

Large-scale movements of common bottlenose dolphins in the NE Atlantic: dolphins with an international courtyard

Ana Dinis^{Corresp., 1, 2}, Carlota Molina^{2, 3}, Marta Tobena⁴, Annalisa Sambolino^{1, 2}, Karin Hartman⁵, Marc Fernandez^{1, 6}, Sara Magalhães⁷, Rui Peres dos Santos⁸, Fabian Ritter⁹, Vidal Martín¹⁰, Natacha Aguilar de Soto¹¹, Filipe Alves^{1, 2}

¹ MARE-Marine and Environmental Sciences, Funchal, Madeira, Portugal

² OOM - Oceanic Observatory of Madeira, Funchal, Madeira, Portugal

³ Department of Animal Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Catalonia, Spain

⁴ Centro I&D Okeanos, University of Azores, Horta, Azores, Portugal

⁵ Risso's Dolphin Research Center, Nova Atlantis Foundation, Pico, Azores, Portugal

⁶ cE3c - Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group, University of Azores, Ponta Delgada, Azores, Portugal

⁷ Mar Ilimitado, Sagres, Portugal

⁸ Futurismo, Pico, Azores, Portugal

⁹ MEER e.V, Berlin, Germany

¹⁰ SECAC Society for the Study of Cetaceans in the Canary Archipelago, Lanzarote, Canary Island, Spain

¹¹ BIOECOMAC, Department of Animal Biology, University of La Laguna, Tenerife, Canary Island, Spain

Corresponding Author: Ana Dinis

Email address: ana.dinis@mare-centre.pt

Wide-ranging connectivity patterns of bottlenose dolphins (*Tursiops truncatus*) are generally poorly known worldwide and more so within the oceanic archipelagos of Macaronesia in the NE Atlantic. This study aimed to identify long-range movements between the archipelagos of Macaronesia that lie between 500 and 1500 km apart, and between Madeira archipelago and the Portuguese continental shelf, through the compilation and comparison of bottlenose dolphin's photo-identification catalogues from different archipelagos: one from Madeira (n=363 individuals), two from different areas in the Azores (n=495 and 176), and four from different islands of the Canary Islands (n=182, 110, 142 and 281), summing up 1791 photographs. An additional comparison was made between the Madeira catalogue and one catalogue from Sagres, on the southwest tip of the Iberian Peninsula (n=359). Results showed 26 individual matches, mostly between Madeira and the Canary Islands (n=23), and between Azores and Madeira (n=3). No matches were found between the Canary Islands and the Azores, and between Madeira and Sagres. There was no individuals identified in all three archipelagos. The minimum time recorded between sightings in two different archipelagos (\approx 460 km apart) was 62 days. Association patterns revealed that the individuals moving between archipelagos were connected to resident, migrant and transient individuals in Madeira. The higher number of individuals that were re-sighted between Madeira and the Canary Islands can be

explained by the relative proximity of these two archipelagos. This study shows the first inter-archipelago movements of bottlenose dolphins in the Macaronesia region, emphasizing the high mobility of this species and supporting the high gene flow described for oceanic dolphins inhabiting the North Atlantic. The dynamics of these long-range movements strongly denotes the need to review marine protected areas established for this species in each archipelago, calling for joint resolutions from three autonomous regions belonging to two EU countries.

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7 Aguilar de Soto¹¹, Filipe Alves^{1,2}

8

9 ¹ MARE - Marine and Environmental Sciences, Funchal, Madeira, Portugal

10 ² OOM - Oceanic Observatory of Madeira, Funchal, Madeira, Portugal

11 ³Department of Animal Biology, Ecology and Environmental Sciences, University of Barcelona,
12 Barcelona, Spain

13 ⁴Centro I&D Okeanos, University of Azores, Horta, Azores, Portugal

14 ⁵Nova Atlantis Foundation, Risso's Dolphin Research Center, Pico, Azores, Portugal

15 ⁶cE3c - Centre for Ecology, Evolution and Environmental Changes /Azorean Biodiversity Group
16 and University of Azores, Azores, Portugal

17 ⁷Mar Ilimitado, Sagres, Portugal

18 ⁸Futurismo, Pico, Portugal

19 ⁹MEER e.V., Berlin, Germany

20 ¹⁰SECAC Society for the Study of Cetaceans in the Canary Archipelago, Arrecife, Lanzarote,
21 Spain

22 ¹¹BIOECOMAC, Department of Animal Biology, University of La Laguna, Tenerife, Spain

23

24 Corresponding Author:

25 Ana Dinis

26 Ed. Madeira Tecnopolo, Caminho da Penteada, Funchal, 9020-105, Madeira, Portugal

27 Email address: ana.dinis@mare-centre.pt

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29 Abstract

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31 poorly known worldwide and more so within the oceanic archipelagos of Macaronesia in the NE
32 Atlantic. This study aimed to identify long-range movements between the archipelagos of
33 Macaronesia that lie between 500 and 1500 km apart, and between Madeira archipelago and the
34 Portuguese continental shelf, through the compilation and comparison of bottlenose dolphin's
35 photo-identification catalogues from different archipelagos: one from Madeira (n=363
36 individuals), two from different areas in the Azores (n=495 and 176), and four from different
37 islands of the Canary Islands (n=182, 110, 142 and 281), summing up 1791 photographs. An
38 additional comparison was made between the Madeira catalogue and one catalogue from Sagres,
39 on the southwest tip of the Iberian Peninsula (n=359). Results showed 26 individual matches,

40 mostly between Madeira and the Canary Islands (n=23), and between Azores and Madeira (n=3).
41 No matches were found between the Canary Islands and the Azores, and between Madeira and
42 Sagres. There was no individuals identified in all three archipelagos. The minimum time
43 recorded between sightings in two different archipelagos (≈ 460 km apart) was 62 days.
44 Association patterns revealed that the individuals moving between archipelagos were connected
45 to resident, migrant and transient individuals in Madeira. The higher number of individuals that
46 were re-sighted between Madeira and the Canary Islands can be explained by the relative
47 proximity of these two archipelagos. This study shows the first inter-archipelago movements of
48 bottlenose dolphins in the Macaronesia region, emphasizing the high mobility of this species and
49 supporting the high gene flow described for oceanic dolphins inhabiting the North Atlantic. The
50 dynamics of these long-range movements strongly denotes the need to review marine protected
51 areas established for this species in each archipelago, calling for joint resolutions from three
52 autonomous regions belonging to two EU countries.

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55 Introduction

56 The common bottlenose dolphin *Tursiops truncatus*, (hereafter “bottlenose dolphin”), like other
57 cetaceans, faces a variety of threats such as water pollution, incidental capture (by-catch) or
58 vessel collisions (Wells & Scott, 2018). Coastal and pelagic variations or ecotypes of bottlenose
59 dolphins have been described based on morphological, ecological and genetic differences
60 (Oudejans et al., 2015). The well-studied populations of coastal bottlenose dolphins exhibit a
61 variety of horizontal movements, including seasonal migrations, year-around home ranges,
62 periodic residency, and a combination of occasional long-range movements and repeated local
63 residency (Shane, Wells & Würsig, 1986; Wells & Scott, 2018). However, much less is known
64 about the ranging patterns of pelagic bottlenose dolphins (Wells & Scott, 2018). It is crucial to
65 gain a better understanding of the ranging patterns of this species in order to establish suitable
66 conservation measures. Apart from small scale movements of bottlenose dolphin studied in
67 greater depth (e.g. Reynolds, Wells and Eide., 2000; Silva et al., 2008; Tobeña et al., 2014;
68 Hwang et al., 2014; Dinis et al., 2016), information from long-distance and inter-archipelagos
69 movements is scarce. Insufficient information on long-distance movements may result in higher
70 emphasis on residency (Bearzi, Bonizzoni & Gonzalvo, 2011), when in fact individuals may
71 leave the study area more frequently than initially thought. Previous studies of pelagic bottlenose
72 dolphin populations in the NE Atlantic area suggested that these populations have a high gene
73 flow and are genetically less differentiated (Querouil et al., 2007; Louis et al., 2014).
74 Additionally, different residency patterns and individual movements within each archipelago
75 were identified for the Azores (Silva et al., 2008), the Canary Islands (Tobeña et al., 2014) and
76 Madeira (Dinis et al., 2016), with just a portion of the individuals being classified as residents.
77 These results indicate large individual home ranges, but there is no evidence of the connectivity
78 of the populations between these oceanic archipelagos. A recent photo-identification study
79 demonstrated the connectivity of pilot whales within the Macaronesia biogeographical region

80 (Alves et al., 2019), also highlighting the importance of such studies for conservation. Hence, it
81 can be speculated that other highly mobile species like bottlenose dolphin can also perform long-
82 range movements in this region (Silva et al., 2008; Dinis et al., 2016). We investigated for the
83 first time horizontal large-scale movements of this species between the archipelagos of Madeira,
84 Azores and the Canary Islands, i.e. within the biogeographical region of Macaronesia, and with
85 the Portuguese continental shelf, covering an area of more than 1600 000 km². The present study
86 aims to the better understanding of the bottlenose dolphin connectivity among these remote
87 oceanic archipelagos, and to help in this species' future conservation and management efforts.

88

89

90 **Materials & Methods**

91

92 STUDY AREA

93 The study area included the oceanic archipelagos of Madeira, Azores and the Canary Islands in
94 the Macaronesia region, plus an adjacent coastal area along the Iberian Peninsula (Fig. 1).
95 Macaronesia consists of island archipelagos located in the Northeast Atlantic Ocean, off the
96 coasts of Europe and West Africa (Almada et al., 2013). It has a unique marine fauna, which has
97 been influenced by West Africa, the Mediterranean Sea and continental western Europe (Floeter
98 et al., 2007; Almada et al., 2013), making this region an ideal habitat for a high number of
99 cetacean species (Pérez-Vallazza et al., 2008; Freitas et al. 2012; Silva et al., 2014; Alves et al.,
100 2018b).

101

102 PHOTO-IDENTIFICATION DATA

103 Dolphin movements were determined through the cross-comparison of photo-identification
104 catalogues held by eight organizations in Portugal and Spain (Table 1). The Madeira catalogue
105 was compiled by OOM and comprised 363 individuals collected between 2004 and 2016, and
106 sighted mainly off the south coast of Madeira. Two catalogues from the Azores were included,
107 one containing 176 individuals from Pico and Faial islands collected between 2003 to 2007
108 compiled by Nova Atlantis Foundation, and a second one with 495 individuals from Pico, Faial,
109 São Miguel and Terceira islands, collected between 2004-2016 compiled through a citizen
110 science platform called MONICET. A third set of raw data from the Azores (Pico and Faial
111 islands), containing 201 photos, from which 42 individuals were identified by OOM, collected
112 by a whale-watching company (Espaco Thalassa), between 2014 and 2016 was added. From the
113 Canary Islands, four catalogues from two institutions and from different islands were used: one
114 from La Gomera with 182 individuals (2004-2015); one from Tenerife with 110 individuals
115 (2014); one from La Palma with 142 individuals (2010-2011 and 2015), all compiled by SECAC
116 and one with 281 individuals (2001-2011), that included photos from La Gomera, El Hierro and
117 La Palma, compiled by BIOECOMAC, using their own data and data from a local NGO (MEER
118 e.V.). The catalogue from Sagres contained 359 individual photographed from 2001 until 2016
119 and was compiled by the whale-watching company Mar Ilimitado.

120

121 PHOTO-IDENTIFICATION PROCEDURES

122 The catalogues were built using different sources, ranging from whale watching operators to
123 research teams and independent photographers and were constructed by creating a dataset of
124 capture histories, using individual information taken by photographs (following Würsig and
125 Jefferson, 1990). Photographs were graded according to their level of focus, contrast, exposure
126 and angle of the dorsal fin; and level of distinctiveness of the individuals was graded according
127 to the number of nicks and notches present in the dorsal fin. Only good quality photos and
128 distinct and very distinct individuals were used in this analysis in order to enhance the reliability
129 of the matches (Urian et al. 2015). Whenever a match was found and confirmed, the same
130 identification number as that of the individual stored in the database was assigned, but, if there
131 were no match, a new identification number was attributed to that individual and it was added to
132 the catalogue as a new individual (Dinis et al. 2016). The matching procedure was conducted
133 through the comparison of natural markings like nicks and notches on the dorsal fin, and the
134 shape of the fin (Würsig and Würsig, 1977). In all the catalogues, with the exception of the one
135 made by BIOECOMAC, the comparison was conducted by the same researcher by naked eye,
136 and confirmed by a second experienced researcher. If doubts persisted, a third experienced
137 researcher would double-check. In the catalogue compiled by BIOECOMAC, dorsal fin images
138 were entered into a digital database using the software Darwin 2.0 (Eckerd College), a trailing
139 edge contour was extracted, which was identifiable from both sides (Auger-Méthé and
140 Whitehead, 2007), and the software was used to assist the matching of individual dolphins
141 (Tobeña et al. 2014).

142

143 MACARONESIA CATALOGUE: PHOTO-IDENTIFICATION ANALYSIS

144 The Macaronesia catalogue was compiled following the procedures described above, by naked
145 eye, always by the same researcher. When a match was found, a new identification code (the
146 Macaronesia identification code) was created, both pictures of the dolphin were added to the
147 catalogue and both locations were indicated in the capture history dataset. Only dolphins seen in
148 two or more locations were included in this catalogue and only matches with 100% certainty
149 were used.

150

151 ASSOCIATIONS

152 The study of the association patterns was made for Madeira archipelago data, including the
153 individuals that were seen in more than one archipelago. It aimed to investigate the residency
154 pattern of these individuals attributed previously in Madeira and their connectedness with the
155 other dolphins identified in this archipelago. Individuals from the Madeira catalogue, seen in
156 association with other individuals between 2004 and 2016 were used in this analysis.
157 Associations between individuals were analyzed according to residency patterns established for
158 this archipelago (Dinis et al., 2016): individuals that were sighted during three seasons in one
159 year and in more than two consecutive years were considered residents; individuals that were

160 seen only once were considered transients, and the remain individuals were categorized as
161 migrants. A social network diagram was created using NetDraw 2.160 (Borgatti, 2002) to
162 visualize individual association.

163

164

165 **Results**

166

167 PHOTO-IDENTIFICATION ANALYSIS

168 There were 26 dolphins with matches: 23 between Madeira and Canary Islands (≈ 500 Km apart),
169 and three individuals between the Azores and Madeira (≈ 1000 Km apart). No matches between
170 the Canary Islands and the Azores were found. Likewise, none of the individuals were seen in all
171 three archipelagos, nor between Madeira and Sagres (Fig.2). The 23 matches between Madeira
172 and the Canary Islands (occurred on three of the four studied islands in the Canary Islands,
173 mainly with El Hierro ($n=6$, ≈ 570 Km) and La Palma ($n=14$, ≈ 460 Km) (S1 Table). The results
174 also showed back and forth movements made by Tt_MAC_8 and Tt_MAC_12, between Madeira
175 and the Canary Islands., representing a round-trip of approximately 920 Km (Fig.3). Moreover,
176 two individuals were seen within the Canary Islands, and then off Madeira several years later:
177 Tt_MAC_3 was sighted seven times intermittently off El Hierro in 2004, 2008, 2009, then was
178 photographed off La Palma in 2010, and sighted two times off Madeira in 2014 and in 2016.
179 Tt_MAC_4 was first seen off El Hierro in 2009, then sighted off the neighboring island of La
180 Gomera in 2010, was observed again in El Hierro in 2010 and 2011, and eventually sighted off
181 Madeira in 2015 (S1 Table). Four individuals (Tt_MAC_7, 11, 13 and 17) were sighted off La
182 Palma on the same date (on 24th May 2011) and then sighted together off Madeira on 13th
183 August 2011 with less than 3 months between re-sightings (Fig.4). Tt_MAC_9, 12, 14 and 15
184 were sighted in the same time frame and in the same locations (Table S1).

185 The three individuals seen first in the Azores and last off Madeira were sighted three
186 (Tt_MAC_24), nine (Tt_MAC_25) and 10 (Tt_MAC_26) years apart. Tt_MAC_24 was seen in
187 Pico island, which represents a distance to Madeira of approximately 1200 Km, while
188 Tt_MAC_25 and 26 were sighted off São Miguel which represents a distance to Madeira of
189 roughly 950 Km. No movements from Madeira to Azores were recorded (Fig.5).

190 Tt_MAC_17 was photographed off La Palma and then off Madeira within 62 days, presenting
191 the minimum time interval that an individual travelled between two archipelagos, covering
192 around 460 Km within this timeframe.

193

194 ASSOCIATIONS

195 The social network diagram (Fig 6) incorporated 332 individual dolphins, catalogued in Madeira
196 archipelago, and presents three clusters grouped by residency patterns. Seventeen dolphins were
197 seen both in the Canary Islands and in Madeira associated with all categories of residency
198 patterns. Two dolphins seen both in Azores and Madeira (Tt_MAC_24 and 25) associated with

199 migrant individuals seen both in Madeira and in the Canary Island (Tt_MAC_3 and 20), and the
200 third (Tt_MAC_26) was seen in association with transient dolphins.

201

202 **Discussion**

203 This study shows that 26 bottlenose dolphins photo-identified off Madeira moved between, at
204 least two Macaronesian archipelagos, demonstrating that this species' population covers wide
205 areas in the NE Atlantic. These 26 individuals correspond to 7.1% of the 363 catalogued
206 dolphins in the Madeira archipelago, similarly to what was found for UK and Irish waters
207 (approximately 6%, Robinson et al., 2012). Only a few studies described long-distance
208 movements (>1000 km) of bottlenose dolphin around the world (e.g. Wood, 1998; Wells et al.,
209 1999; Robinson et al., 2012), and none covered these three archipelagos of the Macaronesia
210 region so far, thus this study expands our knowledge of the species in this area of the NE
211 Atlantic. Previous examples of wider-scale movements based on photo-identified bottlenose
212 dolphins come from Argentina (Würsig, 1978), Ireland (O'Brien et al., 2009), Mediterranean Sea
213 (Gnone et al., 2011) and eastern North Pacific Ocean (Defran et al., 2006; Hwang et al., 2014).
214 For example, off Argentina, one individual travelled 300 km, while off the coast of Ireland, an
215 individual travelled a distance as large as 650 km. The distances reported here for the individuals
216 that moved between Madeira and the Canary Islands are comparable to these ones, and if we
217 consider the round-trip, the distance travelled is even larger, similar to the 965 Km covered by a
218 dolphin that travelled from Mexico to the USA, described by Hwang et al. (2014). The distance
219 travelled by Tt_MAC_24 seen off Pico island as well as off Madeira Island, represents a distance
220 of approximately 1200 km, one of the highest distances recorded so far for this species. It comes
221 closer to the 1277 km an individual travelled between UK and Ireland (Robinson et al., 2012).
222 The inshore waters of the oceanic archipelagos within the NE Atlantic waters offer a sheltered
223 place where bottlenose dolphins can feed, when compared to the offshore waters nearby (Silva et
224 al., 2008; Dinis et al., 2016). Possibly, when food resources are scarce, some individuals may
225 travel longer distances to where similar, and more abundant food resources may be available. In
226 less productive habitats such as oceanic waters, animals can be expected to have larger home
227 ranges because there is a need to range further to find sufficient food (Silva et al., 2008; Bräger
228 and Bräger, 2019).

229 The fact that the Madeira archipelago and the Canary Islands share many biogeographic, and
230 likely also oceanographic characteristics (Freitas et al., 2019), might explain the higher number
231 of matches between these two archipelagos. One would also expect that the dolphins prefer to
232 travel these comparably shorter distances because it would imply less effort as compared to the
233 distance between the Azores and the Canaries. The back and forth movements we found
234 demonstrate that at least some of the bottlenose dolphins in Macaronesia have very large home
235 ranges that include more than one archipelago.

236 Although we could not determine the sex of the dolphins seen in more than one archipelago, for
237 male bottlenose dolphins, long-distance movements could also serve to get access to receptive
238 females outside their own population. I.e., young adult males could be driven to seek for females,

239 as described for Indo-pacific bottlenose dolphin (*Tursiops aduncus*) in Shark Bay, Australia
240 (Connor, Smolker & Richards, 1992), and thereby also increasing gene flow between
241 populations. In this way, population viability could be improved and genetic differences within
242 the NE Atlantic bottlenose dolphin populations may perhaps decrease, as confirmed by a study
243 that compared individuals from the Madeira and Azores archipelagos (Querouil et al., 2007).
244 Tobeña and colleagues (2014), in a study reporting inter-islands movements within the Canary
245 Islands, described two individuals that were seen over a long period of time (three and four
246 years). These two individuals are Tt_MAC_3 and 4 in this study, suggesting that even
247 individuals that were considered resident in an area or having a high degree of site fidelity may
248 undertake long-range movements from time to time. Another cross-Macaronesian study (Alves et
249 al., 2018a) reported a group of five socially related short-finned pilot whales with strong site
250 fidelity to Madeira which made a round trip to the Azores archipelago, covering approximately
251 2000 km, highlighting the importance of caution when assigning residency patterns to smaller
252 areas in oceanic waters. Similarly, in the study of long-range movements of bottlenose dolphins
253 (Robinson et al., 2012), the far ranging individuals had been considered to belong to discrete
254 resident populations in the UK and Ireland.

255 Four individuals (Tt_MAC 7, 11, 13, 17) were seen together off La Palma and were encountered
256 thereafter in Madeira (Fig.4). Our results also showed that other Macaronesian individuals
257 (Tt_MAC_9, 12, 14 and 15) were documented during the same period in both archipelagos,
258 indicating stable social association, which may persist during, or even favor, long-range oceanic
259 journeys.

260 Bottlenose dolphins' social structure vary between locations, and even individuals from the same
261 community may behave differently (Gowans, 2019; Genov et al. 2019). Our network analysis
262 showed that the Macaronesian bottlenose dolphins were seen with transients, migrants and
263 resident dolphins, including one resident that has a high level of centrality (Dinis et al., 2016).
264 This indicates that some far-ranging dolphins are connected to individuals that play a central role
265 for connectivity of local network as social brokers (Lusseau & Newman, 2004). Individuals
266 exhibiting extended home ranges can have a fundamental role, contributing to a genetic
267 variability in oceanic dolphin communities, which otherwise would be genetically isolated
268 (Louis et al., 2014).

269 The minimum period of time between the re-captures in different archipelagos (Canary Islands to
270 Madeira) was 62 days. Satellite-monitored movements of an individual bottlenose dolphin off
271 Florida showed that the dolphin moved 581 km in 25 days (Mate et al., 1995). In Japan, one
272 tagged bottlenose dolphin travelled about 604 km in 18 days (Tanaka, 1987). Therefore, the time
273 period documented in this study is comparatively long, but the actual time it took the dolphins to
274 cover the distance from one archipelago to the other remains unknown. In one study using
275 satellite telemetry (Klatsky, Wells & Sweeney, 2007), the authors determined a mean travel
276 distance of 28.3 Km/day for three offshore bottlenose dolphins, which suggests that the dolphins
277 reported here could have covered the distance within a time period well below 62 days.

278 Alternatively, they may also have travelled a (much) longer distance within those 2 months.

279 The fact that we did not find any match between the Madeira archipelago and the Portuguese
280 continental shelf should not exclude the assumption that some individuals may undertake these
281 even longer trips. A previous study on bottlenose dolphin populations of the NE Atlantic (Louis
282 et al., 2014) found no genetic structure between the Azores archipelago and individuals from
283 several parts of the NE Atlantic, including the shelf-edge.

284 Connectivity studies can be a monitoring tool when assessing ranging patterns over wider areas,
285 as has been regularly made for large whales (e.g. Robbins et al., 2011; Bertulli et al., 2013;
286 Carpinelli et al., 2014). We now know that at least some bottlenose dolphins perform extreme
287 mobility throughout the Macaronesia region. This has multiple implications for conservation and
288 management efforts designed for this species: Firstly, management units may not be separable
289 and their connectivity must be taken into account e.g. when establishing marine protected areas
290 (MPAs). Connected populations will have to be considered coherently within conservation
291 frameworks such as the European Union Habitats & Species Directive (HD). Bottlenose dolphins
292 inhabiting Macaronesia waters are, as in other places, subject to many threats like fisheries
293 interaction (by-catch), overfishing, pollution, vessel strikes, stress caused by human recreational
294 activities such as whale-watching and climate change, among others (Reeves, 2018). In the
295 Macaronesia region a large number of marine protected areas were designed to protect bottlenose
296 dolphins, but with different levels of protection (Hoyt, 2011). Some of these are SACs (Special
297 Area of Conservation) designated as part of the Natura 2000 network under the European Union
298 HD. Most marine SACs thereby only cover coastal areas, rather than reaching offshore. While
299 the establishment of MPAs is a step forward to protect bottlenose dolphins (Hoyt, 2011; Silva et
300 al., 2012) in this region, more has to be done in terms of mitigations measures, as many of the
301 established SACs still lack management plans. In the Azores, it has been demonstrated that the
302 established areas are not sufficient mainly because they are not covering the complete home
303 range of the dolphins (Silva et al., 2012). The same applies to the Canary Islands and to Madeira
304 archipelago. Our results confirm that the bottlenose dolphins' home range in Macaronesia
305 includes more than one archipelago and the offshore waters around them. This means that SACs
306 should be expanded to include offshore waters allowing protection measures to be more
307 effective. Such an expansion would have positive side effect for other highly mobile species, like
308 the short-finned pilot whale, that are known to use this area widely, too (Alves et al., 2019).

309

310 **Conclusions**

311 This study provides first evidence of large-scale connectivity of bottlenose dolphin communities
312 between Macaronesia archipelagos, highlighting the strength of combining photo-identification
313 catalogues from different areas, and can be seen as a first step to review the established
314 boundaries of the existing MPAs (SACs) for this species in Macaronesia. This will require a
315 considerable effort, because there are three different autonomous communities (Madeira, Azores
316 and Canary Islands) involved, belonging to two EU member states (Portugal and Spain).
317 Nevertheless, it would correspond to an adaptive and ecosystem-based management approach

318 and serve the coherent protection of the species across borders – all aspects that the EU HD
319 strives to achieve.

320

321

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335 **References**

336 Almada VC, Toledo JF, Brito A, Levy A, Floeter SR, Robalo JI, Martins J, Almada F. Complex
337 origins of the Lusitania biogeographic province and northeastern Atlantic fishes. *Front Biogeogr.*
338 2013;5: 20–28. doi: 10.21425/F5FBG14493

339

340 Alves F, Alessandrini A, Fernandez M, Hartman KL, Dinis A. Home sweet home? Wide-ranging
341 movements of socially stable resident delphinids (*Globicephala macrorhynchus*). *Scientia*
342 *insularum*. 2018a; doi: 10.25145/j.SI.2018.01.004

343

344 Alves F, Alessandrini A, Servidio A, Mendonça AS, Hartman KL, Prieto R, Berrow S,
345 Magalhães S, Steiner L, Santos R, Ferreira R, Marrero J, Ritter F, Dinis A, Martín V, Silva M,
346 Aguilar N. Complex biogeographical patterns support an ecological connectivity network of a
347 large marine predator in the north-east Atlantic. *Divers Distrib.* 2019; 25: 269-284.

348 doi:10.1111/ddi.12848

349

350 Alves F, Ferreira R, Fernandes M, Halicka Z, Dias L, Dinis A. Analysis of occurrence patterns
351 and biological factors of cetaceans based on long-term and fine-scale data from platforms of
352 opportunity: Madeira Island as a case study. *Mar Ecol.* 2018b; 39, 2:

353 e12499.doi.org/10.1111/maec.12499.10.1111/maec.12499

354

355 Auger-Méthé M, Whitehead H. The use of natural markings in studies of long-finned pilot whale
356 (*Globicephala melas*). *Mar Mamm Sci.* 2007; 23, 77–93. [https://doi.org/10.1111/j.1748-](https://doi.org/10.1111/j.1748-7692.2006.00090.x)

357 7692.2006.00090.x

358

- 359 Bearzi G, Bonizzoni S, Gonzalvo J. Mid-distance movements of common bottlenose dolphins in
360 the coastal waters of Greece. *J Ethol.* 2011; 29, 369–374. doi.org/10.1007/s10164-010-0245-x
- 361 Borgatti SP. NetDraw: Graph visualization software. Harvard, MA: Analytic Technologies,
362 2002.
- 363
- 364 Bertulli CG, Rasmussen MH, Tetley MJ. Photo-identification rate and wide scale movement of
365 common minke whales (*Balaenoptera acutorostrata*) in the coastal waters of Faxaflói and
366 Skjálfandi Bays, Iceland. *Journ of Cetacean Res and Manag.* 2013; 13, 39–45.
- 367
- 368 Bräger S, Bräger Z. Movement Patterns of Odontocetes Through Space and Time. In Würsig, B,
369 editor. *Ethology and Behavioral Ecology of Odontocetes.* Springer; 2019.
- 370
- 371 Carpinelli E, Gauffier P, Verborgh P, Airoidi S, David L, Di-Meglio N, Cañadas A, Frantzis A,
372 Rendell L, Lewis T, Mussi B, Pace DS, de Stephanis R. Assessing sperm whale (*Physeter*
373 *macrocephalus*) movements within the western Mediterranean Sea through photo-identification.
374 *Aquat Conserv Mar Freshwat Ecosyst.* 2014; 24(Suppl 1):23–30. doi.org/10.1002/aqc.2446
- 375
- 376 Connor RC, Smolker RA, Richards AF. Two levels of alliance formation among male bottlenose
377 dolphins (*Tursiops* sp.). *Proc Natl Acad Sci U S A.* 1992; 89(3), 987-990. doi:
378 10.1073/pnas.89.3.987
- 379
- 380 Defran RH, Weller DW, Kelly DL, Espinosa MA. Range characteristics of Pacific coast
381 bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. *Mar Mamm Sci.* 1999;
382 15(2), 381-393. doi: 10.1111/j.1748-7692.1999.tb00808.x
- 383
- 384 Dinis A, Alves F, Nicolau C, Ribeiro C, Kaufmann M, Cañadas A, Freitas L. Bottlenose dolphin
385 *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the
386 Madeira Archipelago (North-East Atlantic). *Afr J Ma. Sci.* 2016; 38(2), 151-160.
387 doi.org/10.2989/1814232X.2016.1167780
- 388
- 389 Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WF, Wirtz P, Edwards AJ,
390 Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcón JM, Bowen BW, Bernardi G. Atlantic
391 reef fish biogeography and evolution. *J Biogeogr.* 2018; 35: 22–47. doi.org/10.1111/j.1365-
392 2699.2007.01790.x
- 393
- 394 Freitas L, Dinis A, Nicolau C, Ribeiro C, Alves F. New records of cetacean species for Madeira
395 Archipelago with an updated checklist. *Bol Mus Mun Fun.* 2012; 62(334): 25-43.
- 396
- 397 Freitas R, Romeiras M, Silva L, Cordeiro R, Madeira P, González JA, Wirtz P, Falcón JM, Brito
398 A, Floeter SR, Afonso P, Porteiro F, Vieira-Rodríguez MA, Neto AI, Haroun R, Farminhão

- 399 JNM, Rebelo AC, Baptista L, Melo CS, Martínez A, Núñez J, Berning B, Johnson ME, Ávila
400 SP. Restructuring of the ‘Macaronesia’ biogeographic unit: A marine multi-taxon
401 biogeographical approach. *Sci Rep.* 2019; 9, 15792. doi.org/10.1038/s41598-019-51786-6
402
- 403 Genov T, Centrih T, Kotnjek P, Hace A. Behavioural and temporal partitioning of dolphin social
404 groups in the northern Adriatic Sea. *Mar Biol.* 2019; 166(1), 11.
405
- 406 Gnone G, Bellingeri M, Dhermain F, Dupraz F, Nuti S, Bedocchi, D, Moulins A, Rosso M,
407 Alessi J, McCrea RS, Azzelino A, Airoidi S, Portunato N, Laran S, David L, Di Meglio N,
408 Bonelli P, Montesi G, Trucchi R, Fossa F, Wurtz M. Distribution, abundance, and movements of
409 the bottlenose dolphin (*Tursiops truncatus*) in the Pelagos Sanctuary MPA (north-west
410 Mediterranean Sea). *Aquat Conserv* 2011; 21(4), 372-388.
411
- 412 Gowans S. Grouping Behaviors of Dolphins and Other Toothed Whales. In Würsig B. editor.
413 *Ethology and Behavioral Ecology of Odontocetes.* Springer; 2019.
414
- 415 Hoyt E. *Marine Protected Areas for Whales, Dolphins and Porpoises: A world handbook for
416 cetacean habitat conservation and planning.* 2 nd ed. Routledge; 2011.
417
- 418 Hwang A, Defran R, Bearzi M, Maldini D, Saylan CA, Lang, AR, Dudzik KJ, Guzòn-Zatarain
419 OR, Kelly DL, Weller DW . Coastal range and movements of common bottlenose dolphins off
420 California and Baja California, Mexico. *Bulletin of the Southern California Academy of
421 Sciences.* 2014; vol. 113, no. 1. <https://doi.org/10.3160/0038-3872-113.1.1>
422
- 423 Klatsky, LJ, Wells, RS, Sweeney, JC. Offshore Bottlenose Dolphins (*Tursiops truncatus*):
424 Movement and Dive Behavior Near the Bermuda Pedestal. *J Mammal*, 2007; 88(1): 59-66.
425 doi.org/10.1644/05-MAMM-A-365R1.1
426
- 427 Louis M, Viricel A, Lucas T, Peltier H, Alfonsi E, Berrow S, Brownlow A, Covelo P, Dabin W,
428 Deaville R, de Stephanis R, Gally F, Gauffier P, Penrose R, Silva MA, Guinet C, Simon-Bouhet
429 B. Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-
430 East Atlantic. *Mol Ecol.* 2014; 23 (4), 857-874. doi.org/10.1111/mec.12653
431
- 432 Lusseau D, Newman MEJ. Identifying the role that animals play in their social networks. *Proc R
433 Soc Lond B.* 2004; (Suppl) 271:S477–S481. doi: 10.1098/rsbl.2004.0225
434
- 435 Mate B, Rossbach KA, Nieukirk SL, Wells RS, Irvine AB, Scott MD, Read AJ. Satellite-
436 monitored movements and dive behavior of a bottlenose dolphin (*Tursiops truncatus*) in Tampa
437 Bay, Florida. *Mar Mamm Sci.* 1995; 11:452-463. doi.org/10.1111/j.1748-7692.1995.tb00669.x
438

- 439 O'Brien JM, Berrow SD, Ryan C, McGrath D, O'Connor I, Pesante G, Burrows G, Massett N,
440 Klötzer V, Whooley P. A note on long-distance matches of bottlenose dolphins (*Tursiops*
441 *truncatus*) around the Irish coast using photo-identification. *J Cetacean Res Manag.* 2009; 11(1),
442 71-76
443
- 444 Oudejans MG, Visser F, Englund A, Rogan E, Ingram SN. Evidence for distinct coastal and
445 offshore communities of bottlenose dolphins in the north east Atlantic [published correction
446 appears in *PLoS One.* 2015; 10 (5):e0128259]. doi:10.1371/journal.pone.0122668
447
- 448 Pérez-Vallazza C, Álvarez-Vázquez R, Cardona L, Pintado C, Hernández-Brito J. Cetacean
449 diversity at the west coast of La Palma Island (Canary Islands). *J Mar Biol Assoc UK.* 2008;
450 88(6), 1289-1296. doi: 10.1017/S0025315408001239
451
- 452 Querouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A, Alves F, Matos J, Mendonça
453 D, Hammond PS, Santos RS. High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*)
454 of the North Atlantic. *Conserv Genet.* 2007; 8(6), 1405. doi.org/10.1007/s10592-007-9291-5
455
- 456 Reeves, RR. Conservation In: Perrin WF, Würsig B, Thewissen JGM and Kovacs KM, editors.
457 *Encyclopedia of marine mammals*, third ed. Academic Press; 2018. pp. 361-364.
458
- 459 Reynolds JE, Wells RS, Eide SD. *The bottlenose dolphin: biology and conservation.* Gainesville:
460 University Press of Florida; 2000.
461
- 462 Robbins J, Rosa LD, Allen JM, Mattila DK, Secchi ER, Friedlaender AS, Stevick PT, Nowacek
463 DP, Steel D. Return movement of a humpback whale between the Antarctic Peninsula and
464 American Samoa: A seasonal migration record. *Endanger Species Res* 2011; 13, 117–121. doi:
465 10.3354/esr00328
466
- 467 Robinson KP, O'Brien J, Berrow S, Cheney B, Costa M, Elsfield SM. Discrete or not so discrete:
468 long distance movements by coastal bottlenose dolphins in UK and Irish waters. *J Cetacean Res*
469 *Manag.* 2012; 12(3):365-371
470
- 471 Shane SH, Wells RS, Würsig B. Ecology, behavior and social organization of the bottlenose
472 dolphin: a review. *Mar Mamm Sci* 1986; 2, 34–63. doi:10.1111/j.1748-7692.1986.tb00026.x
473
- 474 Silva MA, Prieto R, Cascão I, Seabra MI, Machete M, Baumgartner MF, Santo RS. Spatial and
475 temporal distribution of cetaceans in the mid-Atlantic waters around the Azores, *Mar Biol Res.*
476 2014; 10:2, 123-137, doi: 10.1080/17451000.2013.793814
477

- 478 Silva MA, Prieto R, Magalhães S, Seabra MI, Machete M, Hammond PS. Incorporating
479 information on bottlenose dolphin distribution into marine protected area design. *Aquat Conserv.*
480 2012; 22(1), 122-133. doi.org/10.1002/aqc.1243.
481
- 482 Silva MA, Prieto R, Magalhães S, Seabra MI, Santos RS, Hammond PS. Ranging patterns of
483 bottlenose dolphins living in oceanic waters: implications for population structure. *Mar Biol.*
484 2008; 156(2), 179.
485
- 486 Tanaka, S. Satellite radio tracking of bottlenose dolphins *Tursiops truncatus*. *Nippon Suisan*
487 *Gakkaishi*.1987; 53:1327–1338. doi.org/10.2331/suisan.53.1327
488
- 489 Tobeña M, Escánez A, Rodríguez Y, López C, Ritter F, Aguilar N. Inter-island movements of
490 common bottlenose dolphins *Tursiops truncatus* among the Canary Islands: online catalogues
491 and implications for conservation and management. *Afr J Ma. Sci.* 2014; 36(1), 137-141. doi:
492 10.2989/1814232X.2013.873738
493
- 494 Urian K, Gorgone A, Read A, Balmer B, Wells RS, Berggren P, Durban J, Eguchi T, Rayment
495 W, Hammond PS. Recommendations for photo-identification methods used in capture-recapture
496 models with cetaceans. *Mar Mamm Sci.* 2015; 31, 298–321. https://doi.org/10.1111/ mms.12141
497
- 498 Wells R, Rhinehart HL, Cunningham-Smith P, Whaley J, Baran M, Koberna C, Costa DP. Long
499 distance offshore movements of bottlenose dolphins. *Mar Mamm Sci.* 1999; 15 (4), 1098-1114.
500 doi.org/10.1111/j.1748-7692.1999.tb00879.x
501
- 502 Wells RS, Scott MD. Common Bottlenose dolphin (*Tursiops truncatus*). In: Perrin WF, Würsig
503 B, Thewissen JGM and Kovacs KM, editors. *Encyclopedia of marine mammals*, third ed.
504 Academic Press; 2018. pp. 361-364.
505
- 506 Wood CJ. Movement of bottlenose dolphins around the south-west coast of Britain. *J Zool.*
507 1998; 246(2), 155-163. doi.org/10.1111/j.1469-7998.1998.tb00144.x
508
- 509 Würsig B. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops*
510 *truncatus*) in an Argentine bay. *The Biological Bulletin*, 1978; 154(2), 348-359.
511
- 512 Würsig B, Jefferson T. Methods of photo-identification for small cetaceans. In Hammond P.S.,
513 Mizroch S.A. and Donovan G.P. (eds) *Individual recognition of cetaceans: use of photo-*
514 *identification and other techniques to estimate population parameters*. Report of the International
515 Whaling Commission, special issue 12, 1990; Cambridge: International Whaling Commission,
516 pp. 43–52.
517

518 Würsig B, Würsig M. The photographic determination of group size, composition, and stability
519 of coastal porpoises (*Tursiops truncatus*). *Science*, 1977; 198(4318), 755-756. doi:
520 10.1126/science.198.4318.755
521
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Table 1 (on next page)

Summary of the photo-identification data used in this study

1 Table 1. Summary of the photo-identification data used in this study.

Number of individual dolphins	Source	Period	Location
363	Oceanic Observatory of Madeira (OOM)	2004-2016	Madeira island
176	Nova Atlantis Foundation	2003-2007	Pico (Azores)
495	MONICET Project-University of Azores	2004-2016	Pico, Faial, São Miguel and Terceira (Azores)
42	Espaço Thalassa	2014-2016	Pico and Faial (Azores)
182	SECAC	2004-2015	La Gomera (Canary Islands)
110	SECAC	2014	Tenerife (Canary Islands)
142	SECAC	2010-2011	La Palma (Canary islands)
281	BIOECOMAC-University of La Laguna/NGO MEER e.V.	2001-2011	La Palma, La Gomera and Tenerife (Canary islands)
359	Mar Ilimitado	2007-2015	Sagres

Figure 1

Map showing the study area

(A) Sagres, (B) Azores, (C) Madeira, (D) Canary Islands (extracted from Natural Earth:

<https://www.naturalearthdata.com/>)

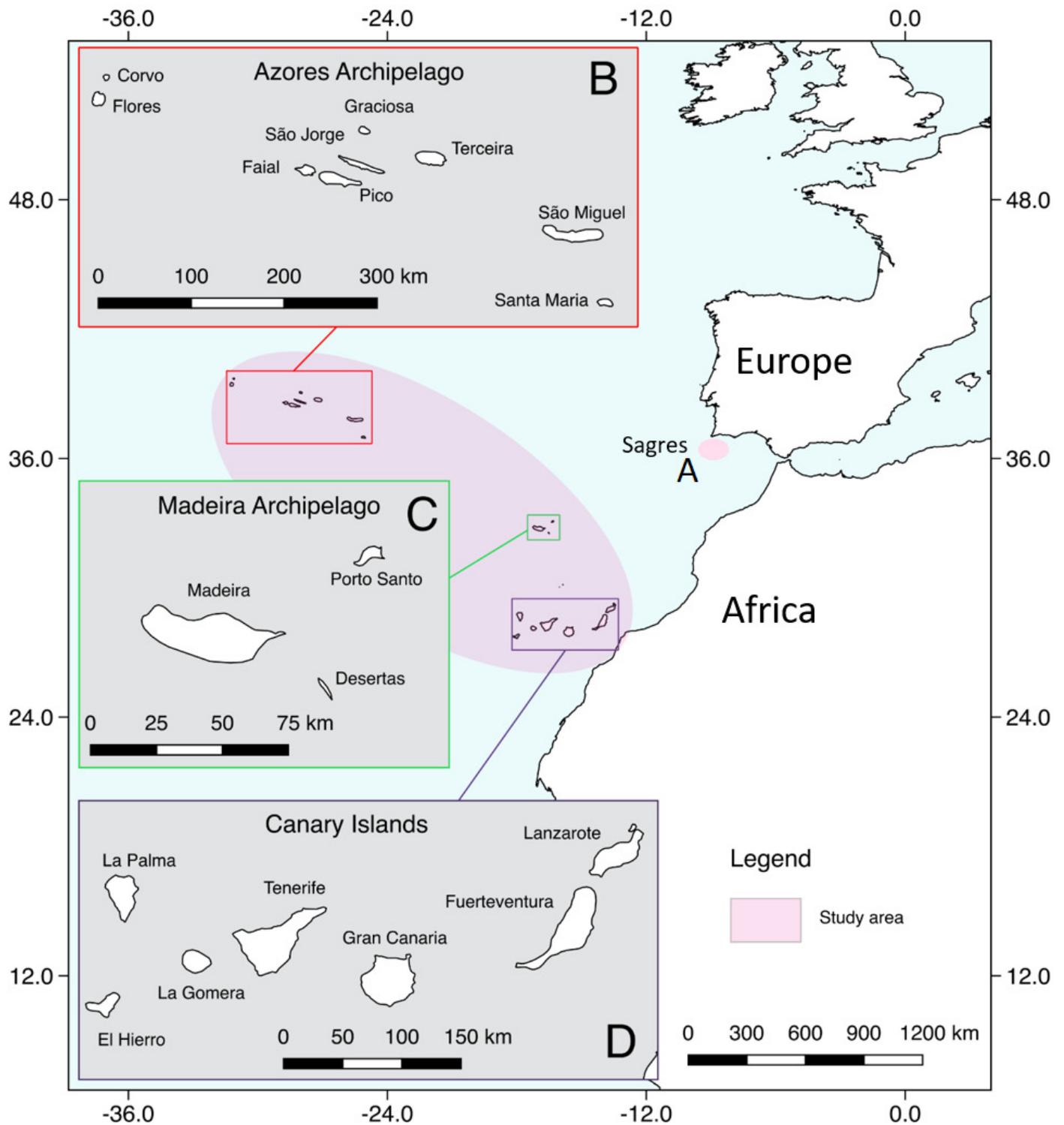


Figure 2

Number of individuals in the catalogues and the number of individuals with matches, distributed by areas.

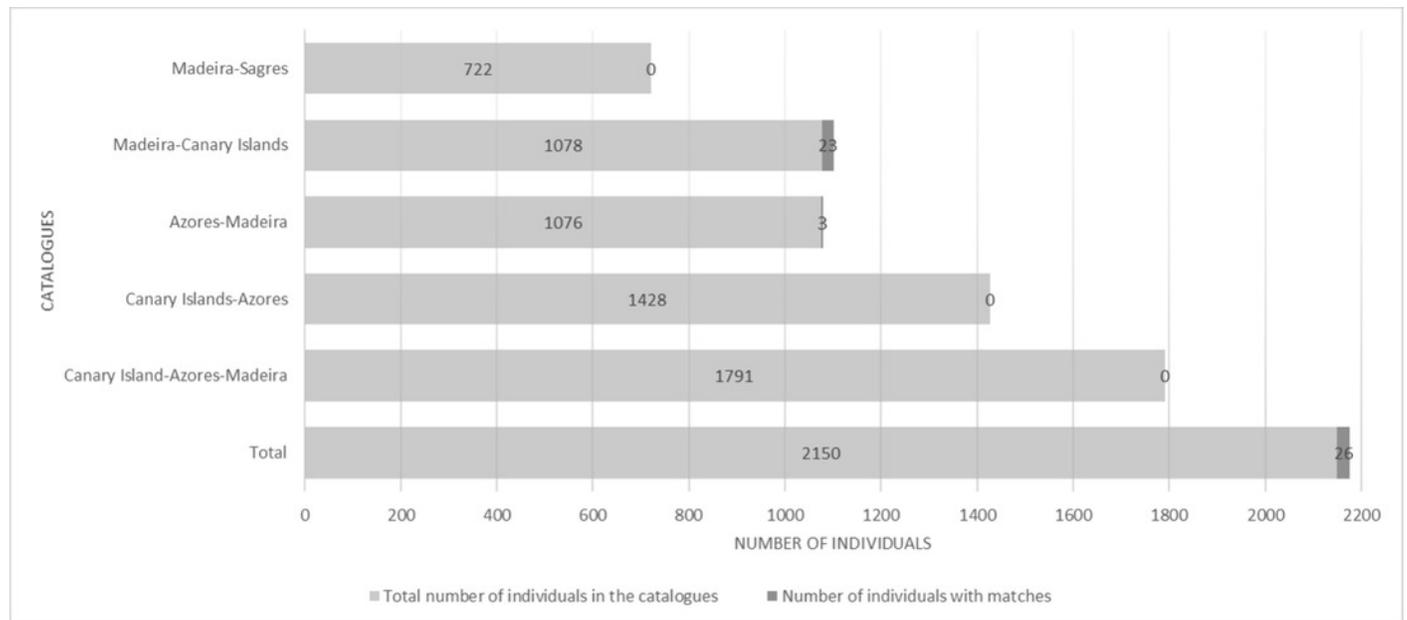


Figure 3

Map showing the two-way movements of two bottlenose dolphins between Madeira and Canary Islands (round-trip of ≈ 920 Km) .

The dots are just figurative and do not reflect the exact location of the dolphins. Illustration by E. Berninsone©ARDITI.

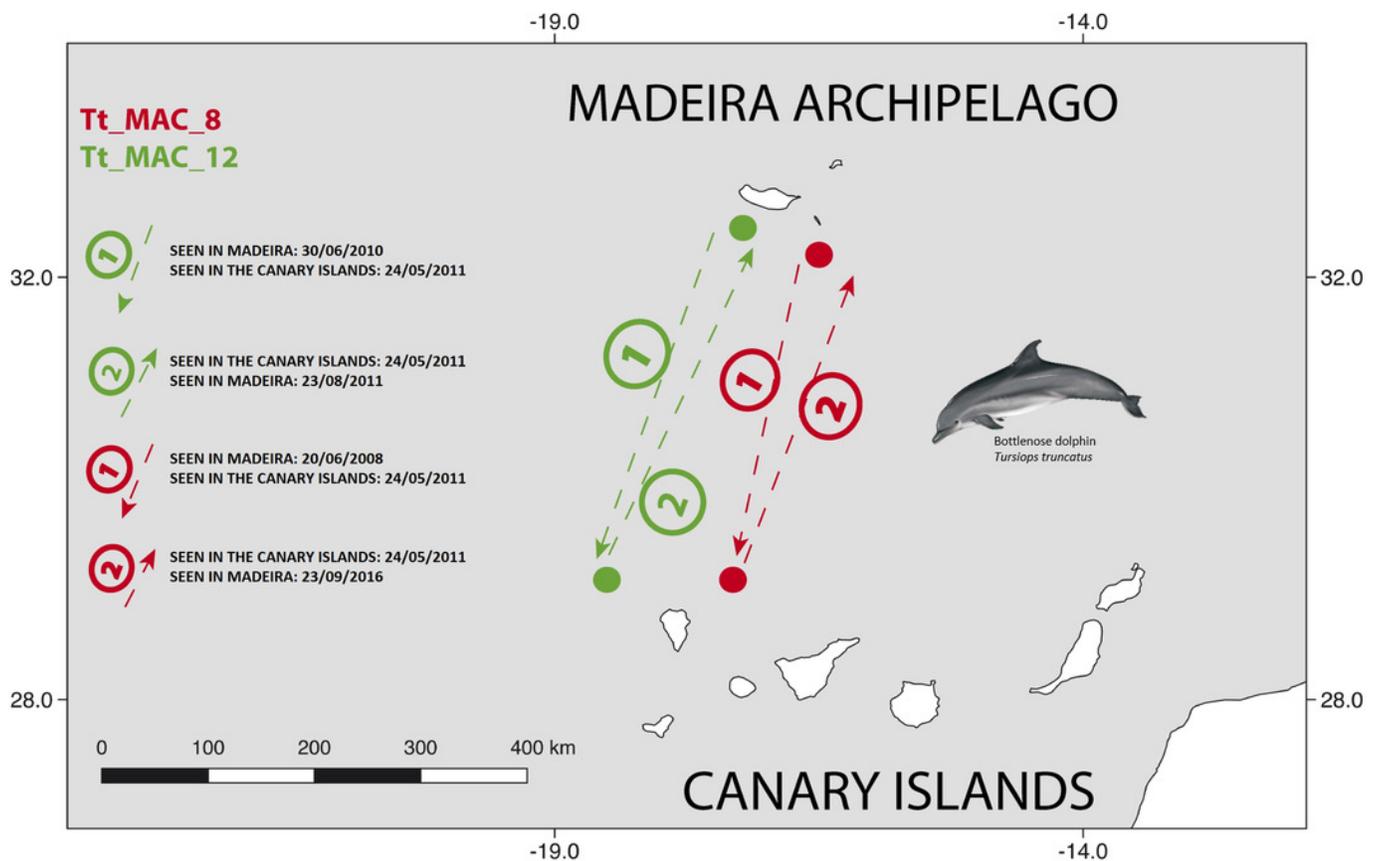


Figure 4

Map showing the movement of four bottlenose dolphins between the Canary Islands and Madeira (≈ 500 Km).

The dots are just figurative and do not reflect the exact location of the dolphins. Illustration by E. Berninsone©ARDITI.

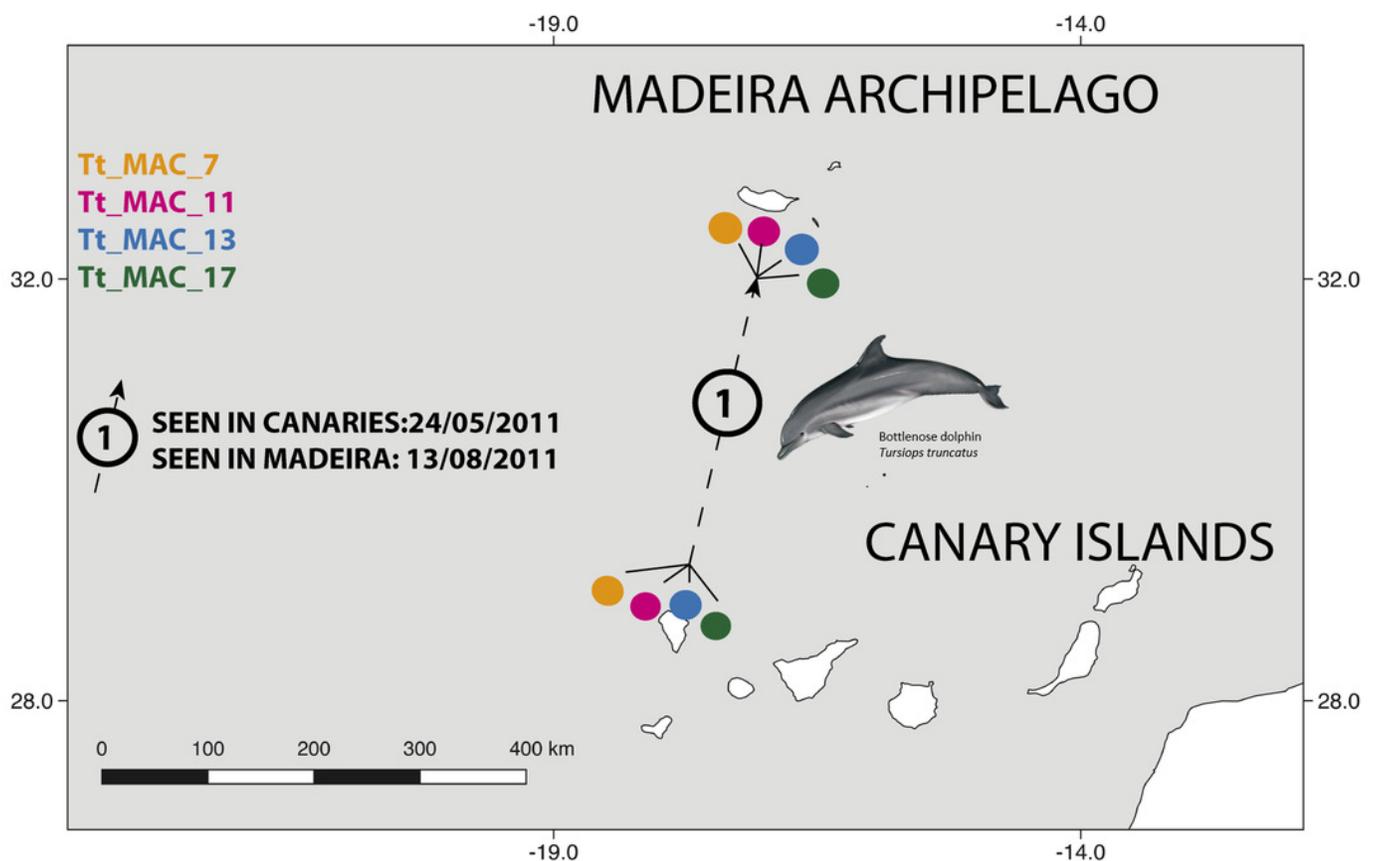


Figure 5

Map showing the movement of three bottlenose dolphins between the Azores and Madeira archipelagos (≈ 1000 Km)

The dots are just figurative and do not reflect the exact location of the dolphins. Illustration by E. Berninsone©ARDITI.

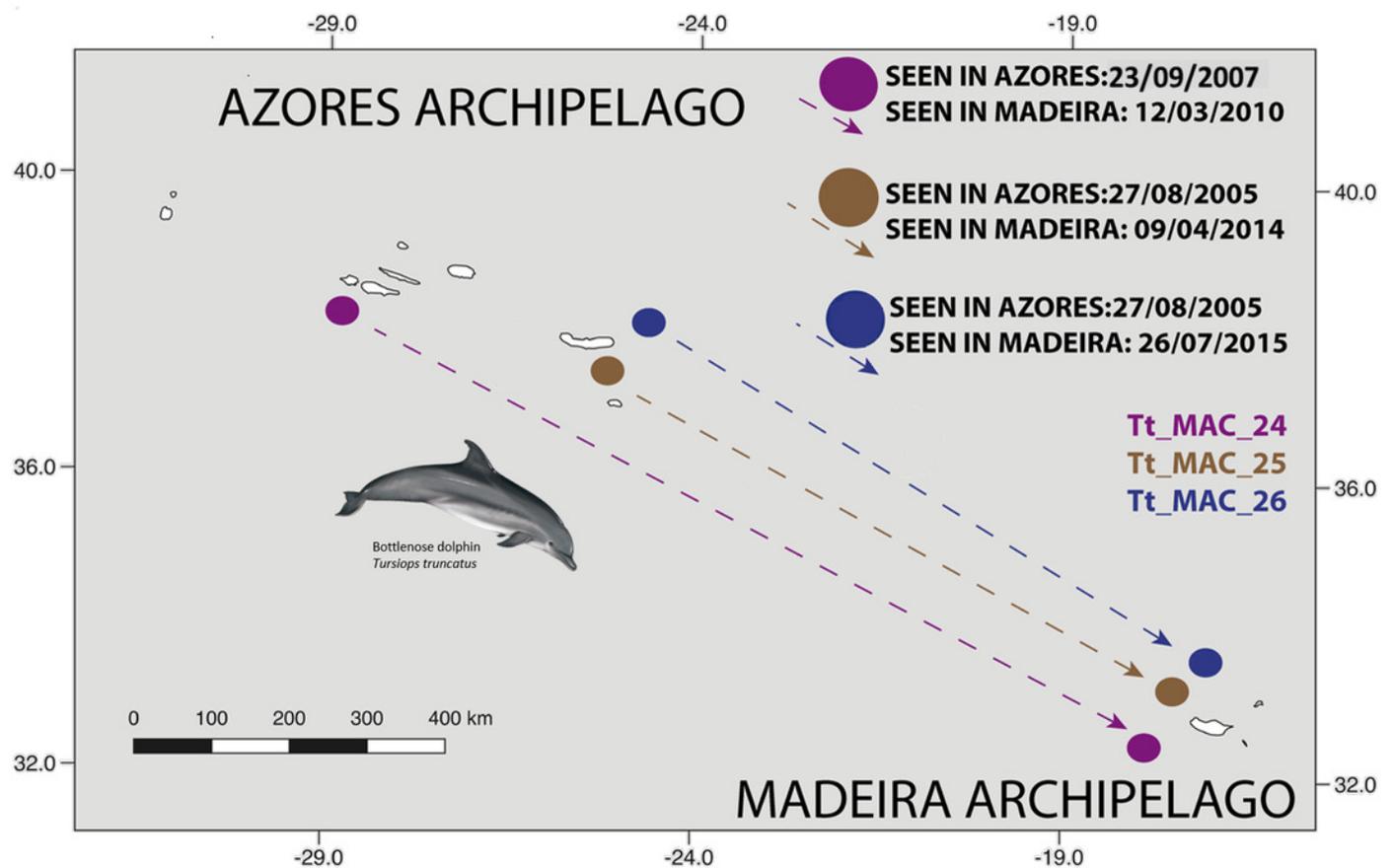


Figure 6

Social network diagram illustrating the associations between the dolphins with different residency patterns identified in Madeira, and the 20 dolphins seen in association in more than one archipelago.

Individual dolphins are represented by nodes and associations by the lines between nodes. Nodes color and shape indicates the archipelago of capture and residency pattern in Madeira archipelago.

