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Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas based on genotype matching

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ABSTRACT

Humpback whales of the South Pacific breed near island groups north of the Antarctic feeding grounds referred to by the International Whaling Commission as Areas V and VI. For this reason, it has generally been assumed that Oceania humpbacks are part of the Group V and VI stocks, however, there is little direct evidence connecting these habitats. Here we present new records of migratory connections based on genotype matching (up to 17 microsatellite loci, sex and mitochondrial DNA). A total of n = 1,756 samples (n = 1,065 unique genotypes) were collected from six winter breeding grounds and a total of n = 214 samples (n = 175 unique genotypes) were collected from Antarctic feeding Areas I-VI. Comparison of genotypes revealed 5 matches representing migratory connections: 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 feeding areas, this survey has doubled the number of connections previously documented by *Discovery* marking and recovery, and provides the first direct evidence of migration between New Caledonia and Area V.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*, Borowski, 1781) congregate during the austral winter near island groups throughout the South Pacific. The islands of the South Pacific (referred to here as Oceania), range from New Caledonia in the west to the Society and Austral Islands of French Polynesia in the east, and lie directly north of the humpback Antarctic feeding grounds referred to by the International Whaling Commission (IWC) as Areas V and VI. For this reason, it has generally been assumed that humpbacks that winter in Oceania are part of the so-called Group V and VI stocks. However, unlike the historic tagging studies of humpbacks taken by coastal whaling stations in eastern Australia and New Zealand (Chittleborough 1965; Dawbin 1964b, 1966), there is little direct evidence connecting the breeding grounds of Oceania to Antarctic Areas. Tagging and recovery of *Discovery* marks documented only four cases of migratory connections between the breeding grounds of Oceania and the Antarctic (Table 1, Figure 1): one between Fiji and Area IV, one between Tonga and Area V and two between Tonga and Area I (Dawbin 1966). There are no *Discovery* mark records connecting Antarctica to other historically known grounds such as New Caledonia, Vanuatu and Samoa (Townsend 1935), or the more recently described breeding grounds around the Cook Islands and the Society Islands of French Polynesia (Gannier 2004; Hauser *et al.* 2000; Poole 2002). More recently, photo-identification

studies have documented a degree of interchange among breeding grounds of Oceania (Garrigue *et al.*, 2000, 2002) and between Oceania and migratory corridors along eastern Australia and New Zealand (Constantine *et al.* 2007). However, to date, there has been limited matching between Oceania and Antarctic catalogues with no evidence of interchange. 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 (Clapham *et al.* 2008).

Here we present new records of migratory interchange based on genotype matching (microsatellite, sex and mitochondrial DNA) between non-lethal samples collected throughout Oceania and those collected from Antarctic feeding Areas. Genotype matching is increasingly being used in the study of migratory animals including humpback whales (Berube *et al.* 2004, Pomilla and Rosenbaum 2005).

METHODS AND RESULTS

A total of n = 1,756 samples (sloughed skin and biopsy samples), including n = 1,112 samples described by Olavarria *et al.* (2007), were collected from six winter breeding grounds: New Caledonia, Tonga, Samoa, Cook Islands, French Polynesia and Pacific coast of Colombia (Table 2). Samples from Oceania were collected primarily by members of the South Pacific Whale Research Consortium during synoptic surveys from 1999 to 2005 but also include smaller numbers of samples collected during surveys of some regions dating back to 1991. Samples collected from the Colombian breeding grounds (the Gorgona Islands and coastal Colombia) were collected by members of Project Yubarta from 1991 to 1998. A total of n = 214 samples (biopsy only) were collected from Antarctic feeding Areas I-VI. These samples were collected from 1991 to 2005 during circumpolar surveys by the International Decade of Cetacean Research and Southern Ocean Whale Ecosystem Research (IDCR/SOWER) of the IWC, and during more localized surveys of the Antarctic Peninsula by the Chilean Antarctic Institute (INACH), and of Area I by Southern Ocean Global Ocean Ecosystems Dynamics (SO-GLOBEC).

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). Up to 17 microsatellite loci were amplified for each sample using previously published primers (GT211, GT575, GT23 (Berube *et al.* 2000) GATA417, GATA28 (Palsboll *et al.* 1997) Ev1, Ev14, Ev21, Ev37, Ev94, Ev96, Ev104 (Valsecchi and Amos 1996) 464/465 (Schlotterer *et al.* 1991) rw26, rw31, rw4-10, rw48 (Waldick *et al.* 1999)). Microsatellite loci were amplified individually in 96- or 384-well format with MJ PTC-225 (MJ Research) and multiplexed in three sets for automated sizing on an ABI 9730xl (Applied Biosystems). Molecular identification of sex and sequencing of the mitochondrial (mt) DNA control region (460 bp) followed methods described in detail by Olavarria *et al.* (2007). Data organisation and initial analyses of microsatellite alleles, sex and mtDNA haplotypes were conducted with the program GenAlEx (Peakall and Smouse 2006).

Variation in the number of microsatellite loci amplified successfully suggested relatively poor quality DNA for some samples, particularly from sloughed skin. Following a quality control (QC) review, samples with fewer than 9 microsatellite loci were deleted from the dataset, leaving a total of n = 1,601 QC samples from breeding grounds and n = 197 QC samples from Antarctic feeding Areas, with an average of 13.5 loci each. Unique genotypes within breeding grounds and within feeding areas were resolved with the program CERVUS (Marshall *et al.* 1998) using a criteria that required exact matching for at least 8 loci, supported, in most cases, with control region haplotypes and sex. Given the large number of loci and the potential for false exclusion due to allelic drop-out and other genotype error (Waits and Leberg 2000, Waits *et al.* 2001), the initial comparison allowed for mismatches at up to three loci. Average probability of identity (PI) for the minimum criterion of 8 matching loci ranged from 1.68×10^{-6} to 2.55×10^{-12} as calculated following Paetkau *et al.* (1995). Given these low values, we assumed that genotypes matching at 8 or more loci were likely to represent replicate samples (true recaptures) of the same individual whales and any mismatching loci were likely to represent genotype error (Hoffman and Amos 2005). With these criteria, the n = 1,798 QC samples resolved n = 1,065 unique genotypes from the six breeding grounds and n = 175 unique genotypes from the Antarctic feeding areas (Table 2).

Comparison between the n = 1,065 unique genotypes from the breeding grounds and n = 175 from the feeding areas revealed 5 matches representing migratory connections: 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) (Table 3, Figure 1). All matches were supported by at least 12 microsatellite loci with maximum PI $< 1.1 \times 10^{-14}$ and a maximum $PI_{sib} < 4.1 \times 10^{-5}$, as well sex and mtDNA haplotype. Genotypes of two samples (sample codes Mno91Tg008 and MnoA51581) included a 'soft match' at three loci i.e. one sample was a homozygote for one allele of the other sample. We repeated these genotypes, confirming that this initial inconsistency was the result of allelic drop-out.

DISCUSSION

Our genotype survey has doubled the number of connections documented by *Discovery* marking, despite the relatively small number of samples from the Antarctic feeding areas. This study provides the first direct evidence of migration between New Caledonia and Area V, further evidence is also provided for a relatively strong connection between Tonga and Areas VI and I, as well as for the previously established connection between the Pacific coast of Colombia and the Antarctic Peninsula (Area I; Stevick *et al.* 2004, Stone *et al.* 1990).

Information on the migratory connections between breeding grounds in the South Pacific and the Antarctic has important implications for management. Humpback whales were hunted intensively throughout the Southern Hemisphere, with more than 200,000 killed during the 20th century (Clapham and Baker 2002). As a consequence, humpback whales disappeared from many regions of the Southern Hemisphere (Chapman 1974). While some regions have shown evidence of strong recovery in abundance (e.g., Bannister 1994; Paterson *et al.* 1994), the numbers of humpback whales in surveyed breeding grounds of Oceania remains low (Garrigue *et al.*, 2004; Gibbs *et al.*, 2006; SPWRC *et al.*, 2006). In an effort to understand the history of this exploitation and the current status of stocks, the IWC has committed to a Comprehensive Assessment of southern hemisphere humpback whales (IWC 1998). One of the challenges of this Comprehensive Assessment is the allocation of historical catches from the Antarctic feeding areas to breeding grounds for the purposes of modelling the historical trajectory of each stock (Baker and Clapham 2004). The available genotype matches and *Discovery* mark recoveries suggest that catches from Areas V, VI and at least the western edge of Area I must be taken into account for an assessment for Tonga, historically considered to be a component of Group V, or more recently, of Breeding Stock E. Given the Government of Japan's plans to renew hunting of humpback whales in the Antarctic for scientific purposes, a more urgent challenge is understanding the mixing of individuals from relatively abundant breeding stocks, such as those from the coasts of Australia, with those from relatively small and slowly recovering stocks, such as those from Oceania (Gales *et al.* 2005). The demonstration of migration from New Caledonia to Area V, the location of Japan's proposed hunting in the austral summer of 2008/09, confirms concerns that whales from small breeding stocks in the South Pacific are at risk from hunting in Area V.

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Table 1: Summary of migratory connections between humpback whales from breeding grounds of Oceania and feeding areas of the Antarctic based on *Discovery* marking and recovery.

	Oceania	Feeding Area	Remarks (reference)
1	Fiji 27 July 1957 17° S, 179° E,	Antarctic Area IV 30 Nov, 1964 55 ° S 87 ° E	Sex unknown #14810. Reported as recaptured in a fin whale however 20 fin and 1 humpback whale were caught on this day and more than likely a mistake was made during processing as to which animal the tag come out of. (Mikhalev and Tormosov 1997)
2	Tonga,, 17 Oct, 1952 21o02'S,175o08'W	Antarctic Area I, 3 Feb, 1957 68o01'S, 95o45'W	male (Dawbin 1964a) (Brown 1957, summarised in Dawbin 1964),
3	Tonga 21oS, 175oW	Antarctic Area I 60-68S, 83-115W,	Sex unknown. The record reads, "found in cooker". The range of recovery reflects the uncertainty in the movement of the vessel over three days that the whale might have been in the cooker (Tormosov 1996)
4	Tonga 6 August, 1958 21o02'S,175o08'W	Area V 28 Dec, 1957 66o37'S, 174o48'E (tagged)	female with calf (Dawbin 1959)

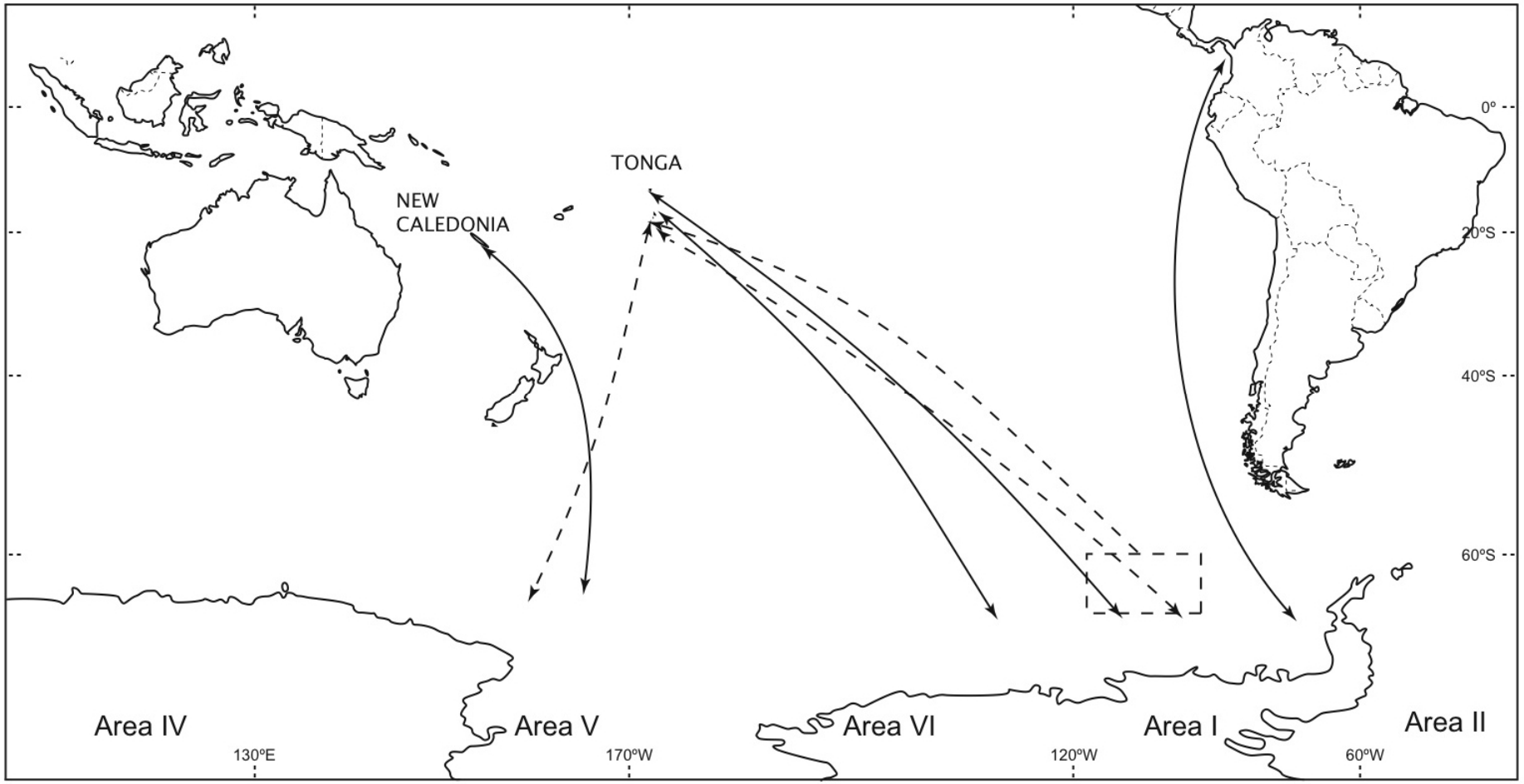
Table 2: The total number of unique genotypes (assumed to represent individual whales) sampled in each region of Oceania and the Antarctic.

Region	**years**	**N-QC samples**	**N unique genotypes**
Oceania breeding grounds			
New Caledonia	1995-2005	581	385
Tonga	1991-2005	496	368
Samoa	2001	2	1
Cook Islands	1996-2005	206	111
French Polynesia	1997-2004	176	118
Colombia	1991-1998	140	111
Total Breeding		1601	1094
Antarctic feeding Area			
Antarctic Peninsula (part of IWC AreaI)	1989-1999	83	73
Antarctica –region unknown	2001	3	3
Antarctica Area I	1994, 2001	15	13
Antarctica Area II	2005	1	1
Antarctica Area III	1992 – 2005	13	11
Antarctica Area IV	1999	51	46
Antarctica Area V	1991- 2004	9	9
Antarctica Area VI	1990, 2001	22	19
Total Feeding		197	175
TOTAL		1798	1269

Table 3: Summary of migratory connections between humpback whales from breeding grounds of Oceania and feeding areas of the Antarctic based on matching genotypes (PI, probability of Identity; PIsib, Probability of Identity for siblings)

	Sample codes	**Location**	**Date**	**Sex**	**mtDNA**	**Number of matching loci**	**PI** PI_{sib}
1	Mno01A51580	Area 1, 67'31S 114'20W	7 Feb 2001	Female	SP1	14	2.0×10^{-18} 2.2×10^{-6}
	Mno03Tg014	Tonga, 18'38S 174'8W	28 Aug 2003	Female	SP1		
2	Mno01A51553	Area VI, 67'14S 129'31W	26 Jan 2001	Male	SP83	13	3.8×10^{-18} 7.3×10^{-6}
	Mno03Tg107	Tonga, 19'54S 174'40W	22 Aug 2003	Male	SP83		
3	Mno01A51581	Area I, 68'26S 114'27W	11 Feb 2001	Female	SP13	15	1.7×10^{-18} 2.6×10^{-6}
	Mno91Tg008	Tonga	Oct 1991	Female	SP13		
4	Mno01A51546	Area V, 62'26S 171'6W	9 Jan 2001	Female	SP26	12	1.1×10^{-14} 4.1×10^{-5}
	Mno97NC016	New Caledonia	1997	Female	SP26		
5	MnoIWC94H101	Area I, 67'03S 71'18W	7 Feb 1994	unknown	SP8	15	4.4×10^{-18} 1.4×10^{-6}
	Mno91Co005	Gorgona Island, Colombia	?1991	Male	SP8		
	Mno91Co011	Gorgona Island, Colombia	?1991	Male	SP8		

Figure 1: Migratory connections between breeding grounds of Oceania and the Antarctic established by genotype matching (solid lines) and *Discovery* marking (dashed lines). The dashed box represents uncertainty in the exact location of the recovery of one of the *Discovery* tags (tag 3, Table1).



Appendix table of genotype data.

Sample Name	464 /465	Ev1	Ev14	Ev21	Ev37	Ev94	Ev96	Ev104	GATA 28	GATA 417	GT 211	GT 23	GT 575	rw 31	rw 4-10	rw 48
Mno01A51580	139/143	123/123	131/141	109/115	212/218	214/214	153/165	149/149		207/214	106/110	111/111	145/155		204/204	114/118
Mno03Tg014	139/143	123/123	131/141	109/115	212/218	214/214	153/165	149/149	147/175	207/214	106/110	111/111	145/155	106/120	204/204	114/118
Mno01A51553	139/139	123/123	131/137	109/109	214/216	212/212	163/171	149/151	187/191		100/116	111/111	153/163	106/114		112/116
Mno03Tg107	139/139	123/123	131/137	109/109	214/216	212/212	163/171	149/151	187/191	218/274		111/111	153/163	106/114	196/204	112/116
Mno01A51546	143/143	123/123	131/131	115/115	192/220	214/216	147/159	149/149			106/106	101/115	151/153			116/116
Mno97NC016	143/143	123/123	131/131	115/115	192/220	214/216	147/159	149/149	147/175	214/218	106/106	101/115	151/153	106/106	204/204	116/116
Mno01A51581	133/137	123/123	131/131	111/111	196/214	208/214	159/161	149/149	147/147	207/214	108/110	111/115	145/149	106/106	194/204	116/116
Mno91Tg008	133/137	123/123		111/111	196/214	208/214	159/161	149/149	147/147	207/214	108/110	111/115	145/149	106/106	194/204	116/116
MnoIWC94H101	139/143	125/127	129/135	109/111	200/206	208/214	163/163	149/149	147/147	203/218	108/112	111/115	147/151	114/116	196/206	116/116
Mno91Co005	139/143	125/127	129/135	109/111	200/206	208/214	163/163	149/149	147/147	203/218	108/112	111/115		114/116	196/206	116/116
Mno91Co11	139/143	125/127	129/135	109/111	200/206	208/214	163/163	149/149	147/147	203/218	108/112	111/115		114/116	196/206	116/116