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1 Abundance of humpback whales in Oceania using photo-identification and  
2 microsatellite genotyping

3 Running head: Oceania humpback whale population estimate

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### 9 **ABSTRACT**

10 Estimating the abundance of long-lived, migratory animals is challenging but  
11 essential for managing populations and anthropogenic impacts. Our study  
12 provides the first estimates of abundance and trend of an endangered population  
13 of humpback whales (*Megaptera novaeangliae*) on their breeding grounds in  
14 Oceania, South Pacific. We used fluke photo-identification (1999-2004, n = 660  
15 individuals) and microsatellite genotypes (1999-2005, n = 843 individuals) to  
16 estimate abundance with open capture-recapture statistical models. Total  
17 Oceania abundance and trend were estimated based on data from four primary  
18 and five secondary sampling sites across the region. The best estimate of total  
19 abundance for Oceania was 3520 whales (CV = 0.1) in 2005, based on a  
20 POPAN super-population model which includes resident whales and those  
21 migrating through the surveyed areas. A genotype-based POPAN abundance  
22 estimate from 2003 (N = 2361, CV = 0.11) was considered the most plausible for  
23 the combined abundance of the four primary survey areas and was similar to a

Pradel model ( $N = 2304$ , 95% CV = 1586 – 3406) using the same male-specific dataset. True abundance in the wider Oceania area is likely to fall between these two POPAN estimates, and a Pradel model showed no significant trend in abundance during the study period. Our results confirm that Oceania is the least abundant humpback whale breeding population in the Southern Hemisphere. The lack of a detectable trend contradicts the recovery seen in almost all other humpback populations throughout the world, and the whales in this area warrant continued study and management attention.

KEY WORDS: Humpback Whale, *Megaptera novaeangliae*, Oceania, South Pacific, Capture-Recapture, Genotyping, Photo-Identification

### INTRODUCTION

Managers depend upon abundance estimates to evaluate the status of populations and the effects of human activities. Whilst some species congregate in relatively discrete areas (e.g., Walton et al. 2005, Rayner et al. 2007), challenges arise when estimating abundance for endangered species that undertake extensive seasonal migrations and range over large, poorly defined areas. For long-lived, slow-breeding species with large home ranges, such as baleen whales, there are several challenges to estimating abundance especially when managing recovering populations (Hammond 1990, Stevick et al. 2003).

Humpback whales (*Megaptera novaeangliae*) congregate to breed during the winter months in Oceania (South Pacific) waters from western New Caledonia

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(~160°E) to the French Polynesian archipelago (~120°W) (Garrigue et al. 2002, Poole 2002) (Fig. 1). Individuals migrate seasonally from these areas to productive Antarctic feeding grounds, but the specific connections and routes taken between areas are not well understood. It is generally assumed that whales breeding throughout the islands and coral atolls of western Oceania migrate past New Zealand and possibly eastern Australia to the International Whaling Commission (IWC) Antarctic management areas known as Areas V (130° E - 170° W) and VI (120° - 180° W) to feed (Dawbin 1964, Dawbin 1966, Garrigue et al. 2000, Constantine et al. 2007, Garrigue et al. 2010, Valsecchi et al. 2010). The central and eastern migratory routes from Oceania are not yet well defined, but matches have been made to Areas V, VI and I (Steel et al. 2008, Hauser et al. 2010, Robbins et al. 2011). Recent satellite telemetry work has shown migration to the productive summer feeding grounds through the open waters south of eastern Oceania where no large land-masses exist along the migration path (Hauser et al. 2010).

In 1999, the South Pacific Whale Research Consortium (SPWRC) initiated a coordinated, synoptic survey of four primary island regions across Oceania; New Caledonia, Tonga (Vava'u), the Cook Islands and French Polynesia (Moorea and Rurutu). Eight additional sites were also surveyed in some years, including Vanuatu, Samoa, American Samoa, Fiji, Niue, and the other Tongan island groups (Ha'apai, Niuatoputapu and Eua) (Fig. 1).

A wide range of research tools have been used in this region, including: photographic identification (photo-ID), the collection of skin biopsy (or sloughed

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skin) samples for genetic analysis, acoustic recordings of song and satellite telemetry. Analyses to date have yielded information on humpback whale distribution, movements, regional abundance, behaviour, genetic differentiation and diversity (Helweg et al. 1998, Garrigue et al. 2004, Olavarria et al. 2007, Garrigue et al. 2010, Hauser et al. 2010, Garland et al. 2011, Garrigue et al. In Press a). Prior work has been particularly informative regarding the structure of the breeding population within Oceania. For example, photo-ID and genetic studies have shown evidence of individual fidelity to specific breeding areas within Oceania, but also exchange among areas (Garrigue et al. 2002, Olavarria et al. 2007, Garrigue et al. In Press a). Satellite telemetry, genetics and photo-ID data suggest that at least one area (the Cook Islands) may mostly function as a migratory corridor than a consistent breeding site (Hauser et al. 2010, Garrigue et al. In Press a). Finally, research to date suggests extremely low levels of interchange between Oceania and east Australia (Anderson et al. 2010, Garrigue et al. In Press b) and whilst the degree of separation of these two populations is still not completely understood, there is evidence that differences occur.

One continuing area of study is the recovery status of humpback whales in Oceania. The late 19<sup>th</sup> century saw the beginning of humpback whale hunts in the South Pacific and 20<sup>th</sup> century whaling was responsible for more than 45,000 whales being killed in the Southern Ocean regions associated with Oceania (Areas V and VI). The greatest impact was rendered by illegal Soviet whaling (1947-73), which killed 25,474 humpbacks in the region south of Oceania in the

1 1959-60 and 1960-61 summer seasons; over 20,000 of these were from Area V  
2 south of east Australia and New Zealand (Clapham et al. 2009).

3 Since commercial whaling ceased, evidence for the recovery of South Pacific  
4 humpback whales has been variable. Strong increases in abundance have been  
5 observed in east Australia (Paterson et al. 2001, Noad et al. 2006 a; Paton et al.  
6 In Press) while the numbers of humpback whales in adjacent Oceania waters  
7 appear to remain low, including areas where numerous whales were previously  
8 reported e.g., Fiji and New Zealand (Dawbin 1959, Gibbs et al. 2006). Of interest  
9 are reports of humpback whales further east than observed prior to whaling  
10 (Poole 2002, Poole 2006, Gibb 2009); the feeding ground origins of these whales  
11 have not yet been determined.

12 Here we report the first estimates of abundance and trend for the endangered  
13 humpback whales that breed in Oceania. Open capture-recapture population  
14 models generated estimates using datasets of humpback whale fluke photo-ID  
15 images, and microsatellite genotypes obtained from skin samples from 1999-  
16 2005.

## 18 **METHODS**

### 19 *Study regions*

20 Dedicated surveys for humpback whales were conducted during the austral  
21 winters of 1999 to 2005 (referred to as the 'synoptic years') during which effort  
22 was relatively similar in four primary study areas: New Caledonia, Tonga, the

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Cook Islands and French Polynesia (Fig. 1; see Garrigue et al. (In Press a) for study site details). However, breeding habitat in Oceania spans a wide range of islands, reefs and atolls from New Caledonia in the west to French Polynesia in the east and directed or opportunistic surveys have been conducted at other sites in one or more synoptic years (see supplementary materials). We used available data from American Samoa, Fiji, Niue, Samoa and Vanuatu to investigate the effects of spatial bias and sample size on our estimates.

### *Microsatellite database*

Biopsy and sloughed skin samples were collected from six breeding regions in Oceania (New Caledonia, Tonga, Cook Islands, French Polynesia, Samoa and American Samoa) between 1999 and 2005. Total cellular DNA was isolated from skin tissue by digestion with Proteinase K, followed by a standard phenol:chloroform extraction method (Sambrook et al. 1989, Baker et al. 1994). Up to 17 microsatellite loci were amplified for 1447 samples using previously published primers (GT211, GT575, GT23 (Bérubé et al. 2000), GATA417, GATA28 (Palsbøll et al. 1997), Ev1, Ev14, Ev21, Ev37, Ev94, Ev96, Ev104 (Valsecchi & Amos 1996), 464/465 (Schlötterer et al. 1991) and rw26, rw31, rw4-10, rw48 (Waldick et al. 1999). Microsatellite loci were amplified individually in a 96- or 384-well format with MJ PTC-225 (MJ Research), and co-loaded in four sets for automated sizing (size standard 500LIZTM) on an ABI 3730xl (Applied Biosystems). Peaks were reviewed and allele bins were allocated using GeneMapper (Applied Biosystems), with all automated calling double-checked by

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eye (Bonin et al. 2004). Molecular identification of sex and sequencing of the mtDNA control region (470 bp) followed previously used methods (Olavarria et al. 2007).

Data organisation, analyses of microsatellite allele frequency and analysis of probability of identity for each microsatellite locus and mtDNA were conducted using GenAlEx (Peakall & Smouse 2006). CERVUS (Marshall et al. 1998) and DROPOUT (McKelvey & Schwartz 2005) were used to identify whether any amplified loci were error prone. Based on these analyses, one locus (rw26) was removed from the dataset.

Variation in the number of microsatellite loci amplified successfully suggested relatively poor quality DNA for some samples, particularly from sloughed skin. Following a quality control (QC) review, samples with fewer than 10 successfully amplified microsatellite loci were deleted from the dataset, leaving a total of 1305 QC samples, with an average of 15.2 microsatellite loci each. Given the large number of loci and the potential for false exclusion due to allelic dropout and other genotype error (Waits & Leberg 2000, Waits et al. 2001), the initial comparisons allowed for mismatches at up to three loci.

Genotypic error rates were calculated per allele (Pompanon et al. 2005), using the internal control samples amplified in every PCR. Unique genotypes were resolved with the program CERVUS using criteria that required exact matching for at least 8 loci, supported by control region haplotypes and sex where available. The average probability of identity for the minimum criterion of 8 matching loci ranged from  $1.68 \times 10^{-6}$  to  $2.55 \times 10^{-12}$  (depending on the particular



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combination of 8), calculated following Paetkau et al. (1995). Pairs of genotypes that matched at 8 loci but mismatched at 1 - 3 loci were reviewed and repeated if necessary to verify the individuals' identity or difference.

### *Photo-identification database*

Humpback whales were individually identified from photographs of the ventral fluke pattern (Katona et al. 1979) between 1999 and 2004 from the four primary regions and the other regions listed above. Regional catalogues were compiled and reconciled each year for within-region matches. The regional catalogues were then matched by rational pair-wise comparisons in order to determine between-region re-sightings and a fully reconciled, quality controlled Oceania catalogue was created (Garrigue et al. In Press a). To ensure consistency (Friday et al. 2000) all images were reviewed for quality by one researcher (RC) using the criteria developed for the SPLASH project in the North Pacific (Calambokidis et al. 2008).

### **Capture-recapture analysis**

#### *Datasets*

Two sets of encounter histories were constructed for each individual in the study. The first was based only on sightings in the four primary regions (SYN), whilst the second also included sightings in the five secondary areas (ALL). Each capture occasion consisted of one winter survey season. For the genotype

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dataset they spanned 1999-2005, but there were no data available in 2004 from Tonga and the Cook Islands, while for the photo-ID dataset, encounter histories spanned 1999-2004. Since genetic samples were not available for Tonga and the Cook Islands in 2004, we explored the sensitivity of estimates to this uneven sampling by removing all captures from 2004, and specifying the given sampling intervals (1999-2003, 2005) in the program MARK (White & Burnham 1999).

Humpback breeding grounds and migratory corridors routinely exhibit a male-biased sex ratio which is likely an artefact of migratory behaviour, residency on the breeding ground or other differential behaviour (Brown et al. 1995, Craig & Herman 1997, Palsbøll et al. 1997, Smith et al. 1999). Therefore, for the genotype dataset, data were either analysed as a single group or grouped by sex.

### *Tests of goodness of fit and closure assumptions*

To clarify which models were best to estimate the population, we carried out tests of the goodness of fit of various single state Cormack Jolly Seber (CJS) mark recapture models to the Oceania datasets using the program U-CARE (Choquet et al. 2005). We tested the goodness of fit of models which exhibited 'trap dependence' and 'trap shy' effects, using a CJS framework for the pooled Oceania datasets and for individual regions. Since the data were collected over 6-7 years, several tests were performed to evaluate whether the population has undergone significant input from births and deaths during this time. We performed a variety of tests for population closure using the program

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CLOSETEST (Stanley & Burnham 1999). We pooled datasets for the SYN data into three general regions New Caledonia, Tonga-Cook Islands and French Polynesia. Using these we estimated movement rates between regions and tested a variety of mark recapture models in the multi-strata framework in MARK.

### *Open model abundance estimates*

We estimated the abundance of Oceania using the POPAN formulation of Schwarz & Arnason (1996) as implemented in MARK. This model is an extension of the Jolly-Seber model, and assumes that both captured and un-captured animals are equally likely to be captured on the survey grounds. The POPAN formulation additionally assumes that the animals encountered during the survey periods represent a component of a larger 'super-population', and derives an annual probability of entry of animals from the 'super-population' into the survey regions. Since a number of parameters are non-identifiable in POPAN using time-dependent capture probabilities, we only explored POPAN models with constant (time-independent) capture probabilities.

The Pradel open population model structure (Pradel 1996) was applied to both datasets, co-estimating population growth ( $\lambda$ ) and survival ( $\phi$ ) and deriving abundance estimates from the capture probabilities of the best fitting model under AIC criteria.

**RESULTS**

*Genotype dataset*

Among all samples available from 1999 to 2005, 1305 of the initial 1447 samples (90%) passed the QC criteria of successful amplification at >10 microsatellite loci. Per-allele error rates of 0.58% and per-locus error rates of 1.11% were calculated from the QC dataset; these errors were corrected within the datasets following the initial matching with fewer loci. From the 1305 QC genotypes we identified 843 individuals; 464 males and 285 females, a sex bias of 1.63:1 males to females (95 individuals were of unknown sex). Across Oceania, within-year (1999-2005) sample sizes ranged from 50 to 214 for the SYN dataset, with a total of 94 individuals captured in multiple years (Table 1). The ALL dataset contained within-year sample sizes between 50 and 231, with a total of 117 individuals captured in multiple years (Appendix Tables 1 & 2).

*Photo-ID dataset and recaptures*

A total of 627 individual whales were included in the SYN dataset from the synoptic years. Across Oceania, within-year (1999-2004) sample sizes ranged between 108 and 150 photo-IDs for the SYN dataset, with a total of 93 individuals captured in multiple years (Table 1). When all regions were considered, a total of 660 individual whales were included in the dataset. The ALL dataset contained within-year sample sizes of between 108 and 171 photo-

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1 identifications, with a total of 101 individuals captured in multiple years (Appendix  
2 Table 1).

### 3 4 *Goodness of fit and closure assumptions*

5 Goodness of fit tests for the single-stratum Oceania datasets (photo-ID and  
6 genotype) all returned a significant signal of transience (i.e., a significant number  
7 of individuals seen once and not recaptured) while all other tests were non-  
8 significant, indicating that CJS models with transience represent the best fit to  
9 these datasets. When the genotype datasets were analysed by sex, the  
10 transience signal was highly significant for males only ( $p < 0.001$ , Appendix Table  
11 3). Goodness of fit tests of the multi-strata datasets (each test weighted equally  
12 between the three Oceania strata) did not recover a significant overall transience  
13 signal ( $p = 0.075$  male,  $p = 0.857$  female genotypes;  $p = 0.155$  photo-ID).

14 However,  $\chi^2$  tests of transience within each stratum revealed a significant, male-  
15 specific transience signal ( $p = 0.05$  in 2001 and 2003) within the New Caledonia  
16 stratum.

17 Goodness of fit tests of individual regions were non-significant for Tonga and  
18 French Polynesia, and again revealed a highly significant signal of male-specific  
19 transience in New Caledonia ( $p < 0.01$ , Appendix Table 3). This suggests that the  
20 transience signal originates in New Caledonia, and this heterogeneity in  
21 recapture suggests these individuals are part of a larger Oceania population. For  
22 this reason we argue that open models are currently more appropriate

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### *Abundance estimates: POPAN models*

Estimates of 'super-population' ( $N_{\text{super}}$ ) abundance using the POPAN models are shown in Table 2. This 'super-population' value represents the total number of individuals in the wider region (assuming no mortality component). From this total, a proportion is estimated to enter the survey region each year and therefore available for capture. Annual estimates are derived from these proportions (Figure 2, Appendix Table 4) and are subject to annual mortality also. The initial and final years are not shown because estimates of  $N$  from these years are not fully identifiable and are therefore not biologically interpretable. Total super-population abundance estimates were very similar for the pooled-sex genotype datasets (ALL  $N_{\text{super}} = 3448$ , CV = 0.11; SYN  $N_{\text{super}} = 3307$ , CV = 0.12), while male-specific estimates differed by <100 individuals between the ALL and SYN datasets, but had higher associated precision (Table 2). Super-population estimates (ALL  $N_{\text{super}} = 2133$ , CV = 0.09; SYN  $N_{\text{super}} = 2053$ , CV = 0.11) were lower for the photo-ID datasets compared to the genotype datasets by ~1,300, although levels of precision were similar.

The lowest annual abundances were estimated for the SYN dataset, and were slightly higher when 2004 was excluded (Figure 2). This estimate was also very similar to that obtained by the ALL dataset in the final estimate year (2003). In contrast to the annual estimates, SYN  $N_{\text{super}}$  abundance was higher when 2004 was included (Table 2). The  $N_{\text{super}}$  estimate includes all animals entering the population but does not account for subsequent survival after capture. Estimated apparent survival (deaths and emigrations,  $\phi$ ) in the best fitting model for the

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1 SYN dataset was low ( $\phi = 0.75$ , AICc weight = 0.53). This may explain the low  
2 annual abundances, which are not reflected in the  $N_{\text{super}}$  estimate since survival  
3 is not a component. Overall estimates of male-specific  $N_{\text{super}}$  abundance were  
4 very similar across all three genotype datasets, and doubled (assuming parity of  
5 females) the estimate to 3300 - 3500 whales in the region during the survey  
6 period. Doubling these male-specific estimates yielded total abundance values  
7 similar to those obtained by the combined datasets also.

### 8 *Abundance estimates: Pradel model*

9 Model averaged estimates of population growth ( $\lambda$ ) and apparent survival ( $\phi$ ) in  
10 the Pradel model were within biologically plausible ranges for all datasets  
11 analysed (Table 3). For the genotype datasets, the best fitting model in each  
12 case was  $\phi(.)p(t)\lambda(.)$ , where only capture probability varied over time. We did not  
13 average over any models where two or more parameters were time varying,  
14 since at least one parameter was unidentifiable in all of these models. The SYN  
15 and ALL genotype datasets yielded very similar estimates, with  $\lambda = 1.03$  and  $\phi =$   
16  $0.94 - 0.95$ . The SYN and ALL photo-ID datasets yielded estimates of  $\lambda = 1.06 -$   
17  $1.07$  and  $\phi = 0.96 - 0.97$  (Table 3, Appendix Table 5). No values for survival or  
18 population growth were significantly better fitting to any dataset than  $\phi = 1$  and  $\lambda$   
19  $= 1$  respectively, i.e., there was no significant trend in abundance. Since the sex  
20 ratio of these datasets is skewed towards males, we also analysed the sex-  
21 specific SYN dataset in order to derive male-specific abundance estimates  
22 (Table 3). There was one anomalously low estimate of abundance in this series,  
23 in 2004 ( $N = 891$ ). Since only 24 males were captured across Oceania in 2004,

greater variation in this estimate is to be expected. Precision (CV) of annual p-values ranged from 0.19 - 0.30, with the lowest precision in the initial and final years of estimates. Abundance estimates derived from the Pradel model (genotypes  $N = 2100 - 2800$ , photo-ID  $N = 1630 - 1830$ ) were the smallest among all estimates so far derived from these data. The male-specific estimates ( $N = 1100 - 1400$ , excluding 2004) were 35-60% smaller than the pooled-sex estimates. Therefore doubling these male-specific estimates yields total abundance values similar to those obtained by the combined dataset.

### DISCUSSION

This paper presents the first comprehensive abundance estimates using photo-ID and genotype data for the endangered humpback whales of Oceania. We recommend that the POPAN male-specific super population estimate,  $N = 3520$  ( $CV = 0.1$ ), from the synoptic years is the best estimate for these data. This estimate effectively encompasses animals which remain in the survey areas for some time and transient animals which migrate past to un-surveyed regions without staying. It is also likely to be somewhat positively biased since survival rates are not incorporated.

For a more conservative estimate of breeding ground abundance (in which the effective survival rates have factored out the transients, so animals in un-surveyed regions are not included), we consider that the 2003 male POPAN estimate of abundance from the SYN (2004 excluded) dataset ( $N = 2361$ ,  $CV = 0.11$ , Fig. 2) represents the most plausible abundance of the primary Oceania



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1 survey areas. This value is closely consistent with the abundance estimate from  
2 the ALL dataset and is not influenced by the low effort in 2004, nor by the  
3 potential widening of the survey area over time that could create estimation bias  
4 in the ALL dataset. It is also closely similar to Pradel abundance estimates in this  
5 year (Table 3). In the Pradel model, transients are not likely to be incorporated in  
6 the abundance estimate since this model is conditioned on recaptures, which by  
7 definition do not include transients. We assume that transients are likely to be  
8 members of the Oceania breeding population, possibly from poorly surveyed  
9 regions such as the Chesterfield Reef, offshore seamounts (Garrigue et al. 2010)  
10 or eastern French Polynesia, or animals that are moving through the surveyed  
11 areas, only outside the research periods. We consider that they should be  
12 included as part of the population until any data suggest evidence to the contrary.  
13 Further research in these other areas will help us understand the status of these  
14 transient animals.

15 The estimate of 3520 humpback whales seems to be the most reasonable  
16 estimate of local abundance for the Oceania survey areas. We recognise that  
17 further analysis, using multi-strata models that explicitly incorporate transience in  
18 an open model framework, would be most desirable for this population but  
19 caution that there are substantial uncertainties in the current dataset which do  
20 not easily permit its use in more complex, parameter rich models. Surveys  
21 designed to assess the population size and trend may allow such analyses of  
22 future datasets. Our results support the IUCN 'Endangered' listing for this  
23 population (Childerhouse et al. 2008) and should be considered as a benchmark

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1 in future humpback whale population assessments of the region. It is therefore  
2 the least populous Southern Hemisphere collection of breeding grounds known  
3 to date (Olavarría et al. 2007), despite encompassing an enormous range that  
4 covers much of the South Pacific (Reeves et al. 1999). The population trend  
5 estimates we present here using the POPAN and Pradel models are  
6 indistinguishable from zero, suggesting that for the synoptic years of 1999 -  
7 2005, this population, at least for the surveyed areas, is not recovering at the rate  
8 of neighbouring populations such as east Australia (Paterson et al. 2001,  
9 Paterson et al 2004, Noad et al. 2006 a, Paton et al. In Press).

10 The reasons for the low abundance and lack of a measurable increase in number  
11 may lie in the intensive hunting pressure on humpback whales south of New  
12 Zealand, especially in later years by Soviet whaling fleets on an already severely  
13 depleted stock (Clapham et al. 2009). Whaling in these waters is the most likely  
14 explanation for the dramatic decrease in whale sightings in regions like Fiji and  
15 New Zealand where whales were frequently sighted in the 1950s but which  
16 exhibit only a slow recovery rate today (Dawbin 1956, Gibbs & Childerhouse  
17 2000, Gibbs et al. 2006). Further research on calving rates, mortality and  
18 understanding links to their Antarctic feeding grounds may help understand the  
19 reasons behind this slow recovery rate.

### 20 21 *Comparison of the ALL and SYN datasets*

22 In general, the photo-ID and genotype ALL datasets produced slightly larger  
23 abundance estimates than the SYN datasets, but the magnitude of the difference

1 was not large or significant. This suggests that most whales have been captured  
2 within the synoptic regions, since increasing regional coverage has not led to a  
3 significant increase in abundance. It must be noted that effort in these secondary  
4 areas was low, with the exception of American Samoa. The precision of  
5 estimates for the genotype SYN dataset was slightly better than for the ALL  
6 dataset when all datasets are compared (Table 2). With this in mind, it is unlikely  
7 that increasing the number or range of survey areas will result in a significant  
8 difference to future estimates. If other primary areas were included in future  
9 surveys, for example American Samoa, the research effort would need to be  
10 comparable to the other regions to ensure a robust CV.

11

### 12 *Limitations*

13 We used open mark-recapture models as they were the best fit to our datasets,  
14 whilst recognising that assumptions in these models regarding equal effort  
15 across regions are probably still violated. The pooled Oceania abundance  
16 estimates are based on low capture probabilities ( $<0.1$ ), which are associated  
17 with model instability and substantial variance in abundance estimates within  
18 each model framework. As the survey region is large and data collection  
19 resources limited, it is unlikely that these recapture values will be increased.  
20 Oceania is known to have significant population structuring across breeding  
21 regions (Olavarria et al. 2007), yet our analysis is based on data pooled from  
22 across these regions; pooled models assume similar effort across all regions.  
23 Despite this, the sum of regional estimates of abundance is roughly consistent

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1 with the overall estimate from the pooled dataset, suggesting that the bias  
2 incurred by the difference in regional effort may not be too substantial.

3 The genotype estimates were consistently larger than the photo-ID estimates but  
4 both found fewer than 5000 individuals in Oceania. These differences are likely  
5 driven by a number of factors, including differences in data collection strategies,  
6 different levels of effort over regions and between years, and the differential  
7 availability of various age- and sex-classes of whales for the two survey  
8 methods. For example, whales are thought to be less available for photo-ID  
9 capture when on migration (as they are less likely to show their flukes when  
10 diving (Perkins et al. 1985)) this could be the case for the transient individuals.

11 We are also unable to directly account for any sex specific capture heterogeneity  
12 in the photo-ID data, as the sex of most of these whales is unknown. We hope  
13 that future simulations to explore the causes of these differences will enable us to  
14 better explain this disparity.

15 Given that the sex ratio of genotype captures is not at parity (1.63:1 males to  
16 females), and we have no reason not to expect the sex ratio of the photo-ID  
17 dataset to be similarly skewed, models which do not take this capture bias into  
18 account may underestimate the true abundance of humpback whales utilising the  
19 region. This is because available feeding ground data suggests that the  
20 humpback populations are at sexual parity (Glockner-Ferrari & Ferrari 1990,  
21 Clapham et al. 1995) but a consistent pattern of genetic capture of more males  
22 than females on breeding grounds and migratory routes is emerging (Brown et al.  
23 1995, Craig & Herman 1997, Smith et al. 1999). This suggests that females may

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be less available for genotype or photo-ID capture on the breeding grounds possibly due to sex specific differences in behaviour or residency times (Craig & Herman 1997). We therefore suggest that abundance estimates based on the male-specific genotype data, doubled to attain an equal-sexes estimate of total abundance, represents the most appropriate estimate of true humpback whale abundance in the region surveyed (Palsbøll et al. 1997).

### *Management implications*

Our research supports the recent IUCN Endangered listing (Childerhouse et al. 2008) for this population and the trend of very low recovery rate for this population is of concern as it contradicts almost all other known humpback populations. The sanctuaries created throughout the South Pacific are important in protecting the humpback whales from anthropogenic threats such as habitat degradation (e.g., mining in New Caledonia, gear entanglement) and the rapid growth in whale watching (O'Connor et al. 2009; Schaffar et al. 2010). Surveys in remote areas of Oceania such as eastern French Polynesia, the Chesterfield Islands, Pitcairn Island and remote island groups in Fiji and Vanuatu should be conducted to gather a clearer picture of the Oceania population size and range. The interchange rate between humpback whales from east Australia and Oceania is extremely low but we have yet to determine the degree of isolation between these two regions (Anderson et al. 2010, Garrigue et al. In Press b). We recommend that another population estimate should be undertaken to provide

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further trends of recovery. This will allow ongoing assessment of their recovery which will hopefully be as successful as most others throughout the world.

### **ACKNOWLEDGEMENTS**

This research is a contribution by the South Pacific Whale Research Consortium. We were generously funded by the International Fund for Animal Welfare, French Fonds Pacifique (through Opération Cétacés), the National Marine Mammal Laboratory, the Australian Department of Water, Heritage and Arts' RNHP Fund, and the International Whaling Commission Scientific Committee. Thanks to the NZ MoRST funded Broadband enabled Science and Technology GRID (BeSTGRID) for collaborative data storage space. We thank all our collaborators in and out of the field over the years that this research has taken. Research in New Caledonia was made possible by the Provinces Sud, North and Isles, Inco S.A, Fondation d'Entreprise Total and Total Pacifique and Opération Cétacés was issued a permit by the Province Sud. The Tongan research was conducted under a University of Auckland Animal Ethics permit (CSB) and a research permit issued by the late Tāufa 'āhau Tupou IV, King of Tonga. Research in the Cook Islands was permitted by the Government of the Cook Islands. Research in American Samoa was supported by the American Samoa Division of Marine and Wildlife Resources, the Fagatele Bay National Marine Sanctuary and the U.S. National Park of American Samoa. Research activities were conducted under NOAA fisheries permit 774-1437 and a scientific permit issued by the Government of American Samoa. Research in French Polynesia was permitted

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by the High Commissioner's Office and the Ministry of the Environment and was supported by West Marine Products, Mike Poliza of the Starship Millennium Voyage, the Office des Postes et Telecommunications, Sin Tung Hing Marine and Mercury outboards, Eric Leborgne, Renee Albertson, Hardy Jones-Julia Whitty Productions, Yves Lefevre and the Raie Manta Club, Cine Marine, Marie-Helene Bacconnet, the National Oceanic Society, and Dolphin & Whale Watching Expeditions. We would like to thank our colleagues, especially at the IWC Scientific Committee, who made helpful comments on earlier drafts of this manuscript.

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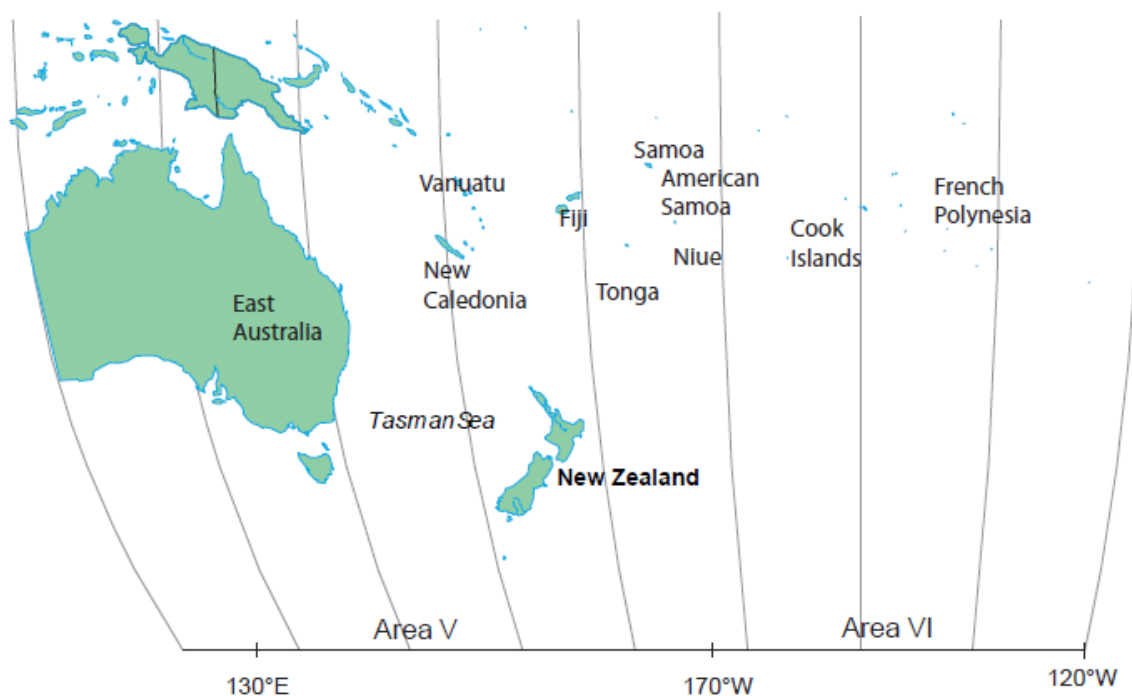
15



1 **FIGURES & TABLES**

2

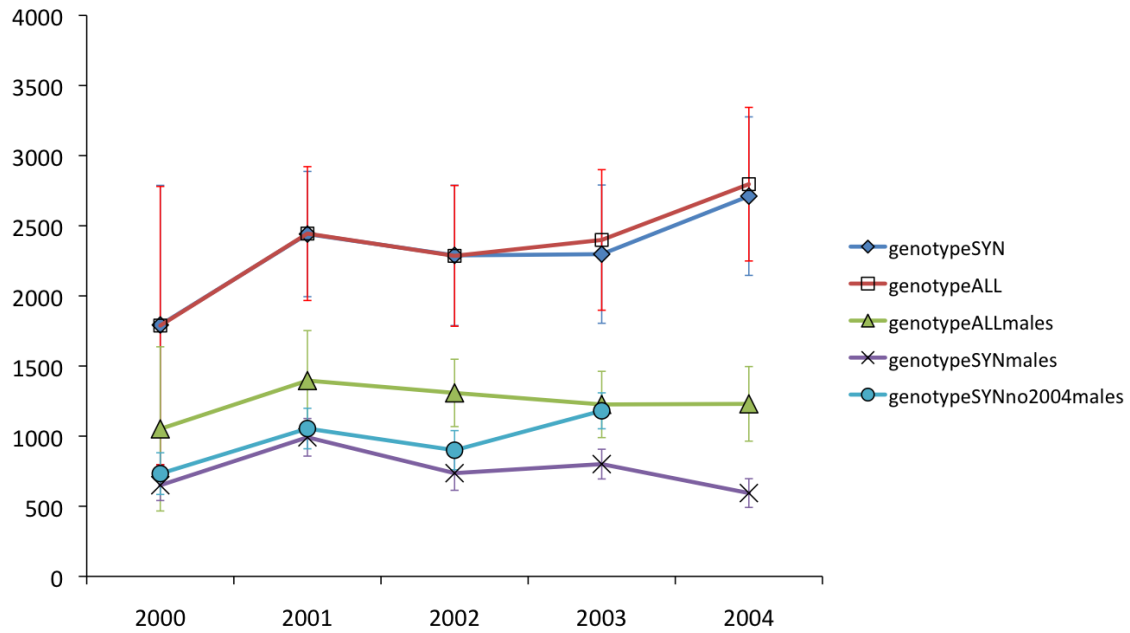
3 Figure 1. Map of Oceania showing the primary and secondary study sites.



4  
5

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- 1 Figure 2. Annual estimates of abundance with associated standard errors shown
- 2 as vertical bars. These are derived from AIC-preferred models for each dataset
- 3 using the Delta method in the POPAN open population model.



4

5

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- 1 Table 1. Summary of humpback whales identified by (A) microsatellite genotypes  
 2 or (B) fluke photographs, shown by year of capture and recapture across the four  
 3 synoptic survey regions (New Caledonia, Tonga, Cook Islands and French  
 4 Polynesia).

### A. Genotypes

Year	1999	2000	2001	2002	2003	2004	2005
Individuals (ind) captured	50	115	181	130	214	79	154
Total ind. captured	50	162	332	445	623	689	807
Number of recaptures	1	2	3				Total
Individuals	76	14	4				94
Year of recapture							
Year of Initial Capture	1999	2000	2001	2002	2003	2004	2005
1999	X	3	7	3	6	2	2
2000		X	4	5	9	3	6
2001			X	9	17	4	8
2002				X	4	2	8
2003					X	2	8
2004						X	4
2005							X

5

### B. Fluke Photographs

Year	1999	2000	2001	2002	2003	2004
Individuals captured	108	124	132	114	150	110
Cumulative # ind. captured	108	226	338	434	551	627
Number of recaptures	1	2	3			Total
Individuals	76	16	1			93
Year of recapture						

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Year of Initial Capture	1999	2000	2001	2002	2003	2004
1999	X	6	13	5	8	6
2000		X	7	8	10	10
2001			X	5	7	8
2002				X	8	2
2003					X	8
2004						X

1

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1 Table 2. Open population POPAN mark-recapture ‘super-population’ abundance  
 2 estimates ( $N_{super}$ ) from photo-ID data and microsatellite genotypes. Estimates  
 3 were AIC weighted using model-averaging in MARK.

4

Dataset	Nsuper	SE	CV	Confidence intervals	Model variation %
Genotype					
ALL – males	1683	222	0.13	1248-2118	5
ALL – females	1050	163	0.16	731-1370	13
ALL – males * 2	3363				
SYN – males	1760	175	0.10	1417-2103	1
SYN – females	1110	125	0.11	864-1355	4
SYN – males * 2	3520				
SYN without 2004- males	1631	162	0.10	1313-1948	1
SYN without 2004- females	1022	114	0.11	798-1246	1
SYN without 2004 – males * 2	3262				
Genotype – all individuals					
ALL	3448	385	0.11	2694-4202	1
SYN	3307	389	0.12	2546-4069	0
Photo-ID					
ALL	2133	201	0.09	1738-2527	4
SYN	2053	231	0.11	1600-2505	7

5

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Table 3. Model-averaged estimates of apparent survival ( $\phi$ ) and apparent population growth ( $\lambda$ ) estimated for pooled SYN Oceania genotype and photo-ID datasets. Capture probabilities over time ( $p_t$ ) for each dataset were estimated from the best fitting AICc-weighted Pradel model in MARK. Abundance was derived by dividing capture probabilities with the number of animals captured in each year ( $p/n$ ). Confidence intervals were derived from the 95% confidence intervals of each capture probability.

Genotype			Genotype males		Photo-ID	
$\phi$	0.95		0.92		0.96	
SE (CI)	0.07 (0.54-1.00)		0.07 (0.64-0.99)		0.07 (0.41-1.00)	
$\lambda$	1.03		0.97		1.07	
SE (CI)	0.07 (0.89-1.17)		0.07 (0.34-1.00)		0.12 (0.82-1.31)	
Year	pt	Nt (CI)	pt	Nt (CI)	pt	Nt (CI)
1999	0.023	2175 (1191-4007)	0.023	1099 (608-2003)	0.06	1824 (1053-3222)
2000	0.051	2243 (1404-3631)	0.052	1340 (846-2150)	0.07	1785 (1140-2839)
2001	0.078	2314 (1575-3444)	0.083	1354 (927-2004)	0.08	1747 (1190-2597)
2002	0.054	2387 (1652-3476)	0.062	1260 (872-1836)	0.07	1710 (1170-2527)
2003	0.087	2461 (1702-3608)	0.099	1152 (793-1703)	0.09	1674 (1108-2575)
2004	0.031	2539 (1587-4091)	0.027	891 (537-1490)	0.07	1639 (983-2784)
2005	0.059	2618 (1543-4525)	0.074	1106 (645-1949)	0.06	1824 (1053-3222)

**SUPPLEMENTARY MATERIAL**

**Appendices**

Appendix Table 1. Numbers of individuals captured by year and total numbers of recaptures across all survey regions (ALL); A. Genotype database summary; B. Photo-ID dataset summary.

A. Genotypes							
Year	1999	2000	2001	2002	2003	2004	2005
Ind captured	50	115	182	130	231	95	162
Total ind captured	50	162	333	446	640	719	843
Number of recaptures	1	2	3				Total
Total Ind	99	14	4				117
B. Fluke Photographs							
Year	1999	2000	2001	2002	2003	2004	
Individuals (Ind) captured	108	124	135	115	171	128	
Total Ind captured	108	226	341	437	570	660	
Number of recaptures	1	2	3				Total
Total Ind	82	18	1				101

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Appendix Table 2. Total genotype captures and recaptures across synoptic regions for males and females.

Males	1999	2000	2001	2002	2003	2004	2005
Individuals captured	25	70	112	78	114	24	82
Total individuals captured	25	92	197	265	358	377	436
Year of recapture							
Year of Initial Capture	1999	2000	2001	2002	2003	2004	2005
1999	X	3	4	0	3	0	1
2000		X	3	3	6	2	6
2001			X	7	10	2	5
2002				X	2	0	4
2003					X	1	5
2004						X	2
2005							X
Year of recapture							
Year of Initial Capture	1999	2000	2001	2002	2003	2004	2005
1999	X	0	3	3	3	2	1
2000		X	1	2	3	1	0
2001			X	2	7	2	3
2002				X	2	2	4

Females	1999	2000	2001	2002	2003	2004	2005
Individuals captured	25	41	58	45	76	26	51
Total individuals captured	25	66	120	158	219	228	277
Year of recapture							
Year of Initial Capture	1999	2000	2001	2002	2003	2004	2005
1999	X	0	3	3	3	2	1
2000		X	1	2	3	1	0
2001			X	2	7	2	3
2002				X	2	2	4



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2003	X	0	2
2004		X	2
2005			X

---

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- 1 Appendix Table 3. Summary of results from U-CARE tests of goodness of fit between the data and various CJS models.
- 2 Tests which are significant at  $p < 0.05$  by one test (\*) or two tests (\*\*) are shown. With the statistic for trap dependence,
- 3 positive values indicate 'trap-shyness' and negative values 'trap-happiness'.

4

	Genotype SYN		Photo-ID SYN	New Caledonia	Tonga	French Polynesia
Test Type	Male	Female				
<i>3.SR</i>						
N(0,1) statistic for transience	4.22**	1.49	2.60**	M: 3.51** F: 1.38	M: 0.50 F: 0	F+M: 0
Log-Odds-Ratio statistic for transience	3.75**	1.08	2.50**	M: 3.67** F: 1.54	M: 1.35 F: 0.59	F+M: 0.36
$\chi^2$	21.35*	3.44	13.2	M: 15.99** F: 4.73	M: 0.74 F: 0	F+M: 0
G2	19.55*	3.44	11.7	M: 15.57** F: 4.73	M: 0.74 F: 0	F+M: 0
<i>3.SM</i>						
$\chi^2$	2.24	0.44	0.70	M: 1.51 F: 0.66	M+F: 0	N/A
G2	2.24	0.44	0.70	M: 1.51 F: 0.66	M+F: 0	N/A
<i>2.CT</i>						
N(0,1) statistic for trap dependence	1.04	2.89*	0.04	M: 0.21 F: 1.90	M: 0.52 F: 0.37	M: 0 F: 0
Log-Odds-Ratio statistic for trap	1.30	2.71*	-0.09	M: 0.21 F: 2.02	M: 1.14 F: 0.84	M:-0.95 F: 1.34

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dependence						
$\chi^2$	4.13	9.43	2.91	M: 1.58 F: 5.31	M: 1.17 F: 0.41	M: 0 F: 0
G2	4.27	9.53*	2.99	M: 1.58 F: 5.31	M: 1.17 F: 0.41	M: 0 F: 0
<i>2.CL</i>						
$\chi^2$	0.66	4.68	0.53	M: 0.19 F: 0.22	M: 0.41 F: 0	N/A
G2	0.66	4.95	0.53	M: 0.19 F: 0.22	M: 0.41 F: 0	N/A

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1 Appendix Table 4. POPAN annual estimates of population abundance, derived from the  
 2 genotype datasets using the Delta method in program MARK. Estimates from the initial  
 3 and final years of data collection have been removed as they are non-interpretable.

4

Year	ALL		SYN		ALL Males		SYN Males		SYN (no 2004) males	
	<i>N</i>	<i>CV</i>	<i>N</i>	<i>CV</i>	<i>N</i>	<i>CV</i>	<i>N</i>	<i>CV</i>	<i>N</i>	<i>CV</i>
2000	1788	0.55	1793	0.56	1052	0.56	650	0.17	733	0.21
2001	2444	0.20	2241	0.18	1396	0.26	992	0.14	1054	0.14
2002	2286	0.22	2289	0.22	1308	0.18	736	0.17	900	0.16
2003	2399	0.21	2298	0.21	1226	0.19	801	0.13	1181	0.11
2004	2797	0.20	2711	0.21	1230	0.22	594	0.17		

5

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1 Appendix Table 5. Model-averaged estimates of apparent survival ( $\phi$ ) and apparent population growth ( $\lambda$ ) estimated for  
 2 pooled Oceania genotype and photo ID datasets. Capture probabilities over time ( $p_t$ ) for each dataset were estimated  
 3 from the best fitting AICc-weighted Pradel model in MARK. Abundance was derived by dividing capture probabilities with  
 4 the number of animals captured in each year ( $p/n$ ). Confidence intervals were derived from the 95% confidence intervals  
 5 of each capture probability.

6

Genotype ALL			Photo ID ALL	
$\phi$	0.94		0.97	
SE (CI)	0.07 (0.59-0.99)		0.06 (0.31-1.00)	
$\lambda$	1.03		1.06	
SE (CI)	0.07 (0.90-1.18)		0.12 (0.83-1.29)	
Year	$p_t$	$N_t$ (CI)	$p_t$	$N_t$ (CI)
1999	0.023	2167 (1187-3993)	0.06	1732 (1015-3018)
2000	0.051	2251 (1408-3645)	0.07	1737 (1122-2732)
2001	0.078	2338 (1594-3474)	0.08	1741 (1201-2556)
2002	0.054	2428 (1692-3513)	0.07	1746 (1215-2535)
2003	0.092	2522 (1773-3636)	0.10	1751 (1193-2613)
2004	0.036	2620 (1687-4099)	0.07	1756 (1095-2867)

**Description of secondary regions**

*American Samoa*

The research in American Samoa focused on the coastal waters of Tutuila (170°0' W and 14°19' S) in 2003 and 2004 (Robbins & Mattila 2006). Densities of whales frequenting these waters (noting that Tutuila is the only island survey to date) are similar to those found in New Caledonia, Tonga and French Polynesia which suggests that American Samoa is an important breeding ground for whales in Oceania. There is interchange between whales from American Samoa and other Oceania regions (Garrigue et al. In Press a).

*Samoa*

Boat-based surveys were conducted in Samoa (173-170° W and 13° S) in 2001. Samoa is approximately 70km north northwest of American Samoa and has nine islands and several seamounts. Research was focused in the waters of one of the main islands, Upolu, with low sighting rates of whales compared to American Samoa (Noad et al. 2006 b).

*Vanuatu*

Research was conducted in the southern islands of Vanuatu (168° E, 17° S) in August 2003 with the majority of whales seen near Tanna (Garrigue et al. 2004). Whales identified in Vanuatu have been re-sighted in New Caledonia and Tonga (Garrigue et al. In Press a).

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### 1 *Niue*

2 Research was conducted in Niue (169°52' W, 19°02' S) in the winter of 2001. Whales  
3 were infrequently sighted but mother-calf pairs are observed and whales have been re-  
4 sighted in Tonga (Garrigue et al. In Press a).

### 5 *Fiji*

6 Fiji (178° E, 18° S) has two main islands with many small islands scattered throughout.  
7 Data were collected from primarily land-based surveys on Lomaiviti Island in 2002 and  
8 2003 (Gibbs et al. 2006). Sighting rates were very low, especially when compared to  
9 data collected from the same site in the 1950s, with no other area in Fiji currently  
10 highlighted as a high density humpback area.