

113   Surveys in the waters around the islands of the archipelago were conducted between 1999 and

114   2012. Survey transects were not systematic but were designed to cross depth contours in a zigzag

115   pattern to provide homogeneous coverage of the whole bathymetric range (Figure 1). A wide

116   variety of vessels was used, including small semi-rigid inflatable boats (survey length 41,218.5 km),

117   opportunistic vessels (whale-watching; survey length 4,566.6 km), sailing boats (survey length

118   8,064.6 km), research vessels (survey length 43,559 km). Eight ferryboats "Naviera Armas" were

119   also used as opportunistic platforms (survey length 12,361.3 km) between the islands of La

120   Gomera, Tenerife, Gran Canaria, and Fuerteventura (Figure 1).

121   Each research platform was always provided with the minimum required set of research equipment

122   (GPS recorder, 7x50 binoculars, digital cameras high definition video camera, hydrophone, and a

123   125 lb power crossbow), and had a minimum of two trained researchers. From different platform

124   heights, depending on the vessel, two observers simultaneously scanned the horizon covering a

125   180° sector in front of the boat (90° each). When a cetacean or a group of cetaceans was detected,

126   searching effort was suspended and data were collected from the group. A "group" was defined as a

127   spatial aggregation of animals, within 1,000 m of each other, that showed similar behavioural

128   activity and interacted with one another over timescales sufficiently short that there were few (or no)

129   changes in group membership (Karczmarski, Würsig, Gailey, Larson, & Vanderlip, 2005). For each

130   encounter, time, GPS position, species, estimated radial distance to the detected group, and group

131   size were recorded. On dedicated research vessels, behavioural observations and group composition

132   were also recorded, and photo-identification and biopsy sample collection conducted.

133   A photographic coverage percentage was assigned in the field, based on the estimated approximate

134   proportion of animals photographed that were observed at sea. Only sightings where the data

135   collection protocol was considered completed at sea were included in the group size

136   estimation and group composition analyses. Based on the data provided by Kasuya and Marsh

137   (1984) and following Heimlich-Boran (1993) interpretations, age/sex classes were defined as: adult

138   male (never found in association with a calf, with a minimum length of 4 m at maturity and a

139   maximum length of 5.8 m), indeterminate (adult female or sub-adult male which did not have a

140   consistent association with a specific immature animal), female (individuals with the physical

141   characteristics of an indeterminate whale and in association with a calf for the entire duration of a

142   sighting), juvenile (animals between 2.5 and 3 m in length, with little developed dorsal muscle);

143   calf (whale with a length between one third and half of an indeterminate animal) neonate (calves for

144   which it was possible to distinguish foetal marks on the body).

145   **Data analysis**

146   **Photo-identification**

147   The photographic material included both colour slides and digital images. All photographic

148   sorting/matching was done visually using Adobe Bridge CS5 software. Focus, contrast, parallax,

149   and relative size of dorsal fin (used for identification - see below) in the picture were used to grade

150   picture quality (Arnbom, 1987; Dufault & Whitehead, 1993, 1995) from "poor" (1) to "excellent"

151   (4) (Baird, Gorgone, et al., 2008; Baird, Webster, et al., 2008; McSweeney, Baird, Mahaffy,

152   Webster, & Schorr, 2009). Individual SFPWs were identified from photographs of their dorsal fins

153   showing naturally occurring marks and notches that allowed left- and right-side photographs to be

154   matched.

155   Dorsal fin silhouettes and scars on the dorsal fin (Bernd Würsig & Thomas A. Jefferson, 1990;

156   Würsig & Würsig, 1977) were used as secondary features to confirm matches and to sort

157   individuals without notches. All the principal matching was conducted by the same person (AS) and

158   an experienced researcher reviewed the final photo-identification catalogue to minimise the chance

159   of false-positive and false-negative matches.

160   Each identified individual was classified for its overall distinctiveness based on its dorsal fin

161   characteristics: number, size and shape of nicks, notches and scars on the leading and the trailing

162   edge of the dorsal fin. The rating followed the ranking scale of 1 to 4, from "not distinctive" to

163   "very distinctive" (Mahaffy et al., 2015). Photo-identification catalogues with the best picture of

164   each animal (from one or both sides) associated with each island were compiled and compared. As

165   many features as possible were used to confirm matches and reduce the possibility of false positives

166   (Scott, Wells, Irvine, & Mate, 1989; Williams, Friedl, & Haun, 1993; Bernd Würsig & Thomas A

167   Jefferson, 1990). The rate of mark change and mark acquisition was assessed by examining images

168   of fins for new notches or changes in notch shape in all re-sightings of individuals. Only good

169   quality photographs (categories 3 and 4) and well–marked animals (distinctiveness 3 and 4) were

170   used in the residency analyses because an assumption of equal capture probability was required.

171   Multiple photographs of the identified individuals were examined to confirm the age-sex

172   classification. In encounters for which the group size estimate at sea was found to be smaller than

173   the number of individuals identified, the sample size obtained by photo-analyses was used as the

174   approximate encounter group size.

175   **Occurrence patterns**

176   Occurrence patterns and distribution were described by considering the number of pilot whale

177   sightings observed and their distribution in relation to the survey location and frequency. To

178   account for the uneven geographical distribution of the survey effort, the study area was divided

179   into a grid of 160 x 61 cells in the range 27º 28' N to 29º 30' N latitude and 12º 58' W to 18º 18' W

180   longitude. Cell area varied between 11.89 and 12.14 square kilometres. The average encounter rate

181   was calculated by dividing the total number of sightings made on effort in each grid cell by the sum

182   of the distance in kilometres covered on effort in each cell. Cells with a total survey effort less than

183   1.414 km (diagonal of a 1 km^2) in any given year were excluded, resulting in a set of 1,598 grid

184   cells used for the analyses.

185   The non-parametric Mann-Whitney U test was used to check if significant differences in group size

186   existed among islands, seasons, and type of groups (male/female and residency patterns).

Residency and site fidelity

188   Four different residency categories were created based on individual re-sighting rates across the

189   whole archipelago, with sampling intervals defined by month and year: "core resident" (SFPWs

190   sighted at least once during each of the four different seasons of at least four different years),

191   "resident" (individuals seen in three or four years and at least two seasons), "occasional"

192   (temporary migrant seen less frequently than "residents", but more than twice), "transient" (whales

193   sighted once or twice in only one season in only one year).

Lagged identification rate

195   SFPWs residence rate was measured by calculating the lagged identification rate (LIR), which

196   represents the probability that an individual identified at any particular time will be identified again

197   in the study area *t* time units later (Whitehead, 2001). LIR computation and model fitting were

198   applied to all sightings of all animals and were carried out using the computer software SOCPROG

199   2.4. (Whitehead, 2009) in MATLAB. Models were fitted to the data using maximum likelihood and

200   binomial loss (Whitehead, 2001), and the quasi Akaike Information Criterion (QAIC) was used to

201   select the best-fitting model (Burnham & Anderson, 2003). The analysis was conducted using a

202   sampling period of 1 day. Jack-knife techniques with 1,000 bootstrap replications were used to

203   calculate confidence intervals and standard errors for each model parameter. Three residency

204   models were fitted to the residency rate data: "closed" (no changes in the individuals present in the

205   area), "emigration/mortality" (individuals could leave the area but never return), "emigration and

206   re-immigration" (individuals could leave and then re-enter the area; Whitehead, 2009; Whitehead &

207   Waters, 1990; Supplementary Material Table S1). Plots of LIR against time were produced for all

208   identified whales in the archipelago and also focusing only on waters off Tenerife to provide

209   indications of the temporal use of the area by individual animals. Movements between Tenerife and

210   La Gomera waters were also analysed.

Ranging patterns

212 Movements represented by re-sightings of identified whales within the archipelago were

213 documented. Linear distance between consecutive re-sightings of photo-identified individuals was

214 measured in GIS software using the "shortest straight swim" distance.

215 GIS software ArcView 3.2 with the Animal Movement extension (Hooge & Eichenlaub, 1997) was

216 used to determine the size of individual ranges and to examine individual ranging patterns. The

217 analysis was performed using the kernel estimator (B. J. Worton, 1989), a probabilistic non-

218 parametric method that attempts to assess the animal's use distribution (UD) within an area

219 (Kernohan, Gitzen, & Millspaugh, 2001) by quantifying the likelihood of finding the animal at any

220 particular location within its range (B. J. Worton, 1989). To decide the minimum number of

221 sightings required in the ranging analysis, bootstrap tests on Minimum Convex Polygon (MCP)

222 range size were run and the shape of the curve relating the size of the ranging area to the number of

223 locations was inspected for each whale. Least-squares cross-validation (LSCV) was used to

224 calculate the bandwidth value (which determines the amount of smoothing applied to the data), and

225 the harmonic mean outlier removal method (White & Garrott, 2012) was applied to identify and

226 remove outlying locations. To minimise autocorrelation (Swihart & Slade, 1985; B. Worton, 1987)

227 multiple sightings of the same individual on the same date were eliminated from the datasets used

228 to determine individual range size and ranging patterns. Schoener's ratio (Schoener, 1981) was

229 calculated for each individual to assess the amount of autocorrelation remaining in the data and the

230 potential effect on the estimates of range size.

231 **3. RESULTS**

232 Between January 1999 and October 2012, 1,782 day-surveys were conducted around the different

233 islands of the archipelago. In total, 109,770 km were covered (10,307 hours), within which 70,620

234 km were spent on effort (5,436 hours) by dedicated survey vessels (Figure 1). Searching effort over

235 the whole Canary archipelago did not vary significantly over years (Kruskal-Wallis test, $H2 =$

236 15.985, $p = 0.192$) or seasons (Kruskal-Wallis test, $H2 = 6.093$; $p = 0.107$). However, the amount of

237 searching effort was not evenly spread amongst different islands in terms of time, distance or area

238 searched (Table 1; Figure 1). The downwind areas of Lanzarote and Fuerteventura were surveyed

239 for 13 years, Tenerife and Gran Canaria for 11 years, La Gomera for 6 years and La Palma and El

240 Hierro for 3 years. Searching effort covered mainly the area around the island of Gran Canaria

241 (42% of the total time); the remainder was mostly spread evenly around the islands of

242 Fuerteventura, Lanzarote, Tenerife and La Gomera (Table 1).

243   In total, 4,242 sightings of 23 cetacean species were recorded. The SFPW was the most frequently

244   seen species, with 1,081 sightings (Figure 2, Table 1). SFPWs were encountered during every day-

245   survey conducted in the waters off Tenerife, with a mean encounter rate (sightings per grid cell) of

246   2.16 (SE = 0.38) sightings 100 km^{-1} (n = 150) surveyed (Supplementary Material Table S2).

247   Significantly fewer sightings were recorded around the other islands (Kruskal-Wallis test, H2 =

248   172.044, p < 0.001), from a mean of 0.64 ± 0.19 sightings 100 km^{-1} off La Gomera (n = 54) to 0 off

249   El Hierro (Supplementary Material Table S2). On 167 occasions they were found associated with

250   other delphinid species, especially with *Tursiops truncatus* (147 sightings) and *Stenella frontalis*

251   (15 sightings). SFPWs were sighted in a wide range of depths, mostly between the 900 m and 1200

252   m isobaths (1077.5 ± 16.9 m, n = 621), and were found in shallower waters in La Gomera compared

253   to Tenerife and Lanzarote–Fuerteventura (Mann-Whitney U test, U=7,162, p=0.006; U = 90,

254   p<0.001, respectively). The distance of sightings from the coast (5.76 ± 0.14 km, n = 625) varied

255   among islands, with greater distances in the eastern islands of Lanzarote-Fuerteventura and Gran

256   Canaria, compared to Tenerife (Mann-Whitney U test, U = 1,572, p < 0.001; U = 1,432, p < 0.001,

257   respectively) and to La Gomera and La Palma (Mann-Whitney U test, U = 114, p < 0.001; U = 111,

258   p = 0.002, respectively).

259   Initial behaviour recorded during the study period included all behavioural categories, which were

260   all observed year-round with no marked differences in frequency, except for socialising which was

261   observed for 77% of the time from June to October.

262   **Group size and composition**

263   Group size ranged from one to 80 individuals, with an overall mean group size of 16 ± 0.4

264   individuals (n = 810). Significantly larger groups were observed in La Gomera (19 ± 1.5) than in

265   Tenerife (16 ± 0.5) (Mann-Whitney, U=21861.5, p=0.015), and in Gran Canaria (Mann-Whitney,

266   U=1022.5, p=0.013), and smaller group sizes were seen in Gran Canaria (13 ± 1.3) compared to

267   Lanzarote-Fuerteventura (20 ± 2.4; Mann-Whitney, U=443.5, p=0.033; Supplementary Material

268   Figure S1a). Seasonal differences in group size were detected only in Tenerife, where observed

269   group sizes were larger in summer and autumn than in spring (Mann-Whitney U test, U = 11,535, p

270   = 0.015; U = 11,631.5, p = 0.003, respectively, Supplementary Material Figure S1b). Group

271   composition showed that SFPWs commonly travel in groups of mixed sex and age. A high

272   frequency of sightings with calves and/or neonates was recorded throughout the archipelago; 82%

273   of the groups encountered included immature animals, with a mean per sighting of 1.3 ± 0.06

274   neonates/calves (n = 803). In Tenerife, where the majority of data were collected, the presence of

275   neonates was highest during the summer months (52%) followed by autumn (31%). Neonates were

276   present in the same groups as presumed adult males in 58.9% of the recorded sightings. Group sizes

277   of sightings with only males (7 ± 0.9, n = 33) were significantly smaller than sightings with no adult

278   males (19 ± 0.92, n = 170; Mann-Whitney U test, U = 774.500, p < 0.001), and when also adult

279   female were present (17 ± 0.7, n = 256; Mann-Whitney U test, U = 7,118, p < 0.001;

280   Supplementary Material Figure S2a). Groups with immature animals were significantly larger (19 ±

281   0.8, n = 382) than groups in which only mature whales (9 ± 0.8, n = 33) were present (Mann-

282   Whitney U test, U = 26,675.5, p < 0.001; Supplementary Material Figure S2b).

Photo-identification

284   During the 629 encounters where photo-identification sessions were conducted, 234,350

285   photographs were taken, of which 190,340 were considered suitable for photo-identification

286   analysis, based on the photographic quality criteria. The overall catalogue of all identified SFPWs

287   in the whole archipelago contained 14,469 dorsal fin photographs belonging to 3,275 unique

288   individuals, within which 1,310 were well-marked individuals identified from good and excellent

289   quality pictures (Table 2). A discovery curve constructed from the overall database (Figure 3)

290   showed continual recruitment of new individuals to the marked population throughout most of the

291   study period (1999-2012), with a temporal plateau reached during 2008. Some levelling off was

292   present in the discovery curve of well-marked individuals in La Gomera, although new well-marked

293   individuals were sighted until the end of the study period in all areas (Supplementary Material

294   Figure S3). A total of 617 (50%) well-marked individuals were seen only once, 191 (15%) twice,

295   and 433 (35%) whales three to 36 (one animal) times (Figure 4). Re-sighting intervals ranged from

296   one day to 11.26 years (112 ± 3.6 days, n = 971): 37.7% of the individuals were recaptured within

297   one year, 25.3% in the following year, and 7.3% over a longer time span (four animals seen in ten

298   years, and five in 11 years between two and seven times).

Distinctiveness and mark change

300   Considering only the mature population, the proportion of re-captured individuals increased as the

301   level of distinctiveness increased, and the mean number of times an individual was re-captured also

302   increased with distinctiveness: 1.5 for non-distinctive, 2.7 for slightly distinctive, 3.1 for distinctive,

303   and 3.8 for very distinctive SFPWs. In total, eighty-two mark-acquisition events or mark-changes

304   were recorded for 64 individuals, but only in seven cases did they result in a change in

305   distinctiveness category. The mark-change rate was estimated to be once every 3.4 to 4.2 years. The

306 low mark-change rate, along with the long-lasting presence of scars persisting over ten years

307 (Servidio 2014), allowed the effect of mark-change to be considered negligible.

308 **Site fidelity and movement patterns**

309 In total, 1,241 well-marked mature SFPWs were classified based on their residency pattern

310 analysis: 255 whales (21%) were considered "residents", and 50 (4%) "core residents", mainly

311 photo-identified in Tenerife (Table 3). Lanzarote and Fuerteventura had almost exclusively

312 "transient" whales, ten SFPWs were recaptured between two and three times in different years in

313 the area ("occasionals"), and only two animals were recaptured between these western islands and

314 Gran Canaria, 11 years apart. Two hundred and eighteen whales were detected at more than one

315 island, of which 27 were identified in Tenerife, La Gomera and Gran Canaria. The "resident" and

316 "core resident" SFPWs in La Gomera ($n = 102$) and Gran Canaria ($n = 35$) were all, except for

317 three animals, also seen in Tenerife, a reflection of the high number of recaptures among these

318 three islands (Table 3 and Supplementary Material Table S3). The highest within-area rate of re-

319 sighting was recorded in the two sub-areas off southwest Tenerife and La Gomera, where some

320 animals ($n = 23$) were documented as moving back and forth, with six animals showing such

321 movements up to four times. Most of the re-captures of the animals moving between Tenerife and

322 La Gomera (96%) and between Tenerife and Gran Canaria (60%) occurred during the warmer

323 months of the year. All residency categories were observed throughout the year but "transient"

324 frequencies were double during warmer months than in the rest of the year. Groups with a mixed

325 composition of residency patterns were also encountered mostly (75%) during summer and autumn.

326 The size of groups formed only by "core residents" and "residents" were significantly smaller (15.6

327 $\pm$ 0.5, $n =170$) than groups containing individuals with a mix of residency patterns (22.8 $\pm$ 1.9, $n =$

328 80); Mann-Whitney U test, U = 17,469.5, p = 0.01).

329 The distance between consecutive sightings of photo-identified SFPWs was mostly less than 10 km,

330 but 1% (n = 38) of inter-sighting distances were between 100 and 170 km, illustrating extensive

331 movements of animals within the archipelago.

332 There was no sex-specific difference in the distances travelled by SFPWs (Mann-Whitney U test, U

333 = 537,187, p = 0.725). However, differences were found among SFPWs of different residency

334 categories (Kruskal-Wallis test, H2 = 86.350, p < 0.001), with the exception of "occasional" and

335 "transient" animals that did not differ statistically (Mann-Whitney U test, U = 2,028.5; p = 0.775).

336 Shorter distances were recorded for "core resident" animals (8.33 $\pm$ 0.65 km, $n = 530$), followed by

337   "resident" animals (13.76 ± 0.62 km, *n* = 1,317), and then by "transient" (26.11 ± 6.01 km, *n* = 43)

338   and "occasional" animals (31.78 ± 2.37 km, *n* =191).

339   **Lagged Identification Rates (LIR)**

340   The best fitting model for the LIR within the entire archipelago was the "emigration +

341   reimmigration" model (Figure 5). An estimated 254 ± 10 of the 1,241 identified whales used in this

342   analysis spent an average of 531 ± 24 days in the Canary Islands before leaving for an average of

343   4,087 ± 941 days (Table 4), i.e. beyond the 4.5 years covered by the dataset used for the analysis.

344   Nevertheless, analyses indicated strong over-dispersion in the data (variance inflation factor =

345   4.82), so results should be interpreted with caution; in particular, the variances of the parameter

346   estimates were likely underestimated.

347   For south-west Tenerife, the best-fitting model was "emigration/mortality" (Table 4), which

348   estimated that 279 of the 717 identified animals had a high level of residency to the area, staying

349   around the island for an average of 2,049 days, a time that was also beyond the 4.5 years of the

350   study. These data were also over-dispersed (variance inflation factor = 3.67) and the results should

351   be interpreted cautiously.

352   For movements between La Gomera and Tenerife, in both directions, the best model was "fully

353   mixed" (Table 4), which is supported by the high number of recaptures recorded between the two

354   areas (Supplementary Material Table S3).

355   **Ranging patterns**

356   Based on the asymptote of the area observation curve, a minimum number of 10 sightings was

357   determined to be an adequate sample size to estimate the size of an individual's range, resulting in a

358   total of 193 animals being selected for this analysis. The small sample size did not allow temporal

359   changes in range size and location to be examined. The mean Schoener's ratio was 1.54 ± 0.03

360   (Supplementary Material Table S4), which can be considered acceptable according to Kenward et

361   al. (2001). The extent of temporal autocorrelation in the data was not investigated. The kernel

362   method gave a mean 95% UD area of 355.90 ± 39.86 km^2, ranging from 46.13 to 3,673.79, and a

363   50% UD core area of 76.95 ± 8.62 km^2 (Supplementary Material Table S4). Even though great

364   variability was found in the estimated core areas (50% UD) among animals, as shown by the high

365   standard error, 71% of all core areas overlapped in a limited area of 57.7 km^2 in southwest Tenerife

and La Gomera (Figure 6a). While most of the individual ranges were limited only to southwest Tenerife (99% of the 50% UD areas and 75% of the 95% UD), the 95% UD showed multiple centres of activity between this area and the southwest areas of La Gomera (26 whales), northeast Tenerife (13 whales), and Gran Canaria (six whales), and three whales had centres of activity in three different areas Figure 6b). The most frequently seen animals seemed to share their range with "transient" animals, which were seen not only when associated with "residents" but also when in isolated groups (Figure S4). There were no significant differences in the ranges (Kernel 50% and 95% UD) between males and females (Mann-Whitney U test, U = 1,334, p = 0.551, N = 120; U = 1,276, p = 0.349, N = 120, respectively).

4. DISCUSSION

SFPWs in the Canary Islands showed significant temporal and spatial variation in patterns of occurrence with higher encounter rates recorded during the warmer months and high variability in island-associated encounter rates. Residency patterns in the archipelago were characterized by a mixture of "residents", "transients", and "occasional" temporary migrants, in agreement with findings for other SFPW populations around oceanic islands (Alves et al., 2013; Mahaffy et al., 2015). "Resident" groups of whales that had ranging areas of limited size and that overlapped considerably were mostly located in southwest Tenerife and La Gomera. The majority (62%) of whales, however, were seen no more than twice and in only one season (defined as "transients").

The inclusion of each individual SFPW in a resident or non-resident category is not definitive because categorization was based on resighting rates which are samples and may therefore change with additional data. However, the "transient" and "temporary migrant" categories that are based on few resightings are most susceptible to this; animals currently categorised as resident are unlikely to change category with additional data.

It is not known whether some animals occurring in the study area are part of a population that uses or moves through it only at certain times. Animals sighted only once could be "transients" passing through the archipelago, have ranges that barely overlap the study area, be behaviourally less likely to be captured, have died or permanently emigrated or simply not have been re-sighted during the study period in the area (Alves et al., 2013). The high percentage of "transients" recorded might also be a consequence of the large size of the study site (109,000 km^2) that did not allow the whole area to be completely and homogeneously covered. Most of the northern windward areas of the islands were excluded, and most of the effort was concentrated in southern coastal leeward waters.

397   This might have resulted in the failure to detect some high use areas, either extensions to identified
398   areas or new areas.

399   Extending the study area to the northern windward areas might result in capturing new previously
400   uncaptured whales, possibly lower the number of whales classified as "transients" and extend the
401   resident distribution. However, long-distance movements for this species should be expected
402   (Aguilar Soto et al., 2008; Sakai et al., 2011; Servidio, 2014), so the size of the study area alone is
403   unlikely to account for the large number of transient whales identified during the study. Indeed, the
404   individuals recaptured between Madeira and the Canary Islands 590.3 km apart (Servidio, 2014)
405   appears not to be an isolated event (Alves et al., 2019)

406   The factors that influence residency patterns of pilot whales and their movements among the islands
407   and archipelagos are poorly understood. They may not be determined by a single factor but instead
408   could be a result of the combination of several and simultaneous variables (McLoughlin &
409   Ferguson, 2000), such as the availability and distribution of resources (food, mates, and shelter; e.g.
410   Abend & Smith, 1999; Alves et al., 2013; De Stephanis, García-Tíscar, et al., 2008).

411   Oceanic islands can be considered generators of biological patchiness (Barton et al., 2000). This
412   and the highly dynamic oceanic ecosystem, in contrast to more productive coastal and inshore areas
413   (Arístegui et al., 2006; Barton et al., 1998), might be responsible for attracting SFPWs from
414   neighbouring ocean regions to the Canary Islands to use the area as a foraging ground on a
415   temporary basis. Conversely, they may also force whales either to travel between familiar and
416   already established feeding sites or to explore larger areas and to venture outside their typical range
417   in search of new food patches, leading to between-island and more pelagic movements. At the same
418   time, the presence of this species year-round, with individuals characterised by a high fidelity to the
419   Canary Islands, indicates that some parts of the archipelago might also offer enough resources to
420   hold a resident population of SFPW.

421   In the western part of the archipelago, the islands offer protection from the prevailing currents,
422   whilst the effect of the anticyclonic gyre, the upwelling filaments and the general pattern of ocean
423   currents increase nutrients and promote organism retention and thus potentially increase the base of
424   the food web supporting increased biodiversity quite close to the coast (Arístegui et al., 2006;
425   Arístegui et al., 1989; Arístegui et al., 1997; Hernández-León, Gomez, & Arístegui, 2007). These
426   deep, productive, and sheltered waters close to the coast thus make these areas especially suitable
427   for raising calves and feeding able to support "resident" insular populations but also visiting
428   "transients". Many movements of the "resident" animals seen in Tenerife were also observed

429 outside their estimated core ranges, with multiple inter-island movements to and from La Gomera

430 and, in some cases, Gran Canaria. Whales were observed to travel repeatedly back and forth

431 between these areas, indicating that these movements were likely ranging rather than dispersal.

432 The eastern islands, conversely, which were visited almost exclusively by "transient" SFPWs in

433 large groups, are characterised by wider continental shelves, unsheltered waters generally open to

434 the effects of the main northerly currents and several mesoscale physical features. It can be

435 speculated that these habitats, including Lanzarote and Fuerteventura, may provide only temporary

436 or less abundant or available prey resources that cannot support resident populations and may

437 therefore be visited infrequently.

438 Different ecological requirements may be responsible for differences in habitat use and for the

439 development of different diving and feeding strategies (Aguilar Soto et al., 2008; Baird, Borsani,

440 Hanson, & Tyack, 2002; Baird et al., 2006; Watwood, Miller, Johnson, Madsen, & Tyack, 2006).

441 Species that are members of the same ecological guild with similar diets may use particular

442 resources in different ways or, more generally, exploit more or fewer resource types, by having a

443 wide or narrow niche range, respectively (generalists or specialists) (Whitehead, 2003), thereby

444 avoiding competition for resources. Niche separation and geographic segregation have been

445 proposed in beaked whale species with similar dietary preferences (MacLeod, Santos, & Pierce,

446 2003). Differences in foraging tactics and therefore in targeted resources at depth have been

447 hypothesised as explaining the spatial segregation of the resident populations of short-finned pilot

448 whales in Tenerife and Blainville's beaked whales in El Hierro (Aguilar de Soto, 2006a). SFPWs

449 seem to feed on prey with more muscle mass rather than on less mobile prey with lower individual

450 caloric value, as do beaked whales (Aguilar de Soto, 2006b). In Tenerife, although there is a high

451 cetacean biodiversity in terms of the number of species found, species other than SFPWs occur only

452 occasionally or in confined areas (Carrillo et al., 2010; SECAC, unpubl data) with almost no

453 overlap with the core range of SFPWs.

454 Ranging behaviour is believed to influence cetacean social structure by limiting the number of

455 potential interactions of each individual to those animals that share analogous ranges (Lusseau et

456 al., 2006). Even though southwest Tenerife represents the area of greatest usage for all the most

457 frequently seen SFPW in the Canary Islands, the "residents" were here often observed (32% of the

458 sightings) interacting with "occasional" and "transient" individuals, which suggests that they might

459 be sharing extensive areas of their ranges.

460   SFPW social structure is believed to be characterised by long term, stable social bonds (Alves et al.,

461   2013; Mahaffy et al., 2015). The similarity in ranging patterns of individuals within the resident

462   groups and their multiple interactions may indicate that these individuals comprise a social

463   community (individuals with long-term site fidelity, nearly all in association with each other; Urian,

464   Hofmann, Wells, & Read, 2009; Whitehead, 2008), but the hypothesis that the common ranges

465   simply result from aggregative behaviour as a response to higher prey availability cannot be ruled

466   out. Although it is impossible to determine if breeding actually takes place during these encounters

467   in the southwest Tenerife, resident SFPWs do not seem to constitute a closed and isolated unit,

468   because they often interact with other animals and share extensive areas of their ranges with non-

469   resident whales. Rather, it seems more likely that there is genetic interchange among whales with

470   different group residency patterns preventing genetic divergence of geographic-based populations,

471   in accordance with results found in Madeira (Alves et al., 2013).

472   Seasonal fluctuation of group size has been described for both short- and long-finned pilot whales

473   (Alves et al., 2013; Cañadas & Sagarminaga, 2000; De Stephanis, Verborgh, et al., 2008; Felleman,

474   Heimlich-Boran, & Osborne, 1991), and can be related to breeding behaviour, with sub-groups

475   regrouping to mate (De Stephanis, Verborgh, et al., 2008). Carrillo et al. (2010) identified Tenerife

476   as an important calving ground for the SFPW, based on the year-round presence of neonates in the

477   area, with a higher frequency between June and October. The seasons when larger group sizes were

478   detected correspond to mating seasons observed in Tenerife by Heimlich-Boran (1993). In this

479   study, in Tenerife a higher frequency of neonates in groups (83%) was recorded during summer and

480   autumn. The gestation period has been estimated for this species to last 14.9 months (Kasuya &

481   Marsh, 1984), so breeding likely occurs mostly during the warmer months, when a high proportion

482   of "transient" and "occasional" whales enter the archipelago and mix with the resident population,

483   forming larger groups of adults of both sexes. Although sex differentiation in this study was based

484   only on qualitative assessment and not supported by genetic studies, observations showed no

485   evidence that sex influenced movement patterns or core range size. In most cases, mixed sex

486   groups, including groups with calves, travelled the greatest distances between the islands providing

487   opportunities for animals associated with different islands to mix (at least among Tenerife, La

488   Gomera and Gran Canaria). Thus, males would have ready access to potential mates and this may

489   explain the lack of evidence for males moving more than females.

490   The southwestern waters of Tenerife, where most of the resident individuals spend most of their

491   time and which results indicate are important for feeding and calving, is also the area with the

492   greatest exposure to human activities that pose a potential risk to SFPWs.

493   As a result of its climatic and oceanographic characteristics, with warm temperatures and calm and

494   productive waters year-round (Arístegui et al., 1994; Barton et al., 2000), the southwestern coast of

495   Tenerife has become a highly developed urban area. Large-scale coastal developments, a growing

496   number of marinas and other coastal infrastructure have been direct consequences of the steadily

497   increasing tourism to this area. Moreover, the majority of the artisanal fisheries of the island operates

498   in the same waters as recreational activities and where boat and ferry traffic are concentrated. The

499   high predictability of observing SFPW in this area has led to this species becoming the main target

500   of a prospering whale-watching industry (in 2008, there were 37 vessels licensed, 625,000 visitors,

501   generating 19.8 million euro of direct gross income; Elejabeita & Urquiola, 2009). It is also one of

502   the species most affected by ship-strikes (Arbelo, 2007; Carrillo & Ritter, 2010; De Stephanis &

503   Urquiola, 2006), making the SFPW the species under most pressure from anthropogenic activity in

504   the archipelago. The importance of southwestern Tenerife waters for resident SFPWs combined with

505   the multiple and high pressure human activities there, makes this a priority area for conservation

506   assessment. The social structure of this population and how this may affect its vulnerability is the

507   subject of another study (Servidio et al, in prep), which will also provide important information for

508   management bodies to take into account when considering mitigation strategies.

509   More widely, the new information presented here can be used to support a more complete

510   assessment of the status of short-finned pilot whale population(s) throughout the entire Canary

511   Islands archipelago. Specifically, this study has established the first and necessary scientific basis

512   required for this species for criterion D1C4 (Range and Distribution pattern) established by OSPAR

513   (OSPAR, 2011) to design and implement an Action Plan with the aim of contributing to Good

514   Environmental Status (GES) of the marine habitat by 2020, as required by the Marine Strategy

515   Framework Directive (MSFD –Directive 2008/56/EC). In this context, the MISTIC SEAS I and II

516   projects (11.0661/2015/712629/SUB/ENV.C2 and 11.0661/2017/750679/SUB/ENV.C2), initiated

517   in 2015 in the Macaronesia Northeast Atlantic sub-region, had the objective to establish a common

518   roadmap to monitor the status of marine mammals, sea turtles, and seabirds and to obtain baseline

519   information for better coordination and implementation of the MSFD. In the Canary Islands the

520   short-finned pilot whales of Tenerife and La Gomera were treated as a management unit (animals of

521   a particular species in a geographical area to which management of human activities is applied)

522   within the archipelago, and were considered a very good potential indicator of GES because of the

523   long and comprehensive data series generated by this study. As a result of the new information on

524   the spatial and temporal distribution of "transients" and island-associated animals highlighted by

525   this study, two Management Units for short-finned pilot whales were identified in the Canary

526   Islands, namely: I – all short-finned pilot whales using coastal waters of the Canary archipelago

527 (transients, occasional visitors and island-associated animals); II – island-associated animals of

528 Tenerife and La Gomera. Thus, it will be possible to monitor the range and distribution of transients

529 using the area as well as island-associated animals, possibly better focus and differentiate pressures

530 impacting the two MUs, and understand the contribution of local factors as drivers of changes in

531 site fidelity.

532 We conclude that different populations of pilot whales seem to be simultaneously present in the

533 Canary Islands. There is a SFPW resident population with a strong site-fidelity to multiple core

534 areas that are characterised by sufficient resources to support its year-round presence. Conversely,

535 there are "transient" animals which, probably driven by inter- and intraspecific competition may

536 travel long distances and may use the archipelago as part of a larger range, within which areas are

537 used temporarily for resting-mating-feeding. The resident population does not seem to be isolated;

538 rather "resident" individuals share ranges and come into contact with other animals from within and

539 outside the archipelago.

540 Further studies supported by genetic analysis and telemetry studies are needed to verify the

541 differences (genetic and behavioural) among individuals with different residency patterns in the

542 Canary Islands. This additional information would strengthen the scientific basis for conservation

543 assessments of SFPWs and allow any management actions to be most effectively focussed.

544

545   **COMPLIANCE WITH ETHICAL STANDARDS**

546   **Conflict of interest:** The authors declare they have no conflict of interest.

547   **Ethical approval:** All applicable international, national, and/or institutional guidelines for the care

548   and use of animals were followed and all necessary approvals were obtained. The official research

549   permission was given by the Ministry of Agriculture, Food and Environment.

563

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Table 1 Total km travelled and surveyed on effort per island, with on and off effort sightings of short-finned pilot whale (SFPW, *Globicephala macrorhynchus*)

Island	At sea km	Day	On effort km	Hr:min	Sightings on effort	off effort
Gran Canaria	42,375.69	1,113	29,529.86	2,278:41	27	25
Fuerteventura	17,672.51	145	10,145.68	694:11	14	12
Tenerife	18,667.42	317	9,976.02	819:40	621	238
La Gomera	12,793.86	162	9,853.16	776:40	69	38
Lanzarote	14,236.27	146	8,190.53	648:46	23	10
La Palma	2,875.69	45	2,084.02	146:10	3	1
El Hierro	1,073.46	18	841.10	72:47	0	0
Total	**109,694.89**	**1,655**	**70,620.37**	**5,436:55**	**757**	**324**

Table 2 Photo-identified SFPWs: picture quality 3 and 4; distinctiveness 3 and 4. Age classes: A=adults, Indet=indeterminates, J=juveniles, C=calves; and N=neonates

Island	Total	A	Indet	J	C	N
Tenerife	760	588	123	35	12	2
La Gomera	271	212	46	11	2	0
Lanzarote-Fuerteventura	282	161	112	7	2	0
Gran Canaria	190	146	31	9	3	1
La Palma	10	9	1	0	0	0
Total	1,310	952	289	57	9	3

Table 3. Number of SFPWs in different residency categories seen in the whole archipelago (top row) and the number in each category seen around each island. Individuals in each category may be included in more than one island because of movement between islands.

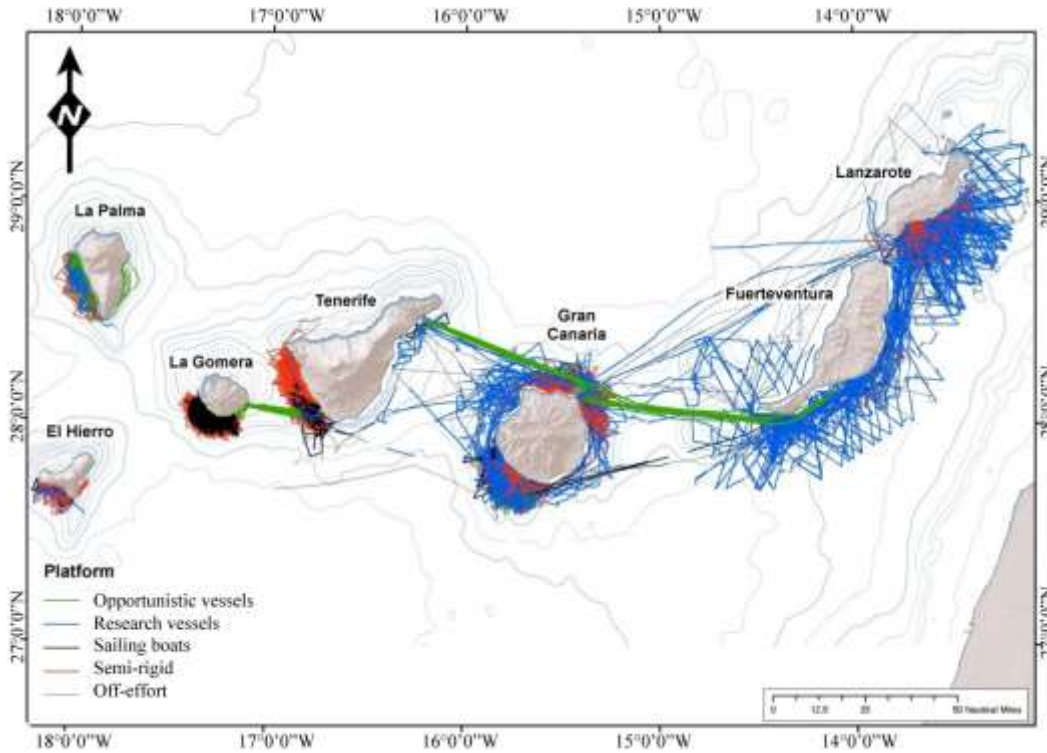| Island	Core Resident	Resident	Occasional	Transient	Tot Ind
Canary Archipelago	50	255	156	780	1,241
Tenerife	50	246	128	287	711
La Gomera	14	88	56	100	258
Lanzarote Fuerteventura	0	0	10	263	273
Gran Canaria	3	22	14	138	177

816 **Table 4** Diagnostics and estimated parameters for the best fitting models of LIRs applied to
817 all individual SFPWs identified in the Canary Islands (1999-2012), and in southwestern
818 Tenerife (2004-2009). Models were also applied to Tenerife and La Gomera to test how
819 SFPWs move between these two islands. td = time lag (τ); a1,a2,a3 = parameters of the
820 models. Values inside the brackets indicate the standard errors of the parameters calculated
821 using bootstrap replications

822

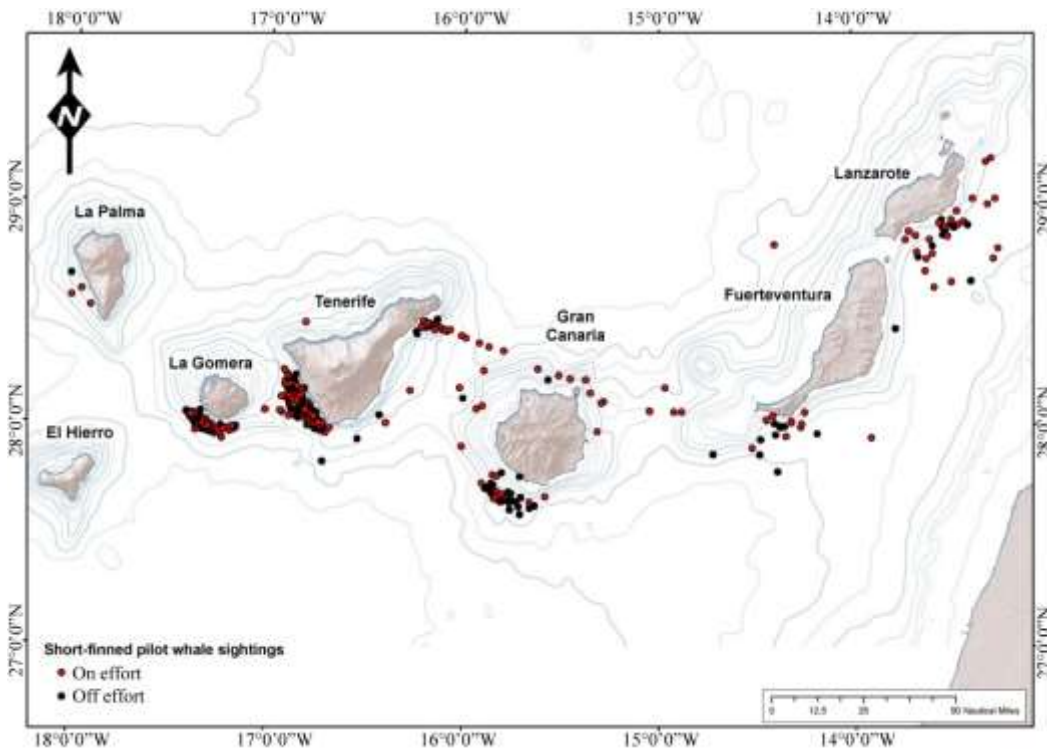| Dataset	Model		Parameters		
			a1	a2	a3
Canary Islands	Emigration+ Re-immigration	$(1/a1)*((1/a3)+(1/a2)*\exp((1/a3+1/a2)*td))/(1/a3+1/a2)$	253.84 (9.93)	530.96 (23.82)	4086.95 (941.43)
Southwest Tenerife	Emigration/ Mortality	$a2*\exp(-a1*td)$	0.0004808 (7.1123e-005)	0.00358 (0.00019)	
		$(1/a1)*\exp(-td/a2)$	279.45 (14.47)	2048.60 (268.28)	
From Tenerife to La Gomera	Fully Mixed	$1/a1$	2718.52 (361.05)		
From La Gomera to Tenerife	Fully Mixed	$1/a1$	1686.18 (221.54)		

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826 **Fig 1** Transects surveyed (1999 - 2012) on board different vessel types: semi-rigid inflatable
827 boats (red), dedicated motor boats (blue), sailing boats (black), and opportunist vessels such
828 as whale-watching boats and ferries (green). Off-effort track-lines are indicated in grey.
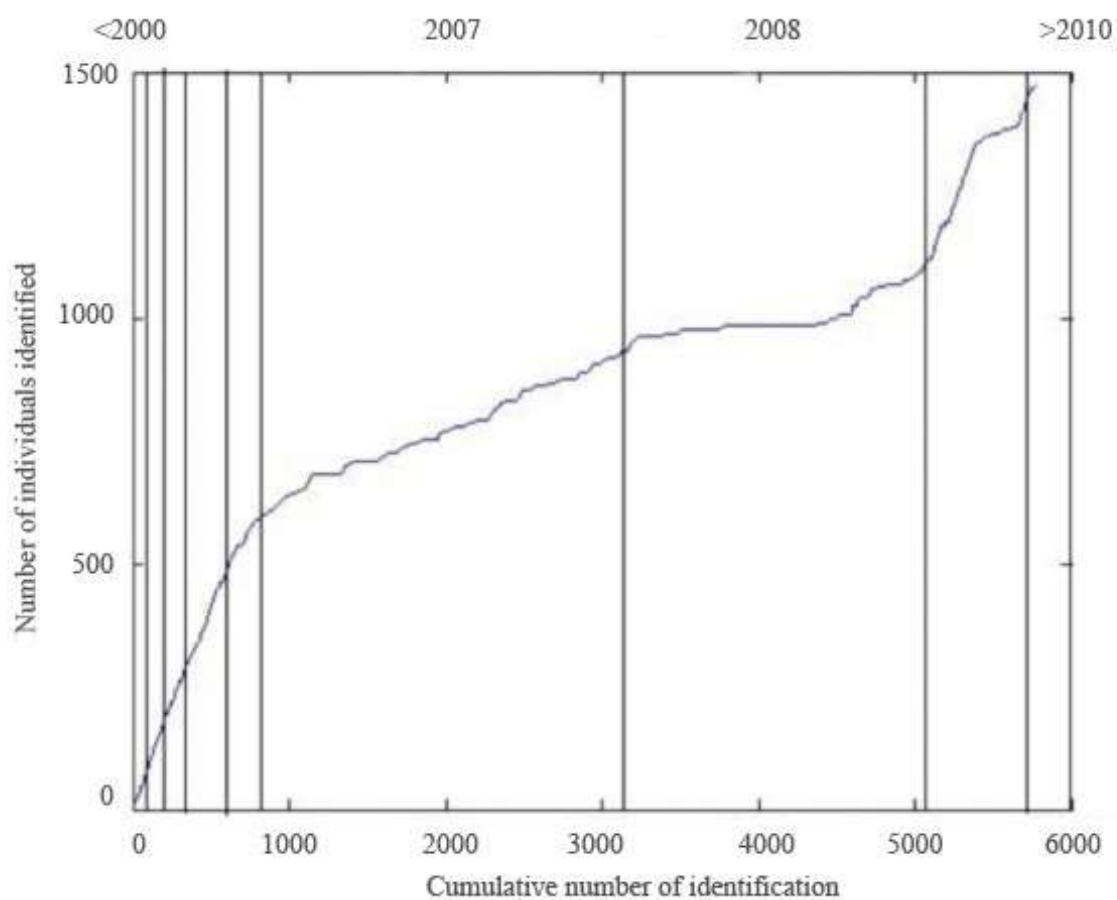
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831 **Fig 2** Short-finned pilot whale (SFPW, *Globicephala macrorhynchus*) sightings (1999-2012)
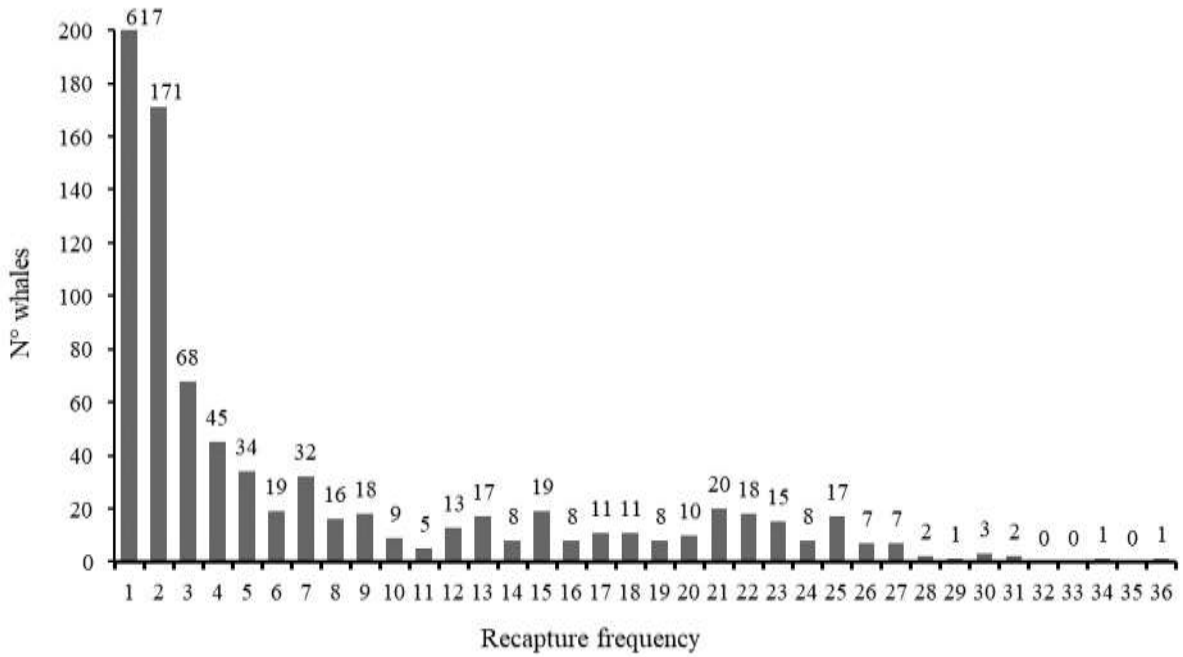
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835 **Fig 3** Discovery curve showing the number of new well-marked SFPWs identified each day.

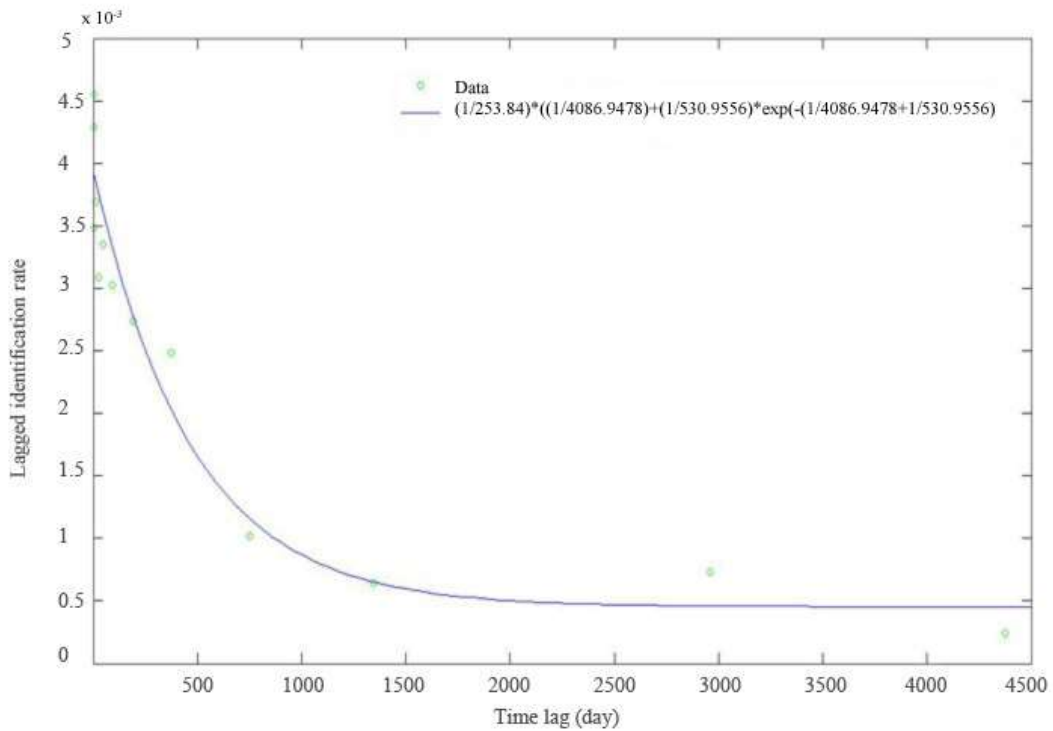836 Vertical lines divide years

837

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839

840 **Fig 4** Frequency histogram of the number of times that uniquely marked SFPWs were
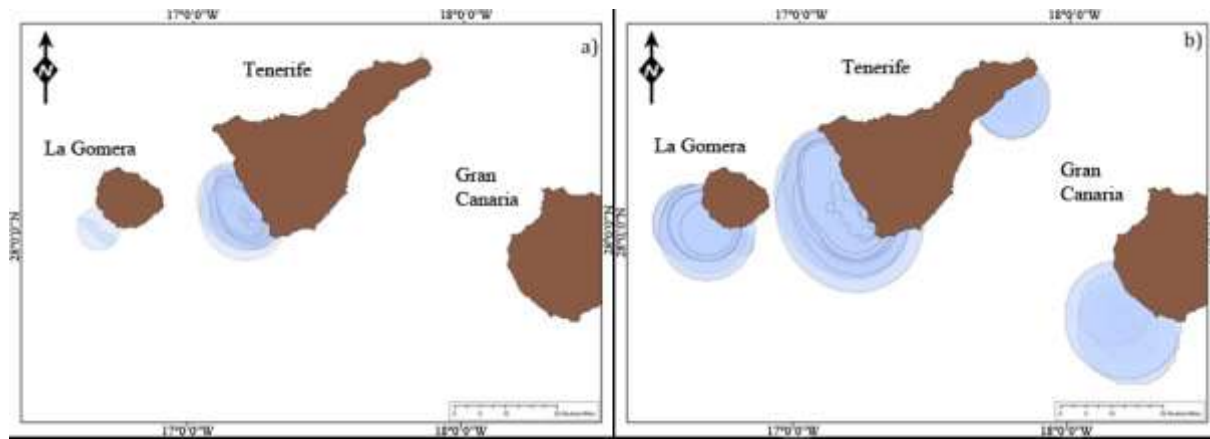841 captured in the Canary Islands

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844 **Fig 5** LIRs for all individual SFPWs identified. Data points are represented as circles and the
845 best fitting model (Emigration + Re-immigration) is displayed as a line

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847

848 **Fig 6a-b** Ranging patterns of the 193 well-marked, adult and indeterminate SFPWs sighted at
849 least ten times, estimated by fixed kernel a) at 50% UD and b) at 95% UD

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