Photo-identification confirms that humpback whales (Megaptera novaeangliae) from eastern Australia migrate past New Zealand but indicates low levels of interchange with breeding grounds of Oceania

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ABSTRACT

Recent photo-identification and genetic studies have identified at least five discrete breeding populations in Australia and Oceania: western Australia (D), eastern Australia (E (i)), New Caledonia (E (ii)), Tonga (E (iii)), French Polynesia and the Cook Islands (F). Also evident are low levels of intermingling among breeding populations consistent with the degree of genetic differentiation. Photo-identification has confirmed linkages between Area V feeding areas and eastern Australia breeding grounds and one genotype match has been reported between Area V feeding areas and Oceania breeding grounds. Recent abundance estimates show strong increases in the eastern Australian population, and some recovery in the New Caledonia and Tonga populations, but with little evidence of recovery at other known Oceania breeding grounds or New Zealand. Studies to date have provided no conclusive evidence of the migratory destination of humpback whales passing through New Zealand waters *en route* between Antarctic feeding areas and tropical breeding grounds. Photo-identification comparisons were undertaken between humpback whale fluke catalogues from eastern Australia (EA, 1315), Oceania east (OE, 513), Oceania west (OW, 166) and New Zealand (NZ, 13). Five matches were found between OE/OW, four matches between OW/EA and three matches between NZ/EA. The data are used to investigate and discuss the migratory destination and breeding ground migratory interchange of humpback whales travelling through New Zealand waters. The data confirm that humpback whales with site fidelity to eastern Australia migrate past New Zealand including through the Cook Strait and Foveaux Strait.

KEYWORDS: HUMPBACK WHALES; PHOTO-ID; MIGRATION; SITE FIDELITY; EASTERN AUSTRALIA; NEW ZEALAND; OCEANIA; ANTARCTIC WATERS; BREEDING GROUNDS; FEEDING AREAS

INTRODUCTION

A comprehensive investigation of humpback whales (Megaptera novaeangliae) migrating through New Zealand waters was undertaken during the 1950s (Dawbin, 1956; 1966; Dawbin and Falla, 1949). After reviewing a range of factors that might influence the migratory routes taken by humpbacks past New Zealand including ocean currents, bottom topography and geography of land masses encountered, Dawbin (1956) concluded that the primary factors determining the migratory route of humpbacks past

New Zealand were feeding behaviour in Antarctic waters and the location of breeding grounds in eastern Australia and the islands of the western Pacific further to the east (Dawbin, 1956; 1964; 1966; Dawbin and Falla, 1949).

Initially, Dawbin considered the breeding ground destinations of humpback whales migrating from Antarctic feeding areas through New Zealand waters, and up along the eastern coast of Australia, were the eastern Coral Sea including the Chesterfields and New Caledonia, with the Tongan Group of islands being the northern limit of north

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bound humpbacks passing New Zealand (Dawbin and Falla, 1949). However, Dawbin subsequently noted that the 'great length of the eastern Australian coastline situated in the tropics should however provide a much more extended area of coastal conditions suitable for breeding than is available at near Pacific Islands' (Dawbin, 1956).

Geographic separation and isolation of discrete breeding groups was considered to occur and to influence breeding ground destinations of migrating humpback whales (Chittleborough, 1965; Dawbin, 1964; 1966; Mackintosh, 1942). The 'Discovery' marking programme²¹ provided the first direct evidence of linkages between polar feeding areas and temperate breeding grounds and intermingling among discrete breeding groups (Chittleborough, 1965; Dawbin, 1959; 1964; 1966; Mackintosh, 1942; Rayner, 1940). This evidence supported the hypothesis that western Australia, eastern Australia and Oceania were discrete breeding grounds with little interchange among individuals and no evidence for permanent exchange of individuals (Chittleborough, 1965; Dawbin, 1964). Dawbin reported links between eastern Australia and Area V22 with occasional interchange between eastern Australia and New Zealand and significant segregation between eastern Australia and the New Zealand/Oceania region (Dawbin, 1959; 1964; 1966).

Members of the South Pacific Whale Research Consortium and the Southern Cross University Whale Research Centre have been undertaking long-term photoidentification, genetic and satellite tagging studies on humpback whales in the Pacific basin and eastern Australia. The studies have substantiated that western Australia (Breeding Stock D) and eastern Australia (Breeding Stock E (i)) are discrete breeding populations (Anderson and Brasseur, 2007; Anderson et al., 2010; Olavarria et al., 2006a; 2006b). The data also substantiated that the IWC Breeding Stock E, which included eastern Australia, New Caledonia and Tonga, should be considered to be three discrete breeding sub-populations; eastern Australia (E (i)), New Caledonia (E (ii)) and Tonga (E (iii)) (Garrigue et al., 2006; Olavarria et al., 2007). The observed limited movements of individual humpback whales between eastern Australia and Oceania (Garrigue et al., 2000; Garrigue et al., 2011) and within Oceania (Garrigue et al., 2002; Garrigue et al., 2010; Hauser et al., 2010; South Pacific Whale Research Consortium et al., 2007) are consistent with the reported levels of genetic differentiation between Breeding Stock(s) E (i), E (ii) and E (iii). Similarly acoustic evidence substantiates low levels of intermingling between Breeding Stock D and E (i) (Noad et al., 2000). Only six movements of humpback whales have been documented, by photoidentification, between Area V feeding grounds and eastern Australia (Franklin et al., 2008a; Kaufman et al., 1990; Rock et al., 2006). Satellite tagging has documented a movement from the Cook Islands to Area VI (Hauser et al., 2010). One recent genotype match was reported between New Caledonia and the Area V feeding area, and also a small number of genotype matches have been reported between Oceania breeding grounds and Area V, VI and I feeding areas (Steel *et al.*, 2008).

Genetic evidence in a recent study suggested that the humpback whales passing New Zealand may be closely related to the New Caledonia (E (i)) population (Olavarria et al., 2006b) and a recent photo-identification matching of the New Zealand Catalogue with the Oceania catalogues produced only 3 matches: two matches with New Caledonia and one with Vava'u, Tonga (Constantine et al., 2006). These studies have demonstrated links between New Zealand and tropical breeding grounds in Oceania but the relationship between New Zealand and Australia has yet to be carefully investigated. Some photo-identification data (Franklin et al. 2008b) and limited telemetry data (Gales et al., 2009; Garrigue et al., 2010) have indicated that whales from eastern Australia migrated past southern New Zealand and that whales from New Caledonia pass near northern New Zealand, respectively. However, there remains considerable uncertainty about the destination of humpback whales migrating past New Zealand from Area V feeding areas.

This paper examines photo-identification data collected from 1999–2004 to investigate movements of individual humpback whales between eastern Australia and Oceania and within Oceania and discuss the breeding ground migratory interchange and migratory destinations of humpback whales travelling through New Zealand waters.

METHODS

Photo-identification data

Vessel-based photo-identification of humpback whale pods in Hervey Bay, Queensland (25°S, 153°E) was undertaken between 1992 and 2005 as part of a long-term study of social behaviour. Photo-identification was also utilised in a study of humpback whales on the northern migration at Byron Bay (28°38'S, 153°38'E) and on the southern migration at Ballina (28°52'S, 153°36'E) between 2003 and 2004. The combined reconciled eastern Australian fluke catalogue for the years 1999–2004, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, consists of 1,315 individuals.

Dedicated surveys of humpback whales in Oceania were conducted between 1999–2004 during the austral winter, in four primary sampling sites: New Caledonia; Tonga; the Cook Islands and French Polynesia. Surveys were conducted in only one or two seasons in other adjacent sampling sites: Vanuatu, Fiji, Samoa, and Niue. Sampling at American Samoa began in 2003. The combined Oceania fluke catalogue for 1999–2004, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, consists of 692 individuals.

A comprehensive description of site sampling effort and the method used to compare the Oceania and eastern Australian catalogues, within and between regions, are fully reported in South Pacific Whale Research Consortium (2007) and Garrigue *et al.* (2011). Although some local site samples, e.g. Vanuatu, Fiji, Samoa and Niue are small, when combined with other sampling sites to create the sites of

²¹ Discovery' marks were stainless steel numbered tags that were fired into the body of the whale and recovered if that animal was captured (Brown, 1978).

²²The International Whaling Commission designated six management areas in the southern hemisphere for baleen whales (except Bryde's whales), areas I–VI. Area v covered the waters between 130°e and 170°w (see review in Donovan, 1991). Some papers refer to the humpback whales from this area as 'group v' humpback whales.

'Oceania West' and 'Oceania East' for analysis (Table 1, below), the combined site samples can be considered random samples from the E (ii) and E (iii) plus F populations, for the purposes of these analyses.

The eastern Australian and Oceania catalogues selected for inclusion in this study were the most recent, fully reconciled, photo-identification catalogues from each of the sample sites at the time of writing and are summarised in Table 1. Photo-identification survey work is still underway in most sites. Sampling site locations are shown in Fig 1.

Statistical analysis

For the analyses, fluke data from New Caledonia and Vanuatu were combined into an Oceania west (OW) catalogue (166) while Tonga, Fiji, American Samoa, Samoa, Niue, Cook Islands and French Polynesia were combined into an Oceania east (OE) catalogue (513). The eastern Australian (EA) catalogue (1,315) and New Zealand (NZ) catalogue (13) were treated as separate population catalogues (Table 1).

Several analyses were conducted investigating the number of matches found between sample site (SITE) and population

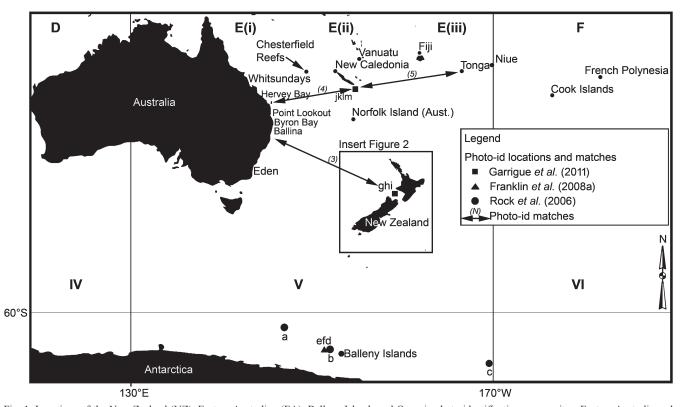


Fig. 1. Locations of the New Zealand (NZ), Eastern Australian (EA), Balleny Islands and Oceania photo-identification survey sites; Eastern Australia and Oceania breeding grounds (E (i), E (ii), E (iii), F); and Antarctic feeding areas IV, V and VI (IWC, 2006) and the photo-id matches reported between NZ/EA, EA/OW and OW/OE.

The circle symbols (a), (b) and (c) show the location of humpback whales reported in Rock *et al.* (2006); whale (a) was sighted in Point Lookout and Eden, (b) in the Whitsundays, Hervey Bay and Eden and (c) in Hervey Bay and Eden. The triangle symbols (e), (f) and (d) show the Balleny Island/EA matches reported in Franklin *et al.* (2008a); whale (d) was sighted in Ballina and (e) and (f) were sighted in Byron Bay and Hervey Bay but in different years. The square symbol marked (g), (h), (i) shows the NZ/EA matches reported in South Pacific Whale Research Consortium (2007); all three were resighted in Hervey Bay, two within the same season; June in NZ and September in Hervey Bay. The square symbol marked (j), (k), (l) and (m) shows the four New Caledonia/Hervey Bay matches reported in South Pacific Whale Research Consortium (2007).

Table 1
Summary of eastern Australian and Oceania reconciled catalogues 1999–2004 by population catalogues (POP)¹ and sampling sites (SITE)².

(A) eastern Australia (EA)		(B) Oceania west (OW)		(C) Oceania ea	st (OE)	(D) New Zealand ³ (NZ)		
Site Flukes (n)		Site	Flukes (n)	Site	Flukes (n)	Site	Flukes (n)	
Hervey Bay	871	New Caledonia	160	Fiji	2	New Zealand	13	
Byron Bay	415	Vanuatu	6	Tonga	282			
Ballina	29			Samoa	1			
				American Samoa	31			
				Niue	2			
				Cook Islands	36			
				French Polynesia	159			
Total EA	1,315	Total OW	166	Total OE	513	Total NZ	13	

¹The pooling of sample site catalogues into the population catalogue groupings of EA, OW, and OE population is based on: Olavarría *et al.* (2006a; 2006b); Anderson and Brasseur (2007) and Anderson *et al.* (2010).

²Although the sample size at some sites is small the combined site effort and samples are consistent with these being random samples from the populations and are considered such for this analysis.

³New Zealand is not considered a discrete population, however for the purposes of this analysis it was treated as such.

catalogues (POP), m_{SITE-POP}: NZ-EA, OW-EA, OE-EA, OW-OE, NZ-OW, NZ-OE. In each case, if the whales sighted at the sample site (SITE) were all members of the population catalogue (POP), the proportion of the SITE catalogue that would be expected to be matched to the POP catalogue should be equal to the proportion of the estimated population that was in the POP catalogue. Alternatively, if the whales sighted at the sample site (SITE) were not all members of the population, the proportion of the SITE catalogue that would be expected to be matched to the POP catalogue would be lower than the proportion of the estimated population in the POP catalogue.

This provides a means of estimating the expected number of matches under a null hypothesis that the whales identified at the SITE were all members of the POP catalogue for testing against the alternative hypothesis that they were not. The analysis is based on a test of association in a 2×2 crosstable of frequencies constructed as 'not seen' or 'seen' at the sample site by 'not seen' or 'seen' in the proposed population (Table 2).

Given these data and estimates, the expected numbers of matches, $_{\rm POP-SITE}$, may be derived from expected equality of proportions, $m_{\rm POP-SITE}/n_{\rm SITE} = n_{\rm POP}/N_{\rm POP}$, and calculated as $_{\rm POP-SITE} = (n_{\rm POP}^* n_{\rm SITE})/N_{\rm POP}$. 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 estimator, = $(n_1 * n_2)/m_2$. The expected frequencies for each of the other cells were obtained in the standard way.

A one-tailed test of association is appropriate because the alternative hypothesis is that the observed frequency of whales seen at both locations will be lower than the expected frequency under the null hypothesis. We used one-tailed p-values from Fisher's Exact Test. This test is preferred over the asymptotic Pearson Chi-Square test when expected frequencies are small.

The sizes of sampling site catalogues ($n_{\rm SITE}$), the sizes of population catalogues ($n_{\rm POP}$) the estimated 2004 population sizes ($N_{\rm POP}$) and the numbers of matches between the sampling site catalogues and the population catalogues ($m_{\rm POP}$), except for the Ballina catalogue (Dan Burns, unpublished data), were derived from Garrigue *et al.* (2011), South Pacific Whale Research Consortium (2006) and Paton *et al.* (2011) and are reported in Table 3.

RESULTS

Matching between the eastern Australian and the Oceania catalogues, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, resulted in: 3 matches between eastern Australia and New Zealand; 4 matches between eastern Australia and Oceania west (New Caledonia, Vanuatu) and 5 matches between

Table 2
Scheme for the cross-tables.

Hypothesised population (POP)							
Sample site (SITE)	Not seen	Seen	Total				
Not seen Seen Total	$\begin{aligned} N_{POP} - n_{SITE} - n_{POP} + m_{POP\text{-}SITE} \\ n_{SITE} - m_{POP\text{-}SITE} \\ N_{POP} - n_{POP} \end{aligned}$	$n_{ ext{POP}} - m_{ ext{POP-SITE}} \ m_{ ext{POP}}$	$N_{POP} - n_{SITE} \\ n_{SITE} \\ N_{POP}$				

 N_{POP} =estimated 2004 population size; n_{POP} =size of the population catalogue; n_{SITE} =size of the sample site catalogue; $m_{POP-SITE}$ =number of whales matched between the population and sample site catalogues.

Table 3

Data summary: sizes of sampling site catalogues, sizes of population catalogues, the estimated 2004 population sizes and the numbers of matches between the sampling site catalogues and the population catalogues.

SITE – POP	NZ-EA	OW-EA	OE-EA	OW-OE	NZ-OW	NZ-OE
Sample site catalogue (n _{SITE}) Population catalogue (n _{POP}) Estimated population size (N _{POP}) Site-population matches (m _{POP,SITE})	13 1,315 7,090	166 1,315 7,090 4	513 1,315 7,090	166 513 3366	13 166 472	13 513 3,366

¹Estimated population sizes (n_{POP}) are based on comparable abundance estimates utilising photo-id data: Baker *et al.* (2006) and Paton *et al.* (2011).

Table 4

Frequencies of whales *not seen* and *seen* in sampling sites by whales *not seen* and *seen* in proposed populations with expected frequencies for site to population matches and Fisher's one-tailed p-values.

SITE – POP	NZ-EA	OW-EA	OE-EA	OW-OE	NZ-OW	NZ-OE
Not seen – Not seen	5,765	5,613	5,262	2,692	293	2,840
Not seen – Seen	1,312	1,311	1,315	508	166	513
Seen – Not seen	10	162	513	161	13	13
Seen – Seen	3	4	0	5	0	0
Expected matches	2.4	30.8	95.1	25.3	4.6	2.0
Fisher's one-tailed p-value	N/A	0.000	0.000	0.000	0.003	0.166

Oceania west and Oceania east (Tonga, Fiji, American Samoa, Samoa, Niue, Cook Islands and French Polynesia). No matches were found between New Zealand and any other of the Oceania catalogues in this comparison (but see Constantine *et al.*, 2006).

The frequencies of whales in sampling sites by whales in proposed populations with the expected frequencies for site to population matches and Fisher's one-tailed p-values are reported in Table 4.

Of the 13 whales sighted in New Zealand, three were matched to the eastern Australian catalogue. This is consistent with the 2.4 expected if the New Zealand whales were all members of the eastern Australian population. With the data falling in the wrong tail of the test distribution this result is entirely consistent with that hypothesis. Of the 166 whales sighted in Oceania west, four were matched to the eastern Australian catalogue. This is considerably and significantly fewer than the 30.8 expected if they were all members of the eastern Australian population. Of the 513 whales sighted in Oceania east, none were matched to the eastern Australian catalogue. This is significantly fewer than the 95.1 expected if they were all members of the eastern Australian population. Of the 166 whales sighted in Oceania west, five were matched to the Oceania east catalogue. This is significantly fewer than the 25.3 expected if they were members of the Oceania east population.

Of the 13 whales sighted in New Zealand, none were matched to the Oceania west catalogue. Although these catalogues were relatively small, this is significantly fewer than the 4.6 expected if they were members of the Oceania west population. However, if it is assumed that the New Zealand 'population' is in fact the eastern Australian population, it would be expected that approximately the same proportion, $p_{\rm NZ-OW}$, of the whales sighted in New Zealand to have been seen in Oceania west as the proportion of the Oceania west whales that were seen in eastern Australia; i.e. $p_{\rm NZ-OW} = 4/166 = {}_{\rm POP-SITE}/13$. On this basis, 0.3 matches would be expected between the NZ and OW catalogues. That no matches were found is consistent with this.

Of the 13 whales sighted in New Zealand, none were matched to the Oceania east catalogue. This is fewer but not significantly fewer than the 2 expected if they were members of the Oceania east population.

DISCUSSION

The result of the comparison between the New Zealand and eastern Australian populations, is consistent with the hypothesis that the whales observed in New Zealand are from the eastern Australian population.

While there is evidently appreciable interchange between the eastern Australian and the Oceania west populations and between the Oceania east and Oceania west populations, the results presented herein support that these are discrete populations. While there may be some interchange between the eastern Australian and the Oceania east populations, the evidence from these data suggests that these populations are discrete.

While there may be some interchange between the Oceania west and New Zealand populations the evidence

from these data suggests that these populations are discrete. The failure to find significance in the comparison between New Zealand and Oceania east (Table 4), may be largely due to the small size of the New Zealand catalogue and the relative small proportion of the Oceania east population in the Oceania east catalogue. However, there is weak evidence in these data indicating that New Zealand and Oceania east are discrete populations.

Movements of humpback whales through New Zealand waters

Dawbin (1956) reported that northbound humpback whales travelling from Antarctic feeding areas approached New Zealand from various directions suggesting widespread lateral dispersion whilst in the Antarctic waters. The northward migration followed three main pathways through New Zealand waters (see Fig. 2). One stream moved along the eastern coastline and was deflected to the northeast, before rounding the northeastern tip and resuming their northerly migration. Another stream passed to the southwest of the South Island through Foveaux Strait and a separate but significant stream passed through Cook Strait between the North and South Island (Dawbin, 1956; 1966).

We speculate that northbound migrating humpback whales travelling from the eastern region of the Area V feeding areas, with site fidelity to the eastern Australian (E (i)) breeding grounds, are likely to pass to the south of the South Island of New Zealand and/or through the Foveaux and Cook Strait from east to west, rather than travel up along the

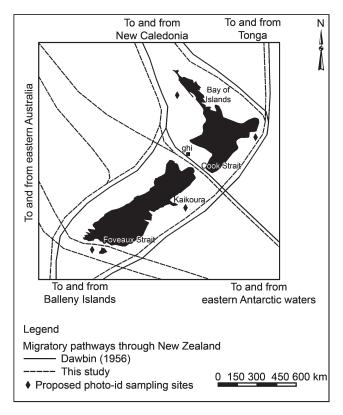


Fig. 2. The migratory pathways and migratory destinations described in (Dawbin, 1956) and the hypothesised migratory pathways and migratory destinations described in this study are shown in solid and broken lines respectively. The additional proposed photo-id sampling sites are shown as diamond shapes. The square symbol marked (g), (h) and (i) are the Cook Straits samples reported in South Pacific Whale Research Consortium (2007).

northeastern coastline of New Zealand. This is supported by the telemetry information in Gales *et al.* (2009).

In contrast, humpback whales with site-fidelity to the New Caledonia (E (ii)) and Tonga (E (iii)) breeding grounds are likely to pass northwards along the eastern coastline of the North Island of New Zealand and after clearing the northern tip of New Zealand, before resuming their migration to New Caledonia (E (iii)) on a northwesterly track, or to the Tongan Islands (E (iii)) on a northeasterly track along the Tongan trench. Two humpback whales sighted in Kaikoura during the northward migration, were also photographed in New Caledonia and Tonga, which suggests this may be the case (Constantine *et al.*, 2006). This is supported by the telemetry data in Garrigue *et al.* (2010).

Dawbin (1956) reported that southbound migrating humpback whales approached New Zealand from the north in narrowly focused pathways. The major proportion of the migration arrived along the western coastline of the North and South Islands, were deflected to the southwest until they rounded the southern tip of the South Island and continued their southern migration to Antarctic waters. Some southbound humpback whales passed around northeastern tip of the North Island (Dawbin, 1956; 1966). This was the case with a humpback whale sighted in New Caledonia, which was also sighted in New Zealand at the Bay of Islands (NE of North Island) during the southern migration (Constantine et al., 2006). An even smaller proportion of the migration, move from west to east through the Cook Strait and Foveaux Strait (Dawbin, 1956).

Humpback whales travelling directly from eastern Australia are likely to approach the western coastline of New Zealand from the east, whereas those migrating from New Caledonia and Tonga would be travelling from the north. Consequently humpback whales from eastern Australia would more likely arrive at, or towards the southern end of, the western coastline of the South Island of New Zealand.

Photo-identification sampling on the southeastern coast of New Zealand and in Cook Strait may therefore represent a sampling bias. Selecting at least three additional sampling sites for systematic photo-identification of humpback whales in New Zealand waters could provide data to determine the destinations of humpback whales passing through the northern waters of New Zealand. These sampling sites could include a site within the Foveaux Strait, a site on the northwestern coast of the North Island, a site on the northwestern coast of the North Island, and a site on the southeastern coast of the South Island, while continuing concurrent sampling in the Cook Strait.

Migration to breeding grounds north of New Zealand

Dawbin (1964) found Discovery mark matches between eastern Australia and Foveaux Strait, at the southern tip of New Zealand and Cook Strait located between the North and South Islands of New Zealand. He stated that the recapture rates of humpbacks marked off eastern Australia and in waters near New Zealand and Norfolk Island indicated that there was significant segregation between groups that migrated along the eastern coast of Australia and those that migrate past islands further east.

Differentiation between eastern Australian (E (i)), New Caledonia (E (ii)) and Tonga (E (iii)) animals has been

substantiated by recent genetic and photo-identification studies (Anderson and Brasseur, 2007; Anderson *et al.*, 2010; Garrigue *et al.*, 2011; Garrigue *et al.*, 2006; Olavarria *et al.*, 2006a; Olavarria *et al.*, 2007; Olavarria *et al.*, 2006b; South Pacific Whale Research Consortium *et al.*, 2007). Over 800 sightings of humpback whales have been reported in New Zealand waters between 1970 and 2007 (Nadine Gibbs, pers. comm.). The majority of sightings were made on the southeast coast of New Zealand off Kaikoura and during systematic surveys conducted in Cook Strait (Constantine *et al.*, 2006; Gibbs and Childerhouse, 2000).

Comparisons of the New Zealand and eastern Australian catalogues for the period 1999–2004, reported herein, resulted in three matches with eastern Australia. All three matches were sighted in the Cook Strait during the early northbound migration and in Hervey Bay during the late southbound migration, two of the matches occurred within the same season (Garrigue *et al.*, 2011). Previous matches between New Caledonia, eastern Australia and New Zealand have been reported (Garrigue *et al.*, 2002; Garrigue *et al.*, 2000) and more recent comparisons of the New Zealand and Oceania catalogues have reported matches between New Caledonia, Tonga and New Zealand (Constantine *et al.*, 2006).

The results reported in this paper confirm that many humpback whales are migrating from Antarctic feeding areas through New Zealand waters to the eastern Australian (E (i)) breeding grounds. Whilst there is some evidence of humpback whales travelling through New Zealand waters to the New Caledonia (E (ii)) breeding grounds to the northwest, and the Tongan (E (iii)) breeding grounds to the northeast of New Zealand, further systematic sampling, at different locations around the northern coastline of New Zealand, is required to fully substantiate the destinations of humpbacks whales travelling through New Zealand waters.

Effect of exploitation and recovery on Pacific migratory destinations

Commercial whaling including some illegal post-war whaling is estimated to have reduced the Area V humpback whale population to 500 individuals or less by the early sixties (Chittleborough, 1965; Clapham et al., 2009). Dawbin (1964) noted that the great decline in humpback numbers between 1959 and 1962 paralleled simultaneous decreases of humpback whales observed in many other South Pacific localities, such as the Chesterfields, Vanuatu and Fiji. Jackson et al. (2008) estimated that the humpback whale preexploitation abundance for eastern Australia and Oceania ranged from around 26,400-31,400 and 16,000-23,000 respectively. These results are similar to the most recent modelling exercise undertaken by the Scientific Committee who estimated pre-exploitation abundance at around 21,600– 29,000 (90% credibility interval) for Breeding Stock E(i) and 11,000–19,600 (90% credibility interval) for Breeding Stock O (IWC, In press).

The humpback population from the eastern Australian (E (i)) breeding grounds has increased over the last fifty years was independently estimated to be around 7,000–8,000 in 2004 (Noad *et al.*, 2011; Paton *et al.*, 2011). The IWC Scientific Committee estimated the 2012 population to be

14,700–18,000 (90% credibility interval) during the modelling exercise referred to above (IWC, In press).

In contrast population levels in Oceania are relatively low. An overall estimate of the humpback population in Oceania by 2004 was 3,827 (CV, 0.12) individuals, with 472 in New Caledonia (E (ii)) and 2,311 in Tonga (E (iii)) (South Pacific Whale Research Consortium *et al.*, 2006). The IWC Scientific Committee estimated the 2012 population to be 4,500–6,000 (90% credibility interval) during the modelling exercise referred to above (IWC, In press). However, it noted that the complexities of eastern Oceania with respect to stock structure and trend information required further investigation.

There is little evidence of humpback whale population recovery in Vanuatu, Fiji and Norfolk Island, and no evidence of recovery at the Chesterfields in the Coral Sea (Jackson *et al.*, 2008; South Pacific Whale Research Consortium *et al.*, 2006). Whilst numbers of humpback whales have been observed in New Zealand waters in recent years, no abundance estimate is available for the humpback whales migrating past New Zealand (Constantine *et al.*, 2006; Gibbs and Childerhouse, 2000).

Clapham and Zerbini (2006) have suggested that social aggregation among the surviving Oceania humpback whales (i.e. that whales that once went to now-depleted breeding grounds changed their migratory destination to eastern Australia) may provide an explanation of why the eastern Australian (E (i)) group has recorded relatively earlier and stronger population increase than has been seen in New Caledonia (E (ii)) and Tonga (E (iii)) and why little recovery has been observed in Fiji and no recovery observed in the Chesterfields (see Clapham and Zerbini, (2006) for a discussion of the humpback 'Social Aggregation' Hypothesis).

Further research

Accumulation and comparison of photo-identification data, together with genetic and satellite tagging data obtained across the breadth of the Area V feeding area, would greatly improve our understanding of the level and rate of intermingling among humpback whales from different breeding groups while in Antarctic waters. Data on individual humpback whales, passing through New Zealand waters to breeding grounds in eastern Australia and the western Pacific, offers the opportunity to document and quantify temporary and/or permanent immigration between existing breeding grounds and to monitor and assess recovery of humpback whales in formerly occupied breeding grounds in Oceania.

Conclusions

The data herein supports earlier research that, although low levels of intermingling occur between eastern Australia (E (i)) and Oceania west (E (ii)) breeding ground populations and, Oceania west (E (ii)) and Oceania east (E (iii) and F) breeding ground populations, these populations are discrete breeding populations.

Although based on a small sample size from New Zealand, the results presented here confirm that eastern Australian humpback whales are travelling through southern New Zealand waters en-route from Antarctic feeding areas.

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