Novel insights on large-scale movements of common bottlenose dolphins in the NE Atlantic: dolphins with an international courtyard

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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 up1791 photos. 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 Canaries (n=23), and between Azores and Madeira (n=3). No matches were found between the Canary Islands and the Azores, as well as among the three archipelagos and between Madeira and Sagres. The minimum time recorded between sightings in two different archipelagos (≈460 km apart) was 62 days. Social analysis revealed that the individuals moving between archipelagos were connected to individuals of all known residency patterns established for Madeira. The considerably 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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Abstract

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 up1791 photos. 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 Canaries (n=23), and between Azores and Madeira (n=3). No matches were found between the Canary Islands and the Azores, as well as among the three archipelagos and between Madeira and Sagres. The minimum time recorded between sightings in two different archipelagos (≈460 km apart) was 62 days. Social analysis revealed that the individuals moving between archipelagos were connected to individuals of all known residency patterns established for Madeira. The considerably 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.

Introduction

The common bottlenose dolphin *Tursiops truncatus*, (hereafter “bottlenose dolphin”), like other cetaceans, faces a variety of threats such as water pollution, incidental capture (by-catch) or vessel collisions (Well & Scott, 2018). It is crucial to gain a better understanding of the range of this species in order to establish suitable conservation measures. Costal and pelagic variations or ecotypes of bottlenose dolphins have been described based on morphological, ecological and genetic differences (Oudejans et al., 2015). The well-studied populations of coastal bottlenose dolphins exhibit a variety of horizontal movements, including seasonal migrations, year-around home ranges, periodic residency, and a combination of occasional long-range movements and repeated local residency (Shane, Wells & Würsig, 1986; Wells & Scott, 2018). However, much less is known about the ranging patterns of pelagic bottlenose dolphins (Well & Scott, 2018).

Apart from small scale movements of bottlenose dolphin studied in greater depth (e.g. Reynolds et al., 2000; Silva et al., 2008; Tobeña et al., 2014; Hwang et al., 2014; Dinis et al., 2016), information from long-distance ~~movements~~ and inter-archipelagos movements is scarce. Insufficient information on long-distance movements may result in higher emphasis on residency (Bearzi, Bonizzoni & Gonzalvo, 2011), when in fact individuals may leave the study area more frequently than initially thought. Previous studies of pelagic bottlenose dolphin populations in the NE Atlantic area suggested that these populations have a high gene flow and are genetically less differentiated (Querouil et al., 2007; Louis et al., 2014). Additionally, different residency patterns and individual movements within each archipelago were identified for the Azores (Silva et al., 2008), the Canary Islands (Tobeña et al., 2014) and Madeira (Dinis et al., 2016), with just a portion of the individuals being classified as residents. These results indicate large individual home ranges, but ~~to the present time,~~ there is no evidence of the connectivity of the populations between these oceanic archipelagos. A recent photo-identification study demonstrated the connectivity of pilot whales within the Macaronesia biogeographical region (Alves et al., 2019), also highlighting the importance of such studies for conservation. Hence, it can be speculated that other highly mobile species like bottlenose dolphin can also perform long-range movements in this region (Silva et al., 2008; Dinis et al., 2016). ~~With this study,~~ we investigated for the first time horizontal large-scale movements of this species between the archipelagos of Madeira, Azores and the Canary Islands, i.e. within the biogeographical region of Macaronesia, and with the Portuguese continental shelf, covering an area of more than 1600 000 km2. The present study ~~attempts to be a tool that enables the better~~ understanding of the bottlenose dolphin connectivity among these remote oceanic archipelagos, and ~~to~~ help in this species future conservation and management efforts.

Materials & Methods

STUDY AREA

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

PHOTO-IDENTIFICATION DATA

Dolphin movements were determined through the cross-comparison of photo-identification catalogues held by eight organizations in Portugal and Spain, representing three different archipelagos, and a small area on the coastal Portuguese mainland (Table 1). The catalogues were built using different sources, ranging from whale watching operators to research teams and independent photographers. The Madeira catalogue comprised 363 individuals collected ~~over the period~~ 2004 to 2016, and sighted mainly off the south coast of Madeira. Two catalogues from the Azores were compared, one containing 176 individuals from Pico and Faial islands collected between 2003 to 2007, and a second one with 495 individuals from Pico, Faial, São Miguel and Terceira islands, collected between 2004-2016. A third set of data from this region, containing 201 photos of 42 individuals collected from 2014-2016 was added. From the Canary Archipelago, four catalogues from different islands were used: one from La Gomera with 182 individuals (2004-2015); one from Tenerife with 110 individuals (from 2014); one from La Palma with 142 individuals (2010-2011 and 2015), and one with 281 individuals (2001-2011), that included photos from La Gomera, El Hierro and La Palma. The catalogue from Sagres contained 359 individual photographed from 2001until 2016.

PHOTO-IDENTIFICATION ANALYSIS

The photo-identification analysis was conducted through the comparison of natural markings like nicks and notches on the dorsal fin, and the shape of the fin, from each catalogue (Würsig & Würsig, 1977). The matching procedure was always conducted by the same researcher, and confirmed by a second experienced researcher. If doubts persisted, a third experienced researcher would double-check. When a match was found, a new identification code was created and the dolphin was added to the Macaronesia catalogue. Ambiguous matches were discarded to avoid false positives.

SOCIAL ANALYSIS

Only individuals from the Madeira catalogue, seen in association with other individuals between 2004 and 2016 were used in this analysis. Associations between individuals were analyzed according to residency patterns established previously for this archipelago (Dinis et al., 2016): individuals that were sighted during three seasons in one year and in more than two consecutive years were considered residents; individuals that were seen only once were considered transients, and the remain individuals felled in the category of migrants. This study aimed to analyze social interactions at the level of the community, and not between dyads, thus we included all individuals seen in association, regardless of sighting frequency. A social network diagram was created using NetDraw 2.160 (Borgatti, 2002) to visualize individual association patterns with the Macaronesian individuals separated from the main clusters in order to highlight their associations. Residency pattern was included as an individual attribute.

Results

PHOTO-IDENTIFICATION ANALYSIS

There ~~was a total of~~ 26 individual matches most of which between Madeira and Canary Islands. Additionally, three individuals were seen both in the Azores and the Madeira archipelagos. No matches between the Canary Islands and the Azores were found. Likewise, none of the individuals were seen in all three archipelagos, nor between Madeira and Sagres (Fig.2). The 23 matches between Madeira and the Canary Islands occurred on three of the four studied islands in the Canary Islands, mainly with El Hierro (n=6) and La Palma (n=14) (S1 Table). The results also showed back and forth movements between Madeira and the Canary Islands. E.g., one individual (Tt_MAC_12) was sighted off Madeira on 30th June 2010, then off La Palma on 24th May 2011 and again off Madeira on 23th August 2011. Another individual (Tt_MAC_8) was seen off Madeira on 20th June 2008, then off La Palma on 24th May 2011 and again off Madeira on 23rd and 24th September 2016 (Fig.3). Moreover, two individuals (Tt_MAC_3 and

Tt_MAC_4) were seen within the Canary Islands, and then off Madeira several years later. Tt_MAC_3 was sighted seven times intermittently off El Hierro in 2004, 2008, 2009, then was photographed off La Palma in 2010, and sighted two times off Madeira in 2014 and in 2016. Tt_MAC_4 was first seen off El Hierro in 2009, then sighted off the neighboring island of La Gomera in 2010, was observed again in El Hierro in 2010 and 2011, and eventually sighted off Madeira in 2015 (S1 Table). Four individuals (Tt_MAC_7, 11, 13 and 17) were sighted off La Palma on the same date (on 24th May 2011) and then sighted together off Madeira on 13th August 2011 with less than 3 months between re-sightings (Fig.4), possibly accompanied by Tt_MAC_9, 12, 14 and 15, that were sighted in the same time frame and in the same locations (Table S1).

The three individuals seen first in the Azores and last off Madeira were sighted three (Tt_MAC_24), nine (Tt_MAC_25) and 10 (Tt_MAC_26) years apart. No movements from Madeira to Azores were ~~registered~~ (Fig.5).

Tt_MAC_17 was photographed off La Palma and then off Madeira within 62 days, presenting the minimum time interval that an individual travelled between two archipelagos, covering 450 Km within this timeframe.

SOCIAL ANALYSIS

The network social diagram incorporated 332 individual dolphins, catalogued in Madeira archipelago, including 20 Macaronesian individuals seen in association. The diagram presents three clusters grouped by residency patterns with blue representing resident dolphins; yellow, migrant dolphins and red, transient dolphins. From these, 17 dolphins that were seen both in the Canary Islands and in Madeira associated with all categories of residency pattern and, three were seen both in the Azores and Madeira archipelago associated with migrant and transient dolphins (Fig. 6).

Discussion

This study shows that 26 bottlenose dolphins photo-identified off Madeira moved between three archipelagos demonstrating that this species' population covers wide areas in the NE Atlantic. These 26 individuals correspond to 7.1% of the 363 catalogued dolphins in the Madeira archipelago, similarly to what was found for UK AND Irish waters (approximately 6%, Robinson et al., 2012). Only few studies described long-distance movements (>1000 km) of bottlenose dolphin around the world (e.g. Wood, 1998; Wells et al., 1999; Robinson et al., 2012), and none covered these three archipelagos of the Macaronesia region so far, thus this study expands our knowledge of the species in this area of the NE Atlantic. Previous examples of wider-scale movements based on photo-identified bottlenose dolphins come from Argentina and Ireland. Off Argentina, one individual travelled 300 km (Würsig, 1978), while off Ireland, an individual travelled a distance as large as 650 km (O'Brien et al., 2009). The distances reported here for the individuals that moved between Madeira and the Canary Islands are comparable, although the longest distance reported in this study (Tt_MAC_24, 25, and 26) comes closer to the 1277 km an individual travelled between UK and Ireland (Robinson et al., 2012). The distance travelled by Tt_MAC_24 seen off Pico island as well as off Madeira Island, represents a distance of approximately 1200 km, one of the highest distances recorded so far for this species. The inshore waters of the oceanic archipelagos within the NE Atlantic waters offer a sheltered place where bottlenose dolphins can feed, when compared to the offshore waters nearby (Silva et al., 2008; Dinis et al., 2016). Possibly, when food resources are scarce, some individuals may travel longer distances to where similar, and more abundant food resources may be available. In less productive habitats such as oceanic waters, animals can be expected to maintain larger home ranges because there is a need to range further to find sufficient food (Silva et al., 2008). In a publication about movement patterns of odontocentes species (Sandell & Gittleman, 1989), the authors pointed out that one of the variables known to influence bottlenose dolphin movements appears to be the habitat they occupy in accordance with availability of prey.

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

Although we could not determine the sex of the dolphins seen in more than one archipelago, for male bottlenose dolphins, long-distance movements could also serve to get access to receptive females outside their own population. I.e., young adult males could be driven to seek for females, as described for Shark Bay, Australia (Connor, Smolker & Richards, 1992), and thereby also increasing gene flow between populations. In this way, population viability will be improved and genetic differences within the NE Atlantic bottlenose dolphin populations will decrease, as confirmed by a study that compared individuals from the Madeira and Azores archipelagos (11). Tobeña and colleagues (2014) described two individuals (Tt_MAC_3 and 4 in this study) associated to the Canary Islands, where they were seen over a long period of time (four and three years, respectively), before they were photographed off Madeira. This suggests that even individuals that were considered resident or having a high degree of site fidelity may undertake long-range movements from time to time. Another cross-Macaronesian study (Alves et al., 2018a) reported a group of five socially related short-finned pilot whales with strong site fidelity to Madeira which made a round trip to the Azores archipelago, covering approximately 2000 km, highlighting the importance of caution when assigning residency patterns to smaller areas in oceanic waters. Similarly, in the study of long-range movements of bottlenose dolphins (Robinson et al., 2012), the far ranging individuals had been considered to belong to discrete resident populations in the UK and Ireland.

Four individuals (Tt_MAC 7, 11, 13, 17) were seen together off La Palma and were encountered thereafter in Madeira (Fig.4). This strongly suggests that these individuals travelled together from La Palma to Madeira. Our results also showed that other Macaronesian individuals

(Tt_MAC_9, 12, 14 and 15) were documented during the same period in both archipelagos, indicating stable social association, which may persist during, or even favor, long-range oceanic journeys.

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

The minimum period of time between the re-captures in different archipelagos (Canary Archipelago to Madeira) was 62 days. Satellite-monitored movements of an individual bottlenose dolphin off Florida showed that the dolphin moved 581 km in 25 days (Mate et al., 1995). In Japan, one tagged bottlenose dolphin travelled about 604 km in 18 days (Tanaka, 1987). Therefore, the time period documented in this study is comparatively long, but the actual time it took the dolphins to cover the distance from one archipelago to the other remains unknown. In one study using satellite telemetry (Klatsky, Wells & Sweeney, 2007), the authors determined a mean travel distance of 28.3 Km/day for three offshore bottlenose dolphins, which suggests that the dolphins reported here could have covered the distance within a time period well below 62 days. Alternatively, they may also have travelled a (much) longer distance within those 2 months.

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

Further collaborative research is needed to find out, how prevalent the ranging pattern described here are within the Macaronesian bottlenose dolphins, as well as to find out the sex and age classes involved. What is more, behavioral data can complement this study in the future, thereby giving insight into the driving forces for inter-archipelago connectivity.

Conclusions

This study provides first evidence of large-scale connectivity of bottlenose dolphin communities within the Macaronesia region, and highlights the strength of combining photo-identification catalogues from different areas. Such studies hence can be a monitoring tool when assessing ranging patterns over wider areas, as has been regularly realized for large whales. We now know that at least some bottlenose dolphins perform extreme mobility throughout the Macaronesia region. This has multiple implications for conservation and management efforts designed for this species: Firstly, management units may not be separable and their connectivity must be taken into accounts e.g. when establishing marine protected areas (MPAs). Connected populations will have to be considered coherently within conservation frameworks such as the European Union Habitats & Species Directive (HD). Bottlenose dolphin inhabiting Macaronesia waters are, as in other places, subject to many threats like fisheries interaction (bycatch), overfishing, pollution, vessel strikes, stress caused by human recreational activities such as whale-watching, and climate change, among others. In the Macaronesia region a large number of marine protected areas were designed to protect bottlenose dolphins, but with different levels of protection (Hoyt, 2011). Some of these are SACs (Special Area of Conservation) designated as part of the Natura 2000 network under the European Union HD. Most marine SACs thereby only cover coastal areas, rather than reaching offshore. While the establishment of MPAs is a step forward to protect bottlenose dolphins (Hoyt, 2011; Silva et al., 2012) in this region, more has to be done in terms of mitigations measures, as many of the established SACs still lack management plans. In the Azores, it has been demonstrated that the established areas are not sufficient mainly because they are not covering the complete home range of the dolphins (Silva et al., 2012). The same applies to the Canary Islands and to Madeira archipelago. Our results confirm that the bottlenose dolphins' home range in Macaronesia includes more than one archipelago and the offshore waters around them. This means that SACs should be expanded to include offshore waters and protection measures shall be effective. Such an expansion would have positive side effect for other highly mobile species, like the short-finned pilot whale, that are known to use this area widely, too (Alves et al., 2019).

This study can be seen as a first step to review the established boundaries of the existing MPAs (SACs) for this species in Macaronesia. This will require a considerable effort, because there are three different autonomous communities (Madeira, Azores and Canarias) involved, belonging to two EU member states (Portugal and Spain). Nevertheless, it would correspond to an adaptive and ecosystem-based management approach and serve the coherent protection of the species across borders – all aspects that the EU HD strives to achieve. In that sense, the creation of a large-scale sanctuary in the Macaronesia region, involving different states and international waters, would be the most effective way to protect this and others highly mobile oceanic species on this remote area of the North Atlantic.

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Table 1(on next page)

Summary of the photo-identification data used in this study

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)

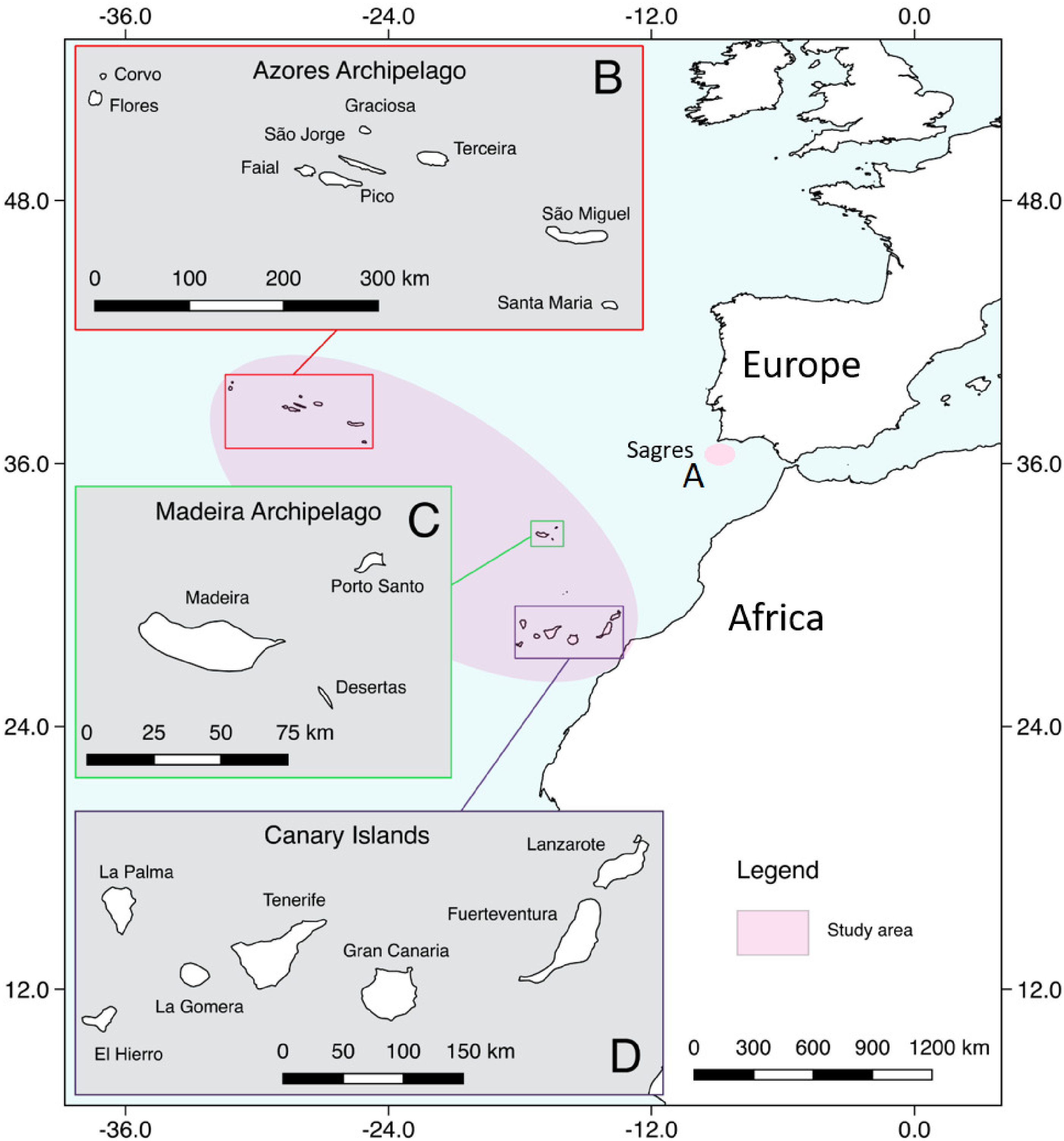
-36.0
-24.0
-12.0
0.0
48.0
36.0
24.0
12.0
Azores Archipelago
B
Corvo
Flores
Graciosa
São Jorge
Terceira
Faial
Pico
São Miguel
Santa Maria
0 100 200 300 km
Europe
Sagres
A
Madeira Archipelago
C
Porto Santo
Madeira
Desertas
0 25 50 75 km
Africa
Canary Islands
Lanzarote
La Palma
Tenerife
Fuerteventura
Gran Canaria
La Gomera
El Hierro
0 50 100 150 km
D
Legend
Study area
0 300 600 900 1200 km

Figure 2

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

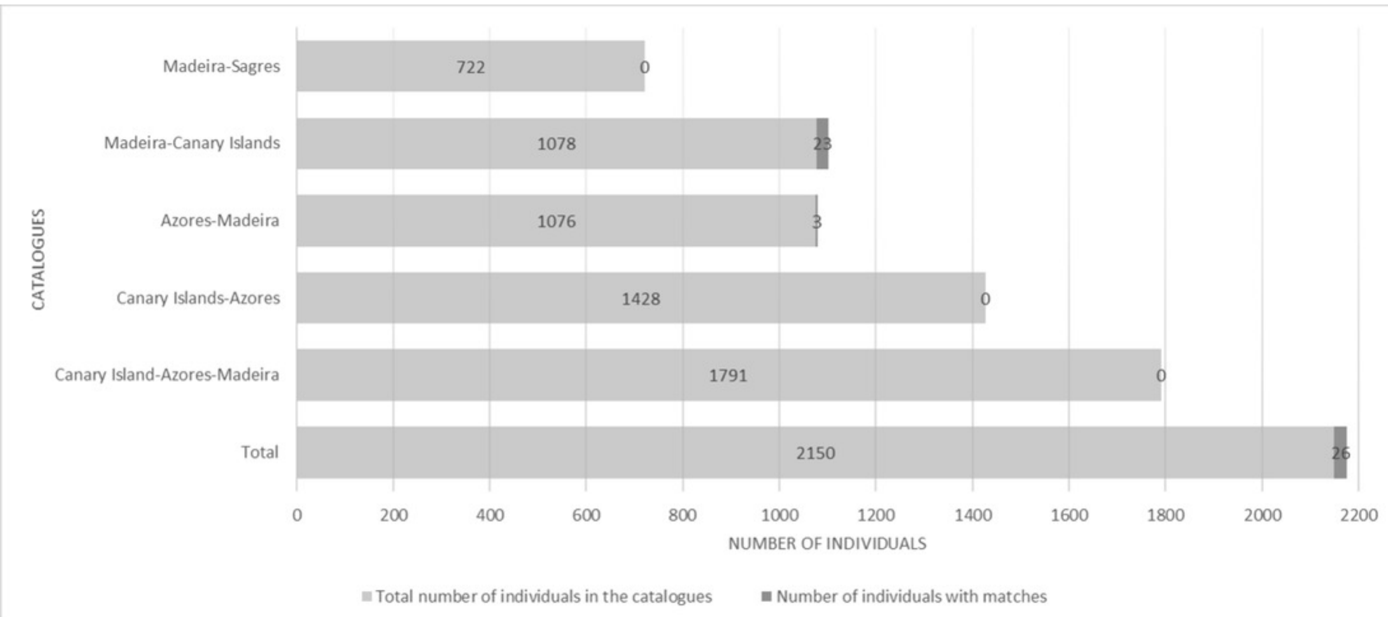

Figure 3

Map showing the two-way movements of two bottlenose dolphin between Madeira and Canary Islands.

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

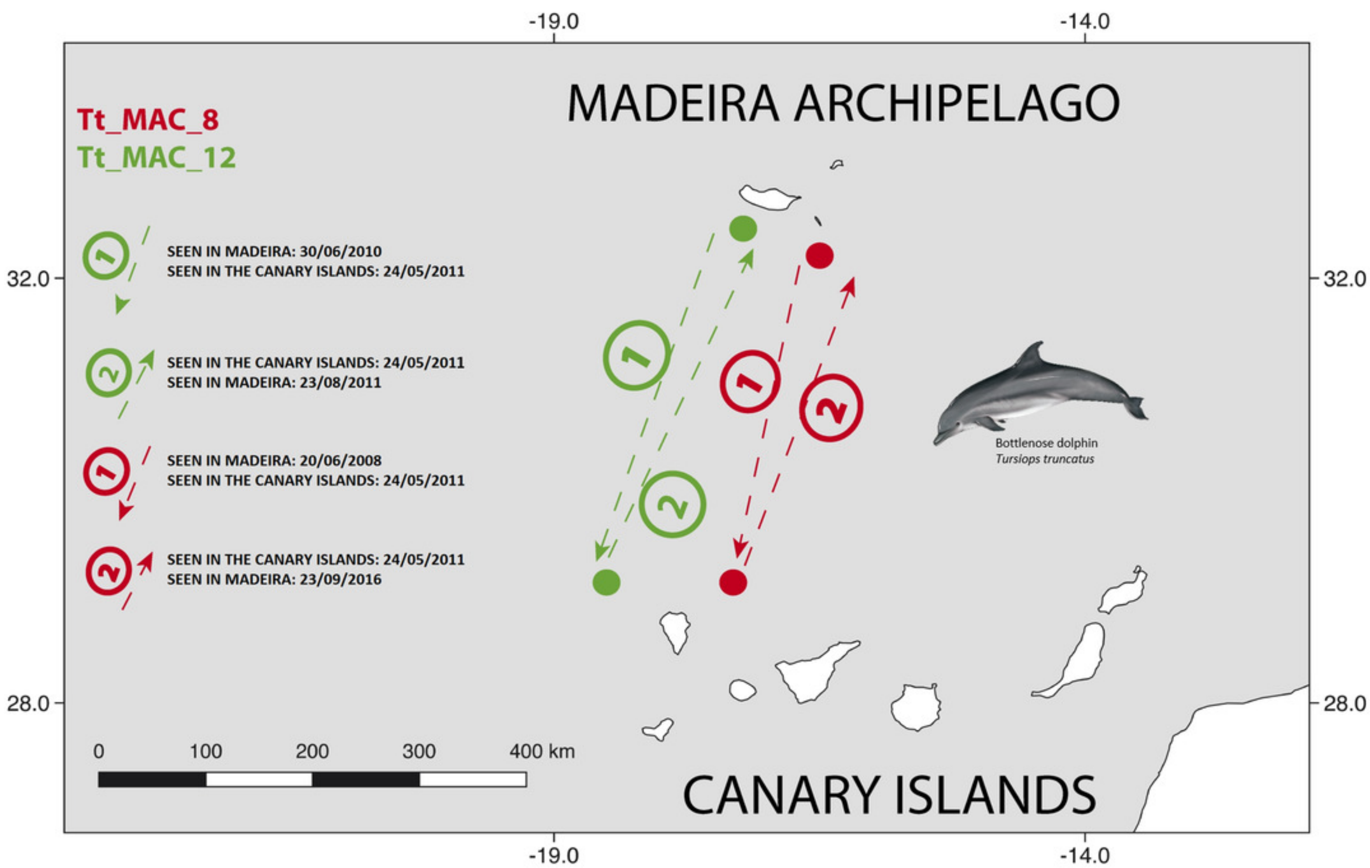

Figure 4

Map showing the movement of four bottlenose dolphin between the Canary Islands and Madeira.

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

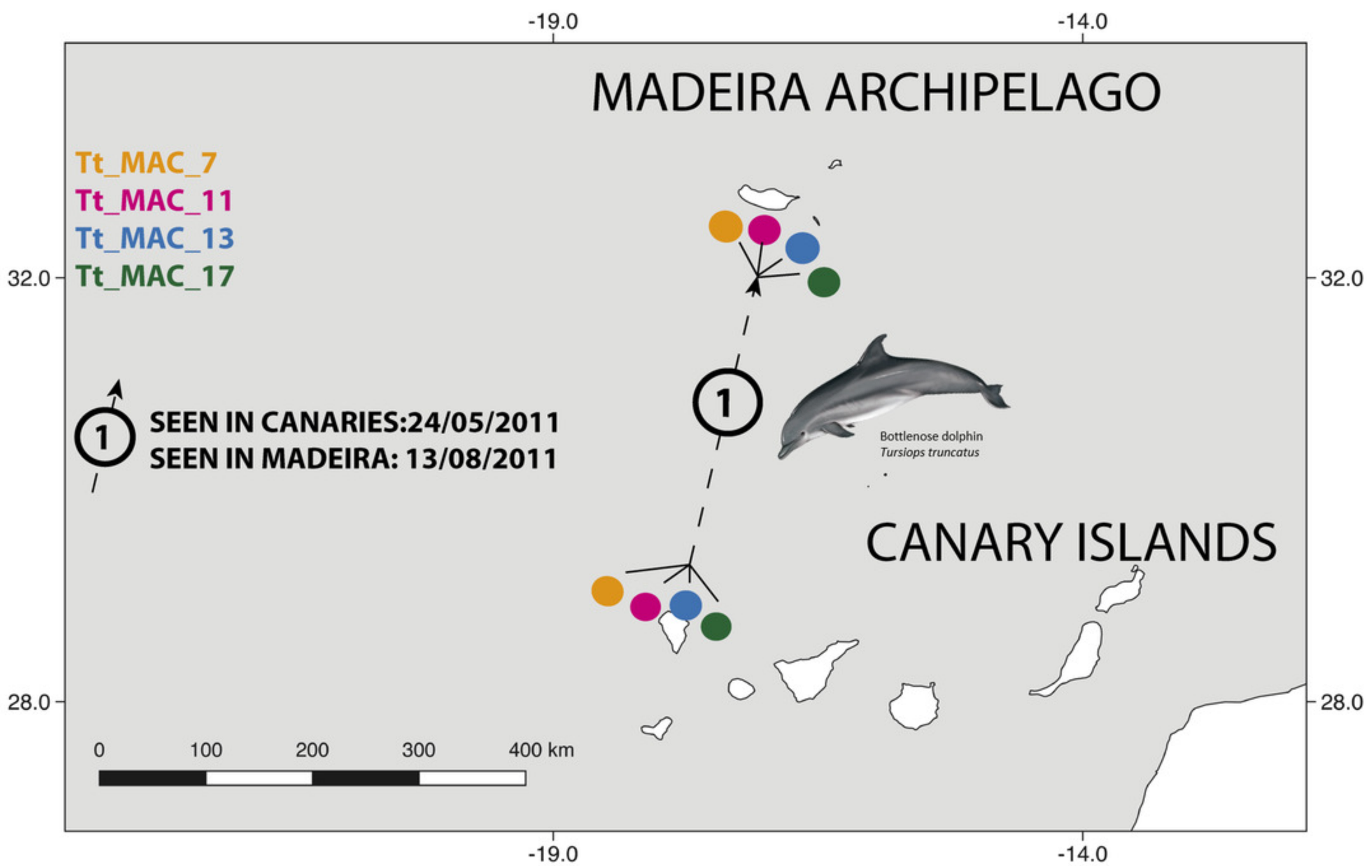

Figure 5

Map showing the movement of three bottlenose dolphin between the Azores and Madeira archipelagos

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

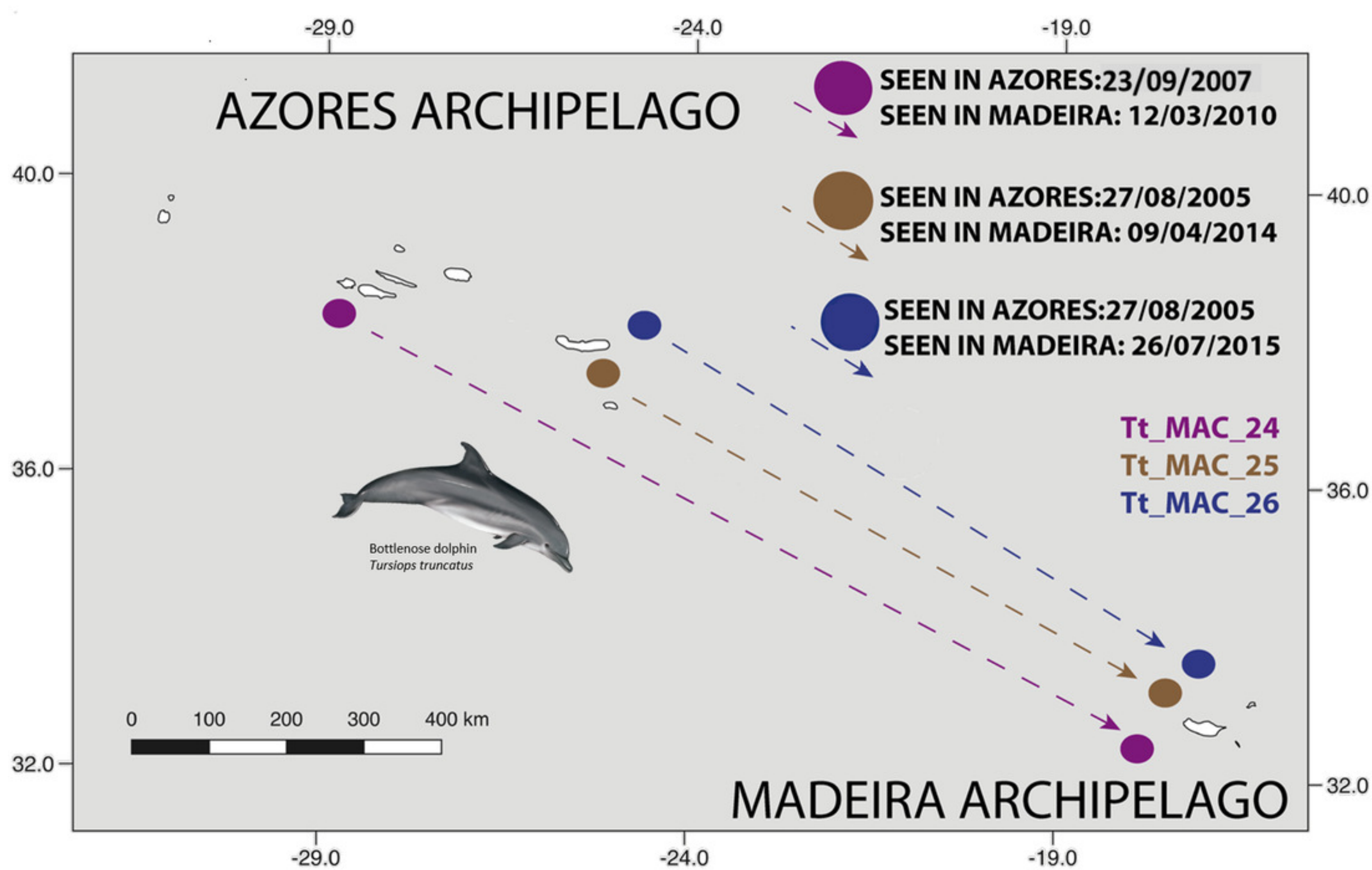

Figure 6

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.