A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, south-west Indian Ocean

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Running title: Tropical dolphin niche segregation

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Abstract

Mayotte in the southwest Indian Ocean is characterized by high dolphin diversity. They may coexist within a fairly small area around the island because they exploit neither the same preferential habitats nor the same resources. This preliminary study aimed to investigate ecological niche segregation among these delphinid communities: the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, the pantropical spotted dolphin, *Stenella attenuata*, the spinner dolphin, *Stenella longirostris*, and the melon-headed whale, *Peponocephala electra*. Two approaches were used. Habitat preferences were investigated by analysing dolphin sighting data and associated physiographical characteristics. Resource partitioning was explored by analysing C and N stable isotopes in skin and blubber biopsies. Only *T. aduncus*, which showed clear association with coastal habitats in the lagoon, differed from the others in terms of habitat preferences, characterised by shallow depth and slope, and proximity to the coast. All other species shared similar oceanic habitats immediately outside the lagoon, these being of higher depth and slope, greater distance from the coast and were not discernable by discriminant analysis. The two *Stenella* species and the melon-headed whale displayed very high overlap in habitat physiographic variables. The analysis of stable isotopes confirmed the ecological isolation of *T. aduncus* and revealed a clear segregation of *P. electra* compared to the two *Stenella* that was not apparent in the habitat analysis. This may reflect ecological differences that were not observable from diurnal surface observations.

Key-words: dolphins, ecological niche, habitats, stable isotopes, south-west Indian Ocean, Mayotte.

1. Introduction

In biological communities, each species has its own unique niche, which provides the conditions and resources needed for its survival. A shared resource in limited supply will bring about competition between members of the same species (intra-specific competition) or between individuals of different species (inter-specific competition). Competition can take two different forms: interference, which is a direct, often aggressive, interaction between individuals, or exploitation-competition, in which individuals interact with each other indirectly, by responding to a resource level which has been depressed by the activity of competitors (Begon et al., 1986).

A niche occupied by a species in the absence of competitors is termed its fundamental niche, whereas in the presence of competitors, species may be confined to a realized niche, which is shaped by the presence of competing sympatric species (Begon et al., 1986). Hence, the coexistence of potentially competing species is often made possible by the differentiation of their realized ecological niches. The first mechanism that allows for niche differentiation is resource partitioning. In this case, different species living in the same habitat exploit the resources differently. For example, predators of different size may feed on prey of different size, hence minimising the overlap between the various predators' prey size ranges. Prey specialization presumably allows for niche partitioning in areas of sympatry (Ballance, 2002). The second mechanism involves spatial (microhabitat differentiation) or temporal separation in the availability of the different resources (these become available at different times of the day or different seasons of the year; Huisman and Weissing, 2001).

Small delphinids belong to numerous species which have similar morphological characteristics. This situation suggests that fine-scale mechanisms allow for the partitioning of habitats and resources when and where the different species live in sympatry. A study of the cetacean community of Great Abaco, Bahamas, has shown that the ecological niches of the four species

70 that permanently live there do not overlap (MacLeod et al., 2004). These species capture prey at
71 different depths of the water column. Other cetacean species are observed in the study area only
72 during the season when prey abundance is sufficiently high to support their presence, while they
73 are competitively excluded for the rest of the year (MacLeod et al., 2004). Indeed, the spatial
74 distribution of marine predators is mainly determined by the distribution and availability of their
75 prey, these in turn varying according to physical, chemical and biological characteristics of the
76 water masses (Forcada, 2002).
77 The dietary ecology of marine mammals and their trophic level can be determined using different
78 methods: traditional methods analyse faeces and regurgitated food of living animals, as well as
79 the stomach contents of dead animals (from strandings or by-catch; e.g. Pusineri et al., 2007). A
80 more recent method for studies of dietary ecology is stable isotope analysis of blubber, skin or
81 muscle samples (Bearhop et al., 1993). The carbon and nitrogen isotope ratios ($^{13}C/^{12}C$ and
82 $^{15}N/^{14}N$, expressed hereafter as $\delta^{13}C$ and $\delta^{15}N$) of a consumer reflect those of its diet, with a slight
83 retention of the heavier isotope and excretion of the lighter one (Das et al., 2003). As a
84 consequence, tissues will be enriched with heavy isotopes at every trophic level. The minor
85 stepwise trophic enrichment of the carbon-isotope ratio limits its use in assessing trophic levels,
86 but enhances its use in tracking carbon sources through a food chain. The carbon isotope ratio of
87 secondary and tertiary consumers should thus reflect the source of carbon at the base of their food
88 chain (Kelly, 2000). The higher enrichment of the nitrogen isotope ratio of consumers compared
89 to their prey makes it very useful for the determination of their trophic level (Kelly, 2000). Thus,
90 both ratios help elucidate trophic relations and habitat use.
91 Mayotte, a volcanic island in the northern Mozambique Channel (southwest Indian Ocean), is
92 characterized by the permanent presence of more than 20 species of cetaceans (Kiszka et al.,
93 2007). Of these, the most important in coastal waters are the Indo-Pacific bottlenose dolphin,

Tursiops aduncus (Ehremberg, 1833), the pan-tropical spotted dolphin, *Stenella attenuata* (Gray, 1846), the spinner dolphin, *S. longirostris* (Gray, 1828), and the melon-headed whale, *Peponocephala electra* (Gray, 1846). The island has a great variety of marine ecosystems offering a large diversity of habitats: coasts, mangroves, an extended lagoon (1100 km^2), different kinds of reefs (fringing, pinnacles, and barrier), a steep insular slope with many submarine canyons and seamounts, and the open ocean (Quod et al., 2000). At least twelve species of delphinids may coexist in a fairly small area around the island because they exploit neither the same habitats nor the same resources (Kiszka et al., 2007). The present study aimed to investigate ecological niche segregation among the resident dolphin community of Mayotte, especially the Indo-Pacific bottlenose dolphin, the pantropical spotted dolphin, the spinner dolphin and the melon-headed whale. We concentrated on these four species as they are of fairly similar size and can be found within the same proximity around Mayotte, in closely-related habitats within a small area and at all seasons (Kiszka et al., 2007). This is particularly so for the two *Stenella* species and the melon-headed whale which are all encountered immediately outside the barrier-reef and in the channels, whereas existing literature suggests that they would be more differentiated habitat-wise, with the spinner dolphin feeding offshore but resting inshore, the melon headed whale being an oceanic squid-eater and the Indo-Pacific bottlenose dolphin dwelling in nearshore coastal habitats (Norris et al., 1994; Silva et al., 2005; Perryman, 2002; Wells and Scott, 2002). Two approaches were used for the study: a comparison of habitat by the analysis of dolphin sighting data and associated behavioural and physiographic characteristics (group size, depth, slope, distance to the coast and proximity to the different kinds of reefs), and the study of habitat and resource partitioning by the analysis of C and N stable isotopes from skin and blubber biopsies.

2. Material and Methods

2.1 Study area

The volcanic island of Mayotte (45°10'E, 12°50'S), which is part of the Comoros archipelago, is located in the northern Mozambique Channel (Indian Ocean) between Madagascar and Southeast Africa. Its surface area is 376 km^2 and it is composed of two main islands and about 30 islets scattered within and around a lagoon. Mayotte is surrounded by a large lagoon-reef complex, whose width varies from 3 to 15 km. Fringing reefs surround the archipelago, an inner double-reef is present off the south-west end of Mayotte, and the barrier reef, which is interrupted by numerous channels, separates the lagoon itself (maximum depth 80 m) from the external slope and more oceanic habitats.

The four species of interest, the Indo-Pacific bottlenose dolphin, the pantropical spotted dolphin, the spinner dolphin, and the melon-headed whale, range in size from about 200 cm and 90 kg for the spinner dolphin to 250 cm and 250 kg for the melon-headed whale (Perrin, 2002a and b, Perryman, 2002, Wells and Scott, 2002).

2.2 Data and sample collection

Data were collected from 1997 to 2005, during small boat-based surveys dedicated to studying marine mammals (Figure 1). Several types of boats were used: a 7 m catamaran equipped with two, four-stroke, 60-hp outboard engines; a 7 m boat equipped with two, two-stroke, 40-hp outboard engines; a 6.4 m cabin boat equipped with an inboard four-stroke and 150-hp outboard engine. Surveys were conducted during daylight hours, i.e. between 0700 h and 1800 h, in sea conditions not exceeding Beaufort 3. The survey vessels did not follow pre-defined transects but sampling covered all habitats within the lagoon and over the external insular slope (Figure 1). Effort varied according to month (Figure 2), with more effort being applied in the austral summer

142 (November to January). When dolphins were encountered, preliminary information records
143 included group size (maximum, minimum, best estimate), geographic position, activity
144 (travelling, resting, foraging/feeding, socialising, milling, play), group classification on the basis
145 of the relative size of individuals (adults, sub-adults, calves), research boat disturbance (bowride,
146 approach, avoidance, no response) as well as group formation (tight, loose, dispersed, variable,
147 convergent; Shane, 1990; Würsig et al., 1998). This study is still on-going and, therefore, only
148 the sighting locations and associated physiographic variables are analysed here.
149 When conditions were optimal (good weather and sea state, dolphins closely approaching the
150 boat), biopsies were collected using a cross-bow (*BARNETT Veloci-Speed® Class*) with Finn
151 Larsen bolts and tips (20-mm). The dolphins were hit below the dorsal fin, when close (3-10
152 meters) to the research boat. Sampling periods spanned all seasons but sample sizes did not allow
153 seasonal comparisons (January, August and December for *T. aduncus*, N=4; January, February,
154 March and October for *S. attenuata*, N=4; February, March, May and October for *S. longirostris*,
155 N=5; March, July and December for *P. electra*, N=4). It was not possible to determine sex, size
156 or age of the individuals biopsied. Blubber and skin biopsy samples were preserved separately in
157 90° ethanol before shipping and subsequent analysis. Biopsy sampling was conducted under
158 scientific permit #78/DAF/2004.
159
160 2.3 Database
161 We constituted a database in which every dolphin observation was associated with the
162 physiographic characteristics (distance to the coast, to the different reefs and to the closest
163 channel, as well as depth and slope of seafloor and the variance of these two parameters)
164 corresponding to the GPS (Global Positioning System) fixes of the observation. The distance data
165 were obtained using GIS (Geographic Information System) software ArcView (ArcGIS 8.2) by

ESRI (Environmental Systems Research Institute). Bathymetric data were obtained from *Service Hydrographique et Océanographique de la Marine* (SHOM). Interpolation of bathymetry data, needed to generate depth and slope data for each sighting, was undertaken with the extension Spatial Analyst by kriging transformation of the raster file into an interpolated data file. This was obtained by calculating the mean value of the twelve points closest to every bathymetric point in a 1 km^2 grid. This interpolated data file thus allowed us to generate depth and slope data over the whole study area and therefore to associate bathymetry data to any dolphin observation in the area.

2.4 Data analysis

The environmental data were first compared between species using basic methods (non-parametric analyses and ANOVA). Then we used multivariate statistical methods including discriminant linear and quadratic analyses to examine how well sightings were assigned to the correct species from the combination of associated physiographic variables. All methods were implemented with the software R (R-2.2.1, R Development Core Team, 2005).

2.5 Stable isotope analyses

Blubber and skin were separated for each biopsy. The ethanol they contained was evaporated at 45°C over 48 h and the samples were ground and freeze-dried (Hobson et al., 1997). Lipids were extracted using cyclohexane (C_6H_{12}) prior to analysis because they are depleted in ^{13}C; if they were not extracted, this would cause a bias in the isotopic signature of ^{13}C (De Niro and Epstein, 1978; Tieszen et al., 1983). Small sub-samples (0.35 to 0.45 mg $\pm$ 0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a continuous-flow isotope-ratio mass spectrometer (Isoprime, Micromass) coupled to an elemental analyser (Eurovector EA 3024).

Results are expressed in δ notation relative to PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation $\delta X = [(R_{sample}/R_{standard}) - 1] \times 10^3$, 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 <0.15‰ and <0.20‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Percent C and N elemental composition of tissues were obtained using the elemental analyzer and used to calculate the sample C:N ratio, indicating a good lipid removal efficiency when <4.

3. Results

3.1 General

Our cetacean sightings comprised 394 positional data for *S. longirostris* (*n* = 208), *S. attenuata* (*n* = 88), *T. aduncus* (*n* = 83) and *P. electra* (*n* = 15) in all sectors around Mayotte (Figure 2) and all seasons (Figure 3). Indo-Pacific bottlenose were mostly found within the lagoon, very often in the immediate proximity of the fringing reef, and to a lesser extent over the North West bank located outside the main barrier reef. The two *Stenella* species were observed all along the barrier reef on its outer side and made only a few incursions into the lagoon. Finally, the melon-headed whale was only seen outside the barrier reef.

3.2 Habitat use and niche partitioning

A preliminary Principal Component Analysis (PCA plot not shown) allowed us to select group size, distance to coast, depth and slope as the set of physiographic variables with least redundancy. Distances to the various reefs and to the nearest channel were heavily redundant

relative to distance from coast and therefore not retained. A simple comparison of the distribution of these variables for the four focal species was performed using Kruskall-Wallis tests (Figure 4). *T. aduncus* is observed at short distances from the coast with shallow bathymetry and moderate slopes, whereas the other three species cannot be significantly differentiated in terms of habitat characteristics. In particular, the two *Stenella* species manifested similar characteristics in group size and environmental preferences. On the other hand, group size differed strongly between *T. aduncus* that lives in small groups (median = 6) and *P. electra* that is mostly found in groups of several hundred individuals (median = 300).

Linear discriminant analysis separated the species according to their environmental characteristics (Figure 5). The predictive power of the linear discriminant analysis was good only for *T. aduncus* which can be explained by its habitat preferences (Table 1, upper part). The other species' habitat characteristics were too similar to permit acceptable predictions. The good prediction for *S. longirostris* might be attributable only to the considerable number of sighting data for this species. Finally, the quadratic discriminant analysis provided slightly better predictive results, especially for *P. electra* (Table 1, lower part).

The different methods used to compare the preferred habitats of the four delphinid species under study all clearly showed that *T. aduncus* differs from the other species in its preferred environmental parameters. *S. attenuata* and S. *longirostris* share similar environmental characteristics. *P. electra* is characterised by a larger group size and deeper depth preference, but resembles *Stenella* in terms of the majority of its other environmental preferences (distance and slope).

3.3 Resource partitioning

Stable isotope ratios were lower in blubber than in skin but the pattern of differences observed between species was similar in both tissues (Figure 6). Skin and blubber of *T. aduncus* have the highest values of $\delta^{13}C$. The two *Stenella* species are not discernable from each other as shown by the extensive overlap in standard deviation for both $\delta^{15}N$ and $\delta^{13}C$, and have the lowest values for $\delta^{13}C$. *P. electra* has the highest $\delta^{15}N$ and a $\delta^{13}C$ values that are intermediate between those for the two *Stenella* species and *T. aduncus*. The intra-specific variance is represented by the standard deviation, which is more important for the $\delta^{13}C$ values than for the $\delta^{15}N$, except in the blubber samples of *T. aduncus* where intra-specific variance in the $\delta^{15}N$ is prevalent.

4. Discussion

The present study comprises a preliminary analysis of habitat and resource use among an assemblage of co-existing tropical delphinids living around Mayotte in the southwest Indian Ocean. The principal finding is that, among the four species of interest, the Indo-Pacific bottlenose dolphin is clearly differentiated from the other species in terms of both habitat preference and stable isotope analyses. From the variables tested here, the other three species can hardly be separated in terms of their preferred habitats but stable isotope analysis revealed a dietary segregation between the melon-headed whale and the two species of the genus *Stenella*. This was not initially evident in the sighting data analyses that described the dolphins' diurnal use of habitats. However, some limitations render these findings preliminary. The sightings constituted presence-only data as the observation effort could not be readily quantified and, hence, the data cannot provide significant information concerning dolphin absence. In this work, we tried to characterise the habitats where dolphins were found, not assess the overall distribution of each species around the island. Nevertheless, the field surveys comprehensively covered the

study area such that all habitats were visited and the sighting data of the four focal species were considered representative of their habitat preference.

The Indo-Pacific bottlenose dolphin, *Tursiops aduncus*, occupies an ecological niche that clearly differs from those occupied by the other study species. *T. aduncus* was observed only inside the lagoon except in the northern part of the island where the reef system is in the form of an open bank outside the lagoon. This species is generally found close to the fringing reef which constitutes the ecosystem where prey of this coastal dolphin may be concentrated. The high $\delta^{13}C$ value in its tissues indicates a benthic carbon source that dolphins more easily access in coastal habitats (Hobson, 1999). This species has indeed been observed feeding near mangroves, along the fringing reefs or over seagrass beds. Its isotopic signature of $\delta^{15}N$ is similar to that of the two *Stenella*, but this cannot be interpreted as an indication of similar trophic levels as the $\delta^{15}N$ values of the local primary producers *versus* those outside the lagoon have not been investigated at this stage.

T. aduncus lives and forages individually or in small groups inside the lagoon, where the water is shallow and large predators are absent, and probably feeds on prey that would not aggregate in large schools (Mann et al., 2000). Indo-Pacific bottlenose dolphins forage over reefs or soft bottom substrata and near the shore relatively close to the island of Mayotte and around Zanzibar (Tanzania) (Amir et al., 2005).

The pantropical spotted dolphin and the spinner dolphin share a barrier reef-associated habitat outside the lagoon. They are also found where the water depth rapidly attains a depth of 100 m. In comparison to the Indo-Pacific bottlenose dolphin, their tissues had a lower $\delta^{13}C$, suggesting it was derived from an oceanic carbon source; oceanic phytoplankton is reported to be ^{13}C-depleted

283 relative to marine phanerogams (Hobson, 1999). Their isotopic ratios suggested their diet
284 comprised oceanic prey.
285 *S. attenuata* and *S. longirostris* can occasionally be observed inside the lagoon where they might
286 take advantage of the safety it provides for resting. This kind of behaviour has been observed in
287 Hawaiian spinner dolphin populations (Norris et al., 1994). *S. longirostris* generally lives in
288 single-species groups from several dozens to several hundreds of individuals, e.g. around the
289 main Hawai'i island (Norris et al., 1994). Their aggregation in large groups might offer some
290 protection against predators but it might also facilitate feeding through communal hunting on
291 large pelagic fish schools. In the present work, *S. attenuata* was rarely observed in single-species
292 groups but was generally found in association with *S. longirostris*, forming important mixed-
293 species groups. Both species might take advantage of a larger group size for safety and foraging.
294 Nevertheless, a large group size increases the potential for intra-specific competition as well as
295 inter-specific competition if the two species feed together. A study in the southwest Atlantic has
296 shown that distributions of spotted dolphins and spinner dolphins may partially overlap (Moreno
297 et al., 2005). Associations of spotted dolphins and spinner dolphins are frequently found in
298 Hawai'i, where the two species travel together while showing many aggressive interactions, but
299 they do not seem to feed together (Psarakos et al., 2003). Conversely, in the Azores, common
300 dolphins, *Delphinus delphis*, and Atlantic spotted dolphins, *Stenella frontalis*, associate and
301 forage together (Clua and Grosvalet, 2001). As *S. attenuata* and *S. longirostris* have similar
302 habitat preferences and similar isotopic signatures, both for carbon and nitrogen, there is no
303 evidence of ecological niche differentiation in these two species. Two options could be
304 investigated in the future: either the two dolphins share the same resources in the same habitats,
305 presumably because food is not limiting there, or they segregate when feeding on different

306 resources but their prey have similar isotopic signatures because they rely on the same carbon
307 source at the same trophic level.
308 The melon-headed whale, *Peponocephala electra*, prefers steep slopes and slightly deeper water
309 than the two *Stenella* species. *Peponocephala electra* forms large groups of several hundred
310 individuals. As it was always observed in a habitat that overlaps with that of the spinner and
311 spotted dolphins, analysis of its habitat characteristics failed to distinguish between it and the two
312 *Stenella* species. This might be due to the fact that melon-headed whale sightings were only made
313 on groups that occasionally approached the island, as the surveys were conducted in a limited
314 area around Mayotte and groups living farther offshore in the open ocean would not have been
315 observed. In this case, our understanding of the preferred habitat of this species remains marginal,
316 being limited to its nearshore fringe. Stable isotope analysis, on the other hand, clearly showed
317 that there is an ecological differentiation between *P. electra* and the two *Stenella* species. Values
318 of $\delta^{13}C$ for *P. electra*'s were intermediate between those of the *Stenella* species and *T. aduncus*.
319 This would suggest that carbon isotopic composition of *P. electra* is influenced more by benthic
320 primary production than that of the two *Stenella* species. *Peponocephala electra* is known for its
321 oceanic habitat (Perryman, 2002), and possible interpretations for its $\delta^{13}C$ include the possibility
322 that it is a deep-diving species that feeds on prey derived from a detritus-based food web unlike
323 the *Stenella* that feed on a phytoplankton-based food web. In addition, *P. electra* clearly differs in
324 its $\delta^{15}N$, this being indicative of a higher trophic level, suggesting its diet includes more
325 carnivorous fish and squid than the spotted and spinner dolphins. Again, as in *T. aduncus*, all
326 sources of primary production should be investigated concerning their $\delta^{15}N$ to adequately
327 interpret the trophic levels.
328

If there is high inter-individual variance in the $\delta^{15}N$ (*versus* $\delta^{13}C$) values within a species, the interpretation is that the species is composed of individuals that have varied feeding habits and prey on organisms at different trophic levels ($\delta^{15}N$) or are found in different habitats ($\delta^{13}C$). A low variance indicates that all the individuals are specialist feeders on similar prey or within the same habitat. Thus, stable isotope variance is sometimes considered a measure of niche width (Bearhop et al., 2004) or at least the inter-individual measure of niche width. Results of our stable isotope analysis indicate that *P. electra* is a fairly specialized feeder, whereas *S. attenuata*, *S. longirostris* and especially *T. aduncus* would be more eclectic feeders, which, in the latter case, is in line with previous studies (Mann et al., 2000).

Detectable differences between the standard deviations in the stable isotope composition in the skin and blubber samples might be attributable to their differential rates in tissue renewal: this takes a few days for epidermis but several months for the collagen matrix of the blubber (Abend and Smith, 1995). The residence time of elements in tissues depends on metabolic turnover rates (Rubenstein and Hobson, 2004). This enables tracking of an animal's foraging history as demonstrated by a study on pilot whales (*Globicephala melas*) in the North Atlantic (Abend and Smith, 1995). *T. aduncus* and the two *Stenella* species clearly differ in the respective isotopic carbon signatures in their skin and blubber, indicating that they feed on trophic webs with different carbon sources over the long term.

Each species' habitat preference is presumably based on their prey distributions (Baumgartner et al., 2000) which, in turn, are related to water depth (Hastie et al., 2005) and, indirectly, bathymetric features that influence currents and productivity (Fiedler, 2002). Foraging behaviour seems to be closely related to submarine habitat characteristics (Hastie et al., 2004). It has been demonstrated that a variable bathymetry contributes to global delphinid abundance, promoting

the regional abundance of different species (Gannier, 2005). The rich marine biodiversity of Mayotte is possibly related to its variety of habitats and these provide numerous ecological niches for delphinid prey.

5. Conclusions

The present study provides preliminary ecological indications of niche differentiation and resource partitioning within the Mayotte delphinid communities. The only species that differs from the others in terms of habitat characteristics is the coastal-dwelling Indo-Pacific bottlenose dolphin, whereas pantropical spotted and spinner dolphins and the melon-headed whale share similar oceanic habitats immediately outside the lagoon. Stable isotope analysis confirmed the ecological specialisation of *T. aduncus* and, in addition to this, revealed a clear segregation of *P. electra*, from to the two *Stenella* species in terms of their feeding that was not apparent in the habitat analysis. This may reflect behavioural differences that were not detectable from diurnal surface observations. Further work should strengthen these conclusions through dedicated sampling of habitat preference and an expansion of the stable isotope studies. These should focus on seasonal changes in food partitioning and the isotopic composition of a series of putative prey species and primary producers characteristic of the inshore-offshore gradient of habitats found around Mayotte.

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Figure captions

Figure 1: Location of the study area and observation routes from July 2004 to August 2005. Isobath (left) and GPS tracks of sighting surveys (right) are shown around Mayotte Island with barrier reef.

Figure 2: General locations of delphinid sightings around Mayotte and its reefs.

Figure 3: Temporal distribution of effort expressed as number of sightings per three-month period.

Figure 4: Delphinid sighting median values, 50, 75 percentiles and outliers of (a) group size, (b) distance to the coast, (c) depth and (d) seafloor slope. Kruskal Wallis tests showed that *T. aduncus* differed significantly in all cases with p-values $<10^{-6}$.

Figure 5: Sighting density for melon-headed whale (dotted line), pan-tropical spotted (black line), spinner (dashed line) and Indo-Pacific bottlenose dolphin (dashed and dotted line) along the first discriminant axis.

Figure 6: Stable isotope ($\delta^{13}C$ and $\delta^{15}N$ in ‰) values in delphinid blubber (right-hand graph) and skin (left-hand graph). Graphs show average values and standard deviations. Black squares represent *S. longirostris* (N=5), whites squares *S. attenuata* (N=4), black diamonds *T. aduncus* (N=4) and white diamonds *P. electra* (N=4).

Table 1: Discriminant analysis: linear and quadratic predictions for the four species. Each sighting was assigned to one of the four study species on the basis of its associated physiographic characteristics. Only *T. aduncus* data were correctly assigned to the right species whereas all others were mostly assigned to *S. longirostris* as they all share similar habitat characteristics.

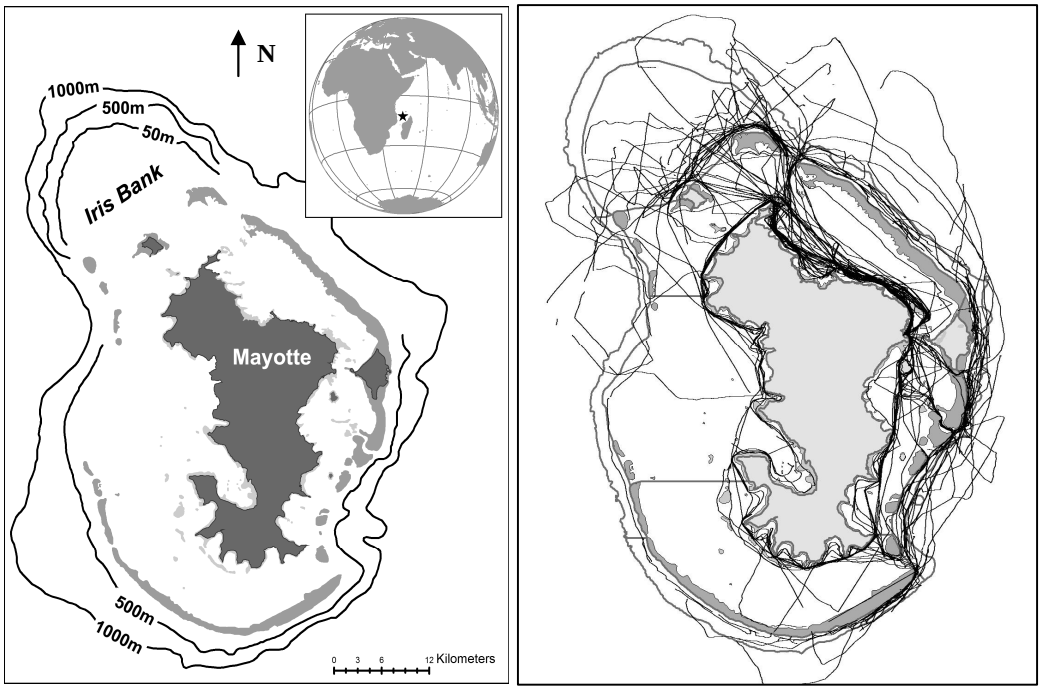
Linear discriminant analysis

	Peponocephala electra	*Stenella attenuata*	*Stenella longirostris*	*Tursiops aduncus*
P. electra	**2**	3	5	0
S. attenuata	1	**3**	1	2
S. longirostris	12	79	**194**	19
T. aduncus	0	2	8	**62**
Good prediction	**14%**	**3%**	**93%**	**77%**

Quadratic discriminant analysis

	Peponocephala electra	*Stenella attenuata*	*Stenella longirostris*	*Tursiops aduncus*
P. electra	**11**	4	4	0
S. attenuata	1	**18**	18	1
S. longirostris	3	46	**131**	4
T. aduncus	0	19	55	**78**
Good prediction	**79%**	**20%**	**63%**	**96%**

Fig.1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598 Fig.2

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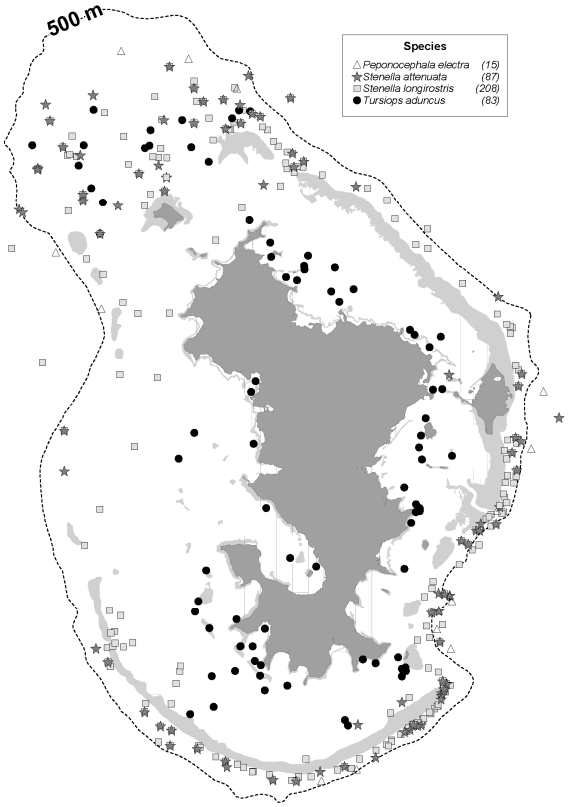

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601 Fig.3

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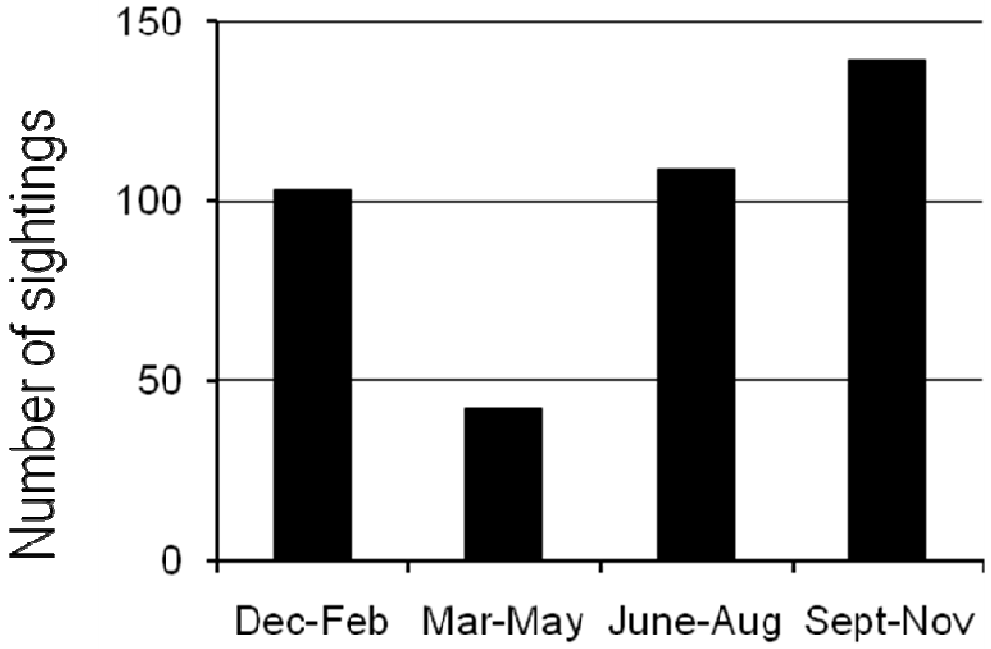

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607 Fig.4

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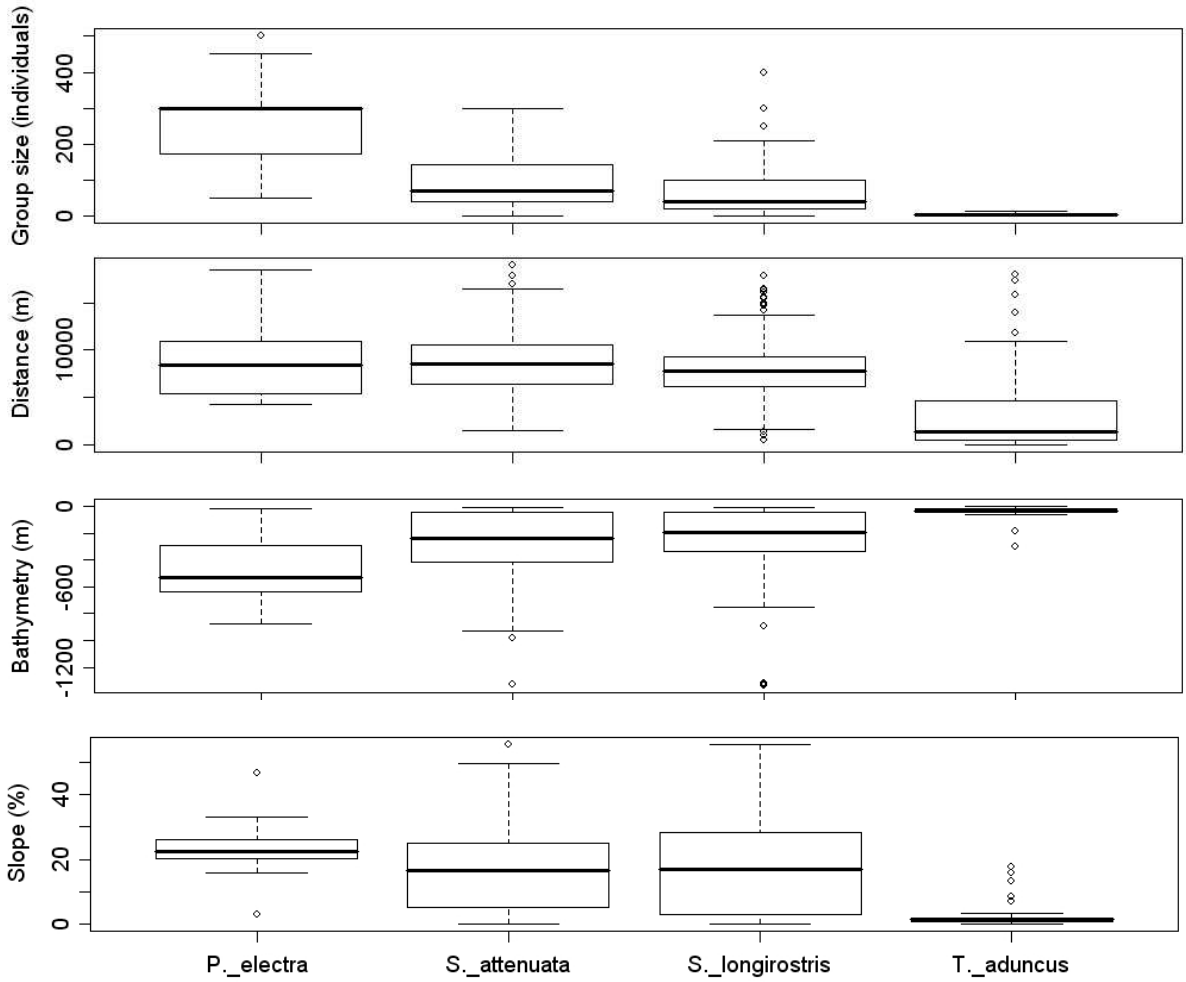

609 Fig. 5

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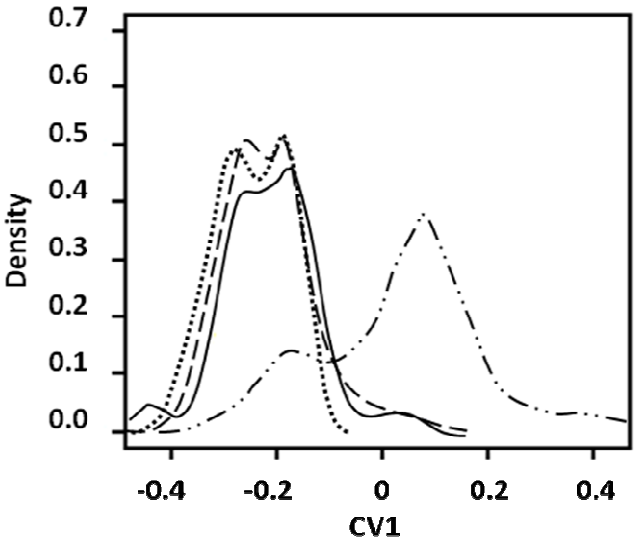

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615 Fig. 6

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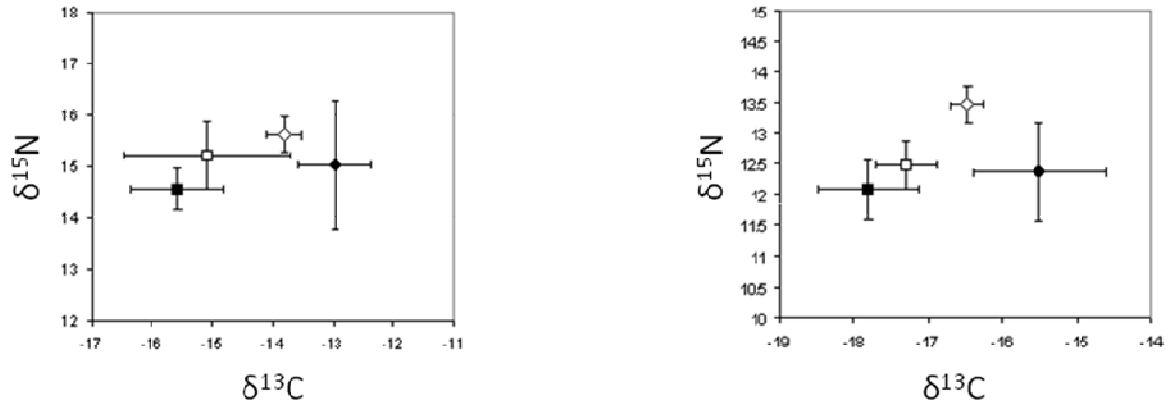
617 Skin Blubber



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