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

Jeremy Kiszka, Peter Ersts, Vincent Ridoux

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J Kiszka[1,2]*, PJ Ersts[3] and V Ridoux[1]

[1] Formerly Observatoire des Mammifères Marins. Direction de l'Agriculture et de la Forêt & Office National de la Chasse et de la Faune Sauvage. BP 103, 97600 Mamoudzou, Mayotte; now LIttoral, ENvironnement et Sociétés (LIENSs), UMR 6250, CNRS-Université de La Rochelle, 2, rue Olympe de Gouges, F-17000, La Rochelle, France

[2]Direction de l'Environnement et du Développement Durable, Collectivité Départementale de Mayotte. BP 101 F-97600 Mamoudzou, Mayotte

[3]Center for Biodiversity and Conservation, American Museum of Natural History, Central Park West at 79th Street, New York, 10024 USA

**Corresponding author, email: jeremy.kiszka@wanadoo.fr*

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 *Tursiops aduncus*, and humpback dolphin *Sousa chinensis*), the outer reef slope (Spinner dolphin *Stenella longirostris*, Pantropical spotted dolphin *S. Attenuate* and melon-headed whale *Peponocephala electra*) and oceanic waters deeper than 500 m (e.g. Blainville's beaked whale *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. ziphiids, 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 immerged 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:

$$H = -\sum_{i=1}^{S} Pi \ln Pi$$

where *Pi* 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 *Peponephala 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 *Kogidae* 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-Drouot 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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References

Anderson RC. 2005. Observations of cetaceans in the Maldives, 1990-2002. *Journal of Cetacean Research and Management* 7: 119-135.

Au DWK, Perryman WL. 1985. Dolphin habitats in the eastern tropical Pacific. *Fishery Bulletin, Washington* 83: 623-643.

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

Baird RW, McSweeney DJ, Webster DL, Gorgone AM, Ligon AD. 2003. Studies of odontocete population structure in Hawaiian waters: results of a survey through the main Hawaiian Islands in May and June 2003. Report prepared under contract no.AB133F-02-CN-0106 from the National Oceanic and Atmospheric Administration, Western Administrative Support Center, Seattle, USA.

Ballance LT, Pitman RL. 1998. Cetaceans in the western tropical Indian Ocean: distribution, relative abundance and comparison with cetacean communities of two other tropical ecosystems. *Marine Mammal Science* 14: 429-459.

Bearzi M. 2005. Aspects of the ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in Santa Monica Bay, California. *Journal of Cetacean Research and Management* 7: 75-83.

Begon M, Townsend CR, Harper JL (eds). 2009. *Ecology: from individuals to ecosystems* (4th edn), Blackwell Publishing, Victoria, Australia.

Brownell RL, Ralls K, Baumann-Pickering S, Poole MM. 2009. Behavior of melon-headed whales, *Peponocephala electra*, near oceanic islands. *Marine Mammal Science* 25: 639-658.

Cañadas A, Sagarminaga R, Garcia-Tiscar S. 2002. Cetacean distribution related to depth and slope in the Mediterranean waters of southern Spain. *Deep-Sea Research I* 49: 2053-2073.

Chapman JL, Reiss MJ (eds). 1999. *Ecology: principles and applications* (2nd edn). Cambridge, UK: Cambridge University Press.

Corkeron PJ. 1990. Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia. In: Leatherwood S, Reeves RR (eds), *The bottlenose dolphin*. San Diego, CA: Academic Press. pp 285–293.

Cubero-Pardo P. 2007. Environmental factors governing the distribution of the bottlenose (*Tursiops truncatus*) and the spotted dolphin (*Stenella attenuata*) in Golfe Duce, South Pacific, off Costa Rica. *Invest. Mar Valparaiso* **.** 35: 15-23.

Dawbin WH. 1966. The seasonal migratory cycle of humpback whales. In: Norris KS (ed.), *Whales, dolphins, and porpoises.* Berkeley: University of California Press. pp 145–70.

Dolar ML, Perrin WF, Taylor BT, Kooyman GT, Alava MNR. 2006. Abundance and distributional ecology of cetaceans in the central Philippines. *Journal of Cetacean Research and Management* 8: 93-111.

Dulau-Drouot V, Boucaud V, Rota B. 2008. Cetacean diversity off La Réunion (France). *Journal of the Marine Biological Association UK* 88: 1263-1272.

Gannier A. 2000. Distribution of cetaceans off the Society Islands (French Polynesia) as obtained from dedicated surveys. *Aquatic Mammals* 26: 111-126.

Gannier A. 2002. Cetaceans of the Marquesas Islands (French Polynesia): distribution and relative abundance as obtained from a small boat dedicated survey. *Aquatic Mammals* 28: 198-210.

Gannier A. 2005. Summer distribution and relative abundance of delphinids in the Mediterranean Sea. *Revue d'Ecologie (Terre et Vie)* 60: 223-238.

Gannier A, Petiau E. 2006. Environmental variables affecting the residence of spinner dolphins (*Stenella longirostris*) in the Bay of Tahiti (French Polynesia). *Aquatic Mammals* 32: 202-211.

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. *Estuarine, Coastal and Shelf Science* 84: 367-374.

Guilmartin M, Revelante N. 1974. The island mass effect on the phytoplankton and primary production of the Hawaiian islands. *Journal of Experimental Marine Biology and Ecology* **16**: 181-204

Guissamulo A, Cockcroft VG. 2004. Ecology and population estimates of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Maputo Bay, Mozambique. *Aquatic Mammals* 30: 94-102.

Hermans A, Pistorius PA. 2008. Marine mammal diversity in the remote waters of Aldabra atoll, southern Seychelles. *Atoll Research Bulletin* 564: 1-7.

Jefferson TA, Barros NB. 1997. *Peponocephala electra*. *Mammalian Species* 553: 1-6.

Jefferson TA, Karczmarski L. 2001. *Sousa chinensis*. *Mammalian Species* 655: 1-9.

Karczmarski L, Cockcroft VG, MacLahan A. 2000. Habitat use and preferences of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. *Marine Mammal Science* 16: 65-79.

Kiszka J, Ersts PJ, Ridoux V. 2007. Cetacean diversity around the Mozambique Channel island of Mayotte (Comoros archipelago). *Journal of Cetacean Research and Management* 9: 105-109.

Kiszka J, Muir CE, Poonian C, Cox TM, Amir OA, Bourjea J, Razafindrakoto Y, Wambiji N, Bristol N. 2008. Marine mammal bycatch in the southwest Indian Ocean: review and need for a comprehensive status assessment. *Western Indian Ocean Journal of Marine Science* 7: 119-136.

Kiszka J, Pusineri C. 2009. Activity budgets of tropical dolphins around Mayotte. Report of Université de la Rochelle, Office National de la Chasse et de la Faune Sauvage and Collectivité Départementale de Mayotte. Mamoudzou, Mayotte (France). 21pp

Kiszka J, Berggren P, Rosenbaum HC, Cerchio S, Rowat D, Drouot-Dulau V, Razafindrakoto Y, Vely M, Guissamulo A. 2009. Cetaceans in the southwest Indian Ocean: a review of diversity, distribution and conservation issues. Report SC/61/O18 to the Scientific Committee of the International Whaling Commission.

Kiszka J, Vely M, Breysse O. 2010. Preliminary account of cetacean diversity and humpback whale (*Megaptera novaeangliae*) group characteristics around the Union of the Comoros (Mozambique Channel). *Mammalia* 74: 51-56.

Leatherwood S, Donovan GP. 1991. Cetaceans and cetacean research in the Indian Ocean Sanctuary In: Leatherwood S, Donovan GP (eds), *Cetaceans and cetacean research in the Indian Ocean sanctuary.* Marine Mammal Technical Report No 3, Nairobi, Kenya: UNEP.

Levine LA, Dayton PK. 2009. Ecological theory and continental margins: where shallow meets deep. *Trends in Ecology and Evolution* 24: 606-617.

MacClanahan TR, Ateweberhan M, Sebastian CR, Graham AJ, Wilson SK, Guillaume MMM, Bruggemann JH. 2007. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series* 337: 1-13.

MacLeod CD, Santos MB, Pierce GJ. 2003. Review of data on diets of beaked whales: evidence of niche separation and geographic segregation. *Journal of the Marine Biological Association UK* 83: 651-665.

MacLeod CD, Hauser N, Peckman H. 2004. Diversity, relative density and structure of the cetacean community in summer months east of Great Abaco, Bahamas. *Journal of the Marine Biological Association UK* 84: 469-474.

MacLeod CD, Zuur AF. 2005. Habitat utilization by Blainville's beaked whales of Great Abaco, northern Bahamas, in relation to seabed topography. *Marine Biology* 174: 1-11.

Mann J. 1999. Behavioral sampling methods for cetaceans: a review and critique. *Marine Mammal Science* 15: 102-122.

Maze-Foley K, Mullin K. 2006. Cetaceans in the oceanic northern gulf of Mexico: distributions, group sizes and inter-specific associations. *Journal of Cetacean Research and Management* 8: 203-213.

Moreno IB, Zerbini AN, Danilewicz D, de Oliveira Santos MC, Simões Lopes PC, Lailson-Brito Jose, Azevedo AF. 2005. Habitat characteristics of dolphins of the genus *Stenella* (Cetacea: Delphinidae) in the southwest Atlantic Ocean. *Marine Ecology Progress Series* 300: 229-240.

Norris KS (ed.). 1991. Dolphin day. The life and times of the spinner dolphin. New York: Norton.

Norris KS, Dohl TP. 1979. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fishery Bulletin, Washington* 77: 821-849.

Norris KS, Würsig B, Wells RS, Würsig M, Brownlee SM, Johnson C, Solow J. 1985. The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Southwestern Fisheries Center Administation Report. LJ-85-06C.

Peddemors VM. 1999. Delphinids in southern Africa: a review of their distribution, status and life history. *Journal of Cetacean Research and Management* **1**: 157-165.

Perryman WL. 2002. Melon-headed whale *Peponocephala electra* Gray, 1846. In: Perrin WF, Wursig B, Thewissen JGM (eds), *Encyclopedia of marine mammals*. San Diego, CA: Academic Press. pp 733–734.

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

Quod JP, Naim O, Abdourazi F. 2000. The Comoros archipelago. In: Sheppard C (ed.). *Seas at the Millennium: an environmental evaluation*. Oxford: Pergamon Press. pp 243-252.

Redfern JV, Barlow J, Ballance LT, Gerrodette T, Becker EA. 2008. Absence of scale dependence in dolphin-habitat models for the eastern tropical Pacific Ocean. *Marine Ecology Progress Series* 363: 1-14.

Rosenbaum HC. 2003. Marine mammals of Madagascar. In: Godman S, Bengston J (eds), *The natural history of Madagascar*. Chicago: University of Chicago Press. pp 213-216.

Ross GJB, Cockcroft VG. 1990. Comments on Australian bottlenose dolphins and taxonomic stock of *Tursiops aduncus* (Ehrenburg, 1832). In: Leatherwood S, Reeves R (eds). *The bottlenose dolphin*. San Diego: Academic Press, 653 pp.

Ross GJB, Heinsohn GE, Cockcroft VGC. 1994. Humpack dolphins Sousa chinensis (Osbeck, 1765), Sousa plumbea (Cuvier, 1829) and Sousa teuszii (Kukenthal, 1892). In: Ridway SH, Harrison R (eds), *Handbook of marine mammals*. Volume 5: The first book of dolphins. pp 23-42.

Scott MD, Shivers SJ. 1990. Distribution and herd structure of bottlenose dolphins in the eastern tropical Pacific Ocean. In: Leatherwood S, Reeves RR (ed.), *The bottlenose dolphin*. San Diego: Academic Press. pp 387–402.

Shane SH. 1990. Behaviour and ecology of the bottlenose dolphin at Sanibel Island, Florida. In: In: Leatherwood S, Reeves RR (ed.), *The bottlenose dolphin*. San Diego: Academic Press. pp 245-265.

Smolker RA, Richards AF, Connor RC, Pepper JW. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* 123: 38-69.

Stensland E, Särnblad A, Carlén I, Bignert A, Berggren P. 2006. Abundance, distribution and behavioral ecology of Indo-Pacific bottlenose (*Tursiops aduncus*) and humpback (*Sousa chinensis*) dolphins off the south coast of Zanzibar. *Marine Mammal Science* 22: 667-682.

Thiele D, Chester ET, Gill PC. 2000. Cetacean distribution in eastern Antarctica (80-150°E) during austral summer of 1995/1996. *Deep-Sea Research II* 47: 2543-2572.

Whitehead H (ed.). 2003. *Sperm whales: social evolution in the ocean*. Chicago, USA: University Chicago Press.

Würsig B, Wells RS, Norris KS, Würsig M. 1994. A spinner dolphin's day. In: Norris KS, Würsig B, Wells RS, Würsig M (eds) The Hawaiian Spinner Dolphin London, University of California Press. pp 65-102.

Würsig B, Lynn SK, Jefferson TA, Mullin KD. 1998. Behaviour of cetaceans in the Northern Gulf of Mexico relative to survey ships and aircraft. *Aquatic Mammals* 24: 41-50.

Table 1: The number of sightings, cumulative number of individuals and group size characteristics of cetaceans encountered around Mayotte from July 2004 to June 2006

Species	Common name	Number of sightings	Frequency sightings (%)	Number of individuals (cumulative)	Frequency of cumulated individuals (%)	Mean group size	Range	SD
Stenella longirostris	Spinner dolphin	177	48.5	9 242	59.7	72.8	3–500	87.1
Stenella attenuata	Pantropical spotted dolphin	85	23.3	2 553	16.5	70.9	3–300	71.9
Tursiops aduncus	Indo-Pacific bottlenose dolphin	64	17.5	414	2.7	6.5	1–15	3.5
Peponephala electra	Melon-headed whale	9	2.5	2 590	16.7	287.8	140–450	84.2
Sousa chinensis	Indo-Pacific Humpback dolphin	7	1.9	17	0.1	2.4	1–3	0.8
Mesoplodon densirostris	Blainville's beaked whale	6	1.6	14	0.1	2.3	1–5	1.6
Grampus griseus	Risso's dolphin	5	1.4	44	0.3	8.8	2–20	6.8
Tursiops truncatus	Common bottlenose dolphin	2	0.5	160	1	80	40–120	–
Pseudorca crassidens	False killer whale	2	0.5	250	1.6	125	100–150	–
Kogia sima	Dwarf sperm whale	2	0.5	3	0.01	1.5	1–3	–
Kogia breviceps	Pygmy sperm whale	1	0.3	6	0.03	6	–	–
Mesoplodon pacificus	Longman's beaked whale	1	0.3	1	0.006	1	–	–
Physeter macrocephalus	Sperm whale	1	0.3	11	0.07	11	–	–
Globicephala macrorhynchus	Long-finned pilot whale	1	0.3	60	0.4	60	–	–
Lagenodelphis hosei	Fraser's dolphin	1	0.3	120	0.8	120	–	–
Feresa attenuata	Pygmy killer whale	1	0.3	4	0.03	4	–	–
TOTAL		365	100	15 489	100	53.8	1–500	

Table 2: Search effort, number of sightings and encounter rates (in parentheses) of cetaceans encountered around Mayotte, July 2004-June 2006

Geographic zone		Number of sightings					
	Effort (h)	Bottlenose and humpback dolphins	Spinner dolphin	Pantropical spotted dolphin	Melon-headed whale	Large toothed whales	Other delphinids
Eastern slope	48.2	0	50 (1.04)	19 (0.39)	2 (0.04)	0	0
Iris Bank	46	10 (0.22)	40 (0.87)	20 (0.43)	1 (0.02)	0	0
North-eastern lagoon	75.7	12/3 (0.2)	0	1 (0.01)	0	0	0
Northern slope	14.4	0	6 (0.42)	2 (0.14)	0	0	1 (0.07)
Northern lagoon	32.5	6 (0.18)	13 (0.4)	3 (0.09)	0	0	0
South-eastern lagoon	52.6	12/2 (0.25)	2 (0.04)	2 (0.04)	0	0	0
Southern slope	23.7	0/1 (0.04)	46 (1.94)	22 (0.93)	0	0	0
Southern lagoon	56.8	16/1 (0.28)	6 (0.11)	2 (0.04)	0	0	0
Western slope	4.8	0	1 (0.21)	1 (0.21)	1 (0.21)	0	1 (0.21)
Western lagoon	22	8 (0.36)	2 (0.09)	1 (0.05)	0	0	0
Total	376.8	64/7 (0.18)	166 (0.44)	73 (0.19)	4 (0.01)	0	2 (0.01)
Entire survey area	441.9	64/7 (0.16)	177 (0.40)	85 (0.19)	9 (0.02)	11 (0.02)	12 (0.03)

Table 3: Depth preferences of the most frequently sighted cetacean species around Mayotte from July 2004-June 2006

Species	Common name	Depth (m)					
		Mean	SD	Range	Median	*Q1*	*Q3*
Stenella longirostris	Spinner dolphin	123.7	187.3	3–1 335	54	25	128.5
Stenella attenuata	Pantropical spotted dolphin	193.7	255.7	5–1 301	74	24	268.3
Tursiops aduncus	Indo-Pacific bottlenose dolphin	23	16	1–57	21	10	35
Peponephala electra	Melon-headed whale	383	286.4	20–845	400	118	560
Tursiops aduncus	Indo-Pacific humpback dolphin	17	7.7	7–28	14	12	22.5
Grampus griseus	Risso's dolphin	1 150	385	762–1 784	1 121	953	1 129
Mesoplodon densirostris	Blainville's beaked whale	1 000	365.5	482–1 524	1 070	782.5	1 143.5

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

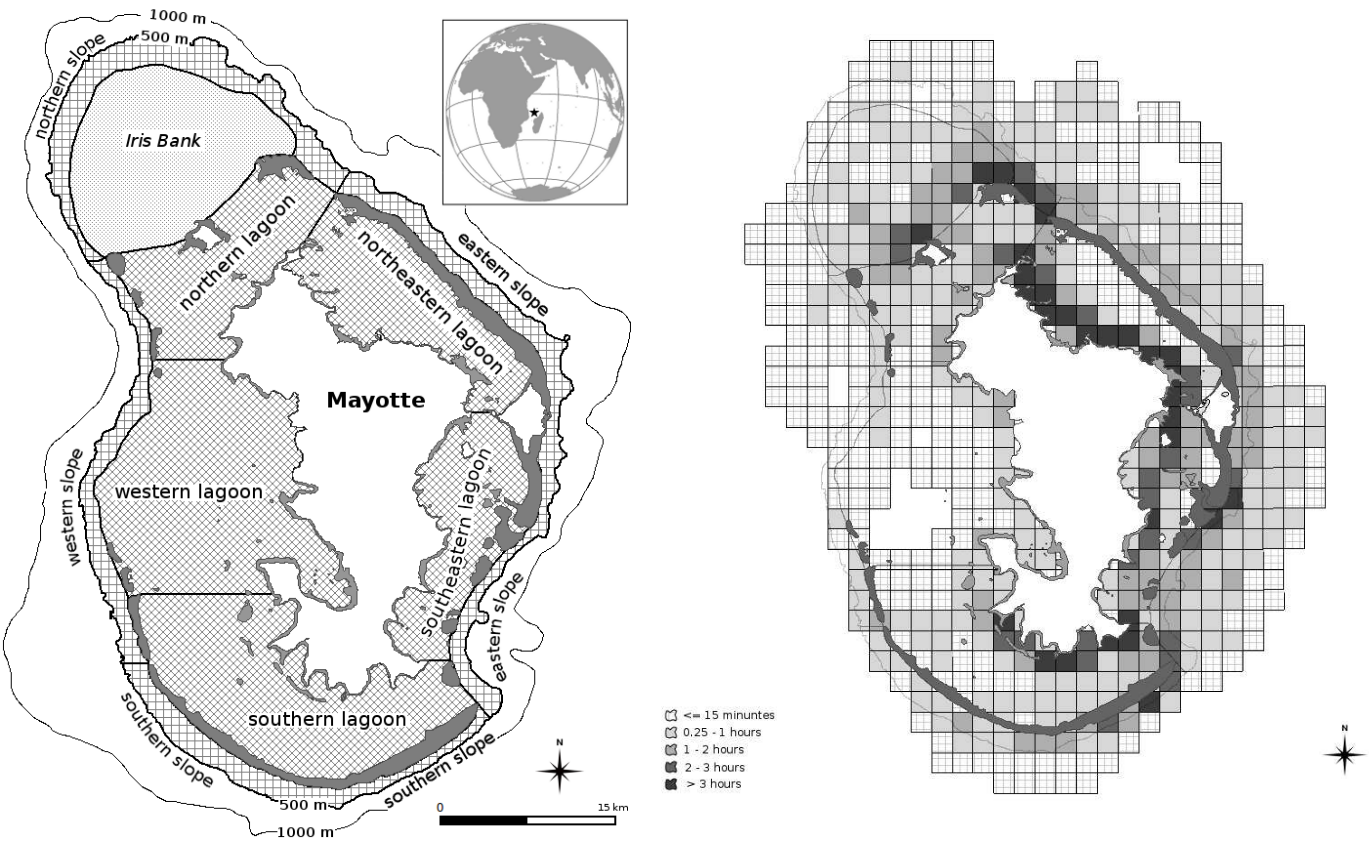

Figure 1

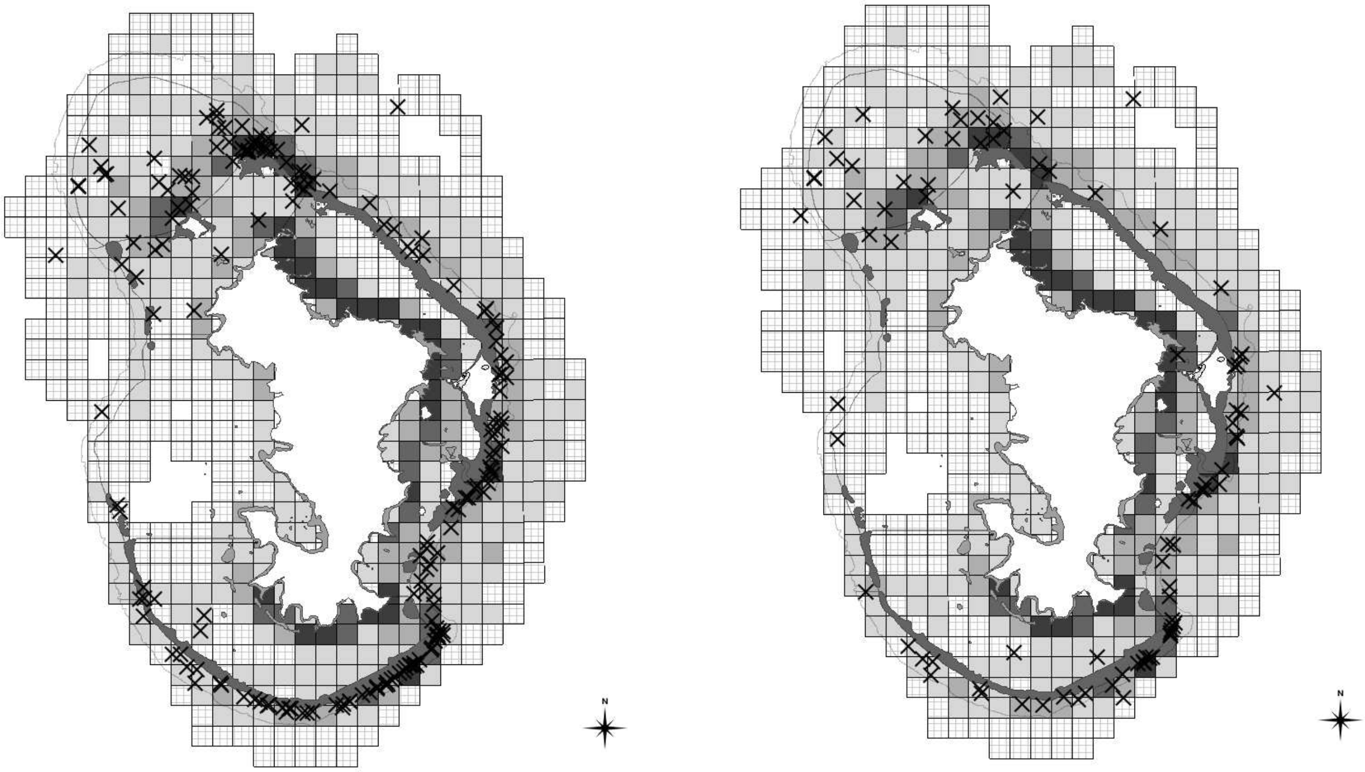

Figure 2

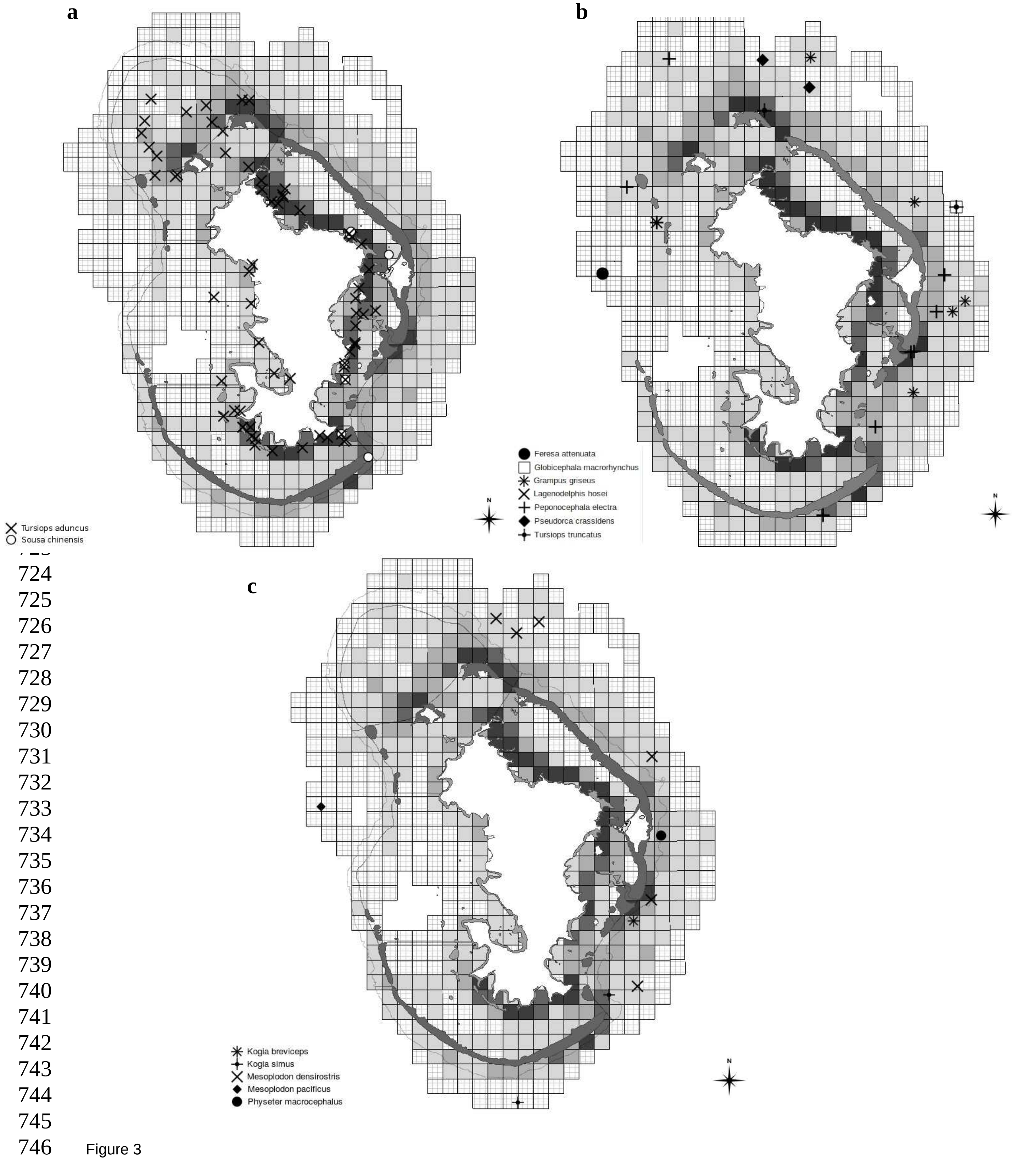
a
Tursiops aduncus
Sousa chinensis
b
Feresa attenuata
Globicephala macrorhynchus
Grampus griseus
Lagenodelphis hosei
Peponocephala electra
Pseudorca crassidens
Tursiops truncatus
N
c
Kogia breviceps
Kogia simus
Mesoplodon densirostris
Mesoplodon pacificus
Physeter macrocephalus
N

Figure 3