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ORIGINAL PAPER

Habitat availability and geographic isolation as potential drivers of population structure in an oceanic dolphin in the Southwest Indian Ocean

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Abstract Delphinid populations show highly variable patterns of genetic diversity and population structure. Previous studies indicate that habitat discontinuities and geographic isolation are major drivers of population division in cetaceans. Spinner dolphins (*Stenella longirostris*) are distributed in all tropical oceans, but they are particularly common around islands and atolls. This species occurs in shallow waters at daytime to rest and socialise, and feeds on offshore mesopelagic prey overnight. Here, we investigated the genetic population structure of spinner dolphins in the Southwest Indian Ocean along a west–east geographic gradient, from eastern Africa to the Mascarene archipelago. We combined analyses of 12 microsatellite loci, mtDNA control region sequences, and sighting data to assess genetic differentiation and characterise habitat preferences of these populations. Significant genetic structure among the three sampled sites (Zanzibar, Mayotte and La Réunion) was observed using both types of molecular markers. Overall, our results indicate that geographic isolation and potentially other factors, such as shallow-water habitats to rest and socialise, may be important drivers of the genetic population structure of insular spinner dolphins in this region.

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Introduction

Understanding factors influencing population connectivity has been a central and long-standing research avenue in marine ecology (e.g. Cowen et al. 2000, 2007; Selkoe et al. 2008). Past studies have shown that the genetic structure of marine populations is driven by a number of processes,

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including water currents, sea floor topography, water temperature and life history (e.g. Fullard et al. 2000; Fontaine et al. 2007; Pelc et al. 2009; Ciannelli et al. 2010; Mendez et al. 2011; 2013). In cetaceans, factors that can lead to discontinuous relationships between genetic and geographic distance include habitat characteristics, intra-species niche partitioning (e.g. foraging specialisation) and kinship, combined with demographic processes (e.g. Hoelzel 2009; Möller et al. 2007, 2011; Louis et al. 2014a, b; Viricel and Rosel 2014).

Besides its fundamental importance in marine ecology, understanding the spatial structure and genetic connectivity of marine populations is also critical for conservation and management purposes. Indeed, while no marine ecosystem is completely unaffected by human activities, threats to populations of marine organisms vary geographically (Halpern et al. 2008). In the Southwest (SW) Indian Ocean for instance, the importance of marine mammal bycatch is spatially variable and it seems to primarily affect inshore species, including coastal delphinids (Kiszka et al. 2009). Thus, delimiting biologically meaningful conservation units (i.e. based on population structure assessments) will be a crucial step towards preserving the marine megafauna of this region.

The spinner dolphin (*Stenella longirostris*) is one of the most abundant and widely distributed tropical delphinids (Perrin 2009). Four subspecies are currently recognised, based on morphological and ecological differences (Perrin and Gilpatrick 1994; Perrin et al. 1999). The Gray's spinner dolphin (*S. longirostris longirostris*), hereafter the spinner dolphin, is primarily an insular subspecies, and its distribution includes the Atlantic, Indian and Pacific Oceans (Perrin and Gilpatrick 1994). In French Polynesia, Hawaii and the Maldives, spinner dolphins enter atolls, sheltered bays and lagoons through reef channels in the morning and leave in the afternoon to feed offshore overnight (Würsig et al. 1994; Anderson 2005; Gannier and Petiau 2006), essentially on mesopelagic prey (Perrin et al. 1973; Dolar et al. 2003). Around the lagoon of Mayotte, in the Mozambique Channel (SW Indian Ocean), spinner dolphins primarily inhabit the outer slope of the barrier reef to rest and socialise, and rarely enter the lagoon (Kiszka et al. 2010a, 2011). During the past 20 years, extensive work has been conducted on the movements, behaviour, social and genetic population structure of insular spinner dolphins, particularly in the Pacific Ocean (Norris et al. 1994; Karczmarski et al. 2005; Oremus et al. 2007; Andrews et al. 2010). These studies highlight that spinner dolphins may form "fission–fusion" societies, with groups forming and separating over short periods of time, such as around the big island of Hawaii (Karczmarski et al. 2005; Andrews et al. 2010). However, social structure may vary according to habitat characteristics and geographic isolation. Indeed, at the remote Midway atoll (Hawaii), spinner dolphins form stable groups with high level of site fidelity, limited emigration/immigration and strong inter-individual associations (Karczmarski et al. 2005). In this region, gene flow is more restricted among populations showing a fluid social structure (the Kona Coast of the island of Hawaii) than among populations with stable social groups (Midway and Kure Atolls) (Andrews et al. 2010).

In the SW Indian Ocean, the spinner dolphin is one of the most common small cetacean species in tropical and subtropical waters, particularly around islands and reef complexes off Zanzibar (Amir et al. 2002), Mayotte (Kiszka et al. 2010a, 2011) and the Comoros archipelago (Kiszka et al. 2010c), La Réunion (Dulau-Drouot et al. 2008; Condet and Dulau-Drouot 2016), Madagascar (Rosenbaum 2003) and Mauritius (Webster et al. 2015). Spinner dolphins are rarely observed in open ocean waters (>2000 m), but can occur for short periods of time between islands (particularly in island chains), mostly when undertaking overnight foraging trips (e.g. Kiszka et al. 2011; Mannocci et al. 2014; Thorne et al. 2012). As this species occurs in coastal and reef-associated waters, spinner dolphins are impacted by human activities, including past hunting and bycatch off Zanzibar (Stensland et al. 1998; Amir et al. 2012), direct hunting and bycatch in southwestern Madagascar (Razafindrakoto et al. 2008) and disturbance from dolphin-watching activities such as on the west coast of Mauritius (Webster et al. 2015). However, the geographic extent of the influence of such direct and indirect effects on populations is unknown.

This study aims to characterise genetic diversity and population structure of spinner dolphins in the SW Indian Ocean, particularly from Zanzibar (Tanzania), Mayotte (Comoros archipelago) and La Réunion (Mascarene archipelago) (Fig. 1). These islands were selected because they are located along a west–east gradient, from continental waters of Africa (Zanzibar) to the most isolated and remote oceanic islands (La Réunion). We also characterise depth preferences of spinner dolphins at these sites to evaluate their reliance on shallow-water habitat and to estimate habitat size around the two oceanic islands. Resting habitat availability has been suggested to influence population size and dispersal in other island-associated spinner dolphin populations (Andrews et al. 2010). We evaluate the relationship between our estimations of genetic diversity and habitat size: islands with more suitable habitats are expected to sustain greater population sizes, which would maintain greater genetic diversity. Geographic distances separating the coasts of the three sites are greater than 900 km. Considering previous knowledge gathered in the Pacific (Andrews et al. 2006; Oremus et al. 2007; Andrews et al. 2010), we hypothesised that geographic isolation is a major driver of the genetic population structure of spinner

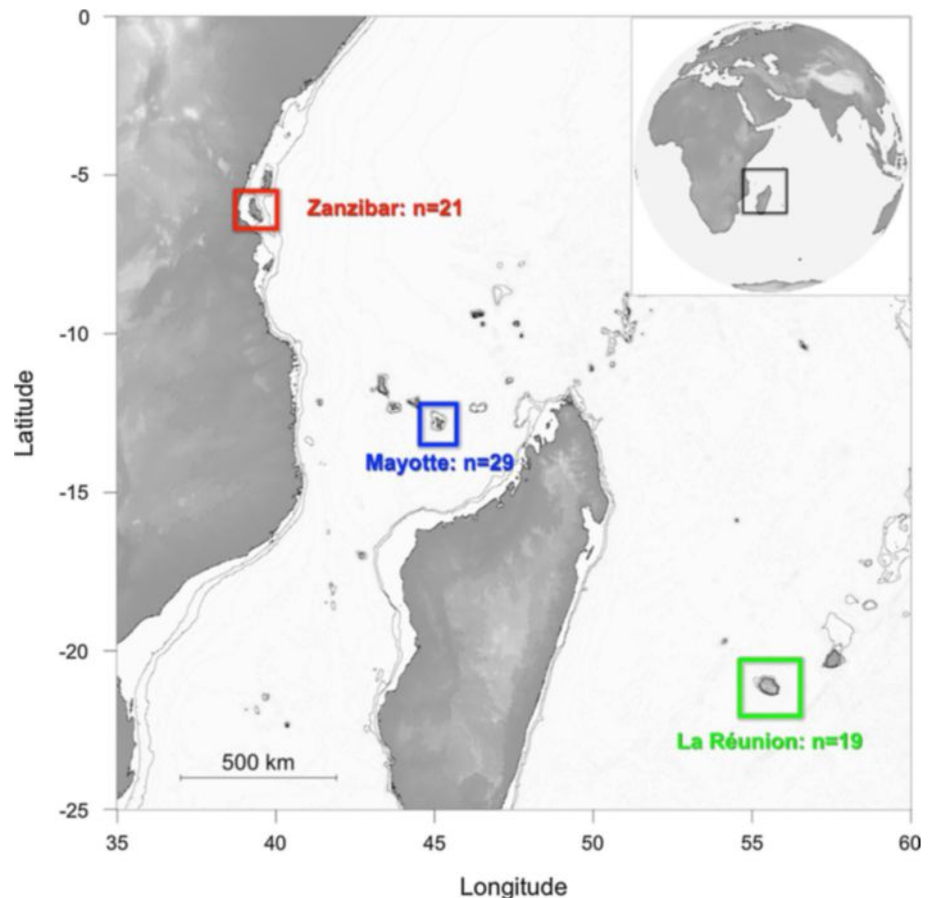


Fig. 1 Study area and sample locations. Sample sizes are indicated for each site. The 200-m and 1000-m isobaths are represented by *darker lines*

dolphins in this region and that sampled islands should contain genetically distinct populations.

Materials and methods

Sample collection and DNA extraction

In total, tissue samples collected from 69 individual spinner dolphins off Zanzibar ($n = 21$), Mayotte ($n = 29$) and La Réunion ($n = 19$) were available for this study (Fig. 1). For Zanzibar, muscle tissues were collected from bycaught animals in drift gillnets between 2000 and 2004 and were stored frozen at −20 °C. Samples from Mayotte and La Réunion were collected during dedicated biopsy surveys undertaken in territorial waters from 2006 to 2011 from small boats. Biopsy attempts were made opportunistically, when groups and individuals were easily approachable and when conditions were optimal (Beaufort < 2, dolphins closely approaching the boat). Optimal weather conditions allowed stability of the research boat and better chances to sample the animals successfully and safely (Kiszka et al. 2010b). Blubber and skin biopsies were collected using a crossbow (BARNETT Veloci-Speed® Class, 68-kg draw weight and BARNETT Panzer V Class, 68-kg draw weight) with Finn Larsen (Ceta-Dart, Copenhagen, Denmark) bolts and tips (dart 20 mm long, 7 mm diameter). Biopsy samples were preserved individually in 90 % ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under French scientific permit #78/DAF/2004 (September 10, 2004) and permit #032/DAF/SEF/2008 (May 16, 2008) for Mayotte and MC/2009/336 for La Réunion. Genomic DNA was extracted from ~25 mg of tissue (muscle or skin) using a Nucleospin Tissue kit (Macherey–Nagel) following the manufacturer's protocol.

Microsatellite genotyping and mitochondrial DNA (mtDNA) sequencing

Twelve microsatellite loci previously optimised for *S. longirostris* were genotyped (Table 1). PCR reactions included ~20 ng of genomic DNA, 0.5 U Taq polymerase, 0.25 mM dNTPs, 1.5 mM $MgCl_2$, 1X PCR Buffer, 0.125 µM of each primer in a 20 µL final volume. PCR profiles were as follows: initial 5-min denaturation step at 94 °C followed by 35 cycles of 30 s at 94 °C, 30 s at a specific annealing temperature (see Table 1), 45 s at 72 °C, and by a final 7-min extension step at 72 °C. All PCRs were conducted in

Table 1 Twelve microsatellite loci genotyped in this study

Locus	Ta (°C)	References	Number of alleles	H_o	H_e
415/416	45	Amos et al. (1993)	12	0.772	0.889
GT575	60	Bérubé et al. (2000)	10	0.679	0.778
GT6	60	Caldwell et al. (2002)	6	0.635	0.676
AAT44	55	Caldwell et al. (2002)	10	0.770	0.710
KWM12a	46	Hoelzel et al. (1998)	10	0.889	0.844
MK5	50	Krützen et al. (2001)	13	0.786	0.912
MK6	50	Krützen et al. (2001)	18	0.879	0.931
GATA98	54	Palsbøll et al. (1997)	9	0.655	0.804
PPHO142	50	Rosel et al. (1999)	9	0.804	0.810
PPHO131	57	Rosel et al. (1999)	12	0.755	0.834
EV1	47	Valsecchi and Amos (1996)	16	0.868	0.902
EV94	54	Valsecchi and Amos (1996)	25	0.772	0.925

PCR annealing temperature (Ta), reference, number of alleles, observed (H_o) and expected (H_e) heterozygosity are given for each locus

a Techne TC-5000 thermocycler. PCR products were visualised using polyacrylamide gels on the LICOR 4300 DNA Analyser. Allele sizes were determined by eye using a size standard and by two different researchers to ensure consistency in scoring.

A portion of the mtDNA control region was amplified using primers Dlp-1.5 (5′-TCACCCAAAGCT GRARTTCTA-3′) (Baker et al. 1998) and Dlp-8G (5′-GGAGTACTATGTCCTGTAACCA-3′) (Dalebout et al. 2005). PCR reactions included 0.5 U Taq polymerase, 0.25 mM dNTPs, 1.5 mM $MgCl_2$, 1X PCR Buffer, 0.125 µM of each primer and ~50 ng of genomic DNA in a 50 µL reaction volume. PCRs were conducted in a Techne TC-5000 thermocycler using the following profile: initial 5-min denaturation step at 94 °C followed by 35 cycles of 30 s at 94 °C, 30 s at 54 °C, 45 s at 72 °C, and by a final 7-min extension step at 72 °C. PCR products were purified and sequenced by Genoscreen (Lille, France). Sequences were edited in Chromas sequence viewer v. 2.33 (Chromas Technelysium) and were aligned using BioEdit version 5.0.6 (Hall 1999).

Microsatellite analyses

We tested for departures from Hardy–Weinberg or linkage equilibrium within each sampled site using Genepop version 4.2 (Raymont and Rousset 1995) with 10,000 dememorizations, 1000 batches and 10,000 iterations per batch. The sequential Bonferroni technique (Holm 1979) was applied to correct for multiple tests. The presence of null alleles and scoring errors was assessed using Micro-checker version 2.2.3 (van Oosterhoot et al. 2004) within each site. We searched for potential duplicates within biopsied animals by comparing their multi-locus genotypes (i.e. searching for identical genotypes in the dataset and for genotypes with less than three different alleles overall) using Genalex version 6.41 (Peakall and Smouse 2006). The mitochondrial haplotypes of samples with matching microsatellite genotypes were compared to confirm they were duplicates of the same individual. We investigated whether related individuals were included in the dataset by calculating maximum-likelihood estimates of pairwise relatedness using ML-Relate (Kalinowski et al. 2006). To avoid biases in population inferences that could result from family structure (Anderson and Dunham 2008), we removed one individual from each pair of potential relatives, i.e. individuals showing a pairwise relatedness value greater than 0.45 (as in Viricel and Rosel 2014). Allele richness, observed and expected heterozygosity were calculated using FSTAT version 2.9.3.2 (Goudet 1995) and Arlequin version 3.5.1.2 (Excoffier and Lischer 2010), respectively. These molecular diversity indices were calculated for the whole dataset and for each site separately.

Population structure was assessed using a Bayesian approach implemented with Structure version 2.3.4 (Pritchard et al. 2000), which infers the number of populations (K) present in a dataset based on assumptions of Hardy–Weinberg and linkage equilibria within populations. Analyses were conducted using the admixture and correlated allele frequencies models, with and without prior information on individual location (option “LOCPRIOR”). Including prior information on sample locations can improve population inferences, particularly when the level of population differentiation is weak or recent (Hubisz et al. 2009). To verify that using prior information did not artificially result in distinct clusters, we conducted additional Structure runs with the LOCPRIOR option after randomizing the sample location information in the input file. Three randomized input files were created. All Structure runs included 300,000 Markov chain Monte Carlo iterations and

a 50,000 step burn-in. Ten replicate runs were performed for K values between 1 and 5. Convergence was assessed by examining *alpha* and likelihood plots and by comparing individual membership probabilities across replicate runs. The best K was chosen by comparing mean log probabilities among K values, and when $K = 1$ was ruled out, by applying Evanno's method using ΔK (Evanno et al. 2005).

To assess genotypic variation among individuals and among the three locations, we applied a principal component analysis (PCA) to the microsatellite data using the package adegenet (Jombart 2008) in R v. 3.1.2 (R Core Team 2015). In the PCA, allele frequencies were scaled using the centring option. An analysis of molecular variance (AMOVA, Excoffier et al. 1992) was conducted in Arlequin version 3.5.1.2. (Excoffier and Lischer 2010) to estimate genetic differentiation among the three islands. Pairwise F_{ST} estimates were calculated, and significance was assessed using 10,000 permutations. We tested for isolation by distance (IBD) by conducting a Mantel test comparing pairwise genetic distances ($F_{ST}/(1 - F_{ST})$, Rousset 1997) with log-transformed (base 10) geographic distances among sampling locations. Geographic distances between population pairs were calculated as the Euclidean distance between the approximate centres of the areas where samples were collected. The Mantel test was performed using IBDWS version 3.23 (Jensen et al. 2005) with 10,000 randomizations. Finally, we investigated the occurrence of private alleles in each population identified using Genalex version 6.41.

MtDNA sequence analyses

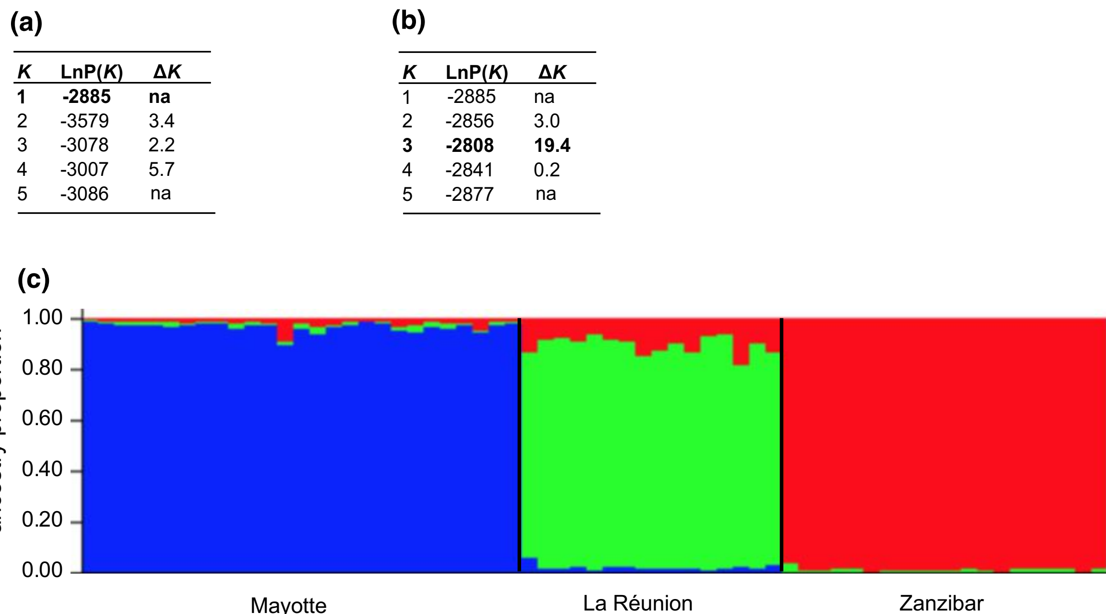
Diversity indices (haplotype and nucleotide diversities) were calculated for each site using Arlequin. We used JModeltest version 0.1.1 (Guindon and Gascuel 2003; Posada 2008) and the Akaike Criterion to determine the most appropriate model of substitution given our sequence alignment. AMOVAs comparing the populations identified using Structure were performed in Arlequin. Genetic differentiation was measured using both F_{ST} and Φ_{ST}. For Φ_{ST}, distances between haplotypes were calculated using the model of substitution selected with JModeltest. Significance was assessed using 10,000 permutations. We evaluated IBD as described above for microsatellite data. A median-joining network was constructed using Network version 4.6.1.2 (Bandelt et al. 1999) with default parameters to represent relationships among haplotypes.

Habitat size

In order to relate patterns of genetic structure and availability of habitat used by spinner dolphins, we created spinner dolphin habitat maps based on their depth preferences around Zanzibar, Mayotte and La Réunion. From 2004 to 2008, sighting data were collected around Mayotte ($n = 168$ sightings in 224 days of survey) and La Réunion ($n = 51$ sightings in 278 days of survey) during small-boat dedicated surveys (see Dulau-Drouot et al. 2008; Kiszka et al. 2011 for sampling protocols). For surveys undertaken around Mayotte and La Réunion, the sampling effort did not follow predefined transects and was not homogeneous. However, both surveys covered shallow inshore waters, the outer slope of the reef and deep oceanic habitats (depth > 500 m around Mayotte: Kiszka et al. 2011 and depth > 1000 m around La Réunion: Dulau-Drouot et al. 2008). For Zanzibar, as sighting data were unavailable, we used geographic locations of bycatch events that were recorded during a bycatch monitoring programme coordinated by the Institute for Marine Sciences, University of Dar es Salaam, based on Zanzibar between 2000 and 2007 ($n = 27$ records). These data were used to determine habitat preferences of spinner dolphins using depth as the main variable. We chose to focus habitat analyses on depth as it was previously identified as one of the main explanatory variables explaining spinner dolphin distribution patterns in this region (Kiszka et al. 2011; Condet and Dulau-Drouot 2016) and in other parts of the world (e.g. Thorne et al. 2012). Depth data were extracted from the GEBCO_2014 Gridded bathymetric dataset (30 arcsecond resolution) hosted on the British Oceanographic Data Center (http://www.bodc.ac.uk). We considered that the preferred habitat corresponded to the depth range where 95 % of spinner dolphin observations were made. Thus, we excluded 2.5 % of the deepest and 2.5 % of the shallowest observations to determine (1) the preferred depth range for Mayotte and La Réunion separately (we did not include Zanzibar in this comparison as observations from Zanzibar come from bycatch events and are thus not directly comparable to sighting data from the other two islands), (2) the overall preferred depth range for the three islands together. For the second calculation, group size information available for sightings around Mayotte was taken into account. Our reasoning was that using group size information (when available) better reflects the preferred habitat of these populations (i.e. observing large groups in an area carries more weight than observing a single individual). We computed the total area available within the depth range limits obtained for the three islands together and mapped these areas for Mayotte and La Réunion. It was not computed for Zanzibar since available habitat within this depth range is virtually infinite along the East African continental shelf relative to the two islands. The retrieval of individual depths, the computation of projected surfaces and the mapping were all performed with the marmap package v0.9.2 (Pante and Simon-Bouhet 2013) in R v3.1.2.

Table 2 Mitochondrial DNA (mtDNA) and microsatellite diversity indices for *Stenella longirostris* from each site: N, sample size; No. haplo, number of haplotypes; π, nucleotide diversity; h, haplotype diversity; AR, allele richness; H_o, observed heterozygosity; H_e, expected heterozygosity

	MtDNA				Microsatellites			
	N	No. haplo	π	h	N	Mean AR	H_o	H_e
Zanzibar	20	9	0.013	0.826	20	7.1	0.747	0.790
Mayotte	19	14	0.015	0.965	27	8.2	0.773	0.835
La Réunion	16	9	0.012	0.900	16	7.5	0.798	0.818


(a)

K	LnP(K)	ΔK
1	**-2885**	**na**
2	-3579	3.4
3	-3078	2.2
4	-3007	5.7
5	-3086	na

(b)

K	LnP(K)	ΔK
1	-2885	na
2	-2856	3.0
3	**-2808**	**19.4**
4	-2841	0.2
5	-2877	na

Fig. 2 Bayesian clustering analysis (structure) results obtained from analysis of 12 microsatellite loci **a** without any prior information and **b** using prior information about sample location ("LOCPRIOR" option). The mean log probability (LnP(K)) is given for each K tested, and the ΔK from Evanno's method is shown between successive K values. **c** The *barplot* represents individual ancestry proportions for the three populations obtained using the "LOCPRIOR" option

Results

Microsatellite data

Each sample was genotyped at 8–12 loci. No significant departure from Hardy–Weinberg or linkage equilibrium was observed (after sequential Bonferroni correction) in the three sampled sites. Furthermore, no scoring errors were identified using Micro-checker. Possible null alleles were detected for loci EV94 and 415/416 in Mayotte; however, since this issue was restricted to one site, we kept these two loci in all analyses. A duplicate sample was identified (100 % matching genotypes and haplotype) in La Réunion, where the same individual was biopsied twice. Five pairs of potential relatives were detected using ML-Relate: two pairs in La Réunion, one pair in Zanzibar and two pairs in Mayotte. Only one individual from each pair was kept in population analyses conducted with both types of markers (mtDNA and microsatellites) to avoid the potential bias of including relatives. The final microsatellite dataset included 63 individuals (Table 2). The number of alleles per locus ranged from six to twenty-five (Table 1). Observed heterozygosity and mean allele richness were similar among the three sites (Table 2).

No population subdivision was found when Structure was run without prior information (Fig. 2a). Conversely, genetic structure was detected when individual location was used as prior information. The most likely number of populations present in the dataset was three based on comparison of the mean log probabilities and ΔK (Fig. 2b), and corresponded to the three sampled sites (Fig. 2c): within each site, all individuals were assigned to the same cluster with high ancestry proportions ($q > 0.8$, mean $q = 0.95$). Randomizing sample locations in the Structure input file and applying the LOCPRIOR option resulted in no structure being detected by the programme (most likely $K = 1$; see Appendix 1 ESM).

Table 3 AMOVA results obtained from analysis of microsatellite data from 63 *S. longirostris* individuals

	Zanzibar	Mayotte	La Réunion
Zanzibar	NA	<0.001*	<0.001*
Mayotte	0.024	NA	0.009*
La Réunion	0.025	0.013	NA

Pairwise F_{ST} values are shown below diagonal and corresponding *p* values above diagonal

* Significant *p* value after sequential Bonferroni correction

Table 4 AMOVA results for mitochondrial DNA sequences

	Zanzibar	Mayotte	La Réunion
Zanzibar	NA	0.050	0.014
Mayotte	0.058*	NA	0.066
La Réunion	0.130*	0.067*	NA

Pairwise F_{ST} and Φ_{ST} values are shown below and above diagonal, respectively

* Significant *p* value after sequential Bonferroni correction

The first principal component of the PCA separated individuals from Mayotte from the other two locations, while the third principal component showed two separate clusters for individuals from La Réunion and Zanzibar (Appendix 2 ESM). Some overlap in the PC space was observed among the three clusters. Together, the first three principal components explained 12.7 % of the total genotypic variation. The AMOVA conducted among the three populations revealed relatively weak, but significant genetic differentiation (overall $F_{ST} = 0.020$ $p < 0.0001$; Table 3). The Mantel test conducted to examine IBD was not significant ($r = 0.21$, $R^2 = 0.04$, $p = 0.51$). Private alleles were detected within each of the three sites (Mayotte: 31; La Réunion: 9; Zanzibar: 11).

MtDNA data

The final control region sequence alignment was 720 bp long and included 28 unique haplotypes (Genbank Accession # KX905105-32 (GenBank)). The sequence alignment included 42 substitutions and no indels. The model selected using JModeltest was Tamura-Nei (Tamura and Nei 1993) with a gamma correction ($\alpha = 0.726$). Analyses of mitochondrial sequences supported the population structure detected using microsatellite loci: significant differences in mitochondrial haplotype frequencies (after sequential Bonferroni correction) were observed among all sites using F_{ST} (overall $F_{ST} = 0.084$ $p < 0.0001$; Table 4). However, none of the pairwise comparisons were significant when distances among haplotypes were incorporated in the AMOVA (i.e. using Φ_{ST}, Table 4). The test for IBD was not significant ($r = 0.96$, $R^2 = 0.93$, $p = 0.17$). There was one shared haplotype between La Réunion and Zanzibar, and three shared haplotypes between Mayotte and Zanzibar. Mayotte and La Réunion had no haplotypes in common (Fig. 3). No obvious phylogeographic structure was observed on the haplotype network.

Habitat size

Comparing the depth distribution data of the two oceanic islands revealed that the preferred depth range of spinner dolphins around La Réunion (16–935 m) was larger than the one calculated for Mayotte (5–175 m). When all observation data are combined, the locations used by 95 % of the individuals sighted around Zanzibar, Mayotte and La Réunion have a depth range of 9–162 m. The total surface available around Mayotte and La Réunion within this depth range (9–162 m) was 1036 and 327 km^2, respectively (Fig. 4). The habitat surface corresponding to spinner dolphins' depth preferences is thus three times larger in Mayotte than in La Réunion.

Discussion

Marine organisms with high dispersal capacities can show weak genetic structure across large geographic distances. For instance, the common dolphin (*Delphinus delphis*) and the Portuguese dogfish (*Centroscymnus coelolepis*) each form a single panmictic population across the eastern Atlantic (Veríssimo et al. 2011; Moura et al. 2013). However, even low levels of genetic differentiation can correspond to restricted levels of dispersal in a demographic sense and can be associated with adaptive divergence (e.g. Knutsen et al. 2011; Aykanat et al. 2015) and therefore represent important findings in terms of conservation and management.

In highly dispersive marine organisms, incorporating spatial information as prior information in genetic analyses can help reveal genetic differentiation (Selkoe et al. 2008), as illustrated in the present study. Indeed, we did not detect any structure when using a Bayesian approach to detect the number of genetically distinct populations based on microsatellite data alone. Including prior information about sample location in the Bayesian analysis allowed retrieving three populations, corresponding to the distinct islands that were sampled. Our results are in accordance with expectations of Latch et al. (2006) and Hubisz et al. (2009), as the F_{ST} estimates we obtained from analysis of microsatellite data fell right in the range where genetic structure can remain undetected without prior information ($0.01 < F_{ST} < 0.03$). This approach (Structure with

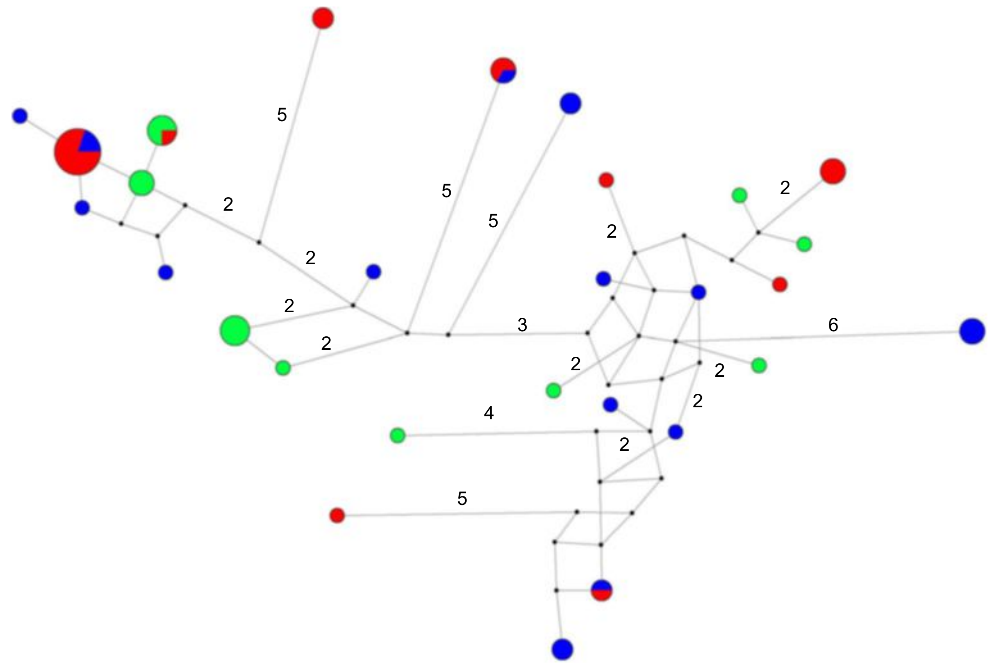


Fig. 3 Median-joining network of 28 mitochondrial control region haplotypes observed in 63 *S. longirostris* individuals. *Filled circles* represent haplotypes, and their size is proportional to their frequency in the dataset. *Circles* are *shaded* in *colours* proportionally to the number of individuals from each population (Mayotte: *blue*; La Réunion: *green*; Zanzibar: *red*). Unsampled or extinct intermediate haplotypes are shown as *black dots*. *Each line* corresponds to one mutational step, except when a number of mutations are adjacent to it

LOCPRIOR: Hubisz et al. 2009) does not seem to falsely inflate genetic structure as shown in previous studies (e.g. Christie et al. 2010; Russello et al. 2012; Viricel 2012). Results from the three randomizations we conducted indicate the genetic clusters we observed using prior information are biologically significant (Appendix 1 ESM). Furthermore, the Mantel test comparing pairwise genetic and geographic distances was not significant, suggesting IBD did not confound our Structure results. The three distinct populations inferred from Structure and observed in the PCA based on nuclear data were supported by the significant genetic differentiation estimated with mitochondrial DNA sequences using F_{ST}. Possible explanations for the lack of significant differentiation observed using Φ_{ST} are that the observed genetic differentiation is recent and that not enough time has passed for new mutations to accumulate within populations or that migration rates among these populations are greater than the mutation rate of the mitochondrial DNA control region. In these cases, incorporating distances among haplotypes in the AMOVA can increase noise in the analysis (Bird et al. 2011), rendering Φ_{ST} less informative than F_{ST}.

The preferred depth range of spinner dolphins we inferred from sighting and bycatch data (i.e. for the three locations analysed together) confirmed that the species is associated with relatively shallow-water habitat at these locations, which corresponds to their resting grounds. The wider depth range observed for the population of La Réunion (also described in Dulau-Drouot et al. 2008) may reflect the very narrow continental shelf of the island, with depth increasing rapidly from the shore, compared to Mayotte. In fact, a recent habitat modelling study showed that despite the wide depth range of spinner dolphin observations around La Réunion, most sightings occur between 51 and 63 m of depth, within a "core habitat" also characterised by flat and light-coloured seabeds (Condet and Dulau-Drouot 2016). Geographic isolation and the reliance of spinner dolphins on appropriate shallow-water resting habitat during daytime are likely factors causing and/or maintaining divergence between populations occupying Mayotte and La Réunion. Although we cannot tease apart the relative role of each of these two factors, hypotheses can be made based on what has been observed in other small delphinid species. Indeed, large geographic distance from continental waters does not seem to be a sufficient driver to cause restricted gene flow in pelagic dolphins found around oceanic islands as illustrated by population structure studies on Atlantic spotted dolphin (*Stenella frontalis*) and common bottlenose dolphin (*T. truncatus*) populations from the Azores: the pelagic morphotypes within these two species form panmictic populations over large distances, from the Azores to offshore waters of the north-western Atlantic at least 4500 km away (Quérouil et al. 2007; Viricel and Rosel 2014). On the other hand, some oceanic island-associated delphinids show restricted gene flow across short distances within an archipelago such as common bottlenose dolphin populations around Hawaii (Martien et al. 2012), or the rough-toothed dolphin (*Steno bredanensis*), which displays long-term site fidelity around the Society Islands (French Polynesia), and fine-scale genetic differentiation between two islands only 170 km apart (Oremus et al. 2012). Thus, daily reliance on near-shore, insular habitats may be a

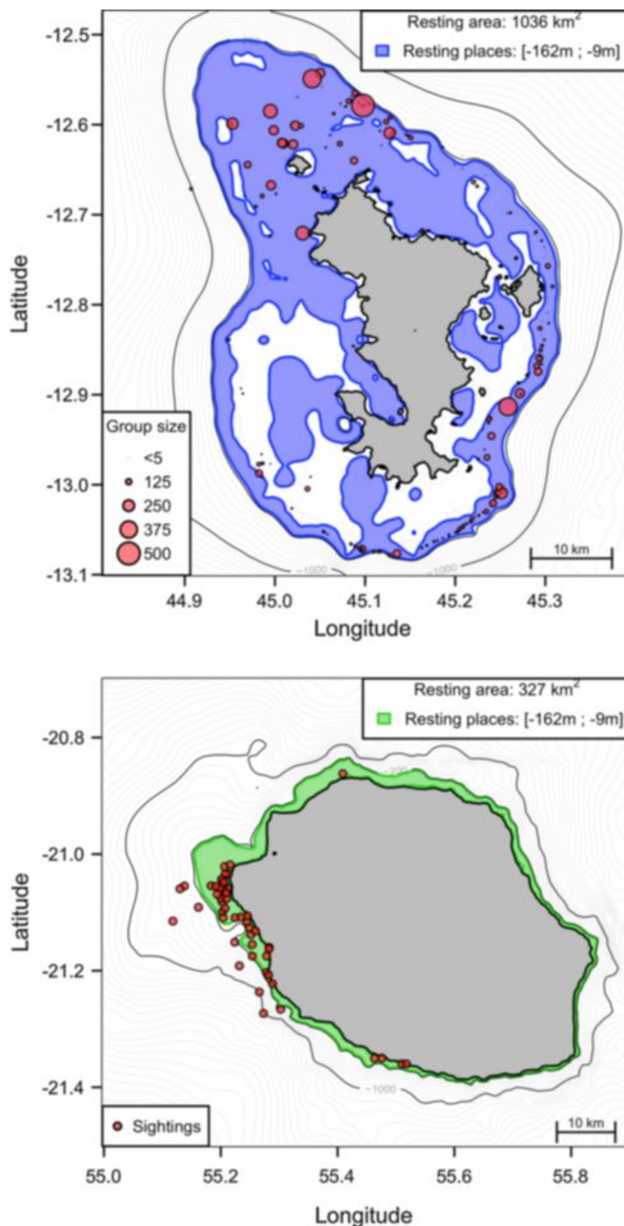


Fig. 4 Maps showing the surface available for daytime resting for spinner dolphins around Mayotte (*top*) and La Réunion (*bottom*). These surfaces were estimated based on the preferred depth range of spinner dolphins in the SW Indian Ocean. Maps include all sightings, including outlier observations that were not used to determine the preferred depth range (see "Materials and methods" section)

predominant driver of population structure in pelagic delphinids, even more so than geographic isolation.

The genetic subdivision we observed is consistent with other studies conducted on *S. longirostris* in the Pacific Ocean, which indicated that insular populations are generally discrete. Levels of genetic differentiation were similar to those observed among Society (French Polynesia) and Hawaii archipelago (Oremus et al. 2007; Andrews et al. 2010). Spinner dolphins found around islands of the Society Archipelago (French Polynesia) form relatively closed communities showing strong island fidelity (Oremus et al. 2007). Gene flow among these communities is restricted, despite the short geographic distances separating some of these islands (i.e. tens of kilometres). Oremus et al. (2007) suggest that these communities are characterised by a metapopulation dynamics, which would explain the high genetic diversity and large island effective population sizes estimated from their molecular data. In the Hawaiian archipelago, fine-scale genetic structure is also observed, but patterns of gene flow vary according to social structure and habitat availability (Andrews et al. 2010). Overall, both the genetic and social structure of this species seems to be influenced by the availability and extent of resting areas (Karczmarski et al. 2005; Andrews et al. 2010). In Hawaiian populations, genetic differentiation increased with geographic distance among islands. In the present study, the tests for IBD we conducted for both types of markers were not significant. We have to note, however, that these tests had low statistical power since only three populations were sampled. Thus, future studies analysing samples from additional islands in the SW Indian Ocean would better allow testing for IBD. Additionally, photo-identification data would complement present findings, as site fidelity may constitute another factor driving population structure in spinner dolphins from the SW Indian Ocean.

The genetic diversity we measured (Table 2) was similar to what has been reported for this subspecies in French Polynesia (Oremus et al. 2007), and was greater than the diversity observed in Hawaii (Andrews et al. 2010). Despite the genetic differentiation of spinner dolphins from La Réunion and Mayotte, the genetic diversity of these two populations is similar to the diversity of spinner dolphins from the coast of Zanzibar. Factors influencing their population genetic diversity include effective population size (linked to drift) and immigration rates. Given the differences in habitat size among the three sites we compared, the respective local population size of the populations occupying these sites may differ. Thus, we hypothesise that the similar levels of genetic diversity we observe in these populations likely reflect low but recurrent gene flow, which may be sufficient to maintain genetic diversity within island communities. Spinner dolphins from the SW Indian Ocean could thus be under a metapopulation dynamics, similar to what findings from Oremus et al. (2007) indicate for populations in the Society Archipelago. Alternatively, the genetic divergence we measured could be recent, and these populations may have so far retained ancestral polymorphisms.

The present study constitutes the first population structure assessment for the spinner dolphin in the SW Indian Ocean, and our findings have important conservation implications. Indeed, the habitat preferences and patterns

of restricted gene flow we identified suggest spinner dolphin populations found off Mayotte and La Réunion are demographically independent from each other. Their differentiation makes them potentially vulnerable if directly impacted by human activities, and spinner dolphins found off these two islands should therefore be treated as two distinct conservation units at the national level. Analysing samples from other islands (e.g. Madagascar, Mauritius) within this region would allow further evaluating the genetic isolation of these populations. Bycatch levels of spinner dolphins in gillnets off Zanzibar (Amir et al. 2002) should be considered as a cause of concern, and this issue highlights the need of a population structure assessment along the east coast of Africa. Protecting important resting habitat is an important step towards the conservation of insular spinner dolphin populations. Dedicated surveys help assessing whether current marine protected areas encompass such habitats (e.g. in La Réunion: Dulau-Drouot et al. 2008) and habitat modelling studies (e.g. Thorne et al. 2012; Condet and Dulau-Drouot 2016) allow identifying key areas where new conservation efforts should be focused.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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