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Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic

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Abstract

Aim: The knowledge of a species biogeographical patterns greatly enhances our understanding of geographical ecology, which can improve identifying key conservation needs. Yet, this knowledge is still scarce for many marine top predators. Here, we aim to analyse movement patterns and spatial structuring of a large predator, the short-finned pilot whale *Globicephala macrorhynchus*, over a wide geographical area.

Location: North-east Atlantic, in Macaronesian archipelagos (Azores, Madeira and Canaries) and Iberian Peninsula (Sagres).

Methods: We used likelihood techniques to estimate residency times and transition probabilities and carried out social analysis from individual photographic

identification data, and analysed year-round distribution from effort-related sightings, collated between 1999 and 2015.

Results: The best-fitting models included emigration and reimmigration and showed different residency times within each archipelago. A total of 26 individual movements from 21 individuals (from a sample of >2,300 individuals) were recorded between Madeira and the neighbouring archipelagos, and heterogeneous transition probabilities were estimated within and between areas. A social network diagram showed associations from animals with distinct residency patterns. Higher significant sighting rates were recorded during autumn in the Azores and Madeira.

Main conclusions: The variation in site fidelity and year-round occupancy among areas of the Macaronesia is consistent with some degree of population structuring, which combined with a connectivity network and seasonal inflows from animals inhabiting offshore waters, support the development of a complex social and geographical ecology in short-finned pilot whales. The combination of techniques applied in this study was an effective way to estimate parameters of movement, which could be a good practice to be used for other scenarios and species.

1 | INTRODUCTION

The movements of individual members of a population can cover a wide range of spatial and temporal scales, resulting in migratory patterns that may overlap or connect with a particular locality (Sprogis, Raudino, Rankin, MacLeod, & Bejder, 2015; Whitehead, 2001). Such connectivity, or functional linkages, between animals (or habitats), can influence population dynamics and viability through a variety of mechanisms, including demographic rescue or the avoidance of inbreeding (Keller & Waller, 2002; Vasudev & Fletcher, 2016). Thus, knowledge of a species biogeographical patterns greatly enhances our understanding of geographical ecology, which can improve identifying key needs for conservation between areas.

Increasing global anthropogenic pressures is leading to population fragmentation in many marine organisms (Halpern et al., 2008; Jones, Srinivasan, & Almany, 2007). Large-sized top predators, such as cetaceans (marine mammals), which play an important role in maintaining the structure and functioning of the environment they inhabit, are especially affected (Bowen, 1997; Roman et al., 2014). The repeated occurrence of top predators in an area may indicate high local prey abundances and, thus, high biological productivity (Joiris, 1991; Jungblut, Nachtsheim, Boos, & Joiris, 2017). Therefore, the understanding of the population ecology and biogeographical patterns of marine top predators is crucial for conservation management. This is even more relevant in the case of highly mobile pelagic predators that can move unrestricted across oceanic areas, where this information is more difficult to obtain, and where their

conservation status is unknown, as in the case of the target species of the present study.

The short-finned pilot whale (*Globicephala macrorhynchus*) is a large-sized delphinid that performs deep vertical dives and presents large horizontal movements (de Soto et al., 2008; Quick et al., 2017; Wells et al., 2013). It has a wide distribution from tropical to warm-temperate waters (Olson, 2009), and on a global scale, its conservation status is described as data deficient and its population trend is unknown (IUCN, 2017). In the north-east Atlantic, the species is considered common in the biogeographical region of Macaronesia (which includes the archipelagos of the Azores, Madeira and Canaries), especially around the Canaries and Madeira where it is consistently among the most frequently sighted cetacean species reported throughout the year (Alves et al., 2018; Servidio, 2014; Silva et al., 2014), but only sporadically in the surrounding waters of the Iberian Peninsula (e.g., Nores & Pérez, 1988).

Insight into the movement patterns of short-finned pilot whales in the study region has been successfully derived from individual photographic identification (hereafter photo-identification). In the Canaries and Madeira, and to a lesser extent in the Azores, it showed that individual whales demonstrate variability in site fidelity and comprise residents, regular visitors and transients (Alves, Quérouil, et al., 2013; Mendonça, 2012; Servidio, 2014). In the Canaries and Madeira, social analyses have showed they live in a well-differentiated society that encompasses several clans, each containing few matrilineal pods/units (Alves, Quérouil, et al., 2013; Servidio, 2014). Additionally, the use of mark–recapture techniques derived high abundance estimates (over 600

individuals) for the south-west of Tenerife Island (Canary archipelago) and lower numbers (approximately half) for the south of Madeira Island (Alves et al., 2015; Servidio, 2014). In Madeira, high survival rates (within the range of other long-lived mammals) have also been estimated (Alves et al., 2015). Moreover, genetic analyses suggested that individuals within the resident, visitor and transient communities inhabiting Madeiran waters may not be genetically isolated but breed across these communities (Alves, Quérouil, et al., 2013). Those analyses also suggested that small groups are made up of related individuals with long-lasting relationships and that large groups are probably temporary associations of smaller groups. The available information on movement patterns for the sampled population supports that these animals display wide-ranging movement patterns and utilize several habitats within the pelagic waters of the Macaronesia, yet little is known of the movement patterns across areas and the relationship among these groups.

The existence of photo-identification data of naturally well-marked short-finned pilot whales collected opportunistically since the late 1990's and regularly since the early 2000's in Macaronesia, and of effort-related sightings collected systematically over the latter period, provided an excellent opportunity to assess movement patterns, connectivity and spatial structuring in this top predator. Our first specific goal was to estimate residency times in each area, thus providing information on the movements into and out of each archipelago. Such estimates are only available for the Canaries (Servidio, 2014), which were compared with data obtained from the other archipelagos. Our second specific goal was to estimate transition probabilities throughout the wide-scale habitat available to short-finned pilot whales in Macaronesia. Our third specific goal was to analyse individual association patterns in order to allow for a visualization of the population linkages and help interpreting the movements in a social context. Finally, the fourth specific goal was to analyse the temporal distribution patterns of this species in Macaronesia, where it is common, and in an adjacent area, where it is sighted only sporadically (Sagres, Iberian Peninsula). The former goals were based on the comparison of an unprecedented number of individual identifications in this species, whereas the latter made use of the longitudinal sighting data sets. Combining both types of data provided a more comprehensive analysis of the short-finned pilot whales movements and contributed to a more general understanding of their occurrence in the north-east Atlantic.

2 | METHODS

2.1 | Study areas

Four areas distributed across the north-east Atlantic were investigated (Figure 1). These included the oceanic archipelagos of the Macaronesia (Azores, Madeira and Canaries) and an adjacent coastal habitat in the Iberian Peninsula (Sagres). The study area spans 20° longitude and 11° latitude from a subtropical to a temperate region,

covering a vast area of the short-finned pilot whale's range in this part of the Atlantic (Olson, 2009).

The Macaronesian archipelagos share natural, geological, climatological and oceanographic aspects, given their volcanic origin and their relative proximity (hundreds of kilometres) (Kim et al., 2008). Nevertheless, there are latitudinal separations, especially between the warm-temperate (Azores, Madeira and Canaries) and tropical (Cape Verde) archipelagos. Spalding et al. (2007) identified ecoregions based on the species that inhabit them, oceanographic characteristics and the presence of specific ecosystems, and considered the Azores, Madeira and Canaries as one province within the Lusitanian ecoregion. While the waters of this province are mainly oligotrophic (Martins et al., 2007), the marine ecosystem off the south-western tip of Europe (Sagres) is influenced by nutrient-enriched cold waters from an upwelling regime off the west Portuguese coast and by outflow from the Mediterranean (Iorga & Lozier, 1999; Lemos & Pires, 2004).

2.2 | Data collection

2.2.1 | Photo-identification data

Photo-identification data from short-finned pilot whales were collated as part of a major collaborative study involving nearly 30 organizations throughout the north-east Atlantic (see authors' affiliations and "Acknowledgments"). These included governmental and nongovernmental, public and private organizations, conducting either dedicated or opportunistic photo-identification surveys.

Most data were obtained from the Azores, Madeira and Canaries, where the species is more frequently observed and where it has been the focus of a number of long-term studies (Alves, 2013; Mendonça, 2012; Servidio, 2014). Three main photo-identification catalogues, one from each of those areas, were used to estimate residency within each area and transition probabilities between areas and to carry out social analysis. In the Azores, the photo-identification data were collected mainly in the south of Faial, Pico and São Miguel Islands (central and east groups), from 1999 to 2015, during dedicated and opportunistic (whale-watching) surveys. In Madeira, the data were collected in the south of Madeira and between Madeira and Desertas Islands, from 2003 to 2015, on platforms of opportunity (whale-watching boats). In the Canaries, the data were collected around all the islands, from 1999 to 2012, during dedicated surveys.

Additional data, which included small photo-identification catalogues and/or isolated photographic material (i.e., individual captures not previously compared to any catalogue), were used to help assess movement patterns between areas. This included data from the Azores collected between 2004 and 2015, from the Canaries between 1993 and 2015 and from Sagres in 2014 and 2015.

In each area, the collection of photographs of short-finned pilot whales followed standard procedures (Würsig & Jefferson, 1990). Photographs were made from a close distance, both on the left- and right-side, independently of age/sex class and dorsal fin distinctiveness. Photo-identification data included location and date. Film

cameras were used in early years, and digital cameras were used starting in approximately 2003. Time constraints limited full photographic coverage of some encounters during the opportunistic surveys.
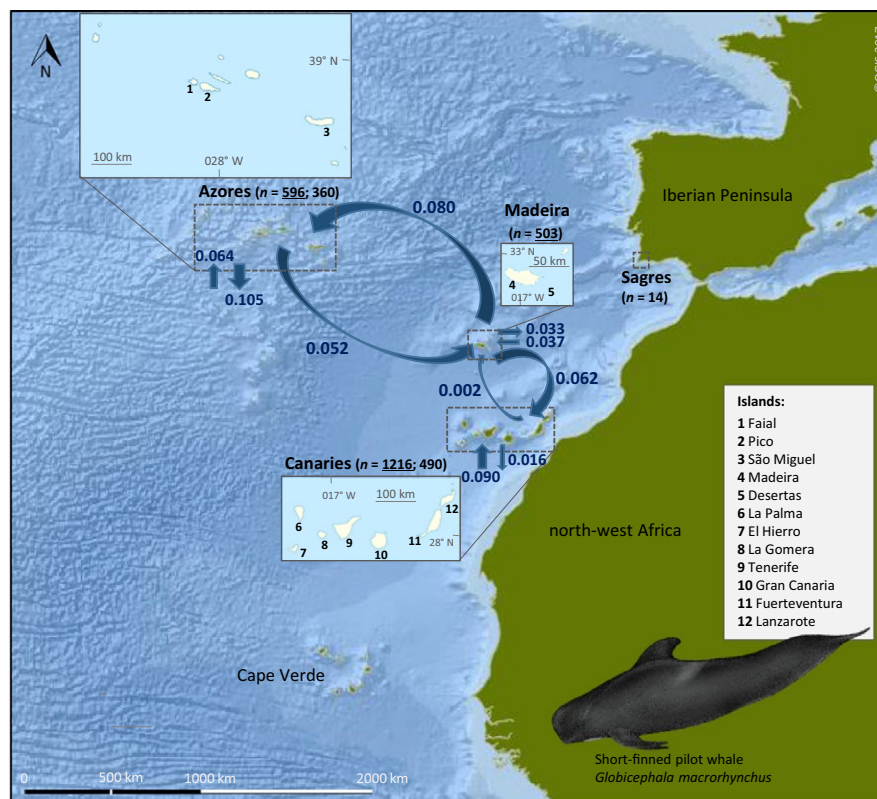
2.2.2 | Sighting data

Different sources of effort-related sightings data collected under favourable conditions (i.e., mainly with Beaufort sea state ≤3) were used to characterize the occurrence of short-finned pilot whales throughout the year in the study area given that this was difficult to obtain with photo-identification data. These were partial and unpublished data from long-term (i.e., decadal) projects carried out in each area to collect data on cetaceans for a number of different aims and are summarized in Table 1. Although the sighting data included the collection of several biological parameters (e.g., group size, behaviour and presence of calves), this study used only data related to the presence of the target species (see "Data analysis—Temporal distribution").

In the Azores, land-based data were preferred to boat-based surveys data, given that the latter were insufficient to characterize

the species occurrence during winter, and were compiled by MARE-IMAR (see affiliations). Sighting data were collected year-round from a vantage point by an experienced lookout that worked for whale-watching companies, from May 1999 to November 2001, and January 2006 to January 2012. The vantage point was situated on the southern coast of Pico Island (central group), and the lookout searched an area of approximately 800 km^2, extending from the shoreline to 22 km offshore, using 15 × 80 mm binoculars. Data on sighting effort were collected for each period of continuous observation (ranging from 1 to 3 hr). Details of this methodology are given in Silva et al. (2014).

In Madeira, sighting data compiled by OOM were collected from nautical surveys on-board platforms of opportunity (whale-watching boats). These included a 15-m ketch and a 23-m catamaran that depart and arrive from Funchal harbour and operate bidaily trips that last 3 hr under daylight, irrespective of the season. The trips search for cetaceans, without any species in particular, and use one experienced observer that scans the area up to the horizon assisted with 7 × 50 binoculars. The surveys were conducted year-round between January 2005 and December 2015, off the south and east of Madeira Island (up to the Desertas Islands). The surveys covered

FIGURE 1 Location of the four areas (and islands) across the north-east Atlantic, where photographic and sighting data of short-finned pilot whales were obtained. *n* (underlined) indicates the number of naturally well-marked catalogued individuals used to estimate residency and transition probabilities, while the nonunderlined indicates the number of additional well-marked whales used to help analysing movement patterns. The arrows width and values illustrate heterogeneous transition probabilities between the Azores, Madeira, Canaries and an outside area (see Supporting Information Appendix S1). These probabilities consider the proportion of the population moving between areas within a period of 10 days, using a parameterized Markov model. The 10-day period should allow movements between these areas, based on their distance and the mean travelling speed of 100 km per day (see "Methods"). The figure is not projected as equidistant, and the migratory pathway between areas is merely schematic. Illustration by Fishpics/ImagDOP [Colour figure can be viewed at wileyonlinelibrary.com]

approximately 800 km^2, up to 20 km off the coast. Details of this methodology are given in Alves et al. (2018).

In the Canaries, sighting and search effort data were collected during dedicated nautical surveys carried out between January 1999 and October 2012 by SECAC. Effort has been heterogeneous in terms of time, sampling areas, observers or platforms used, but have generally covered all months of the year and all islands, up to 30 km of the coast. Details of the methodology of these surveys are given in Servidio (2014).

In Sagres, the access to the cetacean sightings database of the whale-watching and research company Mar Ilimitado was used to provide additional information on the distribution of the target species. Sighting and search effort data were collected during regular bidaily trips (ranging from 1.5 to 2.5 hr) throughout the year, between July 2005 and November 2016. The platforms of opportunity used were rigid inflatable boats that searched for cetaceans in an area of approximately 550 km^2 around the south-western tip of Europe, up to 15 km off the coast.

2.3 | Photo-identification procedures

The compilation of each digital catalogue and the creation of the respective data set of individual-specific encounter (hereafter "capture") histories were based on photo-identification of individuals (Würsig & Würsig, 1977). The catalogues were compiled by MARE-IMAR (and update by OOM), by OOM, and by SECAC, respectively, for the Azores, Madeira and Canaries (see Supporting Information Appendix S2 for the number of captures per year and area).

Fin matching consisted of comparing the best processed image, that is, cropped around the dorsal fin and with adjusted contrast, of each individual that was identified with an alphanumeric code. Matching was based primarily on the number of unique notches on the dorsal fin, which allowed matching left- and right-side independently (Alves, Quérouil, et al., 2013; Urian et al., 2015). A notch was defined as an indentation in the leading or trailing edge of the dorsal fin, identifiable from both sides (Auger-Méthé & Whitehead, 2007). Other secondary features such as fin shape or scars were only used to confirm matches. This study used only well-marked individuals and high-quality images following distinctiveness and photograph quality categories described in Alves, Quérouil, et al. (2013), thus increasing the certainty of matches and minimizing false negatives.

To facilitate photo-identification comparisons, individuals were grouped according to the number of notches present (1, 2, 3, 4 or >4). First, individuals from the same group were compared. If no match was found, then the individual being analysed was compared to individuals from the following or preceding group, that is, with one more or one less notch. This substantially reduced the amount of effort required to match individuals, with a minimum loss of possible matches given the low rate of mark change found in this species in the study area, where a new mark event was recorded every 6.6–8.0 years (mean = 7.3; Alves, Quérouil, et al., 2013), and the duration of this study. Comparison was carried out visually (e.g., Robbins et al., 2011; Wilson, Hammond, & Thompson, 1999) by the same person (AA) at the OOM, and all matches were then confirmed by two experienced researchers (FA and AD). Only matches with 100% certainty by all three researchers were used in the present study.

TABLE 1 Summary of the search effort (in number of days with >2 hr of search effort) and sightings (in number of days with presence) of short-finned pilot whales analysed per month in the Azores, Madeira, Canaries and Sagres. In the Azores, the data were collected from land-based observations in the south of Pico Island between 1999 and 2001 and between 2006 and 2012. In Madeira, data were collected from platforms of opportunity operating in the south of Madeira between 2005 and 2015, whereas in the Canaries they were collected from dedicated boat-based visual surveys around all islands between 1999 and 2012. In Sagres, data were collected from platforms of opportunity between 2005 and 2016

	Azores		Madeira		Canaries		Sagres	
Month	Days with surveys	Days with sightings	Days with surveys	Days with sightings	Days with surveys	Days with sightings	Days with surveys	Days with sightings
1	36	4	286	70	91	18	6	0
2	61	1	248	76	145	38	8	0
3	107	0	282	37	138	23	18	0
4	159	1	280	23	117	23	56	0
5	226	12	313	56	172	39	42	0
6	239	37	324	51	140	39	68	0
7	272	37	337	54	212	54	201	0
8	262	49	340	77	199	74	293	0
9	238	42	320	134	176	30	187	2
10	113	21	257	117	144	42	114	0
11	73	15	288	111	71	20	16	0
12	29	4	252	69	81	25	2	0
Total	1,815	223	3,527	875	1,686	425	1,011	2

2.4 | Data analysis

2.4.1 | Residency in each area

We used likelihood techniques to estimate parameters of movement models (Whitehead, 2001). This allowed dealing with the effort associated in collecting the individual identifications that had been neither randomly nor systematically distributed in space–time. To estimate residency times, we applied the initial models developed by Whitehead (2001). These models provided an opportunity to analyse movements into and out of each archipelago, which is known to occupy only a portion of the animals' range (Alves, Quérouil, et al., 2013; Miralles, Oremus, Silva, Planes, & Garcia-Vazquez, 2016).

The amount of time individuals spent within each area was examined by estimating lagged identification rates (LIRs). The LIR is the probability that an individual identified in the study area at time τ will be identified again within the study area after a certain time lag (Whitehead, 2001). This was estimated only for the Azores and Madeira as LIRs had already been estimated for the Canaries (Servidio, 2014; see "Discussion"), and there were insufficient photo-identification data from Sagres.

Movements into and out of each area were investigated using the capture histories of the catalogued individuals from each area. Sampling period was defined as day and associations as individuals grouped within an encounter. The LIRs were subsequently compared to the expected LIRs from exponential mathematical models (Table 2), and the models were fitted to the data using maximum likelihood and binominal loss (Whitehead, 2009). Given that over

dispersion is an important aspect to consider in mark–recapture data, an estimation of the over dispersion factor, also called variance inflation factor, was obtained by dividing the chi-squared statistic by the number of degrees of freedom (Burnham & Anderson, 2002; Lebreton, Burnham, Clobert, & Anderson, 1992). Whereas a variance inflation factor between one and three is indicative of over dispersion in the data, a value >3 may represent more fundamental problems with the data (Lebreton et al., 1992). Given that the variance inflation factor of the LIRs was <3 in the present study, we proceeded with the analysis. The model with the lowest quasi-Akaike information criterion (QAIC) was selected as providing the best fit to the data (Whitehead, 2009). Precision (_SE_) was estimated using a bootstrap method on each sampling period. The analysis was performed with the compiled version of socprog 2.7 (Whitehead, 2009).

2.4.2 | Movements between areas

Transition probabilities for movements between the Azores, Madeira and Canaries were estimated using a parameterized Markov model developed by Whitehead (2001), making use of Hilborn's (1990) method. 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 potential permanent emigration from all areas during a defined period (Whitehead, 2009). In addition, an undefined area, representing the entire area outside each sampled area, was included in the analysis to account for movements from a specific area to a nonsurveyed area.

TABLE 2 Models fitted to lagged identification rates (LIRs) for short-finned pilot whales captured in the Azores between 1999 and 2015, and in Madeira between 2003 and 2015. The LIRs estimate residence times and movements into and out of the study area. Models ranked by the quasi-Akaike information criterion (QAIC); the lowest (in bold) indicates the best-fitting model and represents the model fitted to the LIR graph. Model parameters: a1 = estimated population size in the study area, a2 = residence time in, a3 = residence time out and a4 = mortality. Parameter values for best-fitting model for the Azores: a1 = 175.3, a2 = 12.7 and a3 = 149.2; and for Madeira: a1 = 57.2, a2 = 5.1, a3 = 4.1 and a4 = 11.5e-05

Area				
Model				
Equation	**Explanation**	**Number of parameters**	**QAIC**	**Summed log likelihood**
Azores				
(1/a1)*((1/a3)+(1/a2)*exp(-(1/a3 + 1/a2)*td))/(1/a3 + 1/a2)	Emigration + reimmigration	3	**298.48**	−1,055.30
(1/a1)*exp(-td/a2)	Emigration/mortality	2	302.05	−1,075.29
(1/a1)	Closed	1	302.70	−1,084.78
(exp(-a4*td)/a1)*((1/a3)+(1/a2)*exp(-(1/a3 + 1/a2)*td))/(1/a3 + 1/a2)	Emigration + reimmigration + mortality	4	306.05	−1,075.28
Madeira				
(exp(-a4*td)/a1)*((1/a3)+(1/a2)*exp(-(1/a3 + 1/a2)*td))/(1/a3 + 1/a2)	Emigration + reimmigration + mortality	4	**53,645.80**	−76,243.16
(1/a1)*exp(-td/a2)	Emigration/mortality	2	53,648.01	−76,251.99
(1/a1)*((1/a3)+(1/a2)*exp(-(1/a3 + 1/a2)*td))/(1/a3 + 1/a2)	Emigration + reimmigration	3	53,649.65	−76,251.47
(1/a1)	Closed	1	53,696.11	−76,323.19

To address the fact that short-finned pilot whales could not move between areas within a day, the sampling period was defined as 10 days (H. Whitehead, Dalhousie University, pers. comm.). We considered that such a period of time should be enough to travel the maximum distance between individual matches used in this analysis (i.e., 1,000 km between São Miguel Island in the Azores and Madeira, see Figure 1 and Table 3). This was based on the mean travelling speed of about 100 km per day obtained from one short-finned pilot whale tracked with a satellite-linked transmitter in the west Atlantic (Wells et al., 2013). That individual travelled nearly 1,500 km during 15 days over abyssal depths, which are similar to the depths occurring between the sampled areas in Macaronesia.

Movements between areas were investigated based on a combined data set of the capture histories of the three catalogues. In the combined data set, the alphanumeric individual code with matches between areas was modified (e.g., Gma_MAC01) in order to identify them during the analysis of transition probabilities. The compiled

data set was truncated to include only data collected between 2004 and 2015. This was due to most effort, and all individual matches between areas have occurred during that period, thus simplifying the modelling. Sagres was not included in the analysis due to insufficient photo-identification data. The analysis was performed with the compiled version of SOCPROG 2.7 (Whitehead, 2009).

The additional photo-identification data were used to help assess movements between all areas, but were not used to estimate transition probabilities, in order to avoid bias in the analysis. The additional data from the Azores and the Canaries obtained from multiples sources could impose false negatives.

2.4.3 | Social analysis

A social network diagram was created using NETDRAW 2.158 (Borgatti, 2002) to illustrate individual association patterns. The analysis was centred on the animals that moved between areas and on those captured together with them (i.e., during the same encounter), covering

TABLE 3 Information on the 21 individuals with matches between areas (A—Azores, M—Madeira and C—Canaries). These total 26 individual movements between areas: five from Madeira to the Azores, nine from the Azores to Madeira, eight from Madeira to the Canaries and four from the Canaries to Madeira. While Gma_MAC09 was obtained from additional data used to help analysing movement patterns, the remaining individuals were used to estimate transition probabilities

From	Individuals ID	Minimum distance travelled (km)	Maximum duration travelling	Area (Island)	No. of captures (of each individual, respectively)	Date of capture
Madeira to Azores						
	Gma_MAC01, 02, 03, 04 and 05	1,000	49 days	M (Madeira)	50, 42, 39, 44 and 51	2003–2015 (regularly)
				A (São Miguel)	2, 2, 2, 2 and 2	02 and 12-June-2015
Azores to Madeira						
	Gma_MAC01, 02, 03, 04 and 05	1,000	77 days	A (São Miguel)	2, 2, 2, 2 and 2	02 and 12-June-2015
				M (Madeira)	50, 42, 39, 44 and 51	2003-2015 (regularly)
	Gma_MAC06, 07 and 08	930	125 days	A (São Miguel)	1, 1 and 1	08-August-2011
				M (Madeira)	1, 1 and 1	11-December-2011
	Gma_MAC09	1,200	1.93 years	A (Pico)	1	11-August-2013
				M (Madeira)	1	16-July-2015
Madeira to Canaries						
	Gma_MAC18 and 19	550	2.83 years	M (Madeira)	1 and 1	10-June-2007
				C (Lanz./ Fuertev.)	1 and 1	12-April-2010
	Gma_MAC20, 21, 22, 23, 24 and 25	590	20 days	M (Madeira)	1, 1, 1, 1, 1 and 1	08-September-2004
				C (La Gomera)	1, 1, 1, 1, 1 and 1	28-September-2004
Canaries to Madeira						
	Gma_MAC14 and 15	520	8.38 years	C (La Gomera)	1	24-February-2006
				M (Madeira)	2 and 1[a]	09-July-2014, 12-August-2015
	Gma_MAC16	480	3.44 years	C (La Palma)	1	16-February-2010
				M (Madeira)	1	25-July-2015
	Gma_MAC17	550	4.88 years	C (Lanz./ Fuertev.)	1	12-April-2010
				M (Madeira)	2	06-March-2015, 29-November-2015

[a]Gma_MAC15 was captured on 09-July-2014.

all their possible associations. Including all (>2,000) individuals would difficult visualization and interpretation, and moreover, a comprehensive social analysis is already available for the Canaries (Servidio, 2014) and Madeira (Alves, Quérouil, et al., 2013).

Area of capture and residency pattern was included as individual attributes. Three residency patterns were considered based on the individual capture histories. Individuals that exhibited multiyear and year-round site fidelity (captured ≥5 times in at least 3 years and 3 seasons, that is, spring, summer, autumn and winter) were termed residents; individuals captured within a 10-day period were termed transients; and individuals that fell between these thresholds were considered visitors (adapted from Alves, Quérouil, et al., 2013).

2.4.4 | Temporal distribution

Monthly sighting rates of short-finned pilot whales were calculated for all four areas. This provided information on year-round species distribution from areas with different habitat use, which helped to understand movements within and between those areas (e.g., indicate possible flows/migratory tendencies). Because the research groups used different methodologies and platforms, which resulted in different detection probabilities, a binomial (presence–absence) approach was applied to all data. This minimized the introduction of potential spatial and temporal correlation in the data (de Stephanis et al., 2008; Panigada et al., 2008). Additionally, it helped standardize the data, thus facilitating data interpretation throughout the studied areas. Nevertheless, comparisons between areas should be made with caution due to having different detection probabilities.

Given the nature of the data, and that consecutive observations were collected close together in space–time, all sightings made during the same day were pooled and considered only as one presence. Days with low coverage (i.e., <2 hr of search effort) were excluded from the analysis to avoid small sample biases. The data were then analysed as the proportion of days (%) with sightings of short-finned pilot whales, taking the number of days with trips (i.e., effort) into account. Month was used as a sampling unit, and the SE was calculated to indicate interannual variability.

Inferential statistics were used to assess whether the monthly sighting rates were significantly different ($\alpha = 0.05$) within each area. Nonparametric tests were used for the data set from the Azores given that the assumptions of parametric tests were not met. A Kruskal–Wallis rank sum test was followed by the Steel–Dwass post hoc test. The one-way ANOVA test, followed by a post hoc Tukey test, was used independently for the data sets from Madeira and Canaries. No tests were used for the data set from Sagres due to insufficient number of sightings. All analyses were carried out using the R 3.4.0 statistical package (R Core Team, 2017).

3 | RESULTS

3.1 | Residency in each area

The best-fitting model for the LIR within the Azores was the Emigration + Reimmigration (Table 2). It indicates that 175

individuals ($SE = 60$), out of 596 used in this analysis, spent an average of 12.7 days ($SE = 4.5$) in the area before leaving for 149.2 days ($SE = 55.6$; Figure 2). The 596 individuals were obtained from 122 sampling periods (of 1 day) and 678 identifications (i.e., captures).

In Madeira, the best-fitting model was the Emigration + Reimmigration + Mortality (Table 2). It indicates that 57 individuals ($SE = 4$), out of 503 used in this analysis, spent an average of 5.1 days ($SE = 4.6$) in the area before leaving for 4.1 days ($SE = 3.8$), with a mortality of <0.001 (Figure 2). The 503 individuals were obtained from 319 sampling periods (of 1 day) and 1,811 identifications.

3.2 | Movements between areas

Twenty-one individuals were identified moving between areas on 26 individual occasions. These include five from Madeira to the Azores, nine from the Azores to Madeira (of which five were from the same individuals that moved from Madeira to the Azores), eight from Madeira to the Canaries and four from the Canaries to Madeira (Table 3). These individuals showed a large degree of variability in site fidelity to
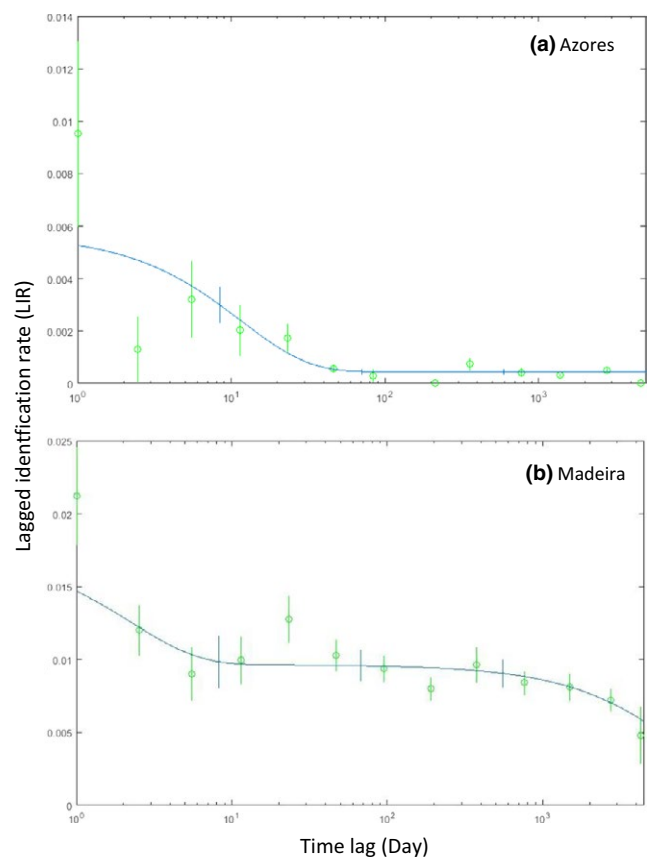
FIGURE 2 Lagged identification rates (LIRs) for short-finned pilot whales captured in (a) the Azores between 1999 and 2015, and (b) Madeira between 2003 and 2015. The graph depicts the probability that an individual captured at time "0" will be identified again at time x within the study area. Line represents the best-fit model according to Table 2, and vertical bars indicate SE calculated using bootstrap method on each sampling period [Colour figure can be viewed at wileyonlinelibrary.com]

each area. While the individuals Gma_MAC01-05 showed strong site fidelity to Madeira, the remaining animals were captured only once or twice in each area. The temporal scale of individual movements between areas ranged from 20 days to 8.38 years (Table 3). Only one individual match (Gma_MAC09) was made by comparisons between a catalogue (from Madeira) with additional data (from Azores, Pico Island) and was also the maximum distance between matches recorded in a straight line (1200 km). The remaining 20 individuals were obtained from the comparison of photo-identification catalogues and thus could be used to estimate transition probabilities. No matches were obtained between the Azores and the Canaries (and vice versa), nor between Sagres with any other area.

Transition probabilities were slightly higher from Madeira to the Azores (0.080), followed from Madeira to the Canaries (0.062) and from the Azores to Madeira (0.052) (Figure 1, Supporting Information Appendix S1). Movements from the Azores to outside areas were higher than vice versa, and movements from the Canaries to outside areas were lower than vice versa. Movements between Madeira and outside areas were similar (Figure 1, Supporting Information Appendix S1). The truncated compiled data set was based on 2,120 individuals obtained from 240 sampling periods (of 10 days) and 3,872 identifications (i.e., captures).

3.3 | Social analysis

The social network diagram comprised 209 individuals from 92 encounters from three areas (three encounters from the Azores, 84 from Madeira and five from the Canaries). Nine individuals were captured in both Madeira and the Azores, 12 in both Madeira and the Canaries and the remaining in single areas (23 in the Azores, 88 in Madeira and 77 in the Canaries) (Figure 3).

A total of 35 individuals were identified as residents, 37 as visitors and 137 as transients. All residents and 73% of visitors were from Madeira, whereas in the Azores all individuals included in the
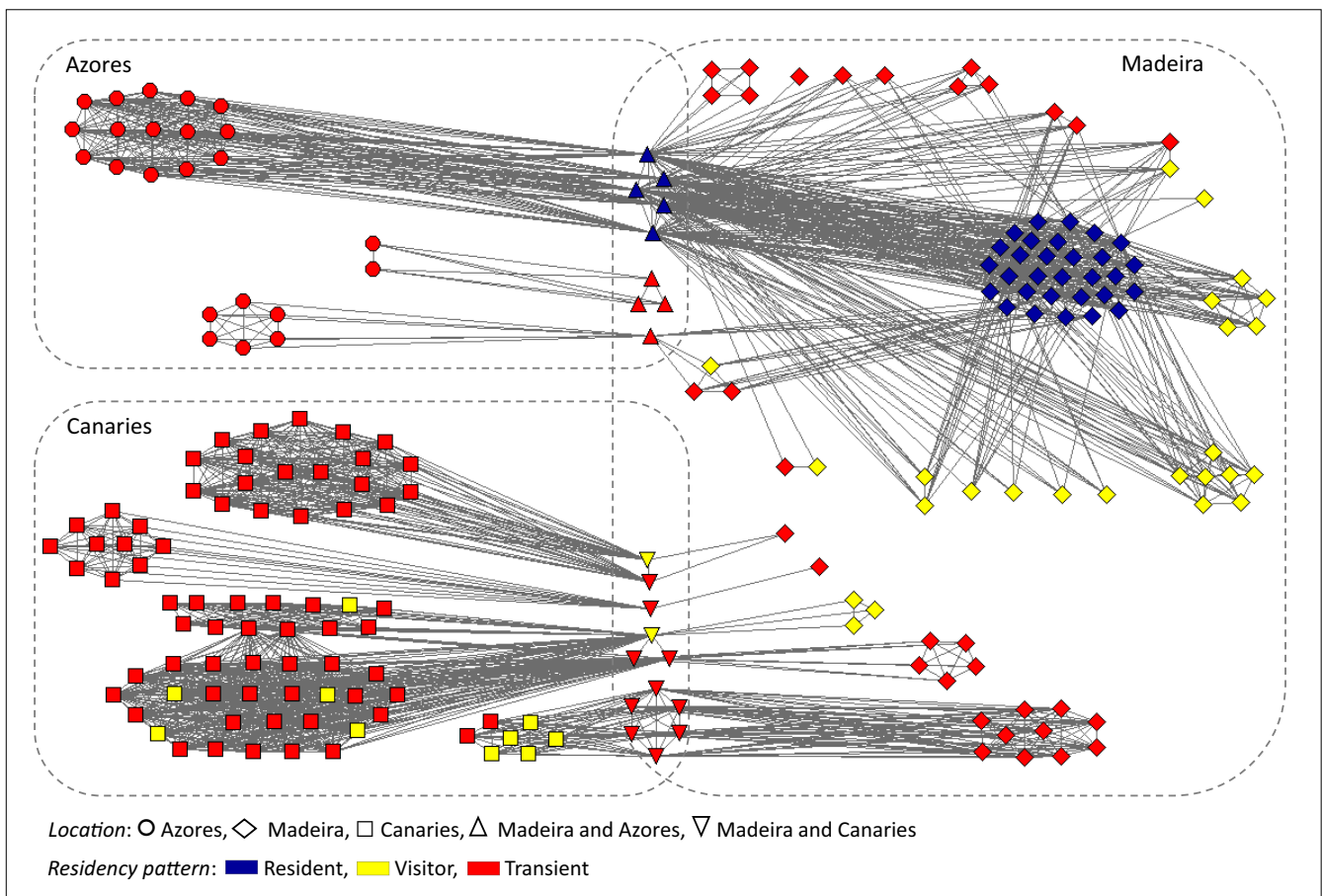
FIGURE 3 Social network diagram showing associations for the 21 short-finned pilot whales captured in different areas of the Macaronesia (nine in Madeira and the Azores [triangle up], and 12 in Madeira and the Canaries [triangle down]). Nodes correspond to individuals, while lines between nodes represent the presence within a group. Symbol shapes and colours indicate individuals' area of capture (Azores, Madeira, Canaries, Madeira and Azores, or Madeira and Canaries) and residency pattern in each area (resident if captured ≥5 times in at least 3 years and three seasons, transient if captured within a 10-day period, and visitor if fell between these thresholds), respectively. The 21 individuals' ID is sequential from top to bottom (i.e., top is Gma_MAC01 and bottom is Gma_MAC25), following the identifications given in Table 3. The residency patterns of these 21 individuals were based on the number of captures for Madeira (Table 3) given that recaptures of these individuals in a single area occurred only in Madeira. The diagram comprises 209 well-marked individuals (based on high-quality images) and shows a complex network diagram involving individuals with different residency patterns from different areas. Note that the absence of social network between the groups Madeira–Azores and Madeira–Canaries does not exclude its possibility [Colour figure can be viewed at wileyonlinelibrary.com]

diagram were identified as transients. In the Canaries, 10 individuals were identified as visitors and the remaining as transients. The diagram shows that five animals identified as residents in Madeira were captured with other animals in the Azores and, similarly, that two animals identified as visitors in Madeira were captured with other animals in the Canaries. It also shows that none of the clusters composed by the individuals captured in Madeira and the Azores were linked to the clusters composed by the individuals captured in Madeira and the Canaries.

3.4 | Temporal distribution

Although there was a heterogeneous distribution in search effort throughout the year in each area (especially in the Azores and Sagres), high coverage was achieved in all calendar months (Table 1, Figure 4). In the Azores, a total of 223 days with sightings were recorded during 1,815 days of land-based observations (corresponding to 12.3% of the surveyed days). In Madeira, short-finned pilot whales were sighted during 875 out of 3,527 surveyed days (24.8%), whereas, in the Canaries, 425 days with sightings were recorded during 1,686 days of surveys on effort mode in the whole period (25.2%). In Sagres, there were only two days with short-finned pilot whale sightings, out of 1,011 days with boat surveys (0.2%) (Table 1). These two sightings were from the same group (based on photo-identification analysis) and sighted one year apart (September 2014 and September 2015).

A general pattern of higher sighting rates was observed during the autumn months, especially in the Azores and Madeira, and less evident in the Canaries (where sighting rates were relatively homogeneous throughout the year). In Sagres, although there were only two days with sightings, these were also recorded near autumn (Figure 4). There were significant differences in the monthly sighting rate in the Azores (p = 0.007), although the post hoc test showed no significant differences in the interactions of all months. In Madeira, significant differences (p < 0.001) were found mainly between the autumn and the remaining months. No significant differences were found in Canaries (p = 0.905).
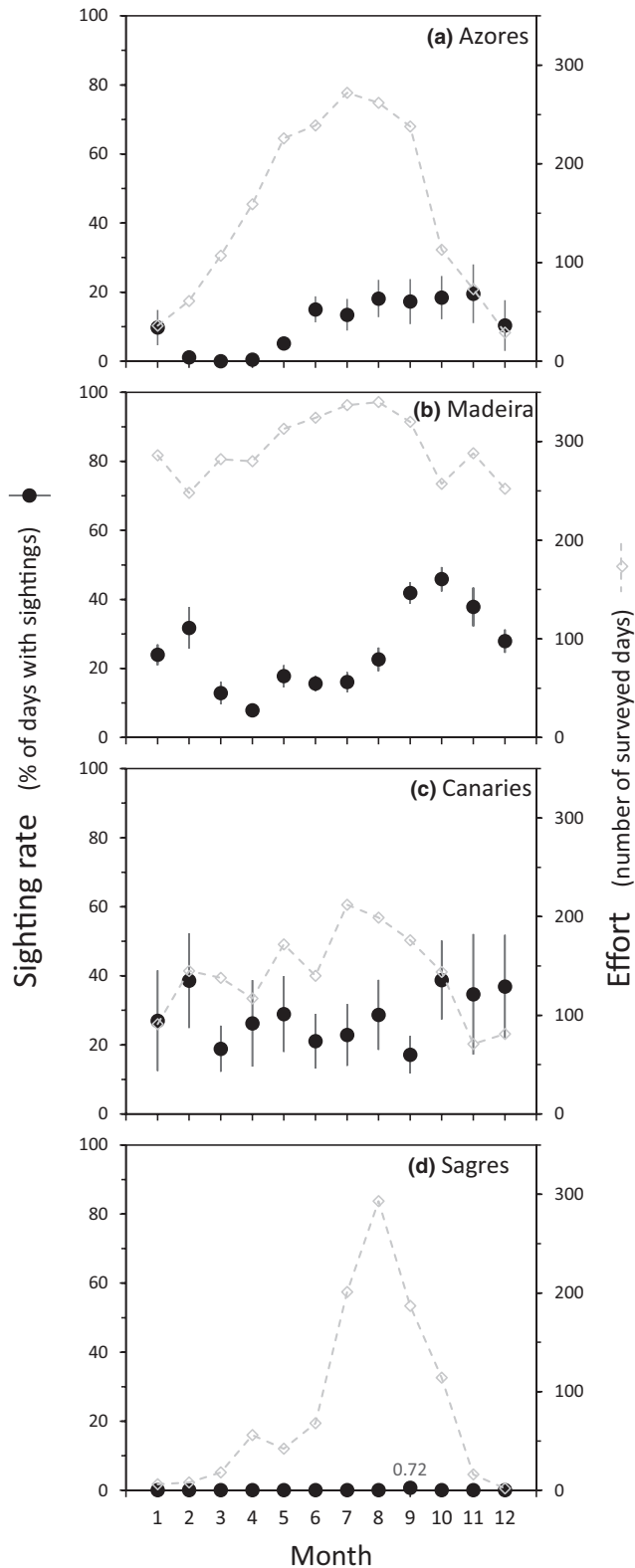
4 | DISCUSSION

Information on the geographical ecology of large marine organisms over a wide scale has relied mainly on the use of satellite telemetry, genetic analyses, sightings or photo-identification data (Amos, Schlötterer, & Tautz, 1993; Benson et al., 2011; Durban & Pitman, 2012; Jungblut et al., 2017; Whitehead, Coakes, Jaquet, & Lusseau, 2008; Whitney, Robbins, Schultz, Bowen, & Holland, 2012). In this study, and although analysed independently, the combination of two noninvasive techniques based on long time-scales of individual photo-identifications and of effort-related sightings was an effective way to estimate parameters of movement and analyse year-round presence of short-finned pilot whales in a large area. By doing so, and addressing movements in a social context, we provide relevant

information on biogeographical patterns and population linkages, which may contribute to the conservation of such large predator species across the north-east Atlantic.

Our investigation showed good agreement between residency times, transition probabilities, social context and temporal distribution in the study area, from which five broad main results have emerged. First, the differences in the number of recaptured individuals between areas suggest spatial structuring. Such heterogeneity was inferred from the number of catalogued individuals compared to the number of identifications (i.e., captures). Madeira, with 503 catalogued individuals from 1,811 identifications (28%), contrasts with the Azores (596 from 678, 88%) and the Canaries (1,216 from 1,578, 77%) (Supporting Information Appendix S2). Nevertheless, such differences could also reflect different local population sizes and the degree of sampling of each. Moreover, the surveyed area in the Canaries covered all islands, while in the Azores and Madeira it covered only a small part of the archipelagos. This likely resulted in a higher percentage of new individuals for the Canaries than if a smaller areas have been used, such as off the south-west of Tenerife or of La Gomera where resident communities are found (Servidio, 2014; FR, unpublished data). Therefore, it is suggested that short-finned pilot whales have higher site fidelity to Madeira, as well as to the Canaries (but in a lesser extent), than to the Azores. Additionally, the fact that the only two sightings (recorded one year apart) in Sagres belong to the same group adds support to the occurrence of spatial structuring in this species.

Second, the best-fitting models for the Azores and Madeira (from the LIR analysis), as well as for the entire Canaries Archipelago (from Servidio, 2014), included emigration and reimmigration, which suggests temporary migration into and out of each area and transiency. Additionally, it shows heterogeneity in residency times between areas. A higher number of individuals spent more time in the Azores and the Canaries than in Madeira, but also left for longer periods in the former areas than in the latter. In the Azores, 175 individuals spent an average of 13 days in the area before leaving for 149 days (SE shown in Results), and in the Canaries, 254 individuals (SE = 10) spent an average of 531 days (SE = 24) before leaving for 4,087 days (SE = 941) (Servidio, 2014), whereas, in Madeira, only a small number of individuals moved more regularly between the study area and an outside area (i.e., within few days, Table 2). This suggests a more constant presence of individuals in Madeira, which supports the previous point. The heterogeneity in residency times between areas suggests different habitat roles and supports species spatial structuring in this region of the Atlantic.

Third, the individual matches between areas together with the social analysis of all its associations indicated some degree of connectivity in Macaronesia. The individual matches occurred in a temporal scale varying from days to nearly one decade, and both ways between Madeira and the Azores, and between Madeira and the Canaries. These individuals showed a large degree of variability in site fidelity, that is, most animals were captured only once or twice, with five captured regularly during 13 years in Madeira (Table 3, Figure 3). Additionally, apart from the five residents in Madeira

FIGURE 4 Mean (±SE) monthly sighting rates (left y-axis) and search effort (right y-axis) for the (a) Azores, (b) Madeira, (c) Canaries and (d) Sagres. Comparisons between areas should be cautious due to using different methods. Data were collected from the following: (a) land-based observations in the south of Pico Island between 1999 and 2001 and between 2006 and 2012; (b) platforms of opportunity operating daily in the south of Madeira Island between 2005 and 2015, (c) dedicated boat-based visual surveys around all Canary Islands between 1999 and 2012 and (d) platforms of opportunity operating daily in the south coast of Sagres between 2005 and 2016. Vertical bars indicate interannual variability. Sighting data were collected from the same area of the photographic data

The fact that most of the individuals that moved were captured only once or twice suggests that the majority of those that move are part of a pelagic population passing through the area, rather than resident groups. This suggests that, as a species, there is variability in home range size. Such variability, which includes large home ranges (>1,000 km in farthest distance), has also been shown in this species in the west Atlantic, which support our findings (Thorne et al., 2017; Wells et al., 2013).

Fourth, the estimates in transition probabilities between areas suggest complex movement patterns within Macaronesia. While transition probabilities were similar (ranging between 5% and 8% of the population) between the Azores and Madeira (both ways) and from Madeira to the Canaries, a much lower percentage (0.2%) was estimated for movements from the Canaries to Madeira. Transition probabilities between each area and an outside area also differed, with more variable values for the Azores and the Canaries, and consistent values for Madeira (Figure 1, Supporting Information Appendix S1), which was consistent with the LIR analysis. This suggests that the area of the Azores is probably more used for passage (i.e., mainly by temporary migrants and transients, and only by a low number of animals with a high degree of site fidelity; frequency of sighting rates shown in Mendonça (2012)), whereas Madeira and the Canaries are visited by temporary migrants and transients but also host a high number of animals with strong geographical fidelity. Nevertheless, the matches, and consequently the transition probabilities, are likely to be underestimated given the possibility of (an undetermined number of) false negatives. Additionally, due to the pilot whales hierarchical social pattern (i.e., living in stable groups of related individuals (Olson, 2009)), the documented 26 individual movements (from at least seven groups, Figure 3, Table 3) may not represent independent movements and could have also contributed for the movement analysis to be underestimated. Although the social network diagram shows that some of the individuals that moved are part of larger groups, in cases when only one or two were captured it could have been due to incomplete sampling or due to having restricted the analysis to well-marked animals from high-quality images. Yet, and although the estimates could be slightly biased, we are confident in the overall results and what they represent.

Fifth, the temporal distribution data showed a general pattern of higher sighting rates during autumn months in all archipelagos, that were captured with animals in the Azores, some transients and visitors that moved between areas were captured with individuals from known (resident and visitor) populations in the destination archipelago (Figure 3). Still important for the social context is to note that the residents and visitors that moved between areas were also captured during other occasions in larger aggregations in Madeira.

especially in the Azores and Madeira. It also showed occasional visits to the south-west tip of the Iberian Peninsula during September. These findings together with the absence of significant intra-annual variations in group sizes in the Azores, Madeira and the Canaries (Alves, Quérouil, et al., 2013; Mendonça, 2012; Servidio, 2014)—which indicates that a higher sighting rate corresponds to an increase in the number of animals in the area instead of a division into smaller units—suggest that some short-finned pilot whales inhabiting pelagic offshore waters move during a particular season of the year to oceanic islands/coastal waters of the north-east Atlantic, especially to those over 32° latitude north. We suggest that these animals represent an undetermined proportion of a metapopulation and that they may live in offshore waters of the Macaronesia or far more out such as of the west or south Atlantic during the rest of the year. Wide inshore/offshore movements mainly associated with foraging activity have been recorded in this species off the east–west coasts of the United States (Shane, 1995; Thorne et al., 2017), but none showed a clear specific seasonal pattern as described in our study. Additionally, higher sighting rates were obtained for Madeira and the Canaries (Figure 4), which support the importance of these two archipelagos for the species. However, the use of different detection probabilities and areas surveyed among regions does not allow having robust conclusions on the comparison between regions. Possible biases include obtaining lower sighting rates from larger areas or from areas less used/preferred by the whales. It is known that short-finned pilot whales prefer habitats located between the 1000 and 2500 m isobaths and in submarine canyons (Abecassis et al., 2015; Thorne et al., 2017), and in our study, those habitats comprised most of the surveyed areas (Alves et al., 2018; Servidio, 2014; Silva et al., 2014), thus minimizing bias. Nevertheless, researchers should standardize a sampling method in future surveys to allow comparing densities.

As an overview, our study has identified individual (or group) variation in site fidelity and year-round occupancy among areas of the Macaronesia, as well as movements between these areas, which suggest ecological spatial structuring. Such a spatial component is consistent with some degree of population structuring, which combined with the connectivity network (between some of the areas/ archipelagos and an outside area) suggest that short-finned pilot whales have developed a complex social and geographical ecology. Although the social analysis has showed that none of the clusters composed by the individuals captured in Madeira and the Azores were linked to the clusters composed by the individuals captured in Madeira and the Canaries, the absence of genetic population differentiation in this species in the study area (Alves, Quérouil, et al., 2013; Miralles et al., 2016) suggests that it may be an artefact of an insufficient sample size and that it supports the findings described here. Ecological spatial structuring has been also suggested for other delphinid populations occupying large areas, that is, over hundreds or thousands of kilometres. Examples include populations of long-finned pilot whales (*Globicephala melas*) in the north Atlantic (Monteiro et al., 2015), of killer whales (*Orcinus orca*) in the northeast of the Pacific and the Atlantic (Dahlheim et al., 2008; Foote, Similä, Víkingsson, & Stevick, 2010), of bottlenose dolphins (*Tursiops*

truncatus) in northern Atlantic and Pacific archipelagos and in the Mediterranean (Baird et al., 2009; Bearzi, Bonizzoni, & Gonzalvo, 2011; Silva et al., 2008; Tobeña et al., 2014) and of false killer whales in Hawai'i (Baird et al., 2008).

In less productive habitats such as oceanic waters, animals are expected to maintain larger home ranges because they need to range further to find sufficient food (Sandell, 1989; Silva et al., 2008). This seems to be a general pattern in large predators (Ford, 1983; Stevick, McConnell, & Hammond, 2002) and has been documented in several marine mammals such as large toothed and baleen whales (e.g., Frantzis, Airoldi, Notarbartolo-di-Sciara, Johnson, & Mazzariol, 2011; Prieto, Tobeña, & Silva, 2017; Stevick et al., 2006). Although an animal's distribution is linked in a scale-dependent manner to the distribution and predictability of their principal prey (Fauchald, Erikstad, & Skarsfjord, 2000; Stevick et al., 2006), other reasons likely contribute to variations in migration and dispersal of marine top predators. These include reproductive strategies, intra- and interspecific competition or, as more recently suggested, physiological maintenance (Durban & Pitman, 2012; Greenwood, 1980; Ramos et al., 2016; Sandell, 1989). In the case of the short-finned pilot whale, most studies investigating their movement patterns and population structure have focused in areas smaller than the species ranging capability (Abecassis et al., 2015; Alves, Quérouil, et al., 2013; Mahaffy, Baird, McSweeney, Webster, & Schorr, 2015). The exception are studies distinguishing (at least) two morphotypes in the Pacific (Oremus et al., 2009; Van Cise, Roch, Baird, Mooney, & Barlow, 2017; Van Cise et al., 2016). Those morphotypes have broad latitudinal ranges, suggesting their distributions are likely driven by complex factors, such as prey distribution, rather than sea surface temperature (Van Cise et al., 2016). In Hawai'i, satellite tagging data combined with active acoustic surveys and oceanographic modelling suggested that the deep mesopelagic boundary prey community is key to a food web that supports insular cetacean populations (Abecassis et al., 2015). In the Canaries and Madeira, bio-logging studies showed that both resident and transient whales made deep dives associated with foraging (Alves, Dinis, et al., 2013; de Soto et al., 2008; Jensen, Perez, Johnson, de Soto, & Madsen, 2011). Despite these studies, a good understanding of the environmental conditions in relation to this species dynamics is still lacking in Macaronesia, so we can only hypothesize that feeding and/or mating or thermal constraints are key drivers of the species complex biogeographical patterns. The use of environmental niche models and satellite-linked telemetry could help explore this further and thus should be considered.

Our study indicates that the adaptive movement of short-finned pilot whales over a wide latitudinal and longitudinal range supports an ecological connectivity network in Macaronesia. This reduces genetic isolation and, due to them being top predators, acts as a biological vector, playing an important role in the ecosystem in this part of the Atlantic. Additionally, short-finned pilot whales are considered abundant from tropical to warm-temperate waters (Olson, 2009). However, based on the present study and on the available literature, we suggest that the species is not homogenously distributed,

nor plays the same ecological role, across its range in the north-east Atlantic (see Alves et al., 2015; de Boer, Saulino, Van Waerebeek, & Aarts, 2016; Hazevoet & Wenzel, 2000; Picanço, Carvalho, & Brito, 2009; Servidio, 2014; Silva et al., 2014). We suggest that the inshore waters of Madeira and the Canaries play an important role for short-finned pilot whales in this part of the Atlantic. Moreover, surveys carried out around all the islands of these two archipelagos showed that the species occurs mainly in the south-east of Madeira Island and in the south-west of Tenerife Island (Alves, 2013; Servidio, 2014). Therefore, these two small areas should be of higher priority in management decisions at both local and broader scale given their importance for the species in the north-east Atlantic. Overall, the wide geographical and oceanic nature of our study, large sample size, combination of two methodologies and the use of robust techniques to investigate movement provided new insights into the biogeographical patterns and population ecology of short-finned pilot whales, which could be a good practice to be used for other scenarios and species.

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CONFLICT OF INTEREST

We have no competing interests.

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BIOSKETCH

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SUPPORTING INFORMATION

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