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Abundance and interchange of humpback whales in Oceania based on fluke photo-identification and DNA profiling

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ABSTRACT

The abundance of humpback whales on breeding grounds from Oceania (New Caledonia to French Polynesia), was estimated using individual identification photographs collected between 1999 and 2004 and microsatellite genotypes collected between 1999 and 2005. Both datasets were reviewed for quality control, resulting in a total photo-ID catalogue of 660 individuals and a genotype catalogue or DNA register of 436 males and 277 females. A number of estimates were calculated using both open and closed models, including sex-specific estimates from the genotypes. The population estimates showed some variation depending on the assumptions of the models and different pooling of the sighting-resighting histories (e.g., by dataset, by sex, by region, or pooled across regions by year). Using closed population estimates, the regional estimates of abundance were greatest for Tonga (N=1,840 using genotypes and N=1,168 CV=0.16 using photo-ID), with about half this number in French Polynesia (N=934 using genotypes and 440 CV=0.23 using photo-ID) and New Caledonia (N=804 using genotypes and 383 CV=0.35 using photo-ID). A Pradel model showed no significant trend in abundance for this population, supporting the conclusion from previous population dynamic models that recovery in the region is much lower than in the adjacent eastern Australia. The genotype database revealed a sex-bias in capture towards males (1.6:1 males : females), so genotypic estimates of abundance were derived by doubling the male-specific estimates, assuming that the true sex ratio is at parity. For the purposes of future modelling efforts intended for completing of the Comprehensive Assessment, we consider the most optimistic estimate of total abundance for Oceania to be 3,520 whales (CV = 0.1) in 2005, using the POPAN model estimate of total 'super-population' abundance. There is a significant transience signal in the dataset, which may indicate that a proportion of the whales captured in the survey region are travelling to areas not yet surveyed in Oceania. The POPAN 'super-population' estimate is therefore favoured because it is inclusive of both animals resident to the surveyed breeding grounds and those migrating past to unsurveyed regions. However it is likely to be positively biased by the assumption of zero mortality over the survey period. Among all other male-derived genotype abundance estimates presented in this study (range of N=1,000-4,800), the male-specific Pradel and POPAN estimates from 2003 were closely similar (doubled estimates of males; POPAN N=2,361 CV=0.11; Pradel N=2,304). We therefore propose the POPAN estimate in 2003 as a reasonable estimate of abundance in the primary survey regions in Oceania, but conclude that true abundance in the wider Oceania area is likely to fall between this estimate and the higher super-population estimate of 3,520 whales.

KEYWORDS: HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, OCEANIA, SOUTH PACIFIC, CAPTURE-RECAPTURE, PHOTO-IDENTIFICATION, GENOTYPING

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) congregate during the winter months to breed in Oceania (South Pacific) waters from western New Caledonia (~160°E) to the French Polynesian archipelago (~120°W) (Townsend, 1935). It is generally assumed that whales found throughout the islands and coral atolls of western Oceania migrate past New Zealand and Norfolk Island and possibly east Australia between the International Whaling Commission (IWC) Antarctic Areas V and VI feeding grounds (Constantine *et al.*, 2007; Dawbin, 1964; Dawbin, 1966; Garrigue *et al.*, 2000; Garrigue *et al.*, 2010). The central and eastern migratory routes are not yet well defined but recent satellite telemetry work has shown migration to the productive summer feeding grounds without passing land (Hauser *et al.*, 2010).

Whaling for humpbacks began in the late 19th century and post-World War II led to more than 45,000 whales being killed in the Southern Ocean region associated with Oceania (Areas V and VI). More than one third (25,192) of these whales were killed during two summer seasons; 1959-60 and 1960-61 (Clapham *et al.*, 2009). The greatest impact was rendered by illegal Soviet whaling (1947-73), which killed more than 13,000 humpbacks in the region south of Oceania in just one summer season (1961-62).

Since whaling ceased in 1978, recovery of breeding grounds in the Oceania region has been variable. Strong increases in abundance have been observed in east Australia (Paterson *et al.*, 2001; Noad *et al.*, 2006 a) while the numbers of humpback whales in the breeding grounds of Oceania appear to remain low, including areas where numerous whales were previously reported e.g., Fiji (Dawbin, 1959; Garrigue *et al.*, 2004; Gibbs *et al.*, 2006). Of interest is reports of humpback whales further east than observed prior to whaling but the feeding ground origins of these whales have not yet been determined (e.g., French Polynesia (Poole, 2006; Gibb, 2009)).

Field studies of the current humpback breeding grounds in Oceania have been in progress since winter 1991. These studies have included photographic identification and the collection of skin biopsy (or sloughed skin) samples and have provided information on the whales' distribution, movements, abundance, behaviour, genetic differentiation and diversity (Garrigue *et al.*, 2004; Garrigue *et al.*, In Press a; Hauser *et al.*, 2010; Olavarría *et al.*, 2007). In 1999, the South Pacific Whale Research Consortium commenced a coordinated, synoptic survey of four primary island regions spread across Oceania; New Caledonia, Tonga (Vava'u), the Cook Islands and French Polynesia (Moorea and Rurutu). An additional eight other regions of Oceania were included in the photo-ID survey, since the above represent a small proportion of the available habitat for humpback whales. These were Vanuatu, Independent Samoa, American Samoa, Fiji, Niue, and the other Tongan island groups; Ha'apai, Niuatoputapu and Eua. A comparison of re-sightings within and between regions found the greatest number of re-sights within regions, while between-region re-sights varied considerably but most were between neighbouring sites (Garrigue *et al.*, In Press a). When the Oceania fluke catalogue was matched to east Australia fluke catalogues, only four matches were found among over 710,000 comparisons suggesting extremely low levels of interchange with east Australia (Garrigue *et al.*, In Press b).

Here we report the results of an exhaustive photo-ID reconciliation (between- and within-region matching) of humpback whale fluke catalogues from the four primary regions of Oceania (1999-2004) and five other regions in Oceania (American Samoa, Independent Samoa, Vanuatu, Niue and Fiji; surveyed from 2003 onwards). Biopsy and sloughed skin samples collected from the four primary study sites were used to obtain microsatellite genotypes of 12-16 loci from 1999-2005. These datasets have been used to derive estimates of abundance for the humpback whales of Oceania using closed and open population capture-recapture models. This summary is intended to contribute towards the upcoming Comprehensive Assessment of Southern Hemisphere Humpback whales for the IWC breeding stocks E2, E3 and F.

METHODS

Study regions

For the purpose of this paper, we define Oceania as the large area of islands in the south-western and south-central Pacific Ocean, stretching from New Caledonia in the west to French Polynesia in the east; geographically, however, Oceania includes a much larger area of island groups in both southern and northern hemispheres (Figure 1). Dedicated surveys for humpback whales in this region were conducted during the austral winters of 1999 to 2004 in four areas: New Caledonia, Tonga, the Cook Islands and French Polynesia. We refer to these as the 'primary study regions' and the years 1999 to 2004 as the 'synoptic years'. A detailed description of the study sites and effort can be found in Garrigue *et al.* (In Press a). It is important to stress that the four primary regions represent only a small proportion of potentially available habitat for humpback whales in Oceania. For this reason, photographs were collected as part of directed or opportunistic surveys in eight other regions or sub-regions of the South Pacific during a subset of the synoptic years.

American Samoa
In American Samoa the research has been focused on the coastal waters of Tutuila (14°19' S and 170°0' W) in 2003 and 2004. Tutuila (the largest island in the group) has the greatest concentration of whales including mother-calf pairs (Robbins and Mattila, 2006). Densities of whales frequenting these waters 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).

Independent 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).

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

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

Photo-identification database
Humpback whales were individually identified from photographs of the ventral fluke pattern (Katona *et al.*, 1979). Regional catalogues were compiled of photographs that could potentially be matched and these were 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 (Garrigue *et al.*, In Press a). All images were then reviewed for quality control using the criteria developed for the SPLASH programme in the North Pacific (Calambokidis *et al.*, 2008). There were five categories for reviewing each photograph and any image that received a score of four or five in any of the categories was judged to be insufficient to be included in the dataset. As recommended by Friday (1997) and Friday *et al.* (2000), the quality control was undertaken by one experienced researcher (RC) to ensure consistency. Once the quality control was completed, a fully reconciled, quality controlled catalogue was created and a rational pair-wise comparison of photographs was undertaken to ascertain matches within- and between-regions (Garrigue *et al.*, In Press a).

Microsatellite database
Biopsy and sloughed skin samples were collected from six breeding regions in Oceania (New Caledonia, Tonga, Cook Islands, French Polynesia, Independent 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) as modified for small skin samples (Baker *et al.*, 1994). Up to 17 microsatellite loci were amplified for 1,447 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 and 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 eye (Bonin *et al.*, 2004). Molecular identification of sex and sequencing of the mtDNA control region (470 bp) followed methods previously described in detail by Olavarría *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 the program

GenAlEx (Peakall and Smouse, 2006). CERVUS (Marshall *et al.*, 1998) and DROPOUT (McKelvey and Schwartz, 2005) were used to identify whether any amplified loci were error prone. High error rates were identified using DROPOUT's DCH test, and CERVUS was then used to investigate whether removal of loci increased the number of high-quality genotype matches. 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. Following a quality control (QC) review, samples with fewer than ten successfully amplified microsatellite loci were deleted from the dataset, leaving a total of 1,305 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 and Leberg, 2000; Waits *et al.*, 2001), the initial comparison allowed for mismatches at up to three loci.

Given these low values, we assumed that genotypes matching at eight or more loci were likely to represent replicate samples (true recaptures) of the same individual whales, and that any mismatching loci were likely to represent genotype error (Hoffman and Amos, 2005) since the probabilities of identity ($P_{(ID)}$) and of sibling identity ($P_{(ID)sib}$) are expected to be sufficiently small to preclude matching by chance in a population of several thousand individuals (Waits *et al.*, 2001). Where samples matched at six to eight loci, we genotyped additional loci in order to verify the match. 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 eight loci, supported by control region haplotypes and sex where available. Under these criteria, the 1,305 QC samples yielded 843 unique genotypes from the six breeding grounds.

Capture-recapture analysis

Datasets

Pooled encounter histories were constructed, covering all regions which have been surveyed in Oceania (including non-synoptic regions American Samoa, Independent Samoa, Vanuatu, Niue and Fiji which were surveyed for 1-3 years in the latter part of the study period), and for synoptic regions only (New Caledonia, Tonga, Cook Islands, French Polynesia); these datasets are referred to as ALL and SYN datasets respectively. Each capture occasion is represented by one winter survey season (the period when humpback whales visit breeding grounds). For the photo-ID dataset, encounter histories spanned 1999-2004 (six occasions), while for the genotype dataset they spanned 1999-2005 (seven occasions), because there was no data available in 2004 from Tonga and the Cook Islands. We explored models for estimating abundance for all of these datasets. For the genotype dataset, since there were a number of individuals of unknown sex, data were either analyzed in *toto* or stratified by sex.

Since genetic surveys were not carried out in 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 MARK.

Regional datasets from New Caledonia, Tonga and French Polynesia were analysed separately. Encounter histories for these regions were generated from the photo-ID and genotype (total individuals, individuals stratified by sex) datasets.

Tests of goodness of fit, closure assumptions

Tests of the goodness of fit of various single state Cormack Jolly Seber (CJS) mark recapture models to the Oceania datasets were carried out 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 Cormack Jolly Seber framework for the pooled Oceania datasets and for individual regions.

Since the data were collected over 6-7 years, a number of tests were performed in order 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 CLOSETEST (Stanley and Burnham, 1999).

Estimating abundance I: 'closed' models

Abundance was estimated from the principal datasets (SYN and ALL) from the SYN dataset with the 2004 capture occasion removed, and for regional datasets (New Caledonia, Tonga and French Polynesia) for each data type using closed models. We investigated the fit of models which vary in capture probability over time (Mt), among individuals within the population (heterogeneity, Mh), and between initial capture and subsequent capture

occasions (behaviour, Mb) and combinations of these models using the program MARK. Model fit was evaluated according to the Akaike Information Criterion (AIC), which penalises the likelihood score of each model with the number of parameters required to fit it. While mark recapture models incorporating genotype error (as mis-identification of individuals) are available, errors were exhaustively identified in the genotype dataset and removed prior to mark recapture analysis. The Type I error in this dataset based on mis-identification was therefore considered to be negligible.

In exploring the effect of heterogeneity, we assumed that the population contains a discrete mixture of two groups of whales (π=2) with different capture probabilities. Mixtures containing any number of groups can be calculated, but since there is no *a priori* reason for choosing one in particular, we opted to choose the simplest model. Model averaging over the best fitting models was carried out using normalised AIC weightings, and yielded averaged estimates of abundance and unconditional standard errors (standard errors accounting for model selection uncertainty) and confidence intervals. The fit of alternative models of capture heterogeneity was also explored using program CAPTURE (capture probabilities varying across the population according to a probability distribution, Otis *et al.*, 1978). We calculated the best-supported models from the variety available in program CAPTURE (using a model selection algorithm described in Otis *et al.*, 1978), since the Mh models incorporating a distribution of capture heterogeneity across the population (e.g., Chao, 1988; Otis *et al.*, 1978) may be a better fit to the data than the discrete mixture model available in MARK.

Estimating abundance: 'open' models

We estimated the abundance of Oceania using the POPAN formulation of Schwarz and 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.

Johnston and Butterworth (2008) recently presented an assessment model which incorporates capture histories directly into a population dynamic model likelihood framework, and can therefore simultaneously co-estimate trend, abundance and interchange directly within this framework. A recent workshop on humpback assessment methodology agreed that the mark recapture model developed within this framework was most similar to the Pradel open population model structure (IWC, 2010). Therefore, in view of the upcoming Comprehensive Assessment of Oceania humpbacks (IWC stocks E2, E3 and F), we also applied the Pradel open population model (Pradel, 1996) to both datasets, co-estimating population growth (λ) and survival (ϕ) and deriving abundance estimates from the capture probabilities of the best fitting model under AIC criteria.

RESULTS

Photo-ID dataset and recaptures

Across Oceania, within-year (1999-2004) sample sizes ranged between 108 and 150 for the SYN dataset, with a total of 93 individuals captured in multiple years (Table 1). When all regions were considered, the ALL dataset contained within-year sample sizes of between 108 and 171, with a total of 101 individuals captured in multiple years (Table 2).

Genotype dataset and recaptures

Among all samples available from 1999-2004, 1,305 of the initial 1,447 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. Average probability of identity (PI) for the minimum criterion of 8 matching loci ranged from 1.68×10^{-6} to 2.55×10^{-12} (depending on the particular combination of 8) as calculated following Paetkau *et al.* (1995).

Among 843 total individuals which exceeded the minimum criteria for inclusion in the quality controlled dataset, 464 were males and 285 were females, with 95 individuals of unknown sex; a sex bias of 1.63:1 males to females. 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). When all regions were considered, the ALL dataset contained within-year sample sizes of between 50 and 231, with a total of 117 individuals captured in multiple years (Table 2).

Goodness of fit and closure assumptions

Goodness of fit tests for the single-stratum Oceania datasets (photo-ID and genotype) all returned a significant signal of transience (*i.e.*, a significant number of individuals seen once and not recaptured) while all other tests were non-significant, indicating that CJS models with transience represent the best fit to these datasets among the models tested. When the genotype datasets were analyzed by sex, the transience signal was highly significant for males only ($p<0.001$, Appendix 3). Goodness of fit tests of individual regions were non-significant for Tonga and French Polynesia, and again revealed a highly significant signal of male-specific transience in New Caledonia ($p<0.01$, Appendix 4). This suggests that the transience signal originates in New Caledonia, and that otherwise standard CJS assumptions are not violated by these data.

There were no significant closure violations detected for any of the datasets analysed, suggesting that the impact of births, deaths, emigration and immigration over the study periods is not significant enough to violate the assumptions of the closed model framework.

Estimating abundance I: 'closed' models

Capture probabilities were low (~0.05 for both sexes and combined) for all genotype datasets (Appendix 5); this is likely to create substantial uncertainty in the derived abundance estimates, with large standard errors. Low capture probabilities drive model instability, so from these low values, it can be predicted that estimates of abundance will vary between models and datasets. Capture probabilities were slightly higher (0.06-0.08) for the photo-ID datasets (Appendix 5).

Genotypic estimates of N by sex were relatively consistent between the ALL and SYN datasets (Table 4), with similar CVs, and abundance estimates differing by <100 individuals. Estimates of abundance were greater by >1,000 individuals when unknown-sex individuals were included and data were not stratified by sex (Table 4). Since 98% (94 of 96) individuals of unknown sex were only sighted once (multiple sightings increasing the probability that sex can be determined from the genetic sample), the pooled region datasets contained a slightly lower percentage of inter-year recaptures (11.9% for ALL, 11.7% for SYN) than the data by sex (13.1% for ALL, 12.9% for SYN). Consequently the probability of recapture was slightly lower (difference in $p<0.01$), with higher associated abundance and poorer precision. Along similar lines, the removal of capture data from 2004 reduced the recapture rate from 11.6% to 10.7%, increased abundance estimates by 300-600 and reduced precision (Table 4).

The percentage by which abundance is determined by variation between the models reflects the level of support given to models with very different abundance estimates. Where variation percentages are low, this either reflects a large AIC difference between the best supported model and other models, or a small AIC difference between models but similar abundance estimates. When low variation is associated with good precision (CV), this suggests the latter scenario. In the case of the closed genotype models, the SYN datasets yielded the lowest CVs and model variation, suggesting that these may be the best-supported estimates among the models described. The most strongly supported model for the SYN dataset (weight=0.86, Appendix 6) allowed capture probabilities to vary by time and between the sexes (Mt*sex) while the most strongly supported model for the ALL dataset (weight 0.75, Appendix 7) allowed capture probabilities to vary by time only (Mt). In contrast, the Mth Chao model was the most strongly preferred for both datasets by program CAPTURE (Appendix 1), which yielded similar, slightly larger, estimates of abundance (<200 individuals) for females but substantially larger estimates for males (800-900 individuals); mean values for each (MARK and CAPTURE) model outcome were outside 95% confidence intervals of the other.

For the complete SYN dataset (including both sexes + unknowns) only one model was supported, a model where capture probability varied over time and was heterogeneous across the population (Mth AICc -5276, weight = 1.00, Appendix 8) for the pooled SYN dataset (all individuals). This estimate (N=5118, CV=0.47) was 40% larger than the next most strongly supported model (Mtbh AICc -5250, weight = 0.00, N=2936, CV=0.14). However under the Mth Chao model implemented in CAPTURE (Appendix 1), estimated abundance was substantially less (N=3995, CV=0.11). This estimate instability is likely driven by the low capture probabilities; models tend to converge to similar values as capture probabilities increase. Similarly, the complete ALL dataset also supported a model where capture probability varied over time and was heterogeneous across the population (AICc -5577, N=4887, CV= 0.39); this abundance estimate was 60% larger than the estimates yielded by other less strongly supported models, with a combined model-averaged estimate of N=4273, CV=0.54. The poor precision of the model-averaged estimate reflected the large difference in abundance estimates between AICc-supported models. Program CAPTURE supported a similar model (Mth Chao) and yielded a similar estimate of abundance (N=4048, CV=0.11, Appendix 1).

Estimates of abundance from the photo-ID datasets were also similar (<50 individuals different) between the ALL and SYN datasets (Table 4), with good precision (CV=0.08 and 0.15 respectively). The most strongly

supported model incorporated time dependent capture probabilities (Mt) for both datasets. The ALL dataset also provided equal support to a heterogeneous model (Mth), but the heterogeneous mixture proportions (between 0-1) in this model were >0.99 so this model was effectively equivalent to a time-variant model with zero heterogeneity. Photo-ID abundance estimates were significantly smaller (<2000 individuals) than all combined-sex estimates from the genotype datasets (Table 4). Abundance estimates yielded by CAPTURE (recommended model Mh Jackknife) were congruent with the SYN estimate in MARK (<100 individuals different), while the ALL dataset yielded a significantly smaller abundance estimate under the Mbh Pollock model (N=1110 CV=0.05) (Appendix 1, Table 4).

In general, the genotype and photo-ID ALL datasets tended to produce larger abundance estimates than the SYN datasets, but the magnitude of the difference was not large or significant (with the exception of the pooled-sex genotype datasets, which have very poor precision). This suggests that most whales have been captured within the synoptic regions, since increasing regional coverage has not led to a significant increase in abundance. It must be noted though that effort in these secondary areas was low, with the exception of American Samoa. The precision of estimates for the genotype SYN dataset was slightly better than for the ALL dataset when all datasets are compared (Table 4).

Regional estimates of abundance were greatest for Tonga (genotype males x 2 N=1840), with the biggest disparity in abundance between the sexes also (1.86:1 males: females). Genetic abundance of whales in New Caledonia and French Polynesia was ~50% lower, and confidence intervals for French Polynesia were very wide, reflecting the small yearly sample sizes collected from this region and correspondingly low capture probabilities (Table 5). The combined abundance of these three regions is not significantly different from the pooled abundance estimates presented in Table 4.

Estimating abundance II: 'open' models

Annual estimates of abundance using the POPAN models are shown in Figure 2, and 'super-population' (N_{super}) estimates are shown in Table 6. 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. Annual estimates are derived from these annual proportions (Figure 2) and are subject to annual mortality also. 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 (N_{super} = 3,448 for ALL and 3,307 for SYN), while male-specific estimates differed by <100 individuals between the ALL and SYN datasets, but had higher associated precision (Table 6).

The lowest annual abundances were estimated for the SYN dataset. The SYN dataset (2004 excluded) yielded slightly higher annual abundances relative to the SYN (2004 included) estimates (Figure 2). The SYN (2004 excluded) 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_{super} abundance was higher when 2004 was included (Table 6). The N_{super} estimate includes all animals entering the population but does not account for subsequent survival after capture. Estimated apparent survival (deaths and emigrations, ϕ) in the best fitting model for the SYN dataset was particularly low (ϕ = 0.75, AICc weight = 0.53), which may explain the low annual abundances, which are not reflected in the N_{super} estimate since survival is not a component. Overall estimates of male-specific N_{super} abundance were very similar across all three genotype datasets (Table 5), and doubled (assuming parity of females), they estimate a total of 3,300-3,500 whales in the region during the survey period. Doubling these male-specific estimates yielded total abundance values similar to those obtained by the combined datasets also.

Model averaged estimates of population growth (λ) and apparent survival (ϕ) in the Pradel model were within biologically plausible ranges for all datasets analysed (Table 7). For the genotype datasets, the best fitting model in each case was $\phi(.)p(t)\lambda(.)$, where only capture probability varied over time. We did not average over any models where two or more parameters were time varying, since at least one parameter was unidentifiable in all of these models. The SYN and ALL genotype datasets yielded very similar estimates, with λ =1.03 and ϕ = 0.94-0.95. The SYN and ALL photo-ID datasets yielded estimates of λ = 1.06-1.07 and ϕ = 0.96-0.97 (Table 8). No values for survival or population growth were significantly better fitting to any dataset than ϕ = 1 and λ = 1 respectively, *i.e.*, there was no significant trend in abundance. Since the sex ratio of these datasets is skewed towards males, we also analyzed the sex-specific SYN dataset in order to derive male-specific abundance estimates (Table 7). There was one anomalously low estimate of abundance in this series, 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 (N=2100-2800 genotypes, N=1630-1830 fluke photographs) 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, which is a much lower percentage than that derived by the closed models. Therefore doubling these male-specific estimates yields total abundance values similar to those obtained by the combined dataset.

Recommendations for the Comprehensive Assessment

While the datasets we examined here did not significantly violate closed model assumptions during goodness of fit testing (Appendix 1), these data were collected over a long time period, with varying effort across regions and over time. We therefore consider that the open models of mark recapture probably represent a better fit to these datasets, while recognising that assumptions in these models regarding equal effort across regions are probably still violated (see 'Caveats'). Since the sex ratio of genotype captures is not at parity (1.63:1 males to females), and we have no reason not to expect the sex ratio of the photo-ID dataset to be similarly skewed, we recommend choosing open model abundance estimates based on the male-specific genotype data and doubling this to attain an equal-sexes estimate of total abundance. The range of abundance estimates from these data across these models was 1,800-2,700 under the Pradel model (Appendix 12) and 1,200 to 2,800 under the POPAN model (Table 8). Estimates of total ('super-population') abundance in POPAN ranged from 3,200-3,500. Since the POPAN model considers all captured whales to be members of a larger 'super-population', this framework will include the transients known to be in the dataset from goodness of fit testing, although they are not explicitly modelled as such. In the Pradel model such transients are not likely to be incorporated in the abundance estimate since this model is conditioned on recaptures, which by definition do not include transients. In the absence of data to the contrary at present, we assume that transients are likely to be members of the Oceania breeding population, possibly from poorly surveyed regions such as the Chesterfield Reef or eastern French Polynesia, and consider that they should be included as part of the population until any data suggest evidence to the contrary. We therefore tentatively recommend the POPAN male-specific 'super-population' estimate (e.g. genotype SYN N=3,520, Table 5) as the most optimistic estimate of abundance in Oceania in 2005. This estimate effectively encompasses animals which calve and breed in the survey areas and 'transient' animals which migrate past to un-surveyed regions. It is also likely to be somewhat positively biased since survival rates are not factored. 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=2,362, CV=0.11) probably represents the abundance of the principal Oceania survey areas. This value is closely consistent with the abundance estimate from the ALL dataset and is not influenced by the low effort in 2004, nor by the potential widening of survey area over time that could create estimation bias in the ALL dataset. It is also closely similar to Pradel abundance estimates in this year (Table 4). This value therefore seems to be the most reasonable estimate of local abundance for the Oceania survey areas, although we recognise that further analysis, using multi-strata models that explicitly incorporate transience in an open model framework, would be most desirable for this population.

DISCUSSION

This paper presents the first comprehensive abundance estimates using quality controlled photo-ID and genetic data for Oceania. Whilst recognising caveats around this dataset, the POPAN male specific 'super popuation' estimate of N=3,250 is the best estimate for these data. This work has advanced a preliminary population estimate for the region which used photo-ID data only (Baker *et al.*, 2006). Abundance in Oceania was found to be very low, ranging between 2,000-4,000 whales. It is therefore the least abundant breeding ground among all those estimated for the Southern Hemisphere, despite an enormous range area covering much of the South Pacific. The population trend estimates we present here using the POPAN and Pradel models are indistinguishable from zero, suggesting that for the synoptic years of 1999-2005, this population is not recovering at the rate of neighbouring populations such as east Australia (Jackson *et al.*, 2009; Noad *et al.*, 2006 a; Paterson *et al.*, 2001). This information should therefore be considered in future population assessments of the region. The reasons for the low abundance and lack of trend are likely grounded in the intensive hunting pressure on humpback whales south of New Zealand, especially in the later years by the Soviet whaling fleet on an already severely depleted stock (Clapham *et al.*, 2009). Whaling in these waters is the most likely explanation for the dramatic decrease in whale sightings in regions like Fiji where whales were frequently sighted in the 1950s but show only very slow recovery rates today (Gibbs *et al.*, 2006).

The population estimates presented here show some variation depending on the assumptions of the models and the sampling method used. The genotype estimates were consistently larger than the photo-ID estimates but both found fewer than 5,000 individuals in Oceania. These differences are likely driven by a number of factors, including differences in data collection strategies, different levels of effort over regions and between years, and the differential availability of various age- and sex-classes of whales for the two survey methods. For example,

whales are less available for photo-ID capture when on migration (as they are not fluking). We hope that future simulations to explore the causes of these differences will enable us to explain this disparity more fully.

Regional estimates of abundance were greatest for Vava'u, Tonga and the abundance of whales in French Polynesia and New Caledonia was about 50% lower than Tonga. Tonga is the region with the highest levels of interchange within Oceania (Garrigue *et al.*, In Press a) and may form a junction between the eastern and western Oceania whales. The Cook Islands had very low rates of genetic recapture and no photo-ID recaptures during the synoptic years and it appears that the Cook Islands may form part of the migratory corridor for at least a portion of the whales in Tonga (Hauser *et al.*, 2010; Garrigue *et al.*, In Press a). The low abundance and wide confidence intervals for French Polynesia reflects the small sample sizes with low recapture rates. The presence of humpback whales in French Polynesia is of interest as this area was used by whalers passing on their way to the whaling grounds but it was never mentioned as an area where whaling occurred. Olavarría *et al.* (2007) found high levels of genetic diversity in this population that was distinct from other regions of Oceania. Analysis of song across Oceania shows that, despite a clear east to west trend in song transmission across Oceania, there are elements of song in French Polynesia that are of unknown origins (Garland *et al.*, 2009). Whilst there is interchange between French Polynesia and other Oceania regions, including across to New Caledonia, this is at a low level compared to other regions (Garrigue *et al.*, In Press a) and suggests there may be as yet undiscovered aggregations of whales elsewhere in the French Polynesian archipelago and connections with South America (Gibb, 2009). It is also possible that connections between New Caledonia, other parts of western Oceania and east Australia have yet to be discovered; the Chesterfield Islands may be a link between these areas (Anderson *et al.*, 2010).

The genotype analysis showed a male bias in captures (1.63:1 males to females), but the bias is less than that seen in other humpback breeding grounds and migratory corridors (Brown *et al.*, 1995; Craig and Herman, 1997; Palsboll *et al.*, 1997; Smith *et al.*, 1999), where the ratio has been ~2.4:1 males to females. A strongly significant signal of 'transience' (whales captured once only) was found for males genotyped in New Caledonia. These males may be migrants travelling through New Caledonian waters en route to another un-surveyed breeding ground (*e.g.*, Chesterfield Reef to the north) or to the breeding regions associated with east Australia. There was no corresponding signal of transience in the female population; this may reflect differential behaviour but also may be a consequence of the lower capture frequency of females, since migrating females will be correspondingly less likely to be captured than migrating males. Combined mark recapture analysis of fluke and genotype datasets from Oceania and east Australia will be very informative in resolving this question.

There was only a slight, non-significant increase in the population estimates when whales were included outside of the four primary areas across the synoptic years. It is important to note that, apart from American Samoa, effort was limited to a single short season in most of the secondary areas. This may explain their lack of effect on the population estimates. Nonetheless, movements of whales between regions during and since the synoptic surveys is very interesting (Garrigue *et al.*, In Press a; SPWRC, 2008; 2009). Oceania is a large region with numerous atolls and islands that remain un-surveyed, but information from small island states and vessels that ply some of the more remote waters suggests that to date there do not appear to be areas near land that have large unsurveyed humpback populations. Whale habitat is not restricted to landmasses and we know of at least one aggregation of humpbacks over a seamount south of New Caledonia (Garrigue *et al.*, 2010) and it may be that others exist. Recent reports of humpback whales in the waters around Pitcairn Island are interesting (Pers. Comm. Ginny Silva, Pitcairn Island High Commission) and these new reports will be investigated by members of the South Pacific Whale Research Consortium. It has now been determined that the interchange rate between humpback whales from east Australia and Oceania is extremely low and these two populations are effectively isolated from each other (Anderson *et al.*, 2010; Garrigue *et al.*, In Press b). This means that 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) and the rapid growth in whale watching (O'Connor *et al.*, 2009; Schaffar *et al.*, In Press). More importantly, the feeding grounds of this population, which are poorly defined, require protection from unregulated whaling and whilst the proposed catch of humpback whales as part of the JARPA II programme (Nishiwaki *et al.*, 2007) has not occurred, it may be reinstated.

Caveats

The pooled Oceania abundance estimates are based on low capture probabilities (<0.1), which are associated with model instability and substantial variance in abundance estimates within each model framework. Since the region under survey is extremely large and data collection resources very limited, it is unlikely that these recapture values will be increased. Oceania is also known to have significant population structuring across breeding regions (Olavarría *et al.*, 2007), yet the analysis we present here is based on data pooled from across these regions. The pooled models assume similar effort across all regions, however data collection methods and approaches have varied both by regions and over time. Variable effort across regions may be to some extent

reflected in the consistent support for models with heterogeneity of capture. Despite this, the sum of regional estimates of abundance is roughly consistent with the overall estimate from the pooled dataset, suggesting that the bias incurred by the difference in regional effort may not be too substantial. Goodness of fit tests has revealed a 'transience' signal in the data, which was localised to New Caledonia males. The models described here for estimating abundance do not explicitly include a transience component; models which specifically include a transience component may therefore represent an improved fit to these data.

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Table 1. Numbers of individuals captured and recaptured by year across all principal (synoptic) survey regions; A summarises the Photo-ID dataset and B summarises the Genotype database.

A. Fluke Photographs

	1999	2000	2001	2002	2003	2004
Individuals (Ind.) captured	108	124	132	114	150	110
Total Ind. captured	108	226	338	434	551	627

Number of re-captures	1	2	3	Total
Individuals	76	16	1	93

Year of recapture

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

B. Genotypes

	1999	2000	2001	2002	2003	2004	2005
Individuals captured	50	115	181	130	214	79	154
Total Ind. captured	50	162	332	445	623	689	807

Number of re-captures	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

Table 2. Numbers of individuals captured by year and total numbers of recaptures across all survey regions (ALL); A summarises the Photo-ID dataset and B summarises the Genotype database.

A. 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 re-captures	1	2	3			Total
Total Ind.	82	18	1			101

B. 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 re-captures	1	2	3				Total
Total Ind.	99	14	4				117

Table 3. 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

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
2003					X	0	2
2004						X	2
2005							X

Table 4. Closed population mark recapture abundance estimates from microsatellite genotypes (by sex and for all individuals) and photo-ID fluke data. Estimates are AIC_c weighted using model-averaging in MARK. Abundance estimates shown in italics are derived by doubling the estimates for males, assuming an equal ratio of both sexes.

Dataset	*p*	*N*	SE	CV	Confidence interval	Model variation %
Genotype – by sex						
ALL – males		1475	198	0.13	1087-1863	45
ALL – females		918	135	0.15	653-1182	49
*ALL – (males * 2)*		*2950*				
SYN – males		1399	158	0.11	1089-1710	6
SYN – females		886	117	0.13	656-1115	2
*SYN – (males * 2)*		*2798*				
SYN without 2004- males		2092	597	0.29	923-3262	21
SYN without 2004- females		1200	474	0.40	271-2130	39
*SYN without 2004- (males * 2)*		*4184*				
Genotype – all individuals						
ALL		4273	2317	0.54	-268-8813	15
SYN		5118	2424	0.47	367-9869	0
Photo-ID						
ALL		1909	149	0.08	1617-2201	0
SYN		1951	291	0.15	1381-2521	17

Table 5. Regional closed population estimates of abundance from photo-ID fluke data and microsatellite genotypes for the three primary study sites (Cook Islands are excluded here as they show very few inter-annual recaptures, so abundance is not estimable). AIC weighted using model-averaging in MARK.

Region	*N*	SE	CV	Confidence interval	Model variation %
New Caledonia					
Genotype – males	402	194	0.48	21-782	16
Genotype – females	306	186	0.61	0-670	20
*Genotype – (males * 2)*	*804*				
Photo-ID	383	135	0.35	119-648	53
Tonga					
Genotype – males	920	207	0.23	514-1327	19
Genotype – females	494	120	0.24	259-728	13
*Genotype – (males * 2)*	*1840*				
Photo-ID	1168	192	0.16	782-1554	5
French Polynesia					
Genotype – males	467	300	0.64	-120-1054	33
Genotype – females	296	172	0.58	-40-632	40
*Genotype – (males * 2)*	*934*				
Photo-ID	440	99	0.23	245-635	27

Table 6. Open population POPAN mark recapture 'super-population' abundance estimates (N_{super}) from photo-ID fluke data and microsatellite genotypes. Estimates were AIC weighted using model-averaging in MARK.

Dataset	N_{super}	SE	CV	Confidence interval	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

Table 7. Model-averaged estimates of apparent survival (ϕ) and apparent population growth (λ) estimated for pooled Oceania genotype 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 SYN		Genotype ALL		Genotype SYN males	
ϕ	0.95		0.94		0.92	
SE (CI)	0.07 (0.54-1.00)		0.07 (0.59-0.99)		0.07 (0.64-0.99)	
λ	1.03		1.03		0.97	
SE (CI)	0.07 (0.89-1.17)		0.07 (0.90-1.18)		0.07 (0.34-1.00)	
Year	p_t	N_t *(CI)*	p_t	N_t *(CI)*	p_t	N_t *(CI)*
1999	0.023	2175 (1191-4007)	0.023	2167 (1187-3993)	0.023	1099 (608-2003)
2000	0.051	2243 (1404-3631)	0.051	2251 (1408-3645)	0.052	1340 (846-2150)
2001	0.078	2314 (1575-3444)	0.078	2338 (1594-3474)	0.083	1354 (927-2004)
2002	0.054	2387 (1652-3476)	0.054	2428 (1692-3513)	0.062	1260 (872-1836)
2003	0.087	2461 (1702-3608)	0.092	2522 (1773-3636)	0.099	1152 (793-1703)
2004	0.031	2539 (1587-4091)	0.036	2620 (1687-4099)	0.027	891 (537-1490)
2005	0.059	2618 (1543-4525)	0.060	2720 (1648-4565)	0.074	1106 (645-1949)

Table 8. Model-averaged estimates of apparent survival (ϕ) and apparent population growth (λ) estimated for pooled Oceania genotype 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.

	Photo ID SYN		Photo ID ALL	
ϕ	0.96		0.97	
SE (CI)	0.07, 0.41-1.00		0.06 (0.31-1.00)	
λ	1.07		1.06	
SE (CI)	0.12 (0.82-1.31)		0.12 (0.83-1.29)	
Year	p_t,	N_t (CI)	p_t	N_t (CI)
1999	0.06	1824 (1053-3222)	0.06	1732 (1015-3018)
2000	0.07	1785 (1140-2839)	0.07	1737 (1122-2732)
2001	0.08	1747 (1190-2597)	0.08	1741 (1201-2556)
2002	0.07	1710 (1170-2527)	0.07	1746 (1215-2535)
2003	0.09	1674 (1108-2575)	0.10	1751 (1193-2613)
2004	0.07	1639 (983-2784)	0.07	1756 (1095-2867)

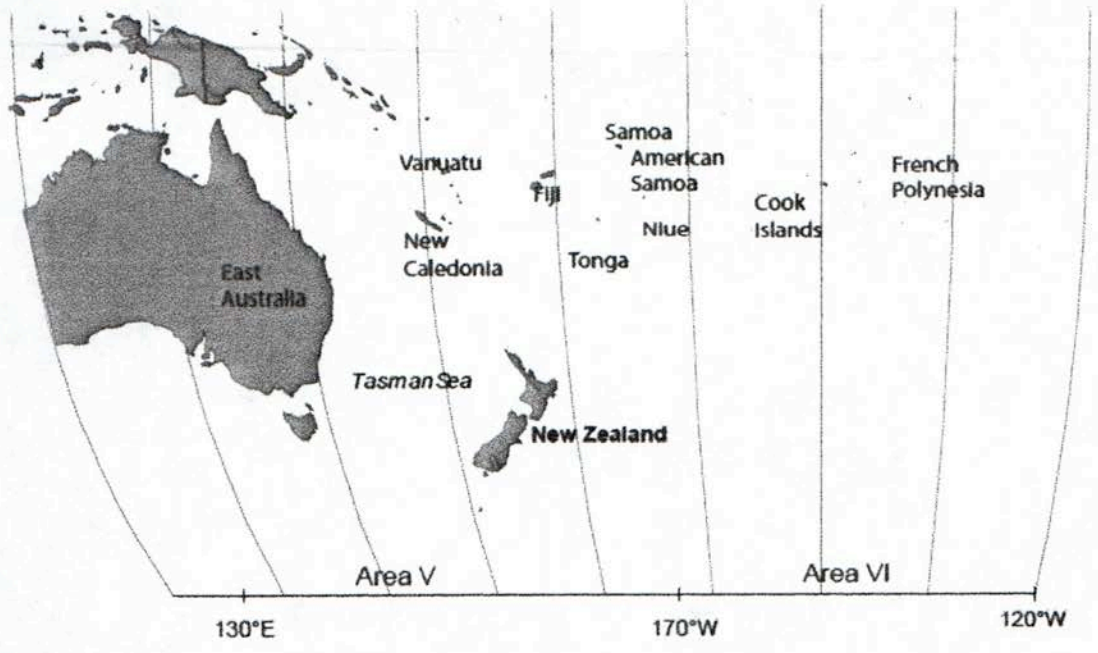

Figure 1. Map of Oceania showing the primary and secondary study sites.

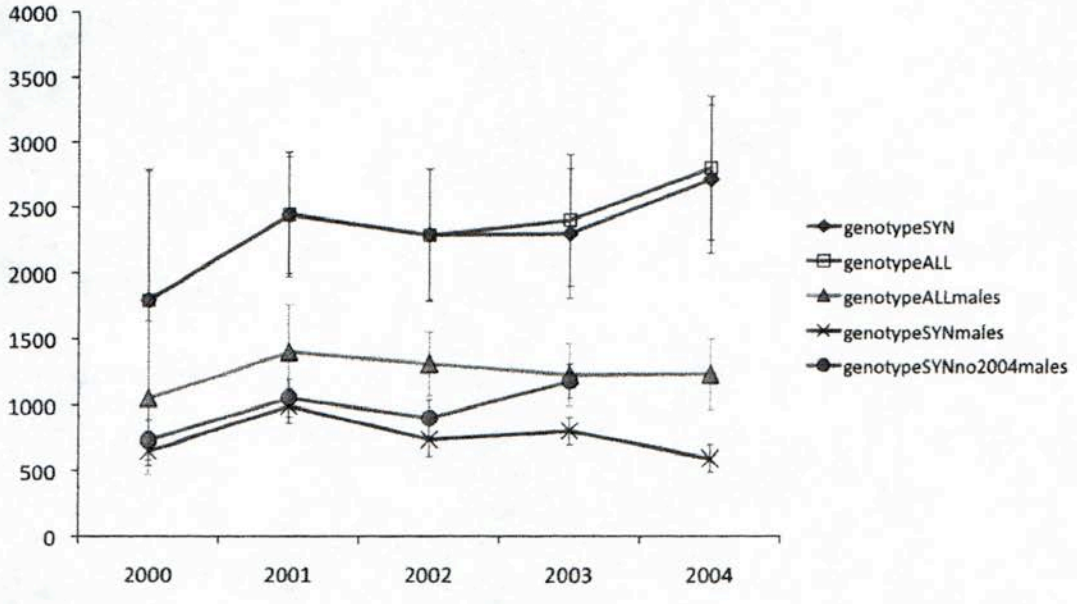

Figure 2. Annual estimates of abundance with associated standard errors shown as vertical bars. These are derived from AIC-preferred models for each dataset using the Delta method in the POPAN open population model.

APPENDIX

Appendix 1. Estimates of abundance of Oceania determined by the best fitting models available in program CAPTURE. [a] Best fitting model was Mtbh (not estimable from the data). Therefore the next best fitting model (model 'support' 0.72) is presented.[b] Best fitting model was Generalised Removals (not appropriate for the data type). Therefore the next best fitting model (model 'support' 1.00) is presented.

Dataset	Best model	*N*	SE	CV	Confidence Intervals
Genotype by sex					
ALL - males	Mth Chao	2379	354	0.15	1801-3206
ALL - females	Mth Chao	991	156	0.15	745-1367
SYN – males[a]	Mth Chao	2202	334	0.15	1660-2985
SYN - females	Mth Chao	1045	175	0.17	772-1470
Genotype – all individuals					
ALL	Mth Chao	4048	443	0.11	3291-5039
SYN	Mth Chao	3995	451	0.11	3226-5009
Photo-ID					
ALL[b]	Mbh Pollock	1110	52	0.05	1020-1223
SYN	Mh Jackknife	1808	70	0.04	1680-1953

Appendix 2. Estimates of regional abundance from synoptic regions using the best fitting models determined in program CAPTURE. [a,b] Best fitting model was Mtbh (not estimable from the data). Therefore the next best fitting models (model 'support' levels 0.84 and 0.96 respectively) are presented.

Region and dataset	Best model	*N*	SE	CV	Confidence Intervals
New Caledonia					
Genotype – males	Chao Mth	680	141	0.21	470-1035
Genotype – females	Mh jackknife	344	34	0.10	288-420
*Genotype – males*2*		*1360*			
Photo-ID	Chao Mth	515	96	0.19	372-757
Tonga					
Genotype – males	Darroch Mt	1022	202	0.20	714-1522
Genotype – females	Darroch Mt	483	114	0.23	319-781
*Genotype – males*2*		*2044*			
Photo-ID	Burnham Mtb	810	1139	1.41	322-7243
French Polynesia					
Genotype – males[a]	M_0	846	576	0.68	291-4969
Genotype - females[b]	M_0	260	119	0.46	124-639
*Genotype – males*2*		*1692*			
Photo-ID	Darroch Mt	554	102	0.18	399-809

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

		Genotype SYN	Photo-ID SYN
Test Type	Male	Female	
3.SR			
N(0,1) statistic for transience	4.22**	1.49	2.60**
Log-Odds-Ratio statistic for transience	3.75**	1.08	2.50**
χ_2	21.35*	3.44	13.2
G2	19.55*	3.44	11.7
3.SM			
χ_2	2.24	0.44	0.70
G2	2.24	0.44	0.70
2.CT			
N(0,1) statistic for trap dependence	1.04	2.89*	0.04
Log-Odds-Ratio statistic for trap dependence	1.30	2.71*	-0.09
χ_2	4.13	9.43	2.91
G2	4.27	9.53*	2.99
2.CL			
χ_2	0.66	4.68	0.53
G2	0.66	4.95	0.53

Appendix 4. Summary of results from U-CARE tests of goodness of fit between the data and various CJS models by region and sex. The Cook Islands are not included since they were not analysed as an independent population. Tests which are significant at $p<0.05$ by one test (*) or two tests (**) are shown. With the statistic for trap dependence, positive values indicate 'trap-shyness' and negative values 'trap-happiness'.

Region	*New Caledonia*		*Tonga*		*French Polynesia*	
Test type	*Males*	*Females*	*Males*	*Females*	*Males*	*Females*
3.SR						
N(0,1) statistic for transience	3.51**	1.38	0.50	0	0	N/A
Log-Odds-Ratio statistic for transience	3.67**	1.54	1.35	0.41	0.67	N/A
χ_2	15.99*	4.73	0.74	0	0	N/A
G2	15.57*	4.73	0.74	0	0	N/A
3.SM						
χ_2	1.51	0.66	N/A	N/A	N/A	N/A
G2	1.51	0.66	N/A	N/A	N/A	N/A
2.CT						
N(0,1) statistic for trap dependence	0.21	1.90	0.52	0.37	0	0
Log-Odds-Ratio statistic for trap dependence	0.21	2.02	1.14	0.84	-0.95	1.35
χ_2	1.58	5.31	1.17	0.41	0	0
G2	1.58	5.31	1.17	0.41	0	0
2.CL						
χ_2	0.19	4.40	0.41	N/A	N/A	N/A
G2	0.19	4.40	0.41	N/A	N/A	N/A

Appendix 5. Annual capture probabilities and associated standard errors (shown in italics), estimated using the best AIC-fitting closed model of each dataset.

Year	1999	2000	2001	2002	2003	2004	2005
Genotype SYN							
Males	0.02	0.05	0.08	0.06	0.08	0.02	0.06
SE	*0.004*	*0.008*	*0.011*	*0.008*	*0.011*	*0.004*	*0.009*
Females	0.03	0.05	0.07	0.05	0.09	0.03	0.06
SE	*0.007*	*0.009*	*0.012*	*0.010*	*0.015*	*0.007*	*0.011*
Genotype ALL							
Males + Females	0.02	0.05	0.07	0.05	0.09	0.03	0.06
SE	*0.003*	*0.006*	*0.008*	*0.006*	*0.009*	*0.004*	*0.007*
SE							
Photo ID SYN	0.06	0.07	0.07	0.06	0.08	0.06	
SE	*0.007*	*0.008*	*0.008*	*0.007*	*0.009*	*0.007*	

Appendix 6. General models, associated parameters and support for best fitting closed models in MARK for the SYN genotype dataset by sex. Nm represents male abundance, Nf represents female abundance. 'Δ AIC' represents the difference in AIC values from the best fitting model. 'Weight' represents the weighting given to each model in the model averaging process, '#Par' represents the number of parameters in the model. 'SE' represents the standard error. [1]p6=c6 constraint imposed in order that parameters are identifiable.

Model	AIC	Model LnL	Δ AIC	D	Weight	#Par	Nm	SE	Nf	SE
$p(t*sex)=c(t*sex)$ Mt*sex	-3461	1.00	0.0	136	0.86	16	1408	147	887	114
$p(t)$, $c(t)$ Mtb[1]	-3457	0.12	4.3	145	0.10	14	1416	202	900	131
$\pi(.)$, $p_{aM}(t)=c_{aM}(t)=p_{bM}(t)+z=c_{bM}(t)+z=$ $p_{aF}(t)+y=c_{aF}(t)+y=p_{bF}(t)+y+z=c_{bF}(t)+y+z$ Mth*sex	-3455	0.04	6.4	151	0.04	12	1151	184	807	108
$p(t*sex)$,$c(t*sex)$ Mtb*sex[1]	-3449	0.00	12.6	131	0.00	25	1335	228	1000	245
$\pi(.)$, $p_a(t)=c_a(t)=p_b(t)+z=c_b(t)+z$ Mth	-3446	0.00	15.2	162	0.00	11	1099	117	960	133
$p(t)$, $c(.)$ Mtb	-3443	0.00	18.1	168	0.00	9	1495	155	950	103
$p(t)$, $c(.*sex)$ Mtb*sex[1]	-3441	0.00	20.0	168	0.00	10	1498	156	946	103
Weighted average							**1399**	**158**	**886**	**117**

Appendix 7. General models, associated parameters and support for best fitting closed models in MARK for the ALL genotype dataset by sex. Nm represents male abundance, Nf represents female abundance. Full details of column headers are defined in the legend for Appendix 5. [1]p6=c6 constraint imposed in order that parameters are identifiable

Model	AIC	Model LnL	Δ AIC	D	Weight	#Par	Nm	SE	Nf	SE
$p(t)=c(t)$ Mt	-3708	1.00	0.0	139	0.75	9	1494	123	918	81
$\pi(.)$, $p_a(t)=c_a(t)=p_b(t)+z=c_b(t)+z$ Mth	-3704	0.11	4.4	139	0.08	11	1712	238	1052	150
$\pi(sex)$, $p_a(t)=c_a(t)+w=p_b(t)+z=c_b(t)+z+w$ Mthb	-3703	0.07	5.5	136	0.05	13	615	111	376	73
$\pi(sex)$ $p_a(t)=c_a(t)=p_b(t)+z=c_b(t)+z$ Mth	-3702	0.06	5.5	139	0.05	12	1580	281	1196	206
$p(t*sex)=c(t*sex)$ Mtsex[1]	-3701	0.04	6.7	132	0.03	16	1544	159	872	107
$\pi(sex)$, $p_{aM}(t)=c_{aM}(t)=p_{bM}(t)+z=c_{bM}(t)+z=$ $p_{aF}(t)+y=c_{aF}(t)+y=p_{bF}(t)+y+z=c_{bF}(t)+y+z$ Mthsex	-3701	0.03	6.7	138	0.03	13	1623	317	1111	195
$p(t)$, $c(t)$ Mtb[1]	-3698	0.01	9.6	139	0.01	14	1510	210	927	132

Model	AIC	Model LnL	Δ AIC	D	Weight	#Par	Nm	SE	Nf	SE
π(sex) p(t*sex)=c(t*sex)+*w* Mtbhsex	-3697	0.00	11.2	130	0.00	19	702	146	409	93
p(t), c(t*sex) Mtb[1]	-3697	0.00	11.4	130	0.00	19	1510	210	927	132
π(sex) p_a(t*sex)=c_a(t*sex)= p_b(t*sex)+*z*= c_b(t*sex) +*z* Mthsex	-3696	0.00	12.0	133	0.00	19	1619	330	916	175
p(t*sex), c(t*sex)[1] Mtbsex	-3688	0.00	20.3	125	0.00	26	702	164	1129	202
Weighted average							**1475**	**198**	**918**	**135**

Appendix 8. General models, associated parameters and support for best fitting closed models in MARK for the SYN genotype dataset (all individuals). Full details of column headers are defined in the legend for Appendix 5.

Model	AIC	Model LnL	Δ AIC	D	Weight	#Par	*N*	SE
π, $p_A(t)=c_A(t) = p_B(t)+z=c_B(t)+z$ Mth	-5276	1.00	0.0	75	1.00	10	5118	2424
p(t), c(t) Mtb[1]	-5250	0.00	25.2	94	0.00	13	2936	417
Weighted average							**5118**	**2424**

Appendix 9. General models, associated parameters and support for best fitting closed models in MARK for the ALL genotype dataset (all individuals). Full details of column headers are defined in the legend for Appendix 5.

Model	AIC	Model LnL	Δ AIC	D	Weight	#Par	*N*	SE
π, $p_A(t)=c_A(t) = p_B(t)+z=c_B(t)+z$ Mth	-5577	1.00	0.0	75	0.71	10	4887	1928
π, $p_A(t)=c_A(t)$ +*y*= $p_B(t)+z=c_B(t)+z+y$ Mtbh	-5575	0.29	1.8	75	0.29	11	2760	2638
p(t)=c(t) Mt	-5561	0.00	15.7	94	0.00	8	2956	235
p(t),c(t)[1] Mtb	-5553	0.00	23.1	92	0.00	13	3054	422
Weighted average							**4273**	**2317**

Appendix 10. General models, associated parameters and support for best fitting closed models in MARK for the SYN photo-ID dataset. 'Δ AIC' represents the difference in AIC values from the best fitting model. 'Weight' represents the weighting given to each model in the model averaging process, '#Par' represents the number of parameters in the model. 'SE' represents the standard error. [1]p6=c6 constraint imposed in order that parameters are identifiable.

Model	AIC	Model LnL	Δ AIC	D	Weight	#Par	*N*	SE
p(t)=c(t) Mt	-3763	0.34	0.0	55	1.00	7	1866	151
π, $p_A(t)=c_A(t) = p_B(t)+z=c_B(t)+z$ Mth	-3762	0.28	0.3	53	0.85	8	1925	192
p(.)=c(.) M_0	-3762	0.21	0.9	66	0.64	2	1871	152
p(.), c(.) Mb	-3760	0.10	2.3	65	0.31	3	2391	951
$p_A(.)=c_A(.) = p_B(.)+z=c_B(.)+z$ Mh	-3758	0.05	3.9	65	0.14	4	1940	198
π, $p_A(.)$, $c_A(.)$, $p_B(.)$, $c_B(.)$ Mbh	-3757	0.02	5.4	65	0.07	5	2417	966
p(t), c(t) Mtb[1]	-3757	0.02	5.9	53	0.05	11	1773	245
Weighted average							**1951**	**291**

Appendix 11. General models, associated parameters and support for best fitting closed models in MARK for the ALL photo-ID dataset. 'Δ AIC' represents the difference in AIC values from the best fitting model. 'Weight' represents the weighting given to each model in the model averaging process, '#Par' represents the number of parameters in the model. 'SE' represents the standard error. [1]p6=c6 constraint imposed in order that parameters are identifiable.

Model	AIC	Model LnL	Δ AIC	D	Weight	#Par	*N*	SE
π, $p_A(t)=c_A(t) = p_B(t)+z=c_B(t)+z$ Mth	-4015	1.00	0.0	58	0.49	8	1908	147
p(t)=c(t) Mt	-4015	1.00	0.0	58	0.49	7	1908	147
p(t),c(t) Mtb[1]	-4008	0.04	6.5	57	0.02	11	1911	251
π, $p_A(.)=c_A(.)$, $p_B(.)=c_B(.)$ Mh	-4006	0.01	9.4	78	0.00	3	1917	148
p(.)=c(.) M_0	-4006	0.01	9.4	78	0.00	2	1917	148
Weighted average							**1909**	**149**

Appendix 12. POPAN annual estimates of population abundance, derived from the genotype datasets using the Delta method in program MARK. Estimates from the initial and final years of data collection have been removed as they are non-interpretable.

Year	ALL		SYN		ALL Males		SYN Males		SYN (no 2004) males	
	N	*CV*	*N*	*CV*	*N*	*CV*	*N*	*CV*	*N*	*CV*
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		