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

WALLY FRANKLIN[1,2,3], TRISH FRANKLIN[1,2,3], NADINE GIBBS[3,4], SIMON CHILDERHOUSE[3,5], CLAIRE GARRIGUE[3,9], ROCHELLE CONSTANTINE[3,10], LYNDON BROOKS[1,8], DANIEL BURNS[1,3], DAVID PATON[3,8,11], MICHAEL POOLE[3,12], NAN HAUSER[1,3,13], MICHAEL DONOGHUE[3,14], KIRSTY RUSSELL[3,10], DAVID K. MATTILA[15], JOOKE ROBBINS[3,16], MEGAN ANDERSON[1,3,8], CARLOS OLAVARRÍA[3,10,17], JENNIFER JACKSON[3,10], MICHAEL NOAD[3,18], PETER HARRISON[1,3,8], PETER BAVERSTOCK[1,19], RUSSELL LEAPER[20], SCOTT BAKER[3,6,10] AND PHIL CLAPHAM[3,7]

Contact e-mail: wally.franklin@oceania.org.au

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

[1] *Southern Cross University Whale Research Centre, Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia.*
[2] *The Oceania Project, PO Box 646 Byron Bay, NSW 2481, Australia.*
[3] *South Pacific Whale Research Consortium, PO Box 3069, Avarua Rarotonga, Cook Islands.*
[4] *Department of Conservation. PO Box, 5086, Wellington, New Zealand.*
[5] *University of Otago, PO Box 56, Dunedin, New Zealand.*
[6] *Marine Mammal Institute, Oregon State University, 2030 SE Marine Science Dr, Newport, OR 97365, USA.*
[7] *U.S. National Marine Mammal Laboratory, Alaska Fisheries Science Centre, Seattle WA 98115, USA.*
[8] *Southern Cross University, PO Box 157, Lismore, NSW 2480, Australia.*
[9] *Opération Cétacés BP 12827 98802 Nouméa, New Caledonia.*
[10] *School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand.*
[11] *Blue Planet Marine, PO Box 5535 Kingston, ACT 2604 Australia.*
[12] *Marine Mammal Research BP698 98728 Maharepa, Moorea.*
[13] *Cook Islands Whale Research Takuvaine Valley PO Box 3069, Avarua Rarotonga, The Cook Islands.*
[14] *Department of Conservation, PO Box 10-420, Wellington, New Zealand.*
[15] *Hawaiian Islands Humpback Whale National Marine Sanctuary, 726 S. Kihei Road, Kihei, HI 96753 USA.*
[16] *Provincetown Center for Coastal Studies, 5 Holway Avenue, Provincetown, 02657 USA.*
[17] *Centro de Estudios del Cuaternario (CEQUA), Plaza Muños Gamero 1055, Punta Arenas, Chile.*
[18] *School of Veterinary Science, University of Queensland, Brisbane QLD 4072 Australia.*
[19] *Centre for Animal Conservation Genetics, Southern Cross University, P.O. Box 157, Lismore, NSW 2480, Australia.*
[20] *International Fund for Animal Welfare (IFAW), 87-90 Albert Embankment, London, SE1 7UD, UK.*

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 programme[21] 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 V[22] 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 photo-identification, 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 photo-identification, 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).

[22]The 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

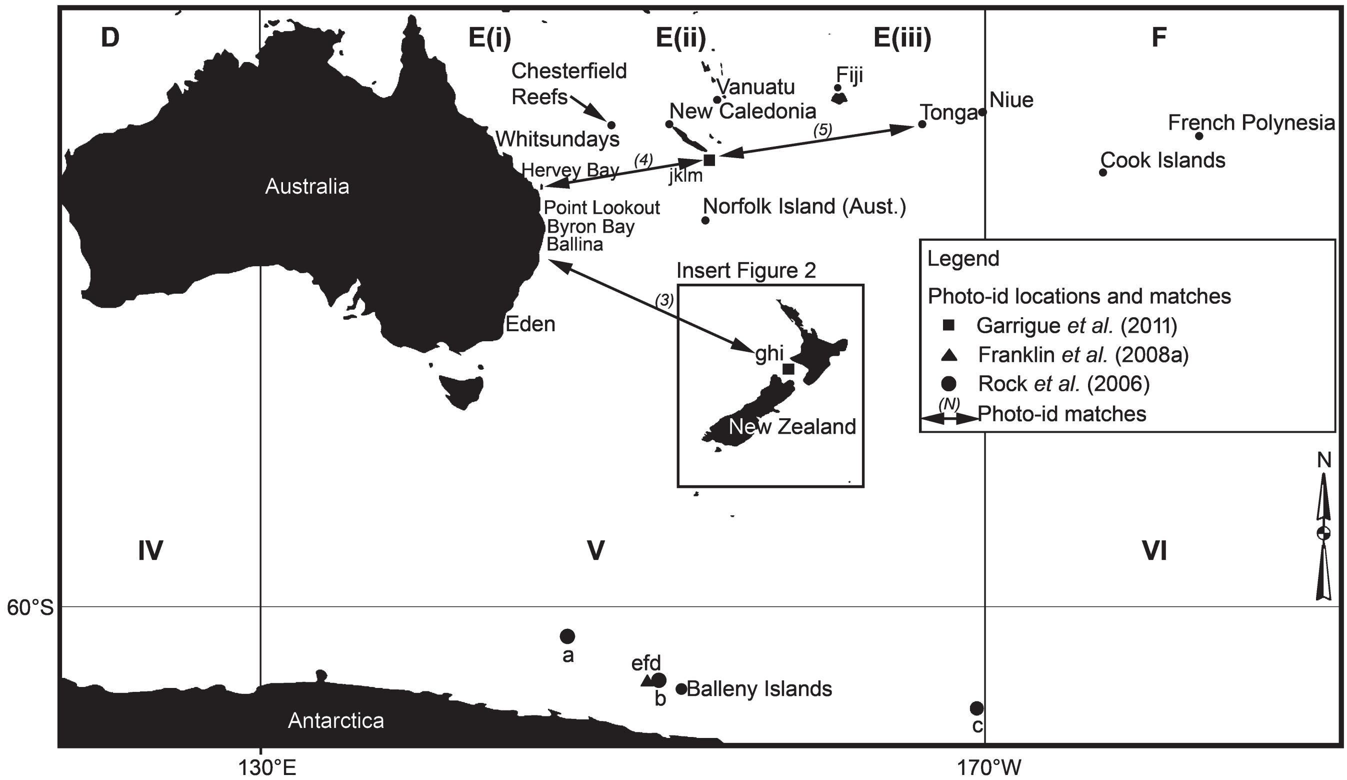

Fig. 1. Locations of the New Zealand (NZ), Eastern Australian (EA), Balleny Islands and Oceania photo-identification survey sites; Eastern Australia and Oceania breeding grounds (E (i), E (ii), E (iii), F); and Antarctic feeding areas IV, V and VI (IWC, 2006) and the photo-id matches reported between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

[1]The 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).
[2]Although 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.
[3]New Zealand is not considered a discrete population, however for the purposes of this analysis it was treated as such.

catalogues (POP), $m_{SITE\text{-}POP}$: 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 cross-table 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, $_{POP\text{-}SITE}$, may be derived from expected equality of proportions, $m_{POP\text{-}SITE}/n_{SITE} = n_{POP}/N_{POP}$, and calculated as $_{POP\text{-}SITE} = (n_{POP}*n_{SITE})/N_{POP}$. 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 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_{SITE}), the sizes of population catalogues (n_{POP},) the estimated 2004 population sizes (N_{POP}) and the numbers of matches between the sampling site catalogues and the population catalogues ($m_{POP\text{-}SITE}$), 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.

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

N_{POP}=estimated 2004 population size; n_{POP}=size of the population catalogue; n_{SITE}=size of the sample site catalogue; $m_{POP\text{-}SITE}$ =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})	13	166	513	166	13	13
Population catalogue (n_{POP})	1,315	1,315	1,315	513	166	513
Estimated population size (N_{POP})[1]	7,090	7,090	7,090	3366	472	3,366
Site-population matches ($m_{POP\text{-}SITE}$)	3	4	0	5	0	0

[1]Estimated 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, $p_{\text{NZ-OW}}$, 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. $p_{\text{NZ-OW}} = 4/166 = {}_{\text{POP-SITE}}/13$. 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

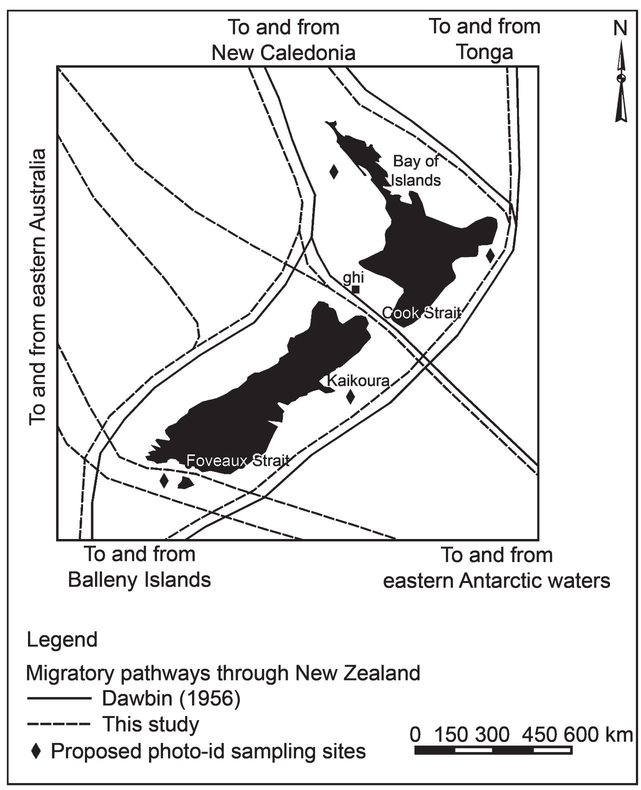

Fig. 2. The migratory pathways and migratory destinations described in (Dawbin, 1956) and the hypothesised migratory pathways and migratory destinations described in this study are shown in solid and broken lines respectively. The additional proposed photo-id sampling sites are shown as diamond shapes. 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 (ii)) 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 the 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 northeastern 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 pre-exploitation 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.

ACKNOWLEDGEMENTS

All authors acknowledge the remarkable contribution of Dr Bill Dawbin and Dr Graham Chittleborough to our understanding of Humpback Whales. We acknowledge Fond Pacifique for funding through Opération Cétacés and the South Pacific Whale Research Consortium for the project of matching the catalogues of east Australia and Oceania. The study of humpbacks undertaken in Oceania by the SPWRC is partly supported by the International Fund for Animal Welfare (IFAW). The long-term study of humpbacks in Hervey Bay being conducted by Trish and Wally Franklin is supported by The Oceania Project and in part by an Australian Research Council Linkage grant with the International Fund for Animal Welfare (IFAW) and the Southern Cross University Whale Research Centre (SCUWRC). We also thank participants in The Oceania Project's Internship program for their financial contribution and assistance to the Hervey Bay study. Research undertaken in Hervey Bay was conducted under research permits issued by the Queensland Parks and Wildlife Service (permit numbers MP2006/020 and WISP03749806). The research undertaken off Ballina and Byron Bay was funded by the Southern Cross University Whale Research Centre and conducted under Scientific Research Permits issued by the Department of the Environment, Water, Arts and Heritage under the EPBC Act 1999 (permit number E2001/0005) and the New South Whales National Parks and Wildlife Service (permit number S10403). We thank Greg Luker of Southern Cross University for providing assistance with figures. The Cook Strait Project acknowledges the Department of Conservation, Dolphin Watch Ecotours, Picton and WWF for their support. We thank John Calambokidis and two anonymous reviewers for their comments, which contributed to the manuscript.

REFERENCES

Anderson, M. and Brasseur, M. 2007. Genetic assessment of Group IV (Western Australia) and V (Eastern Australia) humpback whale population dynamics and migratory interchange. Report to the Department of the Environment, Water, Heritage and the Arts, GPO Box 787, Canberra ACT 2601 Australia.

Anderson, M., Steel, D., Franklin, W., Franklin, T., Paton, D., Burns, D., Harrison, P., Baverstock, P.R., Garrigue, C., Olavarria, C., Poole, M., Hauser, N., Constantine, R., Thiele, D., Clapham, P., Donoghue, M. and Baker, C.S. 2010. Microsatellite genotype matches of humpback whales from eastern Australia to Area V feeding and breeding grounds. Paper SC/62/SH7 presented to the IWC Scientific Committee, June 2010, Agadir, Morocco (unpublished). 11pp. [Paper available from the Office of this Journal].

Brown, S.G. 1978. Whale marking techniques. pp.71–80. In: Stonehouse, B. (eds). Animal Marking: Recognition Marking of Animals in Research. Macmillan Press Ltd, London. 257pp.

Chittleborough, R.G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshwater Res.* 16(1): 33–128.

Clapham, P., Mikhalev, Y., Franklin, W., Paton, D., Baker, C.S., Ivashchenko, Y.V. and Brownell Jr., R.L. 2009. Catches of humpback whales, *Megaptera novaeangliae,* by the Soviet Union and other nations in the Southern Ocean, 1947–1973. *Mar. Fish. Rev.* 71(1): 39–43.

Clapham, P. and Zerbini, A. 2006. Is social aggregation driving high rates of increase in some Southern Hemisphere humpback whale populations? Paper SC/58/SH3 presented to the IWC Scientific Committee, May 2006, St Kitts and Nevis, West Indies (unpublished). 12pp. [Paper available from the Office of this Journal].

Constantine, R., Russell, K., Gibbs, N., Childerhouse, S. and Baker, C.S. 2006. Photo-identification of humpback whales in New Zealand waters and their migratory connections to breeding grounds of Oceania. *Mar. Mammal Sci.* 23(3): 715–20.

Donovan, G.P. 1991. A review of IWC stock boundaries. Rep. int. Whal. Commn (special issue) 13: 39–68.

Dawbin, W.H. 1956. The migration of humpback whales which pass the New Zealand coast. *Trans. R. Soc. NZ* 84(1): 147–96.

Dawbin, W.H. 1959. New Zealand and South Pacific whale marking and recoveries to the end of 1958. *Norsk Hvalfangsttid.* 48(5): 213–38.

Dawbin, W.H. 1964. Movements of humpback whales marked in the southwest Pacific Ocean 1952 to 1962. *Norsk Hvalfangsttid.* 53(3): 68–78.

Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp.145–70. *In*: Norris, K.S. (eds). *Whales, Dolphins, and Porpoises*. University of California Press, Berkeley and Los Angeles. xv+789pp.

Dawbin, W.H. and Falla, R.A. 1949. A contribution to the study of the humpback whale based on observation at New Zealand shore stations. *Proc. Seventh Pac. Sci. Congr.* 4: 373–82.

Franklin, T., Franklin, W., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Ostermann, A., Leaper, R., Baker, S. and Clapham, P. 2008a. Migratory movements of humpback whales (*Megaptera novaeangliae*) between eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. 12pp. Paper SC/60/SH2 presented to the IWC Scientific Committee, June 2008, Santiago, Chile. 12pp.

Franklin, W., Franklin, T., Gibbs, N., Childerhouse, S., Garrigue, C., Constantine, R., Brooks, L., Burns, D., Paton, D., Poole, M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Anderson, M., Olavarría, C., Jackson, J., Noad, M., Harrison, P., Baverstock, P., Leaper, R., Baker, S. and Clapham, P. 2008b. Eastern Australia (E1 breeding grounds) may be a wintering destination for Area V humpback whales (*Megaptera novaeangliae*) migrating through New Zealand waters. Paper SC/60/SH3 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 13pp. [Paper available from the Office of this Journal].

Gales, N., Double, M.C., Robinson, S., Jenner, C., Jenner, M., King, E., Gedamke, J., Paton, D. and Raymond, B. 2009. Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. Paper SC/61/SH17 presented to the IWC Scientific Committee, June 2009, Madeira, Portugal (unpublished). 11pp. [Paper available from the Office of this Journal].

Garrigue, C., Aguayo, A., Amante-Helwig, V.L.U., Baker, C.S., Caballero, P., Clapham, P., Constantine, R., Denkinger, J., Donoghue, M., Florez-Gonzalez, L., Greaves, J., Hauser, N., Olavarria, C., Pairoa, C., Peckham, H. and Poole, M. 2002. Movements of humpback whales in Oceania, South Pacific. *J. Cetacean Res. Manage.* 4(3): 255–60.

Garrigue, C., Forestell, P., Greaves, J., Gill, P., Naessig, P. and Baker, C.S. 2000. Migratory movement of humpback whales (*Megaptera novaeangliae*) between New Caledonia, East Australia and New Zealand. *J. Cetacean Res. Manage.* 2(2): 101–10.

Garrigue, C., Franklin, T., Constantine, R., Russell, K., Burns, D., Poole, M.M., Paton, D., Hauser, N., Oremus, M., Childerhouse, S., Mattila, D.K., Gibbs, N., Franklin, W., Robbins, J., Clapham, P. and Baker, C.S. 2011. First assessment of interchange of humpback whales between Oceania and the east coast of Australia. *J. Cetacean Res. Manage.* (special issue 3): 269–74.

Garrigue, C., Olavarria, C., Baker, C.S., Steel, D., Dodemont, R., Constantine, R. and Russell, K. 2006. Demographic and genetic isolation of New Caledonia (E2) and Tonga (E3) breeding stocks. Paper SC/A06/HW19 presented to the IWC Workshop on Comprehensive Assessment of Southern Hemisphere Humpback Whales, Hobart, Tasmania, 3–7 April 2006 (unpublished). 10pp. [Paper available from the Office of this Journal].

Garrigue, C., Zerbini, A., Geyer, A., Heide-Jørgensen, M.P., Hanaoka, W. and Clapham, P. 2010. Movements of satellite-monitored humpback whales from New Caledonia. *J. Mammal.* 91(1): 109–15.

Gibbs, N. and Childerhouse, S. 2000. Humpback whales around New Zealand. *Conservation Advisory Science Notes* 287: 32pp. Department of Conservation. Wellington, NZ.

Hauser, N., Zerbini, A.N., Geyer, Y., Heide-Jorgensen, M.P. and Clapham, P.J. 2010. Movements of satellite-monitored humpback whales, *Megaptera novaeangliae*, from the Cook Islands. *Mar. Mammal Sci.* 26(3): 679–85.

International Whaling Commission. In press. Report of the Scientific Committee. *J. Cetacean Res. Manage*. (Suppl.) 16.

International Whaling Commission. 2006. Report of the Scientific Committee. Annex G. Report of the Sub-Committee on In-depth Assessment (IA). Appendix 4. Report of the working group on population modelling. *J. Cetacean Res. Manage*. (Suppl.) 8:148–49.

International Whaling Commission. 2011. Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere humpback whales, 4–7 April 2006, Hobart, Tasmania. J. Cetacean Res. Manage. (special issue 3):1–50.

Jackson, J., Zerbini, A., Clapham, P., Constantine, R., Garrigue, C., Hauser, N., Poole, M. and Baker, C.S. 2008. Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. Paper SC/60/SH14 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 12pp. [Paper available from the Office of this Journal].

Kaufman, G.D., Osmond, M.G., Ward, A.J. and Forestell, P.H. 1990. Photographic documentation of the migratory movement of a humpback whale (*Megaptera novaeangliae*) between East Australia and Area V. *Rep. int. Whal. Commn (special issue)* 12: 265–67.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197–300.

Noad, M.J., Cato, D.H., Bryden, M.M., Jenner, M.N. and Jenner, K.C.S. 2000. Cultural revolution in whale songs. *Nature* 408: 537.

Noad, M.J., Dunlop, R.A., Paton, D. and Cato, D.H. 2011. Absolute and relative abundance estimates of Australian east coast humpback whales (*Megaptera novaeangliae*). *J. Cetacean Res. Manage.* (special issue 3): 243–52.

Olavarria, C., Anderson, M., Paton, D.A., Burns, D., Brasseur, M., Garrigue, C., Hauser, N., Poole, M., Caballero, S., Flórez-Gonzalez, L. and Baker, C.S. 2006a. Eastern Australian humpback whale genetic diversity and their relationship with Breeding Stocks D, E, F and G. Paper SC/58/SH25 presented to the IWC Scientific Committee, May 2006, St Kitts and Nevis, West Indies (unpublished). 6pp. [Paper available from the Office of this Journal].

Olavarria, C., Childerhouse, S., Gibbs, N. and Baker, C.S. 2006b. Contemporary genetic diversity of New Zealand humpback whales and their genetic relationship with Breeding Stocks D, E, F and G. Paper SC/A06/HW31 presented to the IWC Workshop on Comprehensive Assessment of Southern Hemisphere Humpback Whales, Hobart, Tasmania, 3–7 April 2006 (unpublished). 8pp. [Paper available from the Office of this Journal].

Olavarria, C., Baker, C.S., Garrigue, C., Poole, M., Hauser, N., Caballero, S., Florez-Gonzalez, L., Brasseur, M., Bannister, J., Capella, J., Clapham, P., Dodemont, R., Donoghue, M., Jenner, C., Jenner, M.N., Moro, D., Oremus, M., Paton, D. and Russell, K. 2007. Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Mar. Ecol. Prog. Ser.* 330: 257–68. [Author: *c.olavarria@auckland.ac.nz*].

Paton, D.A., Brookes, L., Burns, D., Franklin, T., Franklin, W., Harrison, P. and Baverstock, P. 2011. Abundance of east coast Australian humpback whales (*Megaptera novaeangliae*) in 2005 estimated using multi-point sampling and capture-recapture analysis. *J. Cetacean Res. Manage.* (special issue 3): 253–60.

Rayner, G.W. 1940. Whale marking: progress and results to December 1939. *Discovery Rep.* 19: 245–84.

Rock, J., Pastene, L.A., Kaufman, G., Forestell, P., Matsuoka, K. and Allen, J. 2006. A note on East Australia Group V Stock humpback whale movement between feeding and breeding areas based on photo-identification. *J. Cetacean Res. Manage.* 8(3): 301–05.

South Pacific Whale Research Consortium, Baker, C.S., Garrigue, C., Constantine, R., Madon, B., Poole, M., Hauser, N., Clapham, P., Donoghue, M., Russell, K., O'Callahan, T., Paton, D. and Mattila, D. 2006. Abundance of humpback whales in Oceania (South Pacific), 1999 to 2004. Paper SC/A06/HW51 presented to the IWC Workshop on Comprehensive Assessment of Southern Hemisphere Humpback Whales, Hobart, Tasmania, 3–7 April 2006. 10pp. [Paper available from the Officeof this Journal].

South Pacific Whale Research Consortium, Garrigue, C., Baker, C.S., Constantine, R., Poole, M., Hauser, N., Clapham, P., Donoghue, M., Russell, K., Paton, D., Mattila, D.K. and Robbins, J. 2007. Interchange of humpback whales in Oceania (South Pacific) 1999 to 2004 (revised SC/A06/HW55, March 2007). Paper SC/59/SH14 presented to the IWC Scientific Committee, May 2007, Anchorage, USA (unpublished). 10pp. [Paper available from the Office of this Journal].

Steel, D., Garrigue, C., Poole, M., Hauser, N., Olavarría, C., Flórez-González, L., Constantine, R., Caballero, S., Thiele, D., Paton, D., Clapham, P., Donoghue, M. and Baker, C.S. 2008. Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas based on genotye matching. Paper SC/60/SH13 presented to the IWC Scientific Committee, June 2008, Santiago, Chile (unpublished). 9pp. [Paper available from the Office of this Journal].