

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

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Abstract

Little is known about humpback whale (*Megaptera novaeangliae*) dispersal within the Indian Ocean Whale Sanctuary (IOWS). Such information is however critical for conservation and management of this species in the sanctuary as it will help understanding connections among breeding grounds and between breeding and foraging grounds. In October 2011 and 2012, eleven satellite transmitters were deployed on wintering humpback whales in the Comoros islands (Mohéli, n = 6 and Mayotte, n = 5), in the south-western tropical IOWS. 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. Three main dispersal behaviours were identified in both years. Whales either remained at their breeding site for several weeks after tagging (n = 3) or disperse to the northwest (n = 2) or to southwest (n = 3) coast of Madagascar. Whales used the same two sites along the coast of Madagascar in both years suggesting these might be regular stop-overs during migration. One whale then followed the coast up north before going back south along the east coast. Its tag stopped while it was 70 km from the breeding site of Sainte Marie Island. It is the first report of whales visiting the Comoros archipelago (breeding sub-region C2) and both the western and eastern coasts of Madagascar (breeding sub-region C3) during the same breeding season. Finally, two whales were tracked further south towards their Antarctic foraging grounds. One whale followed a south-eastward direction towards the French Sub-Antarctic Islands while the other one travelled to IWC foraging area III, one of the supposed Antarctic foraging areas for humpback whales of breeding stock C. This is the first time movements of humpback whales from this breeding stock are being described and their potential foraging areas in the Southern Ocean identified.

Keywords: marine mammals, migration, satellite telemetry, connectivity, Antarctica, International Whaling Commission

50 1. Introduction

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52 In a context of rapid global environmental changes, investigating dispersal movements of
53 individuals among and within populations has been stressed as a pressing research question
54 (e.g. Grémillet and Boulinier 2009, Ponchon et al., 2012). Individual dispersal between
55 breeding sites is one of the key mechanisms behind the dynamics of the spatial distribution of
56 populations and species ranges, as well as in gene flows within meta-populations (Clobert et
57 al., 2001). This ultimately has important consequences for the management of protected
58 species. Such dispersal behaviour has been mainly described in birds (e.g. Dall et al., 2005)
59 but also in some mammals (e.g. Selonen and Hanski 2010) including humpback whales
60 (*Megaptera novaengliae*). In this species for instance, capture-mark-recapture, genetic and
61 tracking studies have suggested some degree of individual dispersal within a same breeding
62 region (e.g. Cerchio et al., 1998, Lagerquist et al., 2008, Rosenbaum et al., 2009, Garrigue et
63 al., 2011) and among breeding regions (e.g. Stevick et al., 2011).

64

65 Humpback whales undertake extensive seasonal migrations from high latitude foraging
66 habitats to low latitude, coastal waters for calving and mating (Dawbin 1966). In the western
67 Indian Ocean Whale Sanctuary (IOWS), three main breeding sub-regions within the breeding
68 stock C have been described based on historical whaling data and contemporary surveys (e.g.
69 Wray and Martin 1983, Best et al., 1998), photo-identification (Dulau-Drouot et al., 2011,
70 Ersts et al., 2011b), and genetic studies (Rosenbaum et al., 2009). The coastal waters of
71 south-eastern Africa, i.e. from Mozambique to Tanzania constitute the breeding sub-region
72 C1 (Findlay et al., 1994, Fleming and Jackson 2011, IWC 2011), the coastal waters of the
73 northern Mozambique Channel Islands (i.e. Comoros archipelago), the west coast of
74 Madagascar and the southern Seychelles the breeding sub-region C2 and the coastal waters of
75 southern and eastern Madagascar, i.e. Antongil Bay and Sainte-Marie island the breeding sub-
76 region C3 (Rosenbaum et al., 1997, Fleming and Jackson 2011, IWC 2011). A breeding sub-
77 region C4 including the Mascarene Islands has been recently proposed (Dulau-Drouot et al.,
78 2011, Fleming and Jackson 2011, IWC 2011). DNA analyses and recaptures of individuals
79 have suggested connectivity between Mayotte (Comoros Archipelago, C2) and Antongil Bay
80 (Madagascar, C3, Ersts et al., 2011b) but a genetic differentiation between Mayotte and East
81 South Africa/Southern Mozambique (C1) has been detected (Rosenbaum et al., 2009, IWC
82 2011). The connectivity and dispersal movements of humpback whales within and among
83 these breeding sub-regions are, however, far from being fully understood (Pomilla 2006,
84 Pomilla et al., 2006, Cerchio et al., 2009, Ersts et al., 2011b, Fleming and Jackson 2011, IWC
85 2011). Such information is critical for the sustainable management of this species in the
86 IOWS but also for our understanding of breeding habitat selection, migratory fidelity and
87 ultimately individual responses to global environmental changes in large migrating whales.

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89 It is only recently that tracking studies of humpback whales have started to give a better and
90 deeper understanding of dispersal movements in wintering and summering areas in both
91 hemispheres: i.e. North Pacific Ocean, (Mate et al., 1998, Lagerquist et al., 2008), Southern
92 Ocean (Dalla Rosa et al., 2008), South Atlantic Ocean (Zerbini et al., 2006) and North
93 Atlantic Ocean (Heide-Jørgensen and Laidre 2007). Yet to date, tracking studies of humpback
94 whales have never been performed in the IOWS. Here, we aimed at investigating the
95 dispersal of adult humpback whales equipped with Argos satellite transmitters during part of
96 their breeding season in the western IOWS and during their post-breeding migration. This
97 study specifically aimed at (1) investigating how individual whales disperse within and
98 among breeding sub-regions within the same breeding season, (2) assessing if individuals

99 from the same breeding sub-region use similar migratory routes and stop-over sites along
100 these routes, (3) identifying the main foraging area(s) of these whales. This study focused on
101 the breeding sub-region C2, i.e. the Comoros archipelago, where male and female humpback
102 whales come to breed from July to October each year (Kiszka et al., 2010, Ersts et al., 2011a)
103 and for which additional data on population structure and dispersal are critically needed
104 (Fleming and Jackson 2011, IWC 2011).

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2. Material and methods

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2.1 Study area and tag deployment

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2.2 Data analysis

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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 (<http://www.seaturtle.org/stat/>) using a maximum rate of travel of 12 km/h (maximum swimming speed reported for humpback whales, Mate 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. Distance

148 from shoreline and bottom depth were sampled for all daily locations in the STAT database
149 using GEBCO product with 1' spatial resolution (www.ngdc.noaa.gov/mgg/gebco/).

150 **Table 1.** Transmitters deployed on humpback whales *Megaptera novaeangliae* wintering off Mohéli and Mayotte Islands, Comoros
151 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 ¹	SPOT5	11 Oct 2011	12°24'29,4"S 43°36'38,7"E	28	60	11	749
33000	F ²	SPOT5	12 Oct 2011	12°24'43,3"S 43°37'15,9"E	18	98	79	146
37236	F ²	SPOT5	11 Oct 2011	12°24'43,3"S 43°37'15,9"E	0	0	0	0
20157	F ¹	SPLASH	13 Oct 2011	12°26'33,7"S 43°19'44,3"E	0	0	0	0
20690	F ¹	SPLASH	14 Oct 2011	12°27'45,0"S 43°43'23,2"E	8	51	23	506
27261	F ¹	SPOT5	11 Oct 2012	12°57'20,3"S 44°55'41,0"E	18	165	107	471
27262	M ¹	SPOT5	11 Oct 2012	12°59'43,9"S 44°54'29,6"E	20	181	139	460
37227	F ¹	SPOT5	12 Oct 2012	12°59'00,0"S 44°14'00,0"E	20	145	84	1155
37228	F ¹	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 ¹	SPOT5	21 Oct 2012	12°49'16,4"S 44°56'21,6"E	33	150	93	3715

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153 ¹ Determined by molecular analysis (see methods)

154 ² Assumed to be a female because it was the adult individual in a cow-calf pair

155 Chlorophyll a surface concentration was extracted from the STAT database for November 2012
156 using monthly grids obtained from NASA's Ocean Color project MODIS satellite-based sensor
157 (4 km spatial resolution, <http://oceancolor.gsfc.nasa.gov>).
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160 3. Results

161 Eleven satellite transmitters were deployed on individual whales but only eight transmitted
162 locations. Three transmitters probably failed due to a bad position on the whale preventing them
163 from transmitting (i.e. too low on the back of the whale) or due to potential damage to the tag
164 during deployment. Data on deployments of the tags are summarized in Table 1. No strong
165 behavioural reaction to tag implantation other than an apparent short-term increase in swimming
166 speed was noted. The total distance travelled ranged from 146 km (Whale #33000) to 5804 km
167 (Whale #37235).
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169 3.1 No immediate dispersal

170 One individual in 2011 and two in 2012 remained around their respective breeding site for the
171 entire duration of the deployment. Whale #33000, a mother accompanied by a calf, stayed south
172 of Mohéli Island for almost three weeks (Figs 1, 2). It spent most of its time on the continental
173 shelf (i.e. depth < 200 m) moving on average $8.1 \pm 7.9 \text{ km.day}^{-1}$ (mean \pm SD) and was still in
174 Mohéli's coastal waters when its tag stopped transmitting on 30 October 2011. Whales #27261
175 and #27262 were travelling together when they were tagged. Whale #27261 was a mother
176 accompanied by a calf and whale #27262 its escort. The trio remained together around Mayotte
177 for most of the tracking period, alternating between the lagoon's shallow waters and the deeper
178 waters (up to 3300m) outside the barrier reef (mean distance from shore \pm SD = $8.4 \pm 8.8 \text{ km}$,
179 Figs 1, 2). Their mean travel rates were similar: $26.7 \pm 18.6 \text{ km.day}^{-1}$ and $26.2 \pm 21.0 \text{ km.day}^{-1}$
180 (mean \pm SD) for #27261 and #27262, respectively.
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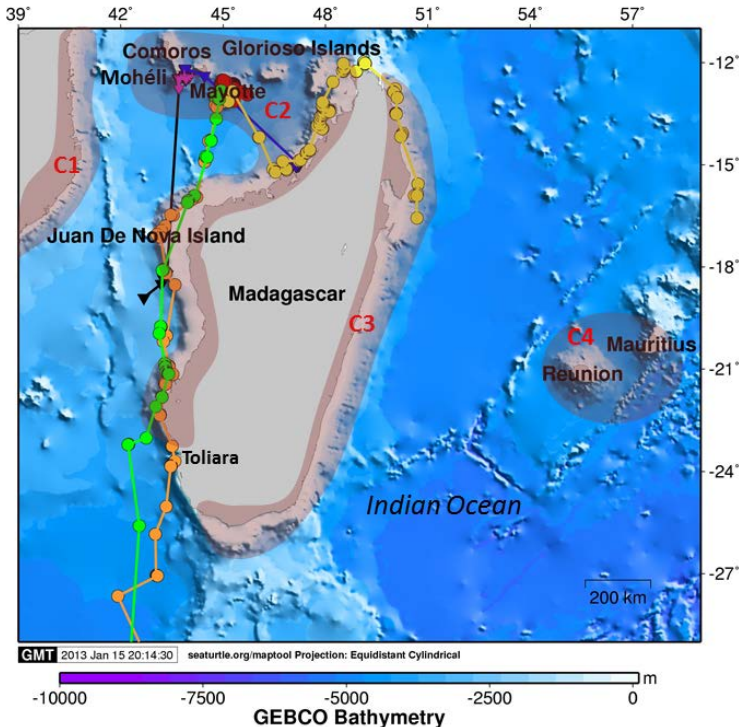
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182 1.1 Dispersal towards northwest and east Madagascar

183 In both years, an individual travelled to the northwest coast of Madagascar only a few days after
184 being tagged at either Mayotte or Mohéli, and then stopped along the coast between Mahajamba
185 Bay and Moramba Bay for a few days (Figs 1, 3). In 2011, the whale #20690, a mother
186 accompanied by a calf, spent three days around Mohéli after tagging before reaching Anjouan on
187 the fourth day. Between both islands, the whale travelled on average $25.6 \pm 5.5 \text{ km.day}^{-1}$ (mean \pm
188 SD). The tag then stopped transmitting for three days. During that time the whale seemed to have
189 crossed from Anjouan towards the north-western coast of Madagascar where it remained for at
190 least 24 hours before transmissions ceased. In 2012, whale #37227, also a mother-calf pair, spent
191 two days in the waters surrounding Mayotte after tagging before moving towards the northwest
192 coast of Madagascar that was reached two days later on 14 October (Figs 1, 3). During the
193 crossing, its travel rate was $134.7 \pm 17.1 \text{ km.day}^{-1}$ (mean \pm SD). It first spent two days in the area
194 where #20690 was last located the year before and then closely followed the coast of
195 Madagascar to the north (mean distance from shore \pm SD = $14.3 \pm 13.9 \text{ km}$). It briefly stopped
196 near Nosy Be, and reached Cape Amber on 23 October before travelling southward along the
197 east coast. During that time, its mean travel rate was $54.3 \pm 51.2 \text{ km.day}^{-1}$ (mean \pm SD). The day
198 transmissions stopped, #37227 was about 90 km south-east of Antongil Bay and 70 km east of
199 Sainte-Marie Island in oceanic waters (~3300m).
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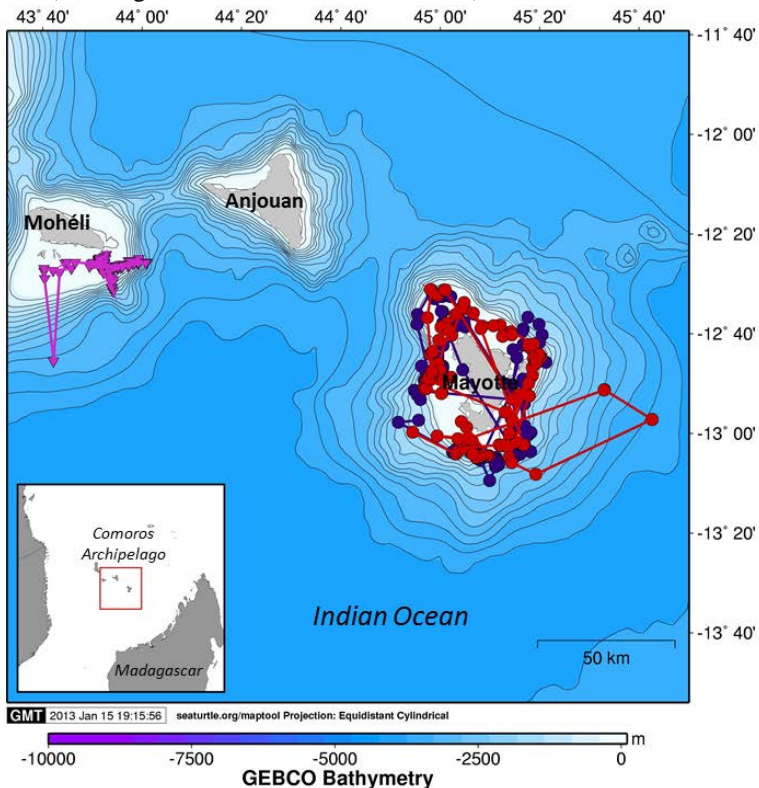
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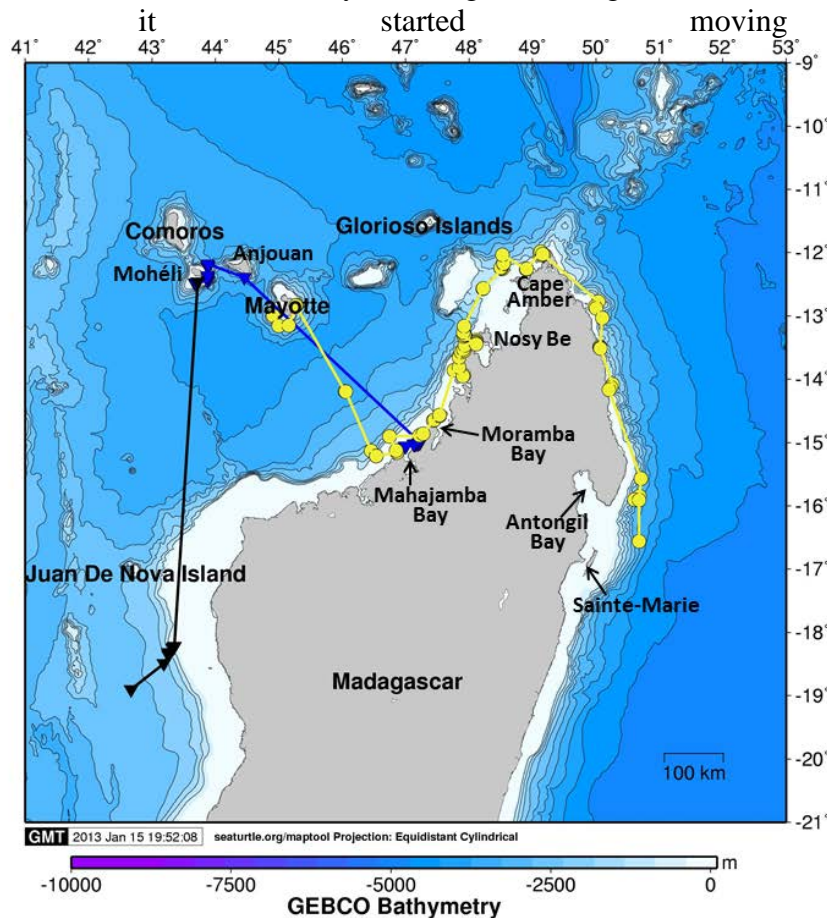
Figure 1: Movement patterns of eight satellite-tracked humpback whales *Megaptera novaeangliae* wintering off Mohéli (#33000: purple triangles, #20690: blue triangles, #22851: black triangles), and Mayotte (#37235: green circles, #37278: orange circles, #37227: yellow circles, #27261: blue circles, #27262: red circles) Islands, Comoros archipelago in 2011 and 2012, respectively. The red-shaded areas represent the breeding sub-regions: C1, C2, C3 and C4 (Fleming and Jackson 2011, IWC, 2011).



229
 230 **Figure 2:** Movement patterns of three satellite-tracked humpback whales *Megaptera novaeangliae*, wintering off
 231 Mohéli (#33000: purple triangles) and Mayotte (#27261: blue circles, #27262: red circles) Islands, Comoros
 232 archipelago in 2011 and 2012. The whales #27261 and #27262 were part of the same group when they were tagged.
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235 **1.2 Dispersal towards southwest Madagascar and the Southern Ocean**

236 The last three individuals all travelled to the southwest coast of Madagascar after being tagged at
 237 either Mayotte or Mohéli. Whale #22851 was travelling together with another adult individual
 238 when it was tagged. Its tag however did not transmit any positions for the next six days. When
 239 the tag started transmitting, the whale was already along the southwest coast of Madagascar, 641
 240 km south of where the tag was deployed off Mohéli (Figs 1, 3). The whale remained in
 241 Madagascar's coastal waters for 14 days moving on average $4.1 \pm 4.5 \text{ km.day}^{-1}$ (mean \pm SD)
 242 before it started moving again

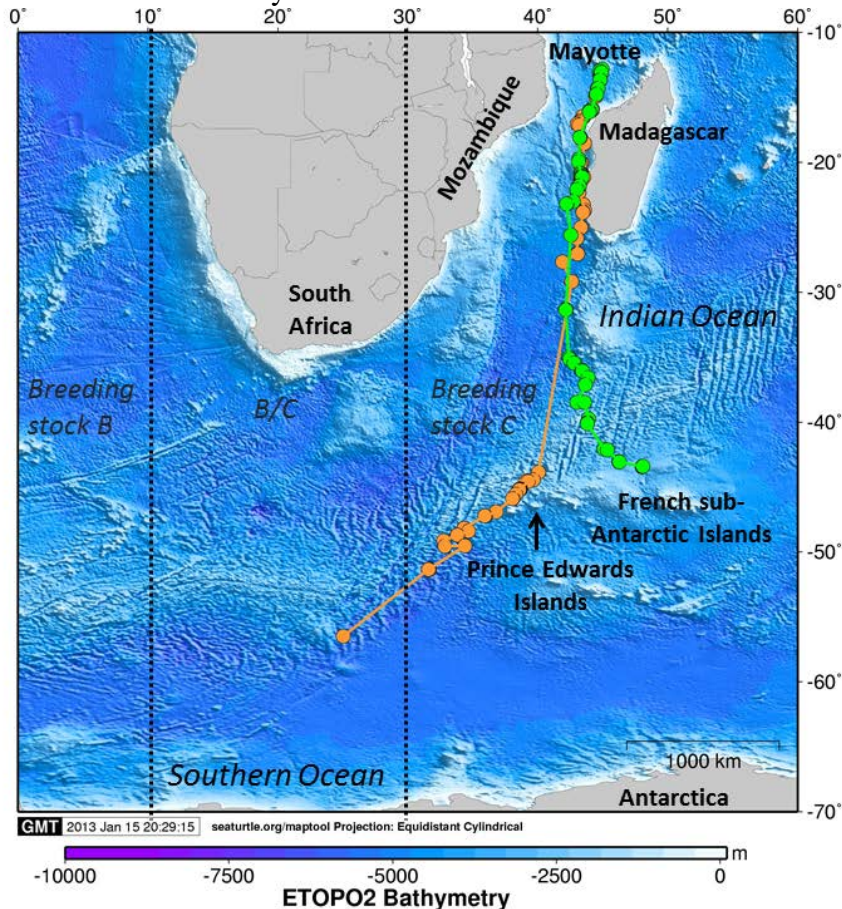


243 **Figure 3:** Migration paths of three satellite-tracked humpback whales *Megaptera novaeangliae*, wintering off
 244 Mohéli (#20690: blue triangles, #22851: black triangles) and Mayotte (#37227: yellow circles) Islands, Comoros
 245 archipelago in 2011 and 2012.
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 248 southwestward into the Mozambique Channel. The last position before the tag stopped
 249 transmitting was about 170 km west from the coast of Madagascar.

250
 251 Whale #37235 and #37278 were part of a group of four adult individuals travelling together
 252 when they were tagged off Mayotte on 21 October. Both whales resumed their southward

253 migration after tagging (Figs 1, 4, 5). They reached the coastal waters of southwest Madagascar
 254 after two days apparently travelling together at a similar rate (#37278: 172.5 ± 22.1 km.day⁻¹ and
 255 #37235, 167.2 ± 37.1 km.day⁻¹, mean \pm SD). They then followed the edge of the continental
 256 shelf (mean distance from shore \pm SD = 66.7 ± 43.1 km) at a slightly slower travel rate until they
 257 reached $\sim 21^\circ$ S on 27 October. On their way south, they stopped for a day in the area where
 258 #22851 stopped for two weeks the year before. The whales then followed two different routes.

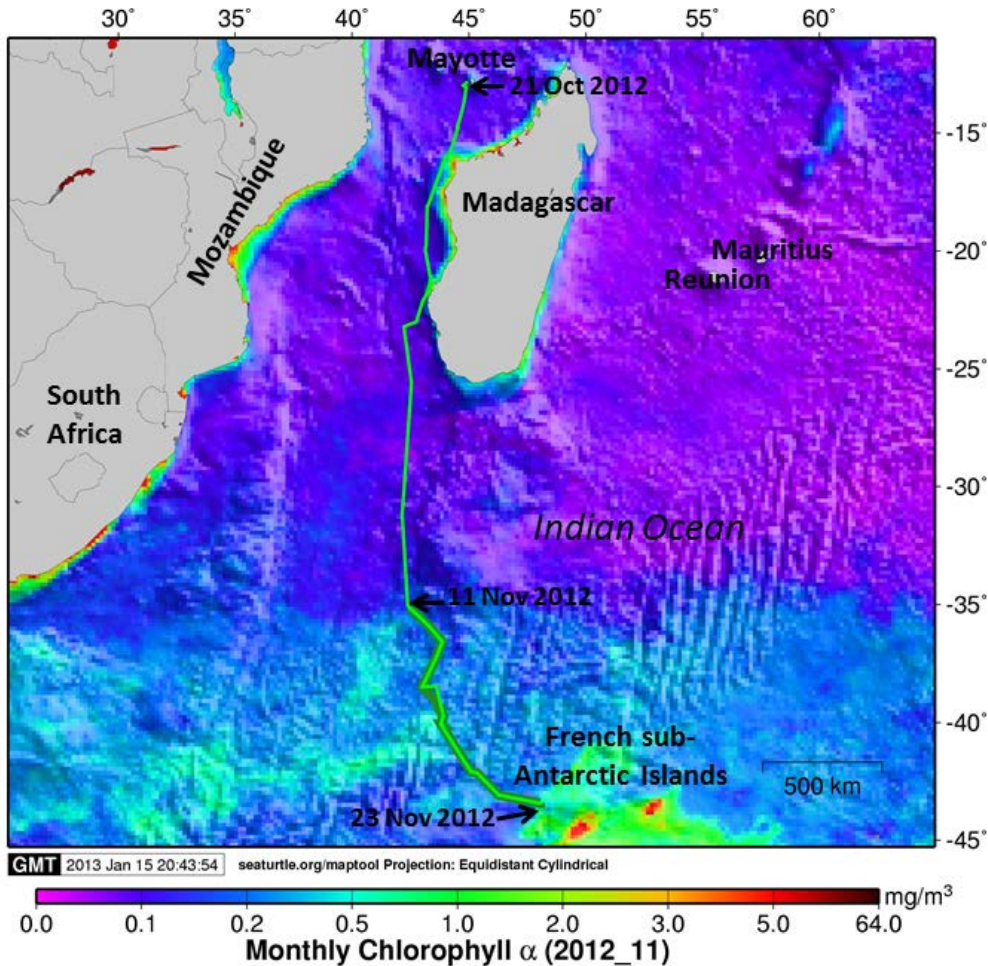


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 260 **Figure 4:** Migration paths of two satellite-tracked humpback whales *Megaptera novaeangliae*, wintering off
 261 Mayotte Island (#37235: green circles, #37278: orange circles), Comoros archipelago in 2012. These two whales
 262 were travelling together when they were tagged. The black dotted line represents the border between the breeding
 263 stock B and breeding stock C (Fleming and Jackson 2011, IWC 2011).
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265 Whale #37278 first spent three days at about 100 km offshore the bay of Toliara in the southwest
 266 moving 38.2 ± 49.2 km.day⁻¹ (Figs 1, 4, 5). On 31 October the whale started migrating south at a
 267 mean travel rate of 116.8 ± 95.4 km.day⁻¹ (mean \pm SD). On 11 November, it changed its main
 268 direction and started travelling south-eastward (150°) towards the French Sub-Antarctic islands
 269 alternating between fast (132.7 ± 36.8 km.day⁻¹) and slow (36.2 ± 38.7 km.day⁻¹) moving periods.
 270 The tag stopped transmitting on 23 November while the whale was 340 km northwest of the
 271 Crozet Plateau in deep (~ 3000 m) and productive waters ($[Chla] = 1$ to 2 mg.m³, Fig 5).

272 Whale #37235 remained close to the west coast of Madagascar (~ 20 km) from 27 to 29 October,
 273 until it reached the bay of Toliara in the southwest. It then left Madagascar's coastal waters and
 274 started travelling offshore in a southward direction at a mean travel rate of 128.6 ± 72.5 km.day⁻¹
 275 (Figs 1, 4). On 3 November, the tag stopped transmitting for 12 days. When transmissions

276 resumed, #37235 was at ~43°S moving south-westward towards Prince Edward Islands (South
 277 Africa). Between 16 and 22 November, the whale's travel rate decreased to an average of $46.8 \pm$
 278 30.9 km.day^{-1} (mean \pm SD) and on 23 November, #37235 was 60km west of Marion Island. It
 279 then resumed travelling south-westward (222°) at a faster travel rate of $122.6 \pm 77.3 \text{ km.day}^{-1}$.
 280 On 7 December, the whale reached 57°22'S, 27°59'E and slowed down to 26 km.day^{-1} . Contact
 281 was lost on 9 December.
 282



283 **Figure 5:** Migration path in relation to monthly chlorophyll a concentration [Chla] of a satellite-tracked humpback
 284 whale *Megaptera novaeangliae*, (#37278: green line) wintering off Mayotte Island, Comoros archipelago in 2012.
 285 The fine green line represents the whale's track from 21 October 2012 to 23 November 2012 while the bold green line
 286 represents the period from 11 November to 23 November 2012 concurrent to [Chla] map.
 287
 288

290 2. Discussion

291 This is the first time humpback whales from IWC breeding stock C have been successfully
 292 tracked within the Indian Ocean Whale Sanctuary and towards their foraging grounds in the
 293 Southern Ocean. A total of 194 days of tracking revealed three main dispersal behaviours

294 adopted by humpback whales at the end of their breeding season in the Comoros archipelago and
295 two potential migratory destinations. Although our sample size of eight successfully-tracked
296 individuals was relatively small, the similarity of the whales' movements between years
297 suggested that the behaviours observed in this study may be characteristic of this region.
298

299 ***4.1 Late departure from the breeding site***

300 In the Comoros archipelago, the peak of the breeding season for humpback whales is considered
301 to be in August, although whales are occasionally observed as late as November (Best et al.,
302 1998, Kiszka et al., 2010, Ersts et al., 2011a). The whales tagged in this study were instrumented
303 relatively late in the breeding season (i.e. October), yet none of them started their migration
304 towards the Antarctic right after tagging. The whales either remained in their breeding region
305 during the entire tracking period or stopped in the coastal waters of Madagascar for varying
306 periods of time (up to two weeks in the same area). Humpback whales fast during the breeding
307 season and their energy stores are depleted when they leave from their breeding site suggesting
308 that the most direct route to their Antarctic foraging ground should be the most common pattern
309 observed amongst late breeders. Surprisingly this was not the case in this study. In particular,
310 three whales stayed in their respective breeding region for at least three more weeks after tagging.
311 Two of them were females accompanied by calves and therefore were probably resting and
312 waiting for the calf to be ready for migration. This is supported by their slow daily travel rates,
313 i.e. between 8 and 27 km.day⁻¹, similar to the travel rates of humpback whale calves estimated by
314 Cartwright and Sullivan (2009) in Hawaii. The third whale seemed to stay closely associated
315 with the mother and calf for most of the tracking period. This individual was a male which
316 escorted the female potentially seeking for mating opportunities, as regularly observed in
317 humpback whales (Pack et al., 2002, 2009).
318

319 ***4.2 Indirect migratory routes and use of stop-over sites***

320 The other five whales started travelling south, either directly or only a few days, after tagging but
321 all of them stopped in the coastal waters of western Madagascar. Their average travel rates
322 during the crossing to Madagascar varied between ~103 km.day⁻¹ and 172 km.day⁻¹ which are
323 comparable to migrating humpback whales in the North Pacific and Southwest Atlantic (Mate et
324 al., 1998, Zerbini et al., 2006, Lagerquist et al., 2008). In both years, a female with her calf
325 reached the northwest coast of Madagascar, suggesting this might be a regular stop-over site for
326 migrating humpbacks from sub-region C2. Before reaching Madagascar, whale #20690 also
327 visited the waters of Mohéli's neighbouring island of Anjouan and most likely the waters of
328 Mayotte. Its tag stopped after one day in Madagascar waters. The other whale (#37227) remained
329 in western Madagascar's coastal waters for nine days. Even though this was not the most direct
330 route to their supposed Antarctic foraging grounds, both whales may have tried to maximize the
331 time spent with their calves in shallow waters (Ford and Reeves 2008). This strategy has been
332 documented in grey whales along the coast of California where migrating mother-calf pairs
333 follow the contour of the shoreline presumably to limit encounters with predators, especially
334 killer whales (*Orcinus orca*) (Ford and Reeves 2008). The last three whales (#22851, #37235,
335 #37278) reached the west coast of Madagascar several hundreds of kilometres south. The two
336 whales travelling together (#37235, #37278) first reached the continental shelf at about 15°S and
337 then followed its edge down to 18°S, i.e. to the area where #22851 spent two weeks the year
338 before. It is well known in other marine species that males may visit multiple rookeries within a
339 single breeding season (Wright et al., 2012). These whales might therefore stopped, after visiting

340 the Comoros archipelago, to mate at another breeding site on their way to the foraging grounds.
341 The slow travelling rate of one individual ($\sim 4 \text{ km.day}^{-1}$, #22851) in this area may also suggest
342 that this whale stopped there for foraging before resuming its migration to the south. Shrimp
343 trawlers and other fisheries operating in this area (Razafindrainibe 2010, Le Manacha et al., 2011)
344 suggest that these are productive waters. Similarly, the two whales which were tracked further
345 south slowed down regularly during their journey suggesting that they might have foraged en
346 route. Opportunistic feeding behaviour during stopovers along the migratory route has previously
347 been reported in humpback whales (Mate et al., 2007, Lagerquist et al., 2008).

348

349 ***4.3 Migratory destinations***

350 The Walters Shoal, a shallow bank south of Madagascar, has been previously identified as an
351 important stop-over site for humpback whales during their migration, however, the only whale
352 (#37378) in our study which travelled relatively close to Walters Shoal did not seem to stop there.
353 Instead, this whale travelled south-eastward towards the French sub-Antarctic islands and was
354 moving slowly northwest of the Crozet plateau when contact was lost. A phytoplankton bloom
355 occurs north of the Crozet plateau annually from September to January (Venables et al., 2007)
356 probably creating favourable foraging conditions for migrating humpback whales in that area. It
357 is not clear, however, if the Crozet plateau was the whale's final migratory destination or if it
358 travelled further east after the tag stopped. The whale (#37235) followed a different migratory
359 route. This individual migrated south-westwards along the South-West Indian Ridge and first
360 slowed down in an area northwest of the Prince Edward Islands where other large top predators
361 including marine mammals and seabirds have previously been reported foraging (Jonker and
362 Bester 1998, Nel et al., 2001, de Bruyn et al., 2009). It then resumed travelling south-westward
363 and 49 days after it was tagged near Mayotte contact was lost at about 57°S , 27°E , i.e. in IWC
364 feeding ground III previously defined as the main feeding ground of humpbacks whales from
365 breeding stock C (Fleming and Jackson 2011, IWC 2011). This is the first description of the
366 migratory route of a humpback whale from breeding stock C towards the IWC feeding ground III.

367

368 ***4.4 Movements between breeding sub-regions within the same breeding season***

369 Five out of the eight tagged whales visited Madagascar's coastal waters on their way to their
370 foraging grounds. Four remained on the west coast travelling through or stopping at areas where
371 high sighting rates of humpback whales (including competitive groups) have previously been
372 reported in late October/early November, in particular off Toliara in the southwest but also
373 further north off Nosy Be (Cerchio et al., 2009, Best et al., 1998). The relationship of these
374 whales breeding on the west coast of Madagascar to those breeding on the east coast or in the
375 Comoros archipelago is however unknown. Our results are the first to suggest a connection
376 between these sites within the same breeding season and to show that whales from the breeding
377 sub-region C2 stop over along the west coast of Madagascar during their southward migration.

378

379 In this study, one female humpback after travelling northward along the west coast of
380 Madagascar crossed the Cape Amber and travelled southward along the east coast. Photo-
381 identification comparisons and genetic analysis have previously suggested a strong between-year
382 connection between the Comoros archipelago and eastern Madagascar (Pomilla et al., 2006,
383 Ersts et al., 2011b) but this is the first report of whales visiting the Comoros archipelago and both
384 the western and eastern coasts of Madagascar during the same breeding season. In other words,
385 humpback whales might use breeding sub-regions C2 and C3 during the same breeding season

386 which may have important implications for population estimates and to revise the definition of
 387 IWC breeding sub-regions. These results indeed suggest that these two sub-regions may be
 388 considered as one single region.

389
 390

391 **3. Acknowledgements**

392

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412 **4. References**

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