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Cetacean diversity off La Réunion Island (France)

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The waters of La Réunion, a French island located in the south-western Indian Ocean, have never been investigated for cetacean diversity. Dedicated daily surveys were conducted in 2004–2007 to assess cetacean diversity off the western and southern coasts of the island. A total of ten species was observed during the survey period, including two baleen whales and eight odontocetes. Four additional species that had not been observed at sea were reported stranded. The most frequent delphinid species were the Indo-Pacific bottlenose, the spinner and the common bottlenose dolphins, which were observed year-round. Photo-identification data showed a high recapture rate of Tursiops aduncus*, strongly suggesting a resident population. The humpback whale uses the coastal waters of La Réunion seasonally, during winter. The high proportion of mother–calf pairs indicated that La Réunion might represent a breeding area for this species. Pantropical spotted dolphin, melon-headed whale and Fraser's dolphin were sighted at a medium frequency, in offshore waters, and tended to favour the southern part of the island. Three coastal species were frequently using the newly created Marine Protected Area (MPA), supporting the view that cetacean conservation issues have to be included in the MPA management plan currently in progress.*

Keywords: cetacean, diversity, distribution, Indian Ocean

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INTRODUCTION

In 1979, the entire Indian Ocean was declared a cetacean sanctuary by the International Whaling Commission, to provide protection from commercial whaling to great whales. Since the creation of the sanctuary, some cetacean studies have been conducted within the Indian Ocean, both in oceanic and coastal waters, including off the eastern coast of Africa, Madagascar, Zanzibar, Mayotte, Mauritius and the Seychelles and Comoros archipelagos (for a review see Leatherwood & Donovan, 1991; De Boer *et al.*, 2002; Kiszka *et al.*, 2007). To date, published data for La Réunion Island (France) is scarce and the cetacean community is largely unknown. Dedicated cetacean research has never been undertaken around the island and strandings have been recorded consistently only since 1998. However, opportunistic sightings of spinner, spotted, common and bottlenose dolphins and other unidentified species, have been reported, in association with marine birds (Jaquemet *et al.*, 2004) and oceanic species including Risso's dolphins, killer whales, false killer whales and short-finned pilot whales have been reported to interact with offshore long-line fisheries (Poisson *et al.*, 2001).

La Réunion (55°33′E 21°07′S) is an oceanic island located 700 km east of Madagascar, on a submarine plateau which stretches over 2000 km northward from La Réunion to the Seychelles. Together with Mauritius and the Rodrigues Islands, they form the Mascarene archipelago. La Réunion is a young volcanic island, where coral reefs are discontinuous and fringe less than 10% of the coastline. The continental shelf of La Réunion is very narrow and the depth increases very rapidly near the shore (Figure 1). Sea surface temperatures (SSTs) vary from 23.4°C in winter to 28°C in summer (Conand *et al.*, 2007). The waters of La Réunion are characterized by low productivity, as indicated by the extremely clear blue waters found around the island year-round. In February 2007, a Marine Protected Area (MPA) was created on the western coast of the island, stretching over 40 km of coastline, and including waters to a depth of 30–50 m (1 km offshore on average).

In 2004, dedicated cetacean surveys were initiated in La Réunion coastal waters, with the aim of assessing species diversity around the island and collecting behavioural and photo-identification data from the main species encountered. Data collected during these surveys are presented here to provide an overview of the cetacean communities occurring in the area and some preliminary information on their occurrence and distribution.

MATERIALS AND METHODS

In 2004–2007, dedicated boat surveys were conducted on a daily basis throughout the year off La Réunion. These surveys were independent of whale-watching activities and aimed to search the entire survey area, which extended over 1000 km^2 (Figure 1). Surveys were conducted in coastal waters and up to 11 km (6 nautical miles) offshore, in the southern and western waters of La Réunion. Survey effort was constrained by the size of the vessels and port locations. Two 5 m long inflatable boats were used, at an average speed of six knots. Depending on weather conditions, the boats were launched at different locations along the coast: Saint Pierre, Etang Salé, Saint-Leu, or Saint Gilles.

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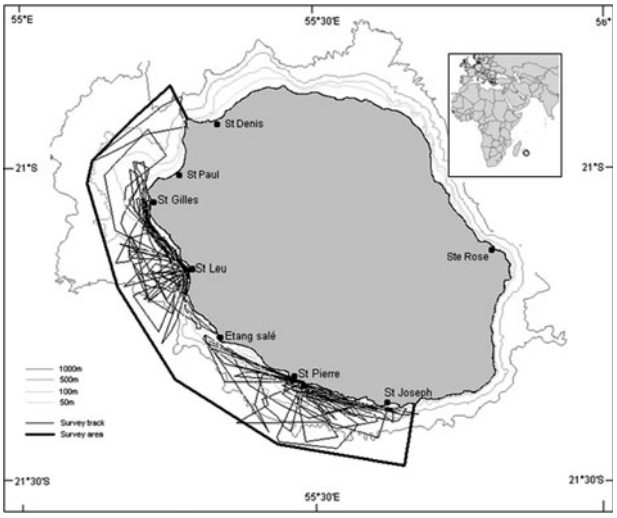

Fig. 1. Survey area and spatial distribution of effort undertaken in 2007.

Watches were undertaken by two to five observers searching the sea surface with the naked-eye. Species identification, group size estimate, time, duration of sighting, position (within 100 m from the group sighted), and behaviour data were recored. Four activity categories were distinguished as follows (Stensland *et al.*, 2006):

- Socializing: some members of the groups displaying surface behaviours such as leaping, chasing and/or engaged in physical contact with one another, including mating.
- Foraging: repeated and co-ordinated dives in varying directions, sometimes associated with observation of prey at the surface or in the dolphin's mouth.
- Travelling: dolphins moving steadily in one direction at a constant speed.
- Resting: slow movements as a tight group, sometimes logging.

When sighting positions were not obtained from a global positioning system (GPS), locations were determined by triangulation from landmarks (30% of sightings). Observer bias was relatively consistent because data were systematically collected by two of the co-authors (V.B. and B.R.), who owned the two survey boats. Only surveys with an average Beaufort sea-state of 3 or less were considered for inclusion.

With regard to observation effort, GPS positions along the vessel's track were only systematically collected in 2007 (Figure 1). Time was the only effort variable consistently reported throughout the four years and was thus used for the analysis. For each species, the encounter rate was computed for each month and expressed as the number of sightings per hour of searching effort. For the most common species, non-parametric Kruskal–Wallis tests were used to assess significant difference in monthly encounter rates. To describe species diversity, a Shannon diversity index, which takes into account both the number of species (species richness) and the evenness with which individuals are distributed among species, was calculated as follows (Begon *et al.*, 1996):

$$H = -\sum \mathrm{P}i \ln \mathrm{P}i$$

where P*i* is the ratio of the number of individuals of species *i* divided by the total number of individuals observed. Bottom depth at sighting position was acquired from Service Hydrographique et Océanographique de la Marine nautical charts, when an accurate position was available. Distance from shore was obtained using the Mapinfo© distance tool. For the most common species encountered, photo-identification was undertaken using digital cameras (Canon 10D and 20D), with a 75–300 mm zoom lens. All photographs were examined and individuals identified based on the size and location of notches on the dorsal fin (for dolphins) or on the ventral side of the fluke (for humpback whales). Individuals were considered adequately identified if the marks were large enough to be recognizable in any good-quality photograph.

RESULTS

Survey effort

In 2004–2007, 278 daily surveys were undertaken, representing a total of 1246 h of survey effort. Survey effort was spread relatively evenly throughout the months, except in June where monthly effort was increased significantly (Figure 2). Yearly survey effort ranged from 201.5 to 415 h and monthly effort averaged 18, 32, 35 and 24 h in 2004, 2005, 2006 and 2007 respectively (Figure 2).

Species accounts

During the survey period, ten different species of cetacean were encountered out of 238 sightings. The four most common species were first sighted during the first year, and additional species were encountered in subsequent years (Table 1). The overall Shannon diversity index was 0.999.

INDO-PACIFIC BOTTLENOSE DOLPHIN (*TURSIOPS ADUNCUS*)

The Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) was the most frequent species encountered in the study area, with a mean of 0.072 sightings per hour (Table 2). Identification was based on external morphology: *T. aduncus* possessed ventral spots and individuals were relatively smaller,

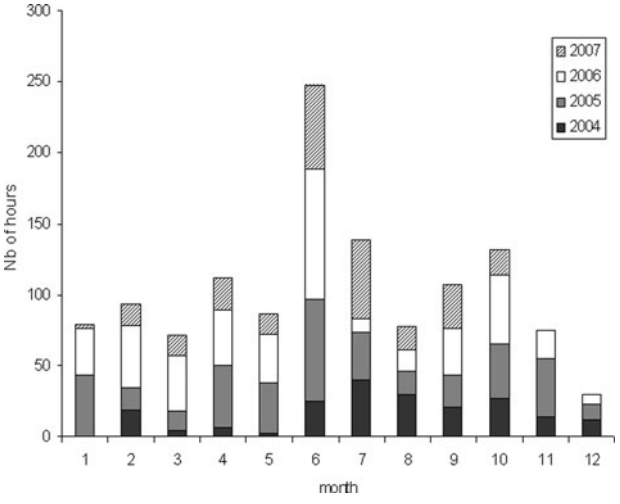

Fig. 2. Distribution of survey effort (in hours) per month and per year.

Table 1. Number of cetacean sightings per species, per year and, in parentheses, the total estimated number of individuals.

Species	2004	2005	2006	2007	Total
Tursiops aduncus	18	41	21	9	89 (838)
Tursiops truncatus	3	5	9	3	20 (908)
Stenella longirostris	10	10	5	4	29 (1473)
Stenella attenuata	–	1	8	1	10 (793)
Lagenodelphis hosei	–	3	2	1	6 (950)
Peponocephala electra	–	4	4	3	11 (4250)
Globicephala macrorhynchus	–	–	1	0	1 (50)
Physeter macrocephalus	–	–	–	1	1 (8)
Megaptera novaeangliae	13	12	13	32	70 (117)
Balenoptera bonaerensis	1	0	0	1	1 (1)
Total	44	76	63	51	238 (9388)

with a longer and more slender beak, compared to *T. truncatus* (Perrin *et al.*, 2007). The Indo-Pacific bottlenose dolphin used shallow waters (mean bottom depth of 20 m) and was always observed in waters less than 80 m deep, therefore very close to shore (Figure 3). Among all sightings, 43.2% were located in the newly created MPA. Group sizes were relatively small, with a mean of 8 individuals per school. Over the four years, *T. aduncus* was sighted every month and no consistent seasonal trend was observed (Figure 4). The monthly encounter rate did not vary significantly between months (Kruskal–Wallis test = 9.154, $P = 0.608$, df = 11). Calves were observed in 37.5% of the groups (from 1 to 2 calves per group) and were encountered each month, except in August and December. Three activity types were commonly observed: resting (44.2% of the sightings), socializing (18.6%, half of which involving mating) and foraging (10.5%). In 26.7% of the sightings, the main activity of the group could not be determined. Fifty-seven individuals were photographically identified, with 56% of them being seen more than once. Re-sightings occurred between months (27 dolphins seen in different months) and between years (20 dolphins seen in different years). Seven dolphins were seen in 5–8 different months.

Table 2. Mean water depth, distance to the shore, group size and encounter rate of cetacean species sighted during the 2004–2007 surveys, off the western and southern coast of La Réunion.

Species		Water depth (m)	Distance to shore (km)	Group size	Encounter rate (sighting/h)
Tursiops aduncus	Mean	21.9	0.65	8.2	0.072
	N	73	73	80	45
	SD	18.8	0.76	5.8	0.069
	Range	3–80	0.1–4.9	1–30	
Megaptera novaeangliae	Mean	67.1	1.12	1.7	0.064
	N	60	60	68	45
	SD	126.9	1.12	0.8	0.126
	Range	5–660	0.1–5.4	1–6	
Stenella longirostris	Mean	182.2	2.16	51.2	0.023
	N	22	22	28	45
	SD	223.7	1.88	45.1	0.041
	Range	3–720	0.1–5.6	5–200	
Tursiops truncatus	Mean	425.6	3.35	47.8	0.018
	N	18	18	19	45
	SD	248.4	1455.3	31.3	0.038
	Range	100–950	1.2–6.0	10–100	
Stenella attenuata	Mean	881.0	6.38	79.3	0.009
	N	10	10	10	45
	SD	465.6	3.27	42.5	0.029
	Range	100–1400	1.0–11.0	3–150	
Peponocephala electra	Mean	822.7	6.07	477.3	0.008
	N	11	11	11	45
	SD	197.1	2.28	323.5	0.018
	Range	500–1800	3.7–10.0	100–1000	
Lagenodelphis hosei	Mean	776.7	6.07	158.3	0.004
	N	6	6	6	45
	SD	228.6	2.92	111.4	0.014
	Range	500–1100	3.3–10.0	50–300	
Globicephala macrorhynchus	Mean	1250	1110	50	0.001
	N	1	1	1	45
	SD	–	–	–	0.004
Balenoptera bonaerensis	Mean	10	100	1	0.001
	N	1	1	1	45
	SD	–	–	–	0.004
Physeter macrocephalus	Mean	550	7300	8	0.002
	N	1	1	1	45
	SD	–	–	–	0.01

N, sample size; SD, standard deviation.

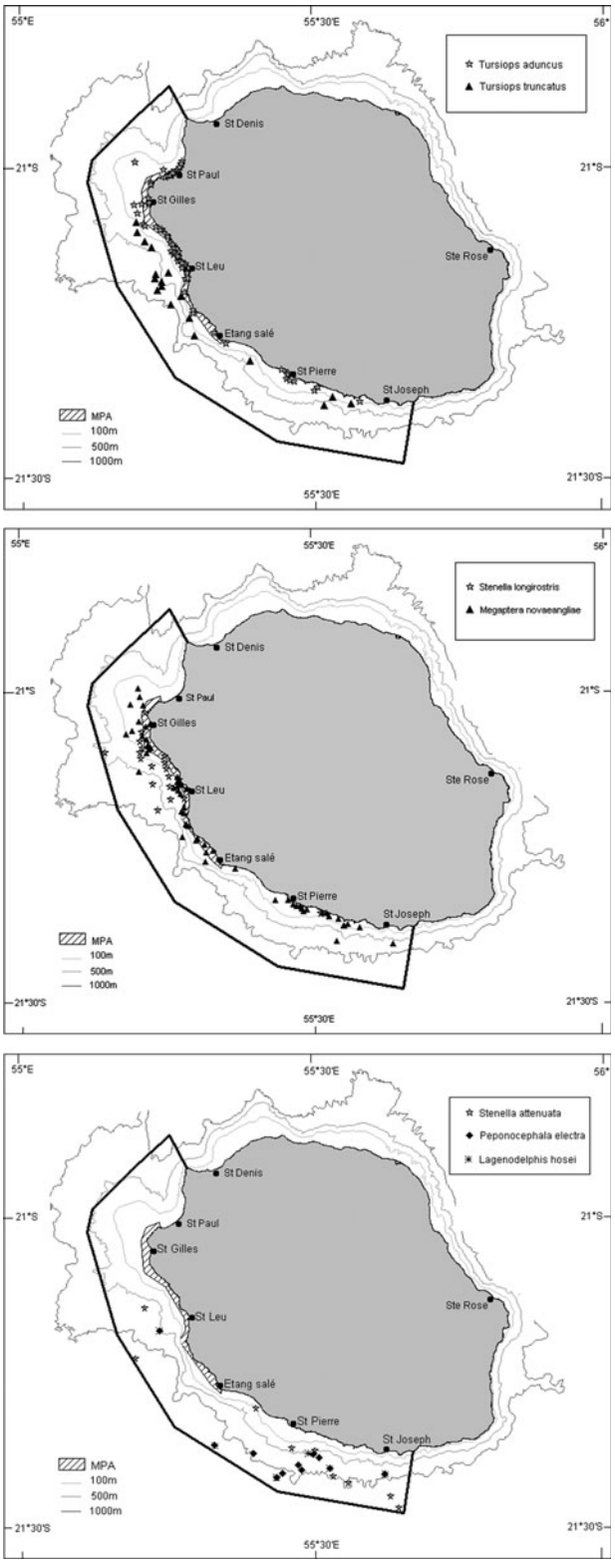

Fig. 3. Maps showing sightings positions of the main species encountered during 2004–2007 surveys and location of the Marine Protected Area (MPA).

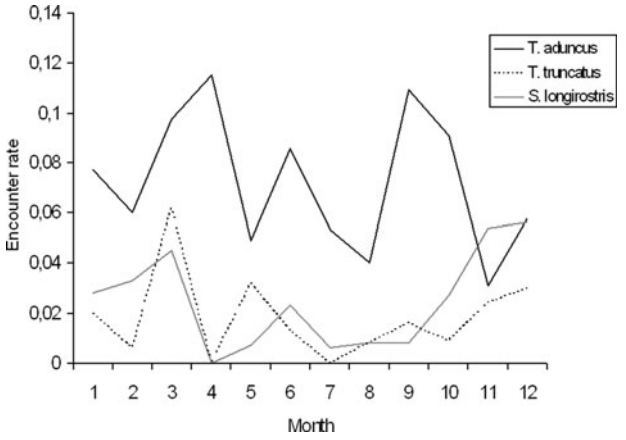

Fig. 4. Monthly encounter rate (sightings/h) of the three most frequent delphinid species encountered in 2004–2007 off La Réunion.

COMMON BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

Common bottlenose dolphins (*T. truncatus*) were also observed in the study area, although at a lower encounter rate (0.018 sightings per hour) than *T. aduncus* (Table 2). The species used deeper waters (425.6 m on average) and were thus generally observed further offshore (from 1.2 to 6 km from the coast) (Figure 3). *Tursiops truncatus* occurred in larger groups from 10 to 100 animals, with a mean group size of 48 individuals. The species was observed each month, except in April and July. No noticeable seasonal trend was observed in sighting rate (Figure 4) and monthly encounter rate did not vary significantly (Kruskal–Wallis test = 8.216, $P = 0.694$, df = 11).

SPINNER DOLPHIN (*STENELLA LONGIROSTRIS*)

With a mean of 0.023 sightings per hour, the spinner dolphin was the second most frequent delphinid species (Table 2). It was sighted in all months except April. Although the monthly encounter rate seemed to increase in October–March (Figure 4), this trend was not significant (Kruskal–Wallis test = 8.993, $P = 0.623$, df = 11). The species showed a wide depth range, with sightings occurring in very shallow waters (3 m) as well as in 720 m deep waters (Table 2). Subsequently spinner dolphins were observed as close as 100 m from shore and up to 5.6 km offshore, with 26.7% of the sightings occurring within the MPA boundaries. There was a significant relationship between bottom depth at sighting position and time of the day, with groups sighted in the late afternoon tending to occur in deeper waters than morning sightings (Pearson correlation = 0.608, $P = 0.003$). However, no clear relationship was observed between dolphin activities and bottom depth at the sighting position. Group sizes were highly variable, ranging from 5 to 200 individuals, with a mean of 51 dolphins per group. Group size appeared to vary according to the activity of the group: spinner dolphins involved in foraging were observed in larger groups (124 ind/group on average) than resting dolphins (16 ind/group on average) and this difference was statistically significant (Mann–Whitney *U*-test = 20, $P = 0.014$). However, no clear relationship appeared between group size and bottom depth (Pearson correlation = 0.020, $P = 0.933$) or distance to shore (Pearson correlation = 0.025, $P = 0.915$). In 14% of spinner dolphin sightings, they were associated with *T. aduncus* and in one occasion with a humpback whale.

PANTROPICAL SPOTTED DOLPHIN (*STENELLA ATTENUATA*)

The pantropical spotted dolphin was sighted at a lower rate (0.009/h) than the species mentioned above (Table 2). Groups were generally large, comprising an average of 79 individuals. The spotted dolphin was mainly sighted in deep waters at a mean bottom depth of 881 m and at a mean distance of 6.4 km from shore (Figure 3). On one occasion spotted dolphins were seen in a mixed group with Fraser's dolphins and melon-headed whales.

MELON-HEADED WHALE (*PEPONOCEPHALA ELECTRA*)

The melon-headed whale had a similar mean sighting rate to that of the Pantropical spotted dolphin. Melon-headed whales had the largest mean school size of all species encountered (477 ind/school), with groups ranging from 100 to over 1000 individuals. As a result, this species accounted for 45.3% of all cetaceans by number, with an estimate of 4250 animals seen over the four years (Table 1). Melon-headed whale sightings were restricted to deep waters ranging from 500 to 1800 m and were observed at an average of 6 km offshore. Subsequently, most sightings occurred in the southern part of the study area, which includes the 1000 m depth contour (Figure 3). Melon-headed whales showed a very distinctive resting behaviour, with all individuals of the groups logging at the sea surface. The majority of sightings (54.5%) were associated with Fraser's dolphins.

FRASER'S DOLPHIN (*LAGENODELPHIS HOSEI*)

Fraser's dolphin sightings occurred at a relatively low rate (0.004/h). Sightings were always associated with schools of melon-headed whales. Fraser's dolphin depth range (500–1100 m) was thus similar to that of the melon-headed whale. This species was generally observed in tightly-packed groups of 50 to 300 individuals and was often seen porpoising (i.e. leaping clear of the water).

SHORT-FINNED PILOT WHALE (*GLOBICEPHALA MACRORHYNCHUS*)

The short finned pilot whale was one of the rarer species, with only one sighting occurring on the edge of the study area, 11 km offshore, at a bottom depth of 1250 m. The group sighted comprised 50 individuals.

SPERM WHALE (*PHYSTER MACROCEPHALUS*)

Sperm whales were sighted once in the study area, 7.3 km off the western coast, at a bottom depth of 550 m. The group included eight whales observed together at the surface. All whales fluked-up as the survey boat was approaching the group.

HUMPBACK WHALE (*MEGAPTERA NOVAEANGLIAE*)

The humpback whale was the second most frequent species encountered (0.064/h) and was present around the island from early June to early November. First sightings of the season were on 13 June 2004, 4 June 2005, 14 June 2006 and 9 June 2007. Last sightings were on 11 October 2004, 6 November 2005, 22 October 2006 and 27 October 2007. Apart from three sightings that occurred beyond the 500 m depth contour, whales were all observed in waters less than 100 m deep, thus usually very close to shore (Table 2), except in areas where the 100 m contour lies further offshore such as between Saint-Paul and Saint Gilles (Figure 3). In this particular area of the western coast, whales were encountered up to 5.6 km from the shore. Most sightings of a mother with calf (81.8%) were observed in waters less than 50 m, while 37.5% of the sightings without calf were found in those shallow waters (<50 m). The newly created MPA encompasses 26% of humpback whale sightings recorded during the study period. Out of the 70 humpback whale sightings, 41% consisted of single animals, 50% of paired individuals (59% of which were mothers with calves) and 7% of groups of three individuals (mother, calf and escort). An active group of six whales was encountered on one occasion. New-born calves were mainly observed during August–October. The number of photo-identified individuals per season ranged from nine to 15, with a total of 29 whales (and two calves) photo-identified. During the study period, no match was observed between years. As to within-year re-sightings, six identified whales were re-sighted once within the same season: four whales were observed at 1–2 d intervals, while one individual was re-sighted two months after its first identification and one mother with its calf was observed over one month.

ANTARCTIC MINKE WHALE (*BALAENOPTERA BONAERENSIS*)

On one occasion in July 2004, one Antarctic minke whale was sighted very close to shore, in 10 m deep waters. The whale was approaching the boat and was observed for up to one hour.

DISCUSSION

Data limitation

The main limitation of this study was that sighting data were not consistently associated with effort data (i.e. regular GPS positions along the vessel's track were recorded only in 2007). This was due to the fact that surveys were undertaken by a local non-governmental organization that, although experienced in detection, species identification and photo-identification, did not have scientific background input regarding cetacean studies until late 2006. As a result, spatial distribution of effort was not available for the overall study period and stratification of effort according to depth could not be undertaken. It is likely that effort was not uniformly distributed within the study area, but this could not be quantified appropriately. Despite this methodological failure

limiting spatial analysis, these results provide a reliable assessment of the cetacean species occurring in La Réunion, where cetacean communities have never been investigated, and an insight into their relative frequency and distribution.

Sighting rate was expressed per hour in this study, which limited comparisons with other studies where frequencies are often expressed per distance unit. Moreover, regional comparisons were not straightforward due to different sampling units used in different studies. In this work, sighting rate was computed per month. Future distribution surveys should aim to apply line-transect methodology, for regional comparisons and abundance estimates to be undertaken and to contribute to a long-term monitoring of cetacean communities off La Réunion.

This study covered the western and southern coast of La Réunion and demonstrated that the west coast of the island, leeward, provides suitable survey conditions throughout the year. Further surveys should be focused on the northern and eastern parts of the island, which have never been investigated. The eastern coast is exposed to dominant winds and provides limited sea access, thus surveys would require larger survey boats.

Species diversity

This four year survey provides the first description of cetacean populations inhabiting La Réunion coastal waters. The ten species sighted were expected subtropical species that had all been previously reported in the south-western Indian Ocean. To date, a total of 30 species of cetaceans are known to occur in the south-western Indian Ocean (Kiszka *et al.*, 2007).

During the survey period, ten species were observed at sea over a surface area of 1000 km^2. Opportunistic sightings of right whale have also been reported in the study area in 1993, by the Natural History Museum of La Réunion (Ribes, personal communication), and in 2003 by the Aquarium de La Réunion (Durville, personal communication). During bird surveys conducted within 30 nautical miles of the western coast of La Réunion, Jaquemet *et al.* (2004) reported sightings of common dolphins (*Delphinus delphis*) in association with marine birds; a species which had not been observed during our study. Four additional species that had not been observed at sea during this study were reported stranded (dead or alive) on La Réunion coastline. These included one striped dolphin (*Stenella coeruleoalba*), two pygmy sperm whales (*Kogia breviceps*), one pygmy killer whale (*Feresa attenuata*), and probably a true beaked whale (*Mesoplodon mirus*) (V.G. Cockcroft, personal communication), over the 1998–2007 period (Van Canneyt, 2005; Stranding Network of La Réunion, unpublished data).

There is no comparative data on local cetacean communities available. The two large scale surveys conducted in the western Indian Ocean that included transects in the vicinity of La Réunion reported two sightings of *Mesoplodon* sp., one sighting of minke whale and one of spotted dolphin (Corbett, 1994; Ballance & Pitman, 1998). In terms of the number of species recorded, the coastal waters of La Réunion appear to host a species richness similar to that of other oceanic islands. Seven delphinid species (Shannon diversity index = 1.86) were reported off the Marquesas Islands, French Polynesia (Gannier, 2002), and 12 off the Society Islands (Shannon diversity index = 1.57) (Gannier, 2000), nine dolphin species around the Galapagos Islands (Smith & Whitehead, 1999), 11 species around the Cape Verde archipelago (Reiner, 1996), and 14 odontocete species in Hawaiian waters, including waters over 4000 m deep (Baird *et al.*, 2003). As to other small islands of the western Indian Ocean, eight species were reported off Mauritius (Corbett, 1994) and nine species were identified from bycatch data around Zanzibar, Tanzania (Amir *et al.*, 2005). Higher numbers of species were reported in the Maldives (20 species), Mayotte (17 species) and Comoros (14 species), probably due to a greater variety of habitat types (including large lagoon/atoll) and to the fact that these are archipelagos, rather than isolated islands (Anderson, 2005; Kiszka *et al.*, 2006a,b). However, comparisons are difficult as the number of species observed is a function of the temporal and spatial distribution of effort, which is very uneven between these survey areas.

Distribution and habitat use

The Indo-Pacific bottlenose dolphin showed a very narrow depth range and was confined to very shallow waters within 3 km of the coastline, suggesting a habitat restricted to waters within the 80 m depth contour. This outer limit appeared to be consistent with the species habitat range described in the literature (Ross *et al.*, 1987; Ross & Cockroft, 1990; Stensland *et al.*, 2006). This restricted spatial range suggests little possible movement and gene exchange with other populations in the area (Mauritius being the nearest island, 210 km apart). The restricted inshore habitat also makes this species particularly exposed to human activities, especially dolphin watching, which is increasing in the area. The common species of bottlenose dolphin (*Tursiops truncatus*) showed a distinctive distribution pattern, with all sightings occurring in 100–950 m deep waters. Therefore the spatial distribution of the two *Tursiops* species did not overlap. Group sizes also differed significantly, with *T. truncatus* usually forming larger groups. The simultaneous occurrence of *T. truncatus* and *T. aduncus* has been reported in Mayotte (Kiszka *et al.*, 2006b) and South Africa (Peddemors, 1999). It is not clear whether one or both species inhabit Madagascar's waters (Rosenbaum, 2003).

The spinner dolphin used a wider depth range (3–700 m) with a spatial distribution overlapping with the two *Tursiops* species: *T. truncatus* in deeper waters (>100 m deep) and *T. aduncus* in shallow waters (<50 m deep), with which it sometimes associates. The results show a tendency for the spinner dolphin to use inshore waters in early morning and to move further offshore later in the afternoon, which might suggest a daily pattern in habitat use. Further data are required to assess whether the coastal waters of the western coast of La Réunion provide a resting area for spinner dolphins. In fact, Würsig *et al.* (1994), who studied spinner dolphin daily movement patterns in Hawaii, demonstrated that dolphins were using inshore waters in early morning to rest/socialize and were heading offshore in the late afternoon to feed overnight. This inshore–offshore daily pattern has also been reported in several areas such as in the Maldives (Anderson, 2005), in Tahiti, French Polynesia (Gannier, 2006) and probably also occurs off Mauritius (Cadinouche, 2006). Spinner dolphins involved in foraging formed significantly larger groups than those observed resting. Other authors have reported large daily variation in spinner

dolphin school size. In Hawaii spinner dolphins merge into larger feeding aggregations at night (Norris & Johnson, 1994).

In La Réunion, the humpback whale was generally observed in waters less than 100 m deep, with mother–calf pairs favouring shallower waters (≤50 m) compared to sightings without calf. Ersts & Rosenbaum (2003) reported that females with calves in Antongil Bay, Madagascar, show a strong preference for waters less than 20 m, and referred to their need to seek out near-shore regions to protect the calf against rough sea conditions and/or large predators. Our results are thus consistent with a pattern of habitat preference on wintering ground based on social organization (Ersts & Rosenbaum, 2003).

The remaining species used deeper waters of the study area, were encountered less frequently and occurred in larger groups. The pantropical spotted dolphin was the least restricted species in terms of depth range (100–1400 m). The Fraser's dolphin and the melon-headed whale seem to prefer deeper waters (500–1800 m). These two species were mainly sighted in the southern part of the island, characterized by a steeper slope and where the 1000 m depth contour lies within 11 km of the shore (i.e. within the survey area). Melon-headed whales formed particularly large groups and although they showed a medium sighting rate, appeared to be the most abundant species in terms of estimated number of animals encountered. Bottom depths and group sizes of species observed off La Réunion were within the ranges reported in other locations of the Indian Ocean (Ballance & Pitman, 1998; Anderson, 2005).

The single sighting of short-finned pilot whales occurred on the outer limit of the study area (11 km offshore). Although this species was rare in the study area, it was frequently reported by local fishermen around offshore FADs (fish aggregating devices). Short-finned pilot whales were also reported to interact with offshore long-line fisheries, together with Risso's dolphin (*Grampus griseus*), killer whale (*Orcinus orca*) and false killer whale (*Pseudorca crassidens*) (Poisson *et al.*, 2001). The sperm whale, which was sighted once during our survey, is also reported by fishermen beyond the study area (>11 km offshore) and was reported as the most frequent species sighted during the large scale survey conducted within the western Indian Ocean (Ballance & Pitman, 1998). These observations suggest that pantropical spotted dolphin, melon-headed whale and Fraser's dolphin favour deep waters over the island slope, while pilot and sperm whales would tend to use further oceanic waters, beyond the survey area. Further offshore surveys including passive acoustic sampling are encouraged to confirm the occurrence and seasonal trends of these latter two species around the island.

The Antarctic minke whale was observed in very shallow water (<10 m), which was unexpected.

Minke whales have been mostly recorded in oceanic areas of the south-western Indian Ocean (Kasuya & Wada, 1991; Corbett, 1994; Eyre, 1995; IFREMER, personal communication).

Temporal variations

The humpback whale, which counts among the most common species sighted, was the only species showing a clear seasonal pattern, being only observed during the southern winter in La Réunion coastal waters. The species was observed around the island for a period of five months, from early June to early November, when the monthly SST ranged between 25.1 and 23.4°C (Conand *et al.*, 2007). This is consistent with the general migration pattern of the species, moving from the Antarctic feeding ground to lower latitude breeding areas in winter and with the average SST (24.6°C) observed on other wintering areas (Rasmussen *et al.*, 2007). Rasmussen *et al.* (2007) suggested that at a basin scale the distribution of wintering humpback whales is influenced by water temperature, while the availability of suitable habitat is significant at a fine scale. Humpback whales are seen over the same period in other areas of the south-western Indian Ocean (designated as wintering stock C by the International Whaling Commission) such as off Madagascar, along the East African coast (from South Africa to Kenya), around Mayotte and the Comoros (Findlay *et al.*, 1994; Best *et al.*, 1995, 1996; Rosenbaum *et al.*, 1997; Kiszka *et al.*, 2006a,b). Humpback whales are also reported around Mauritius (Corbett, 1994). In contrast, the northern Indian Ocean appears to host a resident population of humpback whales, with some individuals inhabiting the Arabian Sea year-round (Whitehead, 1985; Minton *et al.*, 2002).

The consistent observation of new-born calves strongly suggests that La Réunion represents a breeding/calving area for humpback whales. Although no recording was performed, humpback whale songs were also heard in the area during the season. Further studies should aim to include systematic acoustic recordings to confirm that reproductive activity is actually taking place in La Réunion (Tyack, 1981). During the winter season, the time interval between individual recaptures ranged from a few days to up to two months, suggesting that at least some whales showed a relatively long residency around the island. However, further photo-identification data are needed to confirm the average residency time of humpback whales in La Réunion coastal waters. Over the four years surveyed, whales wintering in La Réunion had never been re-sighted in subsequent years, suggesting changes in wintering destination from one year to the next. The migration pattern of humpback whales visiting the Mascarene Islands has never been investigated at a large scale, due to a lack of data for La Réunion, Mauritius and Rodrigues (Best *et al.*, 1998; Ersts *et al.*, 2006; Pomilla *et al.*, 2006; Rosenbaum, 2006). Comparing the La Réunion photo-identification catalogue initiated during this study with those maintained in other areas of the western Indian Ocean should provide insights into whether the Mascarene Islands should be considered as a sub-region (C4) of the East African breeding stock (IWC, 2006).

During the four years surveyed, Indo-Pacific bottlenose, common bottlenose and spinner dolphins were sighted consistently throughout the year, demonstrating a regular occurrence of these three species in La Réunion waters. The photo-identification data collected over these four years showed both within and between year re-sightings of individual Indo-Pacific bottlenose dolphins, with some individuals being observed year-round (in up to 8 different months). These results suggest that a resident population of *T. aduncus* inhabits La Réunion coastal waters. Some identified dolphins were seen only once (N = 25), supporting the need for photo-identification effort to be continued and extended to the northern and eastern part of the island, where cetacean surveys have never been undertaken. Calves were observed year-round, which tended to suggest that calving did not occur seasonally. Further analysis of photo-identification data will provide a better understanding of the

home range and habitat use of this local population. Year-round resident populations of *T. aduncus* have been observed off the southern coast of Zanzibar (Stensland *et al.*, 2006, in eastern Australia (Chilvers & Cockeron, 2003) and off Japan (Shirakihara *et al.*, 2002). A photo-identification catalogue has been recently initiated for bottlenose and spinner dolphins with the objective of providing further insight into the degree of residency of these two species. For other species, the number of sightings was too low to assess any seasonal trend in occurrence.

Inter-specific associations

Mixed species groups have long been noted in different species of mammals. Functional explanations for mixed species groups usually fall within two categories: foraging advantages and predator avoidance (Stensland *et al.*, 2003). Fifteen multi-species associations were recorded during this study, with six species involved. The most common association occurred between the spinner dolphin and the Indo-Pacific bottlenose dolphin. These associations of spinner and bottlenose dolphins occurred in shallow waters, within the depth range of *T. aduncus* (<50 m), mostly during the morning, in tight groups. Although sample size was too small to assess whether these associations were related to any specific activity, dolphins might associate to increase group size and thereby reduce predator pressure while resting. In Hawaii, Norris & Dohl (1980) suggested that spinner dolphins seek out spotted dolphin groups in order to get protection while resting in the company of the more alert spotted dolphins. Ballance & Pitman (1998) reported that in the pelagic western Indian Ocean *Stenella longirostris* was frequently associated with *S. attenuata* which was not observed during this study. Around La Réunion, spinner dolphins might favour entering inshore waters to rest, which might explain why they tend to associate more with the inshore Indo-Pacific bottlenose dolphin rather than with offshore spotted dolphins. Mixed species associations might be particularly important in La Réunion where areas of white sand bottom are scarce. Würsig *et al.* (1994) found that spinner dolphins favour shallow sandy bottom sites when resting. A white sandy bottom might allow dolphins to better localize predators during this period, when echolocation is stopped and dangers such as sharks have to be detected visually (Würsig *et al.*, 1994).

Fraser's dolphin was always sighted in association with melon-headed whales, suggesting that these two species have similar habitat requirements. Over the four years Fraser's dolphin was never observed without the melon-headed whale. This strong association pattern suggests that this behaviour provides a real functional advantage for at least one of the species (rather than both species selecting consistently the same site because they are sharing the same resources). Fraser's dolphin may seek protection by joining larger schools of melon-headed whales, which always occurred in larger numbers. Association of these two species is well-known (Jefferson & Barros, 1997) and has already been reported in the Indian Ocean, for example in Mayotte (Kiszka *et al.*, 2006b) and the Maldives (Anderson, 2005). A mixed group of three species was observed on one occasion: melon-headed whales, Fraser's dolphins and pantropical spotted dolphins, forming a group of around 700 individuals.

CONCLUSIONS

The waters of La Réunion are used by at least three species sighted year-round (Indo-Pacific bottlenose, common bottlenose and spinner dolphins) and one consistently using coastal waters seasonally (humpback whales). The three most common species (Indo-Pacific bottlenose dolphin, spinner dolphin and humpback whale) appear to utilize the newly created MPA (45 km^2), which was not purposefully designed for cetaceans. It is hoped that this study will raise awareness on the importance of the area as an ecological niche for cetaceans and will provide useful information for guiding local conservation and management decisions. Concrete cetacean conservation measures need to be included in the MPA management plan, especially to control whale and dolphin watching activities (performed by some professional operators but mostly by yachtsmen), which are increasing off the western coast of La Réunion. Other than the uncontrolled growth of this activity and the absence of official guidelines to approach cetaceans, no major threats to cetaceans have been detected for this area. The southern part of the island, which includes deeper waters and a steeper slope, appeared to provide a suitable habitat for offshore species. This region therefore provides the opportunity to study poorly known cetacean populations relatively close to shore. This research opportunity should be exploited further.

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