Movements of humpback whales in Oceania, South Pacific

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ABSTRACT

To investigate movements of humpback whales among breeding and migratory areas of Oceania in the South Pacific Ocean, comparisons of individually identified whales were undertaken using catalogues from New Caledonia, Tonga, New Zealand, the Cook Islands and French Polynesia. These locations probably represent wintering grounds or migratory areas for the Group V and VI stocks, as recognised by the International Whaling Commission for management purposes. Comparisons were also made to small samples of photos from Colombia, Ecuador and the Antarctic Peninsula, representing wintering and feeding grounds of the Group I stock. Overall, the combined catalogues contained photographs of 912 individual whales, 767 of which were from Oceania. Twelve fluke matches were made, indicating movement between the following areas: New Caledonia and New Zealand (2); New Caledonia and Tonga (6, plus one made by dorsal fin); Tonga and the Cook Islands (2); the Cook Islands and French Polynesia (1, plus one made by dorsal fin); and between Ecuador and the Antarctic Peninsula (1). These results add to previously known connections between eastern Australia and the westerly component of Oceania (New Caledonia, Tonga and New Zealand). The data also suggest little movement between Oceania and Area I (western South America and the Antarctic Peninsula), although sample sizes for the latter region were too small to conclude this with certainty. The documented movement of some whales among portions of Oceania indicates that stock assessments based on combining regional estimates of abundance are likely to be positively biased, although this may be countered by problems of heterogeneity in sampling effort and whale distribution. In contrast with the recovery exhibited in Area IV and in the western portion of Area V, humpback whale abundance appears to remain low in Oceania, presumably because of overexploitation in the feeding grounds of Area VI and the easterly component of Area V.

KEYWORDS: HUMPBACK WHALE, SOUTH PACIFIC, OCEANIA, NEW ZEALAND, MIGRATION, BREEDING GROUNDS, POPULATION STRUCTURE

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) in the Southern Hemisphere are traditionally considered to form five or six distinct stocks or 'groups', which remain isolated year-round (Mackintosh, 1942; 1965; Chittleborough, 1965). During the summer feeding season, these Groups are distributed more or less discontinuously into six Antarctic Areas historically recognised by the International Whaling Commission (IWC) for the purposes of management (Donovan, 1991). Each winter whales from these feeding areas are thought to migrate to discrete breeding and calving grounds in tropical and near-tropical latitudes along continental and insular coastlines. Evidence for these population divisions came initially from the discontinuous, seasonal distributions of humpback catches and migratory movement by Discovery-marked individuals during periods of commercial whaling. More recently, the distribution of mitochondrial (mt) DNA diversity and movement by naturally marked individuals have been used to confirm and refine these divisions (Stone *et al.*, 1990; Baker *et al.*, 1994; 1998; IWC, 1999; 2000b; 2001; Garrigue *et al.*, 2000).

Referred to here as Oceania, the islands of the South Pacific, from New Caledonia in the west to French Polynesia in the east and including New Zealand, lie directly north of the Antarctic Area V and VI feeding grounds. For this reason, it is generally assumed that humpbacks that winter in Oceania are part of the Group V and VI stocks. Unlike the classic studies of Group IV and V humpbacks by Dawbin (1966) and Chittleborough (1965), however, there is little direct evidence connecting these wintering grounds to Antarctic Areas or to the known migratory corridors along eastern Australia and around New Zealand. Only a handful of Discovery marks placed on the wintering grounds were recovered by Antarctic whaling ships or from shore-based operations in Australia and New Zealand. There is no historical evidence of migratory movement or interchange among the winter grounds of Oceania.

Humpbacks in the Southern Hemisphere were subject to intensive commercial exploitation during the 20th century, with more than 200,000 killed over a seven-decade period (Clapham and Baker, 2001). Almost a quarter of this total represents previously unreported catches by the Soviet Union, which conducted a massive campaign of illegal whaling following the Second World War (Yablokov *et al.*, 1998). Some of the earliest recorded hunting of humpbacks in the Southern Hemisphere was conducted by American whaling vessels near the 'Friendly Isles' of the Kingdom of Tonga and in the vicinity of Chesterfield reef systems, northwest of New Caledonia (Townsend, 1935). While some

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regions of the Southern Hemisphere have shown evidence of strong recovery (e.g. Bannister, 1994; Paterson *et al.*, 1994), the numbers of humpback whales in surveyed regions of Oceania appear to remain low (Abernethy *et al.*, 1992; Gibbs and Childerhouse, 2000; Garrigue *et al.*, 2001).

Since 1991, a number of research projects have been initiated in various parts of Oceania, including New Caledonia, Tonga, the Cook Islands and French Polynesia. These projects have employed photo-id and tissue collection to study the occurrence, distribution, behaviour, abundance, genetics and habitat use of humpbacks at each study site (e.g. Garrigue and Gill, 1994; Baker *et al.*, 1998). This paper reports the results of a comparison of photographic catalogues from these areas, as well as from New Zealand. Photos from Oceania were also compared with more distant study sites off South America and the Antarctic Peninsula to investigate whether the range of Oceania animals extends to the easternmost margins of the Pacific. These comparisons took place as part of two workshops on humpback whales in the South Pacific held at the University of Auckland in March 2000 and April 2001 (Donoghue and Baker, 2000; Anon., 2001). The results provide the first direct evidence of movement among some areas of Oceania and a preliminary assessment of isolation from regions beyond Oceania.

METHODS

Study areas

For the purpose of this paper, Oceania is defined as the large area of islands in the southwestern and south central Pacific Ocean, stretching from New Zealand and New Caledonia in the west to French Polynesia in the east (Fig. 1); geographically, however, Oceania includes a much larger area of island groups in both Southern and Northern Hemispheres. Dedicated surveys for humpback whales in this region were conducted during the austral winter in four areas: New Caledonia; Tonga; the Cook Islands; and French Polynesia. These areas are described separately below. A small sample of opportunistically collected photographs was also available from New Zealand. It is important to stress that the great majority of islands in Oceania have never been surveyed for the presence of humpback whales, and their use of most of the potentially available habitat is therefore unknown.

New Caledonia

New Caledonia lies between 18° and 23°S and between 158° and 172°E. It consists of one main island and three groups of smaller ones plus many uninhabited atolls, including Chesterfield which was used as a whaling area by the American whaling ships during the 19th century (Townsend, 1935).

Humpback whale surveys were conducted sporadically beginning in 1991 (Garrigue and Gill, 1994), and for three months (July, August and September) each austral winter from 1995 on (Garrigue *et al.*, 2001). The primary study site covers approximately 1,000km^2 and is located in the southeastern portion of the lagoon off the main island. A total of 277 days of surveys from small boats have been conducted since 1995.

Tonga

The Tongan archipelago is a series of volcanic islands and coral atolls extending from 15° to 23°S and from 173° to 177°W. Tonga consists of three major island groups thought to constitute the primary area of humpback whale density: Tongatapu in the south; the Ha'apai group in the middle; and the Vava'u group in the north. Hunting of humpback whales is known to have occurred in Tonga during the 19th century by American whaling ships (Townsend, 1935) and hunting continued at a low level by local whalers until banned by Royal decree in 1978.

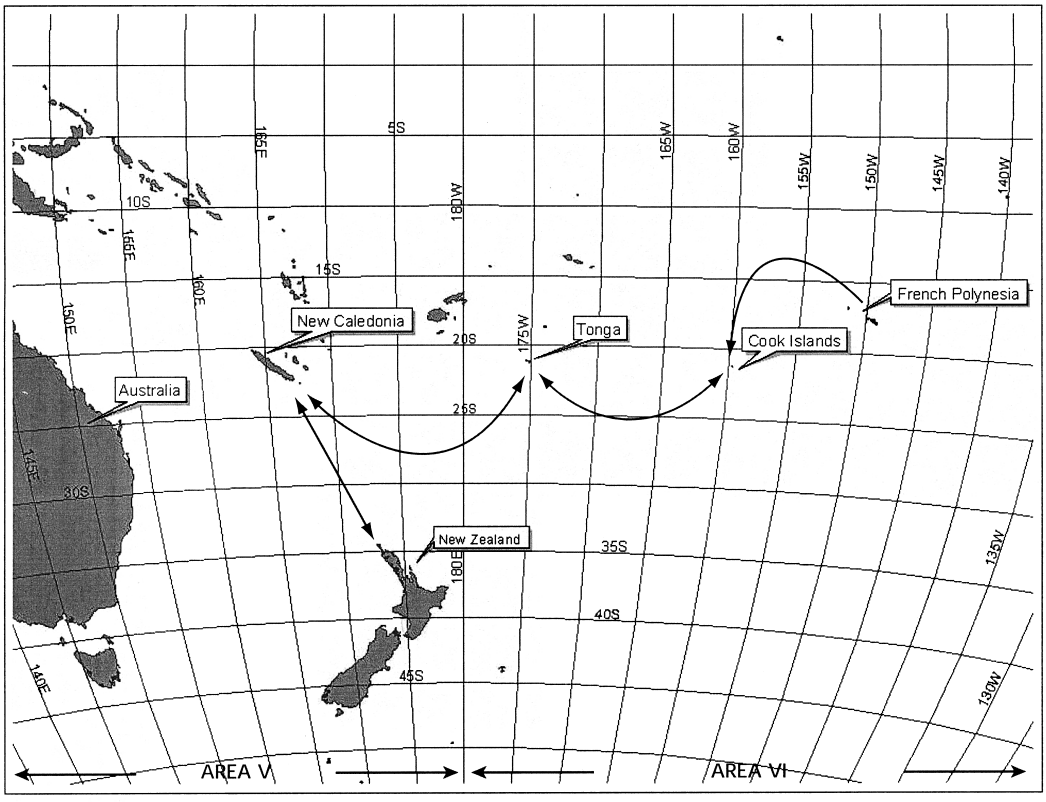

Fig. 1. Map of Oceania, showing the principal study areas.

Vessel-based surveys and the collection of individual identification photographs were initiated in 1991 (Abernethy *et al.*, 1992). Each of the three main island groups has been surveyed in at least one year but most of the field effort from 1994-2000 was concentrated around Vava'u. The majority of fieldwork was conducted in August and early September, although work in some years included late July and early October. The length of the field season varied yearly from approximately 10 days to more than six weeks.

Cook Islands

The Cook Islands extend from 8° to 23°S and from 156° to 167°W, and consists of a few high islands and numerous atolls scattered over approximately 2,000,000km^2 of the southwestern South Pacific. These islands are divided into two groups, the Northern Cooks and the Southern Cooks; the latter include nine islands and atolls lying between latitudes 18°S and 22°S. Little or no whaling took place in this region in the 20th century and records of earlier (historical) catches there are sparse. Surveys for humpback whales in the Southern Cook Islands began with an exploratory three-week project in 1998 and continued with three-month field efforts in both 1999 and 2000 (Hauser *et al.*, 2000). To date, the survey has been focused on three locations: (1) Palmerston Atoll, a small atoll lying at 18°04'S, 163°10'W on the northwestern margin of the Southern Cook group; (2) Aitutaki, an island located at 18°55'S, 159°47'W, roughly 300km east of Palmerston; and (3) Rarotonga, an island located at 21°14'S, 159°48'W, roughly 430km southeast of Palmerston. A total of 110 days of surveys have been conducted.

French Polynesia

French Polynesia lies between 8° and 27°S and 134° to 155°W in the central South Pacific Ocean. It comprises five groups of islands: the Marquesas; the Tuamotu atolls; the Gambiers; the Society Islands; and the Australs. Sightings of humpback whales throughout French Polynesia's waters have been submitted to a sighting and stranding network since 1988 (Poole, 1993; Poole and Darling, 1999).

The nearshore waters of Moorea (17°30'S and 149°50'W) situated 18km northwest of Tahiti in the Society Islands, have been the primary study area for fieldwork since the beginning of dedicated research in 1991. Boat-based observations were conducted on both dedicated vessels and on platforms of opportunity. Additional shore and boat-based observations of humpback whales were begun in 1999 at Rurutu (22°30'S and 151°15'W) in the Austral Islands, approximately 570km SSW of Moorea. For the 1999 and 2000 seasons, the fieldwork was mainly conducted from the end of July to November for a total of 148 days.

Photo identification

Humpback whales were individually identified from photographs of the ventral fluke pattern (Katona and Whitehead, 1981). Although some of the research projects concerned used variation in other markings (notably dorsal fin shape or lateral pigmentation) to recognise individuals, only fluke photos were employed in the primary comparisons described here. Photos were taken with 35mm cameras equipped with zoom or telephoto lenses and either black and white print or colour slide film.

Regional photographic catalogues as well as some digital video images from the principal study sites were compared by participants at two four-day workshops convened at the University of Auckland, New Zealand in March 2000 and April 2001 (Donoghue and Baker, 2000; Anon., 2001). To help establish the eastern extent of movement among whales seen in Oceania, additional comparisons were made between some of these sites and small sample sizes of photos from the eastern Pacific (Ecuador and Colombia) and the Antarctic Peninsula. All matches were confirmed by at least three participants at the workshop. A large catalogue of individual identification photographs from Eastern Australia (Kaufman *et al.*, 1993) was not considered at the workshops because of constraints on time and the variable quality of the published photographs. However, previous complete comparisons to this catalogue have established interchange between eastern Australia and New Caledonia (see below; Garrigue *et al.*, 2000).

To evaluate the relative magnitude of migratory interchange, the within-region return index and the between-region interchange index were calculated following Baker *et al.* (1986) and Calambokidis *et al.* (2001). The return index of within-region annual resights, was calculated as:

$$Rij = Mi, j / (Ai*Bi) *1000$$

Where

Ai = number of whales marked in all the years before 2000;
Bi = number of whales identified in 2000; and
Mi, j = number of whales marked in any previous years and resighted in 2000.

An interchange index of between-region resights was calculated as:

$$Rij = Mi, j / (A1*B2) *1000$$

Where

A1 = number of whales identified in region A;
B2 = number of whales identified in region B; and
Mi, j = number of whales resighted in both regions.

The indices were considered to be zero when there were no whales sighted within or between regions (i.e. when $Mi, j = 0$).

RESULTS

The number of individual identification photographs varied considerably across regions (Table 1). The largest catalogues available for the comparison were for Tonga ($n = 337$ unique individuals), New Caledonia ($n = 206$) and French Polynesia ($n = 171$). The smallest catalogue was for New Zealand ($n = 6$). Larger catalogues exist for Colombia and the Antarctic Peninsula but were unavailable for the current comparison. In all, fluke photographs were available of 912 individual whales, of which 767 came from Oceania.

Comparison of 767 individual identification photographs represented by the regional catalogues revealed eleven matches among the five regions of Oceania; an additional two matches were made by non-systematic comparisons of dorsal fin photos. Matches were made between New Caledonia and New Zealand and Tonga; between Tonga and the Cook Islands; and between the Cook Islands and French Polynesia. Two of the matches were from sightings in a single winter season. One whale was seen in the Cook Islands on 19 and 23 August 1999, then in Tonga on 12 October 1999. One whale seen in French Polynesia in August 1998 matched an animal identified in the Cook Islands on 19 September 1998. The directional movements are varied and indicated no preferential direction (Table 2). One animal identified in New Zealand and New Caledonia has been resighted three times in the latter region. There

Table 1

Results of comparisons of photo-id catalogues among areas, with sample sizes of identified individuals used (*n*) and years of effort. Photos taken in 2000 were not compared to collections from Colombia or Ecuador. * Includes one match reported by Garrigue *et al.* (2000); † Does not include one match by dorsal fin; ‡ Does not include one match made by dorsal fin.

Area	*n*	Years	NZ	TG	CI	FP	AP	CO	EC
New Caledonia (NC)	206	1991-2000	2*	6†	0	0	0	0	0
New Zealand (NZ)	6	1994-2000		0	0	0	0	0	0
Tonga (TG)	337	1991-2000			2	0	0	0	0
Cook Islands (CI)	53	1998-2000				1‡	0	0	0
French Polynesia (FP)	171	1992-2000					0	0	0
Total for Oceania	**767**								
Antarctic Peninsula (AP)	60	1994-95						0	1
Colombia (CO)	20	1992-98							0
Ecuador (EC)	59	1996							

Non-systematic comparison to the published catalogue for eastern Australia resulted in four matches to New Caledonia, and one to Tonga (TG9103 and EO495, Kaufman *et al.* 1993).
Authors responsible for regional catalogues or comparisons: C. Garrigue and J. Greaves for NC; C.S. Baker, R. Constantine and M. Donoghue for NZ and TG; N. Hauser, H. Peckham and P. Clapham for CI; M. Poole, FP; A. Aguayo, C. Olavarria for AP; S. Caballero and L. Florez-Gonzalez for CO; J. Denkinger and C. Pairoa for EC.

were no matches between Oceania and either Ecuador, Colombia or the Antarctic Peninsula but sample sizes are small. One match made between Ecuador and the Antarctic Peninsula is not discussed further here.

Table 2

Directional movement of the resighted whales in between Tonga (TG), New Caledonia (NC), New Zealand (NZ), Cook Islands (CI), French Polynesia (FP). The * indicates a match with dorsal fin.

NC	→	TG	
1994		1999	
1		1	
1997		1996	
1*		1*	Female
1998		1999	
2		2	Males
1998		2000	
1		1	
NC	←	TG	
2000		1996	
1		1	Male
2000		1998	
1		1	Male
NZ	→	NC	
1994		1997, 1999, 2001	
1		1	Female
NZ	←	NC	
1998		1994, 1999	
1		1	Male
TG	→	CI	
1998		2000	
1		1	
TG	←	CI	
1999		1999	Male
1		1	
CI	←	FP	
2000		1997	Female?
1*		1*	
1998		1998	
1		1	

The between-region interchange indices were small in comparison to the within-region return indices from New Caledonia, Tonga and French Polynesia (Table 3). Only New Caledonia and New Zealand showed a relatively high resighting index suggesting a close migratory connection, although the sample size from New Zealand is very low. The absence of within-region returns in the Cook Islands could indicate that this region is part of an extended migratory corridor rather than a primary destination.

Table 3

Between-region interchange indices (normal text) and within-region return indices (in *italics*).

Area	NC	NZ	TG	CI	FP
New Caledonia (NC)	*2.21*	1.62	0.09	0	0
New Zealand (NZ)		0	0	0	0
Tonga (TG)			*0.55*	0.11	0
Cook Islands (CI)				*0.00*	0.11
French Polynesia (FP)					*0.58*

DISCUSSION

The results provide the first direct evidence of interchange or migratory movement among wintering grounds of Oceania. However, interchange was limited to adjacent wintering regions and the rate of interchange was considerably less than expected from the within-region return indices for New Caledonia, Tonga and French Polynesia. This limited interchange suggests that, with the possible exception of the Cook Islands, each region is demographically independent and should be recognised as an individual stock. Differences in within-region return indices could indicate differences in the strength of migratory fidelity or, more likely, differences in the abundance of whales visiting each region. The close migratory connection between New Caledonia and New Zealand is consistent with historical assumptions about migration patterns in eastern Group V (Dawbin, 1966). However, the absence of resightings between Tonga and New Zealand suggests a closer affinity of Tonga with Group

VI than previously assumed. Alternatively, a component of the Tongan stock could have been eliminated by intensive Soviet whaling in eastern Area V (see below).

The results also add to previously established connections between eastern Australia and the westerly component of Oceania. To date, four matches have been made between eastern Australia and New Caledonia (Garrigue *et al.*, 2000), two matches between New Caledonia and New Zealand (Garrigue *et al.*, 2000; this paper), and one match between Eastern Australia and Tonga (reported here for the first time; see notes in Table 1). No evidence was found of interchange between Oceania and Area I (western South America and the Antarctic Peninsula), although the sample sizes for the latter region were too small to conclude this with confidence. The direct evidence of movement within Oceania but not between Oceania and Group I is consistent with previous analyses of mitochondrial DNA gene flow among humpback whales in the Southern Hemisphere (Baker *et al.*, 1998; Caballero *et al.*, 2000; Olavarría *et al.*, 2000). Since no photographs were available of humpback whales from the high-latitude portions of Group V and VI at the time of the study, it is not possible to clarify the relationship between Oceania and the feeding grounds of the Antarctic.

Although rates cannot yet be quantified, the documented exchange between some regions has implications for stock assessment. Specifically, regional estimates of abundance will likely be positively biased because of the potential for whales to move among regions and be recorded more than once. On the other hand, the vast area involved (relative to the survey effort), in combination with heterogeneity in the distribution of individual whales, makes it unlikely that all whales were equally available for sampling. This could result in a negative bias of abundance for the region as a whole.

Currently there are preliminary estimates of abundance for only two regions of Oceania: New Caledonia (approximately 314 for 2000, Garrigue *et al.*, 2001) and Tonga (approximately 770 in the year 2000, Baker *et al.*, 2001). However, all of the observers participating in this comparison note from sighting density data that the abundance of humpbacks remains relatively low, and is clearly well below the levels that once supported large-scale commercial whaling. The apparent lack of recovery in Oceania contrasts sharply with the situation for neighbouring Eastern Australia (western Area V), and in Areas III and IV, where sighting surveys demonstrate consistently high rates of increase in recent years (Bryden *et al.*, 1990; Best, 1993; Bannister, 1994; Paterson *et al.*, 1994; IWC, 2000a). Although survey effort relative to humpback whales in New Zealand waters has been largely opportunistic, research and tourism directed at other cetaceans have consistently covered the former coastal habitat of humpbacks. It is clear from the small number of reported sightings that this species remains rare locally (Gibbs and Childerhouse, 2000). Indeed, New Zealand appears to be one of several areas where populations of mysticetes that were virtually extirpated by whaling have not been repopulated by immigration from elsewhere; this may be due to the effective loss of the cultural memory of a particular migratory route or destination (Clapham and Hatch, 2000).

With the exception of New Zealand, where humpbacks were hunted consistently from numerous shore stations (Dawbin, 1966), little whaling was conducted on the wintering grounds of Oceania itself during the 20th century. Humpbacks were taken in Tonga and near New Caledonia by 19th century whaling vessels and (following European introduction) by Tongan families from the 1890's until 1978, using open boats and hand harpoons. Tongan whaling was small in scale, with annual catches prior to the early 1960's probably not exceeding 30-40 whales (Dawbin, 1959). No reliable data are available on the numbers taken by the more recent local Tongan hunting, but it is known that the hunt focused on mothers and calves, and struck and lost rates of up to 3:1 (relative to whales killed and secured) have been estimated (IWC, 1981). Nine whales have been reported to be killed by locals at Rurutu between 1930 and 1959 (M. Poole, unpublished data).

However, it is now clear that thousands of humpbacks were removed from Oceania by illegal Soviet hunting in the Antarctic; indeed, almost 13,000 humpbacks were taken in a single season (1959/60) from western Area V and eastern Area VI feeding grounds (Mikhalev, 2000). It is therefore not surprising that abundance in wintering grounds of Oceania remains low. Until the locations of all the illegal Soviet catches are published, the total number of humpbacks killed in Area VI will remain uncertain. In light of this, it is suggested that an assessment of current trends and abundance in Oceania is critical to understanding variability in recovery of Southern Hemisphere humpback whales. The work summarised here represents the preliminary framework for such an assessment.

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