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Structure of a toothed cetacean community around a tropical island
(Mayotte Island, Mozambique Channel)

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We describe the structure of a toothed cetacean community around the island of Mayotte
(South-West Indian Ocean, 45°10’E, 12°50’S), using data collected from small boat-based
surveys conducted between July 2004 and June 2006. In all, 16 odontocete species were
recorded. Diversity (Shannon-Weaver index) was particularly high along the outer slope of
the barrier reef. Patterns of spatial distribution underscore the existence of three main
cetacean habitat types: the inner lagoon (Indo Pacific bottlenose dolphin \textit{Tursiops aduncus},
and humpback dolphin \textit{Sousa chinensis}), the outer reef slope (Spinner dolphin \textit{Stenella}
\textit{longirostris}, Pantropical spotted dolphin \textit{S. Attenuate} and melon-headed whale
\textit{Peponocephala electra}) and oceanic waters deeper than 500 m (e.g. Blainville’s beaked
whale \textit{Mesoplodon densirostris}). Group characteristics were highly variable among species,
with oceanic small delphinids characterised by larger group sizes than strictly coastal and
non-delphinid oceanic species. The outer slope of the barrier reef appears to be of primary
importance in terms of density and diversity of odontocetes around Mayotte. Results support
the hypothesis that a number of cetacean species, particularly several delphinid species, are
dependant on coral reef complexes.

Keywords: barrier reef slope, cetaceans, community composition, distribution, encounter
rates, Indian Ocean, Mayotte, odontocetes
Introduction

A biological community can be defined as the populations of organisms that co-exist in an ecosystem (or habitat). Descriptions of biological communities may consider all taxonomic groups in an ecosystem or be limited to a single functional or taxonomic group (e.g. marine top predators or cetaceans respectively). Characterising biological communities is necessary not only for understanding ecosystem structure and functioning (including trophodynamics), but for providing baseline information against which effects of ecosystem changes can be gauged and to identify critical areas for conservation management. Cetaceans perform a role as top predator in various marine ecosystems (e.g. coastal, slope-associated and oceanic, etc.). The distribution, diversity and group characteristics of cetacean communities have been described for marine ecosystems from polar to tropical waters, including Antarctic waters (Thiele et al. 2000), the Mediterranean Sea (Gannier 2005), off the Bahamas (MacLeod et al. 2004), the Gulf of Mexico (Maze-Foley and Mullin 2006), the South-West Atlantic (Moreno et al. 2005) and in French Polynesia (Gannier 2000, 2002). These studies, conducted at the scale of oceanic basins, regions or archipelagos, have shown that cetacean species partition their habitat according to a number of abiotic and biotic environmental variables, such as physiography and primary production. Most cetacean habitat studies have found that depth was one of the primary environmental features explaining cetacean distribution (e.g. Cañadas et al. 2002).

The diversity and density of marine top predators including cetaceans at local (insular or archipelago) scales appears to be high relative to ocean-basin or regional scales (Gannier 2000, 2002, Baird et al. 2003). Similar to continental margins, where the land plunges to the deep oceanic waters, insular slopes potentially provide more abundant resources and perform essential functions such as nutrient cycling (Levin and Dayton 2009). Turbulence and vertical mixing in island channels are believed to create nutrient-rich conditions around archipelagos (Gilmartin and Revelante 1974). The formation of these isolated, nutrient-rich regions, especially in the oligotrophic regimes of the tropics where ocean productivity is generally low, is the primary reason why islands and archipelagos can serve as ‘oases’ of biodiversity. These oases are of critical importance for conservation and management actions that require examination over a range of spatial and temporal scales. Despite this, relatively few studies of cetacean community structure around tropical islands and atolls have been conducted thus far (MacLeod et al. 2004, Anderson 2005, Dulau-Drouot et al. 2008, Hermans and Pistorius 2008).
Mayotte is characterised by diverse ecosystems that are in close proximity to each other, i.e. mangroves, fringing reefs, a large semi-closed lagoon, barrier and double-barrier reef systems, and deep oceanic waters within a few kilometres from shore (Quod et al. 2000). The cetacean community is mostly composed of delphinids but it also includes large odontocetes (e.g. ziphids, kogiids, physeterids), blue whales *Balaenoptera musculus* and humpback whales *Megaptera novaeagliae*. Although some of the species recorded are rare, all are present year-round, with the exception of humpback whales.

In view of the growing need to identify critical areas for marine biodiversity conservation, both locally and regionally, this paper describes the general structure of the odontocete community encountered around the island of Mayotte. We present the diversity of species occurring in the island’s surrounding waters in relation to the main habitat types and provide details on the spatial distribution and encounter rates of the most common species.

**Materials and methods**

**Study area**

Mayotte (45°10'E, 12°50'S) is situated in the northern Mozambique Channel and is part of the Comoros archipelago (Figure 1). The island is almost entirely surrounded by a 197 km long barrier reef, with a second double-barrier in the south-west and the immersed reef complex of Iris Bank in the north-west. There are a series of deep passes through the reefs, some of which are the sites of ancient rivers (Quod et al. 2000). The area of the lagoon and surrounding reef complexes is about 1 500 km² with an average of 20 m and a maximum depth of 80 m in the western, older region of the lagoon. There are some 20 small islets in the lagoon, ranging from 1 ha to 242 ha, each of which is surrounded by fringing reefs. There are approximately 670 ha of mangrove forests around the main island, especially in protected bays (Quod et al. 2000). The insular slope on the exterior of the barrier reef is very steep and contains many submarine canyons. Broad canyons, with numerous volcanoes and landslides, deeply incise the slope (Audru et al. 2006).
Data collection

Between July 2004 and June 2006, small boat-based surveys were undertaken in the waters surrounding Mayotte. Several types of boats were used: a 7-m catamaran equipped with two four-stroke, 60-hp outboard engines; a 7-m boat equipped with two two-stroke, 40-hp outboard engines; and a 6.4 m cabin boat equipped with one four-stroke, 150-hp outboard engine. Surveys were conducted throughout the study period during daylight hours between 07:00h and 18:00h, in sea conditions not exceeding Beaufort 3. Survey vessels did not follow pre-defined transects but every attempt was made to sample each habitat type within the surrounding waters of Mayotte, i.e. coastal areas (mangrove fronts, fringing reef), lagoon waters, barrier reef-associated areas (inner and outer slopes) and oceanic/slope waters (>500 m). Constant GPS logging was used to collect geographic positions every five seconds between departure from and return to the harbour, using a hand-GPS Garmin Gecko®. When cetaceans were encountered, standard sighting data were recorded; i.e. species, group size (maximum, minimum, best estimate) and geographic position. For small aggregations of cetaceans, group size was defined as the number of animals at the surface within five body lengths of each other (Smolker et al. 1992). Large aggregations of small delphinids often consisted of a super group, comprised of several smaller animal units or aggregations (typically 2-20), spaced several dozen-hundreds meters apart (typically 50-200 m), moving in the same direction and exhibiting similar patterns of behaviour. For these large aggregations, group size reflects the size of the super group not the individual aggregations.

Data analysis

Only data for odontocetes were used in this study. Ten geographic zones were defined around the island, based on their general location and environmental characteristics (see Figure 1, Table 2). These geographic zones were grouped into three broad habitat categories to assess cetacean diversity for each habitat type: inner lagoon, outer reef slope (depth <500 m) and oceanic waters (depth >500 m). Encounter rate was defined as the number of sightings per unit of effort (N sightings/effort), expressed in hours. Species richness (S), which is the number of species present in an area, was considered to be an inappropriate measure of diversity on its own because it fails to take into account whether each species is rare or common. Therefore the Shannon-Weaver index (H) was also employed. The Shannon-Weaver index is one of several diversity indices used to measure diversity in categorical data. This diversity measure is derived from information theory and measures the order (or disorder) observed within a particular system. In ecological studies, this order is characterised by the number of individuals observed for each species in the sample plot:
where $P_i$ is the relative abundance of each species. The Shannon-Weaver index was calculated for the whole study area and for each of the three broad habitat categories.

Values of the median, minimum and inter-quartile ranges of depth are provided to describe bathymetric preferences for each species. Depth data provided by Service Hydrographique et Océanographique de la Marine were associated with each sighting location using an overlay technique in a GIS. After GPS track data were downloaded a track point for each second was estimated using interpolation. The tracking data were then post-processed to isolate portions of track spent ‘on effort’, which were subsequently used to calculate the effort within each 2 km$^2$ and geographic zone (Table 2, Figure 2).

**Results**

**General**

Between July 2004 and June 2006, more than 441 hours were spent in ‘search mode’, actively searching for marine mammals around Mayotte. Search effort did not vary across months and years (Kruskal-Wallis test: $H = 4.167$; df = 3: $p = 0.244$). Because the main harbour is located on the north-east coast, observation effort was greater off the east coast, in the south and the north. The western portion of the lagoon and deep oceanic waters were surveyed less (Table 1, Figure 1). Melon-headed whales *Pepenella electra*, pantropical spotted dolphins *Stenella attenuata* and spinner dolphins *S. Longirostris* had the largest group sizes (mean = 287.8, 70.9 and 72.8 respectively; Table 1), and were frequently encountered on the outer reef slope. More coastal species, such as Indo-Pacific humpback whales *Sousa chinensis* (mean = 2.4) and bottlenose dolphins *Tursiops aduncus* (mean = 6.5), had the smallest group size (Table 2).

**Diversity and distribution**

During this study, 16 odontocete species were recorded (species Richness), including 11 *Delphinidae* belonging to nine genera, two *Ziphiidae*, two *Kogiidae* and one *Physeteridae* (Table 1). The Shannon-Weaver index of diversity for the entire region was 1.76, but the index varied between geographic zones: $H = 0.57$ for the inner lagoon (four species recorded), $H = 1.31$ for the outer reef slope (five species) and $H = 0.62$ for the oceanic waters (12 species). The higher index for the outer-reef slope area was due to equitability in
abundance between the species present in this area (reflected in their group sizes) – a
community with an equitable distribution of abundances between species is more diverse
than a community with variable species abundances. Conversely, in oceanic waters, there
was greater variability in group sizes between species (high group size in delphinids vs. low
in the largest toothed whales), lowered the index. Spatial distribution of cetaceans
encountered around Mayotte was highly variable. Spinner and pantropical spotted dolphins
had similar distributions along the outer-reef slope and on the Iris Bank and were rarely
observed inside the lagoon (Figure 2). Indo-Pacific bottlenose and humpback dolphins Sousa
chinensis were observed mainly inside the lagoon and the former were also regularly
observed on the Iris Bank, in waters <40 m (Figure 3a, Table 3). Melon-headed whales were
found on the outer reef slope area and in the shallower waters of the Iris Bank, but were
never sighted inside the lagoon (Table 1 and 3, Figure 3b).

The other delphinids were oceanic species and were observed farther offshore, including
common bottlenose dolphins (mean depth at encounter, MDE=509 m), Risso’s dolphins
Grampus griseus (MDE=1,150), Fraser’s dolphins Lagenodelphis hosei (MDE=336 m), false
killer whales Pseudorca crassidens (MDE=1 168 m), short-finned pilot whale Globicephala
macrorhynchus (MDE=996 m) and pygmy killer whales Feresa attenuata (MDE=1,593 m,
Figure 3b). Although rarely encountered, larger toothed whales such as Blainville’s beaked
whale Mesoplodon densirostris (Table 3), pygmy sperm whales Kogia breviceps (MDE=705
m), dwarf sperm whales (K. sima) (MDE=919 m) and Longman’s beaked whales Indopacetus
pacificus (MDE=1 945 m), were also observed in deep waters off the barrier reef and over
the slope (Figure 3c).

**Encounter rates**

Encounter rates were derived for the coastal species (Indo-Pacific bottlenose and humpback
dolphins), pantropical spotted and spinner dolphins, melon-headed whales, oceanic
delphinids, and the large toothed whales (beaked and sperm whales) in each geographic
zone (Table 2). Although search effort varied between geographic zones, certain trends were
apparent, especially for the most common species, once sightings were standardised for this.
For coastal species, the highest encounter rate was in the western portion of the lagoon
(0.36 group h⁻¹), in the south-eastern lagoon (0.25 group h⁻¹) and on the Iris Bank (0.22 group
h⁻¹). Spinner dolphins were encountered regularly on the eastern outer slope (1.04 group h⁻¹),
but more frequently along the southern slope (1.94 group h⁻¹). A similar trend was found for
pantropical spotted dolphins in the latter area (0.93 group h⁻¹). Beaked whales were rarely
encountered and only in waters deeper than 500 m.
Discussion

To date, at least 31 cetacean species have been recorded in the south-west Indian Ocean, including 23 odontocetes (Kiszka et al. 2009). The odontocete community around Mayotte has a number of notable characteristics. Species richness within the area is high, especially in waters deeper than 500 m (12 species recorded vs. five in the outer-reef slope area and four inside the lagoon). The Shannon-Weaver index was significantly lower in oceanic waters (>500 m) and inside the lagoon, because of the high variability of abundance among species in these regions. For example, in oceanic waters, delphinids have a significantly higher abundance (defined by group size) than beaked whales and sperm whales. Conversely, on the outer-reef slope, species richness is lower (five species) but abundance there is more similar among species, making the outer-reef slope community more diverse.] A previous description of cetacean diversity around Mayotte by Kiszka et al. (2007) documented the presence of 17 species, of which 15 were odontocetes. There was also an unsubstantiated sighting (photographic evidence lacking) of a ginkgo-toothed beaked whale *Mesoplodon ginkgodens*. Our study did not confirm the presence of *M. ginkgodens* but added the pygmy sperm whale *Kogia breviceps* to the species list for Mayotte waters. In addition, the killer whale *Orcinus orca* has been observed on several occasions by whale-watching operators in the recent years (N Bertrand, Sea Blue Safari, pers. comm.). The species richness of the odontocete community around Mayotte is high relative to other tropical islands and archipelagos such as La Réunion in the Mascarenes (eight odontocete species; Dulau-Drouet et al. 2008), Great Abaco in northern Bahamas (seven odontocete species; MacLeod et al. 2004), Aldabra in southern Seychelles (12 odontocete species; Hermans and Pistorius 2008), and the whole Hawaiian archipelago (14 odontocete species; Baird et al. 2003). However, certain oceanic species that have been recorded in the South-West Indian Ocean have not yet been recorded around Mayotte. These include Cuvier’s beaked whale *Ziphius cavirostris*, the rough-toothed dolphin *Steno bredanensis* and the striped dolphin *Stenella coeruleoalba*. Their absence in this study may be an artefact of lower observation effort undertaken in offshore waters. Overall, the high diversity of odontocetes recorded around the island may be linked to the diversity of habitat types encountered there, especially in comparison to other oceanic islands that do not have lagoon or/and extended coral complexes. However, it remains difficult to compare study areas directly, because the number of species recorded is also linked to the spatial and temporal distribution of effort.

Detailed descriptions of the distributions of four delphinid around Mayotte are provided by Gross et al. (2009). Our study confirms that around the island, the Indo-Pacific bottlenose
dolphin has a coastal and shallow-water distribution. The coastal affinity of this species has been documented in other areas of the south-west Indian Ocean, such as at La Réunion (Dulau-Drouot et al. 2008) and off the south coast of Zanzibar (Stensland et al. 2006). Another species documented in our study, the Indo-Pacific humpback dolphin, was encountered infrequently, which precluded detailed analysis of its distribution and habitat characteristics. Along the outer-reef slope, spinner and pantropical spotted dolphins were encountered regularly; these were the most abundant cetacean species found around Mayotte. A comparative habitat analysis by Gross et al. (2009) confirmed that these two species overlap in their distributions, as well as in their isotopic niches, which could indicate possible competition between these sibling species. Habitat features of spinner dolphin around Mayotte are slightly different from those in other areas. In French Polynesia, Hawaii, and the Maldivian atolls, these dolphins enter atolls, sheltered bays and lagoons through reef channels in the morning and leave in the afternoon to feed overnight (Würsig et al. 1994, Anderson 2005, Gannier and Petiau 2006). Around Mayotte, the spinner dolphins under study generally inhabited the outer-reef slope, within a greater depth range than has been previously reported (Norris et al 1994, Gannier and Petiau 2006). In addition, their mean school size of 72.8 animals was slightly higher than in other areas, such as La Réunion (mean = 51.2) and in the Maldives (mean = 58.2) (Anderson 2005). The reasons why spinner dolphins do not regularly use lagoonal waters around Mayotte, even though the habitat conditions appear to be ideal for this species, remain uncertain. One possibility is that they are excluded from the lagoon by the presence of Indo-Pacific bottlenose dolphins, a larger, and possibly more dominant, territorial species. Pantropical spotted dolphins demonstrate a wide range of distribution and habitat characteristics around Mayotte, utilising both shallow and oceanic waters along the outer-reef slope. This species was most frequently observed close to the reef on the outer-reef slope. In Golfo Dulce, along the Pacific coast of Costa Rica, pantropical spotted dolphin occur in shallow waters (mean = 92.7 m; Cubero-Pardo 2007), whereas at La Réunion, the species is only encountered in relatively deep waters (mean = 881 m; Dulau-Drouot et al. 2008).

Melon-headed whales have been reported at a number of island groups, including the Hawaii archipelago, the Philippines, French Polynesia and in the Indian Ocean (Gannier 2000, 2002, Baird et al. 2003, Anderson 2005, Dolar et al. 2006, Kiszka et al. 2007, 2010, Dulau-Drouot et al. 2008, and Brownell et al. 2009). They are generally accepted as having a global distribution, preferring deep tropical and warm-temperate waters (Perryman 2002). In contrast to areas such as Hawaii, La Réunion and the Gulf of Mexico, melon-headed whales around Mayotte were encountered in shallower waters, in the vicinity of the barrier reef where they appeared to engage in resting/socialising behaviour. This daylight behaviour,
which has been observed in other areas throughout the species’ range (Brownell et al. 2009),
suggests that melon-headed whales use shallower waters to rest and socialise, but feed in
deeper waters (probably on the slope).

Several large oceanic delphinids (e.g. Risso’s dolphin, short-finned pilot whale, false killer
whale), beaked whales (e.g. Blainville’s beaked whale) and sperm whales (sperm whale,
dwarf and pygmy sperm whales) were encountered during our study, but relatively
infrequently. These species are found throughout the south-west Indian Ocean (Leatherwood
and Donovan 1991, Kiszka et al. 2009), preferring the slope and oceanic waters (Baird et al.
2003, Whitehead 2003, MacLeod and Zuur 2005). However, the encounter rate for
Blainville’s beaked whales was particularly high around Mayotte (0.09 groups h⁻¹ in waters
>500 m), similar to the rate as observed off Little Bahama Bank in the Caribbean (0.07
groups h⁻¹, MacLeod and Zuur 2005) but higher than in the main Hawaiian Islands (0.012
groups h⁻¹; RW Baird, pers. comm. Cascadia Research Collective). The abundance of
beaked whales encountered around Mayotte could be attributed to the number of broad
submarine canyons that deeply incise the outer slope of the island, which may concentrate
the main prey of these teuthophageous predators (MacLeod et al. 2003, Audru et al. 2006).

It is evident that the outer-reef slope is of primary importance in terms of density and diversity
of odontocetes around Mayotte. This particular habitat (or collection of habitats) provides
resting and foraging areas for several species, such as spinner dolphins, pantropical spotted
dolphins and melon-headed whales (Norris and Dohl 1979, Würsig et al. 1994, Brownell et
al. 2009). Many oceanic species also make regular incursions into these habitats, including
the short-finned pilot whale, which have been observed in close proximity to the barrier reef
around Mayotte while resting. Shallow waters that provide protected areas with few
predators, in close proximity to oceanic foraging habitats, apparently provides an attractive
environment for cetaceans. The affinity of cetaceans for the outer reef slope suggests
probable dependence of the cetaceans on coral reef systems as major feeding and resting
areas. The current decline of coral reefs, both at the global and regional scale in the western
Indian Ocean (MacClanahan et al. 2007), should be considered as a possible long-term loss
of toothed cetacean habitat.

Conclusion

The lagoon and adjacent outer-slope waters of Mayotte support a high diversity of toothed
cetaceans, particularly delphinids. This community includes coastal, semi-pelagic/oceanic
and oceanic species. The high diversity of species combined with the sizes of aggregations
underline the importance of Mayotte to cetaceans. It is noteworthy that there is a large overlap in the distribution of several delphinid, especially in species living along the outer-reef slope, as shown by Gross et al. (2009). Because species should occupy their own niche, some fine-scale segregation processes should occur, which need to be assessed through in-depth habitat analyses. Our results provide important, previously unavailable, descriptive information that is critical for conservation and management efforts. Human activities, especially maritime traffic fishing pressure and disturbances from commercial whale and dolphin watching activities, are escalating in the coastal and lagoon waters of Mayotte. Further effort is needed to assess the spatial and temporal interactions between maritime human activities and cetaceans around this rapidly developing island.

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<td>Pantropical spotted dolphin</td>
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**Figure legends**

**Figure 1:** Mayotte Island, showing (a) the subareas defined for encounter rate calculations and (b) spatial representation of search effort during July 2004-June 2006.

**Figure 2:** Spatial distribution of (a) spinner dolphins *Stenella longirostris* and (b) pantropical spotted dolphins *Stenella attenuata* encountered around Mayotte during July 2004-June 2006, in relation to search effort.

**Figure 3:** Spatial distribution of (a) coastal dolphins (*Tursiops aduncus* and *Sousa chinensis*), (b) oceanic dolphins and (c) the large toothed whales encountered around Mayotte during July 2004-June 2006, in relation to search effort.
Figure 3