Discovery mark tagging provided the first evidence of linkages between Eastern Australian and Oceania Humpback whale breeding grounds and the Antarctic Area V feeding areas. Early investigation of movements of humpback whales in the Western Pacific led to the view that the Balleny Islands and the Ross Sea were the summer destination for humpbacks from Eastern Australia and the Oceania breeding grounds. Recent photo-identification studies provided further evidence of low levels of migratory interchange and complex linkages within Oceania and between Eastern Australia and Oceania. We report here the migratory movement of three humpback whales (Megaptera novaeangliae) between Eastern Australia (El breeding grounds) and the Area V Antarctic feeding area in the vicinity of the Balleny Islands. Using photo-identification techniques, comparisons between a Balleny Island humpback whale catalogue (n = 11 individuals), and existing humpback whale catalogues from Eastern Australia (n = 3120 individuals) and Oceania (n = 725) individuals), yielded three matches to Hervey Bay, Byron Bay and Ballina in Eastern Australia and no matches to Oceania. Only three previous individual photo-identification matches have been reported between Eastern Australia (El breeding grounds) and Antarctic Area V feeding areas in the vicinity of the Balleny Islands and the Ross Sea. Only one genotype match has been reported between Antarctic Area V feeding areas and Oceania breeding grounds. An analysis of the frequencies of whales seen and not seen in the Balleny Islands, Oceania and Eastern Australia, relative to the expected frequencies, based on the estimated population sizes.
INTRODUCTION

Discovery mark tagging provided the first evidence of migratory interchange of humpback whales between the breeding grounds of Eastern Australia and Oceania, and also linkages between the feeding and breeding areas within Areas IV, V and VI (Chittleborough, 1959; Dawbin, 1964; Paton and Clapham, 2006; IWC, 2006). Investigation of migratory movement of humpback whales in the Western Pacific led Dawbin (1949, 1956) to consider that the Balleny Islands and the Ross Sea were the summer destination for humpback whales that travel along the coasts of Eastern Australia and other parts of the Pacific and through New Zealand waters. Further evidence of the complexity of migratory interactions amongst Oceania breeding grounds (including New Caledonia, Vanuatu, Tonga, Samoa, American Samoa, Cook Islands, Fiji, Niue and French Polynesia) and the New Zealand and Norfolk Island migratory corridors was obtained from long term photo-identification studies of humpbacks undertaken by members of the South Pacific Whale Research Consortium (SPWRC) and the Southern Cross University Whale Research Centre (Abernethy et al. 1992; Hauser et al. 2000; Garrigue et al. 2002; Garrigue et al. 2007A; Poole, 2002; Poole, 2006; Gibbs and Childerhouse, 2004; Donoghue, 2008; Franklin et al. 2008).

Recent photo-identification matching between Eastern Australian fluke catalogues (i.e. Hervey Bay and Byron Bay) and ten regional Oceania fluke catalogues for the period 1999 to 2004 (Garrigue et al. 2007B), provides further evidence of the low levels of migratory interchange and illustrates the complexity of linkages between Eastern Australia and Oceania (Donoghue, 2008; Franklin et al. 2008). To date, only three individual photo-identification matches (Fig 1) have been reported between humpback whales that migrate along the Eastern Australian (EI breeding group) coast and Antarctic Area V feeding areas in the vicinity of the Balleny Islands and the Ross Sea (Kaufman et al. 1990; Rock et al. 2006). No photo-identification matches have been reported between any of the Oceania breeding grounds and Area V or Area VI Antarctic feeding areas. However, one recent genotype match was reported between New Caledonia and the Antarctic Area V feeding area, and a small number of genotype matches have been reported between Oceania breeding grounds and Antarctic Area I and VI feeding areas (Steel et al. 2008).

The Balleny Islands are located in the Ross Sea at 67°S, 163°E, and are included within the Southern Ocean Whale Sanctuary that was declared at the 46th meeting the International Whaling Commission (IWC) in 1994 (Fig 1).

Here we use photo-identification matches to document the migratory movements of individual humpback whales between the Balleny Islands (Antarctic Area V feeding area) and Hervey Bay, Byron Bay and Ballina on the eastern coast of Australia (EI breeding grounds). The data are used to investigate the summer feeding areas of Eastern Australian Humpback whales.

METHODS

Field data collection

Observations of humpback whales were undertaken in close proximity to the Balleny Islands (67°S, 163°E), from the 14th to the 25th February 2006 during a marine biodiversity research cruise organised...
by the New Zealand Ministry of Fisheries. Sightings of humpback whales ranged between latitudes 66°10’26°S and 67°34’77°S and longitudes 162°20’00°E and 164°49’66°E. The Balleny Islands (BI) fluke catalogue consists of n = 11 individuals.

Vessel-based photo-identification of humpback whales in Hervey Bay, Queensland (25°S, 153°E) was undertaken between 1999 and 2005 as part of a long-term study of the behaviour and ecology of humpbacks by two of the authors (TF and WF). The reconciled Hervey Bay (HB) fluke catalogue for 1999-2005 consists of n = 1556 unique individuals. Photo-identification studies of humpback whales were undertaken on their northern migration at Byron Bay (BB) (28°38 S, 153°38 E) and southern migration at Ballina (BA) (28°52 S, 153°36 E). Fluke catalogues from these studies comprise of 916 fluke photographs (BB, 1999-2005) and 648 fluke photographs (BA, 2003-2005), respectively. The combined and reconciled Eastern Australian fluke catalogues consists of n = 3120 individuals.

Dedicated surveys of humpback whales in Oceania were conducted between 1999 and 2004 during the austral winter in four primary sites: New Caledonia; Tonga; the Cook Islands; and French Polynesia. Surveys were conducted in only one or two seasons in other South Pacific sites: Vanuatu, Fiji, Samoa, and Niue. Surveys at American Samoa began in 2003. New Zealand surveys began in 2004 and surveys at Norfolk Island began in 2003. The reconciled Oceania Fluke Catalogue for 1999-2004 consists of n = 735 individuals made up of Tonga, 282 individuals; New Caledonia, 160 individuals; French Polynesia, 159 individuals; New Zealand, 41 individuals; Cook Islands, 36 individuals; American Samoa, 31 individuals; Vanuatu, Niue, Samoa and Fiji. 11 individuals and Norfolk Island, 5 individuals. The reconciled Oceania catalogue was used for this matching, as it is the only period for which full reconciliation of each regional catalogue has been completed. The locations of the photo-identification research sites are shown in Fig 1.

Photo-identification comparisons

The methods used to compare the Oceania and Eastern Australian catalogues, both within and between regions, is fully reported in Garrigue et al. 2007A and Garrigue et al. 2007B. Comparisons of each of the 11 individual Balleny flukes were made to each of the 3120 individuals in the combined Eastern Australian Fluke Catalogues, and to each of the 735 individuals in the combined Oceania Fluke Catalogues.

Statistical analysis

Two analyses were conducted, one investigating the matches found between the Balleny Islands (BI) and Eastern Australian (EA) catalogues, and one investigating the lack of matches between the Balleny Islands and Oceania (OC) catalogues.

In the Eastern Australia-Balleny Islands case, if the whales sighted near the Balleny Islands were members of the Eastern Australian population, the proportion of the BI catalogue expected to be matched to the EA catalogue would be equal to the proportion of the Eastern Australian population that were in the EA catalogue and alive and available for capture near the Balleny Islands. For example, if one third of the Eastern Australian population were in the EA catalogue and alive at the time the Balleny Islands was sampled, we would expect about a third of the BI catalogue to be matched to the EA catalogue. Alternatively, if the whales sighted near the Balleny Islands were not members of the Eastern Australian population, the proportion of the BI catalogue we would expect to be matched to the EA catalogue would be less than the proportion of the Eastern Australian population alive and in the EA catalogue.
The same rationale can be applied in the Oceania Balleny Islands case. In each case, this rationale provides a means of estimating the number of matches likely to occur under the single population and separate populations hypotheses. Given this rationale and the estimates described below, each of the analyses may be based on a test of association in a 2x2 cross-table of frequencies constructed as 'not seen' or 'seen' near the Balleny Islands by 'not seen' or 'seen' in Eastern Australia / Oceania (Table 1 a and b).

Table 1

<table>
<thead>
<tr>
<th>Scheme for the cross-tables</th>
<th>Eastern Australia - Balleny Islands matches</th>
<th>Oceania - Balleny Islands matches</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Eastern Australia - Balleny Islands matches</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern Australia</td>
<td>Not seen</td>
<td>Seen</td>
</tr>
<tr>
<td>Balleny Islands</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Not seen</td>
<td>$N_{EA} - n_{BI} - n_{EA} + m_{EA-BI}$</td>
<td>$n_{EA} - m_{EA-BI}$</td>
</tr>
<tr>
<td>Seen</td>
<td>$n_{BI} - m_{EA-BI}$</td>
<td>$m_{EA-BI}$</td>
</tr>
<tr>
<td>Total</td>
<td>$N_{EA} - n_{EA}$</td>
<td>$n_{EA}$</td>
</tr>
</tbody>
</table>

$N_{EA} = $ Total Eastern Australian (EA) 2006 population estimate

$n_{EA} = $ Estimate of number of living whales in 2006 from the EA catalogues

$m_{EA-BI} = $ Number of whales matched between EA and Balleny Islands

$n_{BI} = $ Number of whales identified at Balleny Islands

(b) Oceania - Balleny Islands matches

Oceania

<table>
<thead>
<tr>
<th>Balleny Islands</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>$N_{OC} - n_{BI} - n_{OC} + m_{OC-BI}$</td>
<td>$n_{OC} - m_{OC-BI}$</td>
<td>$N_{OC} - n_{BI}$</td>
</tr>
<tr>
<td>Seen</td>
<td>$n_{BI} - m_{OC-BI}$</td>
<td>$m_{OC-BI}$</td>
<td>$n_{BI}$</td>
</tr>
<tr>
<td>Total</td>
<td>$N_{OC} - n_{OC}$</td>
<td>$n_{OC}$</td>
<td>$N_{OC}$</td>
</tr>
</tbody>
</table>

$N_{OC} = $ Total Oceania (OC) 2006 population estimate

$n_{OC} = $ Estimate of number of living whales in 2006 from the OC catalogues

$m_{OC-BI} = $ Number of whales matched between OC and Balleny Islands

$n_{BI} = $ Number of whales identified at Balleny Islands

Given these data and estimates, the expected numbers of matches, $m_{EA-BI}hat$ and $m_{OC-BI}hat$, may be derived from the equal proportions rationale presented above, $m_{EA-BI}hat = (n_{EA} \cdot n_{BI}) / N_{EA}$ and $m_{OC-BI}hat = (n_{OC} \cdot n_{BI}) / N_{OC}$ respectively. 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-Peterson estimator, $Nhat = (n_1 \cdot n_2) / m_2$. 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 corresponds to the single population case, and the alternative hypothesis to the relatively separate populations case. 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 fewer (and never more) 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 analysis required estimates of the Eastern Australian and Oceania populations (NeA, Noc) for 2006 and estimates of the number of individuals in the EA and OC catalogues that were alive in 2006 and potentially available for capture near the Balleny Islands (nEA, nOC). Our estimate of the Eastern Australian population in 2006 was based on the Noad et al. (2005) estimate of 7090 in 2004 with an expected rate of increase of 10.6%. Our estimate of the number of individuals in the EA catalogue that were alive in 2006 and potentially available for capture near the Balleny Islands was based on the number of individuals collected into the catalogue between 1999 and 2005 with an expected mortality rate of 4% per annum (Clapham et al. 2001). Our estimate of the Oceania population in 2006 was based on the Baker et al. (2006) estimate of 3827 between 1999 and 2004. Our estimate of the number of individuals in the OC catalogue that were alive in 2006 and potentially available for capture near the Balleny Islands was based on the number of individuals collected into the catalogue between 1999 and 2004 with an assumed mortality rate (= birth rate) of 4% per annum.

Few data are available from the Balleny Islands and therefore the analysis was intended to be indicative rather than conclusive. As the data are estimates, we calculated p-values for variation of ±10% in the estimated numbers of whales in the EA and OC catalogues that were alive and available for capture near the Balleny Islands.

RESULTS

Comparison of the Balleny Islands Catalogue to the Eastern Australian Catalogue found three matches of individual whales, whereas no matches were found from a comparison of the Balleny Islands Catalogue to the Oceania Catalogues. One of the individual whales sighted in the Balleny Islands was sighted in Ballina three years earlier and two of the individual whales sighted in the Balleny Islands were sighted in both Byron Bay and Hervey Bay but in different years (Fig. 2).

Eastern Australia - Balleny Islands matches

Assuming a 10.6% annual increase from 7090 in 2004 yielded an estimated Eastern Australian population in 2006 of 8673 whales.

The 3120 individuals recorded in the EA catalogue between 1999 and 2005 were assumed to have been captured at a constant rate of 446 whales per annum. Application of an estimated mortality rate of 4% per annum yielded an estimated 2772 whales in the catalogue that were alive and available for capture near the Balleny islands in early 2006.

Table 2 reports the frequencies of whales ‘not seen’ and ‘seen’ near the Balleny Islands by ‘not seen’ and ‘seen’ in Eastern Australia based on these estimates together with the size of the Balleny Islands catalogue (n = 11) and the number of Balleny Islands to Eastern Australia matches (n = 3). The expected frequencies shown there were derived on the assumption of independence corresponding to an hypothesis that the whales seen in both places were members of the same population.
Table 2

Observed and expected frequencies of whales *not seen* and *seen* near the Balleny Islands by *not seen* and *seen* in Eastern Australia.

<table>
<thead>
<tr>
<th>Balleny Islands</th>
<th>Frequency</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>Observed</td>
<td>5893</td>
<td>2769</td>
<td>8662</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>5893.5</td>
<td>2768.5</td>
<td>8662</td>
</tr>
<tr>
<td>Seen</td>
<td>Observed</td>
<td>8</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>7.5</td>
<td>3.5</td>
<td>11</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>5901</td>
<td>2772</td>
<td>8673</td>
</tr>
</tbody>
</table>

The one-tailed p-value from Fisher’s exact test for the data in Table 2 was 0.512 indicating no evidence of dependency. Indeed, the observed and expected frequencies could not have been closer with 3 (or 4) whales seen at both sites. Thus there was no evidence to reject the null hypothesis that the whales seen near the Balleny Islands were from the Eastern Australian population.

By way of context for this result, the null hypothesis (at \( p < 0.05 \)) would have been rejected were no matches to have been found (\( p = 0.014 \)), but not if as few as one match had been found (\( p = 0.089 \)). Alternatively, if 3 matches were to have been found then the number of Balleny Islands flukes would have had to exceed 21 for the null hypothesis to have been rejected (for 22 Balleny Islands flukes, \( p = 0.046 \)).

With a 10% lower estimate of the number of whales alive and in the EA catalogue, the expected number of matches was 3.1 and the p-value was 0.614; with 10% higher estimate, the expected number of matches was 3.8 and the p-value was 0.431.

(b) Oceania - Balleny Islands matches

It was assumed that there was no increase in the Oceania population from the 2004 estimate of 3827 whales (Baker et al. 2006).

The 735 individuals recorded in the Oceania catalogue between 1999 and 2004 were assumed to have been captured at a constant rate of 122.5 whales per annum. Application of an estimated mortality rate of 4% per annum yielded an estimated 639 whales in the Oceania catalogue that were alive and available for capture near the Balleny islands in early 2006.

Table 3 reports the frequencies of whales ‘*not seen*’ and ‘*seen*’ near the Balleny Islands by ‘*not seen*’ and ‘*seen*’ in Oceania based on these estimates together with the size of the Balleny Islands catalogue (\( n = 11 \)) and the number of Balleny Islands to Pacific matches (\( n = 0 \)). The expected frequencies shown there were derived on the assumption of independence corresponding to an hypothesis that the whales seen in both places were members of the same population.
Table 3
Observed and expected frequencies of whales not seen and seen near the Balleny Islands by not seen and seen in Oceania.

<table>
<thead>
<tr>
<th>Oceania</th>
<th>Frequency</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balleny Islands</td>
<td>Observed</td>
<td>3177</td>
<td>639</td>
<td>3816</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>3178.8</td>
<td>637.2</td>
<td>3816</td>
</tr>
<tr>
<td>Seen</td>
<td>Observed</td>
<td>11</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>9.2</td>
<td>1.8</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td>3188</td>
<td>639</td>
<td>3727</td>
</tr>
</tbody>
</table>

The one-tailed p-value from Fisher's exact test for the data in Table 3 was 0.134. Thus, although the data provide weak evidence to reject the null hypothesis that the whales seen near the Balleny Islands were members of the Oceania population, the samples were not large enough to provide a level of significance sufficient to conclude that they were not.

With no matches being found, the null hypothesis (at p < 0.05) would have been rejected and the alternative hypothesis of two separate populations accepted only if there were at least 900 whales in the OC catalogue that were alive and available for capture near the Balleny islands in early 2006.

With a 10% lower estimate of the number of whales alive and in the OC catalogue, the expected number of matches was 1.7 and the p-value was 0.166; with 10% higher estimate, the expected number of matches was 2.0 and the p-value was 0.107.

DISCUSSION

Only six photo-identification matches have been reported between the Eastern Australia (E1 breeding grounds) and Southern Ocean Antarctic Area V feeding areas. The three matches reported here, between the Balleny Islands and Hervey Bay, Byron Bay and Ballina, and the three previously reported matches in Rock et al. (2006). All six individual humpbacks photographed in the Area V feeding area and/or around the Balleny Islands show frequent, long-term site-fidelity to either the Eastern Australian migratory corridor utilised by the Eastern Australian (E1) breeding group or to locations within or near the putative terminus of the Eastern Australian (E1) breeding group within the Great Barrier Reef lagoon (Kaufman et al. 1990; Rock et al. 2006, Trish Franklin unpublished data), (Fig. 1 and Fig. 2).

While based on limited data from the Balleny Islands, our results are consistent with the hypothesis that the whales seen near the Balleny Islands were members of the population that migrates up the east coast of Australia. It would have been necessary, given the present sizes of the catalogues, to have found no matches between the Balleny Islands and the Eastern Australian catalogues, or given the 3 matches we did find, for the Balleny Islands catalogue to have exceeded 21 individuals to reject this hypothesis.

While we did find weak evidence against the hypothesis that the whales seen near the Balleny Islands were members of the population that migrates into Oceania, there were insufficient data to confidently
conclude that they were not members of that population. Given that no matches were found between the Balleny Islands and Oceania catalogues, the null hypothesis (at p = 0.05) would have been rejected in favour of the two separate populations hypothesis only if there had been at least 900 whales in the Oceania catalogue that were alive and available for capture near the Balleny Islands in early 2006.

Previous research (Olavarria et al. 2007) has concluded that the Eastern Australian and Oceania humpback whale populations are relatively separate, although some migratory interchange has been observed (Garrigue et al. 2007A; Franklin et al. 2008). Franklin et al. (2008) suggest that humpback whales with site-fidelity to Eastern Australia may use the New Zealand migratory corridor to the south of the South Island and or pass through the Foveaux Straits or Cook Straits when travelling to and from the Antarctic Area V feeding areas in the vicinity of the Balleny Islands or the Ross Sea.

If we assume that the data presented here indicate that the whales seen both in Eastern Australia and near the Balleny Islands were very likely to have been members of the same population, then the whales observed near the Balleny Islands were unlikely to also be members of the Oceania population. While the finding of no matches between the Oceania and Balleny Islands catalogues is consistent with this argument, the small catalogues sizes make it difficult to completely rule out some potential interaction with Oceania. Given the recognized differences between Eastern Australian and Oceania breeding stocks, the most parsimonious explanation is that the individuals at the Balleny Islands are likely to be part of the Eastern Australian population based on the limited data available from the Balleny Islands. Consequently further collection of humpback whale photo-identification fluke data, either in the vicinity of the Balleny Islands, the Ross Sea and or from across the Area V feeding areas, will be important in clarifying the migratory linkages between Oceania and Eastern Australian breeding grounds.

Collection of photo-identification data on individual humpbacks in Antarctic feeding areas and systematic comparison with established and growing fluke catalogues from the migratory corridors and tropical breeding grounds can significantly add to our understanding of the migratory movement of individual humpbacks between and within Southern Hemisphere feeding areas, breeding grounds and migratory corridors.

Long-term photo-identification of individual humpbacks combined with genetic analysis and satellite-tagging offer an effective and non-lethal means to provide data to address questions on the biology, behaviour, abundance and ecology of Southern Ocean humpback whale populations.

ACKNOWLEDGMENTS

We acknowledge Fond Pacifique for funding through Opération Cétacés and the South Pacific Whale Research Consortium 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). Research undertaken in Hervey Bay was conducted under research permits issued by the Queensland Parks and Wildlife Service (permit numbers MP2006/020 and WISP034-9806). 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 the New Zealand Ministry of Fisheries for providing access to the Balleny Islands data. The Department of Conservation, Dolphin Watch Ecotours and WWF provided support for the New Zealand project. We thank Greg Luker of Southern Cross University for providing Figure 1. The authors also thank Emeritus Professor Peter Baverstock for his valued comments.
LITERATURE CITED


Figure 1. Locations of the Balleny Islands; the Eastern Australian and Oceania photo-identification survey sites; Eastern Australia and Oceania breeding grounds (E1, E2, E3, F); Antarctic feeding areas IV, V, VI and I (IWC, 2006). The symbols marked (a), (b) and (c) show the location of individual whales reported in Rock et al. (2006) and the symbols marked (d), (e) and (f) show the location of the matches reported herein. Whale (a) was sighted at Point Lookout and Eden; whale (b) was sighted in the Whitsundays, Hervey Bay and Eden; whale (c) in Hervey Bay and Eden (Rock et al. 2006). Whale (d) was sighted in Ballina; whales (e) and (f) were sighted in both Byron Bay and Hervey Bay but in different years (see photo-id details in Figure 2).
Figure 2: Photographs and dates of the confirmed individual photo-identification matches between the Balleny Islands (BI), Hervey Bay (HB), Byron Bay (BB) and Ballina (BA). Left column: Individual e in Fig. 1; seen in BB, HB and BI. Central column: Individual f in Fig. 1; seen in BB, HB and BI. Right column: Individual d in Fig. 1; seen in BA and BI.

Photo-identification data:
Hervey Bay (HB), Trish Franklin;
Balleny Island (BI), Franz Smith;
Byron Bay (BB), Dave Paton & Daniel Burns;
Ballina (BA), Daniel Burns.