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Ecological niche segregation within a community of sympatric dolphins around a tropical island

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ABSTRACT

Investigating ecological segregation among organisms of a given community is challenging, especially when these organisms share similar patterns of distribution, and similar size and morphology. Around the island of Mayotte, a diversified community of at least four sympatric delphinids is present year round within a very restricted range: the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), the spinner dolphin (*Stenella longirostris*), the pantropical spotted dolphin (*Stenella attenuata*), and the melon-headed whale (*Peponocephala electra*). In addition, the Fraser's dolphin (*Lagenodelphis hosei*) makes temporary incursions into peri-insular waters as well. This study aims to assess niche segregation among this tropical dolphin community. We hypothesized that each species occupies its own distinct niche, defined by the following axes: habitat, resources and time. We analysed habitat in relation to physiography, behavioural budgets and C and N stable isotope values from skin and blubber samples for each species. The results highlighted that habitat and behavioural budgets were relatively distinct among species, with few exceptions. However, in those species living on the outer reef slope where habitat and behaviour were not well discriminated, stable isotope analyses confirmed that species have different trophic levels (mostly reflected through $\delta^{15}N$ values) and/or foraging habitat (mostly reflected through $\delta^{13}C$ values). This study confirms that the use of multiple methodologies (habitat, behaviour and feeding ecology studies) help in discerning ecological niche segregation, especially when examining closely related species within a common restricted range.

KEYWORDS: tropical dolphins, ecological niche, habitats, stable isotopes, carbon, nitrogen, south-west Indian Ocean, Mayotte.

INTRODUCTION

Understanding niche segregation processes is critical in ecology, particularly when investigating the ecology of species communities. A community can be defined as a collection of species that occur together in a common environment, or habitat, the organisms making up the community being somehow integrated or interacting as a society (Chapman & Reiss 1999). Each species has its own unique niche (Grinnell 1924). The ecological niche is a complex set of variables structured along three main axes: habitat (influence of environmental variables), diet (diet composition, trophic level and prey quality) and time (use of habitat and resources according to time, such as seasons and time of day). Sympatric species with similar ecological requirements would compete for resources and their coexistence requires some degree of habitat and resource segregation (Pianka 1974). Similar species that co-occur are thought to compete for resources unless they occupy different physical locations and/or feed on different prey. 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) (Roughgarden 1976). Intra-specific competition may be expressed by sex or age related difference in habitat and resource use and has consequences on social structures. Inter-species competition can take various forms, including direct interference (aggressive behaviour) and exploitation-competition, in which individuals indirectly compete for resources (Begon et al. 1986).

Investigating segregation processes within communities of organisms having similar size and morphology has been particularly challenging. In such communities, niche partitioning is difficult to assess as it can occur over small spatial and temporal scales. For example, in species with similar morphology (e.g. body size, jaw/beak shape, etc.), feeding niches are distinct even when feeding occurs in both species within the same area (MacArthur 1958). Niche segregation has been investigated in a number of top marine predator communities, including large teleost fish (Potier et al. 2004, Ménard et al. 2007), sharks (Estrada et al. 2003, Domi et al. 2005, Papastamatiou et al., 2006), seabirds (Ridoux 1994, Cherel et al. 2008, Jaeger 2009), marine mammals (Das et al. 2003, Whitehead et al. 2003, Praca & Gannier 2008) including delphinids (Pusineri et al. 2008, Gross et al. 2009; Kiszka et al. 2010). Methods used to discriminate niches were variable, including stomach content, stable isotope and heavy metal analyses and habitat assessment (including habitat modelling). For example, niche partitioning has been assessed in polar communities using stable isotope analyses of C and N, such as in Antarctic pinnipeds, showing clear ecological segregation between species (Zhao et al. 2004). Conversely, in tropical sympatric seabirds, important overlap of feeding niches has been found, which may be interpreted by the low productivity of tropical oligotrophic waters, leading these predators to share same feeding resources that are not quantitatively limited (Cherel et al. 2008). In the tropical cetacean community of the Bahamas, it has been shown using a habitat analysis that the ecological niches of four cetacean species (Atlantic spotted dolphin *Stenella frontalis*, Blainville's beaked whale *Mesoplodon densirostris*, Cuvier's beaked whale *Ziphius cavirostris* and dwarf sperm whale *Kogia simus*) do not overlap. Other cetacean species are observed in the area only during the season when prey abundance is sufficiently high to support their presence, while they are competitively excluded for the rest of the year (MacLeod et al. 2004).

Around the tropical island of Mayotte (Comoros, SW Indian Ocean), a great diversity of cetaceans has been found within a limited geographical range, i.e. at least 19 species within an area of 2,500 km² (Kiszka et al. 2007). In this area, high cetacean diversity may be associated by the presence of a wide range of marine habitats within close proximity to one another: turbid mangrove fronts, fringing reef systems, clear lagoon areas, barrier and double barrier reef-associated habitats, a steep insular slope and deep oceanic waters. In some locations around Mayotte lagoon, water depth extends beyond 1,000 m less than 3 km away from the barrier reef. The permanent presence of odontocetes within a restricted range suggests that fine-scale mechanisms allow for the partitioning of habitats and/or resources. The four most common dolphin species there have a size ranging from 1.8 m spinner dolphin (*Stenella longirostris,* the smallest) to the 2.8 m melon-headed whale (*Peponocephala electra*, the largest). Other species include Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), pantropical spotted dolphin (*Stenella attenuata*) and Fraser's dolphin (*Lagenodelphis hosei*) (Kiszka et al. 2007). The Indo-Pacific bottlenose dolphin is typically a coastal species, feeding on inshore prey (Amir et al. 2005) and lives inside the lagoon around Mayotte (Gross et al. 2009). Conversely, the other species of the community are oceanic and primarily occur outside the lagoon and feed on epipelagic to mesopelagic oceanic prey (Dolar et al. 2003, Brownell et al. 2009). A preliminary study of the tropical delphinid community around the island of Mayotte indicated that their ecological niches at least partially, overlapped (Gross et al. 2009). Using sighting data related to environmental variables and stable isotope analyses from biopsy samples, it was shown that Indo-Pacific bottlenose dolphin had a coastal/lagonal distribution, while spinner dolphin, melon-headed whale and pantropical spotted dolphin had similar habitat characteristics along the outer reef slope. Stable isotope analyses from a small amount of biopsy samples allowed species of the community to be discriminated isotopically, except the two congeneric and "sibling" dolphins of the genus *Stenella*, having similar morphological characteristics and frequently forming inter-species aggregations. Methodological constraints and limited sample size are likely to explain the absence of measurable differences between species. Therefore, the present work aims to characterize habitat and resource partitioning among delphinids living in sympatry around the island of Mayotte from multiple lines of evidence, along the following axes: habitat, diet (more particularly trophic level and foraging habitat) and time (seasons and time of day, Table 1). In this study, we hypothesize that each delphinids species occupies its own ecological niche, defined by at least one of the indicator used. Indeed, for any given pair of species, statistical difference should be found for at least one of the variables tested (habitat, stable isotope values and temporal variations). We will investigate habitat of delphinids in relation to physiographical variables, activity budgets and their variability among species and according to time, and stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) from biopsy samples. $\delta^{13}C$ and $\delta^{15}N$ isotopes help elucidate habitat use (e.g. $\delta^{13}C$ values typically vary from ^{13}C depleted in offshore, or pelagic-derived, to ^{13}C enriched from inshore or benthic-derived C) and the position of the consumer in the food chain, respectively (Hobson 1999). They can also reflect local baseline differences in coastal waters (Mallena & Harrod 2008). The use of these isotopes has provided alternative information from which to better understand top predator ecology, including marine mammals (Das et al., 2003). Activity budgets have been investigated for the three most common species (spinner, spotted and Indo-Pacific bottlenose dolphins) in order to compare daily variation in behaviour and habitat utilization. It allows investigating, at a short time scale (time of day), one of the temporal dimension of the niche. We also assessed seasonal variations of habitat preferences, behavioural budgets and stable isotope signatures, as seasonality may be a major factor segregating species among them.

MATERIALS AND METHODS

Study area

Mayotte (45°10'E, 12°50'S) is located in the north-eastern Mozambique Channel, and is part of the Comoros archipelago (Figure 1). The island is surrounded by a 197 km long barrier reef, with a second double-barrier in the southwest and the immerged reef complex of Iris in the northwest. The lagoon and surrounding reef complexes are 1,500 km² with an average depth of 20 m and a maximum depth of 80 m found in the western, older, region of the lagoon (Quod et al. 2000). The insular slope on the exterior of the barrier reef is very steep and contains many submarine canyons and volcanoes (Audru et al. 2006). The island of Mayotte is characterized by the presence of high cetacean diversity (19 species including 12 delphinids; Kiszka et al. 2007). The most common species are the spinner dolphin (*Stenella longirostris*), the pantropical spotted dolphin (*Stenella attenuata*), the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and the melon-headed whale (*Peponocephala electra*); these occur on a year-round basis (Kiszka et al. 2007).

Data and sample collection

From July 2004 to April 2009, small boat based surveys were undertaken around Mayotte. Several types of boats were used to collect data: 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 cruiser equipped with one, four-stroke, 150-hp outboard engine; and a 10.8-m cabin cruiser equipped with two, four-stroke, 115-hp outboard engines. Surveys were conducted throughout the study period during daylight hours between 07:00 h and 18:00 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, lagonal waters, barrier reef associated areas (inner and outer slopes) and oceanic or slope waters (>500 m). When delphinids were encountered, standard sighting data were recorded: species, group size (maximum, minimum, best estimate), geographic position and behavioural activity. The predominant activity was defined as the behavioural state in which most animals (> 50%) of the group were involved at each instantaneous sampling. Typically, more than 90% of the animals in a group were engaged in the same activity.

In order to measure behaviour of the focal dolphin species and determine their behavioural budgets, focal group follows were used (Mann 1999). While one of the preferred option in behaviour sampling is to follow a focal individual (Mann 1999), this method was not suitable for large aggregations of oceanic dolphins. In addition, following groups, rather than individuals, is more suitable for behavioural studies as appropriate conditions for individual sampling are rare in diving cetaceans (Whitehead 2004). Individual follows were generally possible in the easily identifiable Indo-Pacific bottlenose dolphins, but not on each occasion, as some individuals were not identifiable, but for comparative purposes, we used a focal group protocol, which has been used in other studies on similar models (Neumann & Orams 2006). The encountered group was approached slowly (typically at 2-3 knots), from the side and rear, with the vessel moving in the same direction as the animals. Groups were scanned, including all individuals, to negate attention being drawn to only specific individuals or behaviours (Mann 1999). During focal follows, dolphin behaviour was recorded every 5 minutes. Five categories of behavioural states were defined: milling, resting, travelling, feeding/foraging (hereafter foraging), and socializing as defined in previous studies (e.g. Norris & Dohl 1979, Bearzi 2005, Neumann & Orams 2006, Degrati et al. 2008). Feeding was characterised by loose to disperse group formations and dolphins were observed swimming in circles, and pursuing fishes (prey observed at the surface). Preys were frequently seen at the surface during foraging activity. In bottlenose dolphins, large preys were frequently exhibited by the animals at the surface. Travelling consisted of persistent and directional movements of all the individuals of a group. Milling was characterised by non-directional movements of the dolphin, with frequent changes in heading. Socialising consisted in frequent interactions between individuals in the form of body contacts, with high-speed movements, frequent changes in direction and aerial displays. Resting was characterised by low level of activity, with groups in tight formations, with little evidence of forward propulsion. Surfacings are slow and relatively predictable.

For stable isotope analyses, biopsy attempts were made 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. 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). A conical plastic stopper caused the bolt to rebound after the impact with the dolphin. The dolphins were hit below the dorsal fin when sufficiently close (3-10 m) to the research boat. Approaches of focal groups/individuals were made under power at speeds of 1-4 knots. Blubber and skin biopsy samples were preserved individually in 90% ethanol before shipping and subsequent analysis. The preservative used (ethanol) was the most suitable that could be used due to logistical constraints. It does not affect stable isotope signatures in freshwater zooplankton and benthic macroinvertebrates (Syväranta et al. 2008), bird eggs, blood and muscle (Hobson et al. 1997, Gloutney & Hobson, 1998). The increase in δ^{13}C values is generally considered to be due to the extraction of some lipids but because lipids are depleted in ^{13}C, they are typically extracted (or corrected arithmetically, e.g. Kiljunen et al 2006) to avoid a bias in estimates of δ^{13}C values (De Niro & Epstein 1978, Tieszen et al. 1983), that likely cancels any potential effect of storage in ethanol (Kiszka et al. 2010). Biopsy sampling was conducted under French scientific permit #78/DAF/2004 (September 10, 2004) and permit #032/DAF/SEF/2008 (May 16, 2008) after examination of the project by *Conseil National de Protection de la Nature*.

Muscle samples from several fish species were also collected for stable isotope analyses, especially to investigate trophic interactions between delphinids and potential dolphin preys as well as fish species with clear ecological profiles (see below). Fish specimens were collected in a local fish market. Fish muscle samples were sampled in April 2009 and preserved in ethanol before subsequent analyses. The fish species selected were pelagic, demersal and benthic species from reef associated habitats, i.e. from various environments in the lagoon and surrounding waters, and different trophic levels (herbivorous, planctonophageous and piscivorous): *Hemiramphus far*, epipelagic, inhabiting waters near reef systems and feeding on the pelagic zooplankton; *Mulloidichthys vanicolensis*, demersal on seaward reefs, feeding on small worms and crustaceans; *Siganus argenteus*, demersal, inhabiting coastal and inner reef slopes and feeding on algae; *Scarus russelii*, demersal, inhabiting shallow coastal reef and feeding on algae by grazing on coral bubble and *Caranx melampygus*, demersal and pelagic predator feeding on small schooling fishes (Froese & Pauly 2010). Two species were sampled because they regularly enter the diet of the Indo-Pacific bottlenose dolphin: *Hemiramphus far* and *Caranx melampygus* (J. Kiszka & C. Pusineri, personal observations).

Habitat analyses

We constituted a database in which every dolphin group observation was associated with the physiographic characteristics (distance from the coast, distance from the nearest reefs, depth and slope of seafloor) corresponding to the GPS (Global Positioning System) fixes of the observation. 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. The distance data were obtained using GIS (Geographic

Information System) software ArcView (ArcGIS 8.3) by ESRI (Environmental Systems Research Institute). We represented the distribution of the four dolphin species investigated in relation to the environmental predictors using kernel density plots to view the distribution of species. In order to differentiate species niches, we performed Multidimensional Scaling (MDS), using Euclidian distances between individual habitat characteristics. Metric Multidimensional scaling (MDS) takes a set of dissimilarities and returns a set of points such that the distances between the points are approximately equal to the dissimilarities. It displays the structure of distance-like data as a geometrical picture (Gower, 1966). In other words, the purpose of MDS is to provide a visual representation of the pattern of proximities (i.e. similarities or distances) among a set of objects. This multivariate analysis was used in order to discriminate species in their habitat preferences. Presence-absence models were not used due to heterogeneous sampling of the study area (for further details, see Clarke & Warwick 2001).

In order to complement this multivariate approach, univariate non-parametric pairwise Wilcoxon tests were used to compare species distribution for each environmental variables. Seasonal differences of habitat preferences were investigated using Mann-Whitney U-tests for each species in relation to the four environmental co-variates that were used. Two seasons were considered: rainy/summer (November – April) and dry/winter seasons (May – October). Analyses were performed using Rv2.10.0 (R Development Core Team, 2009).

Behavioural budget analyses

To analyse diel patterns of behaviour, we defined three time-blocks: morning (before 10:00 h), noon (between 10:01 h and 14:00 h) and evening (after 14:01 h). The seasons considered were identical to those used for the habitat analyses (dry/rainy season). Diurnal and seasonal patterns were investigated by assigning a behavioural sequence to a time block or a season. Contingency table analyses were used in order to compare behavioural budgets among species. Nonparametric tests were selected because assumptions regarding normality and homogeneity of variance were not met.

Stable isotope analyses

Blubber and skin were separated for each dolphin biopsy sample. Fish muscle tissues were used for stable isotope analyses. The ethanol was evaporated at 45°C over 48 h and the samples were ground and freeze-dried (Hobson et al. 1997). Lipids were removed from both blubber and skin samples by 2 successive extractions (1 h shaking in cyclohexane at room temperature and subsequent centrifugation) prior to analysis. After drying, 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 (Delta V Advantage, Thermo Scientific, Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Italy). Reference gas were calibrated against International Reference Materials (IAEA-N1, IAEA-N2 and IAEA-N3 for nitrogen; NBS-21, USGS-24 and IAEA-C6 for carbon). Results are expressed in the δ notation relative to PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively, according to the equation:

$$\delta X = \left[\frac{R_{sample}}{R_{s\tan dard}} - 1 \right] \times 1000$$

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 a laboratory standard (acetanilide) indicated that analytical 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 analyzer and used to calculate the sample C:N ratio, indicating good lipid removal efficiency when C:N <4. Differences of stable isotopes values of $\delta^{15}N$ and $\delta^{13}C$ among species were tested using non-parametric Kruskal-Wallis and Mann Whitney U-tests. Seasonal variations were investigated using Mann-Whitney U tests. Like for seasonal variations of habitat preferences, the two seasons considered were rainy (November – April) and dry seasons (May – October).

RESULTS

Field effort and data collected

From July 2004 to April 2009, data were collected during 224 boat-based surveys. A total of 355 sightings of the targeted species were collected (92% of cetacean encounters around Mayotte), *i.e.* 195 for *Stenella longirostris*, 95 for *Tursiops aduncus*, 53 for *Stenella attenuata* and 12 for *P. electra*. The spatial distribution of observation effort and initial encounters is presented in Figures 2a and b. Overall, spatial coverage of effort was heterogeneous, but covered all available habitats around the island, both inside and outside the lagoon.

We collected biopsy samples from the four focal species from December 2004 to April 2009 (*Stenella longirostris*, n=28; *Stenella attenuata*, n=22; *Tursiops aduncus*, n=28 and *Peponocephala electra*, n=20) and from another delphinid species, the Fraser's dolphin (*Lagenodelphis hosei*, n=7), during a single and unique encounter (in association with a group of melon-headed whales) in January 2005. Seasonal distribution of sighting data and biopsy samples was balanced, allowing analyses of seasonal patterns of variation of habitat and stable isotope signatures (Table 2). For fish and stable isotope analyses in muscle samples, sample size was distributed al follows: *Hemiramphus far* (n=5); *Mulloidichthys vanicolensis* (n=5); *Siganus argenteus* (n=5); *Scarus russelii* (n=5) and *Caranx melampygus* (n=2).

Focal follows were performed on 33 groups of spinner dolphins (total time spent=37.1 h: n=466 behavioural sequences), 28 groups of Indo-Pacific bottlenose dolphins (total time spent=25.5 h; n=413 behavioural sequences) and 12 groups of pantropical spotted dolphins (total time spent=16.3 h; n=193 behavioural sequences). The melon-headed whale was not included in the behavioural budget analysis as sample size was too small (4 focal follows). Focal follows were undertaken all around the island.

Habitat differentiation

Table 3 presents distribution of the four species investigated in relation to environmental predictors. Table 4 presents correlations between variables. Only two variables were significantly correlated: distance from the coast and depth ($P = 0.019$). Density plots show that habitat of the four species were not well differentiated, apart along two habitat axes: depth and distance from the coast (Figure 3). For these variables, the Indo-Pacific bottlenose dolphin occurs significantly closer to the shore and in shallower waters, whereas the three other species are not well discriminated. For the MDS, axes 1 and 2 explained 78.4% and 21.2% of the variance, respectively (Figure 4). The plot slightly discriminated the Indo-Pacific bottlenose dolphin, but segregation among the other three species appeared relatively weak. The pairwise comparison (Wilcoxon tests) of species distribution for each variable provided more significant results. For depth, the three species occurring essentially outside the lagoon (*S. longirostris*, *S. attenuata* and *P. electra*) could not be discriminated ($P > 0.05$), while the *T. aduncus* significantly differed from the three others (all $P < 0.001$). Slope did not segregate any species. The variable “distance from the coast” significantly segregated *T. aduncus* from the three other species (all $P < 0.0001$). The variable “distance from the nearest reef” was significantly discriminant among the oceanic species: *S. longirostris* with *S. attenuata* ($P = 0.002$), *S. longirostris* with *P. electra* ($P = 0.03$).

For all variables, *P. electra* and *S. attenuata* were never discriminated ($P > 0.05$). In all delphinid species, no seasonal variation of habitat preferences was observed, for any variable (all $P > 0.05$).

Behavioural budgets

As we used four types of vessel for collecting behavioural data, we tested for a potential boat effect on the data but failed to find a significant difference ($\chi^2 = 3.238$, $df = 4$; $P = 0.569$); therefore, subsequent analyses reflect a pooled data set. In Indo-Pacific bottlenose dolphins, the most frequent activities recorded were milling (32%), travelling (22%) and foraging (16%) (Figure 5). A quite similar pattern was also observed in the pantropical spotted dolphin, with travelling being the prevalent activity (32%), followed by milling (22%) and foraging (18%). In the spinner dolphin, socialising was the most commonly recorded behaviour (28%), followed by travelling (26%) and milling (22%) (Figure 5). Foraging behaviour was not observed in the spinner dolphin. Among the three species, significant differences in activity budgets were found ($\chi^2 = 177.33$; $df = 12$; $P < 0.0001$). These differences were confirmed when performing pairwise comparisons: *T. aduncus* vs. *S. longirostris* ($\chi^2 = 137.50$; $df = 6$; $P < 0.0001$), *T. aduncus* vs. *S. attenuata* ($\chi^2 = 53.42$; $df = 6$; $P < 0.001$) and *S. longirostris* vs. *S. attenuata* ($\chi^2 = 109.18$; $df = 6$; $P < 0.0001$).

Temporal variation of activity budgets

For all species, no significant variations of activity patterns were observed among seasons ($H = 3.816$; $df = 3$; $P = 0.439$). Contrastingly, behaviour patterns varied significantly according to time of day for Indo-Pacific bottlenose dolphin ($\chi^2 = 48$; $df = 5$; $P < 0.001$), spinner dolphin ($\chi^2 = 13$; $df = 5$; $P = 0.002$) and pantropical spotted dolphin ($\chi^2 = 11$; $df = 5$; $P = 0.009$) (Figure 6, a to c). In Indo-Pacific bottlenose dolphins, foraging activities were prevalent during the morning and decreased throughout the day, whereas socializing was more frequent in the afternoon. In spinner dolphins, travelling activities increased along the day and social activities were more observed in the morning and the afternoon, whereas resting behaviour was more predominant around noon time. Finally, in pantropical spotted dolphins, feeding behaviour prevailed during the afternoon, along with travelling.

Activity budgets did not vary with water depth in Indo-Pacific bottlenose dolphin ($H = 2.060$; *df* = 4; $P = 0.725$), spinner dolphin ($H = 5.621$; *df* = 4; $P = 0.229$) and pantropical spotted dolphin ($H = 8.049$; *df* = 4; $P = 0.09$). However, activity budget varied with distance from the coast for Indo-Pacific bottlenose dolphin ($H = 9.542$; *df* = 4; $P = 0.04$; especially increasing foraging activity closer to shore), although not for either spinner ($H = 3.251$; *df* = 4; $P = 0.517$) or pantropical spotted dolphins ($H = 4.201$; *df* = 4; $P = 0.379$). Feeding activities of the Indo-Pacific bottlenose dolphin increased with decreasing distance from coast.

Stable isotope analyses

Stable isotope values of delphinids and fish were significantly different, as shown in figure 7. The most apparent pattern was the higher trophic level of delphinids, reflected by higher δ^{15}N values. In addition, δ^{13}C values in delphinids were lower than in fish.

In delphinids, stable isotope values were lower in blubber than in skin. However, the pattern of differences observed between species was similar in both tissues (Figure 8 and 9). The Fraser's dolphin shows a high marginality in comparison to the other species, with significantly higher δ^{15}N values in the blubber (Figure 8). However, for skin values, overlap was observed with the melon-headed (Table 5). Overall, among species, significant differences in the skin existed for δ^{15}N ($H = 33.6$; *df* = 2; $P < 0.0001$) and δ^{13}C ($H = 53.6$; *df* = 1; $P < 0.0001$). For blubber, significant differences were also found for δ^{15}N ($H = 49.7$; *df* = 1; $P < 0.0001$) and δ^{13}C ($H = 63$;

df = 1; $P < 0.0001$). A similar statistical difference among species for blubber tissue was found, even when excluding the Fraser's dolphin, very different to the four other species (H = 34; *df* = 2; $P < 0.0001$ for δ^{15}N and H = 60; *df* = 2; $P < 0.0001$ for δ^{13}C). The Indo-Pacific bottlenose dolphin had the greatest δ^{13}C values, while the lowest values were observed in the Fraser's dolphin and in the two species of the genus *Stenella*. The melon-headed whale had intermediate values of δ^{13}C, both for skin and blubber (Figures 8 and 9). When looking at pairwise comparisons of δ^{15}N and δ^{13}C values in blubber and skin tissues, however, some degrees of overlap can be observed (Table 5). From skin samples, δ^{15}N values were significantly different between species pairs, except between *S. attenuata* and *T. aduncus* and between *L. hosei* and *P. electra* (U-tests; $P > 0.05$). For δ^{13}C values, overlap was evident between *L. hosei* and the two species of the genus *Stenella*. Finally, for blubber tissue, δ^{15}N values were significantly different between species pairs, except between *S. attenuata* and *P. electra* and between *S. attenuata* and *T. aduncus*. δ^{13}C values showed the highest degrees of overlap, particularly between *S. longirostris* and *S. attenuata*, between *S. attenuata* and *L. hosei*, as well as between *L. hosei* and *P. electra* (U-tests; $P > 0.05$; Table 5). Stable isotope values from fish samples were useful in order to provide a context to interpret values in delphinids. Among fish, significant differences were observed for δ^{13}C (H = 11.2; *df* = 4; $P = 0.02$) and δ^{15}N (H = 11.6; *df* = 4; $P = 0.01$). *Siganus argenteus* and *Scarus russelii* (herbivores) had the lowest trophic position (δ^{15}N), while *Caranx melampygus*, the most predatory species, had the highest trophic level (δ^{15}N). Their foraging habitats were also well discriminated, with *Mulloidichthys vanicolensis* having the highest δ^{13}C values and *Caranx melampygus* with *Hemiramphus far* the lowest (Figure 7). These latter were about 0.5-1.5 ‰ δ^{13}C and 3-4 ‰ δ^{15}N lower than *T. aduncus*.

Seasonal variations of stable isotope signatures were observed in all species for skin and blubber tissues (Table 6). In the two species of the genus *Stenella* and the melon-headed whale, δ^{13}C values were more negative during the rain season. A reverse situation was observed in *T. aduncus* during the rain season; $\delta^{15}N$ values were decreasing for *Stenella* dolphins and *P. electra*, while increased in *T. aduncus*. However, while (sometimes) statistically significant in some cases, seasonal variations appear to be relatively limited.

DISCUSSION

General

This work represents a detailed study on habitat and resource segregation among tropical dolphins around Mayotte, in the southwest Indian Ocean. It integrates several methods implemented over four years, with varying temporal resolutions: from instantaneous sighting data and behavioural observations collected during daylight hours to stable isotope analyses in skin that represents the foraging niche over days or in the blubber which integrates stable isotope signatures over months (Abend & Smith 1995). The indicators were selected for their ability to document the main dimensions of the ecological niche along which segregation might occur: physiographic characteristics describe the spatial dimension of the ecological niche, carbon isotopic signature focuses on the coastal-offshore gradient of the foraging niche, nitrogen isotopic signature expresses the resource dimension of the niche, and the daily activity budget deals with temporal dimension.

Overall, the main finding of this work is that none of the indicators of trophic niche dimensions, examined solely, reveals complete ecological segregation amongst the four species studied, but the combination of all indicators do (Table 7). Hence, physiographic characteristics of habitats used by the dolphins during daylight, when visual observations were possible, only allow the

Indo-pacific bottlenose dolphin to be differentiated from the others. Carbon isotope signatures allow the melon-headed whale to be separated from the *Stenella* dolphins. Finally nitrogen isotopic signature and activity budget identify differences between spinner and pantropical spotted dolphins.

Identifying the limitations of the study is necessary for delineating its validity range. Most daily field trips were undertaken from Mayotte main harbour located on the east coast of the island and were limited to daylight hours. Hence, effort was concentrated in the lagoon and the vicinity of outer slope of barrier reef, within the 1000 m isobath, and nocturnal distribution and activity could not be documented. The resource dimension of the niche was documented in a very integrated way, as C and N isotopic contents of a predator express foraging habitat and trophic level but not diet *per se*, which is only documented by sporadic direct observations when no biological material is available. Also, in stable isotopes analyses, as in most studies relying on the use of ecological tracers transmitted via food (e.g. fatty acids, contaminants, heavy metals), only differences in stable isotope contents are really informative, whereas similarities may result from a variety of prey combinations. Finally, behavioural budget data is limited by our capacity to infer dolphin underwater activity from surface events. In particular, foraging, which is the key activity to consider when investigating segregation mechanisms, can either be associated to no or barely visible surface events or to explicit and often highly dynamic ones. Nonetheless, in a multifaceted approach as the one followed here, the limitations of each indicator tend to be compensated by the others. For instance, stable isotope analyses reveal foraging habitat and trophic level of prey eaten day and night over the past few days or months, which is extremely useful to disentangle the inherent ambiguities of observations limited to daylight hours. Conversely, behavioural data can help identify differences in foraging strategies that cannot be found in stable isotope analyses.

The ecological significance of these indicators will now be interpreted sequentially from those related to the spatial, the resource and finally the temporal dimensions of the ecological niche.

Spatial segregation inferred from direct observations and $\delta^{13}C$ signatures

This study confirms that *T. aduncus* is associated with coastal, shallow water and reef habitats. Its ecological niche clearly differs spatially from the other species of the community. Coastal foraging habitats are confirmed by high $\delta^{13}C$ value indicating a benthic carbon source that is primarily available in coastal environments (France 1995, Hobson 1999). Preference for coastal habitat is reported throughout species range, a preference shared with the Indo-pacific humpback dolphin, *Sousa chinensis*, which is present in very low numbers around Mayotte, but could not be considered in this work.

S. longirostris and *S. attenuata* co-occur in waters along the outer slope of the barrier reef around Mayotte. They overlap extensively, but the latter tends to occur in deeper waters, located further offshore. Low $\delta^{13}C$ values found in both species, with extensive overlap, are in line with foraging habitats located outside the lagoon at epipelagic depths; this interpretation is reinforced by the overlap also found between the two *Stenella* and the Fraser's dolphin, a typically oceanic dolphin. The pattern observed around Mayotte has also been reported from other insular populations, such as off La Réunion where spotted dolphins occur in deeper, more offshore waters than spinners do (Dulau-Drouot et al. 2008). These two species are not restricted to peri-insular waters; instead populations of the two species also dwell in the open ocean (Wade & Gerrodette 1992, Ballance & Pitman 1998). In this situation, extensive overlap in preferred habitat is also observed, as reported from the western South Atlantic and the eastern tropical Pacific (Polachek 1987, Moreno et al. 2005).

For melon-headed whale, a fairly limited number of sightings were collected, allowing only a partial description of its habitat preferences. Nevertheless, habitat physiographic characteristics of *P. electra* as documented in this work were significantly different from *S. longirostris*, but could not be differentiated from *S. attenuata*. The melon-headed whale has a more oceanic distribution than the other species (Brownell et al. 2009) and it is unknown whether the groups seen around Mayotte are mostly oceanic dwellers that occasionally visit peri-insular waters or if they display some group-specific preference for the peri-insular slope, a habitat that they could exploit around all islands, reefs and seamounts from off the northern end of Madagascar to Grande Comore (western Comoros archipelago). Quite interestingly, δ^{13}C values measured in the melon-headed whale are intermediate between the epi- to mesopelagic *Stenella* and Fraser's dolphins and the coastal dwelling Indo-pacific bottlenose dolphin, rather than being identical to the *Stenella* carbon isotopic content as could be expected from the similarity found in physiographic characteristics. This would suggest spatial segregation along a vertical axis, with melon-headed whales foraging deeper and hence closer to detritic carbon sources than *Stenella* spp. do.

Resource partitioning inferred from δ^{15}N signatures

Nitrogen isotopic signatures are the main source of information on resource utilization by dolphins in Mayotte. Direct evidences of resource use are limited to some anecdotal observations of prey hunting or capture by *T. aduncus* and *S. attenuata* (Kiszka & Pusineri, unpublished observations). Carbon isotopic signatures of fish collected in the lagoon also convey some contextual information on plausible prey for the more coastal dolphins. Finally, when comparing trophic levels inferred from δ^{15}N signatures one should only consider in the comparison dolphin species with overlapping $\delta^{13}C$ signatures, i.e. living in the same habitat, because reference levels of $\delta^{15}N$ in oceanic vs. lagoon habitats are unknown.

Indo-pacific bottlenose dolphins isotopic content can be compared to the isotopic values of putative prey fish collected in the lagoon. The herbivorous fish *Siganus argenteus* and *Scarus russelii* have $\delta^{13}C$ values 2-4 ‰ higher than *T. aduncus*, and would therefore unlikely be important components of its diet. In contrast, blue trevally *Caranx melampygus* and blackbarred halfbeak *Hemiramphus far* display carbon and nitrogen signatures about 0.5-1.5 ‰ and 3-4 ‰ lower respectively than *T. aduncus*; such differences fit well with an enrichment of one trophic level. Therefore, these two predatory fish would be plausible major prey for *T. aduncus*. Anecdotal direct observations in Mayotte are in line with this interpretation even if other fishes, like the mullet *Mulloidichthys vanicolensis*, were also observed being preyed upon (Kiszka & Pusineri, unpublished observations). Our result is also consistent with existing information on the diet of the Indo-Pacific bottlenose dolphin in the region (Zanzibar, Tanzania), suggesting this species forages on a large number of prey species, especially reef fish (Amir et al. 2005). Elsewhere, *T. aduncus* is known to feed on fish species that do not aggregate in large schools (Mann et al. 2000).

The two *Stenella* have largely overlapping ranges of both physiographic habitats and carbon isotopic contents, even if *S. attenuata* is seen slightly further offshore and is nonetheless slightly carbon-enriched (higher $\delta^{13}C$ ratios). According to $\delta^{15}N$ values, pantropical *S. attenuata* are on average 1.5‰ higher than spinner dolphins, *i.e.* half a trophic level, which would express some degree of niche segregation between the two species. In addition to this, *S. attenuata* seems to have a wider niche breadth than *S. longirostris.* Pantropical spotted dolphins have been frequently observed feeding close to the barrier reef where their prey aggregate (fishes of the genus Exocoetidae; Kiszka & Pusineri, unpublished observations), in agreement with their slightly higher $\delta^{13}C$ signature. Fine-scale processes allowing niche differentiation between the two *Stenella* species have also been found in other regions, such as in the eastern tropical Pacific (Perrin et al. 1973). Spinner dolphins there are reported to feed at night upon scattering–layer organisms, *i.e.* on vertically migrating mesopelagic fishes, cephalopods and crustaceans, caught in the upper 200 m and occasionally as deep as 400 m (Perrin et al. 1973, Norris et al. 1994, Dolar et al. 2003). Conversely, pantropical spotted dolphins would feed day and night on epipelagic fishes and cephalopods (Perrin et al. 1973).

Melon-headed whales were observed in much the same habitats as pantropical spotted dolphins, but comparatively higher $\delta^{13}C$ values suggested vertical segregation could occur. Nitrogen isotopic content further suggests a slightly higher trophic level (about 1/3 trophic level). Earlier works report mesopelagic fishes and cephalopods, supposedly preyed upon in the upper 700 meters, as the main component of its diet (Young 1978, Brownell et al. 2009). An element of comparison is provided by the Fraser's dolphin, which was added to the study in an attempt to provide isotopic reference for a true oceanic predator; in addition to this, the species is frequently observed forming mixed group with melon-headed whale (Jefferson & Barros 1997, Kiszka et al. 2007, Dulau-Drouot et al. 2008). Not surprisingly, Fraser's dolphins displayed the second lowest $\delta^{13}C$ values, in agreement with their oceanic lifestyle, and the highest $\delta^{15}N$ values, that fit well with the higher trophic level, likely associated with its preference for larger prey already reported elsewhere (Dolar et al. 2003). Studies of stomach contents from the Pacific suggest this species feeds on relatively large mesopelagic fish and cephalopods from near the surface to probably as deep as 600 meters (Robison & Craddock 1983, Dolar et al. 2003). In Mayotte, Fraser's dolphins and melon-headed whales, although generally seen associated, do not overlap in their isotopic niches, the latter being more $\delta^{13}C$ enriched than the former, which could be interpreted as feeding a deeper food source, possibly associated to peri-insular slopes, whereas the Fraser's dolphin would rely on large epi- to-mesopelagic truly oceanic prey. These two species might associate for other reasons than foraging, such as social advantage or vigilance against predators.

Temporal segregation inferred from seasonal patterns and activity budgets

Our study did not reveal seasonal variations of occurrence or habitat preferences as based on the analyses of visual observations; this could be linked to the absence of seasonal variability in tropical environments. On the other hand, stable isotope values displayed significant differences between dry and rain seasons in all species. Oceanic species, i.e. spinner, pantropical spotted dolphins and melon-headed whales, showed similar levels of variation. Conversely, the Indo-Pacific bottlenose dolphin differed. This species only foraged in the lagoon, and, during the rainy season, $\delta^{13}C$ values were enriched, which could be linked to increasing hydrodynamic activity and remobilisation of benthic sources of carbon in the lagoon. It is therefore suggested that all species have the same habitat use year-round, but isotopic content can vary seasonally as a result of hydro-climatic processes.

At a finer time scale, segregation mechanisms could rely on differential daily activity budgets between species; this aspect was investigated in the bottlenose and the two *Stenella* dolphins, but not in the melon-headed whale. Foraging activities of *Tursiops aduncus* were observed throughout the day, but more frequently in the morning, closer to shore. A similar pattern was observed in common bottlenose dolphins (*Tursiops truncatus*) in Florida (Shane 1990). Pantropical spotted dolphins feed during daylight, with an increase in feeding activity along the day. Nocturnal feeding is not excluded for these two species but could not be accessed directly. Spinner dolphins would only feed at night as foraging was never observed during daylight hours. Behavioural ecology of spinner and pantropical spotted dolphins around Mayotte is similar than in other areas, including around Hawaii and in the oceanic eastern tropical Pacific (Perrin et al.

1973, Norris et al. 1994). Our results underline a clear pattern of niche segregation along the time dimension, at least during the day.

Final comments

Three main dimensions define the ecological niche of a species: habitat, diet and time. Our study integrated these three axes to investigate ecological niche segregation among the delphinid community found around Mayotte. Habitat has been assessed through the investigation of the relationships between delphinid distribution and environmental variables (particularly physiography). Trophic level and foraging habitat have been assessed indirectly, through the use of stable isotopes of N and C respectively (De Niro & Epstein 1978, Kelly 2000). Finally, the temporal component of the ecological niche has been integrated through the study of behavioural budgets, especially their diurnal variations that may potentially segregate species' ecological niche. The use of multiple approaches (habitat, behaviour and feeding ecology studies) was most useful to investigate ecological niche segregation, especially when looking at closely related species within a common restricted range. We hypothesize a conceptual scheme of resource partitioning inferred from these measurements:

1 – The Indo-pacific bottlenose dolphin is mostly confined to the inner lagoon or at least in shallow reef-associated habitats. They feed diurnally (possibly nocturnally as well, although this could not be documented), with daily routines that would follow variation in prey catchability during the day, e.g. mullet being often caught close to the coast in the morning, and *Caranx melampygus* and *Hemiramphus far* the rest of the day across the lagoon;

2 – The spinner dolphin lives in outer reef habitats and forage only nocturnally on small mesopelagic prey;

3 – The pantropical spotted dolphins also lives in outer reef habitats, that largely overlap with the spinner dolphins but feed at least partly diurnally and at dawn on epipelagic prey, that include flying fish caught closer to the barrier reef;

4 – The melon-headed whale is seen in the same habitat as pantropical spotted dolphins, but forages deeper over the peri-insular slope.

This ecological segregation is more significant than in other communities, such as in some epipelagic seabirds (Ridoux 1994, Cherel et al. 2008). Conversely, in diving predators such as large pelagic fish and dolphins, ecological niche segregation is clearly distinguishable (Potier et al. 2004, Ménard et al. 2007, Praca & Gannier 2008). This could be related to the low spatial structure of marine ecosystems in tropical and oligotrophic areas. Conversely, clear isotopic and resource-related gradients can be found in subpolar and polar environments over large spatial scale (Jaeger 2009) as well as vertically (including in the tropics), at a small spatial scale in the water column (this study). This vertical gradient is accessible to fish and dolphins, and not in epipelagic seabirds.

Improvement in our understanding of resource partitioning mechanisms among Mayotte delphinids may be obtained in several directions: - investigating acoustically dolphins' nocturnal distribution and activity; - documenting the regional isoscape by analyzing carbon and nitrogen isotopic composition in phytoplankton collected along a coastal-offshore gradient and along a vertical gradient as well; - investigating residency patterns of dolphin groups living around Mayotte by using photo-identification or individual telemetry approaches, in order to establish whether they are genuinely associated to these peri-insular structures, or have a more oceanic lifestyle, occasionally approaching islands.

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REFERENCES

Abend AG, Smith TD (1995) Differences in ratios of stable isotopes of nitrogen in long-finned pilot whales (*Globicephala melas*) in the western and eastern North Atlantic. ICES J Mar Sci 52:837-841

Amir OA, Berggren P, Ndaro SGM, Jiddawi NS (2005) Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania. Estuarine Coastal and Shelf Science 63:429-437

Audru J-C, Guennoc P, Thinon I, Abellard O (2006) Bathymay : la structure sous-marine de Mayotte révélée par l'imagerie multifaisceaux. Geoscience 338:1240-1249

Ballance LT, Pitman RL (1998) Cetaceans of the western tropical Indian Ocean: distribution, relative abundance and comparison with cetacean communities of two other tropical ecosystems. Mar Mamm Sci 14:429-459

Bearzi M (2005) Dolphin sympatric ecology. Mar Biol Res 1:165-175

Begon M, Harper JL, Townsend CR (1986) Ecology – Individuals, Populations and Communities. Blackwell Scientific Publications, Boston, 876 pp.

Brownell RL, Ralls K, Baumann-Pickering S., Poole MM (2009) Behavior of melon-headed whales, *Peponocephala electra*, near oceanic islands. Mar Mamm Sci 25:639-658

Chapman JL, Reiss MJ (1999) Ecology – Principles and Applications. Cambridge University Press, Cambridge, 336 pp.

Cherel Y, Le Corre M, Jaquemet S, Ménard F, Richard P, Weimerskirch H (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. Mar Ecol Prog Ser 366:281-291

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition, Primer-E, Plymouth, UK.

Das K, Lepoint G, Leroy Y, Bouquegneau JM (2003) Marine mammals from the southern North Sea: feeding ecology data from δ13C and δ15N measurements. Mar Ecol Prog Ser 263:287-298

Degrati M, Dans SL, Pedraza SN, Crespo EA, Garaffo G (2008) Diurnal behaviour of dusky dolphins, *Lagenorhynchus obscurus*, in Golfo Nuevo, Argentina. J Mammal 89:1241-1247

De Niro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochimica Cosmochimica Acta 42:495-506

Dolar MLL, Walker WA, Kooyman GL, Perrin WF (2003) Comparative feeding ecology of spinner dolphins (*Stenella longirostris*) and Fraser’s dolphins (*Lagenodelphis hosei*) in the Sulu Sea. Mar Mamm Sci 19:1-19

Domi N, Bouquegneau JM, Das K (2005) Feeding ecology of five commercial shark species of the Celtic Sea through stable isotope and trace metal analysis. Mar Environ Res 60:551-569

Dulau-Drouot V, Boucaud, V, Rota B (2008) Cetacean diversity off La Réunion Island (France). J M Biol Ass UK 88:1263-1272

Estrada JA, Rice AN, Lutcavage ME, Skomal GB (2003) Predicting trophic position of sharks in the north-west Atlantic Ocean using stable isotope analysis. J M Biol Ass UK 83:1347-1350

France R (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar Ecol Prog Ser 124:307-312

Froese R, Pauly D, Eds (2010) FishBase. World Wide electronic Publication. www.fishbase.org, version (05/2010).

Gower JC (1966) Some distance properties of latent root and vector methods used in multivariate analysis. Biometrika 53:325-328

Gloutney ML, Hobson KA (1998) Field preservation techniques for the analysis of stable-carbon and nitrogen isotopes in eggs. J Field Ornitho 69:223-237

Grinnell J (1924) Geography and evolution. Ecology 5:225-229

Gross A, Kiszka J, Van Canneyt O, Richard P, Ridoux V (2009) A preliminary study of habitat and resource partitioning among co-occurring tropical dolphins around Mayotte, southwest Indian Ocean. Estuar Coast Shelf Sci 84:367-374

Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120:314-326

Hobson KA, Gibbs HL, Gloutney ML (1997) Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. Can J Zool 75:1720-1723

Jaeger A (2009) Etude isotopique des variations saisonnières et à long terme de l'écologie alimentaire des oiseaux marins de l'océan austral. PhD Dissertation, University of Paris VI.

Jefferson TA, Barros NB (1997) *Peponocephala electra*. Mammalian Species 153:1-6

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78:1-27

Kiljunen M, Grey J, Sinisalo T, Harrod C, Immonen H, Jones RI (2006) A revised model for lipid-normalising δ^{13}C values from aquatic organisms, with implications for isotope mixing models. J Appl Ecol 43:1213-1222

Kiszka J, Ersts PJ, Ridoux V (2007) Cetacean diversity around the Mozambique Channel island of Mayotte (Comoros Archipelago). J Cet Res Manage 9:105-109

Kiszka J, Oremus M, Richard P, Poole M, Ridoux V (2010) The use of stable isotope analyses from skin biopsy sampled to assess trophic relationships of sympatric delphinids off Moorea (French Polynesia). J Exp Mar Biol Ecol 395:48-54

MacArthur RH (1958) Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599-619

Macleod CD, Hauser N, Peckham H (2004) Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas. J M Biol Ass UK 84:469-474

Mallela J, Harrod C (2008) $\delta^{13}C$ and $\delta\ ^{15}N$ reveal significant differences in the coastal food webs of the seas surrounding Trinidad and Tobago. Mar Ecol Progr Ser 368:41-51

Mann J (1999) Behavioral sampling methods for cetaceans: a review and critique. Mar Mamm Sci 15:102-122

Mann J, Connor RC, Tyack PL, Whitehead H (2000) Cetacean Societies – Field Studies of Dolphins and Whales. University of Chicago Press, Chicago, 433 pp.

Ménard F, Lorrain A, Potier M, Marsac F (2007) Isotopic evidence of distinct feeding ecologies and movement patterns in two migratory predators (yellowfin tuna and swordfish) in the western Indian Ocean. Mar Biol 153:141-152

Moreno IB, Zerbini AN, Danilewicz D, De Oliveira Santos MC, Simoes-Lopes PC, Lailson-Brito Jr. J., Azevedo AF (2005) Distribution and habitat characteristics of dolphins of the genus *Stenella* (Cetacea: Delphinidae) in the southwest Atlantic Ocean. Mar Ecol Progr Ser 300:229-240

Neumann DR, Orams MB (2006) Impacts of ecotourism on short-beaked common dolphins (*Delphinus delphis*) in Mercury Bay, New Zealand. Aquatic Mammals 32:1-9

Norris KS, Dohl TP (1979) Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fish Bull 77:821-849

Norris KS, Würsig B, Wells RS, Würsig M (1994) The Hawaiian Spinner Dolphin, University of California Press, Berkeley, 408 pp.

Papastamatiou YP, Wetherbee BM, Lowe CG, Crow GL (2006) Distribution and diet of four species of carcharhinid shark in the Hawaiian Islands: evidence for resource partitioning and competitive exclusion. Mar Ecol Progr Ser 320:239-251

Perrin WF, Warner RR, Fiscus CH, Holtz DB (1973) Stomach content of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fish Bull 71:1077-1092

Pianka ER (1974) Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences USA 71:2141-2145

Polachek T (1987) Relative abundance, distribution and inter-specific relationship of cetacean shools in the eastern tropical Pacific. Mar Mamm Sci 3:54-77

Potier M, Marsac F, Lucas V, Sabatié R, Hallier J-P, Ménard F (2004) Feeding partitioning among tuna taken in surface and mid-water layers: the case of yellow fin (*Thunnus albacares*) and bigeye (*T. obesus*) in the western tropical Indian Ocean. Western Indian Ocean Journal of Marine Science 3:51-62

Praca E, Gannier A (2008) Ecological niches of three teuthophageous odontocetes in the northwestern Mediterranean Sea. Ocean Science 4:49-59

Psarakos S, Herzing DL, Marten K (2003) Mixed-species associations between Pantropical spotted dolphins (*Stenella attenuata*) and Hawaiian spinner dolphins (*Stenella longirostris*) off Oahu, Hawaii. Aquatic Mammals 29:390–395

Pusineri C, Chancollon O, Ringelstein J, Ridoux V (2008) Feeding niche segregation among the northeast Atlantic community of oceanic top predators. Mar Ecol Progr Ser 361:21-34

Pusineri C, Kiszka J, Barbraud J-C, Ridoux V (2009) Abundance of marine mammals around the island of Mayotte. Report of ONCFS (French Wildlife Service) to Collectivité Départementale de Mayotte.

Quod JP, Naim O, Abdourazi F (2000) The Comoros archipelago. In: Sheppard, C. (Editors), Seas at the Millennium: An Environmental Evaluation. Pergamon Press, Oxford, pp 243-52.

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical # Computing, Vienna, Austria ISBN 3-900051-07-0

Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar Ornithol 22:1-192

Robison B, Craddock JE (1983) Mesopelagic fishes eaten by Fraser's dolphin, *Lagenodelphis hosei*. Fish Bull 81:283-289

Roughgarden J (1976) Resource partitioning among competing species: a coevolutionary approach. Theor Pop Biol 9:388-424

Shane SH (1990) Behaviour and ecology of the bottlenose dolphin at Sanibel Island, Florida. In: S. Leatherwood & R.R. Reeves (Eds.). The Bottlenose dolphin. Academic Press: San Diego (CA): 245-265

Syväranta J, Vesala S, Rask M, Ruuhijärvi J, Jones RI (2008) Evaluating the utility of stable isotope analyses in archived freshwater sample materials. Hydrobiologia 600:121-130

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for δ^{13}C analysis of diet. Oecologia 57:32-37

Wade PR, Gerrodette T (1992) Estimates of dolphin abundance in the eastern tropical Pacific: preliminary analysis of five years of data. Report of the International Whaling Commission 42:533-539

Whitehead H (2004) The group strikes back: follow protocols for behavioral research on cetaceans. Mar Mamm Sci 20:664-670

Whitehead H, MacLeod CD, Rodhouse P (2003) Differences in niche breadth among some teuthivorous mesopelagic marine mammals. Mar Mamm Sci 19:400-406

Wickel J, Jamon A (2009) Inventaire taxonomique actualisé des poissons marins de Mayotte et des bancs récifaux de Geyser-Zélée, Canal du Mozambique. Liste révisée des espèces et élaboration d'une base de données fonctionnelle. Rapport d'études LAGONIA / APNEE Mayotte pour le compte du Service Environnement et Forêt de la DAF de Mayotte.

Young RE (1978) Vertical distribution and photosensitive vesicles of pelagic cephalopods from Hawaiian waters. Fish Bull 76:583-615

Zhao L, Castellini MA, Mau TL, Trumble SJ (2004) Trophic interactions of Antarctic seals as determined by stable isotope signatures. Polar Biol 27:368-373

Tables

Table 1: Methodology used to explore the three main dimensions of the ecological niche in the present study.

	Niche dimensions		
Variables tested	***Habitats***	***Resources***	***Time***
Distribution and associated habitat characteristics	Habitat defined on physiographic aspects (and seasonal variation)		
Activity budget			Daily activity rhythm (and seasonal variation)
N isotopic signature		Trophic level (and seasonal variation)	
C isotopic signature	Habitat along a coastal-oceanic gradient (and seasonal variation)		

Table 2: Seasonal distribution (winter/dry season: May to October; summer/rain season: November to April) of sighting data and biopsy samples collected from December 2004 to April 2009.

	SIGHTINGS		**BIOPSIES**	
Species	Winter	Summer	Winter	Summer
Tursiops aduncus	48	43	12	16
Stenella longirostris	101	67	12	13
Stenella attenuata	13	23	12	10
Peponocephala electra	5	6	10	10
Lagenodelphis hosei	0	1	0	7

Table 3: Distribution of the delphinids in relation to physiographic variables.

	Mean	Median	SD	Q1-Q3
Depth (meters)				
Tursiops aduncus	47.9	32	70.2	19.7 – 45.1
Stenella longirostris	220.7	230.5	175.9	71.7 – 285.7
Stenella attenuata	301.4	276.4	277.2	44.9 – 370.4
Peponocephala electra	486.5	462.2	244.1	274.9 – 666.2
Slope (degree)				
Tursiops aduncus	2.1	0	6.7	0 – 0.8
Stenella longirostris	9.5	0	17.9	0 – 7.9
Stenella attenuata	9.7	0	19.7	0 – 2.9
Peponocephala electra	13.6	0	20.4	0 – 39.8
Distance coast (meters)				
Tursiops aduncus	2001.8	996.2	2169.8	487.6 – 2778.5
Stenella longirostris	5258.8	5068.3	2763.5	3216.6 – 7191.7
Stenella attenuata	6295.3	5771.8	3331.2	3921.7 – 8602.8
Peponocephala electra	6665.6	7086.4	2130.7	5369.9 – 8520.4
Distance reef (meters)				
Tursiops aduncus	1363	509.2	2071.8	268.7 – 1474.1
Stenella longirostris	1059.7	700.4	1144.8	478 – 1320.6
Stenella attenuata	2011.8	1210	1999.5	722 – 2701.9
Peponocephala electra	2452.1	1363.3	3014.8	927.6 – 2563.8

Table 4: Correlation between variables (Pearson's correlation values above the diagonal and associated *P* values below the diagonal).

	Distance coast	Distance reef	Slope	Depth
Distance coast	-	0.27	-0.13	0.01
Distance reef	< 0.001	-	0.13	0.34
Slope	0.020	0.028	-	0.24
Depth	< 0.001	0.731	< 0.001	-

Table 5: Pairwise Mann-Whitney U test p values for each pairs of delphinid species in carbon and nitrogen in skin and blubber.

SKIN				
Nitrogen	*Lagenodelphis hosei*	*Peponocephala electra*	*Stenella attenuata*	*Stenella longirostris*
Tursiops aduncus	0.01	0.001	0.125	< 0.001
Stenella longirostris	< 0.001	< 0.001	< 0.001	
Stenella attenuata	0.01	0.009		
Peponocephala electra	0.232			
Carbon				
Tursiops aduncus	< 0.001	< 0.001	< 0.001	< 0.001
Stenella longirostris	0.339	< 0.001	0.02	
Stenella attenuata	0.157	0.008		
Peponocephala electra	0.008			
BLUBBER				
Nitrogen				
Tursiops aduncus	< 0.001	0.022	0.08	< 0.001
Stenella longirostris	< 0.001	< 0.001	< 0.001	
Stenella attenuata	< 0.001	0.485		
Peponocephala electra	< 0.001			
Carbon				
Tursiops aduncus	< 0.001	< 0.001	0.001	0.001
Stenella longirostris	0.02	< 0.001	0.182	
Stenella attenuata	0.242	< 0.001		
Peponocephala electra	0.112			

Table 6: Pairwise Mann-Whitney U test P values for seasonal differences of stable isotope signatures for each species and type of tissue.

SPECIES/SEASON	BLUBBER	SKIN
Tursiops aduncus		
Dry season	P < 0.001	P < 0.001
Rainy season	P > 0.05	P > 0.05
Peponocephala electra		
Dry season	P > 0.05	P > 0.05
Rainy season	P > 0.05	P < 0.01
Stenella attenuata		
Dry season	P > 0.05	P > 0.05
Rainy season	P < 0.05	P < 0.001
Stenella longirostris		
Dry season	P > 0.05	P < 0.05
Rainy season	P > 0.05	P > 0.05

Table 7: Summary of results obtained for the four indicators of ecological niche dimensions among the Mayotte delphinid community. Different letters denote species that segregate for the indicator being considered.

<table>
<tr><th>Indicators of niche dimensions</th><th><i>Tursiops aduncus</i></th><th><i>Stenella attenuata</i></th><th><i>Stenella longirostris</i></th><th><i>Peponocephala electra</i></th></tr>
<tr><td>Physiographic characteristics</td><td>A</td><td colspan="3">B</td></tr>
<tr><td>Carbon isotopic values</td><td>A</td><td colspan="2">B</td><td>C</td></tr>
<tr><td>Nitrogen isotopic values</td><td colspan="2">A</td><td>B</td><td>C</td></tr>
<tr><td>Daily activity rhythm</td><td>A</td><td>B</td><td>C</td><td>Not investigated</td></tr>
</table>

Figure captions

Fig. 1: Location of the study area.

Fig. 2: Spatial distribution of effort (per 1 km cell) and distribution of dolphin sightings around Mayotte from July 2004 to April 2009.Fig. 3: Density plots of sightings of dolphins around Mayotte in relation to physiographical variables: depth (meters), slope (degree), distance from the coast (meters) and distance from the nearest reefs (meters). Pe: *Peponocephala electra*; Ta: *Tursiops aduncus*; Sl: *Stenella longirostris*; Sa: *Stenella attenuata.*

Fig. 4: Metric Multi-Dimensional Scaling plot of delphinid habitat in relation to physiographical variables. Pe: *Peponocephala electra*; Ta: *Tursiops aduncus*; Sl: *Stenella longirostris*; Sa: *Stenella attenuata.*

Fig. 5: Overall activity budgets for Indo-Pacific bottlenose dolphins, pantropical spotted dolphins and spinner dolphins around Mayotte from 2004 to 2009.

Fig. 6: Within day variations of behavioural budget in spinner dolphin (a), Indo-Pacific bottlenose dolphin (b) and pantropical spotted dolphin (c) around Mayotte from 2004 to 2009.

Fig. 7: Mean (with Standard Errors in bold line and Standard Deviation in thin line) stable isotope values in dolphin skin and fish muscle ($\delta^{13}C$ and $\delta^{15}N$ in ‰).

Fig. 8: Mean (with Standard Errors in bold line and Standard Deviation in thin line) stable isotope values in lipid-treated dolphin blubber.

Fig. 9: Mean (with Standard Errors in bold line and Standard Deviation in thin line) stable isotope values in lipid-treated dolphin skin.

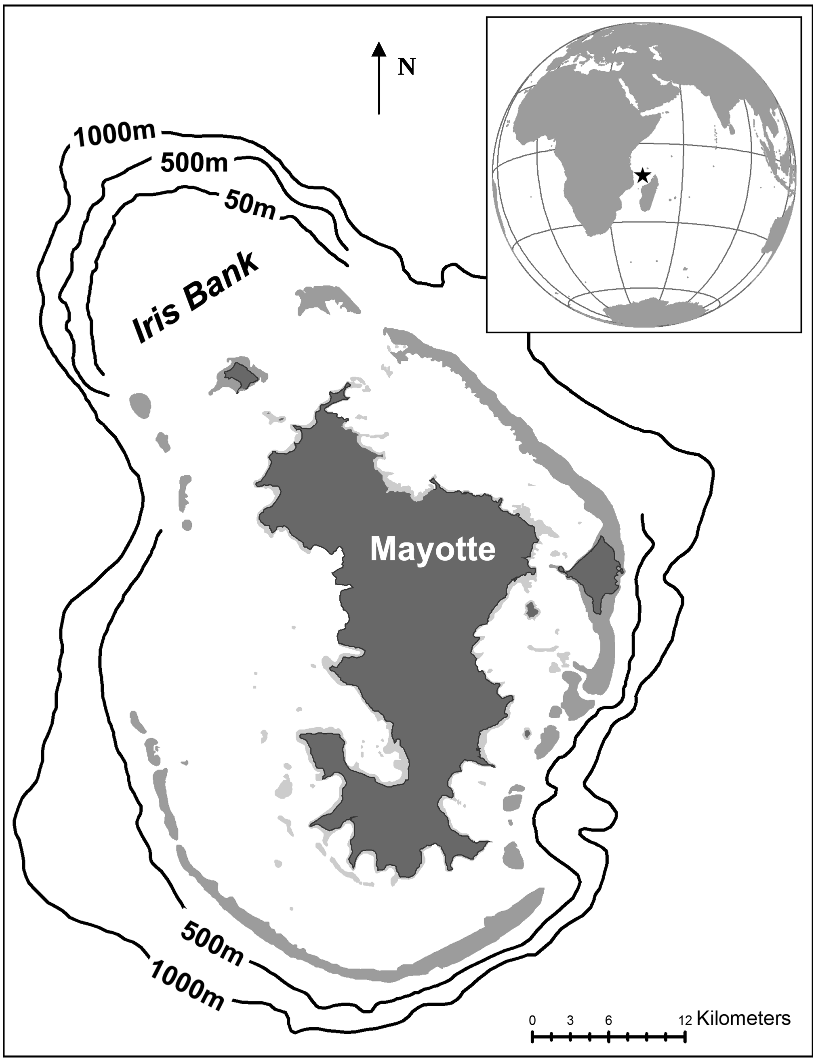

N
1000m
500m
50m
Iris Bank
Mayotte
500m
1000m
0 3 6 12 Kilometers

Fig. 1

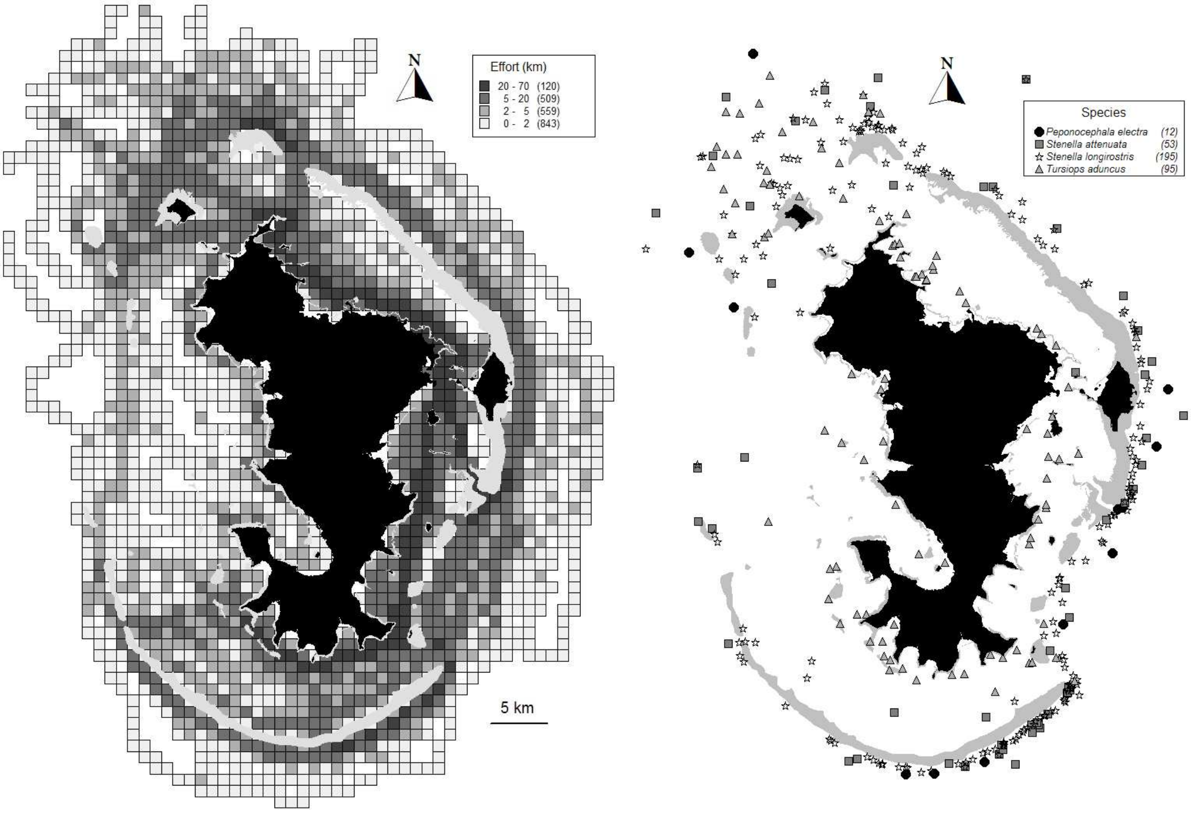

N
Effort (km)
20 - 70 (120)
5 - 20 (509)
2 - 5 (559)
0 - 2 (843)
5 km
N
Species
Peponocephala electra (12)
Stenella attenuata (53)
Stenella longirostris (195)
Tursiops aduncus (95)

Fig. 2

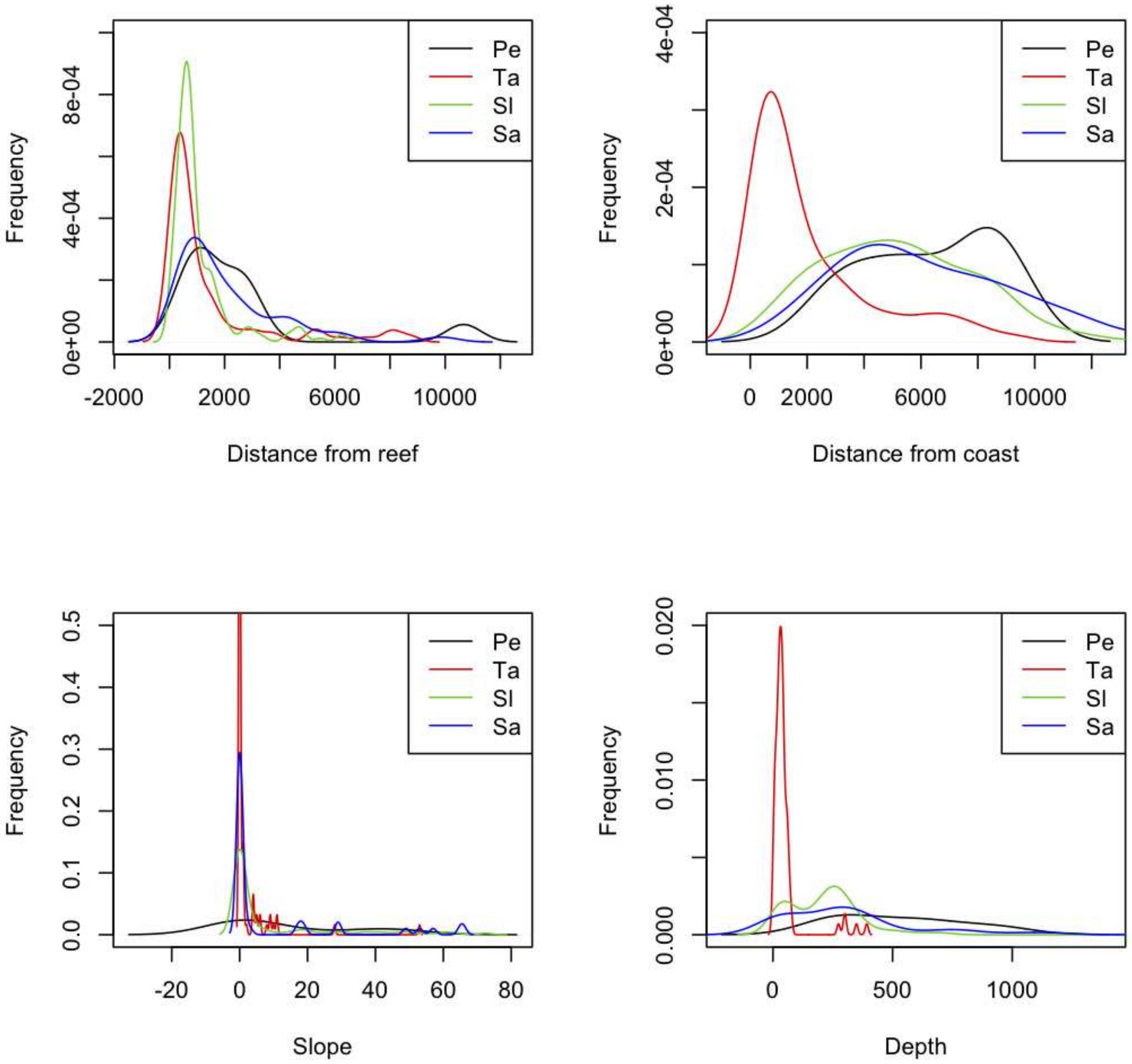

Frequency
0e+00
4e-04
8e-04
-2000
2000
6000
10000
Distance from reef
Pe
Ta
Sl
Sa
Frequency
0e+00
2e-04
4e-04
0
2000
6000
10000
Distance from coast
Pe
Ta
Sl
Sa
Frequency
0.0
0.1
0.2
0.3
0.4
0.5
-20
0
20
40
60
80
Slope
Pe
Ta
Sl
Sa
Frequency
0.000
0.010
0.020
0
500
1000
Depth
Pe
Ta
Sl
Sa

Fig. 3

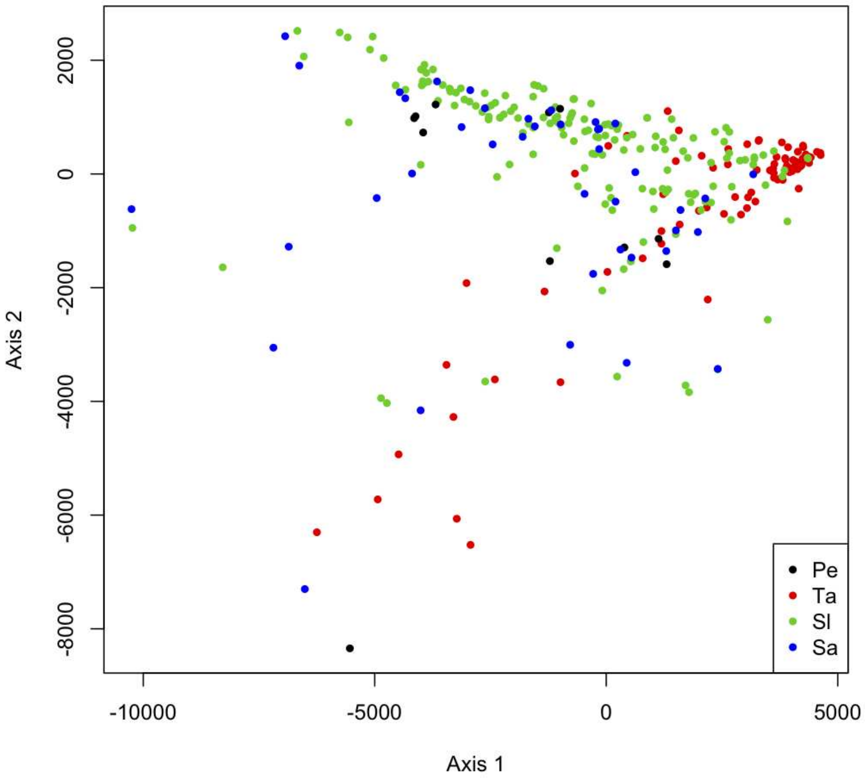

2000
0
-2000
-4000
-6000
-8000
Axis 2
-10000
-5000
0
5000
Axis 1
● Pe
● Ta
● Sl
● Sa

Fig. 4

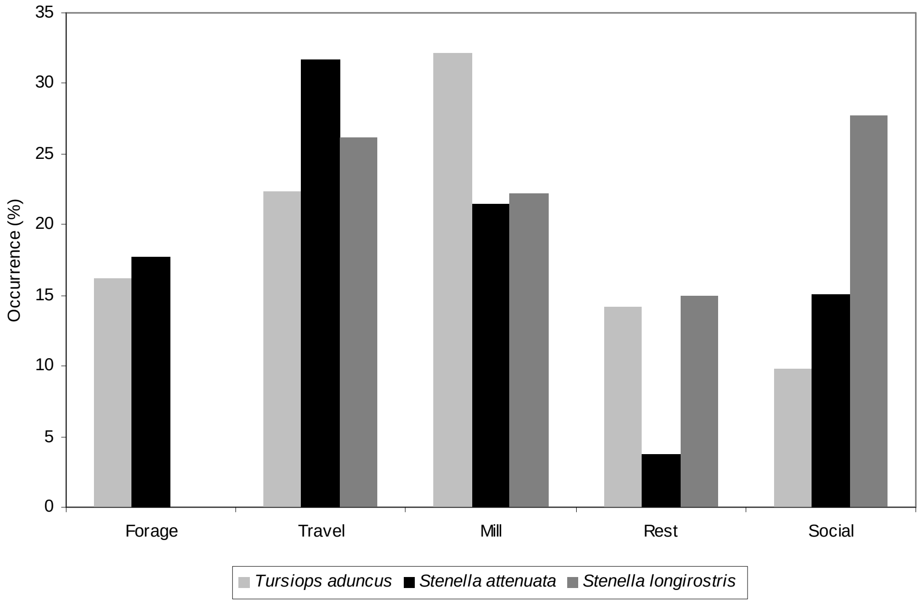

35
30
25
20
15
10
5
0
Occurrence (%)
Forage
Travel
Mill
Rest
Social
Tursiops aduncus
Stenella attenuata
Stenella longirostris

Fig. 5

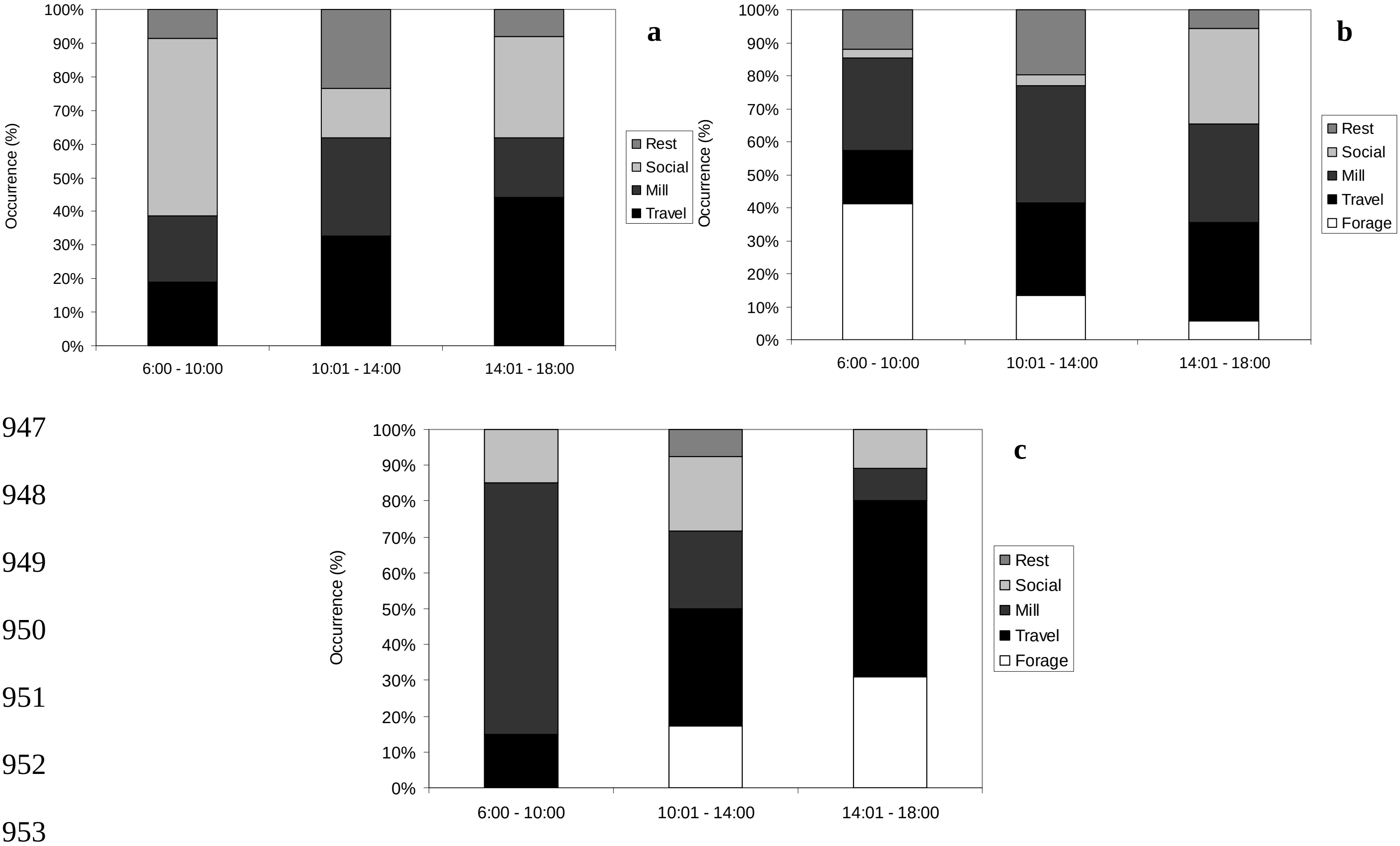

a
b
c
Occurrence (%)
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
6:00 - 10:00
10:01 - 14:00
14:01 - 18:00
Rest
Social
Mill
Travel
Forage

Fig. 6

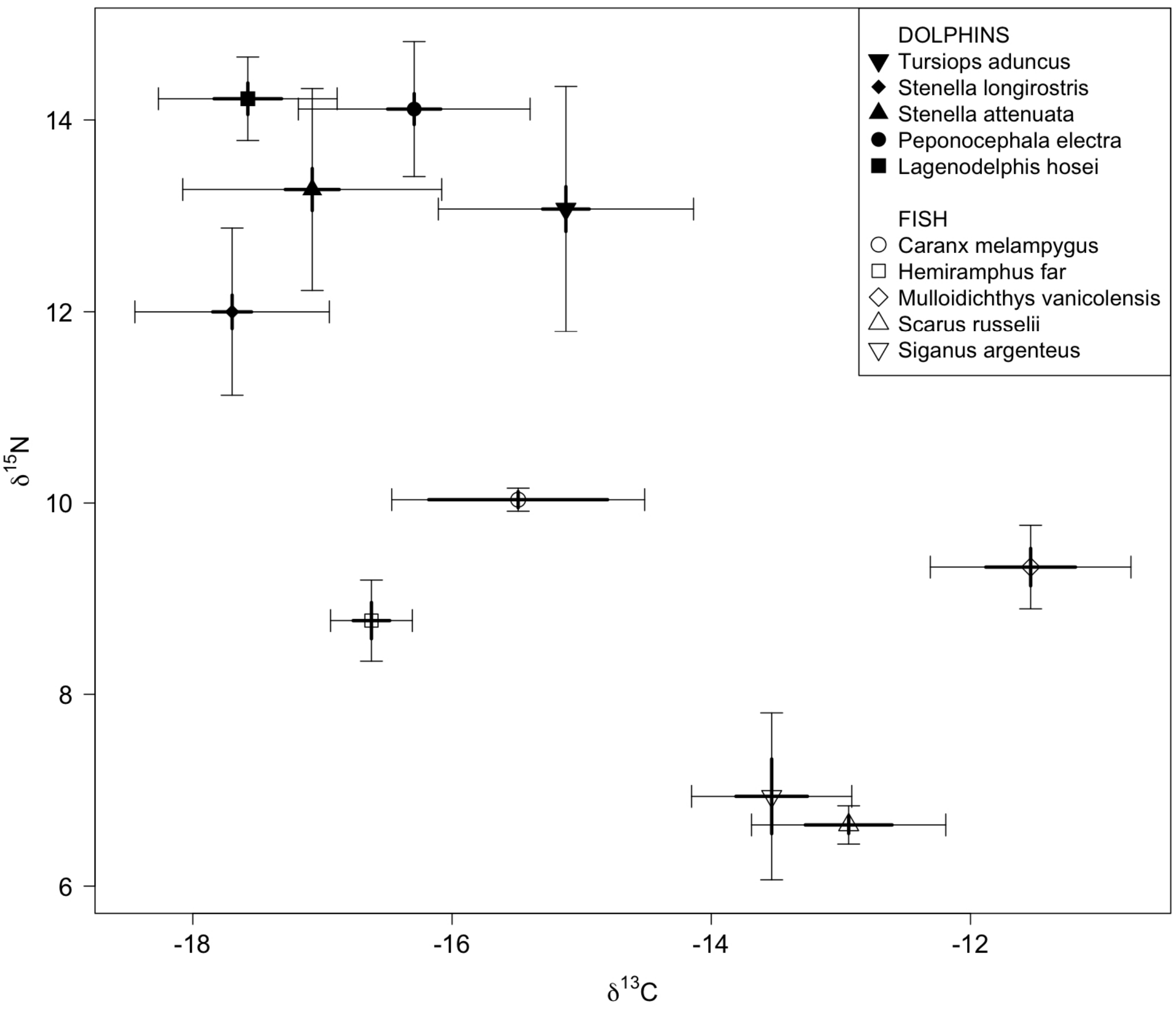
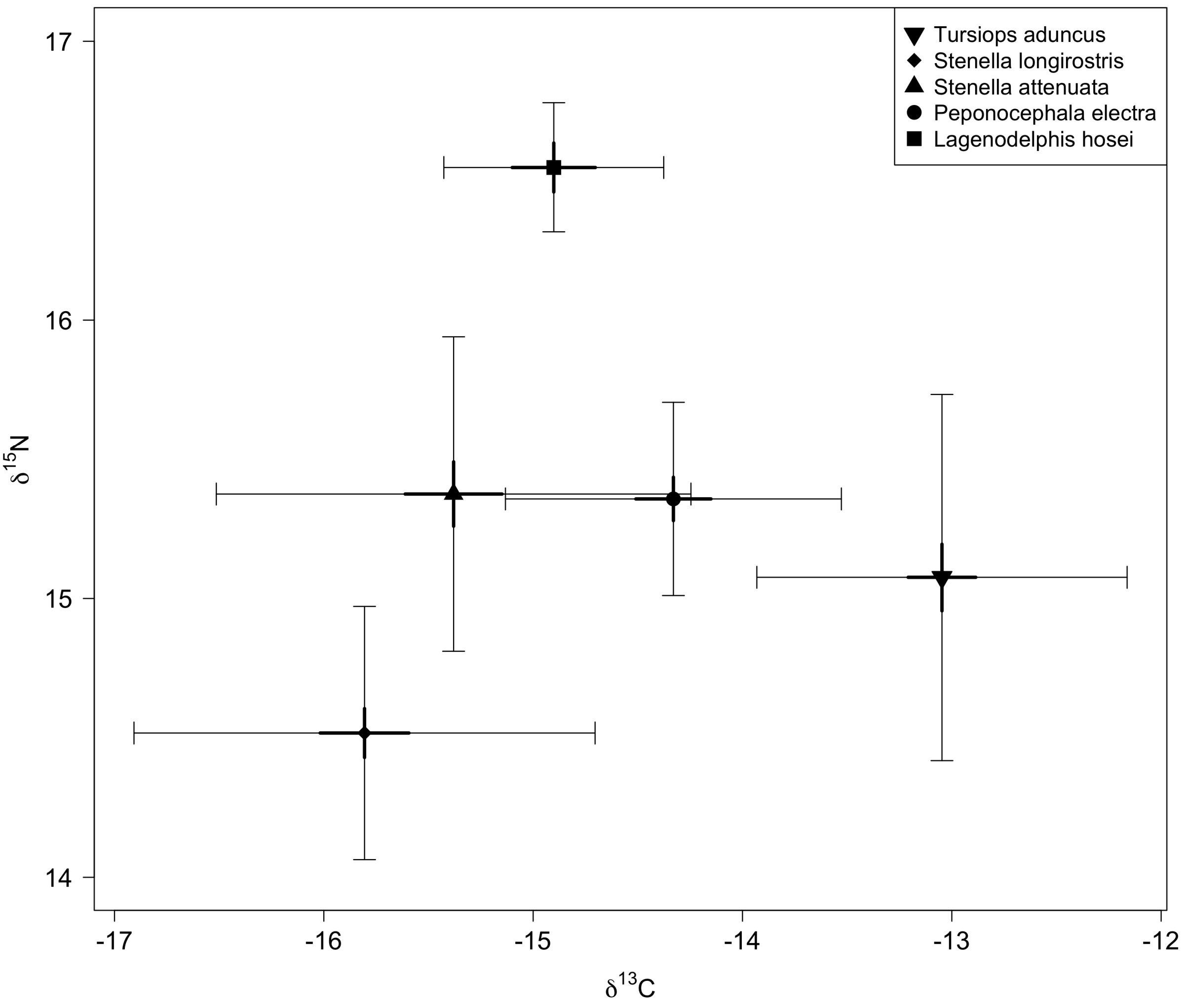

DOLPHINS
Tursiops aduncus
Stenella longirostris
Stenella attenuata
Peponocephala electra
Lagenodelphis hosei
FISH
Caranx melampygus
Hemiramphus far
Mulloidichthys vanicolensis
Scarus russelii
Siganus argenteus
$\delta^{15}N$
14
12
10
8
6
-18
-16
-14
-12
$\delta^{13}C$

Fig. 7



▼ Tursiops aduncus
◆ Stenella longirostris
▲ Stenella attenuata
● Peponocephala electra
■ Lagenodelphis hosei
$\delta^{15}N$
$\delta^{13}C$
17
16
15
14
-17
-16
-15
-14
-13
-12

Fig. 8

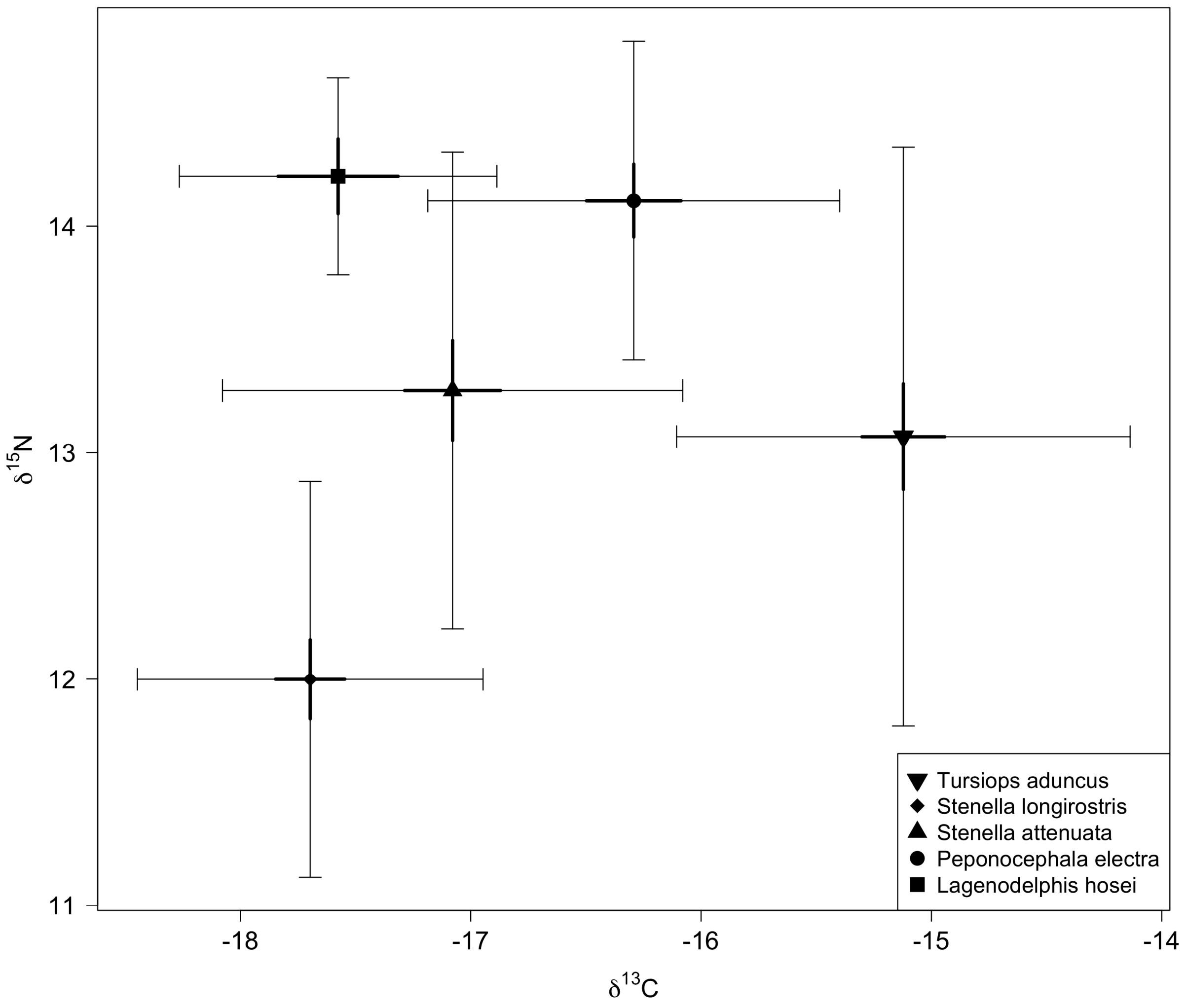

δ15N
δ13C
14
13
12
11
-18
-17
-16
-15
-14
▼ Tursiops aduncus
◆ Stenella longirostris
▲ Stenella attenuata
● Peponocephala electra
■ Lagenodelphis hosei

Fig. 9