Eastern Australia (El breeding grounds) may be a wintering destination for Area V Humpback Whales (Megaptera novaeangliae) migrating through New Zealand waters.

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ABSTRACT
Investigation of the migratory movement of humpback whales past New Zealand in the 1950s and early 1960s suggested that the primary factor influencing the migratory flow past New Zealand was behaviour associated with breeding and feeding. To the north humpback whales gathered in concentrated breeding assemblages, along the Great Barrier Reef, Australia and nearby islands of the Western Pacific, at locations with suitable coastal conditions. To the south humpback whales dispersed widely across the Antarctic Area V feeding areas. Discovery Tag marks provided the first evidence of linkages between Eastern Australia, New Zealand and Oceania and Antarctic Area V feeding areas and also revealed low levels of intermingling of individual humpbacks between isolated tropical breeding grounds in Western Australia, Eastern Australia and Oceania. A simultaneous, near total collapse of the Eastern Australian, Norfolk Island, New Zealand and Oceania stocks occurred in the early 1960's as a result of commercial whaling, particularly the illegal whaling conducted by the Soviets in the Area V feeding areas. Recent photo-identification and genetic studies have identified at least 5 discrete breeding sub-populations in Australia and Oceania; Western Australia (E1), Eastern Australia (E2), Tonga (E3) and Cook Island's and French Polynesia (F). Also evident are low levels of intermingling amongst breeding sub-populations consistent with the degree of genetic differentiation. Photo-identification has confirmed linkages between Antarctic Area V feeding areas and Eastern Australia and one genotype match has been reported between Antarctic Area V feeding areas and Oceania breeding grounds. Recent abundance estimates show steady increases of the Eastern Australian population, some recovery in the New Caledonia and Tonga population with little evidence of recovery at other known Oceania breeding areas and in New Zealand. Studies to date have provided no conclusive evidence of the migratory destination of the New Zealand population traveling from Antarctic Area V feeding areas to tropical breeding grounds. Here we use recent photo-identification data to investigate and discuss the migratory destination of humpback whales traveling through New Zealand waters and suggest the hypothesis that humpbacks with site fidelity to Eastern Australia may migrate past the South Island of New Zealand including through the Cook Strait and Foveaux Strait.
INTRODUCTION

A comprehensive investigation humpback whales (*Megaptera novaeangliae*) using the New Zealand migratory corridor of was undertaken during the 1950's (Dawbin and Falla 1949, Dawbin 1956, Dawbin 1966). Northbound humpbacks traveling from Antarctic feeding grounds approached New Zealand from various directions suggesting widespread lateral dispersion whilst in the Antarctic feeding areas. The northward migrating streams followed three main pathways through New Zealand waters. 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, Dawbin 1966).

Humpbacks migrating southbound, from tropical breeding grounds, approached New Zealand from the north in highly focused streams. The major proportion of the migrating stream 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 Antarctica. Some passed around the northeastern tip of the North Island, and a small proportion passed through the Cook Strait (Dawbin 1956, Dawbin 1966).

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 Antarctica and the location of breeding and mating grounds in Eastern Australia and the islands of the Western Pacific further to the east (Dawbin and Falla 1949, Dawbin 1956, 1964, 1966).

Initially Dawbin considered the breeding ground destinations of humpback whales migrating from feeding Area V 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 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 humpbacks 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 humpbacks (Macintosh 1942, Chittleborough 1965, Dawbin 1964, 1966). The Discovery Mark tagging programs provided the first direct evidence of linkages between polar feeding areas and temperate breeding grounds and intermingling amongst discrete breeding groups (Ravner 1940, Macintosh 1942, Dawbin 1964, 1966, Chittleborough 1965). This evidence supported the hypothesis that Western Australia, Eastern Australia and Oceania were discrete breeding areas with little interchange among individuals and no evidence for permanent exchange of individuals (Dawbin 1964, Chittleborough 1965). Dawbin reported links between Eastern Australia and the Antarctica Area V 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).

Between 1952 and 1962 the total reported catches of humpback whales off Eastern Australia were 7,423 and off Norfolk Island/New Zealand were 3,039. Total post-war catches in the two regions were 15,577 humpbacks (Clapham et al. 2005). Overall 38,146 humpbacks were taken in Area V between 1946 and 1973, with illegal unreported Soviet catches accounting for 22,569 humpbacks, the majority taken by Soviet whalers between 1959 and 1963 (Clapham et al. 2005). The only population estimate of Area V humpbacks available at the time, based on historic sightings data, was considered to be approximately 10,000 individuals (Chittleborough 1965).

Dawbin (1964) reported the total collapse of shore-based whaling off Eastern Australia and Norfolk Island/New Zealand by 1962 and noted that the great decline in humpback numbers between 1959 and 1962 paralleled simultaneous decreases of humpbacks observed in many other South Pacific localities. Chittleborough (1965) calculated that the catchable stock of the Area V humpback population left in 1963, when the IWC prohibited commercial whaling of humpback whales in Antarctica, may have been close to 500 individuals or less.

The Eastern Australian (E1 breeding grounds) humpback population has shown steady increase over the last fifty years and by 2004-2005 was independently estimated to be around 7,000 to 8,000 (Noad et al. 2005, Paton et al. 2006). By comparison population recovery levels in Oceania are relatively low. An overall estimate of the humpback population in Oceania by 2004 was 3827 (CV, 0.12) individuals, with 472 in New Caledonia (E2) and 2311 in Tonga (E3) (Baker et al. 2006). 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 (Baker et al. 2006, Jackson et al. 2006). Low numbers of humpbacks have been observed in New Zealand waters in recent years and no abundance estimate is available for the humpback whales migrating past New Zealand (Gibbs and Childerhouse 2000, Constantine et al. 2007).

Members of the South Pacific Whale Research Consortium and the Southern Cross University Whale Research Centre have recently undertaken photo-identification and genetic studies on humpback whales in the Pacific basin and Western Australia. The studies have demonstrated that Western Australia (breeding area D) and Eastern Australia (breeding area E1) are discrete breeding stocks (Olavarria et al. 2006a, 2006b, Anderson and Brasseur 2007). The data also indicated that the former IWC breeding Area E, which included Eastern Australia, New Caledonia and Tonga, should be considered to be three discrete breeding sub-stocks: Eastern Australia (E1), New Caledonia (E2) and Tonga (E3) (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, 2007b) and within Oceania (Garrigue et al. 2002, 2007a) are consistent with the reported levels of genetic differentiation between breeding Areas E1, E2 and E3. Similarly acoustic evidence supports low levels of intermingling between breeding Area D and E1 (Noad et al. 2000). Only 6 movements of humpback whales have been documented, by photo-identification, between Antarctic Area V feeding grounds and Eastern Australia (Rock et al. 2006, Franklin et al. 2008). One recent genotype match was reported between New Caledonia and the Antarctic Area V feeding area, and also a small number of genotype matches have been reported between Oceania breeding grounds and Antarctic Area VI and I feeding areas (Steel et al. 2008).
Genetic evidence in a recent study suggested that the Humpbacks passing New Zealand may be closely related to the New Caledonia (E2) stock (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. 2007). 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 investigated. Therefore, there remains considerable uncertainty about the destination of humpback whales migrating past New Zealand from Antarctic Area V feeding grounds.

Here we use photo-identification data collected from 1999 to 2004 to investigate movements of individual humpbacks between Eastern Australia and Oceania and between Oceania regions and discuss the migratory destinations of humpback whales using the New Zealand migratory corridor.

METHODS

The Eastern Australian and Oceania catalogues selected for inclusion in this study are the most recent, fully reconciled, photo-identification catalogues from each of the survey regions described below and photo-identification survey work is still underway in most regions. Survey locations are shown in Figure 1.

Vessel-based photo-identification of humpback pods in Hervey Bay, Queensland (25°S, 153°E) was undertaken between 1992 and 2005 as part of a long-term study of humpback whales. The reconciled Hervey Bay (HB) Fluke Catalogue for 1999-2004 consists of n = 1246 individuals. Photo-identification was also utilised in a study of humpback whales on the northern migration at Byron Bay (BB) (28°38'S, 153°38'E) resulting in a 1999-2004 catalogue of n = 598 individuals. Photo-identification on the southern migration at Ballina (BA) (28°52'S, 153°36'E) between 2003 and 2004 resulted in a catalogue of n = 235 individuals. The combined reconciled Eastern Australian Fluke Catalogues, after reconciliation within and between the Catalogues and rejection of photographs of unsuitable quality, consist of n = 1315 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 adjacent sites: Vanuatu, Fiji, Samoa, and Niue. Surveys 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 n = 692, made up of New Zealand, n = 13; New Caledonia, n = 160; Vanuatu, n = 6; Fiji, n = 11; Tonga, n = 282; Samoa, n = 1; American Samoa, 31; Niue, n = 2; Cook Islands, n = 36 and French Polynesia, n = 159.

Matching between the Eastern Australia 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; and 4 matches between Eastern Australia and New Caledonia. No matches were found between Tonga and the other Oceania catalogues. The method used to compare the Oceania and Eastern Australian catalogues, within and between regions, is fully reported in Garrigue et al. 2007a and 2007b.
Statistical analysis

For the purposes of analysis, fluke data from New Caledonia and Vanuatu were combined into an Oceania West (OW) catalogue (n = 166) while Tonga, Fiji, American Samoa, Samoa, Niue, Cook Islands and French Polynesia were combined into an Oceania East (OE) catalogue (n = 513). The Eastern Australian (EA) catalogue (n = 1315) and New Zealand (NZ) catalogue (n = 13) were treated as separate sites.

Several analyses were conducted investigating the number of matches found between sample site (SITE) and proposed population (POP) catalogues, m_{SITE-POP}: NZ-EA, OW-EA, OE-EA, OE-OW, NZ-OW, NZ-OE.

In each case, if the whales sighted at the sample site were all members of the proposed population, the proportion of the SITE catalogue we would expect to be matched to the POP catalogue would be equal to the proportion of the proposed population that were in the POP catalogue. Alternatively, if the whales sighted at the sample site were not all members of the proposed population, the proportion of the SITE catalogue we would expect to be matched to the POP catalogue would be lower than the proportion of the proposed population in the POP catalogue.

This rationale provides a means of estimating the expected number of matches under a null hypothesis that the whales identified at the sample site were all members of the proposed population for testing against the alternative hypothesis that they were not. The analysis may be based on a test of association in a 2x2 cross-table of frequencies constructed as ‘not seen’ or ‘seen’ at the sample site by ‘not seen’ or ‘seen’ in the proposed population (Table 1).

Table 1 Scheme for the cross-tables.

<table>
<thead>
<tr>
<th>Sample site (SITE)</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>N_{POP} - n_{SITE} + m_{POP-SITE}</td>
<td>n_{POP} - m_{POP-SITE}</td>
<td>N_{POP} - n_{SITE}</td>
</tr>
<tr>
<td>Seen</td>
<td>m_{SITE} + m_{POP-SITE}</td>
<td>n_{SITE}</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>N_{POP} - n_{POP}</td>
<td>n_{POP}</td>
<td>N_{POP}</td>
</tr>
</tbody>
</table>

N_{POP} = 2004 population estimate
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

Given these data and estimates, the expected numbers of matches, m_{POP-SITE}hat, may be derived from expected equality of proportions, m_{POP-SITE}hat = (n_{POP} \times n_{SITE}) / N_{POP}, and calculated as m_{POP-SITE}hat = (n_{POP} \times 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, Nhat = (n_{1}\times 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 fewer 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 estimated 2004 population sizes, the sizes of sampling site and proposed population catalogues and the numbers of matches between the sampling site and proposed population catalogues except for the Ballina catalogue (Dan Burns, unpublished data) were derived from Garrigue et al. 2007b and Baker et al. 2006, and are reported in Table 2.

Table 2. Data summary; estimated 2004 population sizes, the sizes of sampling site and proposed population catalogues and the numbers of matches between the sampling site and proposed population catalogues.

<table>
<thead>
<tr>
<th>SITE - POPULATION</th>
<th>NZ-EA</th>
<th>OW-EA</th>
<th>O-EA</th>
<th>OE-OW</th>
<th>NZ-OW</th>
<th>NZ-OE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site catalogue</td>
<td>13</td>
<td>166</td>
<td>513</td>
<td>166</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Population catalogue</td>
<td>1315</td>
<td>1315</td>
<td>1315</td>
<td>513</td>
<td>166</td>
<td>513</td>
</tr>
<tr>
<td>Population size</td>
<td>7090</td>
<td>7090</td>
<td>7090</td>
<td>3366</td>
<td>472</td>
<td>3366</td>
</tr>
<tr>
<td>Site-population matches</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
RESULTS

The frequencies of whales not seen and seen in sampling sites by whales not seen and seen in proposed populations with the expected frequencies for site to population matches and Fisher’s one-tailed p-values are reported in Table 3.

Table 3. 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.

<table>
<thead>
<tr>
<th>SITE - POPULATION</th>
<th>NZ-EA</th>
<th>OW-EA</th>
<th>OE-EA</th>
<th>OE-OW</th>
<th>NZ-OW</th>
<th>NZ-OE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen - Not seen</td>
<td>5765</td>
<td>5613</td>
<td>5262</td>
<td>2692</td>
<td>293</td>
<td>2840</td>
</tr>
<tr>
<td>Not seen - Seen</td>
<td>1312</td>
<td>1311</td>
<td>1315</td>
<td>508</td>
<td>166</td>
<td>513</td>
</tr>
<tr>
<td>Seen - Not seen</td>
<td>10</td>
<td>162</td>
<td>513</td>
<td>161</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Seen - Seen</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Expected matches</td>
<td>2.4</td>
<td>30.8</td>
<td>95.1</td>
<td>25.3</td>
<td>4.6</td>
<td>2.0</td>
</tr>
<tr>
<td>Fisher’s one-tailed p-value</td>
<td>0.444</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.003</td>
<td>0.166</td>
</tr>
</tbody>
</table>

Of the 13 whales sighted in New Zealand, 3 were matched to the Eastern Australian catalogue. This is slightly more than the 2.4 expected if the New Zealand whales were all members of the Eastern Australian population. This result is entirely consistent with that hypothesis.

Of the 166 whales sighted in Oceania West 4 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. While there is evidently appreciable interchange between the Eastern Australian and the Oceania West populations, those populations are relatively separate.

Of the 513 whales sighted in Oceania East, none were matched to the Eastern Australian catalogue. This is many and significantly fewer than the 95.1 expected if they were all members of the Eastern Australian population. While there may be some interchange between the Eastern Australian and the Oceania East populations there is no evidence of any interchange from these data, and those populations are apparently quite separate.

Of the 166 whales sighted in Oceania West, 5 were matched to the Oceania East catalogue. This is considerably and significantly fewer than the 25.3 expected if they were members of the Oceania East population. While there is evidently appreciable interchange between the Oceania East and the Oceania West populations, those populations are relatively separate.

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. While there may be some interchange between the Oceania West and New Zealand populations there is no evidence of interchange from these data, and those populations are apparently relatively separate. However, if we assume that the New Zealand population is in fact the Eastern Australian population,
we would expect approximately the same proportion, \( p_{NZ,OW} \), 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 Eastern Australia; i.e. \( p_{NZ,OW} = \frac{\text{matches}}{13} \). 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 2.0 expected if they were members of the Oceania East population. While failure to find significance here may be largely due to the small size of the NZ catalogue and the relatively small proportion of the Oceania East population in the OE catalogue, there is weak evidence in these data that the New Zealand and Oceania East populations are relatively separate.

DISCUSSION

Dawbin (1949, 1956) noted that the Ross Sea, particularly around the Balleny Islands, "almost certainly represents the summer concentration of humpbacks which pass the coasts of New Zealand, East Australia and other parts of the Pacific" and developed the hypothesis that dispersal across the Antarctic Area V feeding grounds is a primary determinant of the routes taken by humpbacks as they approach New Zealand on their return to winter breeding areas. Recent photo-identification evidence supports this view. Only six photo-identification matches have been reported between the Antarctic Area V feeding areas and breeding grounds to the north (Kaufman et al. 1990, Rock et al. 2006, Franklin et al. 2008). Five of these sightings were in close vicinity to the Balleny Islands (67° S, 163°E), and one was near to the eastern border of the Area V feeding area (69°S, 171°W) (Rock et al. 2006, Franklin et al. 2008). The longitude of the most westerly sighting was 155° 55' E, and the most easterly was at 170° 52' W. The distance between these two sightings was approximately 817 nautical miles (Rock et al. 2006). All of these individuals are reported as having strong site fidelity to Eastern Australia (Kaufman et al. 1990, Rock et al. 2006, Franklin et al. 2008). Franklin et al. (2008), concluded that these sightings suggest that Eastern Australia is the wintering destination for whales sighted in and around the Balleny Islands (Franklin et al. 2008). Accumulation and matching of photo-identification data, obtained across the breadth of the Antarctic Area V feeding grounds (130°E to 170°W), would greatly improve our understanding of the level and rate of intermingling amongst humpbacks from differing breeding groups and the linkages between Area V feeding areas and Pacific breeding grounds.

Dawbin (1964) found Discovery Mark tag 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. The recapture rates of humpbacks marked off Eastern Australia and in waters near New Zealand and Norfolk Island indicated that there was "very highly significant" segregation between groups that migrated along the Eastern coast of Australia and those which migrate past islands further east (Dawbin 1964). Differentiation between the Eastern Australian (E1) breeding grounds, New Caledonia (E2) and Tonga (E3) has been confirmed by recent genetic and photo-identification studies (Olavarria et al. 2006a, 2006b, 2007, Garrigue et al. 2006 and 2007a and b, Anderson and Brasseur 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 south east coast of New Zealand off Kaikoura and during systematic surveys conducted in Cook Strait (Gibbs and
Comparisons of the New Zealand and Eastern Australian Catalogues for the synoptic period 1999-2004, reported herein, resulted in 3 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, and two of the matches occurred within the same season (Garrigue et al. 2007b). Previous matches between New Caledonia, Eastern Australia and New Zealand have been reported (Garrigue et al. 2000, 2002) and more recent comparisons of the New Zealand and Oceania catalogues have reported matches between New Caledonia and Tonga and New Zealand (Constantine et al. 2007).

Dawbin (1956) reported that northbound humpbacks traveling past New Zealand favour the eastern coastline, with part of the stream passing south of the South Island through the Foveaux Strait and part of the stream passing through the Cook Strait, while the rest of the stream traveled to the northeast along the eastern coastline of the North Island of New Zealand until rounding the northern extremity of the North Island. We suggest that humpbacks traveling from the eastern region of the Antarctic Area V feeding areas, with site fidelity to the Eastern Australian (E1) breeding grounds, may be more likely to pass to the south of the South Island of New Zealand and or through the Foveaux and Cook Strait rather than travel up along the north eastern coastline of New Zealand. In contrast humpbacks with site-fidelity to the New Caledonia (E2) and Tonga (E3) breeding grounds may be more likely to pass northwards along the eastern coastline of the North Island of New Zealand and after clearing the northern tip of New Zealand they may then resume their migration to New Caledonia (E2) on a northwesterly track, or to the Tongan Islands (E3) on a northeasterly track along the Tongan trench. Two humpbacks sighted in Kaikoura during northward migration where also photographed in New Caledonia and Tonga (Constantine et al. 2007). Photo-identification sampling on the southeastern coast of New Zealand and in Cook Strait may therefore represent a sampling bias towards whales that are traveling towards the Eastern Australian breeding grounds. A similar pattern of migration may occur during the migration from the northern breeding grounds to Antarctic feeding areas. The majority of southward moving humpbacks favor the western coastline with a small proportion rounding the northern tip of New Zealand to the east and travel down along the eastern coast, as occurred with a humpback sighted in New Caledonia which was also sighted in New Zealand at the Bay of Islands (NE North Island) during the southern migration (Constantine et al. 2007). An even smaller proportion move from west to east through the Cook and Foveaux Straits (Dawbin 1956). Humpbacks from Eastern Australia may approach the western coastline of New Zealand from a shallower angle than those from New Caledonia and Tonga thus possibly arriving at, or towards the southern end of, the western coastline of the South Island of New Zealand.

Selecting at least three additional sampling sites for systematic photo-identification of humpbacks in New Zealand waters could provide data to test the hypothesis proposed above. These 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 of New Zealand and a site on the southeastern coast of the South Island, while continuing concurrent sampling in the Cook Strait.

Chittleborough (1955) reported that, from his sample of 894 humpback whales collected between 1952 and 1962, mainly off Western Australia, he found very low levels of physical maturity, 1.4% in males and 1.8% in females; whereas for a mature baleen stock the range of physically mature individuals was expected to be
between 25° and 35° (Macintosh 1942). He surmised that the most likely reason for this bias was that whalers had intentionally selected for killing larger, older humpbacks. However he noted that between 1957 and 1961 catches from the east coast of Australia contained "a greater accumulation of old males" than found in catches of the same years from the west coast of Australia (Chittleborough 1962, 1965). Dawbin found the catch proportions between Eastern Australia and New Zealand to be in the order of 2:1 and conjectured that, because of the availability of suitable coastal breeding areas along the east coast of Australia, compared to the limited coastal breeding areas around the Islands of the Western Pacific, relative population levels in the two regions may be of similar proportions (Dawbin 1956, 1964). Recent abundance estimates show this to be near to the current proportion of the humpback populations in Eastern Australia and Oceania (Noad et al. 2005, Baker et al. 2006, Jackson et al. 2006, Paton et al. 2006).

It is possible that, after the near total collapse of the Antarctic Area V humpback stock in the early 1960s, the majority of the 500 or so surviving individuals (Chittleborough 1965) may have been whales with site-fidelity to the east coast of Australia. Also there may have been a possibility that surviving immature males and females from groups with site fidelity for locations such as the Chesterfields and Fiji may have been recruited into the surviving Eastern Australian (E1) group or the relatively smaller New Caledonian (E2) and Tongan (E3) groups. This may provide an explanation of why the Eastern Australian (E1) group has recorded relatively earlier and stronger population increase than has been seen in New Caledonia (E2) and Tonga (E3) 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). Recolonisation and population recovery, in formerly populated areas of Oceania, may be dependant on immigration and/or recruitment of humpbacks of, or approaching, mature age breeding status. Photo-identification matches between New Caledonia and Hervey Bay (Garrigue et al. 2007) confirm the movement of male humpbacks between Eastern Australia (E1) and New Caledonia (E2). However a match between New Caledonia and Hervey Bay not included in Garrigue et al. (2007b) documented the movement of a known breeding female between the two regions. The whale was sighted as a singleton in New Caledonia in April 1995 and was subsequently then sighted in Hervey Bay with calves in October 1996, 2000 and 2003. Similarly a female with a calf was sighted in New Caledonia in September 2000 and then re-sighted at Ballina in 2003 with a calf (Claire Garrigue, Dan Burns and Trish Franklin, unpublished data). An unpublished match between Tonga and Eastern Australia has also been observed (Dan Burns, pers. Comm.). Accumulation of photo-identification data of extended life histories of individual humpback whales of known age-class offers the opportunity to document and quantify temporary and/or permanent immigration of individual humpback whales between existing breeding grounds and/or areas formerly occupied by humpback whales.

Recolonisation of formerly occupied breeding areas in Oceania and, the rates of population recovery in currently occupied breeding areas in Eastern Australia and Oceania, may also be determined by the actual available breeding area for female humpbacks who have, or are about to attain breeding age. At some time in the future, the Eastern Australian population may reach a point where some form of density dependence for breeding females will occur. This may give rise to competition amongst younger females for suitable breeding locations generating pressure for them to seek alternative breeding locations. Recent modeling estimated the combined humpback carrying capacity for Eastern Australia as ranging from 40,595 to 44,476 (95% probability range
36,642 - 66,129 (Jackson et al. 2006), compared to current abundance estimates for Eastern Australia (E1) of
7041 (4075 - 10,008 95% CI) in 2005 (Paton et al. 2006) and of Oceania in 2004 of 3827 (CV, 0.12) (Baker et
al. 2006). Given this it is unlikely that density dependence will be a significant feature of the population in the
immediate future, we nevertheless suggest the hypothesis that emigration of some breeding females from Eastern
Australia may be a factor in the future recovery of smaller Oceania humpback whale populations and the future
recolonisation of previously occupied breeding grounds in Oceania. A research priority for the long-term
management of humpback whales in the Southern hemisphere may be the identification, mapping, measurement
and monitoring of humpback whale coastal breeding locations, in both presently occupied Eastern Australian
and Oceania breeding areas, and the formerly occupied breeding areas in Oceania. Assessment of population
abundance trends, migratory interchange and recolonisation also requires the continued maintenance of existing
photo-identification surveys and the implementation of new surveys in areas where recolonisation is found to be
occurring.

Although based on a small sample size from New Zealand, the results presented here support the hypothesis that
some humpback whales using the New Zealand migratory corridor are wintering in Eastern Australia. The data
also supports the findings of earlier research that, although there is intermingling between Eastern Australia (E1
breeding grounds) and Oceania West (E2 breeding grounds) and Oceania West and Oceania East (E3 and F
breeding grounds), these populations are relatively separate. Stratification of photo-identification sampling of
humpback whales in New Zealand waters combined with continued photo-identification surveys in Eastern
Australia and Oceania regions, together with the collection of data on individual humpback whales of known
age-class, could significantly contribute to an understanding of the migratory destinations of humpback whales
using the New Zealand migratory corridor.

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LITERATURE


Dawbin WH, Filla RA (1949) A contribution to the study of the humpback whale based on observations at New Zealand shore stations 7th Pacific Science Congress, p 373-382

Dawbin WH (1956) The migrations of humpback whales which pass the New Zealand coast. Transactions of the Royal Society of New Zealand 84:147-196


isolation of New Caledonia (E2) and Tonga (E3) breeding stocks. The Inter-sessional Workshop for the Comprehensive Assessment of Southern Hemisphere Humpback Whales. Scientific Committee of the International Whaling Commission Hobart, 3 - 7 April 2006 SC/A06/HW19: 1-10


MacIntosh NA (1942) The southern stocks of whalebone whales. Discovery Reports XXII:197-300


Rayner GW (1940) Whale marking: Progress and results to December 1939. Disc Rep 19:245-284


Figure 1. Locations of the New Zealand (NZ), Eastern Australian (EA), Balleny Islands 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 triangle 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 circle symbols (e), (f) and (d) show the Balleny Island/EA matches reported in Franklin et al. (2008); whale (d) was sighted in Ballina and (e) and (f) were sighted in Byron Bay and Hervey Bay but in different years. The diamond symbol marked (i), (h), (g) shows the NZ/EA matches reported in Garrigue (2007a); all three were resighted in Hervey Bay, two within the same season; June in NZ and September in Hervey Bay. The diamond symbol marked (j), (k), (l) and (m) shows the four New Caledonia/Hervey Bay matches reported in Garrigue et al. (2007a).