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

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24 ABSTRACT

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

43

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

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48 INTRODUCTION

49

50 Understanding niche segregation processes is critical in ecology, particularly when investigating  
51 the ecology of species communities. A community can be defined as a collection of species that  
52 occur together in a common environment, or habitat, the organisms making up the community  
53 being somehow integrated or interacting as a society (Chapman & Reiss 1999). Each species has  
54 its own unique niche (Grinnell 1924). The ecological niche is a complex set of variables  
55 structured along three main axes: habitat (influence of environmental variables), diet (diet  
56 composition, trophic level and prey quality) and time (use of habitat and resources according to  
57 time, such as seasons and time of day). Sympatric species with similar ecological requirements  
58 would compete for resources and their coexistence requires some degree of habitat and resource  
59 segregation (Pianka 1974). Similar species that co-occur are thought to compete for resources  
60 unless they occupy different physical locations and/or feed on different prey. A shared resource  
61 in limited supply will bring about competition between members of the same species (intra-  
62 specific competition) or between individuals of different species (inter-specific competition)  
63 (Roughgarden 1976). Intra-specific competition may be expressed by sex or age related  
64 difference in habitat and resource use and has consequences on social structures. Inter-species  
65 competition can take various forms, including direct interference (aggressive behaviour) and  
66 exploitation-competition, in which individuals indirectly compete for resources (Begon et al.  
67 1986).

68 Investigating segregation processes within communities of organisms having similar size and  
69 morphology has been particularly challenging. In such communities, niche partitioning is  
70 difficult to assess as it can occur over small spatial and temporal scales. For example, in species  
71 with similar morphology (e.g. body size, jaw/beak shape, etc.), feeding niches are distinct even

72 when feeding occurs in both species within the same area (MacArthur 1958). Niche segregation  
73 has been investigated in a number of top marine predator communities, including large teleost  
74 fish (Potier et al. 2004, Ménard et al. 2007), sharks (Estrada et al. 2003, Domi et al. 2005,  
75 Papastamatiou et al., 2006), seabirds (Ridoux 1994, Cherel et al. 2008, Jaeger 2009), marine  
76 mammals (Das et al. 2003, Whitehead et al. 2003, Praca & Gannier 2008) including delphinids  
77 (Pusineri et al. 2008, Gross et al. 2009; Kiszka et al. 2010). Methods used to discriminate niches  
78 were variable, including stomach content, stable isotope and heavy metal analyses and habitat  
79 assessment (including habitat modelling). For example, niche partitioning has been assessed in  
80 polar communities using stable isotope analyses of C and N, such as in Antarctic pinnipeds,  
81 showing clear ecological segregation between species (Zhao et al. 2004). Conversely, in tropical  
82 sympatric seabirds, important overlap of feeding niches has been found, which may be  
83 interpreted by the low productivity of tropical oligotrophic waters, leading these predators to  
84 share same feeding resources that are not quantitatively limited (Cherel et al. 2008). In the  
85 tropical cetacean community of the Bahamas, it has been shown using a habitat analysis that the  
86 ecological niches of four cetacean species (Atlantic spotted dolphin *Stenella frontalis*,  
87 Blainville's beaked whale *Mesoplodon densirostris*, Cuvier's beaked whale *Ziphius cavirostris*  
88 and dwarf sperm whale *Kogia simus*) do not overlap. Other cetacean species are observed in the  
89 area only during the season when prey abundance is sufficiently high to support their presence,  
90 while they are competitively excluded for the rest of the year (MacLeod et al. 2004).

91 Around the tropical island of Mayotte (Comoros, SW Indian Ocean), a great diversity of  
92 cetaceans has been found within a limited geographical range, i.e. at least 19 species within an  
93 area of 2,500 km<sup>2</sup> (Kiszka et al. 2007). In this area, high cetacean diversity may be associated by  
94 the presence of a wide range of marine habitats within close proximity to one another: turbid  
95 mangrove fronts, fringing reef systems, clear lagoon areas, barrier and double barrier reef-

96 associated habitats, a steep insular slope and deep oceanic waters. In some locations around  
97 Mayotte lagoon, water depth extends beyond 1,000 m less than 3 km away from the barrier reef.  
98 The permanent presence of odontocetes within a restricted range suggests that fine-scale  
99 mechanisms allow for the partitioning of habitats and/or resources. The four most common  
100 dolphin species there have a size ranging from 1.8 m spinner dolphin (*Stenella longirostris*, the  
101 smallest) to the 2.8 m melon-headed whale (*Peponocephala electra*, the largest). Other species  
102 include Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), pantropical spotted dolphin (*Stenella*  
103 *attenuata*) and Fraser's dolphin (*Lagenodelphis hosei*) (Kiszka et al. 2007). The Indo-Pacific  
104 bottlenose dolphin is typically a coastal species, feeding on inshore prey (Amir et al. 2005) and  
105 lives inside the lagoon around Mayotte (Gross et al. 2009). Conversely, the other species of the  
106 community are oceanic and primarily occur outside the lagoon and feed on epipelagic to  
107 mesopelagic oceanic prey (Dolar et al. 2003, Brownell et al. 2009). A preliminary study of the  
108 tropical delphinid community around the island of Mayotte indicated that their ecological niches  
109 at least partially, overlapped (Gross et al. 2009). Using sighting data related to environmental  
110 variables and stable isotope analyses from biopsy samples, it was shown that Indo-Pacific  
111 bottlenose dolphin had a coastal/lagunal distribution, while spinner dolphin, melon-headed whale  
112 and pantropical spotted dolphin had similar habitat characteristics along the outer reef slope.  
113 Stable isotope analyses from a small amount of biopsy samples allowed species of the  
114 community to be discriminated isotopically, except the two congeneric and "sibling" dolphins of  
115 the genus *Stenella*, having similar morphological characteristics and frequently forming inter-  
116 species aggregations. Methodological constraints and limited sample size are likely to explain the  
117 absence of measurable differences between species. Therefore, the present work aims to  
118 characterize habitat and resource partitioning among delphinids living in sympatry around the  
119 island of Mayotte from multiple lines of evidence, along the following axes: habitat, diet (more

120 particularly trophic level and foraging habitat) and time (seasons and time of day, Table 1). In  
121 this study, we hypothesize that each delphinids species occupies its own ecological niche, defined  
122 by at least one of the indicator used. Indeed, for any given pair of species, statistical difference  
123 should be found for at least one of the variables tested (habitat, stable isotope values and temporal  
124 variations). We will investigate habitat of delphinids in relation to physiographical variables,  
125 activity budgets and their variability among species and according to time, and stable isotope  
126 analyses ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) from biopsy samples.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopes help elucidate habitat use  
127 (e.g.  $\delta^{13}\text{C}$  values typically vary from  $^{13}\text{C}$  depleted in offshore, or pelagic-derived, to  $^{13}\text{C}$  enriched  
128 from inshore or benthic-derived C) and the position of the consumer in the food chain,  
129 respectively (Hobson 1999). They can also reflect local baseline differences in coastal waters  
130 (Mallena & Harrod 2008). The use of these isotopes has provided alternative information from  
131 which to better understand top predator ecology, including marine mammals (Das et al., 2003).  
132 Activity budgets have been investigated for the three most common species (spinner, spotted and  
133 Indo-Pacific bottlenose dolphins) in order to compare daily variation in behaviour and habitat  
134 utilization. It allows investigating, at a short time scale (time of day), one of the temporal  
135 dimension of the niche. We also assessed seasonal variations of habitat preferences, behavioural  
136 budgets and stable isotope signatures, as seasonality may be a major factor segregating species  
137 among them.

138

139

## 140 MATERIALS AND METHODS

141

### **Study area**

142 Mayotte (45°10'E, 12°50'S) is located in the north-eastern Mozambique Channel, and is part of  
143 the Comoros archipelago (Figure 1). The island is surrounded by a 197 km long barrier reef, with

144 a second double-barrier in the southwest and the immersed reef complex of Iris in the northwest.  
145 The lagoon and surrounding reef complexes are 1,500 km<sup>2</sup> with an average depth of 20 m and a  
146 maximum depth of 80 m found in the western, older, region of the lagoon (Quod et al. 2000). The  
147 insular slope on the exterior of the barrier reef is very steep and contains many submarine  
148 canyons and volcanoes (Audru et al. 2006). The island of Mayotte is characterized by the  
149 presence of high cetacean diversity (19 species including 12 delphinids; Kiszka et al. 2007). The  
150 most common species are the spinner dolphin (*Stenella longirostris*), the pantropical spotted  
151 dolphin (*Stenella attenuata*), the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and the  
152 melon-headed whale (*Peponocephala electra*); these occur on a year-round basis (Kiszka et al.  
153 2007).

154

#### 155 **Data and sample collection**

156 From July 2004 to April 2009, small boat based surveys were undertaken around Mayotte.  
157 Several types of boats were used to collect data: a 7-m catamaran equipped with two, four-stroke,  
158 60-hp outboard engines; a 7-m boat equipped with two, two-stroke, 40-hp outboard engines; a  
159 6.4-m cabin cruiser equipped with one, four-stroke, 150-hp outboard engine; and a 10.8-m cabin  
160 cruiser equipped with two, four-stroke, 115-hp outboard engines. Surveys were conducted  
161 throughout the study period during daylight hours between 07:00 h and 18:00 h in sea conditions  
162 not exceeding Beaufort 3. Survey vessels did not follow pre-defined transects but every attempt  
163 was made to sample the whole daylight period as well as each habitat type within the surrounding  
164 waters of Mayotte, *i.e.* coastal areas, lagonal waters, barrier reef associated areas (inner and outer  
165 slopes) and oceanic or slope waters (>500 m). When delphinids were encountered, standard  
166 sighting data were recorded: species, group size (maximum, minimum, best estimate), geographic  
167 position and behavioural activity. The predominant activity was defined as the behavioural state



168 in which most animals ( $> 50\%$ ) of the group were involved at each instantaneous sampling.  
169 Typically, more than 90% of the animals in a group were engaged in the same activity.  
170 In order to measure behaviour of the focal dolphin species and determine their behavioural  
171 budgets, focal group follows were used (Mann 1999). While one of the preferred option in  
172 behaviour sampling is to follow a focal individual (Mann 1999), this method was not suitable for  
173 large aggregations of oceanic dolphins. In addition, following groups, rather than individuals, is  
174 more suitable for behavioural studies as appropriate conditions for individual sampling are rare in  
175 diving cetaceans (Whitehead 2004). Individual follows were generally possible in the easily  
176 identifiable Indo-Pacific bottlenose dolphins, but not on each occasion, as some individuals were  
177 not identifiable, but for comparative purposes, we used a focal group protocol, which has been  
178 used in other studies on similar models (Neumann & Orams 2006). The encountered group was  
179 approached slowly (typically at 2-3 knots), from the side and rear, with the vessel moving in the  
180 same direction as the animals. Groups were scanned, including all individuals, to negate attention  
181 being drawn to only specific individuals or behaviours (Mann 1999). During focal follows,  
182 dolphin behaviour was recorded every 5 minutes. Five categories of behavioural states were  
183 defined: milling, resting, travelling, feeding/foraging (hereafter foraging), and socializing as  
184 defined in previous studies (e.g. Norris & Dohl 1979, Bearzi 2005, Neumann & Orams 2006,  
185 Degradi et al. 2008). Feeding was characterised by loose to disperse group formations and  
186 dolphins were observed swimming in circles, and pursuing fishes (prey observed at the surface).  
187 Preys were frequently seen at the surface during foraging activity. In bottlenose dolphins, large  
188 preys were frequently exhibited by the animals at the surface. Travelling consisted of persistent  
189 and directional movements of all the individuals of a group. Milling was characterised by non-  
190 directional movements of the dolphin, with frequent changes in heading. Socialising consisted in  
191 frequent interactions between individuals in the form of body contacts, with high-speed

192 movements, frequent changes in direction and aerial displays. Resting was characterised by low  
193 level of activity, with groups in tight formations, with little evidence of forward propulsion.  
194 Surfacing are slow and relatively predictable.

195 For stable isotope analyses, biopsy attempts were made when groups and individuals were easily  
196 approachable and when conditions were optimal (Beaufort < 2, dolphins closely approaching the  
197 boat). Optimal weather conditions allowed stability of the research boat and better chances to  
198 sample the animals successfully and safely. Biopsies were collected by using a crossbow  
199 (BARNETT Veloci-Speed® Class, 68-kg draw weight) with Finn Larsen (Ceta-Dart,  
200 Copenhagen, Denmark) bolts and tips (dart 25-mm long, 5-mm diameter). A conical plastic  
201 stopper caused the bolt to rebound after the impact with the dolphin. The dolphins were hit below  
202 the dorsal fin when sufficiently close (3-10 m) to the research boat. Approaches of focal  
203 groups/individuals were made under power at speeds of 1-4 knots. Blubber and skin biopsy  
204 samples were preserved individually in 90% ethanol before shipping and subsequent analysis.  
205 The preservative used (ethanol) was the most suitable that could be used due to logistical  
206 constraints. It does not affect stable isotope signatures in freshwater zooplankton and benthic  
207 macroinvertebrates (Syväranta et al. 2008), bird eggs, blood and muscle (Hobson et al. 1997,  
208 Gloutney & Hobson, 1998). The increase in  $\delta^{13}\text{C}$  values is generally considered to be due to the  
209 extraction of some lipids but because lipids are depleted in  $^{13}\text{C}$ , they are typically extracted (or  
210 corrected arithmetically, e.g. Kiljunen et al 2006) to avoid a bias in estimates of  $\delta^{13}\text{C}$  values (De  
211 Niro & Epstein 1978, Tieszen et al. 1983), that likely cancels any potential effect of storage in  
212 ethanol (Kiszka et al. 2010). Biopsy sampling was conducted under French scientific permit  
213 #78/DAF/2004 (September 10, 2004) and permit #032/DAF/SEF/2008 (May 16, 2008) after  
214 examination of the project by *Conseil National de Protection de la Nature*.

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

230

231

### **Habitat analyses**

232 We constituted a database in which every dolphin group observation was associated with the  
233 physiographic characteristics (distance from the coast, distance from the nearest reefs, depth and  
234 slope of seafloor) corresponding to the GPS (Global Positioning System) fixes of the observation.  
235 Bathymetric data were obtained from Service Hydrographique et Océanographique de la Marine  
236 (SHOM). Interpolation of bathymetry data, needed to generate depth and slope data for each  
237 sighting, was undertaken with the extension Spatial Analyst by kriging transformation of the  
238 raster file into an interpolated data file. The distance data were obtained using GIS (Geographic

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

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

257

### 258 **Behavioural budget analyses**

259 To analyse diel patterns of behaviour, we defined three time-blocks: morning (before 10:00 h),  
260 noon (between 10:01 h and 14:00 h) and evening (after 14:01 h). The seasons considered were  
261 identical to those used for the habitat analyses (dry/rainy season). Diurnal and seasonal patterns  
262 were investigated by assigning a behavioural sequence to a time block or a season. Contingency

263 table analyses were used in order to compare behavioural budgets among species. Nonparametric  
264 tests were selected because assumptions regarding normality and homogeneity of variance were  
265 not met.

266

267

### Stable isotope analyses

268 Blubber and skin were separated for each dolphin biopsy sample. Fish muscle tissues were used  
269 for stable isotope analyses. The ethanol was evaporated at 45°C over 48 h and the samples were  
270 ground and freeze-dried (Hobson et al. 1997). Lipids were removed from both blubber and skin  
271 samples by 2 successive extractions (1 h shaking in cyclohexane at room temperature and  
272 subsequent centrifugation) prior to analysis. After drying, small sub-samples (0.35 to 0.45 mg  $\pm$   
273 0.001 mg) were prepared for analysis. Stable isotope measurements were performed with a  
274 continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific,  
275 Germany) coupled to an elemental analyser (Flash EA1112 Thermo Scientific, Italy). Reference  
276 gas were calibrated against International Reference Materials (IAEA-N1, IAEA-N2 and IAEA-  
277 N3 for nitrogen; NBS-21, USGS-24 and IAEA-C6 for carbon). Results are expressed in the  $\delta$   
278 notation relative to PeeDee Belemnite and atmospheric N<sub>2</sub> for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively,  
279 according to the equation:

280

$$\delta X = \left[ \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

281 Where X is <sup>13</sup>C or <sup>15</sup>N and R is the isotope ratio <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N, respectively. Replicate  
282 measurements of a laboratory standard (acetanilide) indicated that analytical errors were <0.1‰  
283 for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Percent C and N elemental composition of tissues were obtained using the  
284 elemental analyzer and used to calculate the sample C:N ratio, indicating good lipid removal  
285 efficiency when C:N <4. Differences of stable isotopes values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  among species

286 were tested using non-parametric Kruskal-Wallis and Mann Whitney U-tests. Seasonal variations  
287 were investigated using Mann-Whitney U tests. Like for seasonal variations of habitat  
288 preferences, the two seasons considered were rainy (November – April) and dry seasons (May –  
289 October).

290

291

## 292 RESULTS

293

### **Field effort and data collected**

294 From July 2004 to April 2009, data were collected during 224 boat-based surveys. A total of 355  
295 sightings of the targeted species were collected (92% of cetacean encounters around Mayotte),  
296 *i.e.* 195 for *Stenella longirostris*, 95 for *Tursiops aduncus*, 53 for *Stenella attenuata* and 12 for *P.*  
297 *electra*. The spatial distribution of observation effort and initial encounters is presented in Figures  
298 2a and b. Overall, spatial coverage of effort was heterogeneous, but covered all available habitats  
299 around the island, both inside and outside the lagoon.

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

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

315

316

### **Habitat differentiation**

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

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

335

336

### Behavioural budgets

337 As we used four types of vessel for collecting behavioural data, we tested for a potential boat  
338 effect on the data but failed to find a significant difference ( $\chi^2 = 3.238$ ,  $df = 4$ ;  $P = 0.569$ );  
339 therefore, subsequent analyses reflect a pooled data set. In Indo-Pacific bottlenose dolphins, the  
340 most frequent activities recorded were milling (32%), travelling (22%) and foraging (16%)  
341 (Figure 5). A quite similar pattern was also observed in the pantropical spotted dolphin, with  
342 travelling being the prevalent activity (32%), followed by milling (22%) and foraging (18%). In  
343 the spinner dolphin, socialising was the most commonly recorded behaviour (28%), followed by  
344 travelling (26%) and milling (22%) (Figure 5). Foraging behaviour was not observed in the  
345 spinner dolphin. Among the three species, significant differences in activity budgets were found  
346 ( $\chi^2 = 177.33$ ;  $df = 12$ ;  $P < 0.0001$ ). These differences were confirmed when performing pairwise  
347 comparisons: *T. aduncus* vs. *S. longirostris* ( $\chi^2 = 137.50$ ;  $df = 6$ ;  $P < 0.0001$ ), *T. aduncus* vs. *S.*  
348 *attenuata* ( $\chi^2 = 53.42$ ;  $df = 6$ ;  $P < 0.001$ ) and *S. longirostris* vs. *S. attenuata* ( $\chi^2 = 109.18$ ;  $df = 6$ ;  $P$   
349  $< 0.0001$ ).

350

351

### Temporal variation of activity budgets

352 For all species, no significant variations of activity patterns were observed among seasons ( $H =$   
353  $3.816$ ;  $df = 3$ ;  $P = 0.439$ ). Contrastingly, behaviour patterns varied significantly according to time  
354 of day for Indo-Pacific bottlenose dolphin ( $\chi^2 = 48$ ;  $df = 5$ ;  $P < 0.001$ ), spinner dolphin ( $\chi^2 = 13$ ;  $df$   
355  $= 5$ ;  $P = 0.002$ ) and pantropical spotted dolphin ( $\chi^2 = 11$ ;  $df = 5$ ;  $P = 0.009$ ) (Figure 6, a to c). In  
356 Indo-Pacific bottlenose dolphins, foraging activities were prevalent during the morning and



357 decreased throughout the day, whereas socializing was more frequent in the afternoon. In spinner  
358 dolphins, travelling activities increased along the day and social activities were more observed in  
359 the morning and the afternoon, whereas resting behaviour was more predominant around noon  
360 time. Finally, in pantropical spotted dolphins, feeding behaviour prevailed during the afternoon,  
361 along with travelling.

362 Activity budgets did not vary with water depth in Indo-Pacific bottlenose dolphin ( $H = 2.060$ ;  $df =$   
363  $4$ ;  $P = 0.725$ ), spinner dolphin ( $H = 5.621$ ;  $df = 4$ ;  $P = 0.229$ ) and pantropical spotted dolphin ( $H =$   
364  $8.049$ ;  $df = 4$ ;  $P = 0.09$ ). However, activity budget varied with distance from the coast for Indo-  
365 Pacific bottlenose dolphin ( $H = 9.542$ ;  $df = 4$ ;  $P = 0.04$ ; especially increasing foraging activity  
366 closer to shore), although not for either spinner ( $H = 3.251$ ;  $df = 4$ ;  $P = 0.517$ ) or pantropical  
367 spotted dolphins ( $H = 4.201$ ;  $df = 4$ ;  $P = 0.379$ ). Feeding activities of the Indo-Pacific bottlenose  
368 dolphin increased with decreasing distance from coast.

369

370

### **Stable isotope analyses**

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

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

381  $df = 1$ ;  $P < 0.0001$ ). A similar statistical difference among species for blubber tissue was found,  
382 even when excluding the Fraser's dolphin, very different to the four other species ( $H = 34$ ;  $df = 2$ ;  
383  $P < 0.0001$  for  $\delta^{15}\text{N}$  and  $H = 60$ ;  $df = 2$ ;  $P < 0.0001$  for  $\delta^{13}\text{C}$ ). The Indo-Pacific bottlenose dolphin  
384 had the greatest  $\delta^{13}\text{C}$  values, while the lowest values were observed in the Fraser's dolphin and in  
385 the two species of the genus *Stenella*. The melon-headed whale had intermediate values of  $\delta^{13}\text{C}$ ,  
386 both for skin and blubber (Figures 8 and 9). When looking at pairwise comparisons of  $\delta^{15}\text{N}$  and  
387  $\delta^{13}\text{C}$  values in blubber and skin tissues, however, some degrees of overlap can be observed  
388 (Table 5). From skin samples,  $\delta^{15}\text{N}$  values were significantly different between species pairs,  
389 except between *S. attenuata* and *T. aduncus* and between *L. hosei* and *P. electra* (U-tests;  $P >$   
390  $0.05$ ). For  $\delta^{13}\text{C}$  values, overlap was evident between *L. hosei* and the two species of the genus  
391 *Stenella*. Finally, for blubber tissue,  $\delta^{15}\text{N}$  values were significantly different between species  
392 pairs, except between *S. attenuata* and *P. electra* and between *S. attenuata* and *T. aduncus*.  $\delta^{13}\text{C}$   
393 values showed the highest degrees of overlap, particularly between *S. longirostris* and *S.*  
394 *attenuata*, between *S. attenuata* and *L. hosei*, as well as between *L. hosei* and *P. electra* (U-tests;  
395  $P > 0.05$ ; Table 5). Stable isotope values from fish samples were useful in order to provide a  
396 context to interpret values in delphinids. Among fish, significant differences were observed for  
397  $\delta^{13}\text{C}$  ( $H = 11.2$ ;  $df = 4$ ;  $P = 0.02$ ) and  $\delta^{15}\text{N}$  ( $H = 11.6$ ;  $df = 4$ ;  $P = 0.01$ ). *Siganus argenteus* and  
398 *Scarus russelii* (herbivores) had the lowest trophic position ( $\delta^{15}\text{N}$ ), while *Caranx melampygus*,  
399 the most predatory species, had the highest trophic level ( $\delta^{15}\text{N}$ ). Their foraging habitats were also  
400 well discriminated, with *Mulloidichthys vanicolensis* having the highest  $\delta^{13}\text{C}$  values and *Caranx*  
401 *melampygus* with *Hemiramphus far* the lowest (Figure 7). These latter were about 0.5-1.5 ‰  
402  $\delta^{13}\text{C}$  and 3-4 ‰  $\delta^{15}\text{N}$  lower than *T. aduncus*.

403 Seasonal variations of stable isotope signatures were observed in all species for skin and blubber  
404 tissues (Table 6). In the two species of the genus *Stenella* and the melon-headed whale,  $\delta^{13}\text{C}$

405 values were more negative during the rain season. A reverse situation was observed in *T. aduncus*  
406 during the rain season;  $\delta^{15}\text{N}$  values were decreasing for *Stenella* dolphins and *P. electra*, while  
407 increased in *T. aduncus*. However, while (sometimes) statistically significant in some cases,  
408 seasonal variations appear to be relatively limited.

409

410

## 411 DISCUSSION

412

413

### General

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

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

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

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

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

455

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

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

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

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

491

#### 492 **Resource partitioning inferred from $\delta^{15}\text{N}$ signatures**

493 Nitrogen isotopic signatures are the main source of information on resource utilization by  
494 dolphins in Mayotte. Direct evidences of resource use are limited to some anecdotal observations  
495 of prey hunting or capture by *T. aduncus* and *S. attenuata* (Kiszka & Pusineri, unpublished  
496 observations). Carbon isotopic signatures of fish collected in the lagoon also convey some  
497 contextual information on plausible prey for the more coastal dolphins. Finally, when comparing  
498 trophic levels inferred from  $\delta^{15}\text{N}$  signatures one should only consider in the comparison dolphin

499 species with overlapping  $\delta^{13}\text{C}$  signatures, i.e. living in the same habitat, because reference levels  
500 of  $\delta^{15}\text{N}$  in oceanic vs. lagoon habitats are unknown.

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

515 The two *Stenella* have largely overlapping ranges of both physiographic habitats and carbon  
516 isotopic contents, even if *S. attenuata* is seen slightly further offshore and is nonetheless slightly  
517 carbon-enriched (higher  $\delta^{13}\text{C}$  ratios). According to  $\delta^{15}\text{N}$  values, pantropical *S. attenuata* are on  
518 average 1.5‰ higher than spinner dolphins, i.e. half a trophic level, which would express some  
519 degree of niche segregation between the two species. In addition to this, *S. attenuata* seems to  
520 have a wider niche breadth than *S. longirostris*. Pantropical spotted dolphins have been  
521 frequently observed feeding close to the barrier reef where their prey aggregate (fishes of the  
522 genus Exocoetidae; Kiszka & Pusineri, unpublished observations), in agreement with their

523 slightly higher  $\delta^{13}\text{C}$  signature. Fine-scale processes allowing niche differentiation between the  
524 two *Stenella* species have also been found in other regions, such as in the eastern tropical Pacific  
525 (Perrin et al. 1973). Spinner dolphins there are reported to feed at night upon scattering-layer  
526 organisms, *i.e.* on vertically migrating mesopelagic fishes, cephalopods and crustaceans, caught  
527 in the upper 200 m and occasionally as deep as 400 m (Perrin et al. 1973, Norris et al. 1994,  
528 Dolar et al. 2003). Conversely, pantropical spotted dolphins would feed day and night on  
529 epipelagic fishes and cephalopods (Perrin et al. 1973).

530 Melon-headed whales were observed in much the same habitats as pantropical spotted dolphins,  
531 but comparatively higher  $\delta^{13}\text{C}$  values suggested vertical segregation could occur. Nitrogen  
532 isotopic content further suggests a slightly higher trophic level (about 1/3 trophic level). Earlier  
533 works report mesopelagic fishes and cephalopods, supposedly preyed upon in the upper 700  
534 meters, as the main component of its diet (Young 1978, Brownell et al. 2009). An element of  
535 comparison is provided by the Fraser's dolphin, which was added to the study in an attempt to  
536 provide isotopic reference for a true oceanic predator; in addition to this, the species is frequently  
537 observed forming mixed group with melon-headed whale (Jefferson & Barros 1997, Kiszka et al.  
538 2007, Dulau-Drouot et al. 2008). Not surprisingly, Fraser's dolphins displayed the second lowest  
539  $\delta^{13}\text{C}$  values, in agreement with their oceanic lifestyle, and the highest  $\delta^{15}\text{N}$  values, that fit well  
540 with the higher trophic level, likely associated with its preference for larger prey already reported  
541 elsewhere (Dolar et al. 2003). Studies of stomach contents from the Pacific suggest this species  
542 feeds on relatively large mesopelagic fish and cephalopods from near the surface to probably as  
543 deep as 600 meters (Robison & Craddock 1983, Dolar et al. 2003). In Mayotte, Fraser's dolphins  
544 and melon-headed whales, although generally seen associated, do not overlap in their isotopic  
545 niches, the latter being more  $\delta^{13}\text{C}$  enriched than the former, which could be interpreted as feeding  
546 a deeper food source, possibly associated to peri-insular slopes, whereas the Fraser's dolphin



547 would rely on large epi- to-mesopelagic truly oceanic prey. These two species might associate for  
548 other reasons than foraging, such as social advantage or vigilance against predators.

549

#### 550 **Temporal segregation inferred from seasonal patterns and activity budgets**

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

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

571 1973, Norris et al. 1994). Our results underline a clear pattern of niche segregation along the time  
572 dimension, at least during the day.

573

574

#### **Final comments**

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

587 1 – The Indo-pacific bottlenose dolphin is mostly confined to the inner lagoon or at least in  
588 shallow reef-associated habitats. They feed diurnally (possibly nocturnally as well, although this  
589 could not be documented), with daily routines that would follow variation in prey catchability  
590 during the day, e.g. mullet being often caught close to the coast in the morning, and *Caranx*  
591 *melampygus* and *Hemiramphus far* the rest of the day across the lagoon;

592 2 – The spinner dolphin lives in outer reef habitats and forage only nocturnally on small  
593 mesopelagic prey;

594 3 – The pantropical spotted dolphins also lives in outer reef habitats, that largely overlap with the  
595 spinner dolphins but feed at least partly diurnally and at dawn on epipelagic prey, that include  
596 flying fish caught closer to the barrier reef;

597 4 – The melon-headed whale is seen in the same habitat as pantropical spotted dolphins, but  
598 forages deeper over the peri-insular slope.

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

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

616

617

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**Tables**

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

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

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810 Table 2: Seasonal distribution (winter/dry season: May to October; summer/rain season:  
 811 November to April) of sighting data and biopsy samples collected from December 2004 to April  
 812 2009.

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

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823 Table 3: Distribution of the delphinids in relation to physiographic variables.  
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	Mean	Median	SD	Q1-Q3
<b>Depth (meters)</b>				
<i>Tursiops aduncus</i>	47.9	32	70.2	19.7 – 45.1
<i>Stenella longirostris</i>	220.7	230.5	175.9	71.7 – 285.7
<i>Stenella attenuata</i>	301.4	276.4	277.2	44.9 – 370.4
<i>Peponocephala electra</i>	486.5	462.2	244.1	274.9 – 666.2
<b>Slope (degree)</b>				
<i>Tursiops aduncus</i>	2.1	0	6.7	0 – 0.8
<i>Stenella longirostris</i>	9.5	0	17.9	0 – 7.9
<i>Stenella attenuata</i>	9.7	0	19.7	0 – 2.9
<i>Peponocephala electra</i>	13.6	0	20.4	0 – 39.8
<b>Distance coast (meters)</b>				
<i>Tursiops aduncus</i>	2001.8	996.2	2169.8	487.6 – 2778.5
<i>Stenella longirostris</i>	5258.8	5068.3	2763.5	3216.6 – 7191.7
<i>Stenella attenuata</i>	6295.3	5771.8	3331.2	3921.7 – 8602.8
<i>Peponocephala electra</i>	6665.6	7086.4	2130.7	5369.9 – 8520.4
<b>Distance reef (meters)</b>				
<i>Tursiops aduncus</i>	1363	509.2	2071.8	268.7 – 1474.1
<i>Stenella longirostris</i>	1059.7	700.4	1144.8	478 – 1320.6
<i>Stenella attenuata</i>	2011.8	1210	1999.5	722 – 2701.9
<i>Peponocephala electra</i>	2452.1	1363.3	3014.8	927.6 – 2563.8

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

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839 Table 5: Pairwise Mann-Whitney U test p values for each pairs of delphinid species in carbon and  
 840 nitrogen in skin and blubber.  
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<b>SKIN</b>				
<b>Nitrogen</b>	<i>Lagenodelphis hosei</i>	<i>Peponocephala electra</i>	<i>Stenella attenuata</i>	<i>Stenella longirostris</i>
<i>Tursiops aduncus</i>	0.01	0.001	0.125	< 0.001
<i>Stenella longirostris</i>	< 0.001	< 0.001	< 0.001	
<i>Stenella attenuata</i>	0.01	0.009		
<i>Peponocephala electra</i>	0.232			
<b>Carbon</b>				
<i>Tursiops aduncus</i>	< 0.001	< 0.001	< 0.001	< 0.001
<i>Stenella longirostris</i>	0.339	< 0.001	0.02	
<i>Stenella attenuata</i>	0.157	0.008		
<i>Peponocephala electra</i>	0.008			
<b>BLUBBER</b>				
<b>Nitrogen</b>				
<i>Tursiops aduncus</i>	< 0.001	0.022	0.08	< 0.001
<i>Stenella longirostris</i>	< 0.001	< 0.001	< 0.001	
<i>Stenella attenuata</i>	< 0.001	0.485		
<i>Peponocephala electra</i>	< 0.001			
<b>Carbon</b>				
<i>Tursiops aduncus</i>	< 0.001	< 0.001	0.001	0.001
<i>Stenella longirostris</i>	0.02	< 0.001	0.182	
<i>Stenella attenuata</i>	0.242	< 0.001		
<i>Peponocephala electra</i>	0.112			

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843 Table 6: Pairwise Mann-Whitney U test P values for seasonal differences of stable isotope  
 844 signatures for each species and type of tissue.  
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<b>SPECIES/SEASON</b>	<b>BLUBBER</b>	<b>SKIN</b>
<b><i>Tursiops aduncus</i></b>		
Dry season	P < 0.001	P < 0.001
Rainy season	P > 0.05	P > 0.05
<b><i>Peponocephala electra</i></b>		
Dry season	P > 0.05	P > 0.05
Rainy season	P > 0.05	P < 0.01
<b><i>Stenella attenuata</i></b>		
Dry season	P > 0.05	P > 0.05
Rainy season	P < 0.05	P < 0.001
<b><i>Stenella longirostris</i></b>		
Dry season	P > 0.05	P < 0.05
Rainy season	P > 0.05	P > 0.05

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847 Table 7: Summary of results obtained for the four indicators of ecological niche dimensions  
 848 among the Mayotte delphinid community. Different letters denote species that segregate for the  
 849 indicator being considered.  
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<b>Indicators of niche dimensions</b>	<i>Tursiops aduncus</i>	<i>Stenella attenuata</i>	<i>Stenella longirostris</i>	<i>Peponocephala electra</i>
Physiographic characteristics	A	B		
Carbon isotopic values	A	B		C
Nitrogen isotopic values	A		B	C
Daily activity rhythm	A	B	C	Not investigated

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869 Figure captions

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871 Fig. 1: Location of the study area.

872 Fig. 2: Spatial distribution of effort (per 1 km cell) and distribution of dolphin sightings around

873 Mayotte from July 2004 to April 2009. Fig. 3: Density plots of sightings of dolphins around

874 Mayotte in relation to physiographical variables: depth (meters), slope (degree), distance from the

875 coast (meters) and distance from the nearest reefs (meters). Pe: *Peponocephala electra*; Ta:

876 *Tursiops aduncus*; Sl: *Stenella longirostris*; Sa: *Stenella attenuata*.

877 Fig. 4: Metric Multi-Dimensional Scaling plot of delphinid habitat in relation to physiographical

878 variables. Pe: *Peponocephala electra*; Ta: *Tursiops aduncus*; Sl: *Stenella longirostris*; Sa:

879 *Stenella attenuata*.

880 Fig. 5: Overall activity budgets for Indo-Pacific bottlenose dolphins, pantropical spotted dolphins

881 and spinner dolphins around Mayotte from 2004 to 2009.

882 Fig. 6: Within day variations of behavioural budget in spinner dolphin (a), Indo-Pacific

883 bottlenose dolphin (b) and pantropical spotted dolphin (c) around Mayotte from 2004 to 2009.

884 Fig. 7: Mean (with Standard Errors in bold line and Standard Deviation in thin line) stable

885 isotope values in dolphin skin and fish muscle ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in ‰).

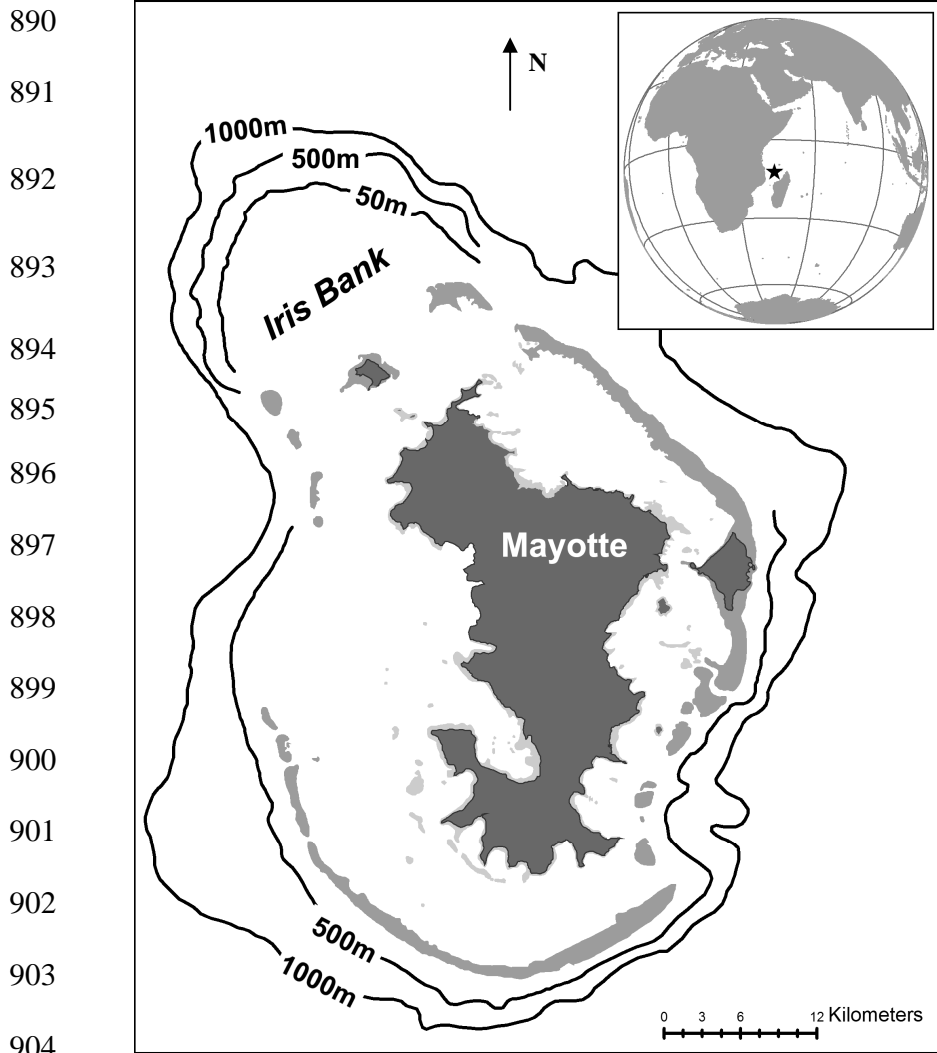
886 Fig. 8: Mean (with Standard Errors in bold line and Standard Deviation in thin line) stable

887 isotope values in lipid-treated dolphin blubber.

888 Fig. 9: Mean (with Standard Errors in bold line and Standard Deviation in thin line) stable

889 isotope values in lipid-treated dolphin skin.





905 Fig. 1

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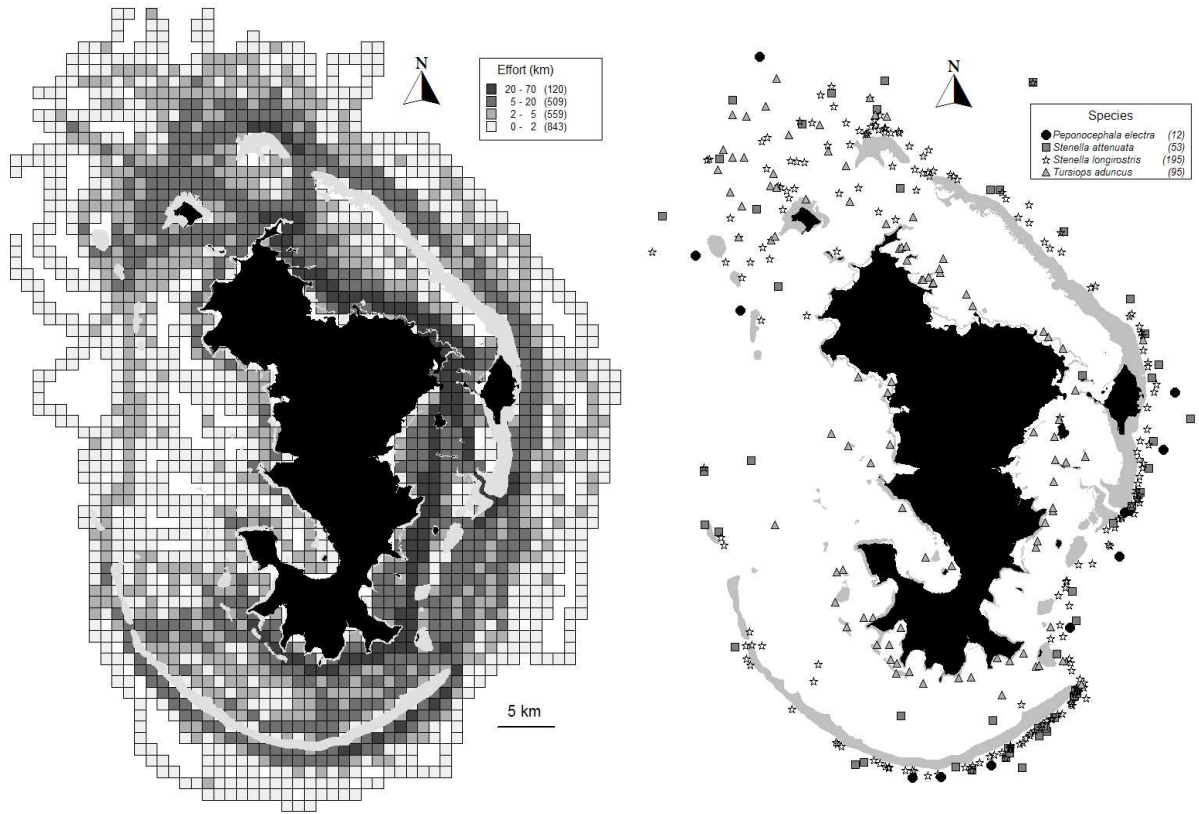
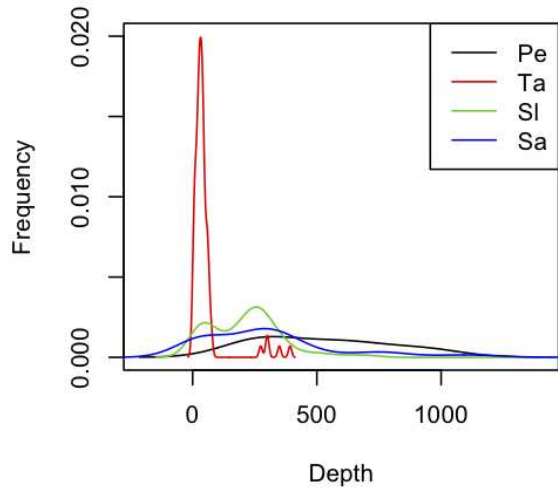
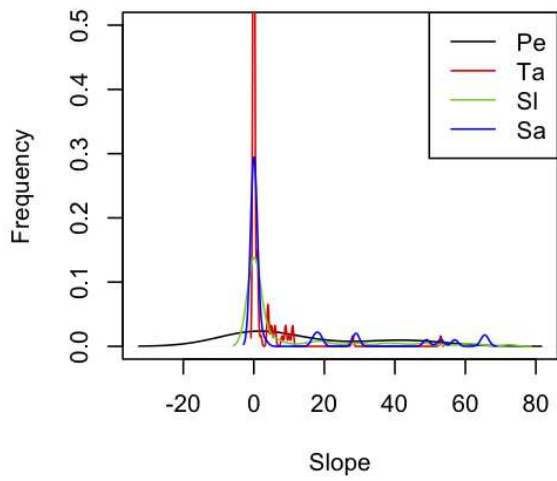
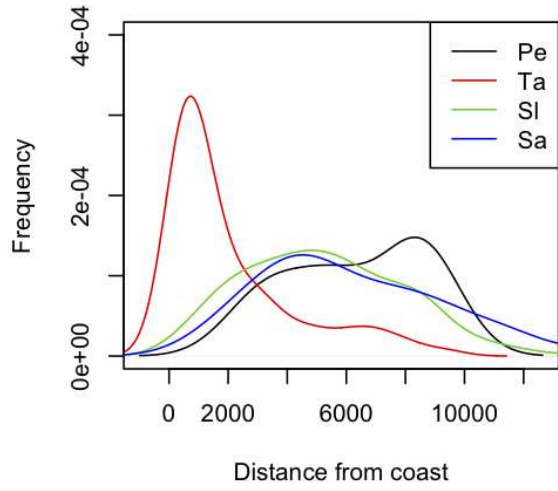
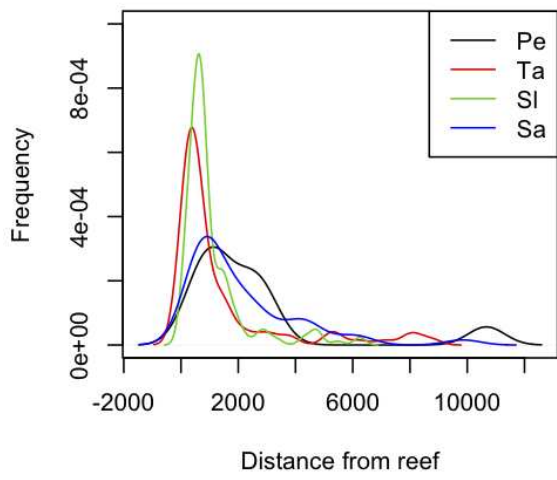


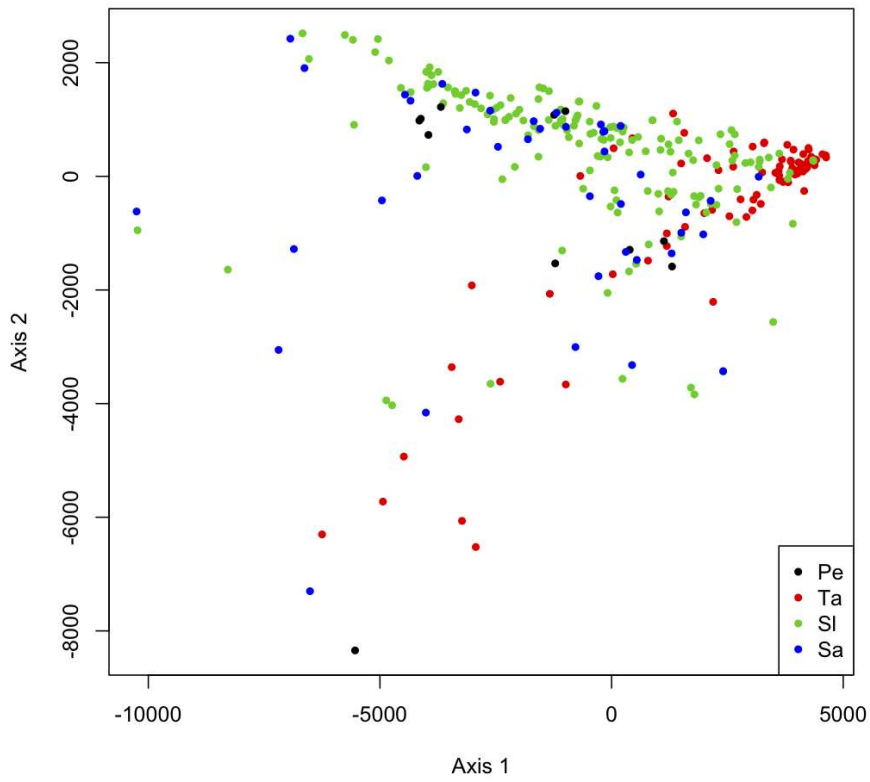
Fig. 2



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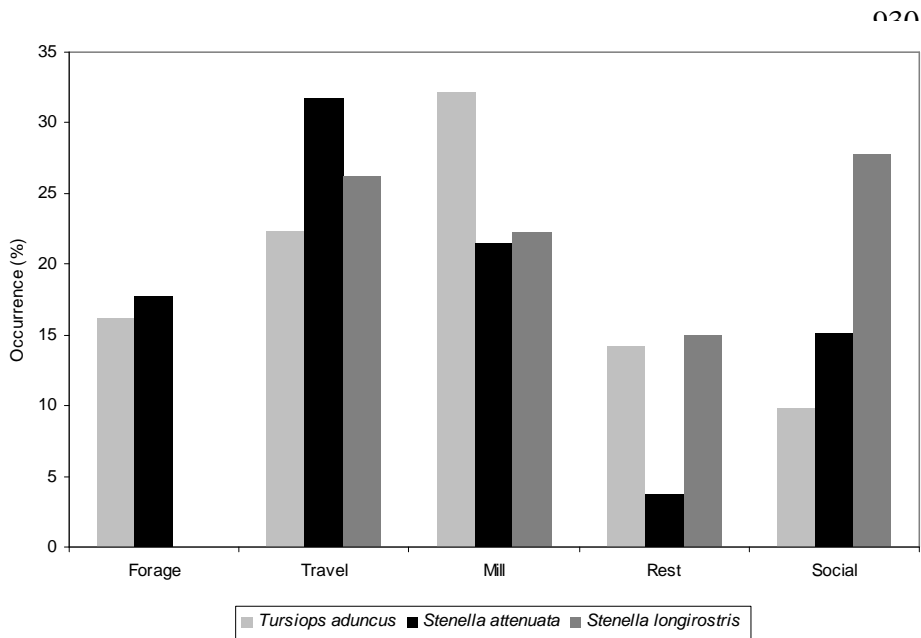
Fig. 3



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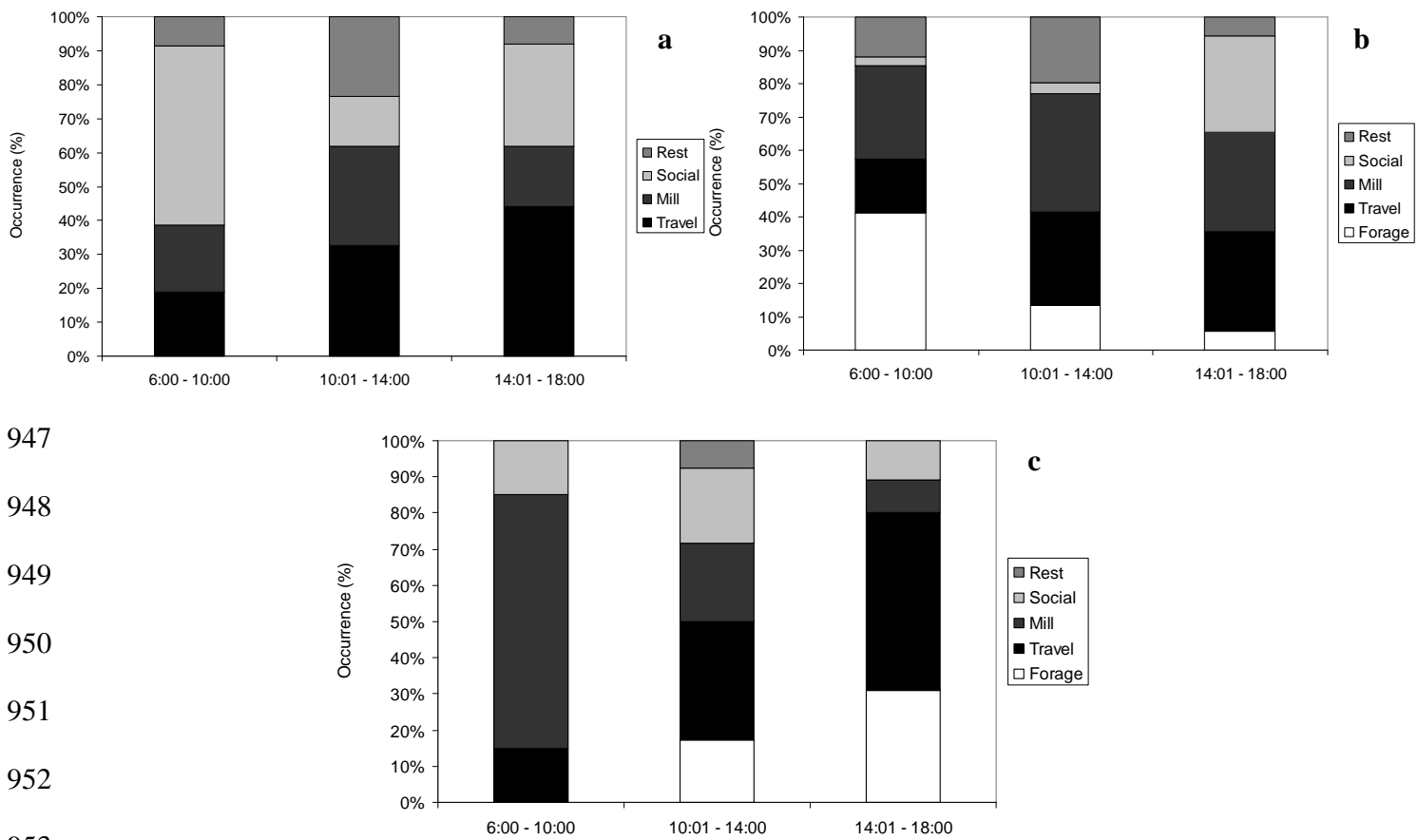
Fig. 4



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Fig. 5



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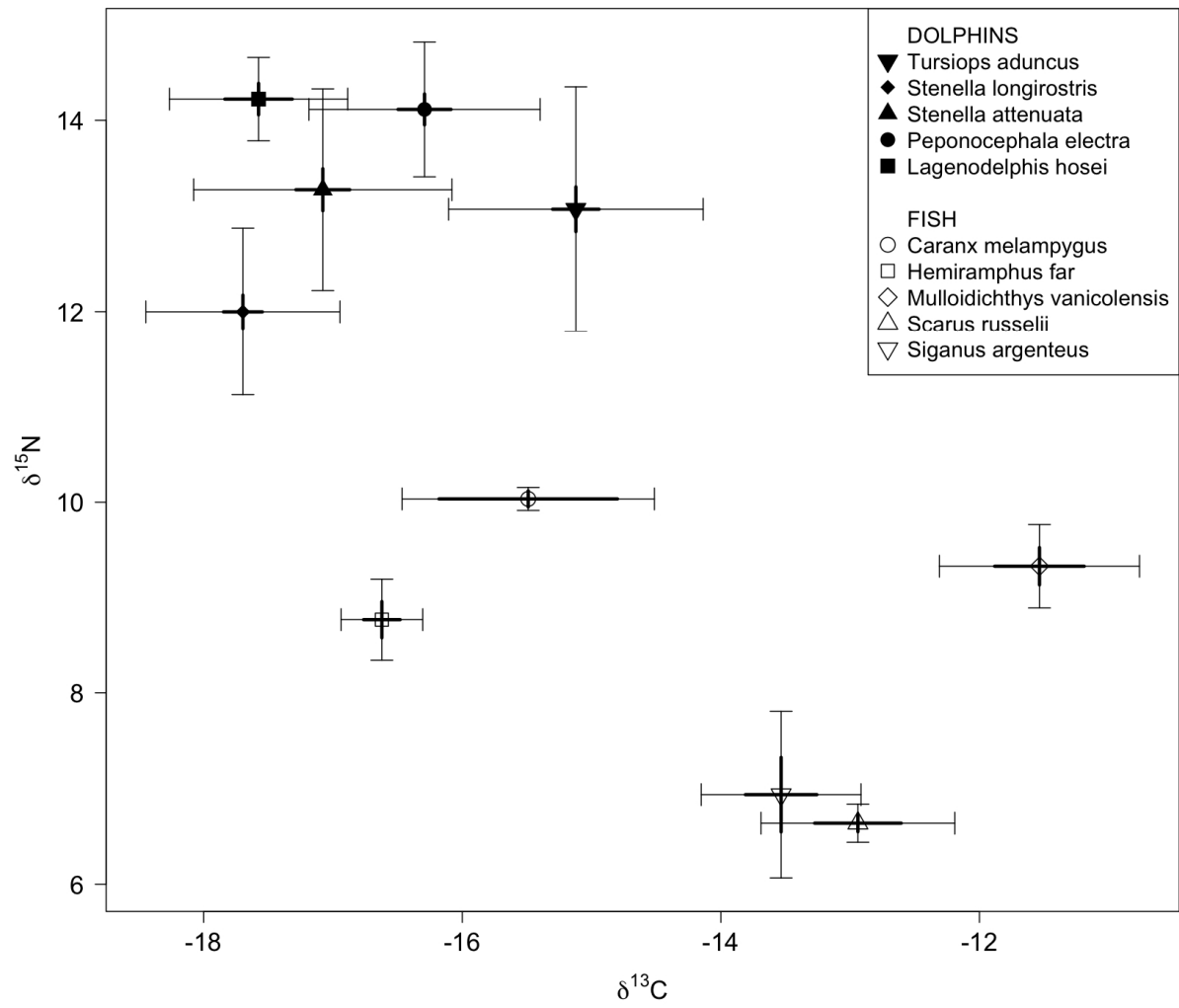
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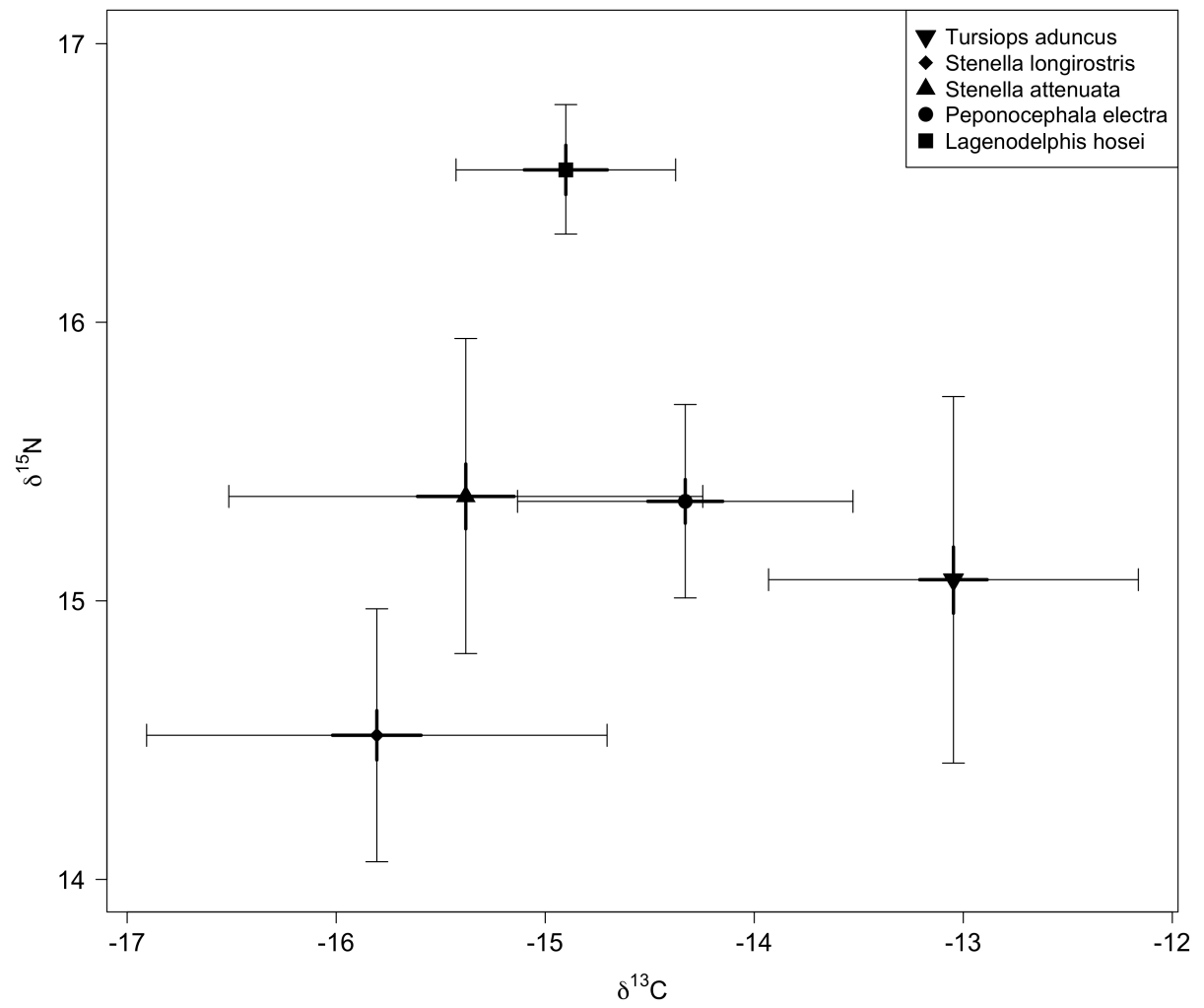
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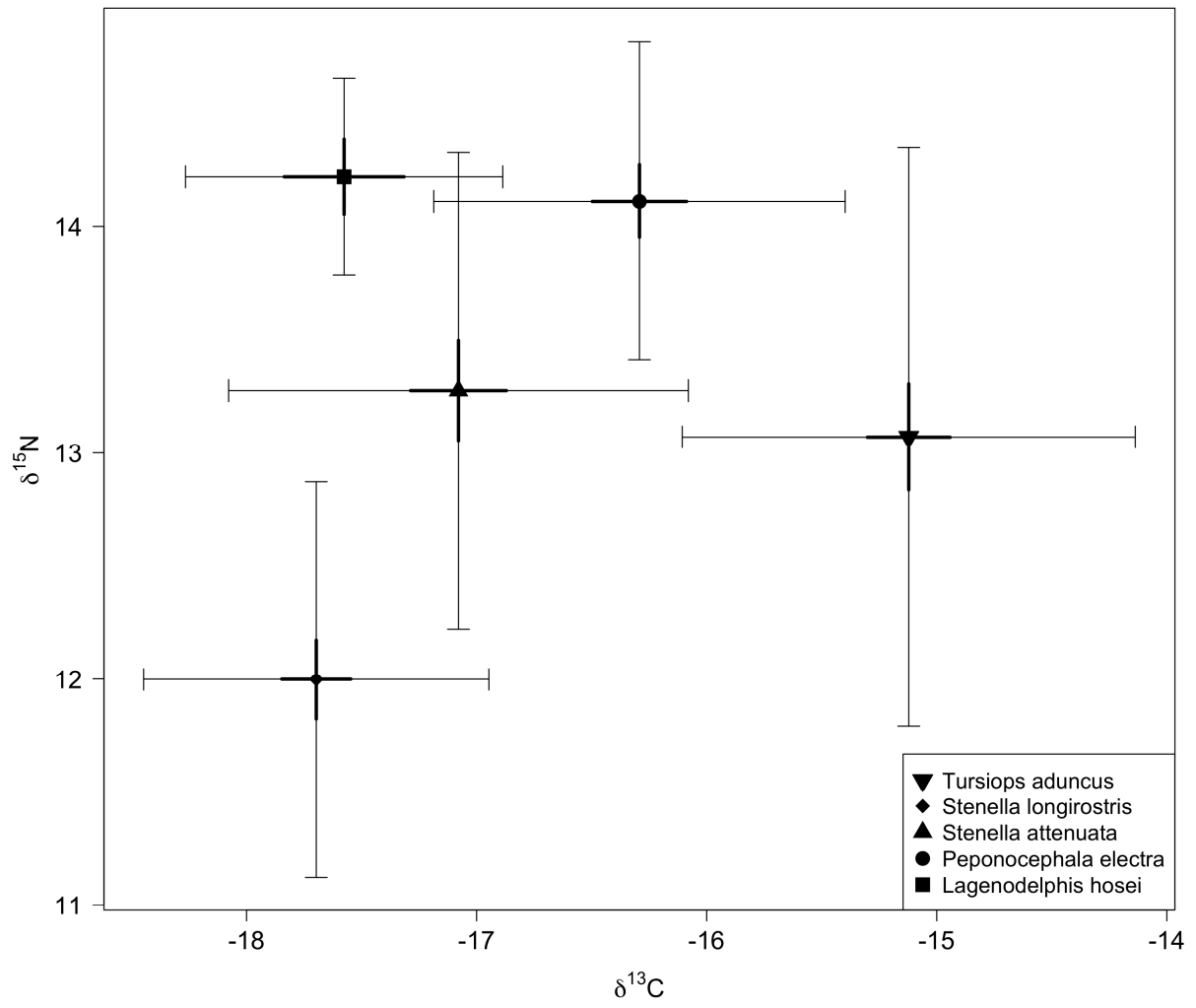


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Fig. 8



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Fig. 9