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Bottlenose dolphin *Tursiops truncatus* group dynamics, site fidelity, residency and movement patterns in the Madeira Archipelago (North-East Atlantic)

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The bottlenose dolphin *Tursiops truncatus* is one of the most frequently sighted cetacean species in the Madeira Archipelago (North-East Atlantic); however, little is known about its population ecology in these waters. Photo-identification undertaken during systematic, non-systematic and opportunistic surveys conducted between 2001 and 2012 was used to assess group dynamics, site fidelity, residency and movement patterns of bottlenose dolphins in the archipelago. Three different patterns of residency were assigned, based on individual sighting histories. Group size ranged between 2 and 90 individuals (median 12), with no significant monthly difference in group size. All resident dolphins formed a core, complex network with migrant and transient dolphins. In contrast, satellite clusters were formed exclusively by transient individuals. The lagged identification rate (LIR) model indicated that a dolphin remained in the area for an average of 90 days, whereas the average time an individual spent outside the study area was approximately 313 days. The Madeira Archipelago appears to be only a section of a much larger home range for this population, with the dolphins exhibiting three different patterns of occurrence that associate with each other. The information gained about this poorly studied population contributes to the overall knowledge of bottlenose dolphins in insular oceanic habitats.

Keywords: Macaronesia, photo-identification, residency, social network

Introduction

Patterns of residency and site fidelity are often indicative of the ecology of a population; evidence of repeated sightings in the same area can be used to establish core areas or ranges of individuals and to identify important habitats. Residency is generally defined based on the amount of time an individual spends in a certain geographic area (Wells and Scott 1990). The parameters used to define residency in studies of cetaceans vary widely and are usually influenced by the local geography, as well as the access of researchers to the population of interest. This often requires long-term studies of populations, which can be particularly challenging when studying highly mobile species, such as bottlenose dolphins *Tursiops truncatus*. Coastal bottlenose dolphins tend to form resident or semi-resident populations across their distribution. For example, bottlenose dolphins are year-round residents in Sarasota Bay, Florida, and the Moray Firth, Scotland (Scott and et al. 1990; Wilson et al. 1997), whereas those identified in Bahia Kino, Gulf of California, and in the Shannon Estuary, Ireland, are not (Ballance 1992; Ingram and Rogan 2003). Studies of bottlenose dolphins around oceanic islands are limited (Baird et al. 2009) and these populations are likely to present different conservation needs than in more neritic areas. The pelagic waters of the Madeira Archipelago are one of the most

isolated oceanic habitats of the North Atlantic (Alves et al. 2013). Residency of animals in isolated oceanic habitats is more difficult to establish than in more enclosed areas. Studies in remote open-ocean systems often rely on site fidelity, the tendency for individuals to return or to remain in the same area over a period of time (Baird et al. 2008). However, bottlenose dolphins inhabiting open habitats tend to occur in large groups, with low site fidelity and extensive movement patterns (Bearzi 2005; Silva et al. 2008).

The size of an area typically surveyed in the open ocean (e.g. 4 818 km² in the Madeira Archipelago; Alves et al. 2013) is much larger than that surveyed in locations such as bays and estuaries (e.g. 336 km²; Martinho 2012). Therefore, lower encounter rates in the open ocean are expected and the definition of residency should be adjusted accordingly. Little is known about residency and movement patterns of bottlenose dolphins in the Madeira Archipelago. Previous studies have shown that these dolphins are one of the most frequently sighted cetaceans both during research surveys and whale-watching trips (Ferreira 2007; Dinis et al. 2009), but more-detailed information about population dynamics is still lacking. Determining whether a population or part thereof is dependent on a specific area is crucial for future management decision-making.

In the past few years, bottlenose dolphins in the Madeira Archipelago have been exposed to an increase in whale-watching activity (Ferreira 2007). The activity was regulated in 2013, limiting the number of participating companies and establishing areas where whale watching is restricted or prohibited, yet potential effects on dolphins remain poorly understood.

This study intends to add knowledge of populations of bottlenose dolphins inhabiting oceanic habitats in order to improve mitigation measures and future conservation management plans for Madeiran waters and for similar isolated oceanic bottlenose dolphin habitats. Long-term photo-identification data of bottlenose dolphins from both systematic and non-systematic research surveys were used to determine group dynamics. Moreover, additional data from opportunistic encounters by whale-watching boats were used to assess the level of residency and site fidelity, as well as to investigate movement patterns within and outside the study area.

Material and methods

Study area, field surveys and photo-identification

The archipelago of Madeira (Portugal) is located in the warm-temperate waters of the North-East Atlantic Ocean (32° N, 17° W), nearly 1 000 km from the European continent and 500 km off the north-west coast of Africa (Figure 1). The archipelago is part of the Macaronesia biogeographic region, which includes Cape Verde, Madeira, the Canary Islands and the Azores, plus a small area of the north-west African coast. Systematic surveys were conducted in eight pre-established sectors around the islands of Madeira, Desertas and Porto Santo in 2001, 2002 and 2004, and from 2007 to 2012 (Figure 2a). Non-systematic surveys were conducted in four pre-established sectors from 2004 to 2007 and from 2010 to 2012 (Figure 2b). These sectors were established after taking into account the nature of the islands' coasts, the bathymetry and the logistics associated with surveying each area. The surveys were part of a larger research programme that aimed to collect baseline distribution data for all cetacean species, and whenever bottlenose dolphins were encountered, photo-identification data were collected. Alves et al. (2013) provide detailed information on the survey methods.

A photo-identification catalogue was compiled and a dataset of capture histories was subsequently created, where a successful photo-identification of an individual in a given sampling event was defined as a capture (Würsig and Jefferson 1990).

Photographs were graded as 'good', 'fair' or 'bad', according to their level of focus, contrast and exposure, the angle of the dorsal fin to the camera and the size of the dorsal fin in the frame. Additionally, the distinctiveness of each frame was graded as 'very distinct', 'distinct', 'slightly distinct' or 'unmarked', based on the number and location of 'nicks' on the dorsal fins. Only good quality and very distinct or distinct photographs were used in this study, in order to enhance the reliability of matches. Calves were excluded from the photo-identification analysis.

All photo processing was done using Darwin© 2.0 (Eckerd College Dolphin Research Group), including cropping the

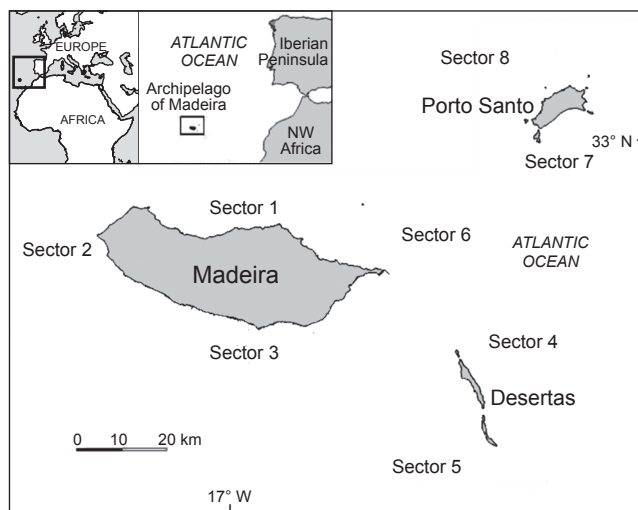


Figure 1: Map of the main study area with the division of the eight sectors used in this study: Sector 1 – Madeira North; Sector 2 – Madeira West; Sector 3 – Madeira South; Sector 4 – Desertas East; Sector 5 – Desertas West; Sector 6 – Channel; Sector 7 – Porto Santo South and Sector 8 – Porto Santo North (adapted from Alves et al. 2013). Inset shows the location of the Madeira Archipelago in the North-East Atlantic

dorsal fin area and adjusting light and contrast. A trailing-edge contour was extracted, which was identifiable from both sides (Auger-Méthé and Whitehead 2007), and the programme was used to compare the extracted fin contour with all others stored in the database. Secondary features, such as fin shape or scars, were used to confirm a match using the naked eye. Whenever a match was found and confirmed, the same identification number as that of the individual stored in the database was assigned. If the programme did not find a match, a visual comparison with all the individuals in the catalogue was attempted, using the number of nicks in the dorsal fin. If there was still no match, a new identification number was attributed to that individual and it was added to the catalogue.

Group dynamics

In this analysis, the term 'group' was used as the sampling unit and was defined as all dolphins sighted within 100 m radius of each other (Wells et al. 1987). Group size was estimated as the average of a count of the minimum number of animals and an estimate of the maximum number. Group composition was determined by counting the minimum number of adults, juveniles and calves present. For this analysis, only data from research surveys from 2004 onwards were considered; whale-watching data were excluded due to lower confidence associated with estimates of group size/composition. Sightings recorded both in search mode and off-effort during the two types of surveys were considered in order to provide more-robust analyses.

A one-way ANOVA was used to investigate whether there were significant differences in group size between months. The assumptions for the ANOVA ($\alpha = 0.05$) analyses were tested using Shapiro–Wilk and Levene's tests. All the analyses were conducted using R 3.0.2

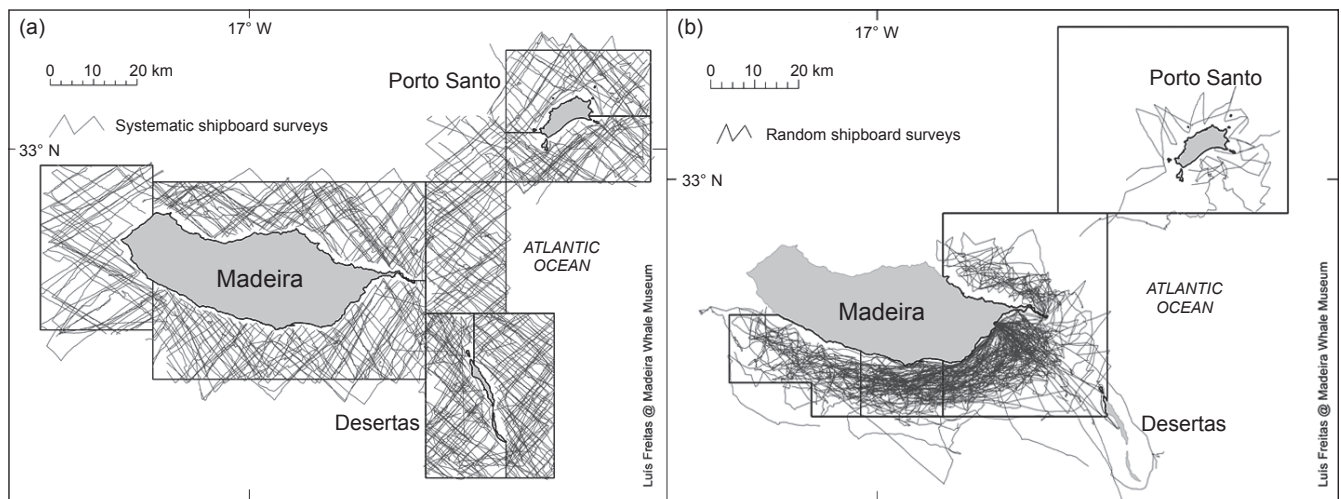


Figure 2: Maps of survey effort within predefined sectors from 2001 to 2012: (a) systematic surveys; (b) non-systematic surveys

software (R Development Core Team 2012). Additionally, the seasonality of groups with calves was investigated and the percentage of encounters that displayed interspecific interactions was calculated.

Site fidelity

Site fidelity was determined by examining the sighting frequency (number of sightings of each individual), number of years observed and mean monthly sighting rate (MMSR). Data from whale-watching boats were included in the analysis of the sighting frequency and number of years observed. The monthly sighting rate was calculated as the proportion of months a given individual was seen in relation to the number of months surveyed during that year. The overall mean was then obtained by averaging this value across the years the animal was observed (Silva et al. 2008). A value of MMSR = 1 implies that an individual was seen in all the surveyed months in the years it was observed in the study area. A Kruskal–Wallis test was used to determine whether MMSR differed with respect to the numbers of years dolphins were sighted. Shapiro–Wilk and Levene’s tests were used to test the associated assumptions.

Residency

Residency in the study area was examined using social network analysis and lagged identification rate (LIR). Social network diagrams were produced with Netdraw 2.136 (Borgatti 2002). Using nodes to represent individuals and lines to link associated individuals, such diagrams graphically display the social organisation within a population.

Only individuals seen in association with other individuals between 2004 and 2012 were used in this analysis. The residency pattern was included as an individual attribute. Residency patterns were assigned to individual dolphins based on their capture histories. The term ‘resident’ was used to designate dolphins that were seen regularly during the study period in the study area (during three seasons in a year and in more than two consecutive years). Following the nomenclature used in capture-recapture studies, ‘transient’

dolphins were defined as those seen just once in the main area (Pradel et al. 1997). Dolphins seen more than once, but in non-consecutive years, were considered ‘migrants’ (Kendall et al. 1997).

The amount of time individuals spent within all the eight sectors of the study area was examined using LIR, calculated in SOCPROG 2.4 (Whitehead 2009). Given that an animal of the study population can be identified only if present in the study area, it is important to assess the potential for the animals to leave the area. LIR provides the probability that an individual observed in the study area at a given time will still be present τ time-lags in the future (Whitehead 2008).

Movements into and out of the whole study area were investigated using photo-identification data of all individuals photographed between 2004 and 2012. LIR was displayed graphically, and models generated in SOCPROG 2.4 (Whitehead 2009) were fitted to the data using maximum likelihood and binomial loss. The model with the lowest quasi Akaike information criterion (QAIC) was selected as providing the best fit to the data (Whitehead 2009).

LIR was calculated using the sighting histories of all individuals, including transients, and represents an average residency rate for the animals that were included in the analysis. The same dataset used for building the social network was also used in the LIR analysis, with an established sampling period of a day.

Movement patterns

Transition probabilities for movements between sectors within the main study area were calculated in SOCPROG 2.4 (Whitehead 2009). In addition, an undefined area representing the entire area outside the study area was included in the analysis to account for movements from a specific sector to a non-surveyed area. Using the same dataset as for the LIR analysis, a parameterised Markov model was used to assess movements among sectors. This model generates estimates for each time-unit in which individuals have a certain probability of moving from one area to another, while accounting for permanent emigration

in a single day (Whitehead 2009). The probability of an individual remaining in the study area one sampling period later (μ) was also calculated following Whitehead (2009), i.e. by subtracting from one the sum of the transition probabilities in its corresponding row.

Results

Group dynamics

Group size and composition were examined for 242 encountered groups between 2004 and 2012, including 185 groups encountered during search (on-effort) mode (Table 1) and 57 encountered opportunistically. Group size ranged from 2 to 90 individuals (median 12). The most common group size was 6–10 dolphins ($n = 56$) (Figure 3). The ANOVA showed no significant differences in group size across months ($F = 1.2$, $df = 11$, $p = 0.23$) (Figure 4).

Calves were present in 26.4% of groups, with the remaining groups consisting either of adults or adults together with juveniles. Groups with calves were seen year-round, with a peak in the early spring and another in late summer/autumn (Figure 5).

In 36 encounters (14.9%), bottlenose dolphins were observed in association with another cetacean species. The short-finned pilot whale *Globicephala macrorhynchus* was the species most commonly found in association with bottlenose dolphins ($n = 23$); on each occasion, a small number of dolphins were seen among the whales. The second most common association was with Bryde's whales *Balaenoptera edeni* ($n = 6$), in which dolphins were seen near a whale when it was feeding.

Site fidelity

Individual sighting histories varied greatly. Some individuals were sighted only once during the study period, others up to 13 times (median = 2). Of the total of 501 individuals catalogued, 108 (21.5%) were resighted in more than one year, with 15 sighted in four or more consecutive and/or non-consecutive years (3.2%) (Figure 6).

Individuals Tt032 and Tt086 were first documented in 2002 and subsequently resighted 12 and 13 times, respectively, during different months and years until 2012 (Appendix). Individual Tt009 was recorded in eight years, i.e. nearly every year of the study period, with the exception of 2004, 2006 and 2009.

The MMSR was generally low (range 0.12–0.45; median 0.23). Although it appeared to increase with the number of years the dolphins were seen, there was no significant relationship ($H = 6.06$, $df = 6$, $p = 0.41$).

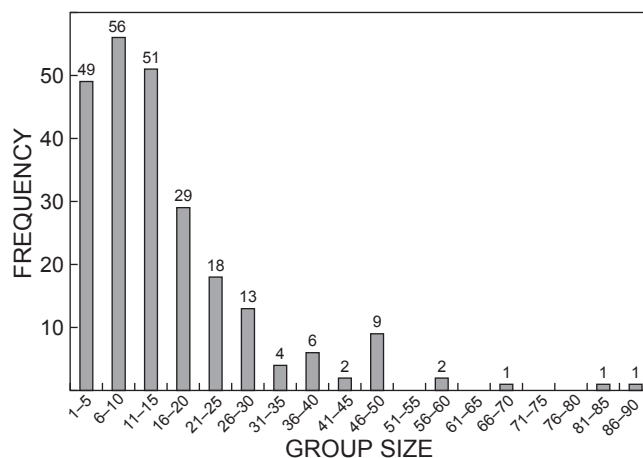


Figure 3: Frequency of group sizes of bottlenose dolphins based on field counts between 2004 and 2012 in the Madeira Archipelago

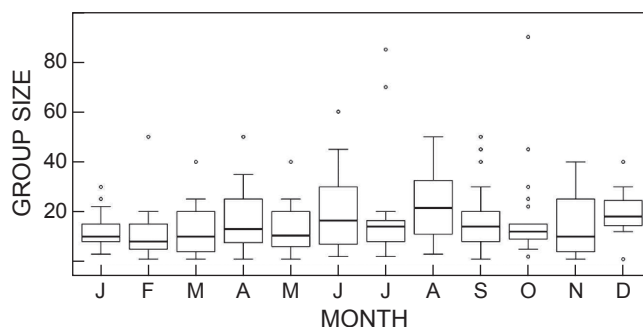


Figure 4: Monthly distribution of group size of bottlenose dolphins. The bottom and top of the box represent the first and third quartiles, respectively; the band inside the box is the median. Vertical bars correspond to maximum and minimum group size and points represent outliers. One-way ANOVA showed no significant difference in group size across months

Table 1: Distance surveyed, number of groups and encounter rate of bottlenose dolphins sighted per year and type of survey from 2004 to 2012

Year	Non-systematic surveys			Systematic surveys			Total	
	Distance surveyed (km)	No. of groups	Encounter rate (sightings per 100 km)	Distance surveyed (km)	No. of groups	Encounter rate (sightings per 100 km)	Distance surveyed (km)	No. of groups
2004	455	17	3.74	652	7	1.07	1 107	24
2005	1 853	17	0.92	—	—	—	1 853	17
2006	2 005	11	0.55	—	—	—	2 005	11
2007	649	6	0.92	919	6	0.65	1 568	12
2008	—	—	—	2 274	15	0.66	2 274	15
2009	—	—	—	500	4	0.80	500	4
2010	953	13	1.36	1 551	10	0.64	2 504	23
2011	3 266	26	0.80	2 510	17	0.68	5 776	43
2012	1 415	20	1.41	1 392	16	1.15	2 807	36
Total	10 596	110		9 798	75		20 394	185

Residency

In total, 441 individuals were seen in association with others over the period 2004–2012. Based on the previously established residency criteria, we assigned 19 residents (4.3%), 41 migrants (9.3%) and 381 transients (86.4%). The social network diagram showed a core network formed by 380 individuals (86.1%) and 12 satellite clusters (range 2–9) with no link to the main cluster, containing a total of 61 dolphins. All individuals present in the satellite clusters were transient, whereas the main cluster comprised dolphins of all three of the residency patterns. The main cluster exhibits the centrality (a measure of a node in the network) of resident dolphins (Figure 7).

LIR analysis revealed that the model in SOCPROG 2.4 that best described the movements of the study population in the Madeira Archipelago was emigration+re-immigration ($a1 = N$; $a2 = \text{res time in}$; $a3 = \text{res time out}$) (Figure 8, Table 2). The model indicates that, on average, 178 individuals were in the study area at any one time and that an individual remained in the study area for an average period

of 90 days. The average time an individual spent outside the study area was estimated at 313 days.

Movement patterns

Transition probabilities were estimated for movements among all sectors within the study area (Figure 2), as well as to an undefined area outside the study area within one day (Table 3). Sectors 2 and 4 were excluded from the analysis on account of the low number of identifications. Sector 3 showed higher probabilities of movements to Sector 8 than movements to any other sector. In addition, movements from Sector 6, which is located between Madeira Island and Porto Santo, were higher to Sectors 1, 7 and 8. Sector 1 was also the area in which dolphins had the highest probability of remaining in the area. The area outside the study area showed relatively high probabilities of movements into it, indicating that dolphins can leave the study area over short periods of time.

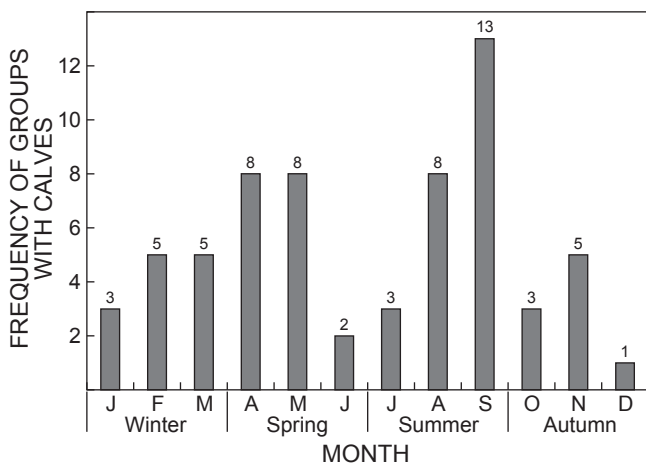


Figure 5: Monthly distribution of bottlenose dolphin groups with calves

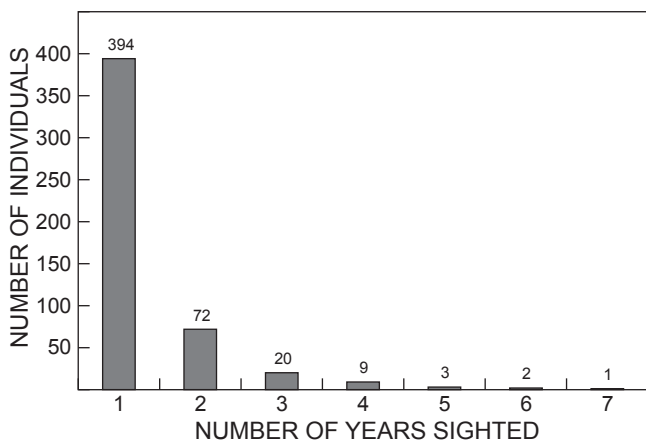


Figure 6: Number of identified bottlenose dolphins in the Madeira Archipelago by number of years in which they were sighted, between 2001 and 2002 and between 2004 and 2012

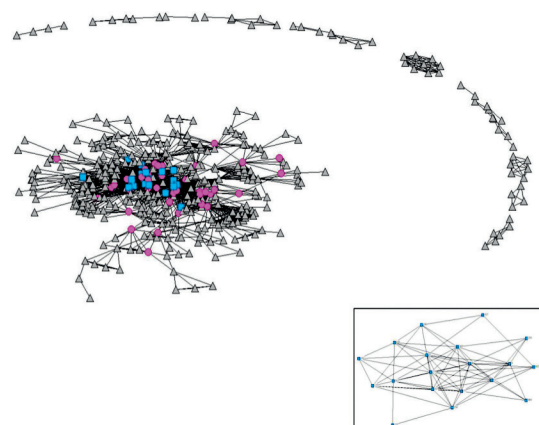


Figure 7: Social network diagram illustrating the associations of 441 dolphins identified in the study area. Individual dolphins are represented by nodes; associations are shown by the lines between nodes. Residents are represented as blue boxes, migrants as pink circles and transients as grey triangles. Inset provides a detailed view of resident dolphins

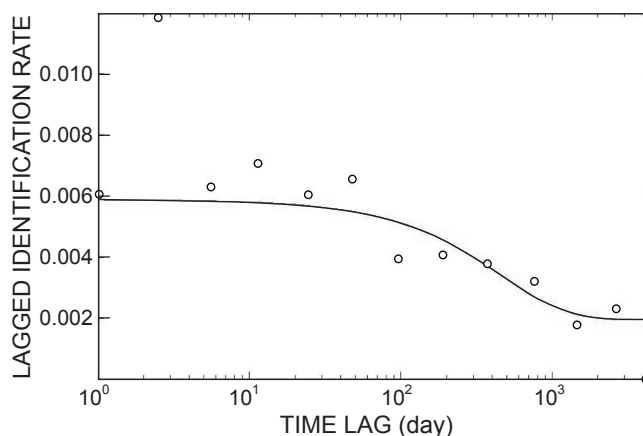


Figure 8: Lagged identification rate (LIR) for all individuals captured between 2004 and 2012, showing the best-fit model from Table 2 (emigration+re-immigration)

Table 2: Models fitted to lagged identification rates (LIRs) for bottlenose dolphins observed in the Madeira Archipelago, using SOCPROG: residence (res) times and movements into and out of the study area, for all individuals captured, between 2004 and 2012. N = estimated population size in the study area; a_1 to a_4 are model parameters; * marks the best-fit model (with the lowest QAIC value)

Model	Maximum-likelihood value for parameters	QAIC value	Summed log likelihood	Mean residence time in study area (days)	Mean residence time outside study area (days)
* $a_1 = N$; $a_2 = \text{res time in}$; $a_3 = \text{res time out}$	$N = 177.890$	7 526.4115	-5 063.831	90.28	312.93
$a_1 = N$; $a_2 = \text{res time in}$; $a_3 = \text{res time out}$; $a_4 = \text{mortality}$	$N = 87.324$	7 528.6852	-5 064.0152	–	–
$a_1 = N$; $a_2 = \text{mean res}$	$N = 200.002$	7 530.5667	-5 067.9744	–	–

Table 3: Probability of individual bottlenose dolphins moving between individual sectors (1–8) and to areas outside the main study area (OUT), within a 1-day period; μ is the probability that an individual remains in a given sector one sampling period later

Sector from	Sector to							μ
	1	3	5	6	7	8	OUT	
1	–	0.1035	0.1180	0.1031	0.1007	0.1081	0.1041	0.9288
3	0.0998	–	0.0994	0.0973	0.1042	0.1267	0.1000	0.3726
5	0.1088	0.1032	–	0.1116	0.0962	0.0965	0.1036	0.3801
6	0.1235	0.0989	0.0748	–	0.1027	0.1040	0.0988	0.3973
7	0.1069	0.0971	0.1040	0.1045	–	0.0977	0.1051	0.3847
8	0.0950	0.1122	0.1071	0.0874	0.1054	–	0.0998	0.3931
OUT	0.0966	0.0979	0.0991	0.1003	0.0894	0.1083	–	0.4084

Discussion

This study provides new information on group dynamics, sighting history, association patterns and probability of movements within and out of the study area of a previously unstudied bottlenose dolphin population in the North-East Atlantic. This work is based on sighting data (242 encounters) and photo-identification data (501 individuals identified) collected over 11 years of surveys and opportunistic whale-watching data.

Group dynamics

The majority of groups of bottlenose dolphins found in the Madeira Archipelago were small (median = 12). This median value was similar to those found in studies of coastal populations of bottlenose dolphins (New Zealand: Constantine 2002; Merriman et al. 2009; Scotland: Einfeld 2003), with other studies also reporting that small groups (3–7 animals) tend to be found in coastal areas (Ben Bearzi et al. 1997; Naceur et al. 2004). One particularly large group in the study area was estimated to consist of 90 individuals, which is consistent with reports that larger groups (up to 35 and as high as 180) are found in offshore waters (Forcada et al. 2004; Cañadas and Hammond 2006). The tendency for bottlenose dolphins to form larger groups when inhabiting more-open, pelagic waters is also observed in other dolphin species (see review by Shane et al. 1986). This might be due to the risk of predation in open habitats and to a change in foraging strategies from predation on solitary prey on reefs or in shallow waters to schooling fish in open water (Norris and Dohl 1980; Wells et al. 1980). In the Madeira Archipelago, it is resident individuals that tend to form small groups typical of

coastal populations, whereas larger groups are likely to be aggregations of transient pelagic dolphins. Lusseau et al. (2003) suggest that features such as geographical isolation and water depth might influence bottlenose dolphin social organisation, which might include group size.

Bottlenose dolphins were recorded in every month of the year in the Madeira Archipelago and groups tended to be larger in summer and autumn, although not significantly so. This is likely owing to the presence of transient pelagic animals during the summer. Groups with calves were recorded year-round, but more often in spring and late summer/autumn. This suggests that there is a preferential period of the year for birthing and calving, as has been reported elsewhere (Wells et al. 1987; Grigg and Markowitz 1997; Mann et al. 2000). Because the risk of predation is low (by e.g. sharks and killer whales) in the Madeira Archipelago, seasonality of birth might be due to the warmer conditions during these months. Mann et al. (2000) suggest that warm water is thermally efficient for small calves or for mothers, but also that food availability might fluctuate sufficiently to favour seasonal births. However, there is insufficient information about prey availability in the Madeira Archipelago to speculate further.

Bottlenose dolphins were associated with other species in 15% of encounters, with short-finned pilot whales being the most frequent associates. Bottlenose dolphins are commonly found in mixed-species groups in pelagic waters (Connor et al. 2000). In the eastern Pacific, a significant increase in mixed groups was found with increasing distance from shore, and 40% of these groups consisted of bottlenose dolphins and short-finned pilot whales (Scott and Chivers 1990). Although common, the interaction is poorly understood. Kraus and Gahr (1971) found scars from squid

suckers on one of two bottlenose dolphins captured in a drive fishery together with a group of 101 pilot whales in the Faeroe Islands. These whales feed extensively on squid (Connor et al. 2000), so the most likely reason for those associations is opportunistic feeding. Recorded associations of bottlenose dolphins with baleen whales might also be related to feeding; whales have been observed lunge-feeding at the surface with bottlenose dolphins in close proximity (AD pers. obs.).

Site fidelity

Despite the large number of dolphins identified and catalogued during the study period ($n = 501$), only a small number of individuals (108 or 21.5%) were resighted in more than one year and an even smaller number (15 or 3.2%) showed long-term site fidelity (i.e. seen in four or more years). Data on sighting frequency indicate that only a small number of dolphins showed high levels of site fidelity. Individuals infrequently resighted also showed some degree of site fidelity to Madeira Island, and individuals seen only once in the study area were likely to be transient pelagic dolphins passing through the archipelago. However, even the individuals with a high level of site fidelity might not always have been present in the study area, because the MMSR was generally low. There was an apparent increase in the MMSR as a function of the number of years an individual was observed, but the relationship was not significant; this is probably due to the fact that few individuals were seen in more than five years. Large populations of dolphins characterised by a low number of resighted individuals are considered typical of open-water habitats (Defran et al. 1999), although they can also occur in coastal environments (Shane 2004). From work conducted in the neighbouring archipelago of the Azores, Silva et al. (2003) speculated that dolphins occurring in the surrounding ocean areas might be drawn to the islands due to the enhanced productivity of waters around them. Hence these island habitats might function as an 'oasis' that attracts several cetacean species that use the area for foraging or as a migration stop. A similar situation appears to occur in the Madeira Archipelago, where different degrees of site fidelity to the islands indicate various patterns of occurrence.

Residency

The Madeira Archipelago seems to have an open population of bottlenose dolphins with only a small proportion (4.3%) of individuals showing residency to the area. All resident dolphins formed a complex network, located in the centre of the main cluster. Satellite clusters were formed exclusively by transient individuals, suggesting that, whereas some transient dolphins mix with residents and migrants, others do not. Individuals Tt86 and Tt32 showed a high level of centrality, indicating that they might act as social brokers that link other individuals, favouring their position in the network (Lusseau and Newman 2004). Similar to the findings of Lusseau and Newman (2004), the removal of those two individuals from the network would not cause the loss of network connectivity. However, some individuals are more important to network connectivity than others, and their removal might cause an effect not immediately evident from a representation of the network (Lusseau

and Newman 2004). The mixture of different patterns of occurrence, represented by residents, transients and migrants, is also apparent in other populations of bottlenose dolphins worldwide (Connor et al. 2000; Silva et al. 2008; Baird et al. 2009), as well as in short-finned pilot whales in the Madeira Archipelago (Alves et al. 2013). In addition, the mixture is reflected in the lack of genetic structure found by Qu  rouil et al. (2007) in the North-East Atlantic, indicating that such associations might serve as a stimulus for gene flow.

From the LIR analysis it was estimated that, on average, an individual remained in the study area for 90 days. Defining some individuals as 'resident', however, does not necessarily imply that they never leave the area; rather, they might travel over a large range that was not covered by our surveys. The LIR curve started to decay after approximately 100 days, indicating that the dolphins leave the area through emigration or mortality. Nevertheless, at about 2.7 years the curve began to level off again, suggesting that some of those individuals that leave the population return to the study area after this period. In addition, this levelling of the LIR curve might be indicative of a mixed population of residents, migrants and transients, as revealed by the social network diagram (Whitehead 2008).

It is emphasised that the terms resident, migrant and transient were assigned according to the sighting frequencies of individuals. Future studies should investigate the possible existence of different communities within the population. Oudejans et al. (2015) pointed out the importance of investigating the existence of primarily 'inshore' and 'offshore' communities for the purpose of long-term management and monitoring of coastal bottlenose dolphin populations.

Movement patterns

Movement probabilities indicate rapid movements among sectors in the Madeira Archipelago. However, survey effort was higher in Sector 3, and hence movements might have been under-represented in the remaining areas. Although transition probabilities were generally low, they seem to indicate movements between Madeira Island and Porto Santo, which are approximately 50 km apart. Sector 1 (Madeira North) had the highest probability of repeated sightings of individuals. Dolphins moving from Sector 3 (Madeira South) showed the highest probability of moving into Sector 8 (Porto Santo North), representing one of the greatest distances covered within the study area. Movements of 50 km in a day by bottlenose dolphins is in accordance with Lynn (1995), who recorded movements up to 55 km in a 12-hour period using radio-tagged dolphins. Similarly, a dolphin was recorded moving 50.2 km in one day in Tampa Bay (Florida) (Mate et al. 1995). Madeira, Desertas and Porto Santo are all within similar ranges.

Sectors 1 and 8 had the highest probabilities of dolphins immigrating from other sectors. They are characterised by having shallower areas than the other sectors. Bottlenose dolphins have been shown to have a preference for shallow waters in other oceanic environments (Silva et al. 2008; Baird et al. 2009, 2013). Further, Dinis (2014) found a strong relationship between depth and the presence of bottlenose dolphins in the Madeira Archipelago, with the majority occurring in depths <1 000 m and no more than

10 km offshore. The strong relationship between depth and the presence of bottlenose dolphins suggests that prey availability plays a fundamental role in dolphin distribution (Fortuna 2006). Hence a potential explanation for movements into Sectors 1 and 8 might include foraging strategies related to the vertical distribution of prey. However, little is known about the diet of bottlenose dolphins in the Madeira Archipelago. In the Azores, Silva (2007) reported the preference of dolphins for shallower waters (100–600 m), where, unlike in open waters, they can take advantage of demersal fish species as well as schooling pelagic prey. A similar strategy might also apply in the Madeira Archipelago. In addition to having shallower waters, Sectors 1 and 8 are relatively exposed. Although the effects of this are unknown, ranging patterns for individuals within a bottlenose dolphin population are driven largely by their particular ecological circumstances (Baird et al. 2009).

The relatively high probability of animals leaving the study area suggests that future studies should include a comparison of identification catalogues with those from neighbouring archipelagos, in order to understand more fully the extent of movements of bottlenose dolphins in Macaronesia.

This study represents a first contribution to knowledge of bottlenose dolphins in the Madeira Archipelago, with the findings having potential management application. The different patterns of occurrence suggest that this population of bottlenose dolphins might segregate into communities that share habitat and resources. This is fundamental in order to distinguish specific management and conservation requirements, and requires further investigation. Despite recent regulation of whale-watching activity, with limits on the number of boats and areas of operation, activity remains highest in summer, mainly in Sector 3, which coincides with one of the peaks in the presence of calves, but the effect is unknown. Furthermore, by preferring shallower waters, the dolphins are subject to increased exposure to anthropogenic interactions, the nature of which requires further study.

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References

Alves F, Querouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L et al. 2013. Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 5: 758–776.

- Auger-Méthé M, Whitehead H. 2007. The use of natural markings in studies of long-finned pilot whale (*Globicephala melas*). *Marine Mammal Science* 23: 77–93.
- Baird RW, Gorgone AM, McSweeney DJ, Ligon AD, Deakos MH, Webster DL et al. 2009. Population structure of island-associated dolphins: evidence from photo-identification of common bottlenose dolphins (*Tursiops truncatus*) in the main Hawaiian Islands. *Marine Mammal Science* 25: 251–274.
- Baird RW, Webster DL, Aschettino JM, Schorr GS, McSweeney DJ. 2013. Odontocete cetaceans around the main Hawaiian islands: habitat use and relative abundance from small-boat sighting surveys. *Aquatic Mammals* 39: 253–269.
- Baird RW, Webster DL, Mahaffy SD, McSweeney DJ, Schorr GS, Ligon AD. 2008. Site fidelity and association patterns in a deep-water dolphin: rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. *Marine Mammal Science* 24: 535–553.
- Ballance LT. 1992. Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science* 8: 262–274.
- Bearzi G, Notarbartolo di Sciara G, Politi E. 1997. Social ecology of bottlenose dolphins in the Kvarneric (northern Adriatic Sea). *Marine Mammal Science* 13: 650–668.
- Bearzi G, Politi E, Agazzi S, Bruno S, Costa M, Bonizzoni S. 2005. Occurrence and present status of coastal dolphins (*Delphinus delphis* and *Tursiops truncatus*) in the eastern Ionian Sea. *Aquatic Conservation: Marine and Freshwater Ecosystems* 15: 243–257.
- Ben Naceur L, Gannier A, Bradai MN, Drouot V, Bourreau S, Laran S et al. 2004. Recensement du grand dauphin *Tursiops truncatus* dans les eaux tunisiennes. *Bulletin Institut National des Sciences et Technologies de la Mer de Salammbô* 31: 75–81.
- Borgatti S. 2002. *Netdraw network visualization*. Harvard, Massachusetts: Analytic Technologies.
- Cañadas A, Hammond P. 2006. Model-based abundance estimates for bottlenose dolphins off southern Spain: implications for conservation and management. *Journal of Cetacean Research and Management* 8: 13–27.
- Connor R, Wells R, Mann J, Read A. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. In: Mann J, Connor R, Tyack PL, Whitehead H (eds), *Cetacean societies: field studies of dolphins and whales*. Chicago: University of Chicago Press. pp 91–126.
- Constantine R. 2002. The behavioural ecology of the bottlenose dolphins (*Tursiops truncatus*) of Northeastern New Zealand: a population exposed to tourism. PhD thesis, University of Auckland, New Zealand.
- Defran R, Weller D, Kelly D, Espinosa M. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. *Marine Mammal Science* 15: 381–393.
- Dinis A. 2014. Ecology and conservation of bottlenose dolphins in Madeira Archipelago. PhD thesis, University of Madeira, Portugal.
- Dinis A, Ribeiro C, Nicolau C, Alves F, Carvalho A, Freitas L. 2009. Common bottlenose dolphin (*Tursiops truncatus*) occurrence, distribution and conservation status in Madeira Archipelago (Portugal). Document SC/61/SM13 presented at the 61st Annual Meeting of the International Whaling Commission, June 2009, Funchal, Madeira.
- Eisfeld S. 2003. The social affiliation and group composition of bottlenose dolphins (*Tursiops truncatus*) in the outer southern Moray Firth, NE Scotland. MSc thesis, School of Biological Sciences, University of Wales, UK.
- Ferreira RB. 2007. Monitoring whale watching activity in Madeira, Portugal. MSc thesis, University of Lisbon, Portugal (in Portuguese).
- Forcada J, Gazo M, Aguilar A, Gonzalvo J, Fernandez-Contreras M. 2004. Bottlenose dolphin abundance in the NW

- Mediterranean: addressing heterogeneity in distribution. *Marine Ecology Progress Series* 275: 275–287.
- Fortuna CM. 2006. Ecology and conservation of bottlenose dolphins (*Tursiops truncatus*) in the north-eastern Adriatic Sea. PhD thesis, University of St Andrews, UK.
- Grigg E, Markowitz H. 1997. Habitat use by bottlenose dolphins (*Tursiops truncatus*) at Turneffe Atoll, Belize. *Aquatic Mammals* 23: 163–170.
- Ingram S, Rogan E. 2003. Bottlenose dolphins (*Tursiops truncatus*) in the Shannon estuary and selected areas of the west-coast of Ireland. Unpublished report to the National Parks and Wildlife Service.
- Kendall W, Nichols J, Hines J. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78: 563–578.
- Kraus C, Gahr M. 1971. On the presence of *Tursiops truncatus* in schools of *Globicephala melaena* on the Faroe Islands. *Investigating Cetacea* 3: 180–182.
- Lusseau D, Newman MEJ. 2004. Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B: Biological Sciences* 271(Suppl. 6): S477–S481.
- Lusseau D, Schneider K, Boisseau OJ, Haase P, Slooten E, Dawson S. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations: can geographic isolation explain this unique trait? *Behavioral Ecology and Sociobiology* 54: 396–405.
- Lynn S. 1995. Movements, site fidelity, and surfacing patterns of bottlenose dolphins on the central Texas coast. MSc thesis, Texas University, USA.
- Mann J, Connor R, Barre L, Heithaus M. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology* 11: 210–219.
- Martinho F. 2012. Residency and behavioural patterns of coastal bottlenose dolphin (*Tursiops truncatus*) in the Arrabida and Troia shores (Portugal). MSc thesis, Universidade de Lisboa, Portugal.
- Mate B, Rossbach KA, Nieukirk SL, Wells RS, Irvine AB, Scott MD, Read AJ. 1995. Satellite-monitored movements and dive behavior of a bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science* 11: 452–463.
- Merriman M, Markowitz T, Harlin-Cognato A, Stockin K. 2009. Bottlenose dolphin (*Tursiops truncatus*) abundance, site fidelity, and group dynamics in the Marlborough Sounds, New Zealand. *Aquatic Mammals* 35: 511–522.
- Newman M. 2004. Analysis of weighted networks. *Physical Review E* 70: 056131 (9 pp).
- Norris KS, Dohl TP. 1980. The behavior of the Hawaiian spinner porpoise, *Stenella longirostris*. *Fishery Bulletin* 77: 821–849.
- Oudejans MG, Visser F, Englund A, Rogan E, Ingram SN. 2015. Evidence for distinct coastal and offshore communities of bottlenose dolphins in the North East Atlantic. *PLoS ONE* 10: e0122668.
- Pradel R, Hines JE, Lebreton JD, Nichols JD. 1997. Capture–recapture survival models taking account of transients. *Biometrics* 53: 60–72.
- Quérouil S, Silva MA, Freitas L, Prieto R, Magalhães S, Dinis A et al. 2007. High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics* 8: 1405–1419.
- R Development Core Team. 2012. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Scott M, Chivers S. 1990. Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In: Leatherwood S, Reeves R (eds), *The bottlenose dolphin*. San Diego: Academic Press. pp 387–402.
- Scott M, Wells RS, Irvine AB. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. In: Leatherwood S, Reeves R (eds), *The bottlenose dolphin*. San Diego: Academic Press. pp 235–244.
- Shane S. 2004. Residence patterns, group characteristics, and association patterns of bottlenose dolphins near Sanibel Island, Florida. *Gulf of Mexico Science* 1: 1–12.
- Shane S, Wells R, Würsig B. 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science* 2: 34–63.
- Silva MA. 2007. Population biology of bottlenose dolphins in the Azores archipelago. PhD thesis, University of St Andrews, UK.
- Silva MA, Prieto R, Magalhães S, Cabecinhas R, Cruz A, Gonçalves J, Santos RS. 2003. Occurrence and distribution of cetaceans in the waters around Azores (Portugal), summer and autumn 1999–2000. *Aquatic Mammals* 29: 77–83.
- Silva MA, Prieto R, Magalhães S, Seabra MI, Santos RS, Hammond PS. 2008. Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. *Marine Biology* 156: 179–192.
- Wells R, Irvine A, Scott M. 1980. The social ecology of inshore odontocetes. In: Herman L (ed.), *Cetacean behavior: mechanisms and functions*. New York: John Wiley and Sons. pp 263–317.
- Wells R, Scott M. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Report of the International Whaling Commission* (Special Issue 12): 407–415.
- Wells R, Scott M, Irvine A. 1987. The social structure of free-ranging bottlenose dolphins. In: Genoways H (ed.), *Current mammalogy*. New York: Plenum Press. pp 247–305.
- Whitehead H. 2007. Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communication in Statistics – Simulation and Computation* 36: 1233–1246.
- Whitehead H. 2008. *Analysing animal societies: quantitative methods for vertebrate social analysis*. Chicago: University of Chicago Press.
- Whitehead H. 2009. SOCPROG programs: analysing animal social structures. *Behavioural Ecology and Sociobiology* 63: 765–778.
- Wilson B, Thompson PM, Hammond PS. 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology* 34: 1365–1374.
- Würsig B, Jefferson T. 1990. Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission* (Special Issue 12): 43–52.

Appendix: Capture histories of the most-resighted bottlenose dolphin individuals

