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Dynamics of short-finned pilot whales long-term social structure in Madeira

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Abstract

The associations of social individuals are normally represented by a social network, which is a static representation of dynamic relationships, generally influenced by spatio-temporal, demographic, environmental and kinship drivers. We examined the social structure of core resident short-finned pilot whales off Madeira, an archipelago in the Northeast Atlantic, delineating their spatial overlapping, temporal evolution, demographic process and site fidelity, between two sub-periods (1997–2013 and 2014–2019). Decades of individual photo-identification work showed that social clusters were formed by preferred companions. The results indicate that this short-finned pilot whale community consists of social clusters, with most individuals showing long-term stability of cluster membership. However, clusters can be also subject to dynamic changes, and sometime split up into two which may be due to an increase in the number of individuals in the original cluster and, consequently, challenges to maintaining associations among individuals in large groups. In general, the probability of associations among core resident individuals within a cluster decreased with time (decreased by half in 18–54 years), which was related to demographic events. All clusters showed highly overlapping distribution areas, suggesting that their social structure is not driven by spatial factors but likely social preferences.

Keywords Dynamic network · *Globicephala macrorhynchus* · Island-associated cetaceans · Madeira archipelago—Northeast Atlantic · Spatial overlap · Social structure

Introduction

Social animals tend to form complex systems of associations among individuals, creating organizational patterns known as social structure (e.g. Whitehead 2008a). Demographic events such as birth, death or migration can affect social structures, sometimes having structure-wide and long-lasting consequences (Shizuka and Johnson 2020). A highly social individual will possibly join (either by immigration or birth) a social structure with multiple connections (e.g. Gero et al. 2013); conversely, the dispersal (either by permanent emigration or death) of a highly social individual will probably reduce the network connectivity (e.g. Elliser and Herzing 2011).

Various cetacean species show different social structure aspects, both at inter and intra-species levels which makes generalization complicated. However, some traits can be shared between species or populations and help us better interpret observations made in other species or populations. For example, several killer whale (*Orcinus orca*) populations have a stable kin-based social structure based on matrilines (e.g. Guinet 1991; Esteban et al. 2016a), where even a lack of dispersal, for both sexes, from their natal groups has been confirmed in some populations (e.g. Bigg et al. 1990; Tavares et al. 2017). Sperm whales (*Physeter macrocephalus*) also have a stable matrilineal social structure; however, males disperse from their natal group (Lyrholm and Gyllensten 1998; Whitehead and Weilgart 2000). Several studies also support the notion of a stable matrilineal kin-based structure for pilot whales (*Globicephala* spp.).

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First, genetic studies in short-finned pilot whales (*Globicephala macrorhynchus*; Fig. A1) show that the most closely related individuals occur within groups which suggest natal philopatry to the group (Alves et al. 2013; Van Cise et al. 2017). Second, mature male long-finned pilot whales (*Globicephala melas*) sampled from drive fisheries in the Faroe Islands neither mate within, nor disperse from their natal groups (Amos et al. 1993). However, the large groups sampled during these fisheries may not reflect typical kin-based group size for pilot whales (Connor 2000). Third, no evidence of sexual segregation has been found in the association networks for long-finned pilot whales (Augusto et al. 2017). Finally, short-finned pilot whales exhibit a long post-reproductive period (Marsh and Kasuya 1984, 1986), which development has been suggested as a result of their demographic structure, i.e. females surviving beyond the point of reproductive cessation (Foote 2008), but also the balance between costs and benefits to aid other group members fitness (Ellis et al. 2018). However, some studies suggest non kin-based social structure for pilot whales, such as multiple matrilines found within mass stranded groups of long-finned pilot whales (Oremus et al. 2013) and among short-finned pilot whales encountered together several times over multiple years (Hill et al. 2019). Other studies question the stability of their associations, short-term associations have been noted in long-finned pilot whales that lasted from hours to days (Ottensmeyer and Whitehead 2003) and, for both species, bachelor groups of young and mature males have been found (Desportes et al. 1992; Mahaffy et al. 2015), suggesting at least temporary male dispersal. Nevertheless, pilot whales are generally assumed as one of the mammals with stable social structure based on preferred associations (Heimlich-Boran 1993; Siemann 1994; Ottensmeyer and Whitehead 2003; de Stephanis et al. 2008; Alves et al. 2013; Servidio 2014; Mahaffy et al. 2015). In summary, there is still much to discover about the social structure of pilot whales, however, these studies indicate an intermediate matrilineal kin-based social structure for pilot whales, with association stability between that of sperm whales and killer whales (Mahaffy et al. 2015).

Social species, with stable long-lasting associations, normally have key individuals which form bonds with individuals of several social units and maintain the interconnection of the complete network (Lusseau and Newman 2004). Cohesion in killer whale social networks appears to be dependent on a small number of key female juveniles (Williams and Lusseau 2006). In fact, deaths due to illegal long-line fishery disrupted social groups of depredating killer whales, resulting in decreased fitness of survivors (Busson et al. 2019). In short-finned pilot whales, older females have fewer calves but lactate longer, which is attributable to the prolonged nursing of their own calves (Kasuya and Marsh 1984; Marsh and Kasuya 1991) and, consequently, the death of an older mother could substantially reduce the survival probabilities of several dependent young, as suggested by Marsh and Kasuya (1991). Stable social structures are thus potentially vulnerable to the removal of certain key individuals.

Short-finned pilot whales (hereafter pilot whales) are one of the most frequently observed species off Madeira (geographic location of Madeira is shown in Fig. 3A) throughout the year (Freitas et al. 2004). Most individuals have low re-sighting rates, with 68% of animals seen only once, named transients; 11% of individuals seen more than five times in at least three years and three seasons, named residents; and the remaining animals (21%) seen more than once but less frequently than the residents, named visitors (Alves et al. 2013). Alves et al. (2013) described a structured society with long-lasting associations and no genetic difference among transients, visitors and residents (Alves et al. 2013). Among the 503 individuals identified in Madeira, twelve visitors and transients were also seen in the Canaries, while nine residents and transients were observed in the Azores, but none of the animals were identified in all three archipelagos (Alves et al. 2019).

In a pelagic population, such as the pilot whales off Madeira (Alves et al. 2013), animals that spend most of their time inshore could be more exposed to anthropogenic threats that tend to concentrate near coastlines, where cumulative risks for marine mammal species have been described (Avila et al. 2018). Although population boundaries in these marine ecosystems are challenging to define (Taylor et al. 2000), the identification of adequate countable units is crucial for effective management of wildlife (Roff et al. 2013).

The aim of this study was to evaluate the social structure, and potential structural changes over time (a period of 22 years), of the pilot whales off the coast of Madeira that spend most of their time in nearshore waters. First, we describe the social structure of most regularly observed individuals, defining social groups with preferred companions, named cluster, calculating several social features between and within those clusters and between two sub-periods. Second, we test if the association probability changed over the entire study period, for all individuals and also within clusters. Third, we evaluate any changes in regards to site fidelity and demographic process. Finally, we evaluate whether individuals from different social clusters exhibited differences in the spatial use of the study area.

Methodology

Data sampling

Field work was conducted during a period of 22 years (1997–2019) in Madeira archipelago, which is in the Central Northeast Atlantic, approximately 1000 km southwest of the Iberian Peninsula. Intraplate volcanism generated the archipelago and a group of seamounts in the surroundings (Geldmacher et al. 2000). Complex bathymetry such as the one found in this region normally provides rich habitat for marine predators (Hazen et al. 2013).

Data was collected from different platforms, beginning opportunistically in 1997, then year-round from dedicated systematic and non-systematic surveys from 2001 onwards and from platforms of opportunity, mainly whale watching (WW) boats, since 2003, and finally from 2010 onwards by observers on board WW boats, trained by the Madeira Whale Museum (MWM). Whenever pilot whales were encountered, dorsal fin pictures were taken of both sides of the individuals, and whenever possible the GPS locations were recorded both from dedicated and opportunistic platforms. From 1997 until 2002, pictures were taken with an analog camera mounted with 70–300 mm lenses, with color slide films. Since 2003 digital cameras were used with image stabilizer lenses ranging from 70 to 400 mm. Animals were considered in the same encounter when they were less than ten body lengths of one another and engaged in similar and/or coordinated behavior (Fig. A1A; Williams and Lusseau 2006) during a day (i.e. the sampling period).

The MWM photo-identification database from 1997 to 2011 (Alves et al. 2013) was reanalyzed to include the use of secondary marks, such as scars, body coloration pattern or dorsal fin shape (Auger-Méthé and Whitehead 2007), to help identify individuals that might gain new primary marks during the long study period. Considering the year-round photo-identification effort, the evolution of temporary marks could be monitored throughout the year, which was previously shown to be robust for mark-recapture analysis (e.g. Verborgh et al. 2021). The database was also updated until 2019, using photo-identification images from both platforms of opportunistic and dedicated surveys. All the dorsal fins present in each photograph were analyzed, recording the identity of each individual based on nicks and notches (primary marks) on the trailing edge of the dorsal fin; distinctiveness (D), to characterize dorsal fin edge primary marks, was classified as: 'no marks' (D0); 'one mark or very small marks' (D1); 'two or more marks' (D2); and 'large or very distinctive marks' (D3). The quality of the dorsal fin picture itself was scored based on focus, angle, size, light, presence of water splashes or water dripping on the trailing edge and the visible percentage of the dorsal fin. To score a picture with the highest quality (Q2 or excellent) the dorsal fin had to be focused, at a perpendicular angle of 270° or 90°, have a large enough size to distinguish features easily, no water in front or on the dorsal fin trailing edge, be perfectly lit and with the trailing edge fully out of the water. A Q1 (good) dorsal fin still had to be well lit to see coloration pattern on the body and dorsal fin completely visible but would not fulfill one of the Q2 requirements. A Q0 (poor quality) dorsal fin was scored whenever one or more of the Q1 requirements were not fulfilled. The apparent age status was also noted based on the presence of fetal folds (newborn), relative size compared to other individuals (calf < 1/3 size of adults, Fig. A1C, juvenile 1/3 to 2/3 size of adult) and body coloration (lighter in non-adults); adults were large individuals with a visible convex shape, due to muscular development, between the blowhole and the dorsal fin. Minimum age was also estimated from the age status given when the individual was first seen. Individuals were classified as 'calves' during their first two years of life, then as 'juveniles' until 7–10 years of age while older animals were recorded as 'adults'. This corresponds with the sexual maturity in females, while males generally reach it later at the age of 17 years (Kasuya and Tai 1993). Therefore, our definition of adults does not reflect fully not exclusively sexually mature individuals of both sexes, but includes also sub-adults males. Genetic sexing of some individuals was also available from Alves et al. (2013).

Matches were made by comparing each new dorsal fin image with the MWM photo-id catalogue. This process was done using the software finFindR (https://github.com/haimeh/finFindR) which has automatic matching functions (Thompson et al. 2022). The individuals that could not be found by the software were searched manually. Then, new individuals that could not be matched were given a new unique alpha-numeric code (GmaXXXX, where XXXX would be a number starting at 0001).

Social structure

Social structure analyses were done on the entire study period and also on two sub-periods to investigate variability of associations over time. The first sub-period included the years 1997–2013 (97–13), and the second sub-period the years 2014–2019 (14–19). The sub-period separation year was due to a low photographic effort year in the study area (Verborgh et al. 2022), and coinciding with the year, 2014, that a WW exclusion zone was defined east of Madeira, where any WW operation is forbidden (Região Autónoma da Madeira 2014). Only data with Q1 and Q2, and marked individuals with D1 to D3 were included in this study. For the social structure analyses (unless detailed otherwise), data was further restricted to individuals observed in more than four years and four seasons (Servidio et al. 2019), and in more than five sampling periods in each sub-period (these whales are named hereafter core resident). Considering the restrictions applied, false negative errors, i.e. not matching two individuals when they are the same, are unlikely to be included in the data set. False positive errors, i.e. matching two individuals as the same when they are different, were highly unlikely to occur, given that specific primary and/or secondary marks had to be clearly observed to be considered a match. Membership in an encounter was used to define when individuals were associated, 'gambit of the group'

(Whitehead and Dufault 1999) during a sampling period. The stringent quality control and the restrictions applied helps to minimize false associations (Whitehead 2008a).

The half-weight association index (HWI) was used to calculate the strength of association between individuals (Whitehead 2008a), as it is one of the most common association indices used among marine mammal species (Weiss et al. 2021), and because it is recommended when there could be incomplete sampling (e.g. not all associates being identified; Whitehead 2008a). HWI ranges from zero (never observed together) to one (never seen apart; Whitehead 2008a). Social differentiation (S) is a coefficient of variation estimate of the true association indices, measured using maximum likelihood; $S < 0.3$ homogeneous, $S > 0.5$ well differentiated, $S > 2.0$ extremely differentiated (Whitehead 2008b). We also calculated the correlation coefficient (r) between the true and estimated association indices, using maximum likelihood; $r = 0.4$ "somewhat representative" and $r = 0.8$ "good" representation (Whitehead 2008a). Standard errors (SE) for S and r were calculated with bootstrap methods (1000 iterations). We used a permutation test (Bejder et al. 1998; Whitehead and Dufault 1999), in which observed associations among individuals were permuted within the sampling sub-periods, controlling for the number of associates of each individual in each sub-period, to test for preferred/avoided associations (Whitehead 2008a) and whether the association patterns observed were different from what might be expected if random. The association matrix was permuted 10,000 times as this stabilized the p values, and each permutation included 1,000 trials (attempts to switch a part of a matrix of associations). HWI, S, r and permutation test within sampling sub-periods were performed with SOCPROG 2.9 (Whitehead 2009).

The distribution of associations between core resident individuals was represented as a social network for the whole study period and both sub-periods. A fast greedy modularity optimization algorithm (Clauset et al. 2004) was used to define the community structure network for the whole study period and both sub-periods, using modularity (M) by gregariousness, where values larger than 0.3 indicate good divisions; resulting communities were named as clusters (Lusseau and Newman 2004). Network visualization and analyses of community structure were performed in R 3.6.1 (R Core Team 2019), with package 'qgraph' (Epskamp et al. 2012). Cluster size was calculated for core resident individuals as the number of individuals per cluster grouped by modularity. We also tested if the structure observed within the core resident individuals was more structured into clusters than expected if random, noting when the observed M was higher than 95% of the network M values calculated from 1,000 randomly generated networks from permuted data (one-tailed; Shizuka and Farine 2016). Furthermore, we tested the robustness of the clusters defined by modularity, r_{com}, by estimating the effect of sampling effort as the probability that a pair of individuals that were assigned to the same cluster in the observed network was assigned to the same cluster in 1,000 bootstrapped networks, with more robust data having values closer to one (Shizuka and Farine 2016). Permutation on M and calculation of r_{com} were done in R 3.6.1 (R Core Team 2019), r_{com} with ASSORNTET (Farine 2014) and "asnipe" (Farine 2019).

Local centrality metrics (e.g. *strength*) of the social structure, as suggested by Silk et al. (2015), are thought to be accurate even when a low proportion of a population have been identified, as it has a linear relationship between a partial (only identifiable individuals) and a full network (all individuals). *Strength*, is the sum of weighted ties for a given individual (Barthélemy et al. 2005), with high values indicating that an individual has strong associations with other individuals. This metric was calculated and averaged across all individuals in the network (all clusters) and within each cluster to determine the robustness of the social structure and evaluate changes along the network structure. The same number of individuals among networks are required to compare those networks (Tantardini et al. 2019), so we further restricted the data to individuals that were observed in both sub-periods (hereafter long-term core resident, LTCR). We tested if the observed *strength* was higher or lower than expected if associations were random (two-tailed), in both sub-periods, by doing permutation tests, swapping observations of two individuals observed in different encounters 1,000 times, recalculating the network after each swap, maintaining the same number of individuals, encounters per individual and same distribution of encounter sizes (Bejder et al. 1998; Farine 2017). We also tested the robustness of the structure within clusters, by conducting permutations in each cluster independently, not swapping individuals among clusters. Furthermore, we compared HWI statistically between periods of LTCR using a matrix correlation test (Spearman mantel test with 10,000 permutations), to test the stability of association patterns across periods. S*trength*, mantel test and permutations were performed in R 3.6.1 (R Core Team 2019), with packages IGRAPH (Csardi and Nepusz 2006), "vegan" (Oksanen et al. 2008) and "asnipe" (Farine 2019), respectively.

Temporal analyses

Standardized lagged association rates (SLAR) were used to estimate the probability that two individuals are associated at a time, and after an interval, the second individual will be a randomly chosen associate of the first (Whitehead 1995). SLAR was calculated for all animals regardless of the number of times they were seen and the cluster they were assigned to, and for the whole study period (Whitehead 2008a), to compare the stability of pairs of individuals in the whole population and within clusters. Considering that the data set is relying also on pictures coming from platforms of opportunity, where probably not all animals in an encounter were photographed in every sampling period, SLAR accounts for cases when not all the true associates of an individual are recorded during a sampling period. Mathematical models of several temporal association patterns were fitted to the observed SLAR (Whitehead 2008a). The best-fitting most parsimonious model was selected using the quasi-likelihood Akaike Information Criterion (QAIC) (Burnham and Anderson 2004), which accounts for over dispersion in the data (Whitehead 1995, 2008a). Standard errors were estimated by jackknife methods (Efron and Gong 1983). A null SLAR was compared to the observed ones, to check if animals associated randomly. SLAR was calculated in the SOCPROG 2.9 program (Whitehead 2009).

Site fidelity and demographic processes

Demographic processes and site fidelity can have different effects on the association patterns of the individuals (Whitehead 1995). We used lagged identification rate (LIR) to assess the presence and absence of individuals in the study area. LIR estimates the probability that an individual in the study area at a time is the same as a randomly chosen individual from the study area after an interval. LIR is constant when the population is closed (no birth, death or migration), and LIR decreases when animals leave the study area through permanent emigration and/or mortality (Whitehead 2001). The best-fitting most parsimonious model were selected using QAIC (Burnham and Anderson 2004). A set of models were fitted to test for closed and open population, including various combinations of emigration, re-immigration and mortality (Whitehead 2001). Confidence intervals were estimated for LIR using 1,000 bootstraps (Whitehead 2007). LIR analysis was done for the whole study period for all animals, and also for each cluster separately. LIR can help in the interpretation of the SLAR, because if one animal leaves the study area then it cannot associate with animals still in it, and if two individuals leave, then we cannot infer their association pattern (Whitehead 2008a). LIR was run in the SOCPROG 2.9 program (Whitehead 2009). Additionally, a turnover of individuals was directly calculated as the percentage of emigrated/dead and immigrated/born individuals over the final number of core resident individuals in the second sub-period for all core resident individuals and, for the different clusters, defined by modularity over the whole study period (see Results; Fig. 1).

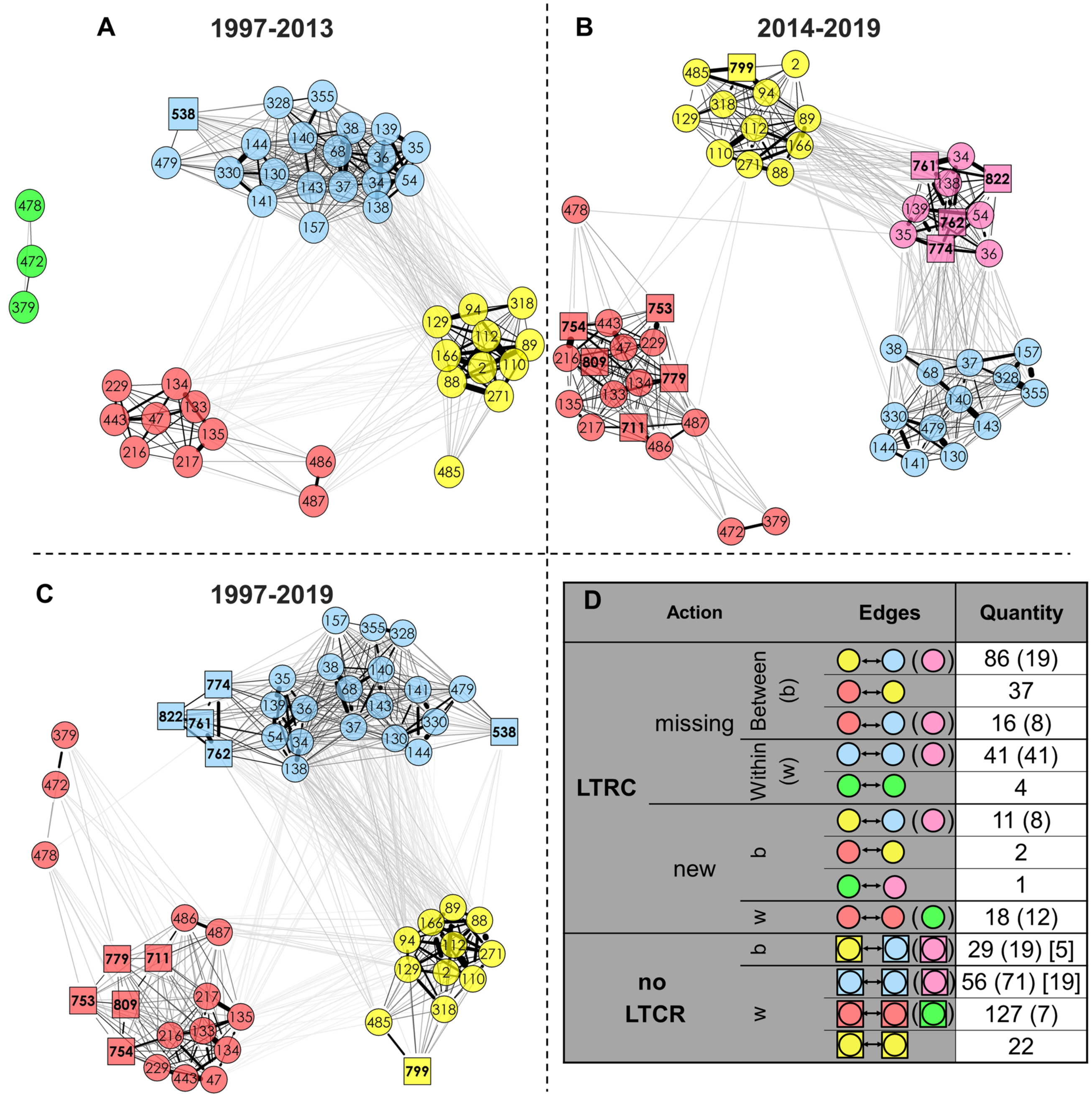
Spatial analyses

We studied the relationship between association among pilot whales and their spatial overlap by estimating the area used by each LTCR individual, and for each cluster. We assigned animals to their corresponding cluster a posteriori and combined the encounters of all individuals of a given cluster (using the three main clusters of the whole study period for LTCR individuals, see Results; Fig. 1), to estimate the area of usage of that cluster. For each cluster, we only used the position of the first individual seen on a sampling day, to avoid spatial correlation. An encounter was assigned to a specific cluster when at least two individuals of that cluster were observed. The areas used were determined by calculating kernel density estimates (KDEs) with the 'ad hoc' method for determining the optimal smoothing parameter (Worton 1989). The fifty percent of density volume contour was used to define their core area, while their home range is represented by the 95% (Beirão-Campos et al. 2016). The overlap between areas of the different clusters and individuals were measured with the home-range (HR) which estimates the proportion of overlap between areas (Kernohan et al. 2001). Typically, the degree of overlap is not reciprocal; overlaps closer to zero in each of these metrics would mean that each cluster/individual uses a specific, separate region in the study area (Kernohan et al. 2001). We analyzed the relation between associations and spatial overlap, to explore the influence of ranging behavior on social interactions during the whole study period. A correlation analysis was performed between the HWI of LTCR and core areas of dyad (pair of individuals) spatial overlap (Mantel Pearson correlation with 1,000 permutations). The spatial analyses were performed in the R environment (R Core Team 2019) with "adehabitatHR" (Calenge 2006) and "vegan" packages (Oksanen et al. 2008).

Results

Data set

Over 900 encounters of pilot whales were recorded in Madeira from 1997 to 2019, of which over 400 were of core resident individuals, based on the analysis of more than 49,000 dorsal fin images (almost 9,000 were of core resident); 1,156 individuals were identified, of which only 54 animals were categorized as core residents (Table 1). All core resident individuals used in this study were either D2 or D3, after applying the restriction of at least five sampling periods, i.e. they were all distinguishable (Table 1). Although the first sub-period is longer than the second (16 years versus five years), the number of individuals identified are similar in both sub-periods, as an increase in the photographic effort is indicated by similar number of



D Action			Edges	Quantity
LTRC	missing	Between (b)	🟡↔🔵 (🟣)	86 (19)
			🔴↔🟡	37
			🔴↔🔵 (🟣)	16 (8)
		Within (w)	🔵↔🔵 (🟣)	41 (41)
			🟢↔🟢	4
	new	b	🟡↔🔵 (🟣)	11 (8)
			🔴↔🟡	2
			🟢↔🟣	1
		w	🔴↔🔴 (🟢)	18 (12)
no LTCR		b	🟨↔🟦 (🟪)	29 (19) [5]
		w	🟦↔🟦 (🟪)	56 (71) [19]
			🟥↔🟥 (🟩)	127 (7)
			🟨↔🟨	22

Fig. 1 Network diagrams for core resident individuals of pilot whales in Madeira in the different sub-periods (**A**: 1997–2013; **B**: 2014–2019; **C**: 1997–2019), where each node represents an individual with its numeric code, each cluster is represented by the color of the node, and the associations are represented by weighted edges which are determined by the HWI among dyads. Animals that were not included in the calculation of *strength* (seen in only one sub-period) are in bold and their nodes are square (i.e. no LTCR). **D** Summary table of the changes in the number of edges (linking dyads) between and within clusters, detailed by *missing* edges and *new* edges compared between sub-periods for LTCR individuals. Changes among individuals of green and pink clusters are given in brackets. *No LTCR* individuals are not present in one of the sub-period, so the number of edges with those individuals are detailed separately (in square brackets are the number of edges for the individual Gma0538 that either emigrated or died during the study period)

sampling periods and an increase in the fins analyzed during the second sub-period. GPS positions were available for most encounters (1997–2019: 68%) and opportunistic sightings (1997–2019: 57%; Table 1).

Social structure

The social structure of the core resident pilot whales in Madeira is well differentiated in both

Table 1 Summarized photographic effort and general results for the core resident pilot whales off Madeira by sub-periods

		1997–2013		2014–2019		1997–2019	
		Total	WW	Total	WW	Total	WW
Sampling periods (SP)		194	172	143	131	337	303
Encounters [GPS]		256 [185]	198 [127]	194 [120]	141 [67]	450 [305]	339 [194]
Fins analysed	Total	1502	1287	8165	5511	9667	6798
	Q1	309	254	5442	3723	5751	3977
	Q2	1193	1033	2723	1788	3916	2821
Individuals (IND)	Total	44		53		54	
	D2	33		39		40	
	D3	11		14		14	
	D1→D2	0		3		3	
	D2→D3	1		2		3	
Mean SP/IND (min–max)		23 (6–46)		12 (6–22)		30 (7–63)	
Mean IND/SP		5		5		5	

Data from opportunistic platforms (WW) are detailed and the number of encounters, from which GPS position was available, are presented in square brackets [GPS]. Details of photographic quality (Q1 and Q2), distinctiveness of individuals (D2 and D3) and change of distinctiveness (D1→D2 and D2→D3) are also shown.

sub-periods (1997–2013: $S \pm \mathrm{SE} = 1.78 \pm 0.17$; 2014–2019: $S \pm \mathrm{SE} = 1.78 \pm 0.12$). The estimated association indices were a good representation of the true association indices for both sub-periods (1997–2013: $r \pm \mathrm{SE} = 0.76 \pm 0.03$; 2014–2019: $r \pm \mathrm{SE} = 0.65 \pm 0.02$). The overall association pattern was not random and preferred/avoided associations were indicated by significantly higher real association indices SD for both sub-periods (1997–2013: real $\mathrm{SD} = 0.20$, random $\mathrm{SD} = 0.18$, $p < 0.01$; 2014–2019: real $\mathrm{SD} = 0.18$, random $\mathrm{SD} = 0.17$, $p < 0.01$).

The maximum modularity defined four clusters for core resident individuals in both sub-periods (Fig. 1 and Table 2), although they were not the same four clusters, the green cluster is only detached in the first sub-period, and in the second sub-period the pink cluster appeared for the first time. Both modularity and *rcom* values for our cluster assignments were relatively high ($M > 0.3$ and *rcom* close to 1), suggesting robust cluster structure and high cluster fidelity with a low propensity for individuals to mix with other clusters (Table 2). The core resident social network for the whole period only differentiated three clusters (Table 2 and Fig. 1); those clusters were used to carry out the temporal and spatial analysis among clusters. In all cases, the grouping structure suggested by modularity is supported by stronger weighted links within clusters than among clusters (Fig. 1).

If clusters are stable associations of individuals, we expect strength within clusters not to decrease notably over time. *Strength* within clusters of LTCR was similar between study sub-periods, though a slight increase was detected in the red cluster and a decrease was detected among individuals of the blue cluster (Table 2). *Strength* was lower than expected if the associations were random, only the yellow cluster had stronger than random associations (Table 2).

Only one individual, belonging to the blue cluster, was absent in the second sub-period (Fig. 1 and Table 2). All individuals belonging to the green cluster in the first sub-period were grouped together with the red cluster in the second sub-period (Fig. 1 and Table 2). The blue cluster split in two, resulting in the creation of the pink cluster during the second sub-period (Fig. 1B). In the pink cluster, apart from the six adult individuals that originally belonged to the blue cluster, we observed four additional individuals, of which one was born during the study, and three new adult individuals that were not identified before. In the yellow cluster there was one new adult individual in the second sub-period. In the red cluster there were five additions in the second sub-period, four births and one new adult individual. In summary, all individuals remained in the same cluster since the first sub-period with the exception of (i) an absent individual (Gma0538); (ii) individuals that formed a new cluster (pink) and (iii) a cluster (green) that joined another cluster (red). Therefore, a low level of cluster changes have been observed over 22 years. In fact, we found a strong and positive correlation among the association indexes of both sub-periods (Mantel test: $r = 0.823$; $p < 0.01$) of LTCR, suggesting that individuals tend to maintain the same pattern of association over time. Individuals were followed on average over 12 years (range: 5–20) and age was estimated from a minimum of 5–27 years old showing strong cluster fidelity. Two adult males and two adult females were previously sexed genetically (Alves et al. 2013) and were identified in the blue and the red cluster.

Table 2 Social network metrics of pilot whales off Madeira; values are given for each sub-period or the overall study period, as indicated, and values were also calculated for clusters defined in the whole study period (Fig. 1C)

Measure	Period	Core resident			
		All clusters	Red	Yellow	Blue
Cluster size	97–13	Mean = 15 (3.86)	13	11	20
	14–19	Mean = 18 (4.49)	18	12	23
	97–19	Mean = 18 (4.89)	18	12	24
Emigration/death	97–13	1	0	0	1
Immigration	14–19	5	1	1	3
Birth	14–19	5	4	0	1
Turnover	97–19	21%	27%	8%	22%
Mean n^o years (min–max)	97–19	10 (5–16)	8 (5–13)	12 (5–16)	10 (5–14)
Mean n^o encounters (min–max)	97–13	24 (5–48)	20 (6–42)	38 (5–48)	19 (6–29)
	14–19	13 (5–24)	14 (5–24)	14 (8–24)	12 (5–18)
Mean HWI (Max)	97–13	0.12 (0.65)	0.23 (0.62)	0.47 (0.70)	0.33 (0.65)
	14–19	0.10 (0.73)	0.28 (0.66)	0.42 (0.67)	0.23 (0.73)
	97–19	0.09 (0.62)	0.22 (0.56)	0.42 (0.68)	0.24 (0.64)
Modularity	97–13	0.50*			
	14–19	0.65*			
	97–19	0.55*			
r_{com}	97–13	0.99			
	14–19	0.97			
	97–19	0.99			
Measure	Period	Long-term core resident (LTCR)			
		All clusters	Red	Yellow	Blue
Strength	97–13	2.96 (1.08)#	2.61 (1.45)#	4.56 (1.22)*	6.19 (1.16)#
	14–19	2.85 (1.12)#	2.91 (1.27)#	4.43 (0.98)*	5.36 (0.72)#

Values within brackets are SD. Significant p value calculated with the permutation test, indicating that observed values were higher (*) or lower (#) than expected if observations were random.

The number of edges between and within clusters also changed with time. The blue and yellow clusters lost more edges between them and gained more new edges with other clusters, especially with the new pink cluster (Fig. 1A, B, D). The blue cluster was also the one with more missing edges within the cluster, while the red cluster is the one with more new edges within the cluster (Fig. 1). The changes in the number of edges with individuals only observed during one of the sub-periods (no LTCR) was more common within their own cluster than with other clusters (Fig. 1A, B, D).

Temporal analyses

The results of the temporal analyses, including all the individuals for the whole study period (Fig. 2A), suggest that associations among pilot whales decrease with time; however, association values remain higher than if association between individuals were random. The model that best fitted the SLAR data (based on QAIC; Appendix Table A1) had terms of exponential decay, which is commonly named as two levels of casual acquaintances, estimating that SLAR declined by half after nearly ten years. SLAR within clusters were significantly higher than expected if association between individuals were random, in general higher than for all the individuals (Fig. 2A). All SLAR curves within clusters had a smooth decline of associations at the end of the study period which is best fitted with a casual acquaintances model (Fig. 2A; Appendix Table A1). For clusters, the SLARs decreased by half after an average of 32 years (red: 23 years, blue: 18 years and yellow: 54 years; Appendix Table A1).

Site fidelity and demographic processes

LIR for all the individuals decayed over short time scales (approximately two days), then stabilized until a marked declined at the end of the study period (Fig. 2B). LIR best model was supported by QAIC ($\Delta QAIC \leq 2$) and included parameters that indicated emigration (approximately 2 years out of the study area), reimmigration (approximately

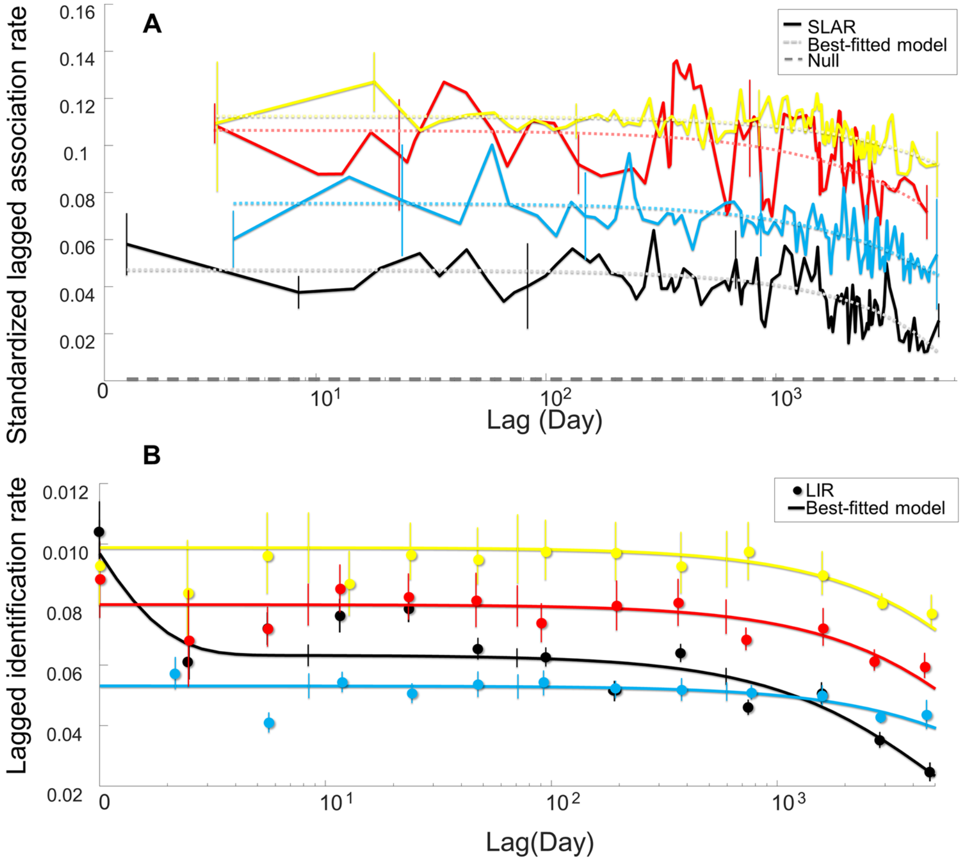


Fig. 2 **A** SLAR of pilot whales in Madeira for the whole study period, including all individuals without restrictions (in black), with a null and a modeled SLAR, and SLAR for individuals belonging to each cluster (in colors), defined by the maximum modularity for the whole study period (Fig. 1C). **B** LIR of all individuals (in black) and by clusters (in colors) for the whole study period. The colors of the curves correspond to the colors of the clusters defined in Fig. 1

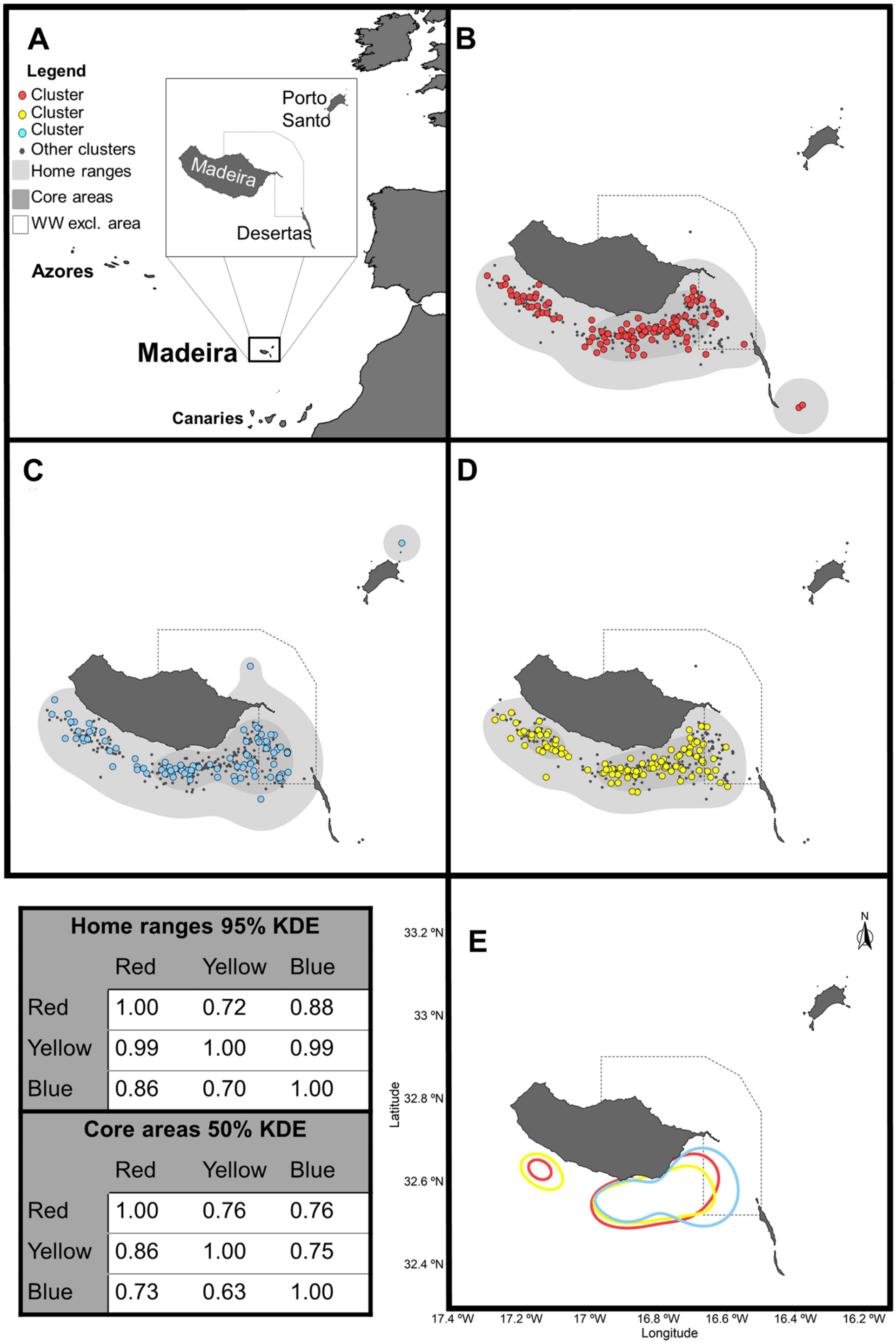
10 months in the study area) and mortality (0.07 individuals/year; Appendix Table A2). When the individuals were classified by their cluster (Fig. 2B), the best model to explain the decline of LIR with time indicated emigration or mortality for all the clusters (Appendix Table A2). For all core resident individuals a turnover of 21% was estimated, and for clusters this turnover ranged from 8 to 27% (Table 2).

Spatial analysis

Spatial distribution slightly influenced the core resident's probability of association; with a significant but weak correlation between HWI and HR (Mantel test: $r = 0.362$; $p = 0.001$), indicating that individuals that used more similar areas tend to show higher HWI. Animals from different clusters had spatially coinciding home ranges, with a large overlap in the 95% KDE among all three clusters and a variable overlap in the 50% KDE core areas (Fig. 3). Note that the gap between the core areas in Fig. 3E is the result of whale watching boats operating from different harbors and with more effort closer to those harbors. Intrinsically the distribution pattern presented in Fig. 3E may be biased and should be considered with caution.

Discussion

In Madeira, core resident pilot whales exhibit a well differentiated structure where not all animals tend to interact with each other but have preferred companions, supporting the division into socially meaningful clusters of varying size and association strength. A well differentiated structure was mostly maintained over time within the core resident pilot whales off Madeira, but slight changes were observed in the configuration of some clusters. The red and yellow clusters only showed small changes in their structure between sub-periods. In contrast, the green cluster, formed initially by three individuals and without any observed associations with other individuals, was later grouped with the red cluster, associating particularly with their new individuals, the ones incorporated during the second sub-period (no LTCR; Fig. 1B, D). The animals from the green cluster could be "new" core resident individuals, or immigrants, which are spending more time in the study area, as these whales are known to sometimes disperse from the study area (Alves et al. 2019). In fact, one of those individuals was previously described as a visitor (Alves et al. 2013), and the other two were not included in previous analyses. Nevertheless, most



Home ranges 95% KDE

	Red	Yellow	Blue
Red	1.00	0.72	0.88
Yellow	0.99	1.00	0.99
Blue	0.86	0.70	1.00

Core areas 50% KDE

	Red	Yellow	Blue
Red	1.00	0.76	0.76
Yellow	0.86	1.00	0.75
Blue	0.73	0.63	1.00

Fig. 3 **A** Study area overview location in relation to south-western Europe with inset and details of the Madeira archipelago, clusters and ranges of short-finned pilot whales and the whale-watch (WW) exclusion zone. **B**–**D** Kernel density estimate (KDE) for each of the three social clusters of LTCR pilot whales in Madeira where the lighter grey area represents their home range (95% KDE), the darker grey area represents their core area (50% KDE) and the WW exclusion zone is delimited by a black dash line. Each dot represents a cluster encounter, with color code following the social clusters classification by modularity for the whole period; B—red, C—blue, D—yellow; and all other cluster encounters are in dark grey. **E** Core areas (50% KDE) for LTCR overlapped, specific values are in the table, together with the overlap of their home ranges (95% KDE). The encounter locations of clusters at the south western Madeira **B**–**D**, and consequently their core areas (**E**; red and yellow clusters) are the result of opportunistic encounters by whale watching boats departing from a different harbour, which should be viewed with caution as the resulting distribution pattern could be biased

of the core resident pilot whale clusters of the first sub-period (Fig. 1A) correspond to previously described resident groups (Alves et al. 2013).

Moreover, the photographic effort evolved over the study period (Table 1), with an increase in photographic equipment quality and photographers' experience. This increase would help to identify more individuals of lower distinctiveness. The number of core resident pilot whales increased during the second sub-period, with ten new individuals (Table 2), of which five were always categorized as adults. They could either be immigrating animals or animals not photographed during the first sub-period, or they acquired marks that allowed us to identify them. However, another five core resident individuals were born during the study period, as they were categorized as calf or juvenile, but still marked, which cannot be assigned solely to the increase in effort. On the other hand, the increase in photographic effort allowed us to separate the study period into two sub-periods with unequal time span, as we had similar number of sampling periods (Table 1). There is an uneven sampling of clusters in the first sub-period, when the yellow cluster was the one most encountered (Table 2) and highly associated with other clusters (Fig. 1A). However, during the second sub-period the mean number of encounters per individuals are more evenly distributed among clusters (Table 2) and fewer edges between clusters are present (Fig. 1B, D), suggesting that the pattern depicted in the second sub-period is more representative.

In nature, extreme changes in stable network structure from one period to another rarely happen (Shizuka and Johnson 2020). After a high poaching period for African elephants (*Loxodonta africana*), some aspects of the stable kin-based community structure were conserved (Goldenberg et al. 2016). However, in fission–fusion systems it is more common to observe a reorganization of associations after a high turnover period. Examples of this have been recorded in Atlantic bottlenose dolphins (*Tursiops truncatus*) after a hurricane, where half of the population dispersed (either died or emigrated), and immigrant individuals incorporated into the existing network which subsequently split into two communities (Elliser and Herzing 2011). Long-term studies and network analysis can help us understand the relationship between demographic events (deaths, births, emigration and immigration) with its ripple effects on the rest of the network (Shizuka and Johnson 2020). In our study, for the overall network there are no apparent changes of the sum of weights of the edges connected to a node, *strength*, between sub-periods (Table 2), and a high correlation of the association matrices was observed between those sub-periods. However, some changes seem to have occurred unequally across clusters, with a moderate turnover caused by the increase in number of individuals during the second sub-period, and its related increase in cluster size, detected in blue and red clusters (Table 2). Mean cluster size increased from 15 individuals in the sub-period 97–13 to 18 individuals in the sub-period 14–19 (Table 2), possibly due to an increase of effort or a real increase of individuals in the clusters, which could have been unmarked calves or juveniles in the first sub-period that acquired new marks or marked individuals entering the population.

In stable societies when group size grows, group cohesion normally decreases, potentially leading to group fission (Stredulinsky et al. 2021). The smaller yellow cluster is the most cohesive with a mean HWI of 0.42 and a significantly higher *strength* than random networks, indicating an association preference between most individuals in this cluster (Table 2). On the other hand, red and blue clusters are less cohesive with about half HWI (0.22–0.24); both clusters also had a significantly lower *strength* than random networks, indicating avoidance between some individuals of the same cluster (Table 2). Both the fission of the blue cluster and the fusion of the original green and red clusters may result in the changes of their cohesiveness, and the increased modularity between the sub-periods. A higher loss of edges were also observed in the blue cluster (Fig. 1) and a decrease of both mean HWI and *strength* over time, probably also related with its fission (Table 2). Increased metabolic requirements in a group has been linked with the decrease in group cohesion, as individuals spend more time foraging to satisfy the nutritional needs of members of a larger group (Stredulinsky et al. 2021). In addition, during this increase in competition for food individuals may spend less time socializing (e.g. Stredulinsky et al. 2021). Group fission among kin-based stable social systems typically occurs between matrilines when the matriarch dies (e.g. Ménard 2017), but also across the matrilines while the matriarch is still alive (Stredulinsky et al. 2021). On the other hand, even with the highest turnover, the red cluster individuals maintain their cohesion, although the red final cluster size was smaller than the blue cluster, which could suggest an optimal cluster size between both magnitudes (Table 2).

Through group fission, individuals may leave their relatives in the original group and even their natal home range, providing a means of dispersal (Lefebvre et al. 2003). However, in the case of pilot whales off Madeira, there is no indication of dispersal outside their natal home range, as all individuals, except one, were present in the last sub-period in the study area. All six individuals that split from the blue cluster were apparently sexually mature adults. They were observed associated with calves during the first sub-period, and three of them were seen associated with calves in the second sub-period, suggesting that the group fission may not be caused by dispersal at sexual maturity. Rather individuals may have split from the group due to an increase in the number of individuals (either by birth or immigration) in the cluster, where such demographic change could have affected the relationships among individuals. The effects of demographic changes were most noticeable in the red cluster where the turnover rate was high. Many edges between the red and other clusters were lost in the second sub-period, while many were established with new individuals in the red cluster (and with individuals from the green cluster; no LTCR, Fig. 1). However, the split of a cluster is a gradual process, considering that they are still sometimes associated, so evidence on dispersal at sexual maturity in short-finned pilot whales should be further investigated. Apart from demographic changes, environmental constraints may also influence group fission in social species (e.g. Lefebvre et al. 2003; Markham et al. 2015). Close monitoring of the associations between individuals, including information on sex, age classes, genetic kinship and/or environmental drivers, may help us understand the dynamics and causes of group fission in pilot whales.

Systematic distance sampling line transect-surveys of all coastal waters of Madeira suggest that pilot whales occur primarily in the channel between Madeira and Desertas islands (Freitas et al. 2014; MISTIC SEAS II 2019), overlapping with the southern part of the WW exclusion zone (Fig. 3A). Individuals using a particular area simultaneously are more likely to associate (Cantor et al. 2012), and perhaps this is even more likely at sea where there are no geographic barriers. In this study, a weak but significant correlation between the social and spatial matrices was detected. In addition, a high degree of home range and core areas overlap between clusters was recorded in the pilot whales off Madeira (Fig. 3). Even when core resident individuals were most likely to use the same area, a modular well differentiated social structure was also detected (Table 2), discarding spatial overlap as a single driver of associations. This suggests the influence of social or ecological drivers for the associations, providing an important line of future inquiry. However, spatio-temporal influences are an important area of research, as individuals can use the same area at different times, and spatial behavior with temporal analyses should be further explored (Genoves et al. 2018).

The temporal probability of association (SLAR) between pilot whales off Madeira was not random, as it never crossed the null SLAR, decreased over time, and displayed dyadic associations generalized as two levels of casual acquaintances, which is usually related to short-term associations. Different social systems can be fitted by the same SLAR model, as model generalization is not prescriptive (Whitehead 2008a). Some **Δ**QAIC values are rather low, suggesting that the best-fitted models are not without uncertainty. Accordingly, LIR was used to help in the interpretation of SLAR (Whitehead 2008a). A decay of LIR was observed among all individuals (Fig. 2B), which could be explained by the large proportion of individuals seen only once, defined as transients (Alves et al. 2013). However, LIR stabilized for years (Fig. 2B & Appendix Table A2), as did the SLAR for all individuals, estimated to decline by half in ten years (Fig. 2A & Appendix Table A1). In general, time also influenced the presence and absence of individuals in the study area (LIR; Fig. 2B and Appendix Table A2), which matched with their corresponding SLAR (Fig. 2A). LIR for all individuals was generalized by a low mortality (0.07/year), emigration and reimmigration of the animals, suggesting that the decay of SLAR was also the result of the natural demographic processes and some individuals being temporarily absent from the study area, as suggested by matches of resident individuals between Madeira and Azores (Alves et al. 2019). SLAR results within clusters were generalized as casual acquaintances with even slower decreases, and the associations in two clusters lasting beyond the study period (red cluster 23 years and yellow cluster 54 years). In fact, the decrease of LIR in the clusters was mostly characterized by a low mortality or emigration of the animals (approximately 0.02/year; Fig. 2B and Appendix Table A2), which is in accordance with another study using this data set (Verborgh et al. 2022). The results of that study, based on robust design mark–recapture, showed a lack of migration and high survival rate for individuals with high site fidelity. Consequently, the small decrease of the association probabilities of the core resident pilot whale clusters observed off Madeira could be due to natural demographic effects, suggesting long-term associations among individuals of the same cluster. The temporal evolution of the associations among individuals of the blue cluster may reflect the split in the group. The blue cluster has the fastest SLAR decline, decaying by half in approximately 19 years, while its LIR decayed in a similar rate as the remaining clusters (0.02/year). Therefore, the fast decline in associations may not be caused only by the loss of individuals (Fig. 2B and Appendix Table A2).

Several hypotheses have been proposed as drivers of the modularity and social differentiation in toothed whales—for example, as a response to the increased threat of male harassment because of their strong sexual size dimorphism (Möller et al. 2012), due to the importance of maternal care which leads to stability in social structure (e.g. Rendell et al. 2019) or the predictability and distribution of resources (Gowans et al. 2007). Weiss et al. (2021) supported all three hypotheses to explain the high modularity in larger marine mammals, as they tend to exhibit greater sexual size dimorphism, have long calving intervals, and have extensive movement ranges because they normally feed on patchy prey. Wide movement ranges have been detected among these pilot whales (Alves et al. 2019). Although the drivers of these movements are still unclear, they could be driven by reproductive or feeding needs, but more data are needed on specific dietary preferences. Rendell et al. (2019) suggests that there are correlations between the stability of social groups of toothed whales with such kin-based stable social systems with the need of maternal care and cooperation, resulting in natal philopatry to the group (e.g. Bigg et al. 1990). Previous studies off the coast of Madeira suggest that natal philopatry for pilot whales, as genetic relatedness was higher within than between groups (Alves et al. 2013). In this study, we found evidences that reinforced the idea of natal philopatry among pilot whales, most probably for both sexes. First, none of the core resident individuals switched between clusters during the present study (except for the individuals within the green cluster or the fission of the blue cluster). Second, two calves and five juveniles, born in the course of the study, were all observed in their natal cluster for the duration of the study and up to 16 years. Finally, the two adult females and two adult males previously sexed by Alves et al. (2013) also stayed in their respective clusters. Continuous monitoring of these individuals could help us understand community responses, such as social dynamics when/if key individuals disperse (e.g. Lusseau and Newman 2004), and could give us a conclusive evidence of natal philopatry to the group (e.g. Bigg et al. 1990) for both sexes in this species.

A high proportion of the encounters recorded in this study were observed from opportunistic platforms (Table 1), increasing the amount of data collected and temporal coverage. However, the robustness of the results was obtained by restricting the analyses to identifiable animals that spend most of their time in the study area, applying methodologies that accounted for missing data and temporally aggregating the data set into periods with sufficient records (Farine 2018). If we want to understand how associations form and evolve over time, a more detailed temporal analysis of social structure and one that compares aggregated networks over shorter time periods is necessary (e.g. Hobson et al. 2013). Such information can only be obtained by an increase of dedicated surveys, where information is collected periodically to detect changes and trends in the associations of individuals.

The study of the social structure can support the conservation of marine mammals (Weiss et al. 2021) by helping to define management units (e.g. Esteban et al. 2016b) or clarifying the way death or removal events influence the population (e.g. Busson et al. 2019). A significant relationship between the connectivity of the social network and prey abundance has been found in the southern resident killer whales off the eastern Pacific (Foster et al. 2012), and between group splitting and low prey abundance in the northern resident killer whales off eastern Pacific (Stredulinsky et al. 2021). Core resident pilot whales could be used as indicators of the environmental status of the archipelago, since their range overlaps with most of the anthropogenic pressures around the islands. In Madeira, pilot whales are potentially subjected to a diversity of anthropogenic pressures, including contaminants, fisheries interactions, maritime traffic and WW activity. Such disturbances may impact both the behavior and physiology of an individual, and changes in these characteristics could affect an individual's vital rates, directly or indirectly (Pirotta et al. 2018). Our study provides important baseline knowledge about the social dynamics of pilot whale core residents of Madeira in two sub-periods, which coincided with prior and after the establishment of a WW exclusion zone in the area (Fig. 1). Furthermore, the second sub-period coincided with an increase in the number of WW boats, which was not related to changes in survival rates (Verborgh et al. 2022). In general, all clusters when in the study area should be receiving the same exposure to WW, as their home ranges highly overlap (Fig. 3) and the species main area of distribution partially coincides with the WW exclusion zone (Freitas et al. 2014; MISTIC SEAS II 2019). We suggest that environmental factors and anthropogenic disturbances should be incorporated as possible drivers of social change in future studies on the Madeiran pilot whales. Such factors have been found to cause shifts in sociality in other species (e.g. Cantor and Farine 2018; Bond et al. 2021).

Using two decades of photo-ID and social network analyses, we showed that core resident pilot whales off Madeira have a clustered society with strong long-term preferred companionships. The networks represented a well differentiated society, with stronger ties among individuals of the same cluster and weaker ties between individuals of different clusters. The predisposition of individuals to a group indicates that not all of the individuals interacted directly with each other, and this heterogeneous interaction pattern was structured into modules of denser associations, named clusters. The spatial overlap of social clusters also suggested minor differences in space use and, consequently, it is an unlikely driver for cluster structure in the social network.

Appendix

See Fig. A1, Tables A1, A2.

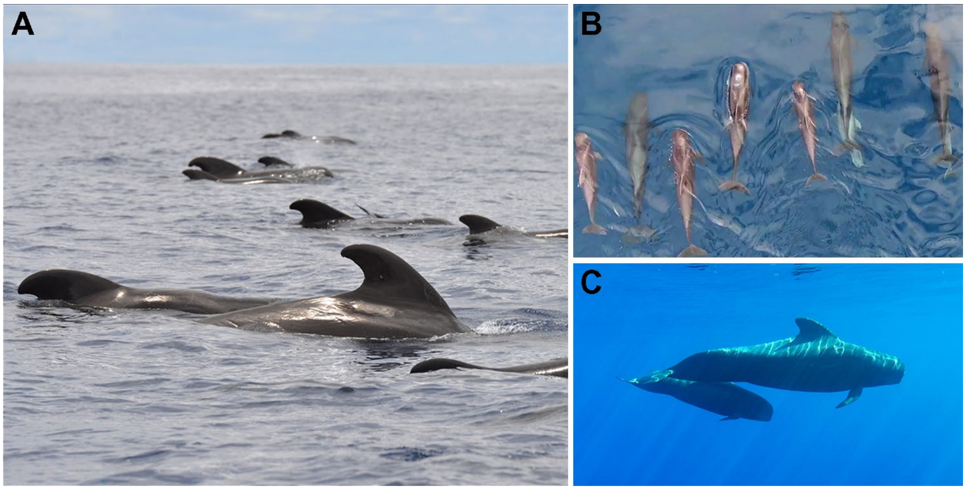


Fig. A1 Short-finned pilot whales(*Globicephala macrorhynchus*) photographed off Madeira island. **A** Boat perspective of a typical group size for this species in this region,a group of around thirteen individuals, as some individuals are submerged and not in the image. **B** Aerial perspective of a group ofnine whales with five individuals submerged. **C** Underwater perspective of an adult and a calf, notice the different body length

Table A1 Models fitted to the empirical standardised lagged association rate (SLAR) found for all pilot whales off Madeira and clusters of core resident individuals 1997–2019, ordered by the lowest Quasi-likelihood Akaike Information Criterion (QAIC) values

	Description of model	Formulae	QAIC	ΔQAIC
All individuals	**2CA**	**$g'(t) = -0.005 \times e^{(0.002 x t)} + 0.05 \times e^{(-9.63 x 10^{-05} x t)}$**	**96,290.73**	**0**
	CA	$g'(t) = 0.05 \times e^{(-1.97 x 10^{-04} x t)}$	96,312.82	22.09
	PC + CA	$g'(t) = 0.03 + 0.11 \times e^{(-1.16 x t)}$	97,006.22	715.49
	PC	$g'(t) = 0.04$	97,017.91	727.18
Red (1)	**CA**	**$g'(t) = 0.11 \times e^{(-8.17 x 10^{-05} x t)}$**	**36,586.06**	**0**
	PC	$g'(t) = 0.09$	36,632.16	46.1
	PC + CA	$g'(t) = 0.09 + 0.06 \times e^{(-1.10 x t)}$	36,634.77	48.71
	2CA	$g'(t) = 0.71 \times e^{(-0.26 x t)} + 0.10 \times e^{(-6.25 x 10^{-05} x t)}$	37,114.97	528.91
Blue (2)	**CA**	**$g'(t) = 0.08 \times e^{(-1.01 x 10^{-04} x t)}$**	**62,606.59**	**0**
	2CA	$g'(t) = -0.02 \times e^{(-0.019 x t)} + 0.08 \times e^{(-1.03 x 10^{-04} x t)}$	62,609.50	2.91
	PC	$g'(t) = 0.06$	62,766.58	159.99
	PC + CA	$g'(t) = 0.06 - 2437.38 \times e^{(-12.11 x t)}$	62,770.53	163.94
Yellow (3)	**CA**	**$g'(t) = 0.11 \times e^{(-3.54 x 10^{-05} x t)}$**	**238,544.09**	**0**
	2CA	$g'(t) = -0.02 \times e^{(-1.11 x t)} + 0.11 \times e^{(-3.56 x 10^{-05} x t)}$	238,547.68	3.59
	PC	$g'(t) = 0.11$	238,610.71	66.62
	PC + CA	$g'(t) = 0.11 - 0.006 \times e^{(-1.08 x t)}$	238,614.68	70.59

The ΔQAIC indicate the relative support for each model. SLAR was fitted to models of preferred companions (PC), casual acquaintances (CA) and combinations of both, such as two levels of casual acquaintances (2CA) (Whitehead, 2008a). The selected model is in bold

Table A2 Models fitted to the lagged identification rate (LIR) found for all pilot whales off Madeira and clusters of core resident individuals from 1997 to 2019, ordered by the lowest Quasi-likelihood Akaike Information Criterion (QAIC) values

	Description of model	Formulae	QAIC	ΔQAIC
All ind	**E + RE + M**	**$R(t)=(e^{(-1.83\times 10\text{\textasciicircum}-04*t)}/39.97\times((1/2.39)+(1/0.80).\ e^{(-(1/2.39+1/0.80)\times t))}/(1/2.39+1/0.80)$**	**138,826.79**	**0**
	E/M	$R(t)=0.006\times e^{(-1.84\ x\ 10-04*t)}$	138,828.66	1.87
	E/M	$R(t)=1/158.29\times e^{(-t/5434.27)}$	138,828.66	1.87
	E + RE	$R(t)=(1/158.28)\times((1/30640878738306.15)+(1/5434.27)\times e^{(-(1/30640878738306.15+1/5434.2705)\times t))}/(1/30640878738306.15)+(1/5434.2705)$	138,830.66	3.87
	C: E + RE	$R(t)=0.004+0.02\times e^{(-140\times t)}$	139,397.07	570.28
	C	$R(t)=0.005$	139,409.11	582.32
	C	$R(t)=1/213.13$	139,409.11	582.32
	E + RE + M	$R(t)=-\ 0.52\times e^{(-2.04\times t)}+0.006\times e^{(-1.84\times 10\text{\textasciicircum}-03\times t)}$	139,989.96	1163.17
Red (1)	**E/M**	**$R(t)=0.08\times e^{(-8.59x10\text{\textasciicircum}-05*t)}$**	**60,341.28**	**0**
	E/M	$R(t)=(1/12.50)\times e^{(-t/11632.74)}$	60,341.28	0
	E + RE	$R(t)=(1/12.40)\times((1/9286.15)+(1/9584.13)\times e^{(-(1/9286.15+1/9584.13)\times t))}/(1/9286.15+1/9584.13)$	60,342.75	1.47
	E + RE + M	$R(t)=(e^{(-8.58\times 10\text{\textasciicircum}-05*t)}/12.15)\times((1/2.27)+(1/76.35).\ e^{(-(1/2.27+1/76.35)\times t))}/(1/2.27+1/76.35)$	60,345.23	3.95
	C	$R(t)=1/14.11$	60,417.18	75.9
	C	$R(t)=0.07$	60,417.18	75.9
	C: E + RE	$R(t)=0.07+0.94\times e^{(-3.97\times t)}$	60,419.16	77.8
	E + RE + M	$R(t)=0.41\times e^{(-0.25\times t)}+0.08\times e^{(-6.75\times 10\text{\textasciicircum}-05\times t)}$	60,722.08	380.8
Blue (2)	**E/M**	**$R(t)=0.05\times e^{(-4.68x10\text{\textasciicircum}-05*t)}$**	**76,882.51**	**0**
	E/M	$R(t)=(1/18.85)\times e^{(-t/21422.63)}$	76,882.51	0
	E + RE + M	$R(t)=(e^{(-4.67\times 10\text{\textasciicircum}-05*t)}/18.98)\times((1/0.06)+(1/62.35).\ e^{(-(1/0.06+1/62.35)\times t))}/(1/0.06+1/62.35)$	76,886.51	4
	E + RE + M	$R(t)=-\ 0.26\times e^{(-4.67x10\text{\textasciicircum}-05\times t)}+0.31\times e^{(-4.67\times 10\text{\textasciicircum}-05\times t)}$	76,886.51	4
	C	$R(t)=1/20.64$	76,917.62	35.11
	C	$R(t)=0.50$	76,917.62	35.11
	E + RE	$R(t)=(1/20.24)\times((1/1.11)+(1/56.23)\times e^{(-(1/1.11+1/56.23)\times t))}/(1/1.11+1/56.23)$	76,921.62	39.11
	C: E + RE	$R(t)=0.05+0.002\times e^{(-1.27\times t)}$	76,921.62	39.11
Yellow (3)	**E/M**	**$R(t)=0.09\times e^{(-3.27\ x\ 10-05*t)}$**	**95,995.09**	**0**
	E/M	$R(t)=(1/10.20)\times e^{(-t/30551.91)}$	95,995.09	0
	E + RE + M	$R(t)=-0.01\times e^{(-0.18\times t)}+0.09\times e^{(-3.33\times 10\text{\textasciicircum}-05\times t)}$	95,998.56	3.47
	E + RE + M	$R(t)=(e^{(-3.27\times 10\text{\textasciicircum}-05*t)}/10.19)\times((1/0.06)+(1/85.54).\ e^{(-(1/0.06+1/85.54)\times t))}/(1/0.06+1/85.54)$	95,999.09	4
	C	$R(t)=0.09$	96,017.63	22.54
	C	$R(t)=1/10.74$	96,019.63	24.54
	C: E + RE	$R(t)=0.09\ -0.005\times e^{(-1.45\times t)}$	96,021.63	26.54
	E + RE	$R(t)=(1/10.68)\times((1/0.34)+(1/54.61)\times e^{(-(1/0.34+1/54.61)\times t))}/(1/0.34+1/54.61)$	96,021.63	26.54

The ΔQAIC indicate the relative support for each model. The models have several biological interpretations: Emigration (E); Reimmigration (RE); Mortality (M); Closed population (C). Model was selected by the one with the minimum QAIC or one that ΔQAIC < 2 and it was visually fitting better the curve. The selected model is in bold

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Author contributions All authors contributed to the study design and data collection. Photo-ID analysis was performed by PV and social structure analyses by RE. The first draft of the manuscript was written by RE and all authors commented on all versions of the manuscript. All authors read and approved the final manuscript.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

References

Alves F, Quérouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C (2013) Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. Aquat Conserv Mar Freshw Ecosyst 23:758–776. https://doi.org/10.1002/aqc.2332

Alves F, Alessandrini A, Servidio A, Mendonça AS, Hartman KL, Prieto R, Berrow S, Magalhães S, Steiner L, Santos R, Ferreira R, Pérez JM, Ritter F, Dinis A, Martín V, Silva M, Aguilar de Soto N (2019) Complex biogeographical patterns support an ecological connectivity network of a large marine predator in the north-east Atlantic. Divers Distrib 25:269–284. https://doi.org/10.1111/ddi.12848

Amos B, Schlotterer C, Tautz D (1993) Social structure of pilot whales revealed by analytical DNA profiling. Science 260:670–672. https://doi.org/10.1126/science.8480176

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

Augusto JF, Frasier TR, Whitehead H (2017) Social structure of long-finned pilot whales (*Globicephala melas*) off northern Cape Breton Island, Nova Scotia. Behaviour 154:509–540. https://doi.org/10.1163/1568539X-00003432

Avila IC, Kaschner K, Dormann CF (2018) Current global risks to marine mammals: taking stock of the threats. Biol Conserv 221:44–58. https://doi.org/10.1016/j.biocon.2018.02.021

Barthélemy M, Barrat A, Pastor-Satorras R, Vespignani A (2005) Characterization and modeling of weighted networks. Phys A Stat Mech Its Appl 346:34–43. https://doi.org/10.1016/j.physa.2004.08.047

Beirão-Campos L, Cantor M, Flach L, Simões-Lopes PC (2016) Guiana dolphins form social modules in a large population with high ranging overlap and small demographic changes. Behav Ecol Sociobiol 70:1821–1830. https://doi.org/10.1007/s00265-016-2188-x

Bejder L, Fletcher D, Bräger S (1998) A method for testing association patterns of social animals. Anim Behav 56:719–725. https://doi.org/10.1006/anbe.1998.0802

Bigg M, Olesiuk P, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Reports Int Whal Commision 12:383–405

Bond ML, König B, Lee DE, Ozgul A, Farine DR (2021) Proximity to humans affects local social structure in a giraffe metapopulation. J Anim Ecol 90:212–221. https://doi.org/10.1111/1365-2656.13247

Burnham K, Anderson D (2004) Multimodel inference understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304. https://doi.org/10.1177/0049124104268644

Busson M, Authier M, Barbraud C, Tixier P, Reisinger RR, Janc A, Guinet C (2019) Role of sociality in the response of killer whales to an additive mortality event. Proc Natl Acad Sci U S A 116:11812–11817. https://doi.org/10.1073/pnas.1817174116

Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Cantor M, Farine DR (2018) Simple foraging rules in competitive environments can generate socially structured populations. Ecol Evol 8:4978–4991. https://doi.org/10.1002/ece3.4061

Cantor M, Wedekin LL, Guimarães PR, Daura-Jorge FG, Rossi-Santos MR, Simões-Lopes PC (2012) Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. Anim Behav 84:641–651. https://doi.org/10.1016/j.anbehav.2012.06.019

Clauset A, Newman MEJ, Moore C (2004) Finding community structure in very large networks. Phys Rev 70:066111. https://doi.org/10.1103/PhysRevE.70.066111

Connor RC (2000) Group living in whales and dolphins. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) Cetacean Societies: Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago and London, pp 199–218

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal, Complex Syst 1695:1–9

de Stephanis R, Verborgh P, Pérez S, Esteban R, Minvielle-Sebastia L, Guinet C (2008) Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. Acta Ethol 11:81–94. https://doi.org/10.1007/s10211-008-0045-2

Desportes G, Andersen LW, Aspholm PE, Bloch D, Mouritsen R (1992) A note about a male-only pilot whale school observed in Faroe Islands. Fróðskaparrit 40:31–37

Efron B, Gong G (1983) A leisurely look at the bootstrap, the jackknife, and cross-validation. Am Stat 37:36–48. https://doi.org/10.1080/00031305.1983.10483087

Ellis S, Franks DW, Nattrass S, Currie TE, Cant MA, Giles D, Balcomb KC, Croft DP (2018) Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. Sci Rep 8:12833. https://doi.org/10.1038/S41598-018-31047-8

Elliser CR, Herzing DL (2011) Replacement dolphins? Social restructuring of a resident pod of Atlantic bottlenose dolphins, *Tursiops truncatus*, after two major hurricanes. Mar Mammal Sci 27:39–59. https://doi.org/10.1111/j.1748-7692.2010.00403.x

Epskamp S, Cramer AOJ, Waldorp LJ, Schmittmann VD, Borsboom D (2012) Qgraph: network visualizations of relationships in psychometric data. J Stat Softw. https://doi.org/10.18637/jss.v048.i04

Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD, de Stephanis R (2016a) Maternal kinship and fisheries interaction influence killer whale social structure. Behav Ecol Sociobiol 70:111–122. https://doi.org/10.1007/s00265-015-2029-3

Esteban R, Verborgh P, Gauffier P, Giménez J, Martín V, Pérez-Gil M, Tejedor M, Almunia J, Jepson PD, García-Tíscar S, Barrett-Lennard LG, Guinet C, Foote AD, de Stephanis R (2016b) Using a multi-disciplinary approach to identify a critically endangered killer whale management unit. Ecol Indic 66:291–300. https://doi.org/10.1016/j.ecolind.2016.01.043

Farine DR (2014) Measuring phenotypic assortment in animal social networks: Weighted associations are more robust than binary edges. Anim Behav 89:141–153. https://doi.org/10.1016/j.anbehav.2014.01.001

Farine DR (2017) A guide to null models for animal social network analysis. Methods Ecol Evol 8:1309–1320. https://doi.org/10.1111/2041-210X.12772

Farine DR (2018) When to choose dynamic vs. static social network analysis. J Anim Ecol 87:128–138. https://doi.org/10.1111/1365-2656.12764

Farine, D.R., 2019. asnipe: Animal Social Network Inference and Permutations for Ecologists. R package version 1.1.12 [WWW Document]. R Packag. version 1.1.12. URL https://cran.r-project.org/web/packages/asnipe/index.html (accessed 8.26.20).

Foote AD (2008) Mortality rate acceleration and post-reproductive lifespan in matrilineal whale species. Biol Lett 4:189–191. https://doi.org/10.1098/rsbl.2008.0006

Foster EA, Franks DW, Morrell LJ, Balcomb KC, Parsons KM, van Ginneken A, Croft DP, van Ginneken A (2012) Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca*. Anim Behav 83:731–736. https://doi.org/10.1016/j.anbehav.2011.12.021

Freitas L, Dinis A, Alves F, Nóbrega F, 2004. Cetáceos no arquipélago da Madeira. Museu da Baleia da Madeira.

Freitas L, Alves F, Ribeiro C, Dinis A, Nicolau C, Carvalho A, 2014. Estudo técnico-científico de suporte à proposta de criação de áreas de operação para a actividade de whalewatching e respectiva capacidade de carga. Relatório técnico do Projecto CETACEOSMADEIRA II (LIFE07 NAT/P/000646).

Geldmacher J, van den Bogaard P, Hoernle K, Schmincke H-U (2000) The 40 Ar/ 39 Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). Geochemistry Geophys Geosystems. https://doi.org/10.1029/1999GC000018

Genoves RC, Fruet PF, Di Tullio JC, Möller LM, Secchi ER (2018) Spatiotemporal use predicts social partitioning of bottlenose dolphins with strong home range overlap. Ecol Evol 8:12597–12614. https://doi.org/10.1002/ece3.4681

Gero S, Gordon J, Whitehead H (2013) Calves as social hubs: dynamics of the social network within sperm whale units. Proc R Soc B Biol Sci 89:141–153. https://doi.org/10.1098/rspb.2013.1113

Goldenberg SZ, Douglas-Hamilton I, Wittemyer G (2016) Vertical transmission of social roles drives resilience to poaching in elephant networks. Curr Biol 26:75–79. https://doi.org/10.1016/j.cub.2015.11.005

Gowans S, Würsig B, Karczmarski L (2007) The social structure and strategies of Delphinids: predictions based on an ecological framework. Adv Mar Biol 53:195–294. https://doi.org/10.1016/S0065-2881(07)53003-8

Guinet C (1991) L'orque (*Orcinus orca*) autour de l'Archipel Crozet comparaison avec d'autres localites. Rev D'ecologie (terre La Vie) 46:321–337

Hazen EL, Suryan RM, Santora JA, Bograd SJ, Watanuki Y, Wilson RP (2013) Scales and mechanisms of marine hotspot formation. Mar Ecol Prog Ser 487:177–183. https://doi.org/10.3354/meps10477

Heimlich-Boran JR (1993) Social organisation of the short-finned pilot whale, *Globicephala macrorhynchus*, with special reference to the comparative social ecology of delphinids. University of Cambridge, Cambridge

Hill MC, Bendlin AR, Van Cise AM, Milette-Winfree A, Ligon AD, Adam C, Deakos MH, Oleson EM (2019) Short-finned pilot whales (*Globicephala macrorhynchus*) of the Mariana Archipelago: individual affiliations, movements, and spatial use. Mar Mammal Sci 35:797–824. https://doi.org/10.1111/mms.12567

Hobson EA, Avery ML, Wright TF (2013) An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. Anim Behav 85:83–96. https://doi.org/10.1016/j.anbehav.2012.10.010

Kasuya T, Marsh H (1984) Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. Reprod. Whales, dolphins porpoises. Proc. Conf. La Jolla, CA (**1981**)

Kasuya T, Tai S (1993) Life history of short-finned pilot whale stocks of Japan and a description of the fishery. Biology of Northern Hemisphere Pilot Whales. Report of the International Whaling Commission, Cambridge

Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM (eds) Radio tracking and animal populations. Elsevier, Amsterdam, pp 125–166. https://doi.org/10.1016/B978-012497781-5/50006-2

Lefebvre D, Ménard N, Pierre JS (2003) Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. Behav Ecol Sociobiol 53:402–410. https://doi.org/10.1007/s00265-002-0578-8

Lusseau D, Newman MEJ (2004) Identifying the role that animals play in their social networks. Proc R Soc Ser B 271:S477–S481. https://doi.org/10.1098/rsbl.2004.0225

Lyrholm T, Gyllensten U (1998) Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. Proc R Soc B Biol Sci 265:1679–1684. https://doi.org/10.1098/rspb.1998.0488

Mahaffy SD, Baird RW, Mcsweeney DJ, Webster DL, Schorr GS (2015) High site fidelity, strong associations, and long-term bonds: Short-finned pilot whales off the island of Hawai'i. Mar Mammal Sci 31:1427–1451. https://doi.org/10.1111/mms.12234

Markham AC, Gesquiere LR, Alberts SC, Altmann J (2015) Optimal group size in a highly social mammal. Proc Natl Acad Sci USA 112:14882–14887. https://doi.org/10.1073/pnas.1517794112

Marsh H, Kasuya T (1984) Changes in the ovaries of the short-finned pilot Whale, *Globicephala macrorhynchus* with age and reproductive activity. Rep Int Whal Comm 6:311–335

Marsh H, Kasuya T (1986) Evidence for reproductive senescence in female cetaceans. Rep Int Whal Comm 8:57–74

Marsh H, Kasuya T (1991) An overview of the changes in the role of a female pilot whale with age. In: Pryor K, Norris KS (eds) Dolphin Societies: Discoveries and Puzzles. University of California Press, Berkelery, pp 281–285

Ménard N (2017) Group Fission. Int Encycl Primatol. https://doi.org/10.1002/9781119179313.wbprim0197

MISTIC SEAS II, 2019. Applying a sub-regional coherent and coordinated approach to the monitoring and assessment of marine biodiversity in Macaronesia for the second cycle of the MSFD Final Technical Report - WP1- Monitoring Programs and Data gathering. https://doi.org/10.13140/RG.2.2.17231.10407

Möller LM, Wiszniewski J, Parra G, Beheregaray L (2012) Sociogenetic structure, kin associations and bonding in delphinids. Mol Ecol 21:745–764. https://doi.org/10.1111/j.1365-294X.2011.05405.x

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos PM, Stevens MHH, Wagner H (2008) The vegan package. Commun Ecol Packag 190:295

Oremus M, Gales R, Kettles H, Baker CS (2013) Genetic evidence of multiple matrilines and spatial disruption of kinship bonds in mass strandings of long-finned pilot Whales, *Globicephala melas*. J Hered 104:301–311. https://doi.org/10.1093/jhered/est007

Ottensmeyer CA, Whitehead H (2003) Behavioural evidence for social units in long-finned pilot whales. Can J Zool 81:1327–1338. https://doi.org/10.1139/z03-127

Pirotta E, Booth CG, Costa DP, Fleishman E, Kraus SD, Lusseau D, Moretti D, New LF, Schick RS, Schwarz LK, Simmons SE, Thomas L, Tyack PL, Weise MJ, Wells RS, Harwood J (2018) Understanding the population consequences of disturbance. Ecol Evol 89:141–153. https://doi.org/10.1002/ece3.4458

R Core Team (2019) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Região Autónoma da Madeira, 2014. Portaria nº 46/2014. Regula a “capacidade de carga” inerente à atividade de observação de cetáceos na Região Autónoma da Madeira.

Rendell L, Cantor M, Gero S, Whitehead H, Mann J (2019) Causes and consequences of female centrality in cetacean societies. Philos Trans R Soc B Biol Sci 374:20180066. https://doi.org/10.1098/rstb.2018.0066

Roff J, Zacharias M, Day J (2011) Marine Conservation Ecology. Earthscan. https://doi.org/10.4324/9781849775540

Servidio A (2014) Distribution, social structure and habitat use of short-finned pilot whale, *Globicephala macrorhynchus*, in the Canary islands. University of St Andrews

Servidio A, Pérez-Gil E, Pérez-Gil M, Cañadas A, Hammond PS, Martín V (2019) Site fidelity and movement patterns of short-finned pilot whales within the Canary Islands: evidence for resident and transient populations. Aquat Conserv Mar Freshw Ecosyst 29:227–241. https://doi.org/10.1002/aqc.3135

Shizuka D, Farine DR (2016) Measuring the robustness of network community structure using assortativity. Anim Behav 112:237–246. https://doi.org/10.1016/j.anbehav.2015.12.007

Shizuka D, Johnson AE (2020) How demographic processes shape animal social networks. Behav Ecol 31:1–11. https://doi.org/10.1093/beheco/arz083

Siemann LA (1994) Mitochondrial DNA sequence variation in North Atlantic long-finned pilot whales *Globicephala melas*. Cornell University

Silk MJ, Jackson AL, Croft DP, Colhoun K, Bearhop S (2015) The consequences of unidentifiable individuals for the analysis of an animal social network. Anim Behav 104:1–11. https://doi.org/10.1016/j.anbehav.2015.03.005

Stredulinsky EH, Darimont CT, Barrett-Lennard L, Ellis GM, Ford JKB (2021) Family feud: permanent group splitting in a highly philopatric mammal, the killer whale (*Orcinus orca*). Behav Ecol Sociobiol 75:56. https://doi.org/10.1007/s00265-021-02992-8

Tantardini M, Ieva F, Tajoli L, Piccardi C (2019) Comparing methods for comparing networks. Sci Rep 9:17557. https://doi.org/10.1038/s41598-019-53708-y

Tavares SB, Samarra FIP, Miller PJO (2017) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behav Ecol 28:500–514. https://doi.org/10.1093/beheco/arw179

Taylor BL, Wade PR, De Master DP, Barlow J (2000) Incorporating uncertainty into management models for marine mammals. Conserv Biol 14:1243–1252. https://doi.org/10.1046/j.1523-1739.2000.99409.x

Thompson JW, Zero VH, Schwacke LH, Speakman TR, Quigley BM, Morey JS, McDonald TL (2022) finFindR: Automated recognition and identification of marine mammal dorsal fins using residual convolutional neural networks. Mar Mammal Sci 38:139–150. https://doi.org/10.1111/MMS.12849

Van Cise AM, Martien KK, Mahaffy SD, Baird RW, Webster DL, Fowler JH, Oleson EM, Morin PA (2017) Familial social structure and socially driven genetic differentiation in Hawaiian short-finned pilot whales. Mol Ecol 26:6730–6741. https://doi.org/10.1111/mec.14397

Verborgh P, Gauffier P, Esteban R, Stephanis R (2021) Demographic parameters of a free-ranging deep-diving cetacean, the long-finned pilot whale. Mar Mammal Sci 37:463–481. https://doi.org/10.1111/mms.12752

Verborgh P, Janssen EH, Esteban R, Gauffier P, Freitas L (2022) Proposing a framework for monitoring demographic parameters in local cetacean populations: the case of short-finned pilot whales in Madeira. Mamm Biol (Special Issue) 102(4). https://doi.org/10.1007/s42991-022-00266-y

Weiss MN, Ellis S, Croft DP (2021) Diversity and consequences of social network structure in toothed whales. Front Mar Sci 8:688842. https://doi.org/10.3389/fmars.2021.688842

Whitehead H (1995) Investigating structure and temporal scale in social organizations using identified individuals. Behav Ecol 6:199–208. https://doi.org/10.1093/beheco/6.2.199

Whitehead H (2001) Analysis of animal movement using opportunistic individual identifications: application to sperm whales. Ecology 82:1417–1432. https://doi.org/10.1890/0012-9658(2001)082[1417:AOAMUO]2.0.CO;2

Whitehead H (2007) Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. Commun Stat Simul Comput 36:1233–1246. https://doi.org/10.1080/03610910701569531

Whitehead H (2008a) Analysing animal societies. The University of Chicago Press, Chicago and London, Nova Scotia, Quantitative methods for vertebrate social analysis

Whitehead H (2008b) Precision and power in the analysis of social structure using associations. Anim Behav 75:1093–1099. https://doi.org/10.1016/j.anbehav.2007.08.022

Whitehead H (2009) SOCPROG programs: analysing animal social structures. Behav Ecol Sociobiol 63:765–778. https://doi.org/10.1007/s00265-008-0697-y

Whitehead H, Dufault S, 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations, In: Slater P, Rosenblat J, SNowden C, Roper T (Eds.) Advances in the Study of Behavior. 33–74 Academic Press, Cambridge

Whitehead H, Weilgart L (2000) The sperm whale: social females and roving males. In: Mann J, Connor RC, Tyack P, Whitehead H (eds) Cetacean Societies: Field Studies of Dolphins and Whales. University of Chicago Press, Chicago, pp 154–172

Williams R, Lusseau D (2006) A killer whale social network is vulnerable to targeted removals. Biol Lett 2:497–500. https://doi.org/10.1098/rsbl.2006.0510

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home- range studies. Ecology 70:164–168. https://doi.org/10.2307/1938423