Habitat partitioning and fine scale population structure among insular bottlenose dolphins (*Tursiops aduncus*) in a tropical lagoon

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ABSTRACT

Among marine organisms, little is known on patterns of intra-species habitat partitioning, whereas many studies have examined niche segregation at the multi-species community level. In this study, we investigated the fine-scale population structure and patterns of within-species habitat use of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a tropical lagoon of the Indian Ocean (Mayotte, 45°10′E/12°50′S). First, we assessed genetic population structure using mtDNA and 14 microsatellite markers to determine if bottlenose dolphins around Mayotte belong to one or several panmictic groups. The analyses revealed no mitochondrial polymorphism and the presence of a single population at Hardy–Weinberg equilibrium. Second, we assessed whether a community structure exists within the bottlenose population. A community is an assemblage of individuals using a common home range. Photo-identification data were used to assess individual home range size and habitat preferences. Home range analysis revealed the presence of at least two communities of bottlenose dolphins around Mayotte: one occurring in the shallower waters inside the lagoon and a second in the vicinity of a deeper reef bank, situated further offshore in the northern part of the island. Stable isotope analyses of $\delta^{13}C$ and $\delta^{15}N$ were performed to detect intra-species segregation of habitat and resource use. However, no significant structure across the population was detected. Nevertheless, this study highlights that, even at small spatial scales, individual and between community variations of habitat preferences occur in bottlenose dolphin populations. Intra-species niche partitioning may explain habitat segregation in these insular delphinids.

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1. Introduction

Understanding patterns of trophic and habitat segregation is critical in ecology, especially to investigate the role of organisms within a community, which is an assemblage of species living together in some common habitat. Answering these questions may be challenging for large marine top predators, due to logistical constraints (Heithaus et al., 2008). Among top marine predators (including cetaceans), a number of studies have investigated patterns of niche partitioning at the community level (assemblage of species interacting as a society), using a variety of methodological approaches and exploring both axes of the ecological niche (Cherel et al., 2008; Kiszka et al., 2010a, 2011; Menard et al., 2007; Papastamatiou et al., 2006; Pusineri et al., 2008). However, limited attention has been given to the study of niche partitioning within a species (except at the ontogenetic scale), especially at

a small spatial scale, e.g. the surrounding waters of an island or a lagoon. A recent study of the long-term movements and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) underlined that this species does segregate for space and possibly resources in the lagoons of Palmyra, which may be (at least partially) due to intra-species competition processes (Papastamatiou et al., 2010). Indeed, within a given system, if resources are limited, processes of habitat and/or resource partitioning within a population may occur. This process may be enhanced in less productive systems and/or in systems where resources are less predictable.

In a number of bottlenose dolphin populations (particularly in the common bottlenose dolphin, *Tursiops truncatus*), it has been shown that a given population may segregate into communities (Chilvers and Corkeron, 2001; Rossbach and Herzing, 1999; Urian et al., 2009; Wells, 1986). Here, a community refers to an assemblage of interacting individuals within the species. Despite the fluidity of bottlenose dolphin societies, characterised by a fission–fusion social structure (Connor et al., 2000), communities, defined by shared patterns of residency and associations, may occur (Wells, 1986). A community is not a closed demographic unit, and community structure is defined by associations among dolphins that show long-term patterns of site

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fidelity (Connor et al., 2000; Wells, 1986; Wells et al., 1996). The origin of community formation has been not investigated in previous studies focussing on bottlenose dolphins, but intra-species niche partitioning may explain the fragmentation of a population into communities. Most studies of resource use and population dynamics treat conspecific individuals as ecologically equivalent. However, between-individual variation can sometimes comprise the majority of the population's niche width. Niche variation facilitates frequency-dependent interactions that can profoundly affect the population's stability and the amount of intra-specific competition (Bolnick et al., 2003). The combined effects of individual foraging specialisation and social forces may well explain community formation in bottlenose dolphins. The formation of communities would contribute to share habitat and resources for individuals, and then reduce intra-species competition. In addition, as a homeotherm large predator with high metabolic expenditure (and therefore energy consuming), this species potentially has an important dependence on abundant, high quality and accessible food resources.

In this study, we aimed to assess the fine scale population structure and patterns of intra-species ecological segregation among Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, hereafter bottlenose dolphins), probably the most abundant top predator living in the waters surrounding Mayotte, mostly in the lagoon and adjacent shallow reef banks (Gross et al., 2009; Kiszka et al., 2010a, 2011). As a preliminary step, we assessed if bottlenose dolphins were resident in the lagoon of Mayotte. In addition, we investigated the global pattern of genetic structure of bottlenose dolphins around the island, especially to determine if one or more populations are present. Then, we tested if communities exist around the island by examining individual ranging patterns and habitat preferences (in relation to physiographic variables). We hypothesized that the origin of community formation is based on one main factor, the ecological constraint (niche partitioning). In order to explore the existence of ecological segregation processes occurring within the species or population, we also used stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ in various tissues (skin, blubber) from biopsy samples. The carbon and nitrogen isotope ratios of a consumer reflect those of its diet. Both isotopes help elucidate trophic relations and habitat use, and may be used to assess niche partitioning, including at sub-species level (Hobson, 1999). In order to investigate the fine scale population structure of Indo-Pacific bottlenose dolphins around Mayotte, we combined photo-identification and biopsy sampling data collected year-round from 2004 to 2008.

2. Materials and methods

2.1. Data and sample collection

Mayotte is located in the northern Mozambique Channel and is part of the Comoros archipelago (Fig. 1). The island is almost entirely surrounded by a 197 km long barrier reef, with a second double-barrier in the southwest and the *Iris* immerged reef complex in the northwest. From July 2004 to October 2008, small-boat based surveys were undertaken around the island of Mayotte. Surveys were conducted throughout the study period during daylight hours between 0700 h and 1800 h in sea conditions not exceeding Beaufort 3. Survey vessels did not follow pre-defined transects but every attempt was made to sample the whole daylight period as well as each habitat type within the surrounding waters of Mayotte, i.e. coastal areas, lagoonal waters, barrier reef associated areas (inner and outer slopes) and oceanic or slope waters (>500 m). Surveys were conducted all year round, and two permanent observers were searching for dolphins. Details on spatial coverage of effort are presented in Fig. 2.

When bottlenose dolphins and other cetaceans were encountered, standard sighting data were recorded: group size (maximum, minimum, most accurate estimate), geographic position (latitude, longitude) and behaviour (Shane, 1990). Standard photo-identification technique
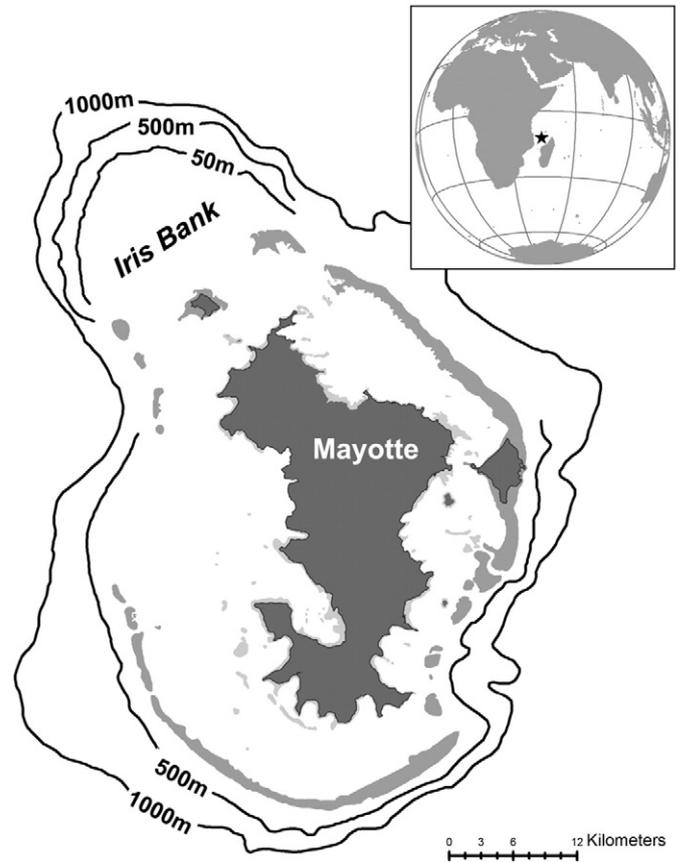

Fig. 1. Location of the study area (*dark grey*: land; *light grey*: coral reefs).

was used to identify individual dolphins using patterns of notches and scars on the dorsal fin (Scott et al., 1990; Würsig and Würsig, 1977), and has been adapted for the use in other marine wildlife such as sea turtles, whale sharks and pinnipeds (Arzoumanian et al., 2005; Forcada and Aguilar, 2003; Schofield et al., 2008). This non-invasive method has been used extensively to investigate demographic parameters, movements, home range and social structure of delphinids, especially the bottlenose dolphin (Bejder et al., 1998; Ingram and Rogan, 2002; Möller et al., 2006; Würsig and Jefferson, 1990; Würsig and Würsig, 1977). In our case, this method has only been used in adult individuals, which have sufficient distinguishable features on the dorsal fin. Images were matched visually, and double-checked by two of the authors (JK and CP).

Stable isotope and genetic analyses were performed using skin and blubber samples. Biopsy attempts were made opportunistically. Biopsies were collected by using a crossbow (BARNETT Veloci-Speed® Class, 68-kg draw weight) with Finn Larsen (Ceta-Dart, Copenhagen, Denmark) bolts and tips (dart 25-mm long, 5-mm-diameter). The dolphins were hit below the dorsal fin when sufficiently close (3–10 m) to the research boat (see Kiszka et al., 2010b for details on biopsy sampling procedure). Blubber and skin biopsy samples were preserved individually in 90° ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under French scientific permits #78/DAF/2004 (September 10, 2004) and #032/DAF/SEF/2008 (May 16, 2008) after examination of the project by *Conseil National de Protection de la Nature*.

2.2. Residency index

Using photo-identification data, a residency index (RI) was calculated following Karczmarski (1999). This index relates the total number of
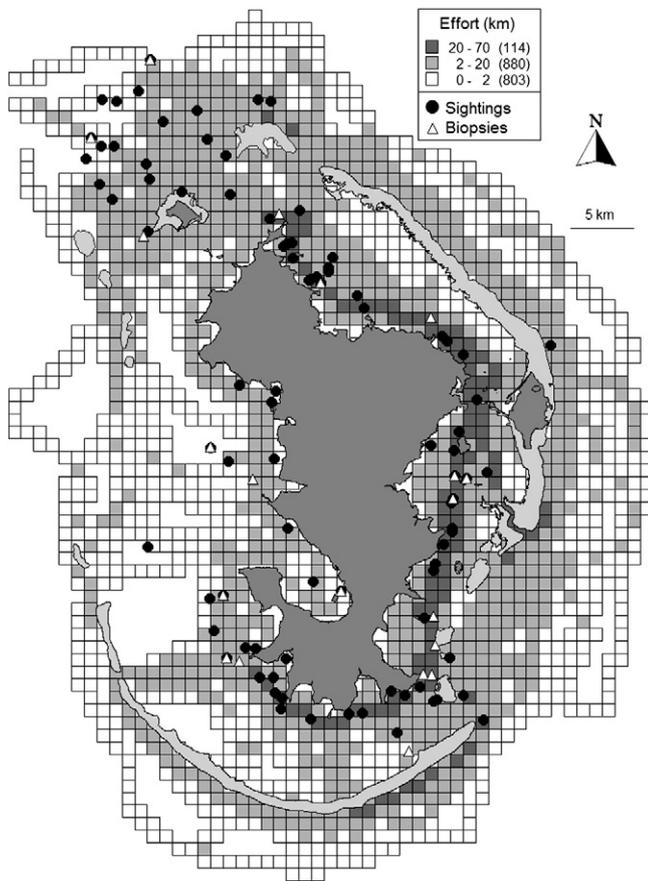
Fig. 2. Distribution of observation effort (expressed in km). Indo-Pacific bottlenose dolphin sightings (white squares) and biopsies (black dots) around Mayotte from 2004 to 2008.

sightings of an individual to the total number of months in which this particular individual was seen: $RI = S \times M/100$, where RI = residence index, S = total number of sightings of an individual, and M = total number of months in which this particular individual was seen. Dolphins that were recaptured on at least 3 occasions were seen on at least 2 different seasons. The seasons that were considered are: rain/summer (November–April) and dry/winter seasons (May–October).

2.3. DNA extraction, PCR, sequencing and genotyping

Total DNA was extracted from skin samples using the Nucleospin® Tissue Kit (Macherey Nagel). The manufacturer protocol was slightly modified as follows: the recommended lysis time was extended to 30 h under permanent agitation and 10 min grinding step using a teflon pestle was added after 5 h of enzymatic digestion. A 254 base pair fragment of the mitochondrial cytochrome b gene was amplified using the protocol and PCR primers described in Jayasankar et al. (2008). The sequencing was performed by Genoscreen corporation (Campus Pasteur, 1 rue du Professeur Calmette, F-59000 Lille, France) using an ABI PRISM® 3730 XL automated DNA Sequencer (Perkin-Elmer Applied Biosystems, Foster City, CA). Sequence data were aligned using ClustalX (Thompson et al., 1994) and ambiguities were manually checked comparing each sequence with its complementary fragment using BioEdit (Hall, 1999).

In addition to mitochondrial analyses, 14 tetranucleotide microsatellite markers were used out of the set of 18 markers designed by Nater et al. (2009). Amplifications were carried out following the protocol and using the primers described in Nater et al. (2009). PCR products were screened on 6.5% polyacrylamide gels using a Li-Cor

NEN Global IR2 DNA sequencer. Allele sizes were determined using a known DNA sequence with the SAGA-GT software (v3.1: Automated microsatellite Analysis Software, LI-COR Biosciences).

2.4. Patterns of population structure

Clustering methods based on Bayesian computations (i.e. Monte Carlo Markov Chains, MCMC) were performed using the software Structure v2.3.1 (Falush et al., 2003; Pritchard et al., 2000). In order to identify potential barriers to gene flow, the number of groups to test (K) required fixing. Then, the software computes the probabilities for each individual of the dataset to belong to each of the simulated group at Hardy–Weinberg equilibrium. We tested values of K ranging from 1 to 10. For each K, ten simulations were conducted in order to compute the inter-simulation variability and the likelihood of the multilocus dataset given K (i.e. $Pr(X|K)$) was computed for each simulation. The most likely value for K is the one maximising $Pr(X|K)$ and minimising the inter-simulation variability. A model with population admixture was used and the parameters of the MCMC were set as follows: burn-in = 50 000 steps, length of the Markov Chain = 200 000 steps.

2.5. Community existence: ranging pattern and habitat analysis

We used the Minimum Convex Polygon method (MCP; Mohr, 1947) to estimate home range areas. This is the most commonly used method to estimate home range in the literature, allowing ready comparisons with other studies (White and Garrott, 1990). It encloses all data points by connecting the outer locations to create a convex polygon. However, in certain situations, it may be uninformative as areas of high utilisation have same values as areas of low utilisation. It is also sensitive to sample size and to outliers and it ignores boundaries, notably the shore line boundary in the case of peri-insular habitats, which excludes animal movement within the home range (Mohr, 1947). In our case, we estimated individual home range for animals with three or more sightings (one sighting is an encounter, only one encounter per day may be considered in the analysis) with the R package fossil (Vavrek, 2011). Due to these restrictions and our limited dataset, absolute home range estimate was not our primary objective, but rather the comparison of home range size and location among individuals in order to identify potential differences among them. However, we took into account the potential bias of home range size estimates due to a varying number of observations depending on the individual. Indeed, we implemented a rarefaction algorithm (in R) to compute a corrected home range size for each individual. The corrected home range size of a given individual was obtained by averaging 1000 values of home range size estimated using only 3 locations randomly selected among the n locations available for that individual (R Development Core Team, 2010).

Individual habitat preferences were also calculated for individuals with more than 3 sightings. We constituted a database in which every individual dolphin sighting was associated with the physiographic characteristics (distance to the coast, to the fringing reef, to the barrier reef and depth) corresponding to the GPS (Global Positioning System) fixes of the observations. For each individual, minimum, maximum, standard deviation and mean values for each variables were calculated. Bathymetric data were obtained from *Service Hydrographique et Océanographique de la Marine* (SHOM) and were included in the GIS procedure, and maps and MCPs were drawn in R v2.11.1 using packages Maps, Mapdata, Argosfilter and Aspace (Becker and Wilks, 2009, 2010; Bui et al., 2009; Freitas, 2010).

In order to identify communities, we used data from individuals sighted on at least 3 occasions (only on separate days over the study period). On the basis of MCP maps, an empirical ranging category has been assigned for each individual to detect the existence of communities within Mayotte' bottlenose dolphins. Then, we conducted a PCA (principal component analysis, PCA function dudi.pca implemented in the

Table 1

Number of bottlenose dolphin photographs (n = 5372) used for photo-identification purposes collected around Mayotte from 2004 to 2008. Grey cells correspond to periods where surveys were not conducted.

Year/month	Jan.	Feb.	March	Apr.	May	Jun.	July	Aug.	Sept.	Oct.	Nov.	Dec.
2004							100	886	229	1	127	698
2005	237	1279	391	1082	1710	1624	12	522	95	454	32	212
2006	1628	560	509	442	350							
2007						126		3	726	690	126	459
2008		29	850	852	1156	193	259	258				

package ade4; Dray and Dufour, 2007) to objectively discriminate communities on the basis of individual habitat characteristics (mean depth preferences, mean distance from the coast, mean distance from the barrier reef) and corrected home range (size in km^2 and location). Each individual was assigned to a ranging category based on MCP maps. For each category, the ellipse pictures the dispersion of the cloud and covers 95% of individual points, the centre of the ellipse being located at the centre of gravity.

2.6. Trophic and habitat segregation using stable isotope analyses

Stable isotope analyses were used to assess segregation patterns of bottlenose dolphins around Mayotte based on their foraging habitat (reflected through $\delta^{13}C$) and trophic level (reflected through $\delta^{15}N$). For dolphin biopsies, blubber and skin were separated for each sample. Analyses were performed in these two tissues. These two tissues have different turnover rates: a few days for epidermis but several months for the collagen matrix of the blubber (Abend and Smith, 1995). The ethanol was evaporated at 45 °C over 48 h and the samples were ground and freeze-dried (Hobson et al., 1997). Because lipids are depleted in $\delta^{13}C$, they were extracted to avoid a bias in the isotopic signature of $\delta^{13}C$ (De Niro and Epstein, 1978; Tieszen et al., 1983). This was done by shaking (1 h at room temperature) in cyclohexane (C_6H_{12}), and subsequent centrifugation prior to analysis. After drying, small sub-samples (0.35 to 0.45 mg ±

0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Italy). Results are expressed in notation relative to PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation:

$$\delta X = \left(R_{sample}/R_{standard} - 1 \right) * 10^3$$

where X is ^{13}C or ^{15}N and R is the isotope ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated that measurement errors were <0.1‰ for $\delta^{13}C$ and $\delta^{15}N$. Percent C and N elemental composition of tissues were obtained using the elemental analyser and used to calculate the sample C:N ratio, indicating good lipid removal efficiency when <4.

3. Results

3.1. Survey effort and sightings

From July 2004 to October 2008, data were collected during 196 independent boat-based surveys. A total of 91 groups of bottlenose dolphins were encountered. Spatial distribution of observation effort covered the interior waters of the lagoon and surrounding deeper waters, outside the barrier reef (Fig. 2). Most effort has been concentrated along the eastern coast, in the north and in the south. The west coast was less surveyed. Bottlenose dolphins were primarily distributed inside the lagoon and close to shore, as well as in the shallow waters of the Iris bank to the north of the island (Fig. 2). Photo-identification effort is presented in Table 1.

3.2. Genetic diversity and population structure

Mitochondrial data consisted of a 254 base pair fragment of the cytochrome b gene. A total number of 29 individuals were sequenced. The analyses revealed no mitochondrial polymorphism, which

Table 2

Allele sizes (bp) and observed frequencies calculated for the unique panmictic population of *Tursiops aduncus* (N = 29) from Mayotte. The GenBank accession number is indicated for each microsatellite marker used.

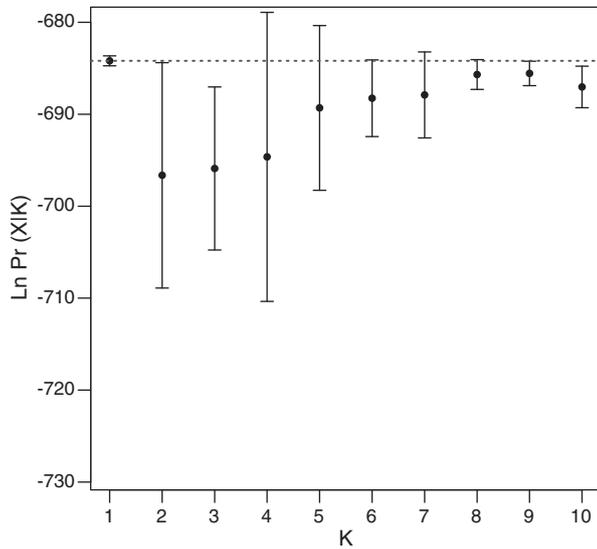| Marker							
EU431965	Allele size	189	193	197			
	Frequency	0.429	0.554	0.018			
EU431966	Allele size	310	314	318	322	326	330
	Frequency	0.196	0.304	0.071	0.375	0.018	0.036
EU431967	Allele size	178	182	186	202		
	Frequency	0.232	0.250	0.500	0.018		
EU431968	Allele size	212	220	224			
	Frequency	0.179	0.536	0.286			
EU431969	Allele size	188	192	196			
	Frequency	0.018	0.946	0.036			
EU431972	Allele size	294	298	302			
	Frequency	0.232	0.679	0.089			
EU431973	Allele size	NA	169	177	181	185	
	Frequency	0.036	0.143	0.500	0.286	0.036	
EU431974	Allele size	299	300	304	308	312	316
	Frequency	0.054	0.232	0.536	0.107	0.054	0.018
EU431976	Allele size	208	212	220	224		
	Frequency	0.089	0.161	0.446	0.304		
EU431978	Allele size	314	334	338	342	346	
	Frequency	0.107	0.268	0.054	0.393	0.179	
EU431979	Allele size	212	220				
	Frequency	0.839	0.161				
EU431980	Allele size	406	410				
	Frequency	0.571	0.429				
EU431982	Allele size	257	261	265	273	277	
	Frequency	0.107	0.518	0.018	0.304	0.054	
EU431983	Allele size	380	384	392	396		
	Frequency	0.036	0.804	0.071	0.089		

Fig. 3. Mean likelihood values (and SD) for various *K*. The horizontal dashed line indicates the position of the highest mean value observed.

suggests a single matriarchal lineage in the Mayotte population. Nuclear markers gave similar results. The genetic diversity was low with allele counts ranging from two to six depending on the locus considered and a multilocus overall gene diversity of less than 0.6 (see Table 2 for allele sizes and observed frequencies). Bayesian simulations revealed no significant structure with a unique panmictic population at Hardy–Weinberg equilibrium around Mayotte being the most likely scenario (most likely *K* = 1; Fig. 3).

3.3. Residency

On average, 67% of the dolphins that we photographed around Mayotte were considered marked (with significant scars and notches allowing individual identification). With respect to the bottlenose dolphins of Mayotte, most individuals were sighted on one (18.6%), two (11.6%), three (15.5%) or four occasions (11.3%). The number of recaptures reached 20 times for one individual (Fig. 4). The two most frequently seen individuals were recorded in 13 and 12 of the 39 months surveyed. Residency index reached a maximum of 2.6 for the most frequently seen dolphin, but for most individuals, this index was below 0.5 (Fig. 4). Overall, 25 individuals (43%) were seen on at least 5 occasions during the study period.

3.4. Ranging patterns and individual habitat preferences

Home range estimate was generated for 43 dolphins. Sample size had a significant effect on home range estimates ($r^2 = 0.4966$; $p < 0.001$, $n = 43$). Corrected home range size varied from 2.14 km^2 (MY71, 3 sightings) to 89.4 km^2 (MY16, 8 sightings) (mean home range = 44.59 km^2: SD = 37.92). Overall, we encountered four types of ranging patterns (Fig. 5). Nine individuals essentially ranged in the north of the island. Twelve individuals essentially ranged around the coastal waters of the island. Nine individuals were primarily distributed in the southern region of the lagoon, and finally, thirteen individuals used both the coastal waters
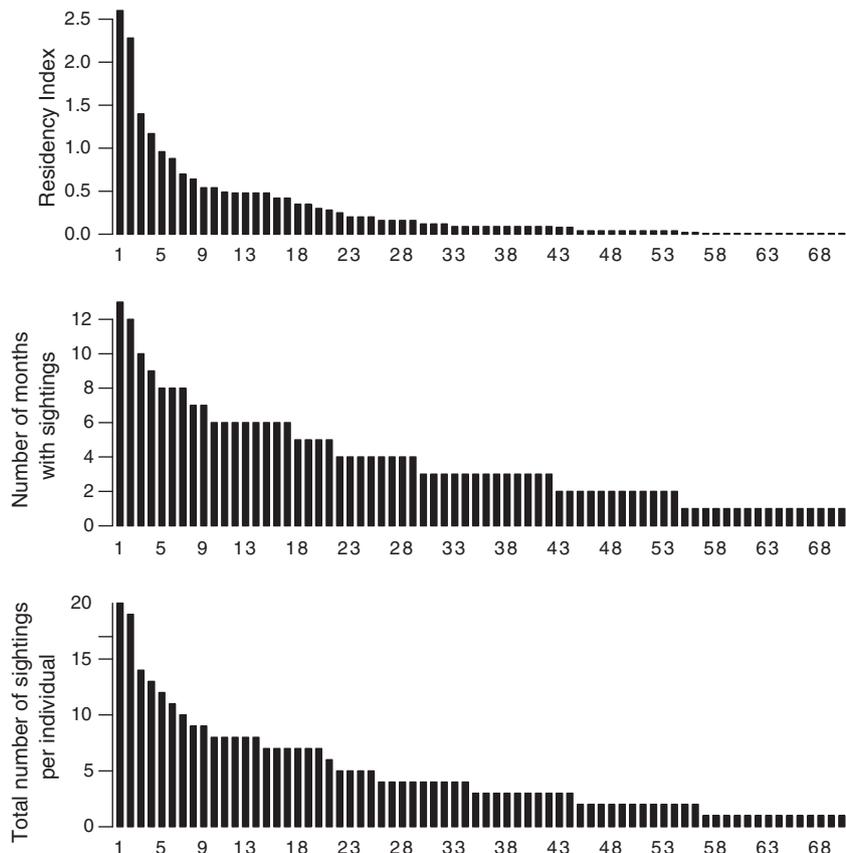

Fig. 4. Sightings of 71 Indo-Pacific bottlenose dolphins around Mayotte from 2004 to 2008: (a) total number of sightings for each identified individual; (b) number of months in which each individual was seen; (c) values of the residency index (RI) calculated for all identified dolphins.

of the lagoon and regularly visited the northern area. These four types have been named as follows: type A (north), type B (coastal waters of the island), type C (south) and type H (hybrid distribution, both coastal waters of the island and north, Fig. 5).

Two main communities were discriminated (Fig. 6). Type "A" typically has a distribution far from shore, in deeper waters (mean = 44.9 m; SD = 6.8) and has a smaller corrected home range (mean = 7.9; SD = 6.4). Types "B, C and H" considerably overlapped, especially in corrected home range size. However, a few differences were observed, especially related to the spatial extent of their home range. The role of the home range size seems negligible in the PCA results. Indeed, the tip of the vector for corr.hr lies far away for the correlation circle indicating a minor role of this variable in the structure observed on both the first and second principal components (F1 and F2). Thus, the home range size is not a factor of primary importance for discriminating group A from groups B, C and H.

Overall, home range size differed significantly between the four ranging patterns defined ($H = 18.891$, $df = 3$, $p < 0.0001$). Habitat, in relation to the three variables considered (depth, distance from shore and from the barrier reef) was also significantly different between the four communities (distance from shore, $H = 23.506$, $df = 3$, $p < 0.0001$; depth, $H = 20.820$, $df = 3$, $p < 0.0001$), except for the variable "distance from the barrier reef" ($H = 2.569$, $df = 3$, $p = 0.463$).

3.5. Habitat and trophic segregation using stable isotopes

We used skin and blubber samples from 31 distinct bottlenose dolphins for stable isotope analyses during the study period. Two individual categories were defined: individuals belonging to the "A" community, essentially living outside the inner lagoon, and individuals belonging to the other communities, mostly living in the inner lagoon (B, C and H; Fig. 7). Stable isotope signatures for skin and blubber were significantly different, both for δ^{13}C ($U = 55$; $p < 0.001$) and δ^{15}N ($U = 91$; $p < 0.001$; Fig. 6). δ^{13}C values were significantly higher in the blubber (mean = −13.05; SD = 0.88; range = −16.16 to −11.77) than in the skin (mean = −15.12; SD = 0.98; range = −17.05 to −12.98). For δ^{15}N, values were also significantly higher in blubber (mean = 15.07; SD = 0.66; range = 13.32 to 16.21) than in skin (mean = 13.07; SD = 1.28; range = 11.44 to 16.15). Variability of values was higher in skin tissues (reflecting intra- and inter-individual differences) than in blubber tissues (only reflecting inter-individual differences), both for δ^{13}C and δ^{15}N (Fig. 7). Overall, for both skin and blubber samples, we found that bottlenose dolphins belonging to community "A" had slightly lower δ^{13}C values. However, no statistical difference was found between stable isotope values in "A" and "B, C, H" community members (δ^{13}C skin: $U = 68$, $p > 0.05$; δ^{13}C blubber: $U = 97$, $p > 0.05$; δ^{15}N skin: $U = 101$, $p > 0.05$; δ^{15}N blubber: $U = 63$, $p > 0.05$).
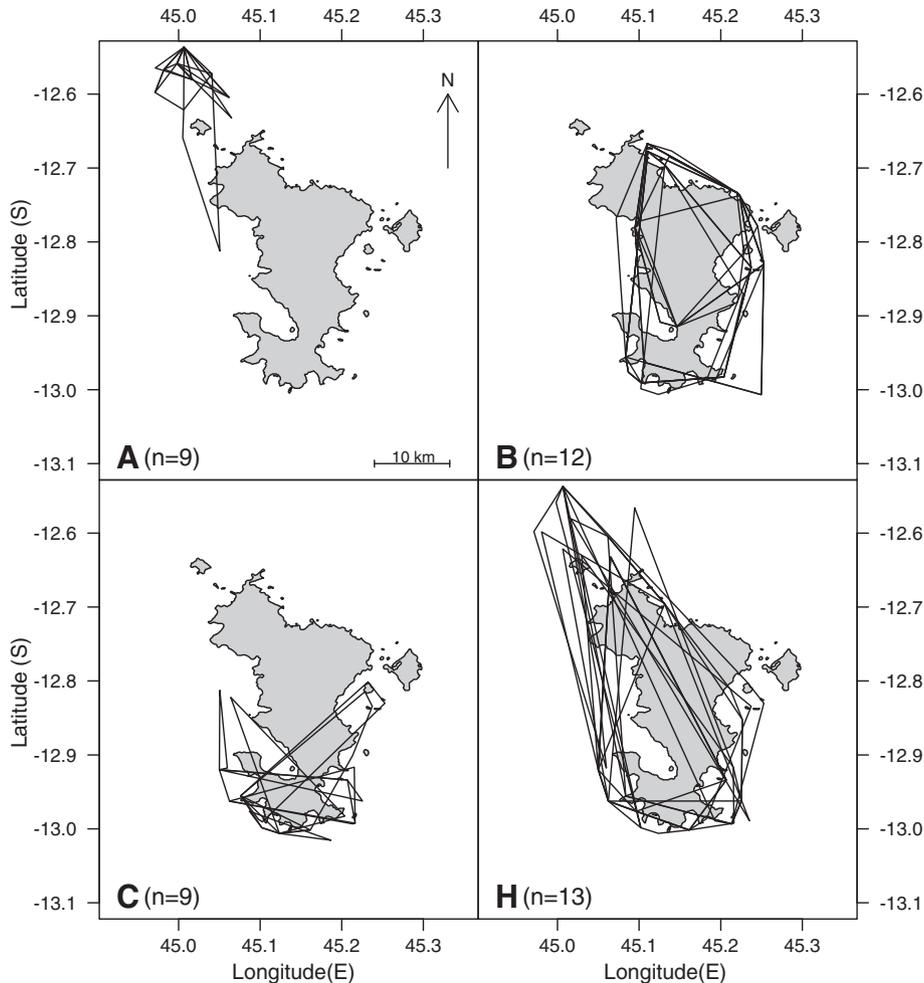

Fig. 5. The four main ranging patterns of Indo-Pacific bottlenose dolphins around Mayotte from 2004 to 2008.
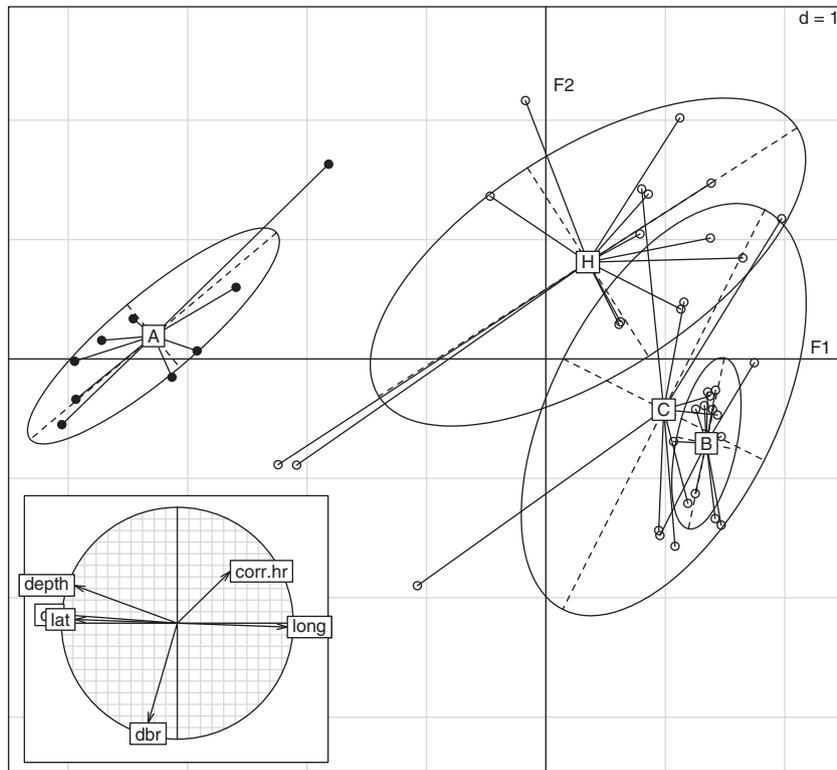
Fig. 6. Principal component analysis showing segregation of individual dolphins of Mayotte from 2004 to 2008 based on their corrected home range size (corr.hr), mean location (lat, long) and habitat preferences: depth, distance from barrier reef (dbr) and from coast (dc, masked by the latitude label). The ellipses represent 95% of the information and the central point is the centre of gravity.

4. Discussion

This study documents intra-species habitat partitioning and fine scale population structure in an isolated population of Indo-Pacific bottlenose dolphins around the island of Mayotte, in the Mozambique Channel. It combines analyses of genetic population structure, residency, ranging patterns, trophic and habitat characteristics to assess the existence of communities around the island. This work is based on the sampling of 29 (genetic analyses) and 31 (stable isotope analyses) dolphins, i.e. around one third of identified individuals and

Fig. 7. Mean (and SD) stable isotope signatures of $\delta^{13}C$ and $\delta^{15}N$ in skin and blubber from biopsy samples (n = 31), in ‰.

photo-identification data over four years (71 individuals identified). This study combines several approaches to answer the question of intra-species habitat partitioning in a small cetacean living in a remote tropical lagoon.

4.1. Evaluation of the study

The main limitation of this study is the low rate of recaptures of dolphins and, consequently, the probable underestimation of the size of individual home range. In addition, the MCP method is known for underestimating home range with small samples (White and Garrott, 1990). The best approach to estimate habitat use and home range in marine animals (and minimise biases) is the study of their movements using GPS and/or Argos satellite tags (Schofield et al., 2007, 2010). However, this approach is logistically difficult in small delphinids, and need further development, especially in terms of tag design, attachment system and deployment. Our definition of communities and ranging patterns is empirical and it is necessary to be cautious with the interpretation of the results. Nevertheless, the differential rate of encounter of identified individuals, according to the spatial coverage of effort, underlines differential individual patterns of distribution. This suggests that the data presented in this work over the four years of the study (i.e. a fairly short period of time), allow documenting some insights of fine scale population structure of Indo-Pacific bottlenose dolphins in this region. It underlines that insular Indo-Pacific bottlenose dolphins may segregate into communities in order to share space and habitat, and, consequently, available habitat and resources.

4.2. Population structure

In terms of genetic population structure, Indo-Pacific bottlenose dolphins form a single panmictic group around Mayotte, with low
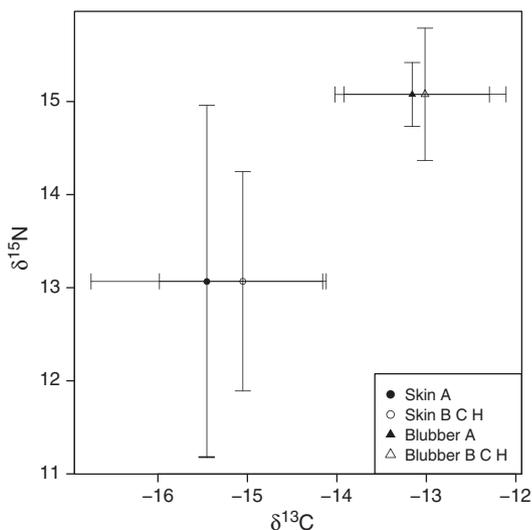
genetic diversity. This low genetic diversity may be attributed to the formation of the population by a limited number of individuals (Barson et al., 2009). Three main situations could explain the genetic profile we observe in this population: (i) bottlenose dolphins of the Mayotte population are totally isolated from surrounding populations; (ii) migrants from surrounding populations may enter Mayotte at a certain frequency, and share the same genetic structure as those of Mayotte; (iii) individuals from surrounding populations may enter Mayotte, but not participate in reproduction, and thus do not contribute to the gene pool of the Mayotte population. This would explain why no signature of admixture has been found. Furthermore, we have the confirmation that the lack of mitochondrial polymorphism at the population level is not due to a poor choice of marker (i.e. a low polymorphism of the cytochrome b marker). Indeed, up to 4% divergence (10 segregating sites) has been found between the mitochondrial sequence of Mayotte individuals and the same gene fragment sequenced in Indo-Pacific bottlenose dolphins from southern India (Jayasankar et al., 2008). Thus the absence of mitochondrial polymorphism likely reflects the fact that a single matriarchal lineage is present in Mayotte.

4.3. Residency

Around Mayotte, Indo-Pacific bottlenose dolphins have a shallow-water and inshore distribution. Numerous within-year and between-year resightings suggest that individuals are resident around the island. However, a number of individuals have never been resighted, but overall; this pattern of residency is relatively similar to other areas of their range (Stensland et al., 2006; Wiszniewski et al., 2009). The relatively high level of residency was expected due to the geographic isolation of the island of Mayotte. The closest island is Anjouan (Union of the Comoros), which is situated 60 km to the west of Mayotte, and the northwest coast of Madagascar, which is situated 280 km to the east of Mayotte, suggesting some degree of isolation of Mayotte Indo-Pacific bottlenose dolphins in the northern Mozambique Channel. This island-associated pattern of residency has been previously documented in similar oligotrophic areas for the common bottlenose dolphin (T. truncatus), around the main Hawaiian Islands (Baird et al., 2009).

4.4. Existence of bottlenose dolphin communities around Mayotte

Based on the ranging patterns of individual dolphins, our results suggest the existence of at least two distinguishable bottlenose dolphin communities around Mayotte despite the absence of geographical barriers to movements. The "type A" (n = 9) community is made of individuals with restricted home ranges, living over higher depths and at longer distances from shore. The second community possibly includes three ranging patterns, "types B, C and H". Individuals in this community have an extended home range and a more inshore distribution. However, some variations within this community have been observed. Twelve individuals (type B) exclusively range in the coastal waters around the island. An intermediate type of ranging pattern (type H, n = 13), very similar to "type B", is characterised by a large home range and intermediate bathymetric range. Type "H" dolphins were also observed outside the lagoon waters, within the type "A" individuals range (type A, n = 9). Finally, 9 individuals (type C) only range in the south of the island, in the coastal waters. Communities "B, H and C" may be different, but our dataset did not show significant differences among them. Conversely, type "A" is significantly different to all other communities. One uses open and deeper waters of a reef bank with higher fish biomass and higher predator presence in the north-west of Mayotte reef complex (type A; Wickel et al., 2010) and the others use more coastal waters located inside the lagoon. Similar spatial segregation has been previously documented, including for bottlenose dolphins and sea turtles from Shark Bay (Western Australia; Heithaus and Dill, 2002; Heithaus et al., 2007). These studies suggest that foraging

distributions reflect a trade-off between predation risk and food availability, and highlight the importance of taking into consideration community context when studying habitat use (Heithaus and Dill, 2002).

The existence of communities has been documented for a number of taxa, such as bottlenose dolphin (especially in T. truncatus), reef sharks (Papastamatiou et al., 2010) and in chimpanzee societies (Goodall, 1986). In bottlenose dolphins, communities are not genetically isolated and individuals may change community membership over time (Wells, 1986; Wells et al., 1996). Among geographical areas, patterns of community home range may be variable. Indeed, communities may overlap in their ranging patterns and live in direct sympatry but differ in their foraging behaviour and social associations (Chilvers and Corkeron, 2001; Lusseau et al., 2005). In other areas such as Tampa bay, in Florida, most communities show little overlap in their ranges (Urian et al., 2009). Our study confirms that the two main communities that were identified (A and B–C, i.e. the "northern community" and the "lagoon community", respectively) show little overlap. However, some substructure among communities B, C and H could occur but more data are clearly needed in order to resolve this issue.

4.5. Origin of community formation

Certain ecological factors may be more likely than others to promote the formation of communities (Urian et al., 2009). These factors can be directly linked to social behaviour, as foraging strategies may be culturally transmitted along matrilines (Krützen et al., 2004; Novacek, 1999). Our stable isotope analyses did not reveal differences of feeding strategies between individuals and communities, especially in the long-term (analyses conducted in the blubber). We also expected that some individuals, such as those from the north (occurring farther from shore), would have lower $\delta^{13}C$ signatures (a pattern that we observed, but that was not statistically significant) and that structure may occur within the population. Indeed, higher values should be observed in dolphins with a more coastal home range, as benthic carbon sources are easier to access in coastal habitats (Hobson, 1999). In the present study, we rather showed a high variance of the stable isotope signatures in skin tissues, revealing a wide inter-individual width of the feeding niche of Indo-Pacific bottlenose dolphins around Mayotte (Bearhop et al., 2004), but not any significant dietary segregation within the population. Consequently, we do not have evidence that bottlenose dolphins use distinct resources at the species level around Mayotte. However, only differences in isotopic signatures are informative whereas similarities do not necessarily imply that individuals share a similar trophic niche, as different foraging strategies may result in similar isotopic signatures. Nevertheless, we showed that some individuals do have different ranging patterns. This could be linked to competition at the species level. Competition is an interaction between individuals, brought about by a shared requirement for resources, and leading to a reduction in survivorship, growth and/or reproduction success (Begon et al., 1986). Here we hypothesize that bottlenose dolphins around Mayotte use similar resources (that can considerably vary over time, cf. stable isotope signature information from blubber). However, they form communities in order to optimize space (and obviously resources) sharing.

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