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Humpback whale (*Megaptera novaeangliae*) post breeding dispersal and southward migration in the western Indian Ocean

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ABSTRACT

Investigating movement patterns of marine migratory species is critical to understand habitat use and population structure, and help inform conservation and management planning. Little is known about humpback whale (*Megaptera novaeangliae*) dispersal and migration in the western Indian Ocean. In October 2011 and 2012, eleven satellite transmitters were deployed on wintering humpback whales from the south-western Indian Ocean breeding stock at the Comoros islands (Mohéli, n = 6 and Mayotte, n = 5). Eight individuals were successfully tracked for 24.3 ± 12.4 days (range = 8–49 days) and travelled between 146 km and 5804 km in total. Whales either remained at their wintering site for several weeks (n = 3) or dispersed along the west coast (n = 4) or east (n = 1) coast of Madagascar where two main stop-over sites were identified. In addition, two individuals travelled along straight paths to distant, potential, foraging areas. One whale reached the French sub-Antarctic islands while the other travelled to one of the supposed Antarctic foraging areas for humpback whales of this breeding stock. This is the first time movements of humpback whales from this area are being described and their potential foraging areas in the Southern Ocean identified. Identification of these dispersal patterns is important for delineation of breeding regions and for allocating abundance estimates to stocks.

1. Introduction

In the context of rapid global environmental changes, investigating dispersal movements of individuals among and within populations has been stressed as a pressing research issue (e.g. Grémillet and Boulinier, 2009; Newson et al., 2009; Ponchon et al., 2012). The dispersal of individuals between breeding sites is one of the key mechanisms behind the spatial dynamics of populations, as well as in gene flows within meta-populations (Clobert et al., 2001). Such dispersal behaviour has been mainly described in birds (e.g. Dall et al., 2005) but also in some mammals (e.g. Selonen and Hanski, 2010) including humpback whales (*Megaptera novaeangliae*). In this latter species, capture–mark–recapture, genetic and tracking studies have suggested some degree of dispersal within the same breeding region (i.e., between breeding sites; e.g. Cerchio et al., 1998; Garrigue et al., 2011; Lagerquist et al., 2008; Rosenbaum et al., 2009) and among breeding regions (e.g. Stevick et al., 2011), between and within breeding seasons.

Humpback whales undertake extensive seasonal migrations from high latitude foraging habitats to low latitude, coastal waters for calving and mating (Dawbin, 1966). In the south-western Indian Ocean, three main breeding sub-regions within the breeding region C have been described by the International Whaling Commission (IWC) based on historical whaling data and contemporary surveys (e.g. Best et al., 1998; Wray and Martin, 1983), photo-identification (Ersts et al., 2011b), and genetic studies (Rosenbaum et al., 2009). The coastal waters of south-eastern Africa, i.e. from Mozambique to Tanzania, constitute the breeding sub-region C1 (Findlay et al., 1994; Fleming and Jackson, 2011; IWC, 2011), the coastal waters of the northern Mozambique Channel Islands (i.e. Comoros archipelago), the west coast of Madagascar and the southern Seychelles, the breeding sub-region C2 and the coastal waters of southern and eastern Madagascar, i.e. Antongil Bay and Sainte-Marie Island, the breeding sub-region C3 (Fleming and Jackson, 2011; IWC, 2011; Rosenbaum et al., 1997). A breeding sub-region C4 including the Mascarene Islands has also been proposed recently (Dulau-Drouot et al., 2011; Fleming and Jackson, 2011; IWC, 2011). DNA analyses and recaptures of individuals have

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suggested connectivity between Mayotte (Comoros archipelago, C2) and Antongil Bay (Madagascar, C3, Ersts et al., 2011b) but a genetic differentiation between Mayotte and East South Africa/Southern Mozambique (C1) has been found (IWC, 2011; Rosenbaum et al., 2009). The connectivity and dispersal of humpback whales within and among these breeding sub-regions are, however, still poorly understood (Cerchio et al., 2009; Ersts et al., 2011b; Fleming and Jackson, 2011; IWC, 2011; Pomilla, 2006; Pomilla et al., 2006). Such information is critical not only for the sustainable management of this species in the southwestern Indian Ocean but also for our understanding of breeding habitat selection, migratory fidelity and ultimately individual responses to global environmental changes.

In the past 10 years, tracking studies of humpback whales have started to give a deeper understanding of dispersal movements in wintering and summering areas in both hemispheres: i.e. North Pacific, (Lagerquist et al., 2008; Mate et al., 1998), South Pacific (Garrigue et al., 2010, 2011), Southern Ocean (Dalla Rosa et al., 2008), South Atlantic (Zerbini et al., 2006), and North Atlantic (Heide-Jørgensen and Laidre, 2007). Yet, tracking studies of humpback whales in the western Indian Ocean have only recently started.

Here, we investigated the dispersal of satellite-tracked adult humpback whales at the end of their breeding season in the southwestern Indian Ocean and during their post-breeding migration. Specifically, this study aimed to investigate (1) how individual whales disperse within and among breeding sub-regions within the same breeding season, (2) assess whether individuals from the same breeding sub-region use similar migratory routes and stop-over sites along these routes, and (3) identify the main foraging area(s) of these whales. This study was carried out in the breeding sub-region C2, i.e. the Comoros archipelago, where humpback whales are known to mate from July to October each year (Ersts et al., 2011a; Kiszka et al., 2010) and for which additional data on population structure and dispersal are needed (Fleming and Jackson, 2011; IWC, 2011).

2. Material and methods

2.1. Study area and tag deployment

The study was conducted in the Comoros archipelago: off Mohéli Island (12°24′S, 43°45′E) between 11 and 14 October 2011 and off Mayotte Island (12°49′S, 45°09′E) between 2 and 20 October 2012. Eleven satellite transmitters were deployed on adult humpback whales (Table 1). Daily searches for whales were conducted from a rigid inflatable boat. When a whale was sighted, it was initially photographed to enable identification using dorsal fin and/or fluke markings prior to instrumentation (Katona and Whitehead, 1981). This avoided double-tagging of the same individual and allowed comparison of the whale's markings with existing individual identifications. A satellite tag was then deployed into the left or right flank of the whale about 0.5–1 m ahead of the dorsal fin and usually within 0.7 m from the midline of the whale's body. Two configurations of satellite transmitters were used: nine transmitters were “implantable” tags (SPOT5, Wildlife Computers, USA, 10 cm long by 2 cm diameter cylinder) while two transmitters were “mini-swing” tags (SPLASH, Wildlife Computers, USA, 53 × 35 × 25 mm). Both types of transmitters were attached to a stainless steel anchoring system equipped with foldable barbs and a triangular sharp tip. The SPOT5 tags were deployed with the ‘ARTS’ (Air Rocket Transmitter System), i.e. a modified pneumatic air gun, at about 8 to 10 m from the whale set at pressure of 11 bars (Heide-Jørgensen et al., 2001). The SPLASH tags were deployed using an 8 m long fibreglass pole at about 4 to 5 m from the whale (Heide-Jørgensen et al., 2003). In 2011, transmitters were configured to transmit everyday from 3 am to 6 pm (GMT), as long as the saltwater switch (SWS) was out of the water while in 2012 transmitters were configured to transmit between 8 am to 8 pm everyday. The sex of eight satellite-tracked humpback whales was determined by molecular analysis (Bérubé and Palsbøll 1996) of genomic DNA extracted using the Qiagen DNeasy Blood and Tissue kit DNA from skin samples obtained by biopsy sampling (Palsbøll et al., 1992). No skin samples could be collected for three individuals but for two of them, we assumed they were female because they were the adult individual in a cow–calf pair.

2.2. Data analysis

Locations were collected via the ARGOS system (https://argos-system.cls.fr). A Location Class (LC) is associated with each location and ranges from A, B, 0, 1, 2, to 3 in increasing order of position accuracy. Argos locations of all qualities but LC 0 were included in route reconstruction (Hays et al., 2001; Witt et al., 2010). The data were then filtered in STAT (Satellite Tracking and Analysis Tool, http://www.seaturtle.org/stat/) using a maximum rate of travel of 12 km/h (maximum swimming speed reported for humpback whales, Mate

Table 1
Transmitters deployed on humpback whales *Megaptera novaeangliae* wintering off Mohéli Island and Mayotte Island, Comoros archipelago in 2011 and 2012.

Whale ID no.	Sex	Tag type	Tagging date	Tagging location	Tag longevity (days)	No. of locations received	No. of locations used	Distance travelled (km)
22851	M[a]	SPOT5	11 Oct 2011	12°24′29.4″S 43°36′38.7″E	28	60	11	749
33000	F[b]	SPOT5	12 Oct 2011	12°24′43.3″S 43°37′15.9″E	18	98	79	146
37236	F[b]	SPOT5	11 Oct 2011	12°24′43.3″S 43°37′15.9″E	0	0	0	0
20157	F[a]	SPLASH	13 Oct 2011	12°26′33.7″S 43°19′44.3″E	0	0	0	0
20690	F[a]	SPLASH	14 Oct 2011	12°27′45.0″S 43°43′23.2″E	8	51	23	506
27261	F[a]	SPOT5	11 Oct 2012	12°57′20.3″S 44°55′41.0″E	18	165	107	471
27262	M[a]	SPOT5	11 Oct 2012	12°59′43.9″S 44°54′29.6″E	20	181	139	460
37227	F[a]	SPOT5	12 Oct 2012	12°59′00.0″S 44°14′00.0″E	20	145	84	1155
37228	F[a]	SPOT5	18 Oct 2012	12°26′05.1″S 43°37′24.4″E	0	0	–	–
37235	Unidentified	SPOT5	21 Oct 2012	12°49′16.4″S 44°56′21.6″E	49	236	127	5804
37278	M[a]	SPOT5	21 Oct 2012	12°49′16.4″S 44°56′21.6″E	33	150	93	3715

[a] Determined by molecular analysis (see Material and methods).
[b] Assumed to be a female because it was the adult individual in a cow–calf pair.

et al., 1998) and a maximum azimuth of 35° between successive locations. Filtered positions were then mapped and tracks were reconstructed for individual whales. For calculating distance and rate of travel for each whale and limiting auto-correlation in the dataset, the location with the greatest spatial accuracy (highest LC) received in each 24 h period (00.00–23.59 UTC) was selected. When more than one location of equal accuracy was received per day, the first location was selected. Both distances from shoreline and bottom depth were sampled for all daily locations in the STAT database using GEBCO product with 1′ spatial resolution (www.ngdc.noaa.gov/mgg/gebco/). Chlorophyll *a* surface concentration was extracted from the STAT database for November 2012 using monthly grids obtained from NASA's Ocean Color project MODIS satellite-based sensor (4 km spatial resolution, http://oceancolor.gsfc.nasa.gov).

3. Results

Eleven satellite transmitters were deployed on individual whales but only eight provided locations (Table 1). Three transmitters probably failed due to a bad position on the whale preventing them from transmitting (i.e. too low on the back of the whale) or due to potential damage to the tag during deployment. No strong behavioural reaction to tag implantation other than an apparent short-term (within 0.5 h) increase in swimming speed was observed. The total distance travelled ranged from 146 km (whale #33000) to 5804 km (whale #37235).

3.1. Dispersal within and among breeding sub-regions

All whales, but one, only dispersed within the breeding sub-region C2 (Fig. 1). One individual in 2011 and two in 2012 remained around their respective wintering site for the entire duration of the deployment. Whale #33000, a mother accompanied by a calf, stayed south of Mohéli Island for almost three weeks (Figs. 1 and 2) moving on average 8.1 ± 7.9 km·day^{-1} (mean ± SD). Whale #27261, a mother accompanied by a calf, and her male escort #27262 remained together around Mayotte for most of the tracking period, alternating between the lagoon's shallow waters and the deeper waters outside the barrier reef. Their mean travel rates were similar: 26.7 ± 18.6 km·day^{-1} and 26.2 ± 21.0 km·day^{-1} (mean ± SD; for #27261 and #27262, respectively). The five other whales travelled to the west coast of Madagascar (i.e. within breeding sub-region C2) either directly or a few days after being tagged. One whale (#37227) then left the breeding sub-region C2 and reach C3 on the east coast of Madagascar. This female closely followed the coast of Madagascar to the north before travelling southward along the east coast at a mean travel rate of 54.3 ± 51.2 km·day^{-1} (mean ± SD). The day transmissions stopped, the whale was about 90 km south-east of Antongil Bay and 70 km east of Sainte-Marie Island.

3.2. Individual migratory routes

In both 2011 and 2012, an individual travelled to the northwest coast of Madagascar only a few days after being tagged at either Mayotte

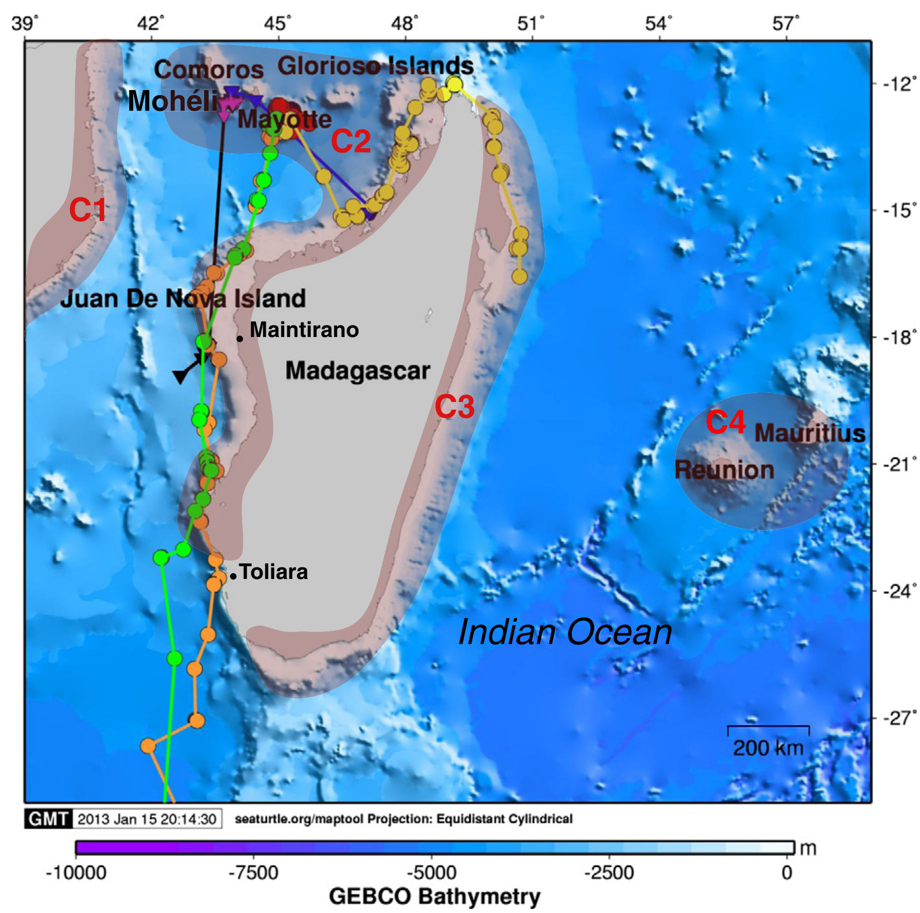

Fig. 1. Movement patterns of eight satellite-tracked humpback whales *Megaptera novaeangliae* wintering off Mohéli Island (#33000: purple triangles, #20690: blue triangles, #22851: black triangles), and Mayotte Island (#37235: green circles, #37278: orange circles, #37227: yellow circles, #27261: blue circles, #27262: red circles), Comoros archipelago in 2011 and 2012, respectively. The red-shaded areas represent the IWC breeding sub-regions: C1, C2, C3 and C4 (Fleming and Jackson, 2011; IWC, 2011).

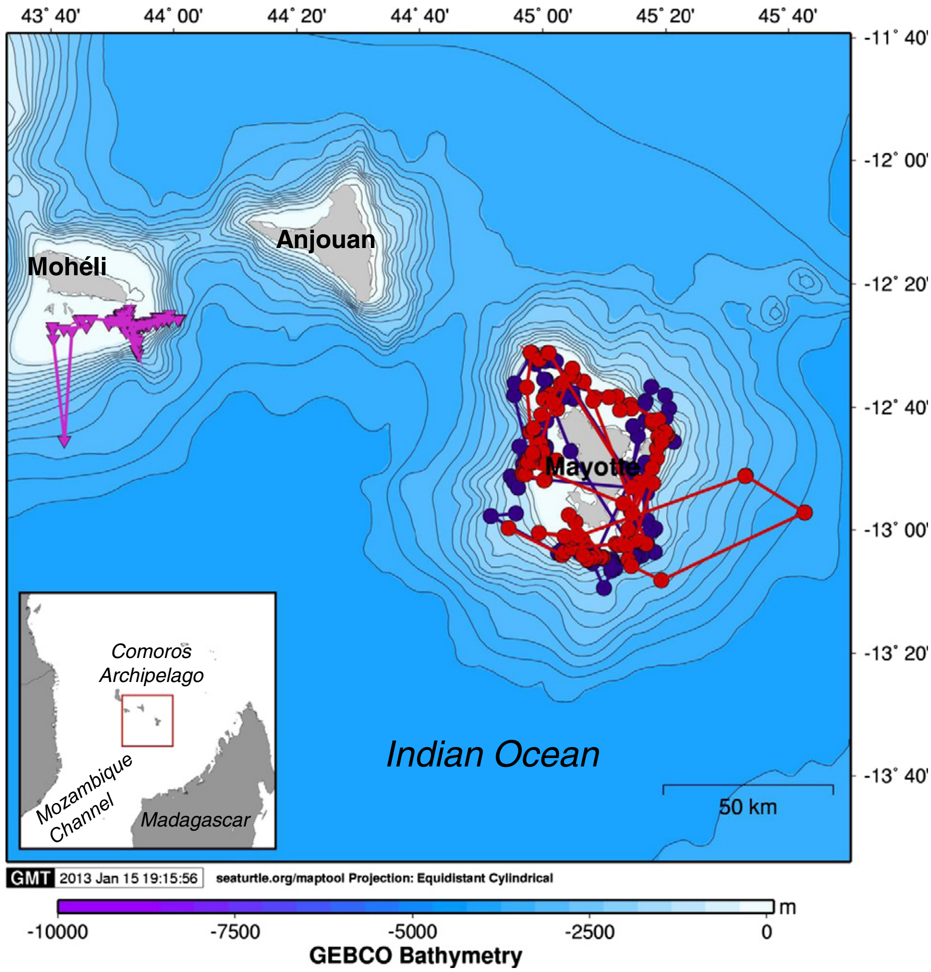

Fig. 2. Movement patterns of three satellite-tracked humpback whales *Megaptera novaeangliae*, wintering off Mohéli Island (#33000: purple triangles) and Mayotte Island (#27261: blue circles, #27262: red circles), Comoros archipelago in 2011 and 2012. The whales #27261 and #27262 were part of the same group when they were tagged.

(whale #37227, mean travel rate ± SD = 134.7 ± 17.1 km·day^{-1}) or Mohéli (whale #20690, mean travel rate = 103 km·day^{-1}), and stopped along the coast between Mahajamba Bay and Moramba Bay for a few days (Figs. 1 and 3). Similarly, three other individuals after being tagged at either Mayotte (whales #37278 and #37235) or Mohéli (whale #22851) travelled southwards to an area along the southwest coast of Madagascar (~70 km west of the town of Maintirano). Whale #22851 was already in this area when first located, six days after tag deployment. This male remained in the area for 14 days moving on average 4.1 ± 4.5 km·day^{-1} (mean ± SD) before returning southwest into the Mozambique Channel. The last position before the tag stopped transmitting was about 170 km west from the coast of Madagascar. The other whales, #37235 and #37278, were part of a group of four adult individuals travelling together when they were tagged, late in the season, off Mayotte. They first reached the coastal waters of southwest Madagascar after two days apparently travelling together at a similar rate (#37278: 172.5 ± 22.1 km·day^{-1} and #37235, 167.2 ± 37.1 km·day^{-1}, mean ± SD, Figs. 1, 4, 5). They then followed the edge of the continental shelf at a slightly slower travel rate until they reached ~21°S. On their way south, they stopped for a day in the area where #22851 stopped for two weeks the year before. After seven days apparently travelling together, the whales took two different routes.

3.3. Potential foraging areas

After leaving Madagascar coastal waters, whale #37278 started migrating south at a mean travel rate of 116.8 ± 95.4 km·day^{-1} (mean ± SD). After a few days, it changed its main direction and started travelling south-eastward (150°) towards the French sub-Antarctic islands alternating between fast (132.7 ± 36.8 km·day^{-1}) and slow (36.2 ± 38.7 km·day^{-1}) moving periods. The tag stopped transmitting while the whale was 340 km northwest of the Crozet Plateau in deep (~3000 m) and productive waters ([Chl*a*] = 1 to 2 mg·m^3, Fig. 5).

Whale #37235 left Madagascar coastal waters and started travelling offshore in a southward direction at a mean travel rate of 128.6 ± 72.5 km·day^{-1} (Figs. 1, 4), its tag then stopped transmitting for 12 days. When transmissions resumed, #37235 was at ~43°S moving south-westward towards Prince Edward Islands (South Africa). For a week, the whale's travel rate decreased to an average of 46.8 ± 30.9 km·day^{-1} (mean ± SD) and on 23 November, #37235 was 60 km west of Marion Island (Prince Edward Islands, South Africa). It then resumed travelling south-westward (222°) at a faster travel rate of 122.6 ± 77.3 km·day^{-1}. Beginning of December, the whale reached 57°22′S, 27°59′E and slowed down to 26 km·day^{-1} before contact was lost.

4. Discussion

This is the first time humpback whales from the so-called breeding stock C defined by IWC (2011) have been successfully tracked within the Indian Ocean and towards their foraging grounds in the Southern Ocean. Although the sample size of eight successfully-tracked individuals was small, the similarity of the whales' movements between years suggested that the dispersal and migratory patterns observed may be characteristic for humpback whales from the southwestern Indian Ocean.

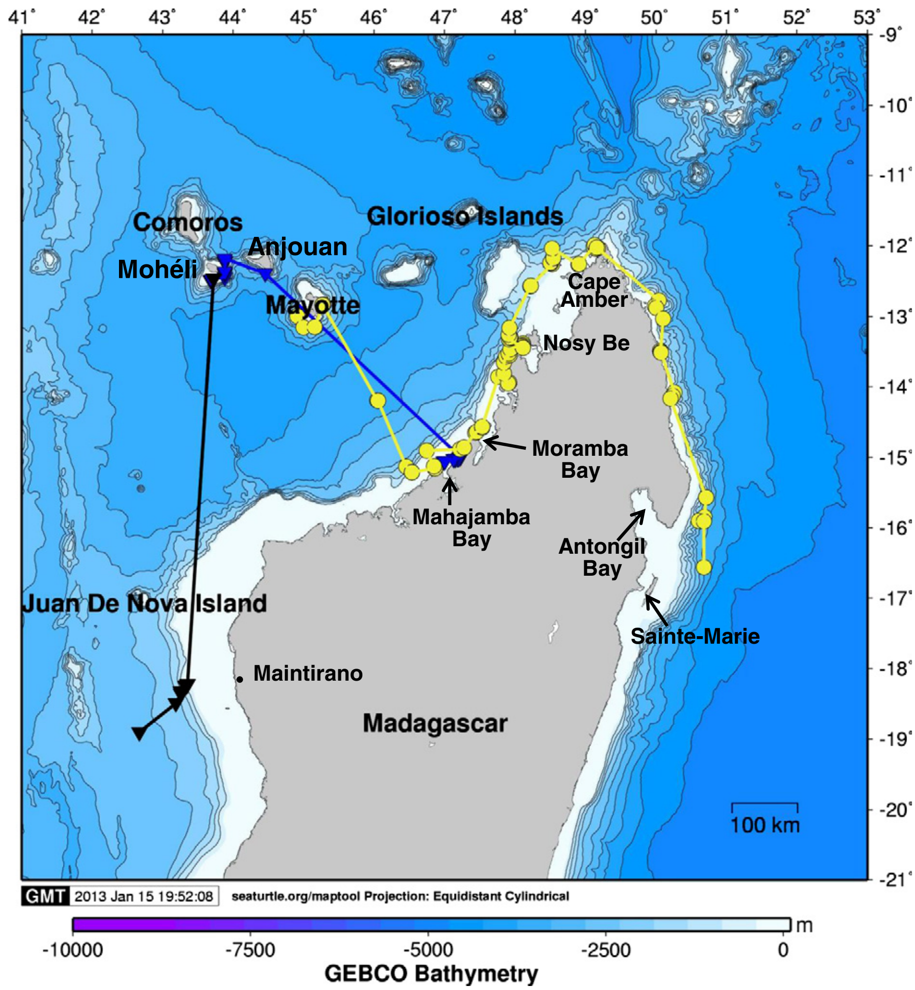

Fig. 3. Migration paths of three satellite-tracked humpback whales *Megaptera novaeangliae*, wintering off Mohéli Island (#20690: blue triangles, #22851: black triangles) and Mayotte Island (#37227: yellow circles), Comoros archipelago in 2011 and 2012.

4.1. Dispersal within and among breeding sub-regions within the same breeding season

The whales tagged in this study were instrumented relatively late in the breeding season (i.e. October, Ersts et al., 2011a; Kiszka et al., 2010), yet several of them did not start their southward migration right after tagging. Some whales remained at their wintering site during the entire tracking period while others stopped in the coastal waters of Madagascar for varying periods of time (up to two weeks in the same area) on their way south. Typically, departure dates from breeding grounds are based on direct observations (e.g. Stevick et al., 2003). Such data can however be biased as individuals may be out of sight of observers. Satellite tracking gives an unequivocal view of departure dates and has for instance been used to record departure dates from breeding grounds in bowhead and humpback whales (Laidre and Heide-Jørgensen, 2012) but also in other taxa such as marine turtles (e.g. Hays et al., 2010) or birds (e.g. Vardanis et al., 2011) and helped improve population modelling (e.g. Hays et al., 2010) and habitat use (Laidre and Heide-Jørgensen, 2012).

Five out of the eight tagged whales travelled through or stopped at areas along the west coast of Madagascar where high sighting rates of humpback whales (including competitive groups) have been reported in late October/early November, in particular off Toliara in the southwest but also further north off Nosy Be (Best et al., 1998; Cerchio et al., 2009). Rate of genetic exchange between whale breeding on the west coast of Madagascar and those breeding on the east coast or in the Comoros archipelago is however unknown. One female was also tracked to the breeding sub-region C3 on the east coast of Madagascar. Photo-identification comparisons and genetic analysis have suggested a strong between-year connectivity between the Comoros archipelago and eastern Madagascar (Ersts et al., 2011b; Pomilla et al., 2006) but this is the first report of whales visiting both the Comoros archipelago and the western and eastern coasts of Madagascar during the same breeding season. In other words, humpback whales might use breeding sub-regions C2 and C3 during the same breeding season which may have important implications for informing the delineations of breeding stocks and subsequently allocating abundance estimates to these stocks. These results suggest that these two, and perhaps three, sub-regions should be considered as one single region.

4.2. Inter-individual variation in migratory routes

Among the eight whales tagged in this study, two individuals (i.e. a female and her male escort) apparently stayed closely associated for most of the tracking period. Two other whales (one male and one unidentified individual) were also travelling together for at least a week during their southward migration. Such temporary associations are often observed in humpback whales (Pack et al., 2002, 2009; Valsecchi et al., 2002).

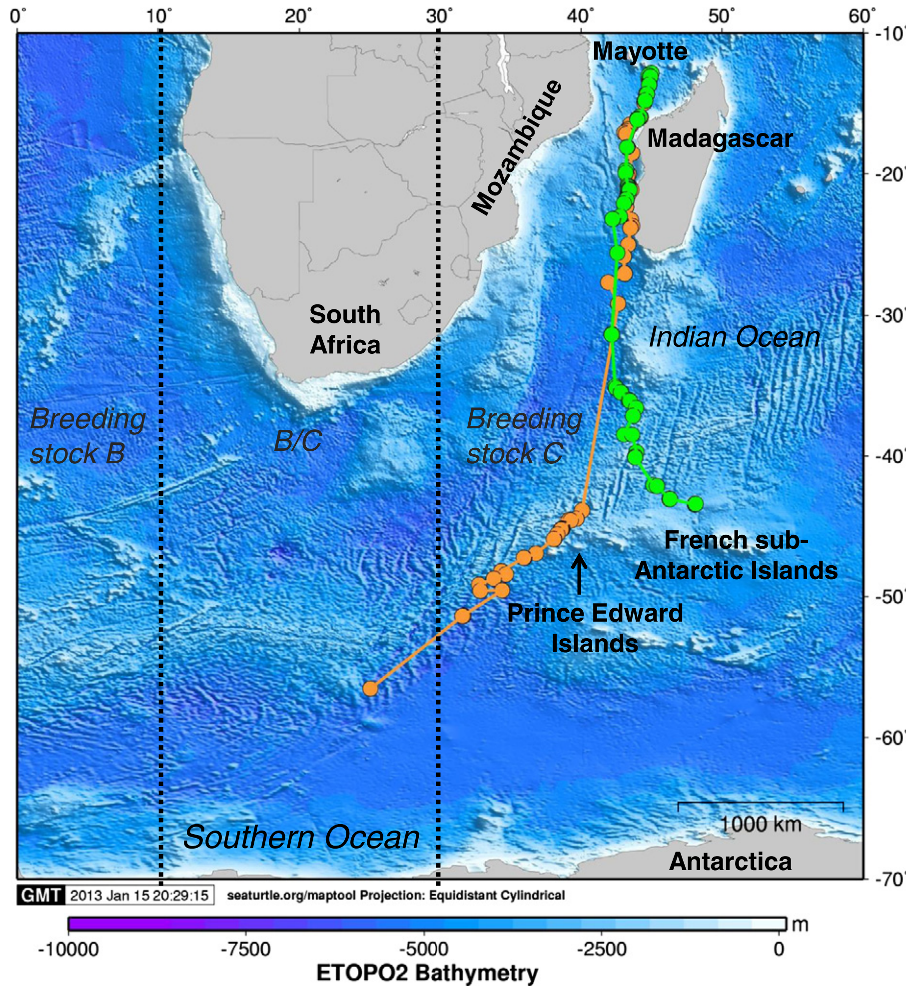

Fig. 4. Migration paths of two satellite-tracked humpback whales *Megaptera novaeangliae*, wintering off Mayotte Island (#37235: green circles, #37278: orange circles), Comoros archipelago in 2012. These two whales were travelling together when they were tagged. The black dotted line represents the border between the IWC breeding stock B and breeding stock C (Fleming and Jackson, 2011; IWC, 2011).

In both years, migrating females with calves did not follow the most direct route to their supposed Antarctic foraging grounds, but instead they remained in coastal waters for most of the tracking periods. This strategy has been documented in grey whales (*Eschrichtius robustus*) along the coast of California where migrating mother–calf pairs follow the contour of the shoreline presumably to limit predation risk by killer whales (*Orcinus orca*) (Ford and Reeves, 2008).

During the straight travelling segments of the whales' migratory routes, average travel rates varied between ~103 km·day^{-1} and 172 km·day^{-1}. These are comparable to travel rates recorded in other migrating baleen whales (Bailey et al., 2009; Heide-Jørgensen et al., 2003; Mate et al., 1998, 2011; Zerbini et al., 2006) and two to three times faster than travel rates recorded in other marine migratory species (e.g. leatherback turtle, *Dermochelys coriacea*, Fossette et al., 2010, whale shark, *Rhincodon typus* Eckert and Stewart, 2001, southern elephant seal, *Mirounga leonina*, McConnell and Fedak, 1996). Humpback whales tracked in the South Atlantic and South Pacific have demonstrated highly directional movements with few stops on the southward migrations (Horton et al., 2011). In this study, two main stop-over sites were identified along the whales' migratory routes on the west coast of Madagascar (i.e. offshore the town of Maintirano and along the coast between Mahajamba Bay and Moramba Bay). Both were visited by several individuals and might therefore be regular stop-over sites for migrating humpback whales. Whales might stop at these sites to rest on their way to their foraging grounds or males might also seek new mating opportunities.

4.3. Potential foraging areas

Opportunistic feeding behaviour during stop-overs along the migratory route has been reported in humpback and right whales (Lagerquist et al., 2008; Mate et al., 2011). While this strategy is common among long-distance migratory birds (e.g. Bairlein and Hüppop, 2004), the use of stop-over sites has not been clearly described in other marine migratory species. The limited sample from this study indicated variable migratory routes as well as several stop-over sites at potential foraging areas. For instance, the slow travelling rate of one individual (~4 km·day^{-1}, #22851) while at its stop-over site along the west coast of Madagascar could indicate feeding but there is only weak evidence of productivity from fishing operations in the area (Le Manacha et al., 2011; Razafindrainibe, 2010).

Another whale (#37278), which travelled south-eastward towards the French sub-Antarctic islands, was also moving slowly northwest of the Crozet Plateau when contact was lost. A phytoplankton bloom occurs north of the Crozet Plateau annually from September to January (Venables et al., 2007, Fig. 5 in this study) creating favourable foraging conditions for marine predators such as birds and mammals (e.g. Bailleul et al., 2005; Péron et al., 2012; Weimerskirch et al., 2005) and potentially humpback whales. It is not clear, however, whether the Crozet Plateau was the whale's final migratory destination or a stop-over and whether it travelled further east after the tag stopped.

Finally, the whale #37235, which migrated south-westward along the South-west Indian Ridge, first slowed down in an area northwest

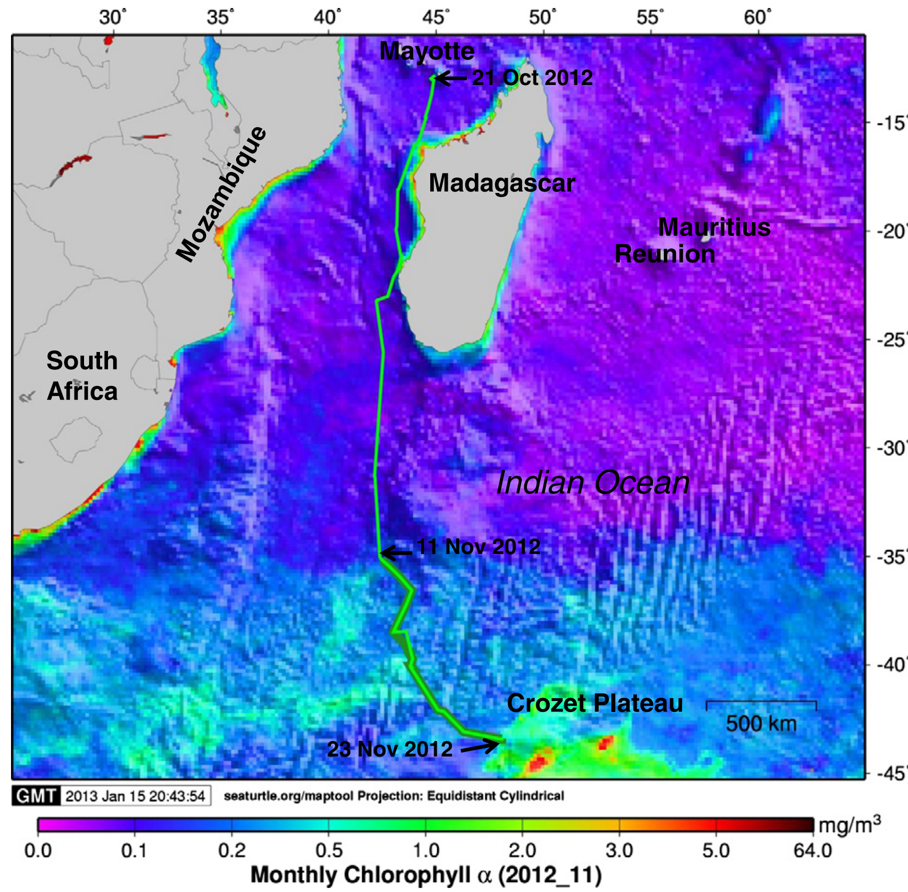

Fig. 5. Migration path in relation to monthly chlorophyll *a* concentration [Chl*a*] of a satellite-tracked humpback whale *Megaptera novaeangliae*, (#37278: green line) wintering off Mayotte Island, Comoros archipelago in 2012. The fine green line represents the whale's track from 21 October 2012 to 23 November 2012 while the bold green line represents the period from 11 November to 23 November 2012 concurrent to [Chl*a*] map.

of the Prince Edward Islands where other large top predators including marine mammals and seabirds have previously been reported foraging (de Bruyn et al., 2009; Jonker and Bester, 1998; Nel et al., 2001). Species tracked in this same area such as leatherback turtles (*D. coriacea*), grey-headed albatrosses (*Thalassarche chrysostoma*) or southern elephant seals generally show sinuous tracks suggesting that they spend time foraging in oceanic meso-scale structures (Jonker and Bester, 1998; Luschi et al., 2003; Nel et al., 2001). On the contrary whale #37235 showed a slow (<50 km·day^{-1}) but relatively straight-line travel through this area (i.e. straightness index = 0.83) suggesting that it may only have opportunistically foraged en route without actively searching for food. The whale then resumed travelling south-westward and 49 days after it was tagged, contact was lost at about 57°S, 27°E, i.e. in IWC feeding ground III previously defined as the main feeding ground of humpback whales from breeding stock C (Fleming and Jackson, 2011; IWC, 2011). This is the first description of the migratory route of a humpback whale from IWC breeding stock C towards the IWC feeding ground III. The whale travelled ~5800 km from its tagging site and this migration distance is comparable to mean migration distances recorded in other baleen whales (e.g. Mate et al., 2011), the leatherback turtle and some migratory fish such as the bluefin tuna (*Thunnus thynnus*) (review in Hein et al., 2012; Hays and Scott 2013).

This study revealed migratory routes, stop-over sites and potential foraging sites of humpback whales from the south-western Indian Ocean. Additional tracks from this area are needed to confirm migratory corridors and get a regional overview of humpback dispersal and migratory patterns.

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