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Migratory round-trip of individually identified humpback whales at the Strait of Magellan: clues on transit times and phylopatry to destinations

Ciclo migratorio de ballenas jorobadas individualizadas del estrecho de Magallanes: indicios sobre la duración de la migración y filopatría en los destinos

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ABSTRACT

Humpback whales undertake seasonal migration between productive high-latitude areas where they feed in summer and low-latitude tropical waters where mating and calving occur during winter. In the eastern south Pacific, the species breeds off Colombia and Ecuador, and feeds primarily in the western Antarctic Peninsula and in the waters of the Strait of Magellan (SM), recently described as a new feeding ground for humpback whales. Comparison of fluke photographs of 62 individuals from the SM obtained during the austral summer from 1999 to 2005 and 1,042 individuals from Colombia, provided conclusive matches for six individuals, with an overall interchange index of 0.093. Eight migratory trips between summer and winter grounds were registered for four whales during a complete migratory round-trip in consecutive years. The minimum distance traveled in a one-way trip ranged from 6,650 to 7,000 km. The duration of the two fastest trips between these migratory destinations was 88 and 99 days, with a mean speed of migration of 76 and 67 km day^{-1} respectively. Five of the whales present in both areas were males and three mitochondrial DNA haplotypes were identified: EM-1 for three individuals, EM-2 for two and EM-3 for the last one, all of which have been previously described for humpback whales from Colombia. All six individuals were seen several days in each season in the SM (as many as 39 days in one case), with an average stay of 72 ± 40 days (n = 20) per year, ranging from 3 to 125 days. On average, each of the six individuals was seen in the SM during 71 ± 18 % of the seven monitored summers. Three individuals were re-sighted in the SM six out of the seven surveyed years, during four to six consecutive years. These results provide the first direct evidence to include humpback whales that feed in the Strait of Magellan as part of the eastern south Pacific population of whales that feed off Colombian waters.

Key words: Colombia, humpback whales, migration, photo-identification, Strait of Magellan.

RESUMEN

La ballena jorobada migra estacionalmente entre latitudes altas donde se alimenta en verano y latitudes bajas donde cría y se aparea en invierno. En el Pacífico sureste, la especie se reproduce en Colombia y Ecuador y se alimenta principalmente al oeste de la península Antártica, y en el estrecho de Magallanes (EM) recientemente descrito como nueva área de alimentación. Al comparar las fotografías de las colas de 62 ballenas individualizadas en el EM durante el verano austral entre 1999 y 2005 con 1.042 individuos de Colombia, se encontró a seis individuos comunes, lo que representa un Indice de Intercambio migratorio de 0,093. Se registraron ocho migraciones para cuatro de estas ballenas entre el EM y Colombia en el ciclo migratorio de años consecutivos. La distancia mínima recorrida en una sola dirección varió entre 6.650 y 7.000 km. La duración de los dos viajes más rápidos registrados entre estos dos destinos fue de 88 y 99 días, con una velocidad promedio de migración de 76 y 67 km día^{-1} respectivamente. Cinco de las seis ballenas comunes entre las áreas fueron machos. Entre las seis ballenas se encontraron tres haplotipos de ADN

mitocondrial todos descritos previamente en ballenas jorobadas de Colombia: tres ballenas con el haplotipo EM-1, dos con el EM-2 y uno con el EM-3. Los seis individuos se avistaron reiteradamente en el EM (hasta 39 días en una estación en un caso), con una permanencia promedio de 72 ± 40 días (n = 20) por año y un rango entre 3 y 125 días. En promedio, estas seis ballenas se vieron durante el 71 ± 18 % de las siete temporadas muestreadas en el EM y tres se registraron seis de lo siete años estudiados, por 4-6 años consecutivos. Esta es la primera evidencia directa para incluir las ballenas jorobadas que se alimentan en el estrecho de Magallanes como parte de la población del Pacífico sureste que se reproduce en aguas colombianas.

Palabras clave: Colombia, ballenas jorobadas, migración, foto identificación, estrecho de Magallanes, ADNmt.

INTRODUCTION

Humpback whales, *Megaptera novaeangliae* (Borowski 1781), undertake the longest known migration to any mammal (Stone et al. 1990, Clapham & Mead 1999). This species inhabits all major ocean basins, and long-distance seasonal migration takes place between productive high-latitude areas where whales feed in the summer and fall, and low-latitude tropical waters where mating and calving occur during winter and spring (Mackintosh 1965). Photographic identification of individual humpback whales has established and confirmed migratory movements all over the world (Kaufman et al. 1990, Stone et al. 1990, Darling & Cerchio 1993, Gill & Burton 1995, Darling et al. 1996, Stevick et al. 1998, 2003).

The migratory destinations of humpback whales in the southeastern Pacific (Area I stock for International Whaling Commission) are partially known. Available information has been gathered from studies based on whaling data (Townsend 1935, Mackintosh 1942, Clarke 1962), and more recently on the identification by naturally marked individuals and on mitochondrial DNA (mtDNA) sequence analysis (Stone et al. 1990, Baker et al. 1998, Flórez-González et al. 1998, Olavarría-Barrera 1999, Caballero et al. 2001, Stevick et al. 2004). The main summer feeding ground, as presently known, for the southeastern Pacific humpback whale stock that breeds off Colombia and Ecuador (Flórez-González 1991, Scheidat et al. 2000, Félix & Haase 2001a), extends along the western coast of the Antarctic Peninsula (WAP) (Omura 1953, Mackintosh 1965, Stone et al. 1990, Stevick et al. 2004), south to the Antarctic Convergence. These summer and winter final migratory destinations are 8,500 km away from each other (Stone et al. 1990). The cold inshore waters of western South America, located in the southern Patagonian fjords and the Strait of Magellan (SM), have recently been described as a summer feeding ground for humpback whales (Gibbons et al. 1998, Gibbons 2003). In accordance with the last report (Gibbons et al. 2003), there is historical evidence of the presence of whales near Carlos III Island in the SM, dated from the 16th century. This species reaches significant concentrations around Carlos III Island from summer to autumn, period during which the authors have also frequently observed an important presence of prey species for humpback whales, such as schooling fishes (herring, *Sprattus fueguensis*) and krill (*Euphausia* sp.). This feeding ground is characterized by (1) containing adults and calves, 13 % of the 62 identified whales are mothers accompanied by calves born that year (J. Capella unpublished data), (2) group sizes with a mode of two individuals (Gibbons et al. 2003), and (3) a sex ratio of 1:1 (V. Sabaj unpublished data)

At present, there is no published data about conclusive wintering origins for individual humpback whales sighted during summer months in the SM. However, indirect data based on pigmentation pattern of flukes (Gibbons et al. 2004) and mtDNA markers (Guerrero 2003) suggest an affinity between humpback whales from the SM and Colombia. Current available evidence indicates that there is no migratory connection between humpback whales from WAP and the SM (Acevedo 2006) or the Southwestern Atlantic Ocean (Brazil) (Stevick et al. 2004, Zerbini et al. 2006). Neither is there any photographic evidence connecting humpback whales from breeding grounds in Brazil to those observed in southwestern America (Stevick et al. 2004).

If humpback whales of the SM belong to the southeast Pacific population, then some individual whales must be common to both the

SM and the main breeding ground from the eastern Pacific Ocean, i.e. the Colombian waters. In this paper we document the migratory destination of six humpback whales from SM to the wintering grounds in Colombia, an estimation of the duration of migration and the site fidelity to these two migratory destinations. We discuss these findings in the context of clues for a short migratory cycle for the Southeast Pacific humpback whales related to strong phylopatry to this newly discovered summer ground.

MATERIAL AND METHODS

Study locations

In high latitudes, the study area encompasses the central sector of the SM around Carlos III Island (53º37' S, 72º21' W), including Whale Sound, Tortuoso Passage, and Jerónimo and Barbara Channels. The study area covers approximately 1,150 km^2 of marine channels where humpback whales feed. Waters are up to 600 m in depth, with a maximum tidal range of less than 4 m, strong current flows and an average surface water temperature ranging between 6 and 8 ºC. The low-latitude study area is situated along the western coast of Colombia, within the waters of the continental shelf (depth < 200 m) and has an average surface water temperature ranging between 26 and 28 ºC (Flórez-González 1991). Three main wintering aggregations of humpback whales are recognized along the coast with some degree of interchange among them (Recalde 2005): Gorgona Island (GI) in the south sector (2º58' N, 78º10' W), Malaga Bay (MB) along the central coast (4º N, 77º10' W) and Tribugá Gulf (TG) in the north (6º N, 77º30' W).

Data collection and management

Searches for humpback whales were carried out on small vessels in each study location, with a minimum of two observers and in good weather conditions (Beaufort Sea state ≤ 3). Sampling in the SM was undertaken during 250 vessel-days from 1999 to 2005, between January and April-May of each year, except 2004, when it continued until June. Boat surveys in Colombia were carried out during the austral winter and spring months (July to October-November) during 1,132 vessel-days from 1986 to 2003 (Table 1) (Fundación Yubarta, Fundación Sentir). Field methods are as described in Flórez-González (1991).

For each sighting, the date was recorded and attempts were made to take photographs of flukes and obtain skin samples of the individuals. Photographs of ventral flukes were taken with 35 mm cameras or digital cameras equipped with 70-210 mm or 300 mm lenses, and ISO 100, 200 and 400 print or slide film. Photographs without a minimum photographic quality were excluded. Skin biopsies were collected in the SM using a 30 mm long bolt with an 8 mm diameter hollow stainless steel tip attached to an arrow propelled by a crossbow (Lambertsen 1987). Skin biopsies were maintained in a solution of 20 % DMSO saturated with NaCl at 7 ºC for later DNA analysis.

TABLE 1

Sampling periods, total effort (Vessel-days), total number of humpback whales identified in Chile and Colombia from 1986 to 2005 (Ni), and global index of phylopatry (Ph)

Periodos de muestreo (en años), esfuerzo total en días de embarcación (Vessel-days), número de ballenas jorobadas identificadas en Chile y Colombia entre 1986 y 2005 (Ni), e índice global de filopatría (Ph)

Region	Area	Sampling years	Vessel-days	Ni	Ph
Chile	Strait of Magellan	1999-2005	250	62	1.34
Colombia	Gorgona Island	1986-1995, 1997, 1999, 2003	764	722	0.37
	Malaga Bay	1993-1998, 2000-2001	313	354	0.53
	Tribuga Gulf	1997-1998, 2000-2001	55	61	0.26

Identifications were made for each one of the four localities (SM, GI, MB and TG) (Table 1).

Duration of migration was defined as the time elapsed from the last date of sighting in a seasonal habitat until the first date sighted in the next migratory destination.

Identification and matching

Humpback whales were individually identified from photographs of the unique patterns of ventral fluke pigmentation (Katona & Whitehead 1981). Matches of humpback whales were found by comparing a collection of 62 adult individuals identified in the SM (Capella & Gibbons unpublished catalog) with a total collection of 1,042 unique individual whales in Colombia. Catalogs from Colombia include Gorgona Island (722), Malaga Bay (354) (Fundación Yubarta unpublished catalog) and Tribuga Gulf (61) (Fundación Sentir and Fundación Yubarta unpublished catalogs), 95 of which are common for two or the three localities.

Migratory connection and phylopatry

Interchange index (I_{bf}) between the SM and Colombia was calculated, as previously described (e.g., Baker et al. 1985, Urbán et al. 1999, Calambokidis et al. 2001):

$$I_{bf} = (m_{bf} / [n_b \times n_f]) \times 1000,$$

where m_{bf} is the number of individual whales seen both in Colombia and the SM, n_b is the number of individuals from Colombia and n_f is the number of individuals from the SM. This index is basically the inverse of the Petersen capture-recapture index. A high value of this index reflects a high probability of recapture due to either a small population or a high interchange of individuals between the two regions.

An index of phylopatry (Ph) was defined as a global rate of recapture. It was calculated to provide a relative quantification of the amount of annual return to specific locations in Colombia and the SM:

$$Ph = (k - n) / n,$$

where k is the total number of whales identified along the period and n is the sum of newly identified individuals each year (not photographed in previous years) for the whole period. A low value in this index indicates a low annual return or low phylopatry to a determined migratory destination, while a high value reflects a high phylopatry.

mtDNA haplotypes and sex determination

Mitochondrial DNA haplotypes were determined from skin biopsies for whales matched between the SM and Colombia. A 441 base pair (bp) fragment near the 5' end of the mtDNA control region (Baker et al. 1993) was amplified by the Polymerase Chain Reaction (PCR) (Saiki et al. 1988) using the following primers designed with the program Primer3 (Rozen & Skaletsky 2000): "Wh2F" (5' TTG TAC AAT AAC GAC AGG GCG AC 3') and "Wh2R" (5' TTT AAA TTA ATA TGG CCC TGA AG 3'). Cycle conditions consisted in a preliminary denaturing period of 2 minutes at 94 ºC followed by 35 cycles of denaturation for 30 seconds at 94 ºC, primer annealing for 30 seconds at 60 ºC, and polymerase extension for 90 seconds at 72 ºC. A final extension period for 15 min at 72 ºC was included. Both strands of cleaned PCR products were sequenced on an ABI-310 Genetic Analyzer (Applied Biosystems Inc., Foster, California, USA) using the Big Dye terminator v1.1 sequencing kit (Applied Biosystems Inc., Foster, California, USA). Sequences were checked visually for possible sequencing errors and corrected manually. Sequences were aligned and edited using the program BioEdit (Hall 1999). For comparative analysis with previously studied humpback whales from Colombia, sequences were truncated to correspond with a 283 bp segment (Baker et al. 1998, Caballero et al. 2001).

The sex of whales was identified by amplification via the PCR and subsequent Taq I digestion of a homologous region of the X and Y chromosomes (Palsbøll et al. 1992). Taq I restriction fragments of the amplified DNA were separated by gel electrophoresis in 3 % agarose at 200 V, and visualized and photographed under UV. The female pattern is characterized by the presence of two bands (439-bp and 182-bp), whereas males show an additional band of 621-bp.

RESULTS

Matches and transit times

Comparison of photographs resulted in conclusive matches of six individuals between the SM and Colombia (Fig. 1) which established a minimum of eleven trips (Table 2). The markings of the fluke for individuals EMa-020, EMa-018 and EMa-033, shown in the accompanying photographs (Fig. 1), showed little or no changes during the intervals between the first and last sightings which ranged from ten to fourteen years.

Four whales were documented moving between summer and winter grounds in a complete migratory round-trip during one year (Table 2 and 3). One whale (EMa-033) was observed at two of our study areas along the Colombian coast in different years. The duration of migration between these migratory destinations varied from 88 days between GI and the SM in 2003-2004 to 265 days between the SM and GI in 2003 (Table 3). The minimum lineal distance between migratory destinations ranged from 6,650 km for the SM to GI to 7,000 km for the SM to TG (Table 3). The two fastest trips recorded here (88 and 99 days from GI to the SM) represent a mean speed of migration of 76 and 67 km day^{-1} respectively (Table 4).

Sex and mtDNA haplotypes

The six matched whales correspond to five males and one female. Among them, three mtDNA haplotypes were identified: EM-1 for three individuals, EM-2 for two and EM-3 for the last one (Table 2).

The alignment of the three haplotypes of the SM Humpback whales with those published revealed that the three of them have been described in Colombia (Baker 1998: Genbank accession numbers AF068069, AF068067 and AF068078; Caballero 2001). They have also been described for the Antarctic Peninsula (AP) feeding ground (Olavarría-Barrera 1999, Olavarría-Barrera et al. 2000). EM-1 is the most frequent haplotype described both in Colombia and AP (Olavarría-Barrera et al. 2000); EM-2 and EM-3 haplotypes have not been described at any other population of Humpback whales analyzed. EM-1 has also been reported from north Pacific humpback whales (Olavarría-Barrera et al. 2000).

Destination fidelity and migratory connection

There is a higher occurrence (number of sightings of specific individuals on different days within a year) and a greater site fidelity to the high-latitude destination compared with the low-latitude destination for all six individuals. They were seen in the SM repeatedly in a particular year (as many as 39 days), with an average stay of 72 ± 40 days (n = 20), ranging from 3 to 125 days (Table 2). On average, each of the six individuals was seen in the SM during 71 ± 18 % of the seven summers sampled. Three individuals (EMa-003, EMa-004 and EMa-020) were re-sighted in the SM six out of seven surveyed years, and during four to six consecutive years (Table 2). In Colombia, five of these individuals were seen only once or twice in total and one individual only (EMa-033) was seen three years out of 17 surveyed years (Table 2). The total photo-identified individuals of humpback whales from the SM and Colombia showed significant differences in the level of annual return, with a mean index of phylopatry of Ph = 1.78 ± 1.35 in a year by year analysis for the six-year period in the SM, in comparison to Ph = 0.59 ± 0.72 for the whole region in Colombia over 17 years (Mann-Whitney U-test, U = 10.0, p = 0.017). The global phylopatry index with the total cumulative data was Ph = 1.34 for the SM and Ph = 0.26 for TG, Ph = 0.37 for MB and Ph = 0.53 for GI in Colombia (Table 1 and 5).

The six humpback whales of the SM matched with Colombia provided an overall Interchange Index of 0.093 (Table 6). The highest degree of interchange was with TG (0.260) as a result of one match, followed by MB (0.091) with two matches and GI (0.089) with four matches (see Table 2 for matches).

DISCUSSION

These results provide the first direct evidence to include humpback whales that feed in the Strait of Magellan as part of the Southeast Pacific population belonging to stock G breeding ground for the southern hemisphere (IWC 1998). In addition to the photographic

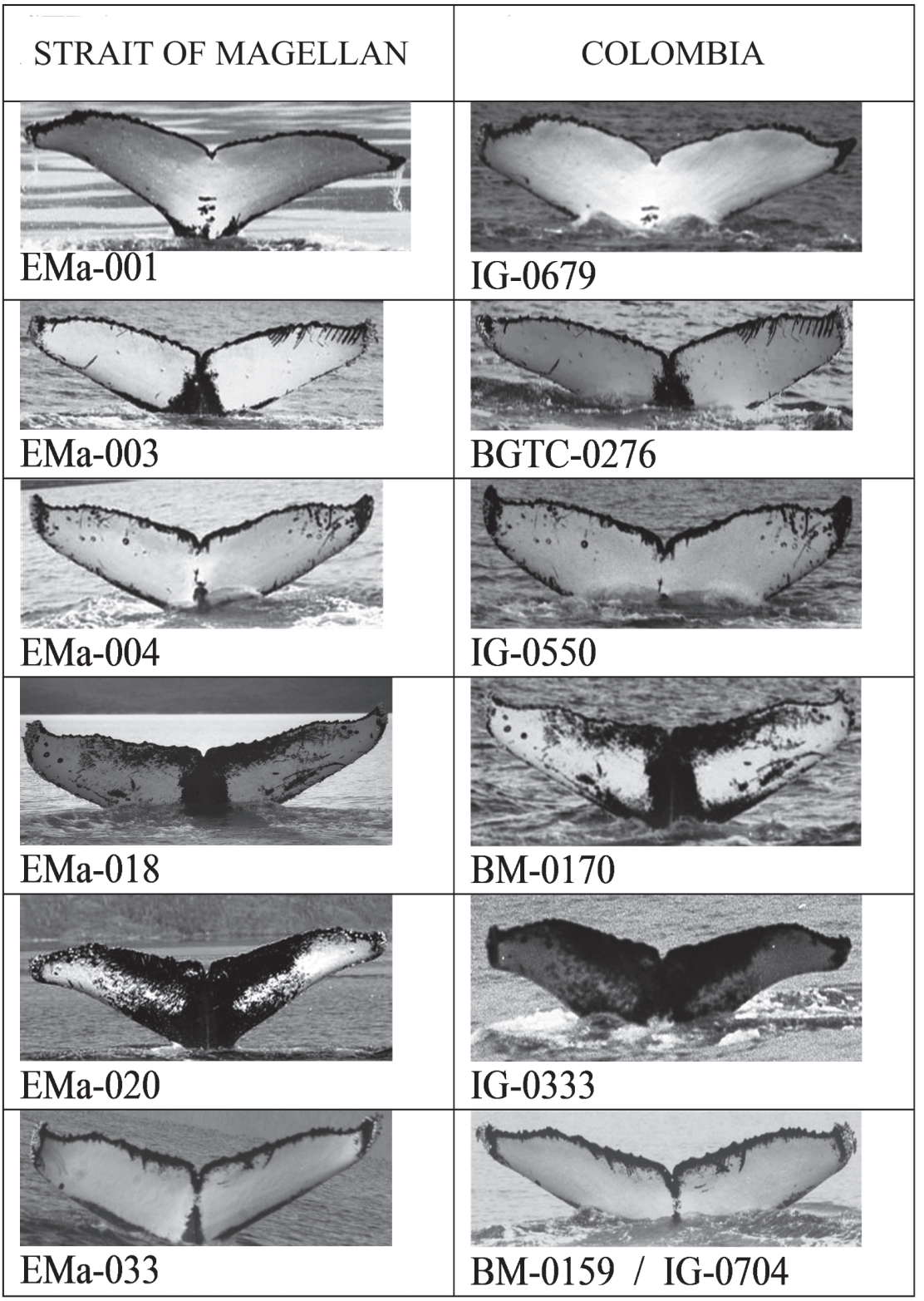

Fig. 1: Fluke photographs of the six individual humpback whales matched between the Strait of Magellan and Colombia.

Fotografías de las colas de seis ballenas jorobadas registradas tanto en el estrecho de Magallanes como en Colombia.

TABLE 2

Matches of humpback whales identified between 1999 and 2005 in the Strait of Magellan and in their wintering grounds off Colombia. Details of sex, mitochondrial DNA haplotypes, dates of the first and the last observation by year and number of days of sightings by locality are shown

Ejemplares de ballena jorobada identificados en el estrecho de Magallanes entre 1999 y 2005 comunes con Colombia. Se muestra el detalle de haplotipo de ADN mitocondrial, fechas de la primera y última observación en el año y el número de días de avistamiento por localidad

		Strait of Magellan				Colombia			
Whale IDnumber	Sex mtDNA haplotype	Year	First observation	Last observation	Number of days	Year	First observation	Last observation	Number of days
EMa-001	MEM-1	1999	15-Jan	-	1				
		2001	21-Feb	-	1				
		2003	29-Mar	-	1	2003 (1)	12-Oct	-	1
		2004	8-Jan	25-Mar	6				
EMa-003	MEM-1	1999	15-Jan	10-May	3				
		2001	13-Feb	-	1	2001 (3)	22-Aug	-	1
		2002	7-Feb	9-Feb	2				
		2003	15-Jan	16-Feb	13				
		2004	19-Jan	16-May	29				
		2005	3-Jan	5-Apr	39				
EMa-004	FEM-1	1999	22-Jan	-	1				
		2000	20-Apr	-	1				
		2002	18-Feb	-	1				
		2003	22-Jan	23-Feb	9	2003 (1)	22-Aug	-	1
		2004	30-Jan	22-Apr	4				
		2005	21-Jan	20-Mar	2				
EMa-018	MEM-2	-				1995 (2)	30-Aug	-	1
		2000	10-Feb	-	1				
		2002	6-Feb	9-Feb	3				
		2003	24-Jan	21-Feb	4				
		2004	7-Feb	18-May	16				
		2005	30-Dec	11-Apr	12				
EMa-020	MEM-2	-				1991 (1)	1-Sep	-	1
		-				1993 (1)	13-Aug	-	1
		2000	10-Feb	-	1				
		2001	13-Feb	-	1				
		2002	6-Feb	9-Feb	2				
		2003	14-Feb	29-Mar	6				
		2004	5-Feb	9-Jun	32				
		2005	21-Jan	9-Apr	16				
EMa-033	MEM-3	-				1995 (2)	23-Aug	20-Sep	2
		-				1996 (2)	31-Aug	22-Sep	2
		2003	22-Jan	9-Feb	8	2003 (1)	2-Nov	3-Nov	2
		2004	11-Feb	9-May	16				
		2005	14-Feb	18-Feb	2				

In Colombia: (1) Gorgona Island; (2) Malaga Bay; (3) Tribuga Gulf

TABLE 3

Duration and distance traveled by individual humpback whales in round-trip migration among the Strait of Magellan and wintering destinations in Colombian coasts

Duración y distancia recorrida por ballenas jorobadas individualizadas en un ciclo migratorio completo entre el estrecho de Magallanes y Colombia

Whale ID number	Migratory destinations inconsecutive years	Duration of the trip(days)	Distance traveled (km)*
EMa-001	Strait of Magellan - Colombia [(1)] (2003)	197	6,650
	Colombia [(1)] - Strait of Magellan (2004)	88	6,650
EMa-003	Strait of Magellan - Colombia [(2)] (2001)	190	7,000
	Colombia [(2)] - Strait of Magellan (2002)	169	7,000
EMa-004	Strait of Magellan - Colombia [(1)] (2003)	180	6,650
	Colombia [(1)] - Strait of Magellan (2004)	161	6,650
EMa-033	Strait of Magellan - Colombia [(1)] (2003)	265	6,650
	Colombia [(1)] - Strait of Magellan (2004)	99	6,650

*minimum lineal distance among localities; [(1)]Gorgona Island, Colombia; [(2)]Tribuga Gulf, Colombia

TABLE 4

Comparative information on distance traveled, duration of the trip, mean speed of the trip for the two fastest individuals recorded in this work and method of recording for different migratory connections of humpback whales. Values were obtained and calculated from data sources

Comparación de la distancia recorrida, duración de la migración, velocidad promedio de viaje de los dos individuos más rápidos registrados en este trabajo y método de registro para diferentes conexiones migratorias de las ballenas jorobadas. Valores obtenidos y calculados a partir de los datos de las fuentes

Trip	Method	Distance traveled (km)	Duration of the trip (days)	Migration rate (km day^{-1})	Source
Antarctic - East Australia	Photo-ID	3,500	216	16	Kaufman et al. (1990)
Costa Rica - California	Photo-ID	5,200	218	24	Steiger et al. (1991)
California - Costa Rica	Photo-ID	5,200	171	30	Steiger et al. (1991)
Japan - Vancouver	Photo-ID	7,900	152	52	Darling et al. (1996)
Dominican Republic - Cape Cod (USA)	Photo-ID	2,351	43	55	Clapham & Mattila (1988)
Alaska - Hawaii	Photo-ID	4,400	79	56	Baker et al. (1985)
Brazil - South west Atlantic	Satellite telemetry	3,640	60	61	Zerbini et al. (2006)
Antarctic - Colombia	Photo-ID	8,350	131	64	Stone et al. (1990)
Colombia - Strait of Magellan	Photo-ID	6,650	99	67	This study
Colombia - Strait of Magellan	Photo-ID	6,650	88	76	This study
Puerto Rico - Cape Cod (USA)	Photo-ID	2,684	34	79	Clapham & Mattila (1988)
Brazil - South west Atlantic	Satellite telemetry	3,720	42	89	Zerbini et al. (2006)
Mexico - Hawaii	Photo-ID	4,700	49	96	Darling & Cerchio (1993)
Alaska - Hawaii	Photo-ID	4,400	39	113	Gabriele et al. (1996)

TABLE 5

Global phylopatry index (Ph) for different areas in wintering and summering regions of humpback whales. Values were calculated from data sources

Índice de filopatría global (Ph) para diferentes áreas de las regiones de verano e invierno de ballenas jorobadas. Valores calculados a partir de los datos de las fuentes

	Regions	Ph	Source
Wintering areas			
	Ecuador	0.01	Félix & Haase (2001c)
	West Indies	0.04	Smith et al. (1999)
	Hawaii	0.13	Glockner-Ferrari & Ferrari (1990)
	Hawaii	0.18	Baker et al. (1986)
	Hawaii	0.24	Perry et al. (1990)
	Mexico	0.24	Urbán et al. (1999)
	New Caledonia	0.38	Garrigue et al. (2001)
	Colombia	0.42	This study
	Japan	0.47	Darling & Mori (1993)
Summering areas			
	Newfoundland	0.08	Katona & Beard (1990)
	Shumagin Island, Alaska	0.22	Witteveen et al. (2004)
	Gulf of Saint Lawrence	0.27	Katona & Beard (1990)
	Greenland	0.28	Katona & Beard (1990)
	California	0.63	Calambokidis et al. (1990)
	South east Alaska	0.76	Baker et al. (1986)
	South east Alaska	0.94	Perry et al. (1990)
	Strait of Magellan	1.34	This study
	Gulf of Maine	1.70	Katona & Beard (1990)
	Gulf of Maine	2.18	Clapham et al. (1993)

matching and the round trip movements of individuals demonstrated here, the haplotypes of the mtDNA belonging to the six individual whales observed both in the SM and Colombian waters also support a strong affinity between those regions. The most common haplotype found in the SM population (V. Sabaj unpublished data) is the dominant one for Gorgona Island and Malaga Bay (Caballero et al. 2001) and it is also present, at a low frequency, in the North Pacific humpback whales (Olavarría-Barrera et al 2000, Caballero et al. 2001). Two of the three haplotypes described for the six matched individuals, as far as we know, have not been described in any population of humpback whales other than Colombia and Antarctic Peninsula, suggesting that this population is isolated from other Pacific populations. This finding is further supported by the high phylopatry index estimated for the SM population as compared to other parts of the world.

Several major migratory connections of humpback whale populations, based on the Interchange Index, have been reported worldwide, such as those between the Mexican coast and the west coast of the United States (California-Oregon-Washington, Urbán et al. 2000), and between Hawaii with SE Alaska and W Gulf of Alaska (Perry et al. 1990), as well as secondary connections, i.e., México-Prince William Sound (Alaska) and Hawaii-British Columbia (Calambokidis et al. 2001). In the Southeast Pacific the main migratory connection is between WAP with Colombia and Ecuador (Stevick et al. 2004), with similar values to those found among main destinations of other populations. The index of Interchange of 0.093 between the SM and Colombia, represents a migratory connection with an

intermediate value, similar to the secondary migratory destinations for Hawaii, México and Dominican Republic (Katona & Beard 1990, Urbán et al. 2000, Calambokidis et al. 2001).

Although our data is limited, it is concordant with the described presence of whales in Colombia from feeding grounds of west Antarctic Peninsula as well as SM. On the other side, given that only 10 % of humpback whales photo-identified in the SM were found in Colombia, other breeding areas, such as Ecuador and Panamá, could be other wintering destinations for SM whales.

The transit registration of EMa-001 between the Strait of Magellan and Colombia in 88 days is the third fastest among the photo-identification data and intermediate among satellite telemetry data available for other parts of the world (Table 4). The only published information about transit time for the SE Pacific population is one photo-identified whale that swam 8,350 km from the Antarctic Peninsula to Gorgona Island in 131 days (Stone et al. 1990), equivalent to 64 km day^{-1} (Table 4). Due to little coverage of the study areas, the resultant element of chance involved in re-identifying individuals and the impossibility of establishing erratic movements and changes in speed for whales, the use of photo-identification to study the movements of whales provides conservative estimates of migration duration and distance traveled. Methods such as the satellite telemetry have provided information with unprecedented accuracy about journeys of individual humpback whales in other populations, showing that none of the whales tagged traveled together, departure timing varied for a period of two months, and periods of both straight line and erratic movements existed (Mate et al. 1998, Zerbini et al. 2006). In the Southwest Atlantic for example, two humpback whales travelled 3,720 and 3,640 km through oceanic waters in a relatively direct pattern, at a mean speed of 89 km day^{-1} and 61 km day^{-1}, respectively (Table 4), and then moved erratically for several hundred kilometres during more than 75 days when they were already in feeding grounds (Zerbini et al. 2006) probably looking for food. Unlike the fastest

TABLE 6

Interchange Index between different migratory connection of breeding and feeding grounds of humpback whales. m_{bf}: individuals matched between breeding and feeding grounds; n_f: number of individuals identified in feeding grounds; n_b: number of individuals identified in breeding ground. Values obtained and calculated from data sources

Índice de Intercambio para diferentes conexiones migratorias entre áreas de reproducción y alimentación de ballenas jorobadas. m_{bf}: individuos encontrados en sitios de alimentación y de apareamiento; n_f: numero de individuos identificados en sitios de alimentación; n_b: número de individuos identificados en sitios de apareamiento. Valores obtenidos y calculados a partir de los datos de las fuentes

Migratory connection	m_{bf}	n_f	n_b	Interchange index	Source
Mexico (coast) - Prince William Sound	1	87	138	0.083	Calambokidis et al. (2001)
Mexico (coast) - South east Alaska	4	429	383	0.024	Urbán et al. (2000)
Mexico (coast) - California-Oregon-Washington	97	597	383	0.424	Urbán et al. (2000)
Hawaii - British Columbia	9	73	1,056	0.117	Calambokidis et al. (2001)
Hawaii - South east Alaska	82	464	634	0.279	Perry et al. (1990)
Hawaii - West Gulf of Alaska	17	95	634	0.282	Perry et al. (1990)
Dominican Republic - Gulf of Maine	32	505	975	0.065	Katona & Beard (1990)
Dominican Republic - Newfoundland	157	1,443	975	0.112	Katona & Beard (1990)
Dominican Republic - Greenland	17	154	975	0.113	Katona & Beard (1990)
Ecuador - West Antarctic Peninsula (AP)	32	535	254	0.236	Stevick et al. (2004)
Colombia - Antarctic Peninsula (WAP)	14	535	79	0.331	Stevick et al. (2004)
Colombia - Strait of Magellan	6	62	1,042	0.093	This study

trips between Hawaii and Alaska, Hawaii and México and Brazil and SW Atlantic (Darling & Cerchio 1993, Gabriele et al. 1996, Zerbini et al. 2006) that occur in open sea, migration between the SM and Colombia covered a distance of 2,000 to 3,000 km longer than those previously mentioned (Table 4) and probably crossed through a set of more coastal sites potentially appropriate for feeding and or reproduction. The fastest migration speed of EMa-001 on 2004 between the SM and Colombia (76 km day^{-1} on average) and the second fastest EMa-033 on the same year (67 km day^{-1} on average), correspond to a speed range for straight line movements of migrating whales in the SW Atlantic (61 to 89 km day^{-1}) (Table 4). The registered time of migration for these two individuals suggests, then, to direct trips without erratic movements. On the contrary, erratic movements could explain the longest durations registered for the same individuals on 2003 (EMa-001:197 days and EMa-033:265 days). Validity of these suggestions will require the use of different techniques as the previously mentioned satellite telemetry.

Considerable site fidelity exists among the six migrating individual whales at the feeding grounds of the SM. Values estimated for their residence times and fidelity are representative of this population: humpback whales stayed in the SM during 57 ± 43 days (n = 102) on average and 60 % of the 62 individuals identified returned for two to six years (J. Capella unpublished data). The global Phylopatry Index for the SM is higher than any one in wintering grounds and is one of the highest worldwide for summering areas (Table 5). However, some movement outside the SM must occur because there is considerable variation in residence times among individuals (2 to 155 days) (J. Capella unpublished data). There are frequent sightings of humpback whales in the Corcovado Gulf area in summer, about 1,000 km north of the SM on the Pacific coast (Gibbons & Capella 2006) and one individual recorded in Carlos III Island was also sighted in Canal Wide, Patagonian fjords region, 365 km north (Gibbons et al. 2003). In contrast, tropical wintering ranges on the west coasts of South America appear to be characterized by a high turnover of individuals with interchange among areas (Flórez-González et al. 1998, Recalde 2005) and a weaker site fidelity, a common fact in breeding areas worldwide (Table 5). The humpback whales off the coast of Colombia and Ecuador show a low level of phylopatry (0.36 and 0.01, respectively, Table 5) and a short residency, with an overall mean of 18 days and 13 days respectively (Capella et al. 1995[1], Scheidat et al. 2000). Our findings indicate that the SM is a recurrent feeding ground destination for at least some of the humpback whales that breed along the coast of Colombia and is unique in the southern ocean outside of the Antarctic region (Clapham & Mead 1999).

It is unknown whether the six individual whales described in this report are representative of the summer migratory destinations of all whales within the stock. Our results and the absence of any evidence of a migratory connection between humpback whales from WAP and the SM (Acevedo 2006), provide important and unique support for the assessment that the Strait of Magellan and its surrounding waters could be a sub-region of the feeding range of the Area I stock. This is consistent with the high level of inter-year return that we observed, also reported by Acevedo et al. (2006).

Our information and those previously published for the Antarctic Peninsula (Stone et al. 1990, Stevick et al. 2004) show that the southeastern Pacific humpback whale population may segregate into at least two separate feeding areas located at variable distances from the breeding region, resembling the north Atlantic and north Pacific humpback whale populations, where some geographically distinct feeding aggregations have been described (Baker et al. 1986, Katona & Beard 1990, Katona & Beard 1991, Stevick et al. 2003). Taken together, our results suggest for Area I stock the existence of a shorter migratory cycle, with final summer destinations at SM, 1,400 km closer than the previously described at WAP.

[1] CAPELLA J, L FLÓREZ-GONZÁLEZ & GA BRAVO (1995) Site fidelity and seasonal residence of humpback whales around Isla Gorgona, a breeding ground in the Colombian Pacific. Abstracts of the Eleventh Biennial Conference on the Biology of Marine Mammals, Orlando, Florida, USA.

The precise migratory routes in the southeast Pacific as well as the movements within the waters of the Patagonian fjords and throughout the western Antarctic Peninsula remain poorly known. Further photographic data from the SM will be necessary to establish, with confidence, the extent of exchange among Colombia and other wintering grounds in eastern Pacific (Ecuador and Panamá). Current evidence does not allow determining the main winter destination. Based on the presence in the SM of a mtDNA haplotype absent in the SE Pacific and Antarctic Peninsula (Sabaj et al. 2004), humpback whales coming from breeding areas that have not been characterized or considered in this study could also feed in the SM (for example the SE coast of Brazil).

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