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Humpback whale connectivity: Preliminary findings on the Oceania to Antarctica migration path via the Kermadec Islands

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ABSTRACT

Our understanding of the connectivity between humpback whale breeding and feeding grounds in the South Pacific region is based on historical *Discovery* tag information with recent data on single individuals. The Southern Ocean Research Partnership – Antarctic Whale Expedition voyage in 2010 found strong links between humpback whales and the Balleny Islands region, with very few whales from Oceania. To determine the feeding grounds of humpbacks breeding in Oceania, we undertook a research voyage to Raoul Island, Kermadec Islands, New Zealand in late September to mid-October 2015. Over 13 days we deployed 25 satellite tags, collected 84 tissue samples for genetic analysis and photo-identified 124 individual whales. Eighteen tags transmitted for longer than 21 days and one tag is transmitting over seven months post deployment. Preliminary data analysis found that whales migrating south past the Kermadecs originate from five different breeding grounds spanning ~3,600 km of Oceania between New Caledonia and the Cook Islands. There were four genotype matches (including two tagged whales originally identified in Tonga from 2003 and 2005) and 13 photo-identification matches. To date there are no matches to mainland New Zealand (primarily whales on the northern migration) or east Australia. Once past the Kermadecs, the humpbacks stopped on feeding grounds spanning ~3,500 km of Southern Ocean between west of the Ross Sea region to the Bellingshausen Sea. Whilst data analysis has yet to be completed, we clearly show that Oceania's humpback whales have feeding grounds spanning IWC Areas V, VI and I; information that will improve our understanding of humpback whale stock recovery.

KEYWORDS: HUMPBACK WHALES, MIGRATION, ANTARCTIC, PACIFIC OCEAN, FEEDING GROUNDS, SATELLITE TAGGING, GENETICS, PHOTO-ID

INTRODUCTION

Our understanding of the migratory routes and the summer distribution of humpback whale (*Megaptera novaeangliae*) populations from Antarctic feeding grounds is based on historical *Discovery* tag data (Chittleborough 1959, Dawbin 1964) with more recent photo-identification, genotype and satellite tag data. Generally, these data are sparse and therefore patterns of distribution and mixing are not well described for most of the Antarctic feeding grounds. Research efforts in areas like the west Antarctic Peninsula (e.g. Friedlaender *et al.* 2006) are providing important local information about feeding behaviour, habitat use and niche partitioning amongst baleen whales. There is an increasing number of satellite telemetry studies informing our understanding of whale movement patterns both on the breeding grounds (e.g., Garrigue *et al.* 2010, Hauser *et al.* 2010) and feeding grounds (e.g., Zerbini *et al.* 2011).

An improved understanding of the movements and mixing of humpback whales around Antarctica is a priority for the International Whaling Commission (IWC) because such information is integral to the Recovery/Stock Assessments, a prerequisite of which is the allocation of catches to particular breeding populations (e.g., Jackson *et al.* 2008, IWC 2015). An improved understanding of the migratory paths and feeding grounds of humpback whales would allow the more appropriate allocation of historical catches made in Areas I-VI. This would improve the accuracy of recovery assessments and estimates of pre-whaling abundance (Carroll *et al.* 2015, IWC 2015).

The IWC population assessment process would benefit from a greater understanding of the distribution and mixing of all Southern Hemisphere humpback whale populations. The Southern Ocean Research Partnership (SORP) - Humpback Whale Connectivity Project has focused on the remote Antarctic Areas V, VI and I, the feeding grounds for the complex E (broadly clustered as east Australia and western Oceania) and F (eastern Oceania) populations. A 2010 survey of 5,800 nm south of 60° between 150°W and 150°E (incorporating parts of Areas V and VI) found that whales encountered feeding mainly in the Balleny Islands region were linked to east Australia, with a few matches to New Caledonia and New Zealand (Constantine *et al.* 2014). This is consistent with previously reported connections between east Australia, New Zealand and the eastern Oceania region (e.g., Constantine *et al.* 2007, Franklin *et al.* 2014, Garrigue *et al.* 2011, Steel *et al.* 2014). The absence of whales linked to the east Oceania breeding grounds meant that a robust understanding of connectivity in the region remained unresolved with the exception of a few individual movement records (Robbins *et al.* 2011, Steel *et al.* 2008).

Extensive commercial whaling during the 20th century drove humpback whales (*Megaptera novaeangliae*) close to extinction. Since the cessation of whaling, humpback populations have been rebuilding (IWC 2015) but the Oceania population, in contrast to the neighbouring east Australian whales (Noad *et al.* 2011), has been slow to recover (Constantine *et al.* 2012). Throughout Oceania there is sub-population genetic structuring as humpbacks typically return to their natal breeding grounds (Olavarría *et al.* 2007). Recent work in the region has shown that different age- and sex-class groups prefer different habitat when on their breeding grounds, but this is not a limiting factor to the recovery of Oceania's whales (Lindsay *et al.* 2016). It has been suggested that the population decline post-whaling meant social aggregations on breeding grounds were fragmented and whales moved to areas of higher density, ultimately leading to higher rates of population increase in some areas (e.g. east Australia) compared to others (e.g., Fiji) (Clapham and Zerbini 2015). The migration distance, feeding opportunities along the migration path (Owen *et al.* 2016) and quality of feeding grounds may also explain slower rates of recovery for some populations.

Since 2008, land-based observations by rangers based on Raoul Island have revealed that the Kermadecs are frequented by humpback whales from mid-September to mid-November as they migrate to their Antarctic feeding grounds. Single four-hour surveys have reported up to 153 whales passing Raoul Island (e.g., Brown 2010) with the peak in sightings mid-September – mid-November (Gibson 2014). In contrast, there are very few sightings of humpbacks on their northern migration; the Kermadecs are a hotspot only during the southern migration. From late September to mid-October 2015, we undertook a multidisciplinary study deploying satellite tags on humpback whales as they

migrated south past Raoul Island, Kermadec Islands, New Zealand. We identified individuals using genetic markers and photo-identification of flukes to determine connectivity between their breeding grounds, their southern migration path and Antarctic feeding grounds.

METHODOLOGY

Data collection

We undertook a research voyage to the Kermadec Islands, New Zealand for a total of 13 days around Raoul Island (29.2500 °S 177.9167 °W from 29th September – 11th October 2015). Raoul Island is part of the Kermadec group and is an active volcanic island approximately half way between Tonga and northern New Zealand, ~1,100km northeast of New Zealand (Figure 1). We were based on the *RV Braveheart*, a 39 m live-aboard ship and deployed two small research vessels (4.8 m and 6.1 m) to undertake satellite tagging, biopsy sampling and photo-identification of individual whales. Opportunistic photographs of the underside of whale flukes (Katona *et al.* 1979) were also taken from on-board the *RV Braveheart*.

The two small vessels conducted non-systematic surveys in a similar area around the island largely dictated by weather conditions. Upon encountering a pod of whales the position (using a handheld GPS), pod size estimate and pod composition (mother-calf pairs and/or adults) were recorded. The 6.1 m vessel was dedicated to deploying Wildlife Computers SPOT 5 satellite tags in adult whales and collecting small tissue biopsy samples from a crossbow equipped with 7x10mm stainless steel cutting tips. They also collected photo-identification images of whale flukes. The 4.8 m vessel was dedicated to collecting small tissue biopsy samples from a Paxarms© biopsy system fitted with 7x10 mm stainless steel cutting tips, the collection of sloughed skin from surface active whales and to the collection of photo-identification images. Whales were also identified by their dorsal fins in an effort to minimise resampling of individuals in the field and allow cross comparison of data at the completion of the study to maximise fluke identification and tissue sample data matches for each whale.

At the end of each day, all tissue samples were prepared so the skin sample was preserved in 70% ethanol and, where present, a blubber sample was stored in aluminium foil and frozen at -20°C. The samples were labelled with a unique identifier and this was reconciled with field data on pod composition and size, and with the digital photographs. The photographs of whale flukes and dorsal fins were sorted by each pod encounter and the unique tissue sample code, satellite tag number and series of photographs were then given an encounter code. This was done independently for each vessel and all data from both vessels were reconciled when back in the lab.

Satellite telemetry

The satellite tags were duty cycled to 10 hours on and two hours off for the duration of the tag transmission. Whale locations were stored in the ARGOS system and downloaded on a weekly basis. Fine-scale analysis of the whales' migration paths and habitat use is currently underway in collaboration with the Australian Antarctic Division and National Marine Mammal Lab – NOAA as part of the SORP - Humpback Whale Connectivity Project.

Genetics

Total genomic DNA was extracted using standard proteinase K digestion and phenol/chloroform methods (Sambrook *et al.* 1989), as modified for small samples by Baker *et al.* (1994). Genetic profiles consisting of sex, mtDNA control region haplotype (470bp) and up to fifteen microsatellite loci (EV1, EV14, EV21, EV94, EV96 and EV104; Valsecchi *et al.* 1996; GATA28 and GATA417; Palsbøll *et al.* 1997; RW18, RW31, RW410 and RW48; Waldick *et al.* 1999; GT23, GT211 and GT575; Bérubé *et al.* 2000) were generated following methods previously described by Olavarría *et al.* (2007) and Constantine *et al.* (2012).

Mitochondrial control region sequences were identified to haplotype using Sequencher v4.7 (Genecodes) and all variable sites were visually inspected. Microsatellite alleles were sized with Genemapper v4.0 (Applied Biosystems) and all automated calling was confirmed by visual inspection (Bonin *et al.* 2004). As a precaution against poor DNA quality, only those samples that amplified at a minimum of 11 microsatellite loci were retained for further analyses (Quality Control dataset).

The program Arlequin v3.1 (Excoffier *et al.* 2010) was used to test for differentiation in mtDNA haplotype frequency between the Kermadec Island population, the migratory corridors of east Australia and New Zealand and the winter breeding grounds in Oceania. The significance of this differentiation was tested with 10,000 random permutations within Arlequin. Replicate genotypes within the Kermadec Island samples were identified using Cervus v3.0 (Kalinowski *et al.* 2007). Individuals identified within the Kermadec Island samples were then compared with a curated database of DNA profiles from 1,052 humpback whales sampled in three breeding grounds of Oceania (New Caledonia, Tonga, American Samoa-French Polynesia); to two DNA databases from the east Australia migratory corridor (Anderson *et al.* 2010, Schmitt *et al.* 2014a); and to a DNA database from the migratory corridor of New Zealand (Steel *et al.* 2014).

Photo-identification

All fluke photographs were quality controlled and only images that showed both sides of the trailing edge of the underside of the fluke were included in the Kermadec Islands catalogue. We included fluke photographs of seven individuals collected prior to this 2015 research voyage, one image from the Department of Conservation rangers based on Raoul Island and four images provided by Natural History New Zealand from a voyage to Raoul Island in late October 2015. All images of high quality to allow matching were entered into the computer programme Fluke Matcher (Kniest *et al.* 2010) and matched to catalogues from the South Pacific breeding grounds from New Caledonia to the Cook Islands, migratory corridors including the Gold Coast, southeast Queensland, New Zealand and Norfolk Island (see Figure 1 for locations) and Antarctic catalogues primarily collected during previous SORP voyages.

Due to the size of many of the catalogues, initial matching has focused on the top 40 chosen by Fluke Matcher but further analysis is underway for the remaining unmatched images outside of the top 40. All matches to date were confirmed by at least two researchers experienced in fluke identification. This work has yet to be completed but, as with previous SORP humpback whale images, the catalogue will be curated with the SORP secretariat at the Australian Antarctic Division and available for other agencies and research groups (e.g., the Antarctic Humpback Whale Catalogue – College of the Atlantic) to match with their catalogue holdings.

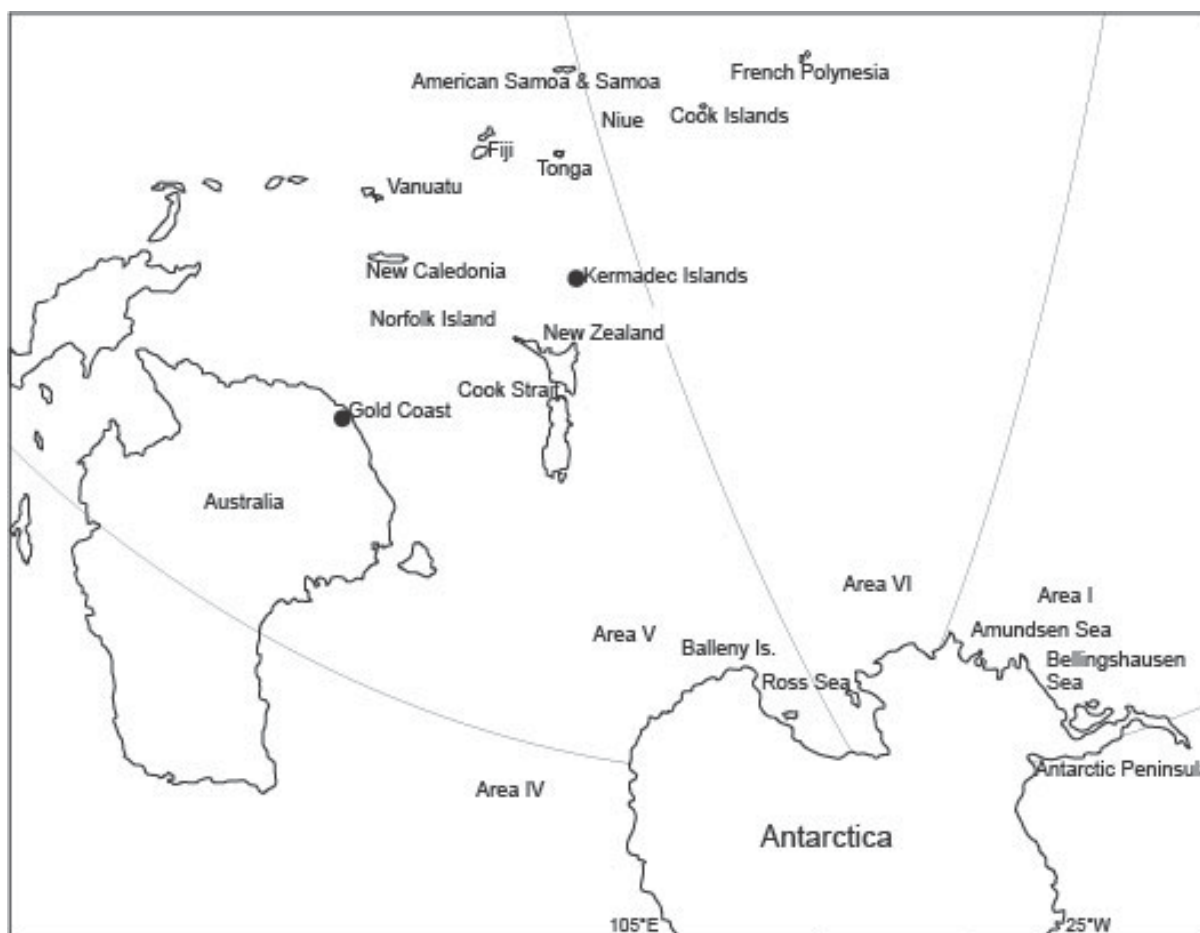


Figure 1. Location of the study site (Kermadec Islands), breeding grounds, migratory corridors and IWC Antarctic feeding grounds (Areas IV, V, VI and I) for humpback whales.

RESULTS

Research progress and effort

Here we report the preliminary results of the research, as one satellite tag is still transmitting, the analysis of microsatellite markers is underway and we are finalising the matching of as yet unidentified whales with images ranked >40 in Fluke Matcher. We are also completing preparation of the photo-identification catalogue allowing online access through the SORP Secretariat. Over 13 days of small-boat based surveys at Raoul, we surveyed 1,480 km around Raoul Island and encountered 127 pods of humpback whales with a cumulative total of 235 adults and 37 calves.

Satellite telemetry

We deployed 25 satellite tags on adult whales; 24 of these were embedded near the whales' dorsal fin with tag PTT112694 detaching from the whale shortly after deployment. Simultaneous to tag deployment, we took a tissue biopsy from 24 of the 25 tagged whales with 23 samples yielding sex identification using molecular markers (10 males: 13 females: 1 unknown). Seven of the 13 tagged females were mothers accompanied by calves.

Eighteen tags transmitted for longer than 21 days and the longest transmission exceeded seven months duration; this tag (PTT102218 - male) is currently transmitting. The tag data showed whales travelling through the Kermadec Island chain then diverging paths as they continued south (Figure 2). Whales were spread ~3,500 km from west of the Ross Sea through to the Bellingshausen Sea, near the west

Antarctic Peninsula. The longest migration from Raoul Island until the whales stopped to feed in Antarctica was approximately 7,000 km and took nine weeks to complete. This does not reflect the entire migration as an approximation of distances between Raoul Island and the potential Oceania breeding grounds show the whale probably travelled ~1,600 km prior to reaching Raoul, then continued to move shorter distances whilst on the feeding grounds. A conservative estimate is ~8,600 km from the breeding to feeding grounds which is similar to long migration distances reported previously (Robbins *et al.* 2011, Stevick *et al.* 2010). The majority of whales travelled in a southeast direction, with four whales migrating to the farthest Bellingshausen Sea region, one whale passed close by mainland New Zealand (a mother with a calf) and four passed the Chatham Rise. Whilst fine-scale analysis of the satellite tracks is underway, in general, the majority of whales stayed in the same feeding ground once in Antarctic waters (Figure 2).

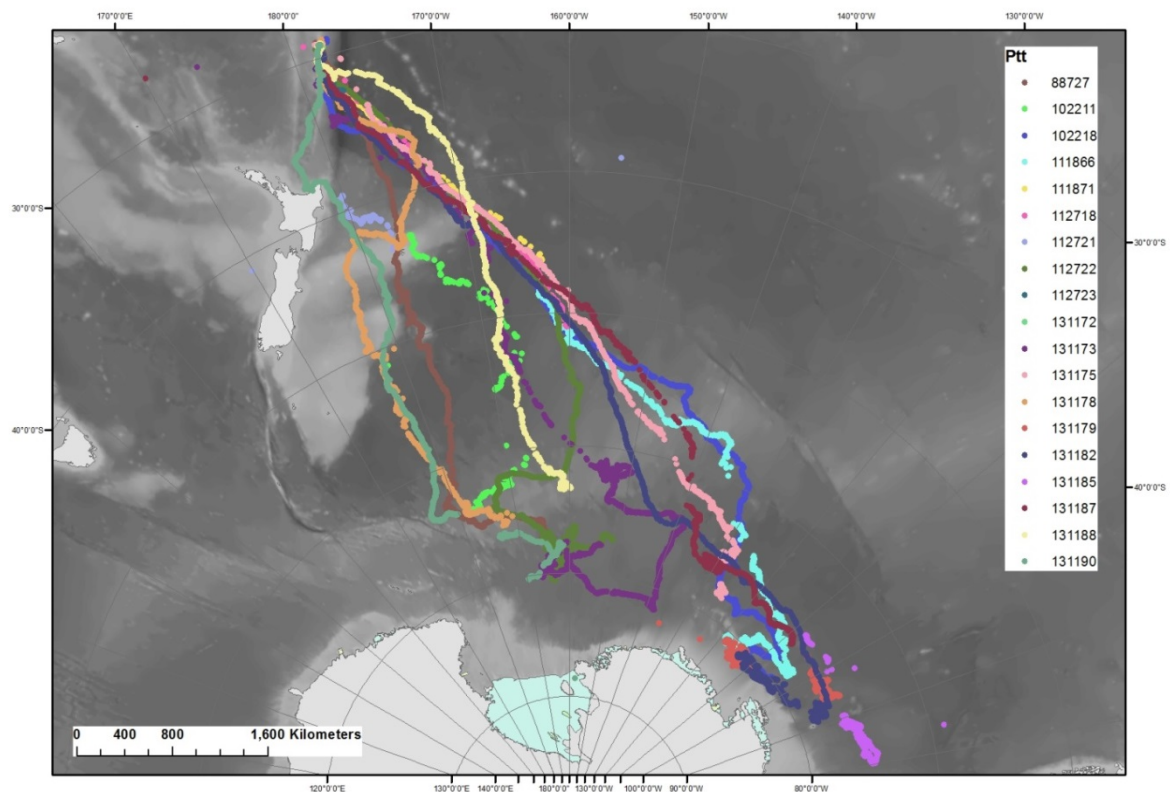


Figure 2. Migration path of humpback whales from Raoul Island to Antarctica from October 2015 until April 2016.

Genetics

We collected 84 small tissue samples either from biopsy systems (n = 70) or sloughed skin (n = 14, including one sample from a dead calf); of these, 54 had a blubber sample attached that will be used for progesterone analysis. Of the 70 biopsy samples, 24 were from satellite tagged whales. Insufficient quantities of DNA were extracted from three samples due to the small amount of tissue and these three samples were discarded. All of the remaining 81 samples passed the Quality Control (QC) criteria of amplification at a minimum of 11 microsatellite loci and were retained for further analysis. Comparison of genetic profiles identified 73 individuals with a female bias (28 males: 45 females). When the genotypes were matched to previously identified whales from Oceania, New Zealand, east Australia and Antarctica, we identified four whales previously sampled on their breeding grounds,

including two of the tagged whales previously sampled in Tonga. There was one match to New Caledonia (female – 1999), two matches to Tonga (female – 2003 and male – 2005) and one match to American Samoa (male – 2009). There were no matches to the migratory corridors of east Australia, New Zealand and Norfolk Island and no matches to any feeding grounds.

Preliminary analysis of the mtDNA has identified 31 haplotypes from 68 individuals with the remaining five individuals being reanalysed to confirm sequencing results. The Kermadec Island samples have no 1:1 relationship with any one population and are significantly different to all other populations at $p = 0.05$, reflecting the diversity of genotype matches to the Oceania breeding grounds (Table 1). A mixed-stock analysis to assign breeding ground origins will be undertaken once the final samples have been re-sequenced and quality controlled.

Table 1. Results of pairwise comparisons for mtDNA haplotype diversity (F_{ST}) between humpback whales sampled at the Kermadec Islands and the migratory corridors of east Australia and New Zealand, and breeding grounds of Oceania. The number in brackets is the number of individuals with sequence used for each population. There were 68 individuals with sequence sampled at the Kermadec Islands.

	Sampling site	F_{ST}	p-value
Migratory corridor	East Australia (316)	0.012	0.000
Migratory corridor	New Zealand (150)	0.008	0.007
Breeding ground	New Caledonia (367)	0.004	0.028
Breeding ground	Tonga (337)	0.005	0.025
Breeding ground	French Polynesia –American Samoa (302)	0.022	0.000

Photo-identification

The Kermadec Islands catalogue includes a total of 136 individual whales identified via the unique pattern of marks on the underside of their flukes. We identified 124 individuals during our field work, received a further five fluke identifications from other sources in 2015 and included an additional seven whales photographed in previous years (2007 - 2013). A total of 44 whales in the Kermadec fluke identification catalogue were biopsy sampled during our field work, including 17 of the satellite tagged whales. The matching of images entered into Fluke Matcher is close to completion with coverage of breeding ground catalogues from New Caledonia to the Cook Islands, migratory corridors of New Zealand, Norfolk Island and southeast Queensland, and photographs from Antarctic waters south of New Zealand primarily from SORP voyages either fully or partially matched (Table 2).

To date, 13 whales from the Kermadec catalogue were matched to their breeding grounds; nine from New Caledonia, and one each from Tonga, Niue, American Samoa and the Cook Islands. There were no matches to mainland New Zealand or east Australia (represented by whales photo-identified at the Gold Coast, Queensland - Vindenes 2015) and no matches to the Antarctic fluke data we have entered in Fluke Matcher, primarily collected on SORP voyages in Areas V and VI.

Table 2. Summary of fluke identification catalogues of humpback whales entered in Fluke Matcher from feeding grounds, migratory corridors and breeding grounds matched to the Kermadec Islands catalogue (n = 136). Note that not all catalogues have been completely matched, as noted in the final column as ‘complete or partial’. Not all catalogues have been entered into Fluke Matcher but work is currently ongoing. The photographs from Antarctica are primarily supplied from previous SORP voyages (Areas V & VI only) and these have been submitted to the Antarctic Humpback Whale Catalogue curated by College of the Atlantic. The east Australia photographs include whales from the northern and southern migration past the Gold Coast, southeast Queensland (SEQ) only.

Location	Catalogue size (Fluke Matcher)	Years included	Complete/ partial
Antarctica	115	1991, 1999, 2002, 2006, 2008, 2010, 2013, 2015	Partial
American Samoa	322	2003 - 2011, 2014, 2015	Partial
Cook Islands	83	1999 - 2008	Complete
East Australia (SEQ)	641	2008 - 2012	Partial
Fiji	15	2002, 2003, 2005, 2008, 2011, 2013	Complete
Kermadec Islands	136	2007, 2008, 2011, 2013, 2015	Complete
New Caledonia	1200	1995-2015	Complete
New Zealand	130	1994 - 1996, 1998, 2001, 2002, 2004- 2013	Partial
Niue	58	2001, 2007 - 2011, 2014, 2015	Complete
Norfolk Island	6	2001, 2002, 2007, 2008	Complete
Samoa	17	2006 - 2008	Partially
Tonga	-	2000, 2002, 2003, 2006 - 2011, 2015	Partially
Vanuatu	7	2003, 2007	Complete

DISCUSSION

Our research has revealed that humpback whales migrating past the Kermadec Islands originate from several Oceania breeding grounds and once past the Kermadecs, then spread widely throughout feeding grounds in Areas V, VI and I. The breeding grounds of individual whales span ~3,600 km of the South Pacific, including New Caledonia, Tonga, Niue, American Samoa and the Cook Islands (IWC Breeding grounds E (ii), E (iii) and F). Preliminary results from the mtDNA analysis show a mixture of haplotypes from across Oceania with possibly some input from the east Australia breeding ground that has yet to be genetically defined (Smith *et al.* 2012). Whilst we have not undertaken an exhaustive match to all data throughout the broader Australia – South Pacific region, largely due to the considerable challenge in matching fluke identification images, we have clearly shown that the Kermadecs are a place of mixing for humpbacks on their southern migration.

The feeding grounds of tagged whales span ~3,500 km from west of the Ross Sea to the eastern Bellingshausen Sea. No whales migrated to the Balleny Islands region providing further support for the possibility that the feeding grounds of whales migrating up the coast of east Australia are largely separate from the feeding grounds of Oceania’s whales (Constantine *et al.* 2014, Gales *et al.* 2009). Several tagged whales travelled to the remote Bellingshausen Sea with the closest approach ~900 km west of the west Antarctic Peninsula. The longest reported round-trip of a humpback whale was recorded from American Samoa to the west Antarctic Peninsula, a return journey of 18,840 km (Robbins *et al.* 2011). Our findings suggest that such long-range movements may not be unusual for Oceania’s humpback whales. These findings are important when considering historical linkages between breeding and feeding grounds and when undertaking stock assessments to determine population recovery (e.g., Carroll *et al.* 2015, Clapham *et al.* 2009, Jackson *et al.* 2008, IWC 2015). We have yet to complete our assessment of the mixing of stocks on the feeding grounds, but it is interesting to note that the two tagged whales originally identified in Tonga (PTT112721 – female and PTT111866 – male) travelled in different directions, with the females tag transmitting for 39 days before stopping near the Chatham Rise, east New Zealand and the males tag transmitting for 163 days where he fed in the Bellingshausen and Amundsen Sea regions (Figure 2). These whales, whilst coming from the same breeding ground, took two different migratory paths. This supports other

findings that whales from the same breeding ground may have different feeding grounds and/or migration paths (e.g., Steel *et al.* 2008, Constantine *et al.* 2014, Gales *et al.* 2009, Garrigue *et al.* 2015).

Only one tagged whale (a mother-calf pair) came within close proximity to mainland New Zealand but there were others that migrated through New Zealand waters past the Chatham Rise. The majority of humpback sightings in New Zealand are of whales on their northern migration (Gibbs and Childerhouse 2000). A land-based survey at Cook Strait, a site of historic whaling, has collected biopsy samples of whales as they travel north. Our genetic analyses clearly show whales migrating past the Kermadecs are not the same whales passing through Cook Strait. There are significant genetic differences at F_{st} and different population mixes, with Cook Strait assigning to the breeding grounds of New Caledonia and east Australia (Steel *et al.* 2014). Our results show that whales using the migratory corridors through New Zealand waters are linked to New Caledonia for northern and southern migrations. Previous research has shown tagged, genotyped and/or photo-identified whales migrating past the Kermadecs and mainland New Zealand (Constantine *et al.* 2007, Garrigue *et al.* 2010, Garrigue *et al.* 2011, Garrigue *et al.* 2016). The Kermadecs, over many years now, is clearly an important part of the southern migration path of many humpback whales from throughout the South Pacific.

Why humpbacks travel from a broad range of breeding grounds to pass this remote group of islands is unknown. It may be an important late season aggregation point (Clapham and Zerbini 2015) for the whales or a resting area. Whale residency time at Raoul Island ranged from periods of <1 day to 21 days with all age- and sex-class groups observed there. Most whales were sighted on a single occasion with the highest resight rate for one whale sighted on five separate days. We also had one tagged whale (PTT 11131172 – female) that remained in the area for 21 days who was sighted with a calf on two separate encounters but five days after the first encounter, the calf was found dead. Despite several hours observing the fresh carcass being scavenged by a sharks and seabirds, there were no sightings of adults in close proximity.

We will continue analysis of these data, in particular the fine-scale tag data to reveal more details about the whales' migration paths and habitat use. With one tag still transmitting we may receive data on the northern migration path. With very few observations of humpback whales at Raoul Island during their northern migration, the whales clearly do not return along the same path as their southern migration. They also do not travel via the New Zealand mainland, so may stay offshore migrating through the large expanse of South Pacific Ocean. There has been some discussion about the different migration paths of east Australian humpbacks (Valsecchi *et al.* 2010) so this is interesting to note with regards to the Kermadec whales. We will undertake a mixed-stock analysis (e.g., Schmitt *et al.* 2014b) and finalise the photo-identification matching. With the challenges associated with accessing the remote Antarctic waters south of the South Pacific, our work at the Kermadecs, the southernmost point with accessible whales in this region, was an effective way of studying these whales. Now we have determined individual feeding grounds, newly developed isoscape models based on isotope markers will allow us to assign feeding grounds and provide baseline data on how future changes may influence their spatial distribution, stock recovery and role in Southern Ocean ecosystem function.

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