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# Remote Antarctic feeding ground important for east Australian humpback whales

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**Abstract** Understanding the dynamics of population recovery is particularly complex when an organism has multiple, remote breeding and feeding grounds separated by one of the longest known migration routes. This study reports on the most comprehensive assessment of humpback whale (*Megaptera novaeangliae*) movements between remote Antarctic waters south of New Zealand and east Australia (EA), and the migratory corridors and breeding grounds of Australia and Oceania. A total of 112 individual whales were identified; 57 from microsatellites and 61 by fluke with 23 % ($n = 26$) matched to sites outside Antarctica. Despite large datasets from other southern regions being included in the comparison, the whales were predominantly linked to EA ($n = 24$). Only two matches to the Oceania catalogues directly north was surprising; therefore the primary feeding grounds of these endangered whales still remain unknown. The confirmation of the Balleny Islands as an important feeding ground for EA whales could provide an insight into reasons behind the rapid recovery of this population. Determining the feeding grounds of Oceania's whales may explain whether prey energetics or migration length are limiting factors to their recovery and will allow an understanding of future ecosystem changes in these whales.

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## Introduction

Migrations are necessary for animals that require spatially separated habitats, such as breeding and feeding grounds, but few mammals undertake long periods of fasting as a consequence of differences in these habitats. For species of concern, understanding all ecological requirements is crucial when determining their recovery. Humpback whales (*Megaptera novaeangliae*) undertake annual migrations between polar feeding grounds and tropical breeding grounds and show population structuring, primarily due to maternal philopatry (Clapham 2009). Most humpback populations are recovering from depletion (Clapham and Baker 2002); however, adjacent populations in the southern hemisphere show highly variable recovery rates (Clapham 2009). The east Australia (EA) humpback whale population is growing at 10.6 % per annum (Noad et al. 2011), which is near the maximum growth rate for the species (Zerbini et al. 2010), whereas neighbouring Oceania subpopulations found on the breeding grounds between New Caledonia and French Polynesia (Fig. 1) are recovering considerably more slowly (Childerhouse et al. 2008; Constantine et al. 2012).

The Antarctic feeding grounds of southern hemisphere humpback whales are remote and largely unsurveyed; therefore, links between the breeding and feeding grounds are poorly understood (Valsecchi et al. 2010; Schmitt et al. 2013). Discovery tags from whaling (Dawbin 1964), genotypes (Steel et al. 2008), satellite telemetry (Garrigue et al. 2010a; Hauser et al. 2010), acoustics (Garland et al. 2013) and photo-identification (Stevick et al. 2010; Robbins et al. 2011) show single movements between defined breeding grounds and feeding areas (International Whaling Commission (IWC) Areas IV–I; Fig. 1) but large feeding aggregations of whales south of NZ have yet to be described.

Determining the Antarctic feeding grounds of southern hemisphere whales may provide important insights into causes behind the different population recovery rates. Previous opportunistic surveys have resulted in six fluke matches between EA and Area V (Fig. 1) feeding grounds (Kaufman et al. 1990; Rock et al. 2006; Franklin et al. 2012). Until now, there has been no comprehensive comparison of whales from Antarctic feeding grounds south of Oceania and EA and links to their migration routes and breeding grounds. We expected Antarctic Area V, spanning the Antarctic waters 130°E–170°W directly south of EA and east of NZ (Fig. 1), to be an important feeding ground for whales breeding in western Oceania as it was an area of historical abundance. Here we conduct the first large-scale research effort using fluke photographs and genotyping to determine the identity of humpback whales on the productive Area V Antarctic feeding grounds south of Oceania.

## Methods

### Photo-identification

Humpback whales were identified from photographs of natural markings on the underside of their flukes (Katona et al. 1979). Photographs were collected during two Antarctic voyages; (1) the Antarctic Whale Expedition (AWE), a dedicated Antarctic cetacean research voyage, from 2 February to 15 March 2010, that surveyed 5,800 nm south of 60° between 150°W and 150°E (Gales 2010). (2) The French Cetacés en Terre Adélie (CETA) programme, with opportunistic cetacean sightings from 10 to 22 January 2010 on the Adélie Land continental shelf between 140 and 146°E (Garrigue et al. 2010b). Images from these two expeditions were combined to make a single catalogue (AWE/CETA) of the best image of each whale and curated on a website at the Australian Antarctic Division. The AWE/CETA catalogue was then matched to existing fluke catalogues from Australia, Oceania and Antarctica resulting in broad coverage of migratory corridors, breeding grounds and other Antarctic waters (Table 1). These catalogues, curated by different researchers, had been internally reconciled so only a single image of each whale existed in the respective catalogues, but many of the catalogues from different

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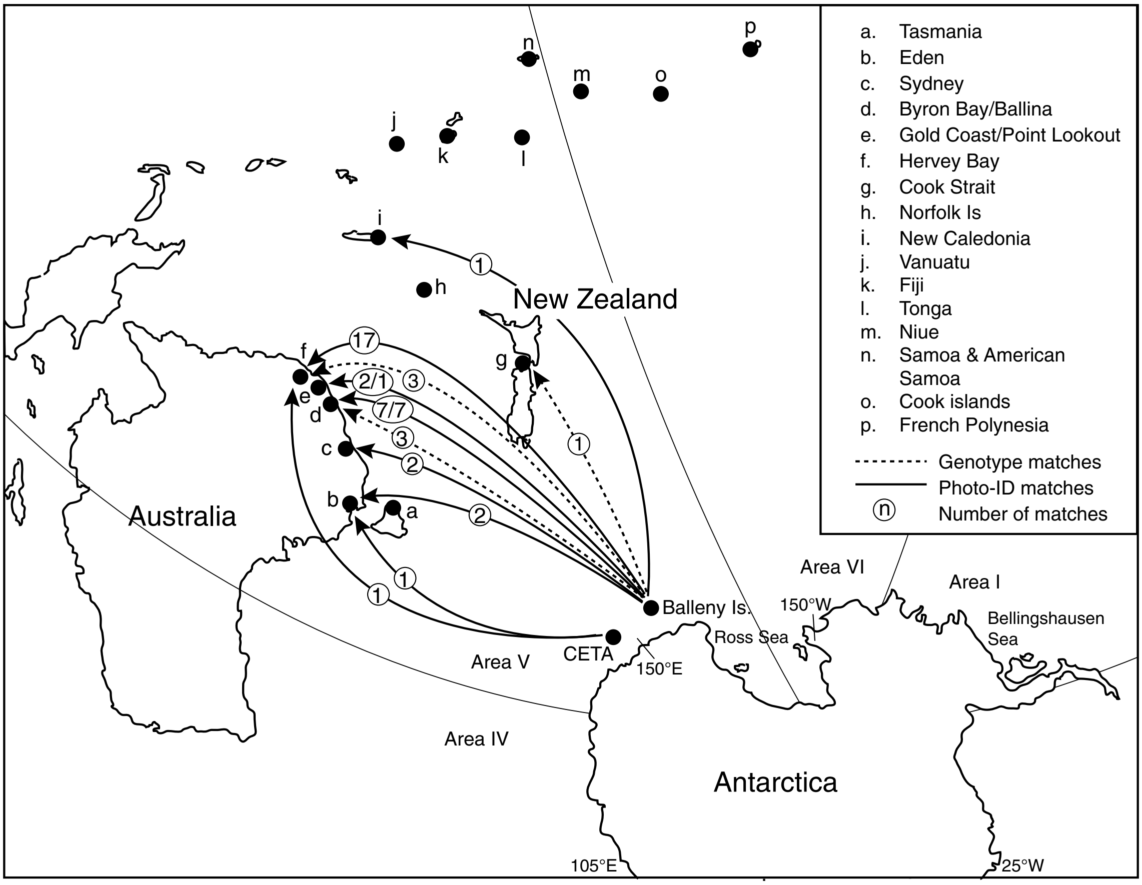

**Fig. 1** Location and number of genotype (*dashed line*) and photo-identification (*solid line*) matches of humpback whales from Antarctica to the migratory corridors and breeding grounds of Australia, New Zealand and Oceania. The Antarctic Whale Expedition survey boundaries of 150°E and 150°W which provided the majority of the data are demarcated. The location of the two matched photographs taken on the French Cetacés en Terre Adélie expedition are noted as CETA

**Table 1** Summary of the regional photo-identification catalogues matched to AWE/CETA

| Location | Breeding, migration, feeding | Total |
|---|---|---|
| West Australia | M; B | 1,664 |
| East Australia | M; B | 9,994 |
| AHWC (assorted) | B | 2,403 |
| AHWC (Antarctic) | F | 1,270 |
| New Zealand | M | 100 |
| Norfolk Island | M | 6 |
| Oceania | B | 1,806 |
| Overall total | | 17,243 |

The Antarctic humpback whale catalogue (AHWC, curated by JA) contains images from the breeding and feeding grounds and hence the delineation of this catalogue into two categories

areas had not been reconciled with each other. While the AWE/CETA catalogue only contains the best image of each whale, the sum of individuals across the other catalogues is likely to include duplicate images of some individuals. Therefore, the total number of images matched to the AWE/CETA catalogue exceeds the actual number of individual whales. This refers primarily to EA where several catalogues of over 1,000 whales exist and to date have not been reconciled.

## Genetic identification

Tissue samples were collected during the AWE using a biopsy rifle system. Total cellular DNA was isolated using an automated Promega Maxwell$^{®}$16 System. Ten microsatellite loci were amplified for each sample (GT211, GT575 (Bérubé et al. 2000), GATA417 (Palsbøll et al. 1997), EV1, EV14, EV37, EV94, EV96 (Valsecchi and Amos 1996) and rw4-10 (Waldick et al. 1999). For each locus, one of the primers within each pair was labelled fluorescently at the 5′ end to allow for visualisation of alleles on an automated ABI 3130 sequencer (Applied Biosystems). Sex was determined using a fluorescent 5′ exonuclease assay producing

**Table 2** Unique genotypes (individual whales) sampled on breeding grounds and migratory routes (details in electronic supplementary material, Table 4)

| Region | No. loci | No. loci shared with AWE | Dataset | Years | No. unique genotypes |
|---|---|---|---|---|---|
| Oceania breeding grounds | | | | | |
| New Caledonia | 17 | 10 | SPWRC | 1995–2005 | 388 |
| Tonga | 17 | 10 | SPWRC | 1991–2009 | 371 |
| Samoa/American Samoa | 17 | 10 | SPWRC | 2001–2009 | 88 |
| Cook Islands | 17 | 10 | SPWRC | 1996–2005 | 108 |
| French Polynesia | 17 | 10 | SPWRC | 1997–2007 | 230 |
| Niue | 17 | 10 | SPWRC | 2008 | 3 |
| Total Oceania | | | | | 1,188 (1,140) |
| Northbound migration | | | | | |
| Byron Bay, EA | 13 | 8 | SCU | 1996–2004 | 337 |
| Eden, EA | 10 | 10 | AMMC | 2008 | 43 |
| Tasmania, EA | 10 | 10 | AMMC | 2006–2008 | 1 |
| Cook Strait, NZ | 17 | 10 | SPWRC | 2003–2009 | 65 |
| Total northbound | | | | | 446 |
| Southbound migration | | | | | |
| Hervey Bay, EA | 13 | 8 | SCU | 1997–2003 | 365 |
| Ballina, EA | 13 | 8 | SCU | 2003–2004 | 63 |
| Eden, EA | 10 | 10 | AMMC | 2008 | 18 |
| Tasmania, EA | 10 | 10 | AMMC | 2006–2008 | 69 |
| Exmouth, WA | 10 | 10 | AMMC | 2007 | 204 |
| Total southbound | | | | | 719 |
| Total breeding and migration | | | | | 2,353 (2,272) |

The number of unique genotypes across the entire region (i.e. between-region matches removed) shown in parentheses

*EA* east Australia, *NZ* New Zealand, *WA* west Australia

Dataset curators are *SPWRC* South Pacific Whale Research Consortium, *SCU* Southern Cross University, Australia, *AMMC* Australian Marine Mammal Centre, Australia

PCR product from the ZFX and ZFY orthologous gene sequences (Morin et al. 2005). Sequencing of 700 bp of the mitochondrial (mt)DNA control region followed Olavarría et al. (2007).

Replicates were identified and removed from within the dataset using GenAlEx (Peakall and Smouse 2012). Genotypes of the remaining individuals were then compared to 2,272 previously typed individuals from Australia and Oceania (Table 2), some of which had been compared previously (Anderson et al. 2010). All datasets included mtDNA control region sequence and sex information (supplementary material, tables 1–3). Initial genotype matching between the datasets was conducted using Cervus (Kalinowski et al. 2007) using 'relaxed' conditions to avoid false exclusion of true matches due to genotyping or standardisation errors. The relaxed conditions required a minimum of six matching loci to confirm identity (Waits and Leberg 2000; Waits et al. 2001; Hoffman and Amos 2005; Morin et al. 2010).

## Results

We identified 112 individual humpback whales (fluke $n = 61$; genotype $n = 57$; of these, both methods $n = 6$). Despite extensive but non-systematic coverage near the humpback whales' preferred habitat near the sea-ice edge, sightings were unevenly distributed even when taking sighting conditions into consideration (Gales 2010). The greatest number of whales was sighted near the Balleny Islands compared to other areas along the survey route (Gales 2010). Subsequently, the majority of whales were photographed ($n = 57$) or biopsied ($n = 56$) near the Balleny Islands (66°55′S 163°45′E) (Gales 2010; Garrigue et al. 2010b) (Fig. 1).

Sixty-one individual whales included in the AWE/CETA catalogue were matched to 17,243 other catalogued images (Table 1). Twenty-five (41 %) whales matched other catalogues (EA = 24, New Caledonia = 1) (Fig. 1) with matches dating back to 1984. Sixteen whales were sighted more than once. Of these, individuals were sighted on average 2.2 times with an average of 6.7 years between the initial sighting and their AWE/CETA sighting when each whale was counted once per location per annum.

Analysis of the mtDNA control region resolved 26 previously described haplotypes (Olavarría et al. 2007) and two new haplotypes. There was a 1:1 sex ratio (28 females/29 males) of genotyped whales. Comparison of the 57 AWE whales to 2,272 unique individuals from other areas (Table 2) resulted in seven matches (EA = 6, NZ = 1) (Fig. 1). Six to ten matching microsatellite loci were considered sufficient to establish a match (pID, $2.3 \times 10^{-7}$, supplementary material, table 4), given the small number of pairwise matches ($57 \times 2{,}272 = 1.3 \times 10^5$).

## Discussion

Our research unequivocally shows the importance of the Balleny Islands region as a feeding ground for EA humpback whales as surprisingly; with the exception of two matches (to the New Caledonia breeding ground and NZ migratory corridor), all matches were to EA whales. The Antarctic feeding areas for whales from the Oceania breeding grounds remain unknown despite the majority of the data being collected at the Balleny Islands, a likely feeding ground south of western Oceania (Fig. 1). We present the most comprehensive matching of individually identified humpback whales undertaken in this poorly surveyed Antarctic region, which provides insight into the ecology of humpback whales.

The Balleny Islands represent a productive part of eastern Antarctica (Atkinson et al. 2009), and this humpback whale feeding ground may provide valuable insights into why the EA subpopulation is recovering rapidly (Noad et al. 2011), in contrast to the endangered Oceania whales (Constantine et al. 2012). Whales are likely to have similar energetic requirements to survive irrespective of the Antarctic feeding ground location (Reilly et al. 2004), and it is possible that regional productivity and the length of migration path may play a role in population recovery. EA whales feed at Eden, south-eastern Australia, on their southern migration before reaching the Antarctic feeding grounds (Stamation et al. 2007). Satellite-tagged humpbacks on their southern migration past east Australia stopped for periods of days to weeks (Gales et al. 2009) at the productive subtropical front passing the south-west coast of the South Island, NZ (Murphy et al. 2001). It has been suggested that they may opportunistically feed on prey patches before they arrive in Antarctic waters. Telemetry could help determine the relationship between whale foraging behaviour on their migratory path and on the feeding grounds by measuring chlorophyll *a* productivity (e.g. Laidre et al. 2010) and niche preferences within the water column (e.g. Friedlaender et al. 2006). Understanding the role of opportunistic feeding grounds to the energetics of humpback whales may provide insights into the different recovery rates of this species.

Despite the essential role of Antarctic waters as the summer feeding grounds for all southern hemisphere whales (de la Mare 1997; Reilly et al. 2004; Nicol et al. 2008), most recent research on humpback whale feeding grounds has been conducted around the Antarctic Peninsula (Thiele et al. 2004; Friedlaender et al. 2006). The potential Antarctic feeding grounds available to Oceania's humpback whales cover a broad and largely inaccessible expanse of the Southern Ocean (Fig. 1). Throughout these waters, there is variation in productivity and sea-ice edge dynamics; both factors are important for humpback whales in Antarctica (de la Mare 1997; Murphy et al. 1998; Holland and Kwok 2012; Bintanja et al. 2013). It would be valuable in the future if researchers working in the poorly studied area between the eastern Ross Sea and Bellingshausen Sea, located west of the Antarctic Peninsula (Fig. 1), could photo-identify whales in these waters. This information may reveal the Oceania whales' feeding grounds. There are a few records of humpback whales from eastern Oceania matching to the waters west of the Antarctic Peninsula (Steel et al. 2008; Robbins et al. 2011), and we suggest that the highly productive waters of the western Antarctic Peninsula may provide the feeding grounds for some of Oceania's humpback whales. Satellite tag deployments and comparing photo-ID and genetic data from Oceania to the Antarctic Peninsula may determine the strength of these linkages.

Our research has shown that the Balleny Islands are important for EA humpback whales. Unfortunately, the feeding grounds of Oceania's humpback whales remain unresolved, and the waters between their breeding grounds and Antarctica remain poorly surveyed. Further investigation of linkages between feeding grounds and migratory paths is vital to resolve whether Oceania's whales are recovering slowly due to resource limitations, migration distance and/or if population declines from historical whaling remains a driving factor.

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