Photo-identification comparison of humpback whale (*Megaptera novaeangliae*) flukes from Antarctic Area IV with fluke catalogues from East Africa, Western Australia and Eastern Australia

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ABSTRACT

Early 'Discovery mark' data together with recent photo-identification, acoustic, genetic and satellite-radio tag data revealed linkages between humpback whales migrating from breeding grounds (C) off East Africa and the Area III feeding area, from Western Australian breeding grounds (D) and the Antarctic Area IV feeding area and the East Australian breeding grounds (E1) and Antarctic Area V feeding area. These data also revealed low levels of intermingling between (E1) and (D) humpback whales in the Antarctic Area IV feeding area consistent with these being separate populations. Greenpeace photographed the ventral tail flukes of 30 individual humpback whales in the Antarctic Area IV feeding area (70°E–130°E) from 2 to 9 January 2008, between 62°47'S and 64°14'S latitude and 80°00'E and 112°57'E longitude. Comparisons of the Antarctic Area IV Greenpeace fluke catalogue (n = 30) with existing reconciled fluke catalogues from East Africa (n = 842), Western Australia (n = 1,558) and Eastern Australia (n = 1,964), yielded no photo-identification matches. An analysis of the frequencies of whales seen and not seen in Antarctica, East Africa, Western Australia and Eastern Australia relative to the frequencies expected to have been seen and not seen, based on the estimated population sizes and the sizes of the catalogues, provided evidence that the Antarctic whales photographed are from a different population to the East African and East Australian populations. There was weak evidence supporting the hypothesis that the Antarctic whales are from the Western Australian population but insufficient data were available to determine a clear outcome. A comparison of the Antarctic Area IV Greenpeace catalogue (n = 30) with other existing African, Indian Ocean, Western and Eastern Australian and/or Antarctic catalogues, together with increased sampling across the humpback whale feeding season in Antarctica and along the Western and Eastern Australian coastline during their winter migration, is likely to provide further evidence of the migratory destination of these humpback whales. It will also add to our limited knowledge of the extent of population overlap within the Antarctic Area III, IV and V feeding areas.

KEYWORDS: HUMPBACK WHALE; PHOTO-IDENTIFICATION; MIGRATORY MOVEMENTS; ANTARCTIC; AFRICA; AUSTRALASIA; FEEDING AREAS; BREEDING GROUNDS; MANAGEMENT AREAS

INTRODUCTION

'Discovery marks' from the 1930s to the 1950s revealed linkages between humpback whales from East Africa (C) breeding grounds and Antarctic Area III feeding area (0°E–70°E), between humpback whales from the Western Australian breeding grounds (D) and Antarctic Area IV feeding area (70°E–130°E), and humpback whales from the Eastern Australian breeding grounds (E1) and Antarctic Area V feeding area (130°E–170°W). Discovery mark data also revealed low levels of interchange of individual humpback whales from breeding grounds D and E1 with Antarctic feeding Area IV and V (Rayner, 1940; Chittleborough, 1965; Dawbin, 1966; IWC, 2011; IWC, 2012).

Recent genetic evidence reports linkages between humpback whales migrating along the West Australian (D) coast and Antarctic Area IV feeding area (Pastene *et al.*, 2013) and low levels of interchange between breeding populations of Western Australia (D) and Eastern Australia (E1) (Anderson, 2013; Schmitt *et al.,* 2014a). Only two previous anecdotal photo-identification matches support linkages between Western Australia and Antarctic Area IV feeding area and mingling between breeding populations of Western Australia (D) and Eastern Australia (E1). One match supports the linkage between Western Australian breeding grounds (D) and Antarctic Area IV feeding area (Gill and Burton, 1995). The lateral body of a humpback whale was photographed on 3 September 1989 at 32°S, 116°E off Perth on the southwest coast of Western Australia during the southern migration and was subsequently matched to a photograph of the lateral body of the same individual humpback whale sighted and photographed on 14 February 1993 at 64°S, 101°E, in the Antarctic Area IV feeding area

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(Gill and Burton, 1995; Fig. 1). A single match supports interchange between humpback whales from Eastern Australia (E1) and Western Australia (D) (Kaufman *et al.,* 2011). A humpback whale tail fluke photograph obtained off North Stradbroke Island (28°S, 154°E) on 15 September 1987 was matched to a fluke photograph obtained off Perth (32°S, 116°E) on 10 October 1995 (Kaufman *et al.,* 2011; Fig. 1). Satellite-radio tag tracking of an individual humpback whale supports linkages between East Africa (C) and Antarctic Area III feeding area (Fossette *et al.,* 2014). Similarly, only one individual humpback whale satellite-radio tag track (Gales *et al.,* 2009; Fig. 1) supports the presence (Andrews-Goff, pers. comm.; Franklin *et al.,* 2017) of East Australian whales in the Antarctic Area IV feeding area. Recent acoustic evidence also reports low levels of interchange between humpback whales from breeding Areas D and E1 (Noad *et al.,* 2000).

This study uses the first large photo-identification dataset to investigate linkages and interchange between breeding grounds C off East Africa, D off Western Australia and E1 off Eastern Australia and the Antarctic Area IV feeding area. The outcome of a photo-identification comparison between a catalogue of individual humpback whales photographed in the Antarctic Area IV feeding area (2008, n = 30), and three large existing regional fluke catalogues from East Africa (2000–2006, n = 842), Western Australia (1990–2007, n = 1,558) and Eastern Australia (1992–2005, n = 1,964) is reported. A novel analysis of the photo-identification data (see statistical analysis below) was used to investigate linkages between each of the three breeding grounds and the Antarctic Area IV feeding area, and the results are discussed.

Table 1

Date and location of humpback whales photographed by Greenpeace in Antarctic IWC Management Area IV feeding area

Whale	Date (dd/mm/yy)	Latitude Deg. mins (S)	Longitude Deg. mins (E)
001	02/01/08	63.34	112.57
002	02/01/08	63.33	112.54
003	02/01/08	63.34	112.57
004	02/01/08	63.34	112.57
005	02/01/08	63.34	112.57
006	02/01/08	63.48	111.47
007	03/01/08	63.25	105.39
008	03/01/08	63.27	104.52
009	03/01/08	63.27	104.52
010	03/01/08	63.25	105.39
011	04/01/08	63.02	102.08
012	07/01/08	62.47	87.04
013	07/01/08	62.47	87.04
014	07/01/08	62.47	87.04
015	07/01/08	62.47	87.04
016	07/01/08	62.47	87.04
017	07/01/08	62.47	87.04
018	07/01/08	62.47	87.04
019	07/01/08	62.47	87.04
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023	07/01/08	62.47	87.04
024	07/01/08	62.47	87.04
025	07/01/08	62.47	87.04
026	07/01/08	62.47	87.04
027	07/01/08	62.47	87.04
028	07/01/08	62.47	87.04
029	09/01/08	64.14	80.01
030	09/01/08	64.14	80.01

METHODS

Photo-identification and fluke catalogues

The Greenpeace International vessel *Esperanza* undertook a non-lethal research program in Antarctica from 7 November 2007 to 8 February 2008. As part of this program, photographs were taken of humpback whales in the Antarctic Area IV feeding area (70°E–130°E) from 2 to 9 January 2008 in locations ranging between 62°47'S and 64°14'S, 112°57'E and 80°00'E (see Table 1 and Fig. 1). The resulting Greenpeace Antarctic Area IV (ANT) catalogue of ventral humpback whale tail fluke photographs consists of n = 30 photo-identified individual humpback whales.

The Wildlife Conservation Society and the American Museum of Natural History Cetacean Conservation and Research Program have conducted photo-identification studies of humpback whales off East Africa since 2000 (Cerchio *et al*., 2008a; 2008b). Photography of humpback whale pods was conducted off Madagascar (C3, 16°S, 50°E) between 2000 and 2006. The resulting East African (EAF) fluke catalogue for the period 2000–2006 consists of n = 842 unique individuals. Only the Madagascar (C3) catalogue was used for this study.

The Centre for Whale Research Western Australia has conducted photo-identification studies of humpback whales off Western Australia since 1990 (Jenner *et al.,* 2001). Photography of humpback whale pods was conducted at Exmouth Gulf (21°40'S, 114°10'E), Dampier (20°20'S, 116°45'E) and the Kimberley region (15°50'S, 123°30'E) between 1990 and 2007. The reconciled Western Australian (WA) fluke catalogue for the period 1990–2007 consists of n = 1,558 unique individuals.

The Oceania Project conducted vessel-based photo-identification of humpback whale pods and individual whales in Hervey Bay, Queensland (25°S, 153°E) between 1992 and 2005 (Franklin *et al*., 2011, Franklin 2012, Franklin 2014). The reconciled Eastern Australian (EA) fluke catalogue for the period 1992–2005 consists of n = 1,964 unique individuals.

The sampling sites and the reconciled fluke catalogues are summarised in Table 2 and the locations of the photo-identification sampling sites and IWC breeding grounds and feeding areas are shown in Fig. 1.

Photo-identification sampling sites for this study: Madagascar (16°S, 50°E); Exmouth Gulf (21°40'S, 114°10'E), Dampier (20°20'S, 116°45'E) and Kimberley (15°50'S, 123°30'E); Hervey Bay (25°S, 153°E). Antarctic Area IV sampling sites for this study (shown as circles in Fig. 1, also see Table 1): (g) 2-Jan-08, (60°S, 112°E), 6 flukes; (h) 3-Jan-08, (63°S, 105°E), 4 flukes; (i) 4-Jan-08, (63°S, 102°E), 1 fluke; (j) 7-Jan-08, (63°S, 87°E), 17 flukes; (k) 9-Jan-08, (64°S, 80°E), 2 flukes.

Other photo-identification and satellite-tag locations mentioned in the text: (a) 3-Sep-89 off Perth, (32°S, 116°E) one lateral body photo; (b) 14-Feb-93, (64°S, 101°E), one lateral body photo (Gill and Burton, 1995); (c) sat-tag commenced, 10-Oct-08, (37°S, 150°E), (d) sat-tag ceased, 3-Feb-09, (61°S, 101°E) (Gales *et al.*, 2009, Andrews-Goff,

Table 2

Summary of East African, Western Australian and Eastern Australian sampling sites (SITE) and the population tail fluke catalogues (POP) of individual humpback whales used in this study.

East Africa (EAF)		Western Australia (WA)		Eastern Australia (EA)	
Site	Flukes (*n*)	Site	Flukes (*n*)	Site	Flukes (*n*)
Madagascar (C3)	842	Exmouth, Dampier and Kimberley	1,558	Hervey Bay	1,964
Total (POP)	842		1,558		1,964

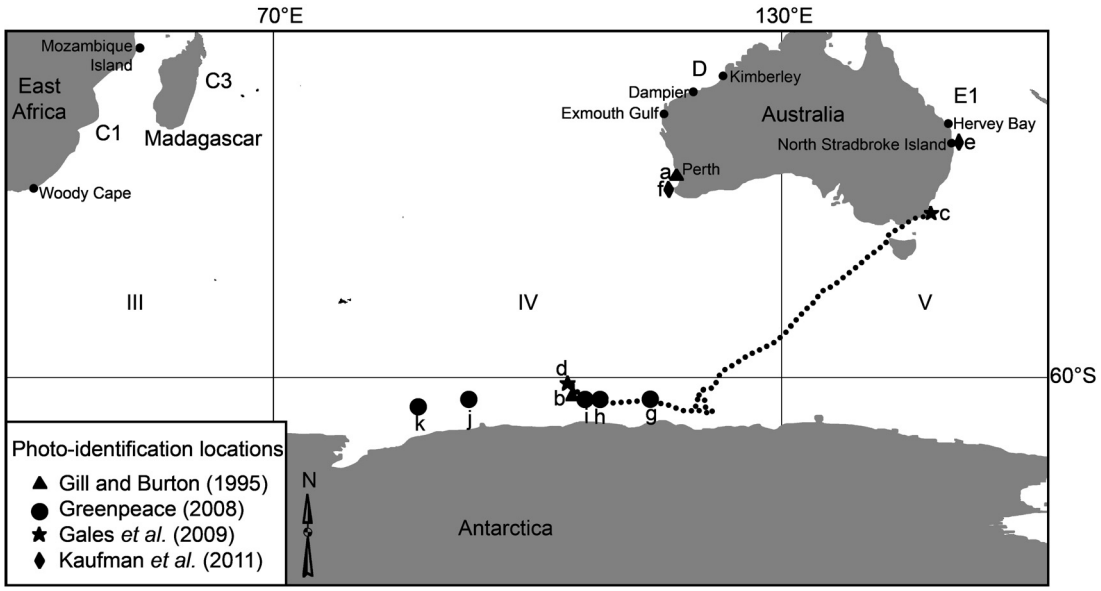

Fig. 1. East African, Western Australian and Eastern Australian photo-identification sampling sites, used in this study; IWC breeding grounds C1, C3, D and E1 and Antarctic feeding Areas III (0°–70°E), IV (70°E–130°E) and V (130°E–170°W); and other photo-identification locations mentioned in text.

pers. comm. and Franklin *et al.*, 2017); (e) 15-Sep-87 (28°S, 154°E) off North Stradbroke Island, one fluke, (f) 10-Oct-95 (32°S, 116°E) one fluke (Kaufman *et al.,* 2011).

Statistical analysis

A novel analysis (first described in Franklin *et al.,* 2012) was conducted to investigate the photo-identification data from Antarctic Area IV (ANT) fluke catalogue and each of the large regional photo-identification datasets from East African (EAF), Western Australian (WA) and the Eastern Australian (EA) fluke catalogues.

The analysis tested the question: are the data available for each region consistent with the hypothesis that the whales sighted in the vicinity of the Antarctic Area IV are from a single population? (single population hypotheses).

The following rationale was used to design the analysis:

(a) If the whales sighted in Antarctic Area IV were members of the EAF, WA or EA population (Table 2), the proportion of the ANT catalogue expected to be matched to the EAF, WA or EA catalogue would be equal to the proportion of the EAF, WA or EA population that were in the EAF, WA or EA catalogue and alive and available for capture in Antarctic Area IV. For example, if one third of the East African population were in the EAF catalogue and alive at the time Antarctic Area IV was sampled, a third of the ANT catalogue could be expected to be matched to the EAF catalogue (single population hypotheses).

(b) Alternatively, if the whales sighted in Antarctic Area IV were not members of the EAF, WA or EA population, the proportion of the ANT catalogue expected to be matched to the EAF, WA or EA catalogue would be less than the proportion of the EAF, WA or EA population alive and in the EAF, WA or EA catalogue (separate population hypothesis).

Given the above rationale and the estimates described below, the analysis may be based on a test of association in a 2 × 2 cross-table of frequencies constructed as *'not seen'* or *'seen'* in Antarctic Area IV by *'not seen'* or *'seen'* in East Africa, Western Australia or Eastern Australia (Table 3).

Looking at these data and estimates, the expected numbers of matches, $\hat{\boldsymbol{m}}_{POP\text{-}ANT}$, may be derived from the equal proportions rationale presented above, $m_{POP\text{-}ANT}/n_{ANT} = n_{POP}/N_{POP}$, and calculated as $\hat{\boldsymbol{m}}_{POP\text{-}ANT} = (n_{POP}*n_{ANT})/N_{POP}$. This is both the standard way of calculating the expected frequencies under a null hypothesis of independence in a cross-table (row total by column total over grand total) and a simple transformation of the Lincoln-Petersen Estimator, $\hat{N}_P = (n_1*n_2)/m_2$. The expected frequencies for each of the other cells were obtained in the standard way. Note that the null hypothesis of independence in the Table 3 corresponds to the single population hypothesis described above.

A one-tailed test of association is appropriate because the alternative hypothesis is that the observed frequency of whales seen at both locations was fewer (and never more)

Table 3
Scheme for cross-tables: East Africa, Western Australia/Eastern Australia (POP) – Antarctic IWC Management Area IV (ANT)

Antarctic IWC Management Area IV (ANT)	East Africa/Western Australia/Eastern Australia (POP)		
	Not seen	Seen	Total
Not seen	$N_{POP} - n_{ANT} - n_{POP} + m_{POP\text{-}ANT}$	$n_{POP} - m_{POP\text{-}ANT}$	$N_{POP} - n_{ANT}$
Seen	$n_{ANT} - m_{POP\text{-}ANT}$	$m_{POP\text{-}ANT}$	n_{ANT}
Total	$N_{POP} - n_{POP}$	n_{POP}	N_{POP}

N_{POP} = Population estimate at 2008 for East Africa, Western Australia and Eastern Australia.
n_{POP} = Estimate of number of living whales in 2008 from the East African, Western Australian and Eastern Australian catalogues.
$m_{POP\text{-}ANT}$ = Number of whales matched between East Africa, Western Australia or Eastern Australia and Antarctic IWC Management Area IV.
n_{ANT} = Number of whales identified in Antarctic IWC Management Area IV.

than the expected frequency under the null hypothesis. A one-tailed *p*-value from Fisher's Exact Test was used. This test is preferred over the asymptotic Pearson Chi-square test when expected frequencies are small (Everitt, 1992).

The analysis required estimates of the East African, Western Australian and Eastern Australian populations (N_{POP}) for 2008 and estimates of the number of individuals in the POP catalogues that were alive in early 2008 and potentially available for capture in Antarctic Area IV (N_{POP}).

RESULTS

Comparison of the Antarctic Area IV catalogue (n = 30) to the East African (n = 842), Western Australian (n = 1,558) and Eastern Australian (n = 1,964) catalogues found no matches (locations are shown in Fig. 1 above).

Analysis: Antarctic Area IV – East Africa

An estimated population of 7715 was obtained for East Africa. This was based on the estimate of the East African C3 population in 2006 at 6,737, CV = 0.31 (Cerchio *et al.,* 2008a). However, to allow for growth between 2006 and 2007 and to take into account that the 2006 estimate may only be an estimate of a sub-region of the C population, as suggested by Cerchio *et al.* (2008a), the upper bound estimate of 7,715, CV = 0.24 was used as a minimum estimate for the East African (C) population in early 2008.

The 842 individuals recorded in the EAF catalogue between 2000 and 2006, were assumed to have been captured at a constant rate of 120.3 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham *et al*. 2001; Zerbini *et al*., 2010), yielded an estimated 748 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 4 reports the frequencies of whales 'not seen' and 'seen' near the Antarctic Area IV by 'not seen' and 'seen' in East Africa based on the above estimates together with the size of the Antarctic Area IV catalogue (n = 30) and the number of Antarctic Area IV to East Africa matches (n = 0). The expected frequencies shown were derived on the assumption of independence corresponding to a hypothesis that the whales seen in both places were members of the same population.

The one-tailed p-value from Fisher's exact test for the data in Table 4 was p = 0.047, indicating that the Antarctic and East Africa data were likely to be from separate populations. With 2.9 matches expected under the single population null hypothesis, it is highly unlikely that no matches would be found unless the data were on whales from separate populations. The null hypothesis would not have been rejected if 1 match had been found (p = 0.197).

Table 4
Estimated numbers and expected frequencies of whales 'not seen' and 'seen' in Antarctica IWC Management Area IV by 'not seen' and 'seen' in East Africa

Antarctic Area IV	Frequency	East Africa		Total
		Not seen	Seen	
Not seen	Observed	6,937	748	7,685
	Expected	6,939.9	745.1	7,685
Seen	Observed	30	0	30
	Expected	27.1	2.9	30
Total		6,967	748	7,715

Analysis: Antarctic Area IV – Western Australia

The estimated Western Australian population of 26,100 in early 2008 was based on the 2007 estimate of Salgado Kent *et al.* (2012) of 26,100 (95% CI = 20,152–33,272). Note: See IWC (2012) for discussion of potential bias of the results in Salgado Kent *et al.* (2012).

The 1,558 individuals recorded in the WA catalogue between 1990 and 2007 were assumed to have been captured at a constant rate of 86.6 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham *et al*., 2001; Zerbini *et al*., 2010, yielded an estimated 1,127 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 5 reports the frequencies of whales 'not seen' and 'seen' near the Antarctic Area IV by 'not seen' and 'seen' in Western Australia based on the above estimates together with the size of the Antarctic Area IV catalogue (n = 30) and the number of Antarctic Area IV to Western Australia matches (n = 0). The expected frequencies shown were derived on the assumption of independence corresponding to a hypothesis that the whales seen in both places were members of the same population.

The one-tailed p-value from Fisher's exact test for the data in Table 5 was p = 0.266, indicating insufficient evidence (i.e. P > 0.05) to reject the null hypothesis that the Antarctic and WA data were from the same population. However, the finding of no matches weakens the argument that the Antarctic data were from the WA population: even a single

Table 5

Estimated numbers and expected frequencies of whales 'not seen' and 'seen' in Antarctica IWC Management Area IV by 'not seen' and 'seen' in Western Australia.

		Western Australia		
Antarctic Area IV	Frequency	Not seen	Seen	Total
Not seen	Observed	24,943	1,127	26,070
	Expected	24,944.3	1,125.7	26,070
Seen	Observed	30	0	30
	Expected	28.7	1.3	30
Total		24,973	1,127	26,100

match (p = 0.626) would have strengthened the case for a single population. The relatively small Antarctic catalogue and the relatively small proportion of the estimated WA population expected to be alive and in the WA catalogue (4.32%) makes for an indefinite conclusion.

Analysis: Antarctic Area IV – Eastern Australia

The Eastern Australian population in early 2008 was estimated at 9,592 whales based on the Noad *et al.* (2011) estimate of 7,090 in 2004 with an assumed rate of increase of 10.6% per annum.

The 1,964 individuals recorded in the EA catalogue between 1992 and 2005, were assumed to have been captured at a constant rate of 140.3 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham *et al*., 2001, Zerbini *et al*., 2010), yielded an estimated 1,527 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 6 reports the frequencies of whales 'not seen' and 'seen' near the Antarctic Area IV by 'not seen' and 'seen' in Western Australia based on the above estimates together with the size of the Antarctic Area IV catalogue ($n = 30$) and the number of Antarctic Area IV to Western Australia matches ($n = 0$). The expected frequencies shown were derived on the assumption of independence corresponding to a hypothesis that the whales seen in both places were members of the same population.

The one-tailed p-value from Fisher's exact test for the data in Table 6 was p = 0.005, indicating that the Antarctic and EA data were from separate populations. With 4.8 matches expected under the single population null hypothesis, it is highly unlikely that no matches would be found unless the data were on whales from separate populations. The null hypothesis would not have been rejected had even one match had been found (p = 0.037).

Table 6

Estimated numbers and expected frequencies of whales 'not seen' and 'seen' in Antarctica IWC Management Area IV by 'not seen' and 'seen' in Eastern Australia

		Eastern Australia		
Antarctic Area IV	Frequency	Not seen	Seen	Total
Not seen	Observed	8,035	1,527	9,562
	Expected	8,039.8	1,522.2	9,562
Seen	Observed	30	0	30
	Expected	25.2	4.8	30
Total		8,065	1527	9,592

DISCUSSION

This study is the first to utilise large humpback whale photo-identification datasets for comparison against a small catalogue from the Antarctic Area IV feeding area to investigate linkages between Area IV feeding area and East Africa, Western Australia and Eastern Australia. The data support the hypothesis that humpback whales feeding in Antarctic Area IV are a separate population from the East Africa and Eastern Australia populations. However, as the East African and Eastern Australian data used in this study are each from one sampling site, there is a possibility that comparison of the Antarctic flukes with other African and East Australian catalogues may yield matches. Consequently, we cannot discount the likelihood that some East African and Eastern Australian humpbacks may feed in the Antarctic Area IV feeding area (see Franklin *et al.,* 2017). In contrast, there is much more recent evidence that some Eastern Australian humpbacks feed in Antarctic Area V in and around the Balleny Islands (Franklin *et al.,* 2008; Franklin *et al.,* 2012; Constantine *et al.,* 2014; Schmitt *et al.,* 2014b).

The limited data from Western Australia and the small Antarctic Area IV catalogue used in this study provided weak evidence to reject the null hypothesis that humpback whales feeding in Antarctic Area IV are from the Western Australian population. Both early 'Discovery mark' data and recent photo-identification data provide support for the hypothesis that Western Australian humpback whales feed in Antarctic Area IV (Rayner, 1940; Chittleborough, 1965; Dawbin, 1966; Gill and Burton, 1995). Moreover, recent genetic data supports linkages between Western Australia (D) and Antarctic Area IV feeding area (Pastene *et al.,* 2013). Consequently, the most likely interpretation of available photo-identification data in this study is that the humpback whales feeding in Antarctic Area IV are from the Western Australian population.

Both early Discovery mark data and recent photo-identification, satellite-tag, genetic and acoustic data support the hypothesis of low levels of overlap, in the Antarctic Area IV feeding area, between Eastern Australian (E1) humpback whales and Western Australian (D) humpback whales (Rayner, 1940; Chittleborough, 1965; Dawbin, 1966; Gales *et al.,* 2009; Andrews-Goff, pers. comm.; Kaufman *et al*., 2011; Anderson, 2013; Schmitt *et al.,* 2014a; Franklin *et al.,* 2017).

The timing and location of sampling in Antarctic Area IV feeding area is likely an important factor in determining the linkages between tropical breeding grounds and Antarctic Area IV feeding area. The humpback whale satellite-radio tagged off Eden in October 2008 (Franklin *et al.,* 2017) travelled down into Antarctic Area IV feeding area during February 2009 whereas the sampling for this study in Antarctica was during January. Moreover, there is a temporal staggering of sexual and maturational classes of humpback whales during the migration to and from Antarctica (Chittleborough, 1965; Dawbin, 1966, 1997; Franklin, 2012). Consequently, sampling in the Antarctic Area IV feeding area throughout December, January and February may yield more useful results for comparison with coastal humpback whale tail fluke catalogues.

Collection of further photo-identification data of humpback whales in Antarctic Area III, IV and V feeding

areas with sampling across the season will assist in further investigation of the linkages between the Antarctic feeding areas and tropical breeding grounds of humpback whales in both the Indian and Pacific Ocean basins, as well as rates of interchange between these different breeding populations during their period in the feeding areas.

The Greenpeace Antarctic Area IV catalogue should also be compared to any other existing West African, East African, Indian Ocean, Australian and/or Antarctic catalogues, as this is likely to provide further data on the migratory destination of these humpback whales and add to our limited knowledge of the extent of breeding population overlap within the Antarctic Area III, IV and V feeding areas.

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