Occurence and residency patterns of humpback whales off Réunion Island during 2004–10

VIOLAINE DULAU-DROUOT*, JACQUES FAYAN+, LAURENT MOUYSSET* AND VIRGINIE BOUCAUD*

Contact e-mail: violaine.dulau@globice.org

ABSTRACT

Dedicated humpback whale surveys were conducted around Réunion Island during 2004–10. Boat-based surveys were conducted from June to October, in the main objective of collecting photo-identification data. For 2004–10, a total of 501 survey trips, representing 1,530 hours of on-searching effort, and 724 humpback whale sightings were achieved. Although effort had a significant influence on the number of sightings, sighting rate was shown to increase significantly from 2007 onwards, with a peak in 2008. Seasonal variations were observed, with significantly higher numbers of sightings occurring in July–September. Larger number of whales, together with increased survey effort, led to larger datasets collected in 2008–10, allowing further investigation of residency pattern. Within-year recaptures from fluke photographs showed that a relatively large proportion (30%) of the identified whales was recaptured on more than one day around the island. Maximum recapture interval reached 64 days, with a mean ranging 22–29 days for 2008–10. Mean residency, estimated from expected lagged identification rate, was 25 days. Mothers with a calf were shown to reside around the island for longer period of time than other individuals. A seasonal pattern of residency was demonstrated, with single capture individuals occurring early in the season, mainly as singleton or pairs, while individuals showing higher recapture interval were present around the island from August to October. Between-year recaptures were reported for 2009–10, with five individuals re-sighted on consecutive years. The fluke catalogue for Réunion includes 312 distinct individuals identified during 2004–10 surveys, together with 21 additional whales captured opportunistically since 2001. The increasing trend in the number of whales, the high residency time observed for 2008–10 and the recent occurrence of inter-annual recaptures suggest that Réunion Island has become an important migratory site for humpback whales within the south-western Indian Ocean (Breeding Stock C). The species might expand its spatial range by occupying new breeding sites (or re-occupying old ones) within the south-western Indian ocean, as a result of population growth.

KEYWORDS: HUMPBACK WHALE; INDIAN OCEAN; BREEDING GROUND; RESIDENCY PATTERN; PHOTO-ID; SURVEY-VESSEL

INTRODUCTION

Réunion Island is a French overseas territory. It is a small (72km long), oceanic island in the south-western Indian Ocean, located 700km east of Madagascar and 250km west of Mauritius. The island shelf is very narrow (200m depth contour lies 3km from the coast on average) and sea depth increases very rapidly near the shore, down to 3,000m deep. Since 2004, ongoing cetacean surveys have been carried out in Réunion's coastal waters (<5 n.miles offshore), and 21 species have observed to date (Dulau-Drouot *et al.*, 2008; Globice, unpubl. data). The humpback whale (*Megaptera novaeangliae*) is one of the most frequent species seen in shallow waters during the southern winter.

The humpback whale is the only species showing a clear seasonal pattern in Réunion. Sightings occur from early June to late October (although few sightings are made in November and rare sightings occurred in December 2007 and 2008 and in February 2009), which is consistent with the general migration pattern of the species. Humpback whales undertake annual migration between high latitude summer feeding areas and low-latitude winter breeding areas (Dawbin, 1966). Although major migratory corridors have been described at the basin scale (Best *et al.*, 1998), knowledge of humpback whale migration pattern in the south-western Indian Ocean is still incomplete. Best *et al.* (1998) proposed three principal migratory streams: one on the east coast of southern Africa, one along the Madagascar Ridge, and one in the central Mozambique Channel. The International Whaling Commission (IWC) designated seven breeding population (stocks A–G) in the Southern Hemisphere (IWC, 1998). The south-western Indian Ocean is considered as Breeding Stock C, sub-divided into 3 major subpopulations (IWC, 2000): C1, along the east coast of South Africa to Mozambique; C2, central Mozambique channel islands (Comoros, Aldabra, Eparses islands); and C3, coastal waters of Madagascar. The possibility of a further breeding sub-region, C4, in the Mascarene Islands (Réunion, Mauritius and Rodrigues) has been proposed (IWC, 2011b). However, because limited information was available, humpback whales from this region were not considered in the assessment of Breeding Stock C conducted recently by the Scientific Commission of the IWC (IWC, 2011a). Although the presence of the species has been reported in Réunion, Mauritius and Rodrigues little published data exist (Corbett, 1994; Dulau-Drouot *et al.*, 2008). There is evidence that whaling on humpback whales took place in Mauritius at the end of the 18th century (logbook from the ship *Asia*, 1791–94), but the Mascarene Islands did not appear to represent a whaling ground for humpback whales in the 19th century (Townsend, 1935). In the 20th century, although modern whaling expanded in South Africa, Mozambique and Madagascar (Tønnessen and Johnsen, 1982), no catch records are available from the Mascarene Islands. Therefore, there is no existing long term data for the species in this area. In this paper results are presented on sighting rate, residency patterns and movements of

* *Groupe Local d'Observation et d'Identification des cétacés (GLOBICE), 30 Chemin Parc cabris, Grand Bois, 97 410 Saint Pierre, La Réunion, France.*
+ *Brigade Nature Océan Indien (BNOI)/ONCFS, 12 Allée de la Forêt – Parc de la Providence, 97400 Saint Denis, La Réunion, France.*

humpback whales in Réunion, from data collected during 2004–10 southern winters.

MATERIAL AND METHODS

Data collection

Dedicated boat surveys were conducted throughout the year off La Réunion (55°33'E, 21°07'S) from 2004 to 2010. Humpback whale data were collected, from June to October, in the coastal waters of the island. Surveys boats of similar sizes (5m long on average) were used and were launched at different locations along the coast: Saint Pierre; Etang sale; Saint-Leu; Saint Gilles; Le Port; and Sainte Marie. The spatial distribution of effort was constrained by general weather conditions, port locations and boat availability. The west coast is sheltered from dominant winds and was therefore mostly covered. Surveys off the northern coast were limited due both to difficult weather conditions during winter and lack of boat available in this area. No boat was available in Saint Rose, so the eastern coast of the island, exposed to dominant winds, was not covered during this study.

During surveys, watches were undertaken by 3–5 observers, searching the sea surface with the naked-eye. The same type of survey boats were used across years, thus the observers were surveying at a consistent height above the water surface. Searching effort was recorded by noting time, GPS position and sea state condition every 15 minutes. When humpback whales were sighted, the group size and composition were recorded, together with behavioural data. This sighting phase dedicated to data collection was considered off-effort. Groups of whales were classified into five categories based on group size and composition and according to behavioural characteristics previously described for this species (Tyack and Whitehead, 1983): singletons, pairs, mother-calf pair, mother-calf-escort and competitive groups. Groups that did not fall into one of these categories were classified as 'undetermined'. Whenever possible during humpback whale encounters, photographs were taken of the ventral side of the fluke and of both sides of the dorsal fin. Digital cameras (*Canon* 10-50D, *Sony* A100) equipped with 75–300mm lenses were used.

Data analysis

Humpback whale sighting rate was computed for each survey trip, by dividing the number of humpback whale sightings by the number of hours on-effort (include only searching phases and excluding time spent on sighting of any cetacean species) and expressed as the number of sightings per hour of searching effort. Mean sighting rates were calculated monthly and annually. A Generalised Linear Model (GLM) analysis was applied to determine whether variations in sightings numbers could be attributed to annual differences, and/or if other factors, such as month surveyed, area prospected and survey effort were expected to have a significant influence. The response variable being count data (number of sightings), a Poisson loglinear regression was applied, including three categorical variables as predictors: 'year'; 'month'; and 'area', with 'effort' as a covariate. The study area was divided into three zones: northern; western; and the southern part of the island (the eastern coast was not surveyed). All statistical tests were conducted using *SPSS*.

Within-year recaptures were assessed by comparing all fluke photographs taken within each year survey. For each individual, the best image of the fluke and, when available, of the right and left side of the dorsal fin were catalogued. The choice of the most representative image was based on both the quality of the photograph and the distinctiveness of pigmentation features of the ventral fluke (Friday *et al.*, 2000). In cases where multiple pictures were needed to allow a complete identification, several fluke photographs were chosen to represent an individual in the catalogue. All photographs of the catalogue were rated for quality on a five-level scale: excellent; good; fair; poor; and not useable. Photographs in the latter category were discarded from the comparison process. The portion of the fluke visible above the surface was also recorded. Flukes were classified into the nine pigmentation categories of the Antarctic Humpback Whale Catalogue (AHWC, *http://www.coa.edu/antarctic*). Photograph not selected for the catalogue were saved in archive files. Comparisons of the fluke catalogue of each year were undertaken to assess between-year recaptures. A 'capture' was defined as the first identification of an individual (based on a photograph of the pigmentation pattern in the ventral surface of the fluke), and a 'recapture' was defined as the subsequent photographic re-identification of the same individual.

Due to the small number of photographs available from 2004–07 and the small number of recaptures recorded these years, only 2008–2010 data were used to assess residency and movement pattern from within-year recaptures. Recaptures of animals identified more than once during the same day were not taken into account, so that within-year recaptures relate only to individuals identified in different days. For individuals re-sighted on multiple days, residence time was assessed by calculating the maximum recapture interval: time interval (in days) between the first capture and the last recapture of the whale. Residency was also investigated using the sighting histories of all individuals (including those seen only once), by computing the lagged identification rate (LIR). The LIR is an estimate of the probability that an individual identified in the study area at any time will be identified again in the study area some time lag later (Whitehead, 2001) and is calculated as follows:

$$R(\tau) = \frac{\sum_{j,k|(t_k - t_j)=\tau} m_{jk}}{\sum_{j,k|(t_k - t_j)=\tau} n_j \cdot n_k}$$

Where n_j is the number of individuals identified on occasion j; m_{jk} is the number of individuals identified on both occasions j; and t_j is the time of identifications at occasion j.

Lagged identification rates were first calculated for all adult whales identified in 2008–10. The LIR was then computed for mothers with a calf separately, to asses any difference in their residency pattern compared to other individuals. The observed lagged identification rates were fitted to exponential mathematical models of residency (Whitehead, 2001). Models were fitted with maximum likelihood methods. The Akaike Information Criterion (AIC) was used to determine the best fitting model and bootstrap

techniques were used to calculate 95% confidence interval and standard errors of LIR and model parameters (Whitehead, 2007). Lagged identification rates computation and residency model fitting were carried out using the computer software *SOCPROG* 2.4 (Whitehead, 2009).

RESULTS

Survey effort and data collected

Searching effort deployed from June to October increased with year, ranging from 120 hours on-effort (29 survey trips) in 2004 to 378 hours (141 survey trips) in 2008 (Table 1). In 2008–10, survey effort was intensified, as a response to the increase abundance of whales; an average of 21, 26 and 34 survey trips were conducted per month in 2008, 2009 and 2010 respectively (Table 1). The spatial coverage of effort tended to expand across years as well, with the northern part of the island being only covered in 2008–10 (Fig. 1). The western and southern parts of the island were covered every year, while the eastern part had never been surveyed during the whale season (Fig. 1).

A total of 720 humpback whale sightings were undertaken from June to October during 2004–10 surveys. The number of humpback whale groups sighted increased with year, to reach a maximum of 272 sightings in 2010 (Table 1). More photo-identification data were collected during 2008–10, as a result of increased survey effort and increased number of whale sightings. Subsequently, the number of individuals identified from fluke photograph increased across years. In 2004–06, 7 individuals were identified per year and 17 in 2007. The number of identified whales increased notably in 2008, 2009 and 2010, with respectively 83, 80 and 116 adult individuals captured. In addition, 12 individuals were photographically identified in years prior to the present survey (9 in 2003, 2 in 2002 and 1 in 2003), although these were not associated with effort data. Furthermore, 9 individuals were identified from fluke photograph taken

Table 1

Details of survey effort carried out during the humpback whale season (June–October) at Reunion Island in 2004–10.

	Number of survey trips	On-effort survey (in hour)	Number of HW sightings	Mean sighting rate (sighting/hour)	Number of identified individuals
2004	**29**	**120.5**	**12**	**0.1**	**7**
June	5	22.3	1	0.04	1
July	7	28.5	6	0.21	5
August	7	27.5	2	0.06	0
September	4	18	2	0.11	0
October	6	24.3	1	0.04	1
2005	**36**	**171.5**	**10**	**0.06**	**7**
June	13	70	7	0.10	5
July	7	36.5	1	0.03	1
August	3	16.5	0	0.00	0
September	5	18.5	2	0.11	1
October	8	30	0	0.00	0
2006	**42**	**192.3**	**13**	**0.08**	**7**
June	18	90.8	3	0.03	0
July	3	10	2	0.20	2
August	4	15	2	0.13	2
September	7	30	1	0.03	2
October	10	46.5	5	0.11	1
2007	**55**	**153.5**	**53**	**0.52**	**17**
June	19	52.4	14	0.27	6
July	13	30.4	12	0.39	6
August	5	12.18	10	0.82	2
September	14	44.6	16	0.36	2
October	4	13.9	1	0.07	1
2008	**91**	**207**	**168**	**1.06**	**83**
June	7	16.6	3	0.18	1
July	19	39.6	24	0.60	7
August	21	53.2	60	1.13	44
September	25	50.3	53	1.05	26
October	19	47.2	28	0.59	4
2009	**107**	**306.3**	**196**	**0.81**	**80**
June	4	12.6	0	0.00	0
July	27	67.8	53	0.78	36
August	33	98.8	50	0.51	30
September	26	77.7	68	0.88	7
October	17	49.4	25	0.51	7
2010	**141**	**378.5**	**272**	**0.92**	**116**
June	5	16.7	0	0.00	1
July	26	76.7	26	0.34	19
August	43	102.7	118	1.15	59
September	36	94.7	105	1.11	31
October	31	87.7	23	0.26	6

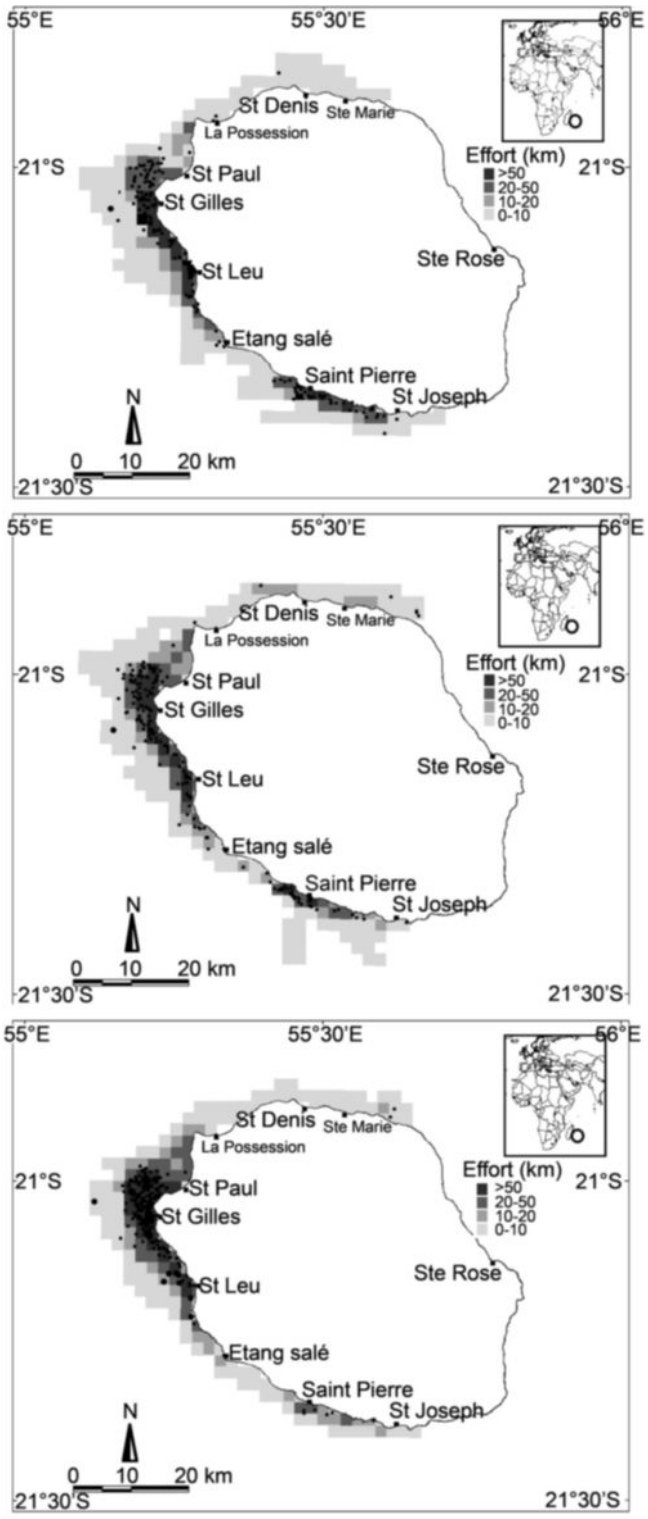

Fig. 1. Map of Réunion showing distribution of effort (2×2km grid) and humpback whales sightings from (A) 2008, (B) 2009 and (C) 2010 surveys.

opportunistically in 2009 and 2010. These additional data were included in when undertaking between-year comparisons.

Sighting rate

The annual sighting rate increased from a mean of less than 0.1 sighting hr^{-1} during 2004–06 to a mean of 0.5 sighting hr^{-1} in 2007, and reached a peak of 1.1 sighting hr^{-1} in 2008 (Table 1). In 2009 and 2010, the mean sighting rates

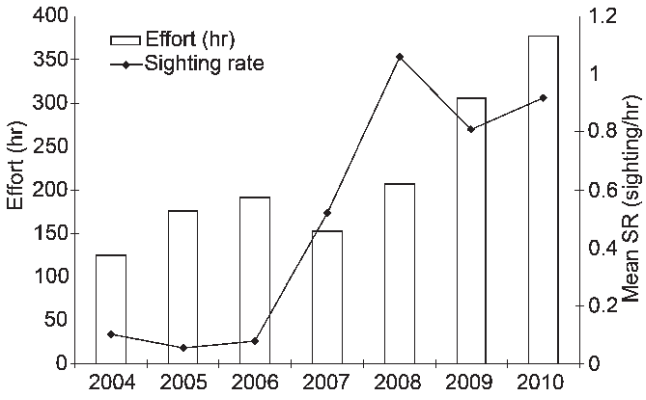

Fig. 2. Humpback whale mean encounter rate (sighting hr^{-1}) observed in 2004–08 in Réunion. Error bars indicate SE. Dotted line indicate a rate of increase of 10.3% from 2004 value.

remained relatively consistent (0.81 and 0.92 sighting/hour respectively), although higher effort was achieved (Fig. 2).

The output of Poisson regression indicates that years, months and effort were highly significant in determining the observed variation in the number of whale sightings, while the area did not appear to be a significant explanatory variable (Table 2). Therefore, for a given month and effort, there was no significant difference in the number of sightings made in different survey areas whereas there was a significant effect of year. The results of the Wald χ^2 tests indicate that the number of sightings was significantly higher in July, August and September, than in October and June (Table 3). Negative parameters for years 2004–07 indicate that the number of sightings was lower over this period than in 2010 (reference year), and the difference was statistically significant for years 2005 and 2006 ($\chi^2 = 1.505$, $p = 0.017$, $\chi^2 = 1.543$, $p = 0.01$, respectively). In 2007 and 2009, the number of sightings was not significantly different to 2010, while in 2008 significantly higher numbers of sightings were observed ($\chi^2 = 1.018$, $p = 0.001$). Therefore, the regression analysis confirms, for a fixed month and effort, an increased humpback whale occurrence in 2007–2010, with a peak observed in 2008. The odd ratios indicated there were 4 times less sightings in 2005 and 2006 than in 2010 and 2.7 times more sightings in 2008 compared to 2010.

Group size and structure

Groups ranged from 1 to 8 individuals, with a mean group size of 2.2 individuals. Of the 720 groups sighted, 26.7% were singletons, 20.7% pairs, 24.9% mother-calf pairs, 8.5% mother-calf-escort, 11.3% competitive groups and 8.3%

Table 2

Overall test of significance of the effect of zone, year, month and effort in the loglinear model.

Tests of model effects (Type III)			
	Wald χ^2	df	*p*
Intercept	0.215	1	0.643
Area	5.202	2	0.074
Year	53.591	6	<0.001
Month	33.993	4	<0.001
Effort	47.113	1	<0.001

Table 3
Analysis of coefficient estimates and the significance of each of the variables included in the loglinear regression.

			95% Wald confidence interval		Hypothesis test			
Parameter	Estimate (β)	Std. error	Lower	Upper	Wald χ^2	Df	p	Odd ratio Exp(β)
(Intercept)	0.279	0.3828	–0.472	1.029	0.530	1	0.467	1.322
Zone=North	–0.752	0.3653	–1.468	–0.036	4.235	1	0.049	0.471
Zone=West	0.123	0.2619	–0.390	0.636	0.221	1	0.638	1.131
Zone=South	0[a]	–	–	–	–	–	–	1
Year=2004	–1.062	0.6084	–2.254	0.130	3.047	1	0.081	0.346
Year=2005	–1.505	0.6307	–2.741	–0.268	5.690	1	0.017	0.222
Year=2006	–1.543	0.5973	–2.714	–0.373	6.678	1	0.010	0.214
Year=2007	–0.043	0.3552	–0.739	0.653	0.014	1	0.904	0.958
Year=2008	1.018	0.2968	0.436	1.600	11.768	1	0.001	2.768
Year=2009	0.399	0.2108	–0.014	0.812	3.583	1	0.058	1.490
Year=2010	0[a]	–	–	–	–	–	–	1
Month=6	–.246	0.4147	–1.059	0.567	0.352	1	0.553	0.782
Month=7	0.558	0.2644	0.040	1.076	4.452	1	0.035	1.747
Month=8	0.656	0.2451	0.175	1.136	7.159	1	0.007	1.927
Month=9	1.140	0.2352	0.679	1.601	23.513	1	<0.001	3.127
Month=10	0[a]	–	–	–	–	–	–	1
Effort (hours)	0.038	0.0056	0.027	0.049	47.113	1	<0.001	1.039
(Scale)	3.307[b]	–	–	–	–	–	–	–

[a]Set to zero because this parameter is redundant (reference variable). [b]Computed based on the Pearson chi-square.

were undetermined. This latter category included mainly groups of 3–4 individuals not showing any surface active behaviour. Therefore, calves were observed in 33% of the sightings. The proportion of each group type varied across months (Fig. 3). Early in the season, in June and July, more than 80% of the sightings consisted of singletons or pairs of individuals. During the season, the number of groups including a calf increased consistently. By October, 64.1% of the sightings consisted of mother-calf pairs or mother-calf-escort groups. Competitive groups were mainly observed in August and September (Fig. 3).

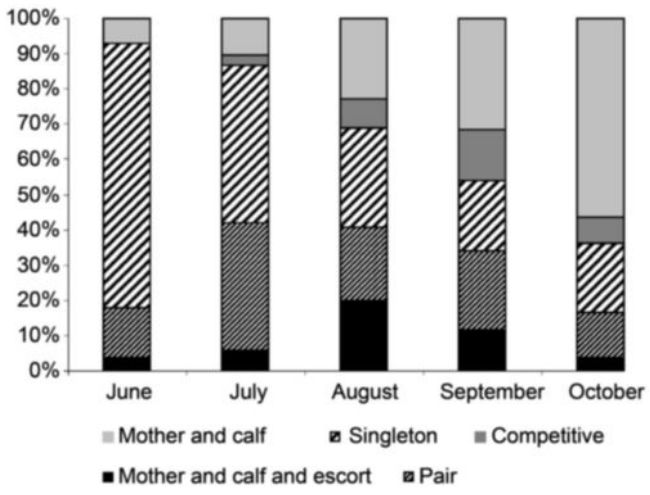

Fig. 3. Monthly distribution of sightings according to group types (2004–10).

Within-year recaptures and time residency

In 2008, 2009 and 2010 within-year recapture rates were relatively high, reaching 30%, 20% and 42% of the 83, 80 and 116 individual identified respectively. Therefore, on average over these three years, 69.4% of the identified individuals were captured only once, while 30.6% were recaptured on more than one day over the season. Overall, there was a trend for individuals captured only once to occur early in the season: 79% of the whales photographically identified in July were single capture individuals while in September and October the majority of the whales identified consisted of recaptures (65 and 68% respectively).

The number of recaptures per individual ranged from 2–7 in 2008 and 2009 and up to 12 in 2010, with most recaptured whales been seen 2–7 times on different days (88%). Although most of the recaptured whales were not seen often, their maximum recapture interval was relatively high and consistent, with a mean of 22 (±SE = 2.8) days in 2008, 29 (±SE = 5.3) days in 2009 and 23 (±SE = 2.3) days in 2010. The longest interval between first and last recaptures was 45, 64 and 60 days in 2008, 2009 and 2010 respectively. Thus, no whale has been observed in Réunion over a period of more than two months within the same year. Among all individuals recaptured on more than one day, 31% were re-sighted after an interval of less than 10 days (28 individuals), 32% were sighted around the island between 11 to 30 days (29 individuals) and the remaining 36% stays over more than 31 days (33 individuals) (Fig. 4). Of the 90 individuals recaptured within 2008, 2009 and 2010 seasons, 11 were females accompanied by a calf and 8 were 'escort'. Mother-calf pairs showed a significantly longer residency than other individuals, with a capture interval of 36 days on average (Table 4), ranging from 19 to 60 days (T-test = 3.59, p = 0.003). Individuals escorting a female with a calf tended to have relatively long residency as well, with a mean capture interval of 28 days, ranging from 19 to 56 days, however, the difference was not significant statistically (T-test = 1.136, p = 0.286).

The residency model best fitting the overall lagged identification rate (Goodness of fit χ^2 = 39.9, df = 39, p = 0.4291) indicates that there were approximately 32 whales (31.7 ±SE = 3.7, 95% CI = 26.3–41.9) in the study area at any one time and the estimated mean residence time of individuals was 25 days (25.1 ±SE = 2.92, 95% CI = 20.5–31.5)

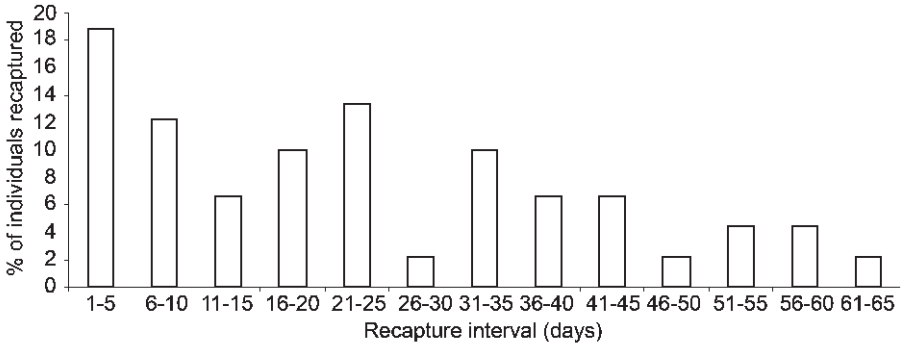

Fig. 4. Distribution of the individuals captured in 2008, 2009 and 2010 off Réunion (in percentage), according to the maximum recapture interval (in days).

When computed separately, the LIR of mother with calf appeared to be higher than those of other individuals, with the observed rates remaining relatively high for of up to 45 days (Fig. 5). Therefore, the probability of recapturing a mother with a calf after its first capture was higher than for other whales, indicating that mothers with calves tended to reside longer in the study area compared to other individuals. The parameter estimates of the fitted model indicate that there were five (4.7 ±SE = 1.37, 95% CI = 2.7–7.8) mothers with a calf at any one time in the study area and their mean residence time was 53 days on average. Other individuals (males or females without a calf) showed a lower probability of being recaptured with lag time (Fig. 5). They occurred in greater numbers, with approximately 30 individuals present at any given time in the study area (29.9 ±SE = 4.1, 95% CI = 23.5–40.9) and were expected to reside for a shorter period of time (24 days ±SE = 3.0, 95% CI = 19.3–30.9).

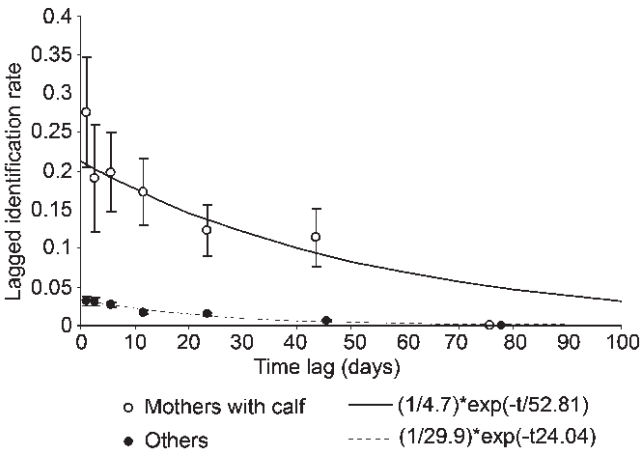

Fig. 5. Lagged identification rate of mother with calf and other individual humpback whales identified in 2008–10 in Réunion, together with the expected lagged identification rates from residency models. Vertical lines are standard error.

Spatial movement

The distance between recaptures of individuals ranged from 0.2 to 75km. On average, the whales moved along the coast at a rate of 3.3km per day, with displacement rate ranging from 0.02km to 52km day^{-1} (Table 4). The maximum distance travelled in one day (52km) correspond to a whale sighted off Saint-Gilles and resighted south of Saint-Pierre the day after. There was no difference in mean displacement rate between mother-calf pairs, escorts and other individuals (Kruskal-Wallis Test = 0.672, $p = 0.715$). Displacement was not significantly correlated with time lag and there was no evidence of any coordinated movement pattern of whales: different whales could either move long distance in one day or remain in the same area for several days. Individuals recaptured on at least seven occasions during 2008–10 are presented in Fig. 6, where re-sightings of mother-calf pairs ($n = 6$), escort ($n = 3$) and other individuals ($n = 3$) were linked with direct separated lines to better visualise long-distance movements. Although most recaptures occurred off Saint Gilles, where most effort was conducted, whales appear to be travelling around the island, and thus using all of the coastline, during their stay in Réunion, independent of whether they are mothers with a calf, escorts or other individuals (Fig. 6).

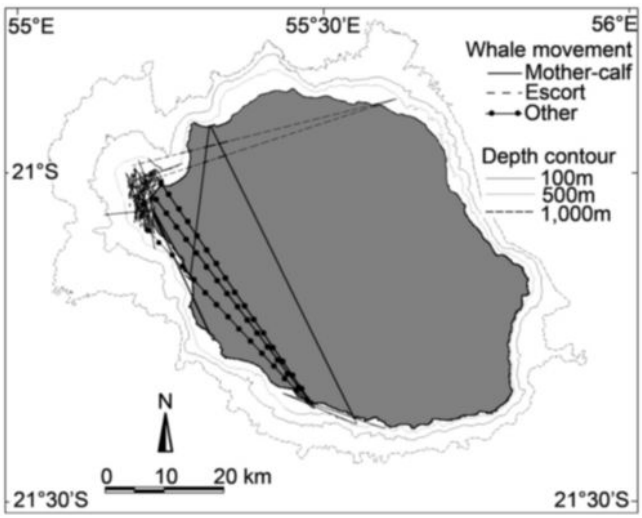

Fig. 6. Map showing re-sightings of whales recaptured seven times or more during 2008–10 season, linked by a direct line to illustrate movements of mother-calf, escort and other individuals separately.

Between-year recaptures

Five between-year recaptures were found during the study period (2004–10). All were first captured in 2009 and recaptured in 2010 at Réunion. Therefore of the 80 individuals identified in 2009, five came back to Réunion the following year. Among them, one individual appeared to be a female, observed with a calf in 2010. The gender of the four other recaptured individuals was not known, although they were all sighted at least once in competitive groups and

Table 4
Descriptive statistics of recapture intervals and displacement rates of individuals recaptured on different days during 2008–10 seasons.

		Recapture interval (days)				Displacement rate (km/day)			
	N	Mean	SD	Min	Max	Mean	SD	Min	Max
Overall	86	23.1	17.9	1	64	3.26	5.10	0.04	28.78
Cow-calf	12	36.6	14.1	19	60	2.17	2.46	0.45	8.55
Escort	8	27.9	17.7	3	56	3.59	3.83	0.68	10.68
Other individuals	68	20.4	17.4	1	64	3.38	5.52	0.04	28.78

were thus involved in reproductive activity. An additional between-year recapture was recorded from an individual first identified in 2003 (before the study period) and recaptured during the 2010 survey at Réunion, when it was sighted 8 times over a 56 day period. This individual was observed both in 2003 and 2010 as escorting a mother with a calf, and was thus suspected to be a male. There was no consistency in the timing of the first capture day between years, with sightings occurring from 2 to 33 Julian days from the date of their initial capture year.

Therefore, taking account of between-year matches, the final catalogue included 312 different individuals captured in Réunion Island during 2004–10 surveys, five of which were recaptured on consecutive years. Fluke photographs of 21 individual whales were also available from previous years (2001–03) and opportunistic photographs (2009–10), allowing a seven year interval recapture. Altogether, the catalogue from Réunion includes 322 individuals identified from fluke photographs up to 2010.

DISCUSSION

The results show a significant increase in humpback whale numbers visiting Réunion during 2007–10 compared to previous years (2004–06). Increases in humpback whale numbers have been inferred in others sites of the south-western Indian Ocean such as in Sainte Marie, on the East coast of Madagascar (F.X. Mayer, pers. comm.) and in Zanzibar (P. Berggren, pers. comm.), although no published data are available from these areas. The increase in sighting frequency observed in Réunion or other localised places might result from an increase in humpback whale population at a regional scale. Using mark-recapture data collected from Antongil Bay in 2000–07 (Cerchio *et al.*, 2008), an annual growth rate of 8% has been estimated for Madagascar (breeding sub-stock C3, Johnston and Butterworth, 2008). However, the increase in humpback whale sightings observed in 2008–10 in Réunion appears to be larger than the medium rate of population increase estimated for Madagascar and exceeds the maximum plausible rate of increase of 11.8% yr^{-1} established from the examination of life-history parameters in humpback whales (Zerbini *et al.*, 2010). Therefore, although part of the rise observed in recent years in Réunion might result from a population growth at a regional level, other factors have to be considered. An increased immigration to Réunion Island might reflect a density-dependent response of whales within Breeding Stock C, whereby whales investigate new sites (or re-occupy historical ones) as other sites are becoming saturated because of recent population growth. First movements of individual humpback whales from Madagascar to Réunion have been reported recently (Dulau-Drouot *et al.*, 2011). Although an analysis of exchange probability has not been conducted yet, these preliminary results tend to support the hypothesis that Réunion might represent an extension of the Madagascar wintering area as oppose to a separate entity (sub-stock C4) within the south-western Indian Ocean. Furthermore, the recent between-year recaptures reported in the present study suggest that some degree of site fidelity might have begun to occur at Réunion. However, most whales captured at Réunion have been sighted in only one year indicating a general trend for whales to use different breeding sites across the years. Studies on major breeding areas of the south-western Indian Ocean have shown low site fidelity between years (Cerchio *et al.*, 2008; Ersts *et al.*, 2006) and evidence of exchanges of individuals between eastern Madagascar and the northern Mozambique Channel (Ersts *et al.*, 2011). Therefore migration movement of humpback whales between breeding sites of the south-western Indian Ocean might be particularly complex. Other environmental factors such as changes in water temperature, might also affect migration routes and choice of breeding areas. However, to date, the forces driving migrations on a fine scale remain unclear (Rasmussen *et al.*, 2007).

Humpback whales were present in coastal waters of Réunion from early June to late October, with a peak in July–September. The consistent occurrence of newborn calves and competitive groups in the present study confirm that Réunion Island represents a breeding area for the species in the south-western Indian Ocean, as suggested in previous studies (Dulau-Drouot *et al.*, 2008).

Within-year recapture results from 2008–10 data showed that an average of 30% of the captured whales were observed on multiple days, with a mean recapture interval ranging from 22–29 days and a maximum residency of 64 days. These recapture rates and intervals are respectively higher and longer when compared to other studies. In Antongil Bay (Madagascar), within-year recapture rate ranged 6–18% of individuals captured on more than one day and mean recapture interval ranged from 3–8 days (Cerchio *et al.*, 2008). In the Pacific, Cerchio (1998) reported that the percentage of recaptured whales in Kauai Island (Hawai'i) ranged from 5–14%, with a mean re-sighting interval of 15 days. Thus, within-year recapture intervals demonstrate relatively high residency of humpback whale in Réunion. These variations might be explained by differences in the size and remoteness of the survey area and survey effort, together with differences in the size and composition of the population. In fact, the probability of recapturing a whale

decreases with increasing survey area and population size. Réunion Island is isolated and relatively small (207km of coastline) with steep underwater slope, restricting humpback whale habitat within 2km from the coast, excepted off Saint Gilles where 100m contour lies 7km from the coast (Dulau-Drouot *et al.*, 2008). Overall, the habitat used by humpback whales around Réunion corresponds to an area of 345km², while Antongil Bay (Madagascar) for example encompasses 1,800km² (Cerchio *et al.*, 2008) with adjacent potential habitat. Furthermore differences in survey effort are observed between studies. In Antongil Bay, Cerchio *et al.* (2008) reported a mean sampling effort of 31 days per season spanning from mid-July to mid-September, while in this study, an effort of 91 to 141 survey trips was achieved from early June to late October in 2008–10. Thus, larger sampling effort, spanning a larger period, might explain the larger recapture intervals obtained in Réunion compared to Madagascar. Réunion being located at a higher latitude compared to Antongil Bay, the breeding season might span a longer period (allowing extended survey effort), as whales might afford to stay longer in southern sites before heading back to Antarctic feeding grounds. Despite an increased effort deployed in 2009 and 2010, relatively consistent recapture intervals were found in 2008–10 in Réunion, suggesting that they are representative estimates of time residency in the survey area. This was confirmed by the lagged identification rate analysis, leading to similar expected residency (25 days).

The results demonstrate a significantly higher residency time for mothers accompanied by a calf compared to other individuals. Furthermore, a seasonal trend was observed in recapture rates, whereby individuals captured in July tended to be sighted only once while the proportion of recaptured individuals increases from August to October. These results suggest that the earlier part of the season encompass mostly individuals with transient residency, while the later part of the season hosts individuals using Réunion coastal waters for a longer period. Therefore, the island seems to represent an 'endpoint destination' for at least some of the whales migrating to Réunion, which remain in coastal waters for a relatively long period (maximum of two months). This seems to be particularly the case for mothers with calves, showing a recapture interval of 36 days on average and expected mean residency (from LIR) of 53 days. Other individuals, including escorts, have also been observed for extended lengths of time (maximum recapture interval of 28 days on average). A seasonal pattern in group structure was also demonstrated, with sightings made early in the season consisting mostly of singletons and pairs of individuals, competitive groups being most frequently observed in August, and mother-calf pairs mainly occurring later in the season, in September and October. This seasonal trend is consistent with the migratory timing described for the species. Both historical catch data and photo-identification studies have demonstrated that humpback whale migration to and from the winter grounds were segregated on the basis of age, sex and reproductive condition (Dawbin, 1997; Graig *et al.*, 2003). Females in late pregnancy or with newborn calves are among the last whales to arrive at the wintering grounds and the last to migrate back to the feeding ground. The year they give birth, females might tend to extend their stay in the feeding ground to maximise their food intake prior to parturition and lactation and to delay their departure from the breeding ground until their calf is sufficiently robust to enhance their chance of survival during their first migration to higher latitude (Graig *et al.*, 2003).

Analysis of spatial movement showed that whales re-sighted on multiple days moved around the island at a rate of 3.3km per day on average. Although the eastern and northern coasts were not or poorly surveyed, opportunistic sightings from land were consistently reported from these areas (Globice, pers. comm.), supporting the view that whales are using the coastal waters of the entire island. In contrast, the majority of captured whales (69% on average for 2008–10) were observed only once. These individuals showing transient residency were mostly encountered early in the season, suggesting a trend for individuals arriving early in the season to stopover in Réunion, before moving to other breeding area such as Mauritius, the Seychelles archipelago or the Tromelin islands. Land based surveys conducted in Tromelin, indicate that this small island of 1km² located 535km North of Réunion also hosts humpback whales during the austral winter, with competitive groups and new born calves being observed there (Globice, unpublished data). Interestingly, no peak of newly identified individuals was observed at the end of the season (the discovery curve flattens out in September–October), suggesting that no (or very few) whales from lower latitude breeding grounds are transiting to Réunion on their southward migration. To date, no inter-regional recaptures of individuals from Réunion have been reported with other sites of the south-western Indian Ocean on the same year, so migration routes are still largely unknown. Further inter-regional comparisons will be encouraged to improve knowledge and understanding of humpback whales migratory movements.

ACKNOWLEDGEMENTS

We thank the Conseil Régional de la Réunion and DIREN-Réunion for having funded part of this study, and all GLOBICE volunteers and BNOI staff who participated to the surveys. We are also grateful to BNOI, Croisière and Découvertes, Excelsus and private boat owners for providing survey platforms; and to external observers who sent opportunistic fluke photographs. Thank you to the anonymous referees, whose useful comments helped in improving the manuscript and to Aurore Fleurette for her help with the statistical analysis.

REFERENCES

Best, P.B., Findlay, K.P., Sekiguchi, K., Peddemors, V.M., Rakotonirina, B., Rossouw, A. and Gove, D. 1998. Winter distribution and possible migration routes of humpback whales, *Megaptera novaeangliae*, in the southwest Indian Ocean. *Mar. Ecol. Prog. Ser.* 152: 287–99.

Cerchio, S. 1998. Estimates of humpback whale abundance off Kauai, Hawaii, 1989 to 1993: evaluating biases associated with sampling the Hawaiian Islands wintering assemblage. *Mar. Ecol. Prog. Ser.* 175: 23–34.

Cerchio, S., Ersts, P., Pomilla, C., Loo, J., Razafindrakoto, Y., Leslie, M., Andrianrivelo, N., Mindon, G., Dushane, J., Murray, A., Collins, T. and Rosenbaum, H.C. 2008. Revised estimation of abundance for breeding stock C3 of humpback whales, assessed through photographic and gentypic mark-recapture data from Antongil Bay, Madagascar, 2000–2006. Paper SC/60/SH32 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 20pp. [Paper available from the Office of this Journal].

Corbett, H.D. 1994. The occurrence of cetaceans off Mauritius and in adjacent waters. *Rep. int. Whal. Commn* 44: 393–98.

Craig, A.S., Herman, L.M., Gabrielle, C.M. and Pack, A.A. 2003. Migratory timing of humpback whales in the central North Pacific varies with age, sex and reproductive status. *Behaviour* 140: 981–1,001.

Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp.145–70. *In*: Norris, K.S. (eds). *Whales, Dolphins, and Porpoises*. University of California Press, Berkeley and Los Angeles. xv+789pp.

Dawbin, W.H. 1997. Temporal segregation of humpback whales during migration in Southern Hemisphere waters. *Mem. Queensl. Mus.* 42(1): 105–38.

Dulau-Drouot, V., Boucaud, V. and Rota, B. 2008. Cetacean diversity off La Reunion island (France). *Journal of the Marine Biological Association of the UK* 88(6): 1263–72.

Dulau-Drouot, V., Cerchio, S., Jouannet, V., Ersts, P., Fayan, J., Boucaud, V. and Rosenbaum, H. 2011. Preliminary comparison of humpback whale photographic identifications indicates connectivity between Reunion (BS C4) and Madagascar (BS C3). Paper SC/63/SH28 presented to the IWC Scientific Committee, June 2011, Tromsø, Norway (unpublished). 10pp. [Paper available from the Office of this Journal].

Ersts, P.J., Pomilla, C., Kiszka, J., Cerchio, S., Rosenbaum, H.C., Vély, M., Razafindrakoto, Y., Loo, J., Leslie, M. and Avolio, M. 2011. Observations of individual humpback whales utilizing multiple migratory destinations in the southwestern Indian Ocean. *African Journal of Marine Science* 33(2): 333–38.

Ersts, P.J., Pomilla, C., Rosenbaum, H.C., Kiszka, J. and Vély, M. 2006. Humpback whales identified in the territorial waters of Mayotte [C2] and matches to eastern Madagascar [C3]. Paper SC/A06/HW12 presented to the IWC Workshop on Comprehensive Assessment of Southern Hemisphere Humpback Whales, Hobart, Tasmania, 3–7 April 2006 (unpublished). 7pp. [Paper available from the Office of this Journal].

Friday, N., Smith, T., Stevick, P. and Allen, J. 2000. Measurement of photographic quality and whale distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. *Mar. Mammal Sci.* 16(2): 355–74.

International Whaling Commission. 2011a. Report of the Scientific Committee. Annex H. Report of the Sub-Committee on Other Southern Hemisphere Whale Stocks. *J. Cetacean Res. Manage. (Suppl.)* 12: 203–26.

International Whaling Commission. 2011b. Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales, 4–7 April 2006, Hobart, Tasmania. *J. Cetacean Res. Manage. (special issue 3)*: 5–50.

International Whaling Commission. 1998. Report of the Scientific Committee. Annex G. Report of the sub-committee on Comprehensive Assessment of Southern Hemisphere humpback whales. *Rep. int. Whal. Commn* 48:170–82.

Johnston, S.J. and Butterworth, D.S. 2008. Updated assessments of Southern Hemisphere humpback whale breeding stock C and its component sub-stocks. Paper SC/60/SH38 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 18pp. [Paper available from the Office of this Journal].

Rasmussen, K., Palacios, D., Calambokidis, J., Saborio, M.T., Dalla Rosa, L., Secchi, E.R., Steiger, G.H., Allen, J.M. and Stone, G. 2007. Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biology Letters* 3(3): 302–05.

Tønnessen, J.N. and Johnsen, A.O. 1982. *The History of Modern Whaling*. C. Hurst and Co., London. i–xx+798pp.

Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica (NY)* 19(1–2): 1–50+6 maps.

Tyack, P. and Whitehead, H. 1983. Male competition in large groups of wintering humpback whales. *Behaviour* 83: 132–54.

Whitehead, H. 2001. Analysis of animal movement using opportunistic individual-identifications: Application to sperm whales. *Ecology* 82: 1417–32.

Whitehead, H. 2007. Selection of models of lagged identification rates and lagged association rates using AIC and QAIC. *Communications in Statistics-Simulation and Computation* 36(6): 1233–46.

Whitehead, H. 2009. SOCPROG programs: analyzing animal social structures. *Behavioural Ecology and Sociobiology* 63: 765–78.

Zerbini, A.N., Clapham, P.J. and Wade, P.R. 2010. Assessing plausible rates of population growth in humpback whales from life-history data. *Mar. Biol.* 157(6): 1225–36.

Date received: June 2011.
Date accepted: November 2011.