



Migratory interchange of humpback whales (*Megaptera novaeangliae*) among breeding grounds of Oceania and connections to Antarctic feeding areas based on genotype matching

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Abstract

Humpback whales (*Megaptera novaeangliae*) congregate to breed during the austral winter near tropical islands of the South Pacific (Oceania). It has long been assumed that humpback whales from Oceania migrate primarily to Antarctic feeding grounds directly south (International Whaling Commission Management Areas V and VI); however, there are few records of individual movement connecting these seasonal habitats. Based on genetic samples of living whales collected over nearly two decades, we demonstrate interchange between the breeding grounds of Oceania and Antarctic feeding Areas V, VI, and I (i.e., from 130°E to 60°W), as well as with the eastern Pacific (Colombia), and the migratory corridors of eastern Australia and New Zealand. We first compared genotype profiles (up to 16 microsatellite loci) of samples collected from Oceania breeding grounds to each other and to those from the eastern Pacific. The matching profiles documented 47 individuals that were present on more than one breeding ground, including the first record of movement between Oceania and Colombia. We then compared the 1179 genotypes from the breeding grounds to 777 from the migratory corridors of east Australia and New Zealand, confirming the connection of these corridors with New Caledonia. Finally, we compared genotypes from breeding grounds to 166 individuals from Antarctic feeding Areas I–VI. This comparison of genotypes revealed five matches: one between New Caledonia and Area V, one between Tonga and Area VI, two between Tonga and Area I (western edge), and one between Colombia and Area I (Antarctic Peninsula). Despite the relatively small number of samples from the Antarctic, our comparison has doubled the number of recorded connections with Oceania available from previous studies during the era of commercial whaling.

Keywords Humpback · *Megaptera novaeangliae* · Migration · Genotyping

Introduction

Humpback whales (*Megaptera novaeangliae*, Borowski 1781) feed during the austral summer in the waters around Antarctica and migrate north during the austral winter to congregate near island groups throughout the South Pacific. These islands (designated here as Oceania) extend from

New Caledonia in the west, to French Polynesia in the east (Fig. 1). Within Oceania, four regional breeding grounds have been described based on the differentiation of mitochondrial (mt)DNA haplotype frequencies; New Caledonia, Tonga, Cook Islands, and French Polynesia (Olavarría et al. 2007). The International Whaling Commission (IWC) recognizes these regions as four 'Breeding Stocks' or substocks, BSE2 (New Caledonia), BSE3 (Tonga), BSF1 (Cook Islands), and BSF2 (French Polynesia) (Fig. 2; IWC 1998, 2015). Samoa and American Samoa are more recently surveyed regions that are considered to be associated with BSE3 (Garrigue et al. 2011a; Robbins et al. 2011).

To the west of Oceania, humpback whales migrating along the eastern coast of Australia are considered to be the western substock of Breeding Stock E (BSE1). To the east,

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whales migrating along the Pacific coast of South America to Colombia and Central America are considered to represent Breeding Stock G (BSG). Both the eastern Australian and Colombian breeding grounds are differentiated from Oceania breeding grounds by mtDNA haplotype frequencies (Olavarría et al. 2006, 2007). Consistent with the genetic evidence for stock structure, photo-identification studies have documented only low levels of interchange among the breeding grounds of Oceania (Garrigue et al. 2002) and between most regions of Oceania and the migratory corridors along eastern Australia (Garrigue et al. 2011b) and New Zealand (Constantine et al. 2007). There has been no recorded movement between Oceania and Colombia (BSG).

The breeding grounds of Oceania lie to the north of Antarctic management Areas V and VI, as referred to by the IWC (Donovan 1991; Fig. 1). However, direct evidence of migratory connections is limited and the migratory destinations for Oceania whales remain poorly described. The first direct evidence of migratory connectivity between Oceania and the Antarctic feeding areas was based on *Discovery* marking and recovery during the era of modern commercial whaling (Clapham and Baker 2009). These are stainless steel tags shot into the back of whales and later recovered when the whale was killed and flensed (Dawbin 1964; Chittleborough 1965; Dawbin 1966). In contrast to the extensive programs of *Discovery* marking and recovery by shore-based whaling stations in eastern Australia and New Zealand (Dawbin 1964; Chittleborough 1965; Dawbin 1966), there was relatively little effort in Oceania (Dawbin 1956). Only four cases of migratory connections between the breeding grounds of Oceania and the Antarctic feeding areas were documented by the recovery of *Discovery* marks prior to the end of commercial whaling and the subsequent illegal Soviet whaling: one between Fiji and Antarctic Area IV (Mikhalev 1997), one between Tonga and Antarctic Area V (Dawbin 1959), and two between Tonga and Antarctic Area I (Brown 1957 as summarized in Dawbin 1964; Mikhalev and Tormosov 1997; Fig. 2 and Online Resource 1). There are no *Discovery* mark records connecting the Antarctic to other historically known South Pacific breeding grounds, such as New Caledonia or Vanuatu (Townsend 1935) or the more recently described breeding grounds around the Cook Islands and the Society Islands of French Polynesia (Hauser et al. 2000; Poole 2002; Gannier 2004).

More recently, photo-identification has confirmed the connectivity of eastern Australia to Antarctic Area V (e.g., Franklin et al. 2008; Constantine et al. 2014) and the Colombian breeding grounds to Antarctic Area I, particularly the Antarctic Peninsula (Stone et al. 1990; Stevick et al. 2004; Rasmussen et al. 2007). To date, however, there have been few published reports of photo-identification matches between Oceania and Antarctic feeding areas, e.g., a single match between New Caledonia and Balleny Island (Area V,

Constantine et al. 2014) and a single match between American Samoa and Area I (Robbins et al. 2011). In the austral winter of 2006, a single whale tagged with a satellite transmitter provided the first record of migration from the Cook Islands to the Antarctic Area VI/I boundary (Hauser et al. 2010).

Records of interchange among breeding grounds and connectivity to the Antarctic feeding grounds are important for understanding the population dynamics and ecological role of humpback whales in the aftermath of commercial whaling (Baker and Clapham 2004). Humpback whales were hunted intensively throughout the Southern Hemisphere, with more than 200,000 killed during the 20th century (Clapham and Baker 2009), resulting in local extirpation before protection by the IWC in 1966 (Clapham et al. 2008). While some regional populations have shown evidence of strong recovery e.g., off the eastern and west coasts of Australia (IWC 2015, 2016; Noad et al. 2016), the numbers of humpback whales in surveyed breeding grounds of Oceania remain low relative to known or presumed historical numbers (Constantine et al. 2012; IWC 2015, 2016).

Here, we use genotype matching (up to 16 microsatellite loci) from non-lethal samples of humpback whales to investigate interchange among breeding grounds of Oceania and to examine interchange with Colombia. Through standardization of laboratory protocols for genotyping, we extend the matching to a large collection of samples from the migratory corridor along eastern Australia (Anderson et al. 2003), extending the previous documentation of interchange based on photo-identification (Garrigue et al. 2011b). We also present new records of migratory connections with feeding areas of the Antarctic, using samples collected during the International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programs of the IWC. For some breeding grounds, this provides the first evidence of migratory destinations since the end of the *Discovery* marking program, more than 50 years ago.

Methods

A total of 2021 samples (biopsy and sloughed skin samples), including 1112 previously described by Olavarría et al. (2007), were collected from six breeding grounds: New Caledonia, Tonga, Samoa, Cook Islands, French Polynesia, and the Pacific coast of Colombia (Table 1). Samples from Oceania were collected primarily by members of the South Pacific Whale Research Consortium during non-systematic surveys from 1999 to 2005, but also include samples collected during surveys dating back to 1991 and as recently as 2009. Samples from the Colombian breeding grounds (Gorgona Island and Bahía Málaga, coastal Colombia) were

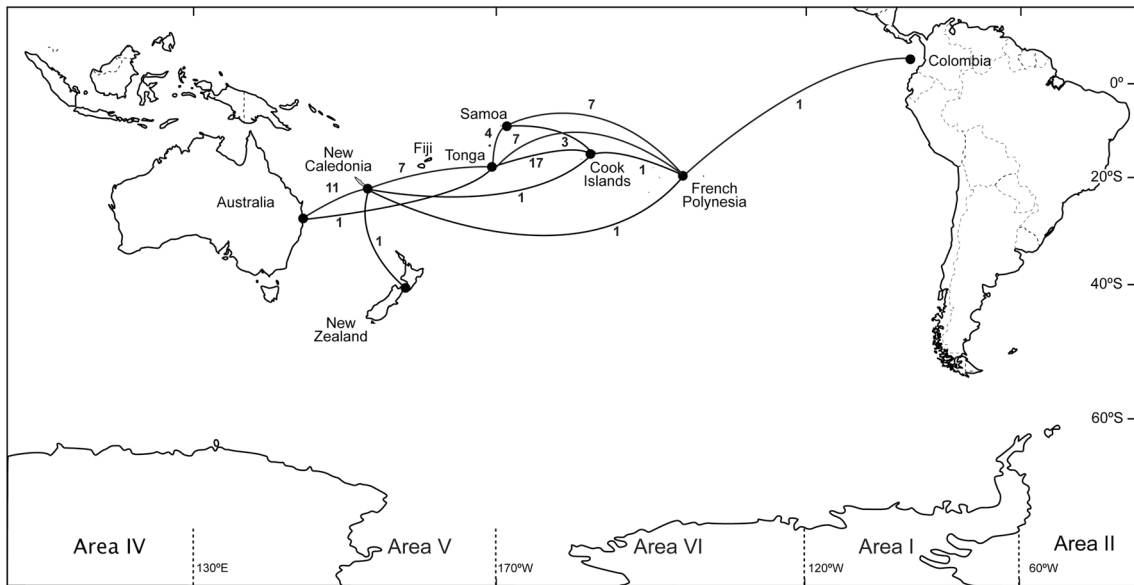


Fig. 1 Movement of individual humpback whales among breeding grounds of Oceania and the eastern Pacific, and the migratory corridors of Australia and New Zealand, as established by genotype matching (solid lines). The approximate boundaries of the Antarctic

Feeding Areas IV, V, VI, and I are shown as dashed lines. One individual was recaptured in three locations, Tonga, American Samoa (Samoa), and the Cook Islands

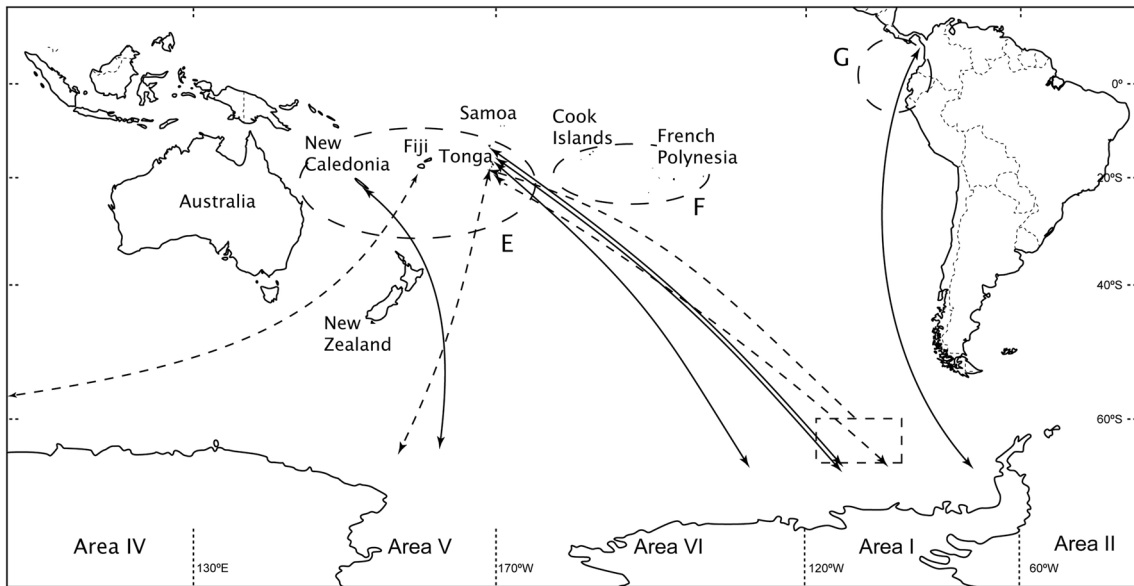


Fig. 2 Migratory connections of humpback whales between breeding grounds of Oceania and the eastern Pacific, and feeding Areas of Antarctica, established by genotype matching (solid lines) as compared to *Discovery* marking (dashed lines). The dashed box represents uncer-

tainty in the location of the recovery of one of the *Discovery* tags (No 4, Online Resource 1). The approximate locations of Breeding Stocks *E*, *F*, and *G* and the boundaries of the Antarctic Feeding Areas IV, V, VI, and I are shown as dashed lines

collected by members of Fundación Yubarta from 1991 to 1999. Samples collected in New Zealand and eastern Australia were considered to represent migratory corridors, rather than migratory destinations, although the corridor of eastern Australia is assumed to represent a proxy for a

primary breeding ground near the Great Barrier Reef (Pater-son and Paterson 1984). In New Zealand, a total of 51 biopsy samples were collected from 2003 to 2007, primarily during the northerly migration through Cook Strait. In eastern Australia, a total of 1526 samples (all sloughed skin) were

Table 1 The collection years, number of samples, and numbers of unique genotypes (representing an individual identification) for humpback whales sampled in each region of Oceania and the Antarctic

Region	Years	^a QC12 ^b samples	^a Unique genotypes	^a Male	^a Female	^a unknown sex
Oceania breeding grounds						
New Caledonia	1995–2005	572	377	212	150	15
Tonga	1991–2005	483	346	225	112	9
American Samoa/Samoa	2001–2009	95	88	64	24	0
Cook Islands	1996–2005	194	98	50	46	2
French Polynesia	1997–2007	309	207	114	86	7
Eastern Pacific breeding grounds						
Colombia	1991–1999	141	111	64	25	22
Total Breeding		1794	(1179)	(698)	(426)	(55)
Migratory corridors						
Eastern Australia ^b	1996–2004	1526	734	403	311	20
New Zealand	2003–2007	45	43	25	10	8
Total Breeding and Corridors		3365	(1943)	(1116)	(744)	(83)
Antarctic feeding Areas						
Antarctic Peninsula (part of IWC Area I)	1989–1999	80	69	23	40	6
Antarctica—region unknown	2001	3	3	0	0	3
Antarctica Area I	1994, 2001	15	13	2	10	1
Antarctica Area II	2005	1	1	1	0	0
Antarctica Area III	1992–2005	13	11	1	4	6
Antarctica Area IV	1999	48	43	19	21	3
Antarctica Area V	1991–2004	9	9	4	3	2
Antarctica Area VI	1990, 2001	19	17	7	8	2
Total feeding		188	(166)	(57)	(86)	(23)
Total		3553	(2104)	(1170)	(827)	(106)

^aQC is the number of samples after quality control, i.e., the number of samples that included genotypes for 12 or more loci (see Methods). The numbers in parenthesis in the rows of Totals are the number of unique genotypes across the entire breeding or feeding region, i.e., with between-region replicates removed

^bEA samples are QC6 i.e., samples that had genotypes for 6 or more loci (Anderson et al. 2010)

collected during both northbound (Byron Bay) and southbound migration (Hervey Bay and Ballina).

Biopsy samples were collected from Antarctic feeding Areas I–VI over the period 1991–2005 during circumpolar surveys by the International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programs of the IWC ($n = 122$). Additional samples were collected during more localized surveys of Antarctic Area I by the Chilean Antarctic Institute (INACH, $n = 65$) and the Southern Ocean Global Ocean Ecosystems Dynamics (SO-GLOBEC, $n = 27$).

For samples from Oceania, New Zealand, and the Antarctic feeding areas, total cellular DNA was isolated from skin tissue by digestion with Proteinase K followed by a standard phenol:chloroform extraction method (Sambrook et al. 1989) as modified for small skin samples (Baker et al. 1994). For samples from eastern Australia total cellular DNA extraction followed methods detailed in (Elphinstone et al. 2003).

Individual identification was based on genotyping methods described in detail by Constantine et al. (2012), and, in

most cases, this was confirmed with molecular identification of sex and sequencing of the mtDNA control region (460 bp) using methods described in detail by Olavarría et al. (2007). For samples from Oceania, Colombia, New Zealand, and the Antarctic, up to 16 microsatellite loci were amplified for each sample using previously published primers (464/465 (Schlötterer et al. 1991); Ev1, Ev14, Ev21, Ev37, Ev94, Ev96, Ev104, (Valsecchi and Amos 1996); GATA417, GATA28 (Palsbøll et al. 1997); rw31, rw4-10, rw48, (Waldick et al. 1999) and GT211, GT575, GT23, (Bérubé et al. 2000); Online Resource 2). Microsatellite loci were amplified individually in 96- or 384-well format with MJ PTC-225 (MJ Research) and co-loaded in four sets for automated sizing (size standard 500LIZ™) on an ABI 3730xl DNA analyzer (Applied Biosystems; Online Resource 2). Peaks were reviewed and allele bins allocated using GeneMapper (Applied Biosystems). Samples from eastern Australia were amplified for a subset of 12 loci and allele sizing bins were standardized using a set of common samples (i.e., allelic standards) as described in Anderson et al. (2003).

Comparisons were not made between eastern Australia and the Antarctic feeding grounds, as these have been reported elsewhere (Anderson et al. 2010).

Data organization and primary analyses of allele frequencies at microsatellite loci and haplotype frequencies for mtDNA sequences were conducted with the program GenAIEx (Peakall and Smouse 2012). Confidence in individual identification was assessed using Probability of Identity (*PI*), defined as the probability that two individuals drawn at random from a given population share identical genotypes for a given set of loci (Paetkau 2003; Pompanon et al. 2005), as calculated in GenAIEx.

Results

Genotype quality control and matching

A total of 2285 samples were genotyped, including identification of sex and sequencing of mtDNA haplotypes for most samples. Variation in the number of microsatellite loci successfully amplified suggested relatively poor quality DNA for some samples. As a measure of quality control (QC), samples with fewer than 12 microsatellite loci were deleted from the dataset. The QC dataset totaled 1794 samples from Oceania and Colombia breeding grounds, 45 samples from New Zealand and 188 samples from Antarctic feeding Areas, with an average of 15.3 loci each (Table 1). Unique genotypes within breeding grounds and feeding areas were resolved with the program CERVUS (Marshall et al. 1998), requiring an exact match for at least eight loci, supported by control region haplotypes and sex where available. Given the relatively large number of loci and the potential for false exclusion due to genotype error (e.g., allelic dropout, (Waits and Leberg 2000; Waits et al. 2001)), the initial comparison allowed for mismatches at up to three loci. Probability of Identity (*PI*) values ranged from 1.3×10^{-5} to 2.1×10^{-12} for the minimum criterion of eight matching loci. Given

these low values, we assumed that genotypes matching at eight or more loci were likely to represent replicate samples (true resamples or ‘recaptures’) of the same individual whales and that mismatching loci were likely to represent genotype error (Hoffman and Amos 2005). Under these criteria, the 2027 QC samples were found to represent 1179 unique genotypes from the six breeding grounds, 43 unique genotypes from New Zealand and 166 unique genotypes from the Antarctic feeding areas (Table 1).

Interchange among breeding grounds and migratory corridors

To document interchange among breeding grounds, we compared unique genotypes from each of the five breeding grounds of Oceania to each other and to available genotypes from the eastern Pacific (Colombia) (Fig. 1). Of the 1227 individuals identified by genotypes, 47 were documented on more than one breeding ground, including one male sampled on three different breeding grounds (1998 in the Cook Islands, 2003 in Tonga and 2009 in American Samoa).

Some interchange was documented among most of the breeding grounds within Oceania and, compared to the previous photo-identification survey (Garrigue et al. 2002), several new and distant connections were found, including the first matches between New Caledonia and French Polynesia, over a four-year interval, and between French Polynesia and Colombia, over an eight-year interval (Table 2). The Cook Islands accounted for a relatively large number of matches, given its small sample size, and included six records of transits within a season (Online Resource 3 and 4).

The 1179 genotypes from the breeding grounds were then compared to those available from the eastern Australia and New Zealand migratory corridors. This revealed 13 matches, which were all between the two corridors and New Caledonia (Table 2) except for one match between eastern Australia and Tonga. Although there was a significant male bias in the combined sample from the breeding grounds and migratory

Table 2 Summary of movement among breeding grounds of humpback whales and adjacent migratory corridors within the South Pacific as documented by genotyping identification and matching

	EA	NZ	NC	Tg	AS/Sa	CI	FP	Co
Eastern Australia	403/311	0	9	1	0	0	0	0
New Zealand	0	25/10	0	0	0	0	0	0
New Caledonia	2	1	<i>212/150</i>	4	0	0	1	0
Tonga	0	0	3	<i>225/112</i>	3	11	6	0
American Samoa/Samoa	0	0	0	1	<i>64/24</i>	1	5	0
Cook Islands	0	0	1	6	2	<i>50/46</i>	0	0
French Polynesia	0	0	0	1	2	1	<i>114/86</i>	1
Colombia	0	0	0	0	0	0	0	<i>64/25</i>

The number of individual whales by sex (males/females) identified by microsatellite genotyping in each breeding ground is shown in the diagonal. The number of males identified on multiple breeding grounds is shown above the diagonal and the number of females below. The italic box indicates breeding grounds of Oceania

corridors (1157 males: 764 females; binomial exact test, $p < 0.001$), there was no evidence of strong sex-bias in movement between breeding grounds or migratory corridors (Table 2): of the 60 individuals documented in two or more regions, 40 were males and 20 were females. This ratio is not significantly different from that of the overall sample from breeding grounds and migratory corridors (Fisher's exact test, $p = 0.38$).

Migratory connections of breeding grounds with Antarctic feeding areas

To document migratory connections between seasonal habitats, we compared unique genotypes from each of the six breeding stocks of Oceania and eastern Pacific to the 166 unique genotypes from Antarctic feeding areas. In contrast to the breeding grounds and migratory corridors, the combined feeding grounds showed a significant female bias (57 males: 86 females, binomial exact test, $p = 0.019$). The comparison of breeding grounds to feeding grounds revealed five matches between the seasonal habitats (Fig. 2): one between New Caledonia and a location close to the eastern margin of Antarctic Area V, one between Tonga and the eastern half of Antarctic Area VI, two between Tonga and Antarctic Area I (western margin) and one between Colombia and Antarctic Area I (Antarctic Peninsula) (Fig. 2; Table 3, Online Resource 4). All matches were supported by at least

13 microsatellite loci, as well as sex and mtDNA haplotype (Table 3).

To assess the support for these matches, we calculated PI and the more conservative probability of identity for full siblings (PI_{sib} , Waits et al. 2001) for each of the three breeding grounds involved in the five migratory connections, using only the loci available for the matching samples (Table 3). Given that the maximum PI for any given breeding ground was 2.1×10^{-12} and the maximum number of pairwise comparisons was 62,582 (i.e., the product of the number of unique genotypes on a given breeding ground and the number of unique genotypes from all feeding areas, Table 1), it is unlikely that any of these five matches was due to chance.

Discussion

We have assembled the most extensive dataset available to date, for genotype identification of individual humpback whales on the breeding grounds of Oceania. With the exchange of reference samples or cross-referencing of allelic ladders, these genotype profiles can be compared between laboratories and provide a searchable 'DNA register' (DeSalle and Amato 2004) to document the migratory return and interchange of individuals for decades to come. Our results complement the use of genotype 'capture-recapture' to estimate the abundance of humpback whales in Oceania (Constantine et al. 2012), and contribute to other records

Table 3 Migratory connections between humpback whales from breeding grounds of Oceania and eastern Pacific and feeding areas of the Antarctic as documented by genotype matching (F, female; M, male; -, missing; mtDNA control region haplotype as described in

Olavarria et al. (2007); PI , probability of Identity; PI_{sib} , Probability of Identity for siblings calculated for the appropriate populations (See Online Resource 4)

	Sample codes	Location	Date	Sex	mtDNA	Matching loci	PI PI_{sib}
1	Mno97NC016	New Caledonia	24 Aug 1997	F	SP26	12	2.4×10^{-13}
	Mno01A51546	Area V 62°26'S, 171°6'W	9 Jan 2001	F	SP26		1.9×10^{-5}
2	Mno03Tg107	Tonga 19°54'S, 174°40'W	22 Aug 2003	M	SP83	13	3.2×10^{-13}
	Mno01A51553	Area VI 67°14'S, 129°31'W	26 Jan 2001	M	SP83		2.1×10^{-5}
3	Mno03Tg014	Tonga 18°38'S, 174°8'W	28 Aug 2003	F	SP1	14	2.5×10^{-16}
	Mno01A51580	Area I 67°31'S, 114°20'W	7 Feb 2001	F	SP1		2.7×10^{-6}
4	Mno91Tg008	Tonga	Oct 1991	F	SP13	15	2.5×10^{-16}
	Mno01A51581	Area I 68°26'S, 114°27'W	11 Feb 2001	F	SP13		2.3×10^{-6}
5	Mno91Co005	Gorgona Island, Colombia	1991	M	SP8	15	3.2×10^{-16}
	MnoIWC94H101	Area I 67°03'S, 71°18'W	7 Feb 1994	-	SP8		2.1×10^{-6}

Latitude and longitude of sample location are provided where available

(genotype and photo-identification) documenting long-range movement of humpback whales (Stone et al. 1990; Bérubé et al. 2004; Pomilla and Rosenbaum 2005; Rasmussen et al. 2007; Robbins et al. 2011; Stevick et al. 2011).

Confirming previous studies, we found a strong male bias in the samples from the breeding grounds and migratory corridors, similar to that reported previously from biopsy samples (Brown et al. 1995; Olavarría et al. 2007), and a significant females bias in samples from the Antarctic feeding areas, similar to that reported in commercial whaling records (Chittleborough 1965). After accounting for the male-biased sample, we did not find evidence of male-biased dispersal (i.e., interchange between breeding grounds), as might be expected from the general pattern of mammalian female philopatry and male dispersal (Greenwood 1980). However, our observations are consistent with other evidence discounting the expectation of a detectable male-biased dispersal in the population structure of humpback whales in the North Pacific (Baker et al. 2013). Despite the absence of demographic evidence for male-biased dispersal, we do not discount the genetic evidence for male-biased gene flow, resulting from occasional alteration among breeding grounds (Baker et al. 2013).

Our matching of genotype profiles among the breeding grounds extended the geographic and temporal range of documented interchange within Oceania. As with previous photo-identification matching, most of the movement was between ‘nearest neighbours’ within Oceania, e.g., New Caledonia and Tonga, Tonga and the Cook Islands. Similarly, there were a relatively large number of matches between the migratory corridors of eastern Australia and the adjacent breeding grounds of New Caledonia but not to other regions of Oceania, despite the relatively large samples size of some regions (e.g., Tonga). There was only a single match with the New Zealand migratory corridor (to New Caledonia) but the sample size was too small to draw any strong conclusions about this connection. Perhaps most notable were the new records of interchange between New Caledonia and French Polynesia, and between French Polynesia and Colombia (BSG). Extending across nearly a decade of sampling and spanning nearly the entire South Pacific, these records confirms the potential for occasional genetic interchange between even the most distant breeding grounds of this ocean basin.

Matches with the Cook Islands accounted for all of the within-season movement between breeding grounds. This is consistent with other evidence suggesting that whales are migrating through the Cook Islands on their way to other destinations (Hauser et al. 2010). Interestingly, the six documented within-seasons transits (three males, three females: Online Resource Table 3) all showed a westerly direction of movement, i.e., the whales were first observed in the Cook Islands and in westerly regions later in the season.

A westerly or northwesterly direction of travel was also observed for seven whales tagged with satellite transmitters in the Cook Islands (Hauser et al. 2010). Although these observations support previous observations that longitudinal movement is an important component of humpback whale migration in the South Pacific, they do not support the hypothesis of a strong sex bias in this component (Valsecchi et al. 2010), given that both sexes are evenly represented in these records. The westerly movement is consistent with a counter-clockwise pattern of migration, also hypothesized by Valsecchi et al. (2010), but could more simply reflect a strong connection of Oceania breeding grounds to Antarctic Area VI. The diagonal connection between these migratory destinations is also supported by recovery of *Discovery* marks, matching of genotype profiles (Fig. 2) and satellite tagging (Garrigue et al. 2010).

Through access to more than 15 years of genetic sampling by the IDCR/SOWER cruises of the IWC, the Chilean Antarctic Institute and the SO-GLOBEC program, we provided the first systematic comparison of migratory connections between the breeding grounds of Oceania and the feeding areas of the Antarctic areas since the end of *Discovery* marking in 1963, a period of more than 50 years. Our genotype survey of living whales has more than doubled the number of connections documented by *Discovery* marking, despite the relatively small number of samples from the Antarctic feeding areas, providing new information on migration between New Caledonia and Antarctic Area V and between Tonga and Antarctic Area VI. The matches also provided further evidence for a connection between Tonga and the western component of Antarctic Area I, as well as for the previously established connection between the Pacific coast of Colombia and the Antarctic Peninsula, in the eastern component of Antarctic Area I (Stevick et al. 2004).

Information on the migratory connections between breeding grounds in the South Pacific and the Antarctic has important implications for management of whales. One of the challenges of assessing the recovery status of humpback whale stocks in the Southern Hemisphere is allocating historical catches from the Antarctic feeding areas to the appropriate breeding stock. This information is needed to accurately model the subsequent trajectory of each stock (Baker and Clapham 2004). The genotype matches reported here and historical *Discovery* mark recoveries suggest that past catches from the eastern component of Antarctic Area V, the whole of Antarctic Area VI and western component of Antarctic Area I should be taken into account for an assessment of Oceania breeding stocks (IWC 2015).

More generally, an understanding of differences in rates of recovery between breeding grounds will require a better understanding of the current connectivity and, perhaps, productivity of the corresponding Antarctic feeding areas (Baker and Clapham 2004). Recently, there has been

considerable progress in the use of ‘mixed-stock’ analyses to understand the contribution of breeding stocks to feeding areas, notably for Colombia (BSG) and Brazil (BSA) in relationship to the Antarctic Peninsula (Area I) (Albertson et al. 2017; Cypriano-Souza et al. 2017). For Oceania, however, it is clear that a quantitative comparison of the relative strengths of these migratory connections and, consequently, a quantitative model of historical catch allocations and current population dynamics will require a larger and more geographically representative collection of samples from the feeding areas, particularly Area VI.

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