# Multistate measurements of genotype interchange between East Australia and Oceania (IWC breeding sub-stocks E1, E2, E3 and F) between 1999 and 2004

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## ABSTRACT

Humpbacks breeding in East Australia (E1) and Oceania (New Caledonia E2, Tonga E3 and French Polynesia F) in the South Pacific are thought to be demographically independent, due to significant differentiation of mitochondrial DNA haplotypes between regions, and notable differences in the trend and pattern of recovery across the South Pacific. Matching of fluke photo-identification and microsatellite genotypes collected across the South Pacific has revealed multiple inter-annual movements between breeding grounds. Total documented movements within Oceania are greater than those documented between Oceania and East Australia, which indicates that East Australia may be more isolated from Oceania than the breeding grounds within Oceania are from each other. A strong contrast in population trend between these regions further supports this observation. A large microsatellite genotype dataset of 1,393 individuals (819 males and 574 females) spanning 1999-2004 is available from all South Pacific breeding grounds. We use this to build the first multistate movement model for the South Pacific region and to estimate rates of inter-breeding ground interchange in a framework that accounts for capture probabilities and survival through time. Thirteen inter-annual, inter-strata movements were identified; 10 males and 3 females. The data are too sparse to permit strong inference regarding movement among breeding grounds. However they do suggest that movements between East Australia and New Caledonia (Oceania) are not significantly different from intra-Oceania movements between New Caledonia and Tonga, indicating that population connectivity levels between East Australia, New Caledonia and Tonga are of similar, low magnitude, despite a pronounced difference in population trend between the East Australia and Oceania regions over the survey period. These results should be taken into consideration when grouping New Caledonia, Tonga and French Polynesia as a single unit for assessment since such an assessment may fail to account for different patterns of recovery and trend within the South Pacific.

## INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) gather to breed at multiple wintering sites scattered across a vast longitudinal range in the western South Pacific (145°E-120°W), along the Great Barrier Reef of eastern Australia (EA), in the lagoons and seamounts of New Caledonia (NC), and among the island atolls of Tonga (TG) and French Polynesia (FP). Fluke photo identification, microsatellite genotypes and satellite telemetry suggest that whales breeding offshore of east Australia, New Caledonia and Tonga may visit a common Southern

Ocean feeding ground in Antarctic Area V (130-180°E) (Chittleborough 1965; Constantine *et al.* 2011; Franklin *et al.* In press-a; Gales *et al.* 2009; Steel *et al.* 2008), travelling via New Zealand, Norfolk Island or the east Australian coastline (Dawbin 1956; Dawbin 1964; Franklin *et al.* 2011; Gales *et al.* 2009; Garrigue *et al.* 2010) while additional eastern migratory routes are hypothesized for whales breeding in Tonga and French Polynesia, some of which travel past the Cook Islands (Hauser *et al.* 2010) to and from wintering grounds in Area VI (180°E-100°W) or even the Antarctic Peninsula (Robbins *et al.* 2011). In addition to the multiple migratory routes and vast distance over which these breeding grounds are spread, additional evidence of demographic isolation between breeding grounds is provided by genetic data, which shows significant differentiation between all regions according to $F_{ST}$ metrics (Olavarría *et al.* 2006; Olavarría *et al.* 2007).

The South Pacific Whale Research Consortium has been conducting field surveys of humpbacks in Oceania since 1991. In 1999, the Consortium began a six-year coordinated survey of the four primary island regions of Oceania; New Caledonia, Tonga (Vava'u), the Cook Islands and French Polynesia (Moorea and Rurutu), collecting fluke photo-identifications and genetic biopsies. These have been coordinated with similar surveys off the coast of east Australia (Anderson 2010; Franklin *et al.* In press-b) in order to facilitate a comparison of population connectivity both within Oceania and between Oceania and east Australia. 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.* 2011). Matches of humpbacks within Oceania suggested relatively higher rates of movement, although movements were still much rarer than resights within individual breeding grounds (Garrigue *et al.* 2007). This led to the Oceania stock structure hypothesis wherein each breeding ground is considered a sub-stock (E1, E2, E3, F) but for population assessment purposes the Oceania sub-stocks E2, E3 and F have been grouped into one combined unit and E1 was assessed as a separate unit (Jackson *et al.* 2009). A recent combined abundance estimate from Oceania suggested a total of roughly 3,000 whales using E2, E3 and F in 2003 (Constantine *et al.* In Press) and found no discernible trend in abundance over the survey period (1999-2005). In contrast a very strong trend in abundance has been documented in E1 over the past 20 years (Noad *et al.* 2011; Noad *et al.* 2008).

To date no structured, quantitative assessment of inter-breeding ground interchange has been carried out, although a large synoptic dataset of individuals based on microsatellite genotypes is available, and spans the five breeding grounds of the South Pacific over the period 1999-2004. Here we attempt the first quantitative analysis of breeding ground interchange using these data and explore the potential of multistate analysis to test whether levels of interchange with East Australia and Oceania are lower than levels of interchange within Oceania. Multistate models were originally developed to analyze situations where animals change state in an unpredictable fashion; be it changes in life history stage or geographical migration between regions (Arnason 1972, 1973). In this study we focus on Cormack Jolly Seber models which condition only on events since initial marking. In these models only survival ($\Phi$), capture ($p$) and movement probabilities ($\psi$) are calculated, where $\Phi_i^s$ represents the probability of an animal alive at time $j$ in stratum $s$ remaining alive at $j$+1 in any stratum, and $\psi_j^{st}$ represents the probability of an animal alive at time $j$ in stratum $s$ moving to stratum $t$ at time $j$+1, conditional on surviving to $j$+1. These multistate models assume that all individuals make their transitions at the same time so this model is appropriate for breeding grounds where movements are expected to occur between breeding seasons rather than within them.

## METHODS

### *Datasets*

Microsatellite genotype data from Oceania were collected and analyzed as detailed in Constantine et al. (In Press) in order to obtain individual, sex specific capture histories over the period 1999 to 2004 with up to 17 genetic loci. For Oceania, all individuals that matched at 8 loci and had 1-3 mismatches were reviewed and re-sequenced if necessary; only individuals which successfully amplified for >10 loci were used (Constantine *et al.* In Press). Similar protocols were applied for East Australia and are detailed in Anderson (2010). We used known-sex genotypes from New Caledonia, Tonga and French Polynesia (males=422, females=264). Data from the Cook Islands was not included as it is very sparse in terms of recaptures, has revealed within-season re-sights with Tonga and French Polynesia, and is thought to be a migratory corridor rather than a breeding ground (Hauser *et al.* 2010). Microsatellite genotype data from East Australia (males=397, females=310) was collected from Byron Bay, Hervey Bay and Ballina over the period 1999-2004 as described in Anderson (2010). Genotypes were compared between the two laboratories in order to ensure standardization of techniques (Anderson *et al.* 2003). Data organization, matching and probability of identity analyses were all conducted using GenAlEx (Peakall & Smouse 2006). Total regional captures are given in Table 1 and recaptures and movements between strata are shown in Table 2. Seven movements between East Australia and Oceania were identified over the study period; six connections with New Caledonia and one with Tonga. Total movements between strata are shown in Figure 1. Regional data from east Australia was collapsed into one stratum (EA) as otherwise recaptures were too sparse.

We used the Program MARK (White & Burnham 1999) multistate model framework, which utilizes a first order Markov process to co-estimate sex-specific and capture probabilities (p), survival ($\Phi$) and movement ($\psi$) (Arnason 1972, 1973; Schwarz *et al.* 1993). Breeding grounds in East Australia, New Caledonia, Tonga and French Polynesia were used as the core strata over the years 1999-2004. Capture probabilities for Tonga were set to zero in 2004 since no samples were available from that year. Genotype data from French Polynesia and from East Australia and Tonga in 1999 was sparse, so we explored data sensitivity to these factors by constructing a second 1999-2004 dataset where French Polynesia was excluded and captures from Tonga in 1999 were excluded. Support for different models was evaluated using the Akaike Information Criterion (AIC) and likelihood ratio testing. Parameter counting was done to ensure that all models were correctly parameterized.

Goodness of fit testing in the Cormack Jolly Seber (CJS) framework was carried out using U-CARE V2.3.2 (Choquet et al. 2005). We tested the goodness-of-fit of the general mark-recapture model over all tests: WBWA, 3G.SR, 3G.Sm, M.ITEC, M.LTEC, along with single- and multi-state tests over all strata. Model over-dispersion was also examined by calculating the median c-hat parameter for the most general, fully identifiable model of each data set. In both cases, estimated c-hat was very close (<0.01) to 1, so this adjustment was not applied to either dataset.

## RESULTS

Goodness of fit testing only revealed one significant result: New Caledonia males gave a slightly significant 'transience' signal via the 3GSR test in 2001 (4.735, p=0.03, Appendix 1). It is notable that when the same Oceania genotype dataset was analyzed without East Australia (Constantine *et al.* In Press), the 3GSR test for transience was significant for males across the whole dataset, and for New Caledonia males in 2001 and 2003.

### *Capture probabilities p*

Capture data became more sparse across the strata from west to east (Table 1). The most strongly supported multistrata models for both datasets are shown in Tables 2 and 3. More complex (time and sex varying) models were significantly favoured for the East Australia and New Caledonian strata according to likelihood ratio testing (Table 5) while simple (time invariant) models were favoured for Tonga and French Polynesia. In East Australia and New Caledonia the most strongly supported models allowed capture probabilities to differ by sex according to an additive model where female capture probabilities were a logit-transformed coefficient of the time-varying male capture probabilities (model s+t: 'sex+time'). Female capture probabilities were uniformly lower than those of males. In Tonga and French

Polynesia there was no significant difference in support between models with sex-specific or fully constrained time-invariant capture probabilities (Table 4).

Capture probabilities were very similar (<1% difference) between the 3- and 4-strata models (Table 6) for EA, NC and TG. They varied between 3-16% across the survey period for EA, 4-17% for NC and were roughly 4% for TG and 3.5% for FP.

*Survival probabilities $\Phi$*

The most strongly supported models all had time and region invariant survival probabilities- there was more support for sex-specific survival models, but in many cases estimated survival for both sexes was singular (i.e. $\Phi$=1, SE=0), suggesting that there was insufficient information over the time period to accurately estimate this parameter. Fixing annual survival to 0.96 (from Barlow & Clapham 1997) yielded models with much weaker AIC support (i.e. higher AIC).

*Movement probabilities $\psi$*

Movement probability estimates were dependent on a small number of documented movements (Figure 1) so as a consequence a number of different movement hypotheses had very similar AICc support, indicating insufficient data to easily distinguish these models. However some generalities could be deduced from the analysis. The best fitting movement models were all time and sex invariant due to the sparseness of documented movements. Where no movements were detected across the survey period (*i.e.* between East Australia and French Polynesia, and between New Caledonia and French Polynesia), estimates were effectively zero ($\psi<10^{-10}$). Fixing $\psi$ to zero between these strata usually yielded identical model results. Bidirectional models (models where movements between each pair of strata were equal) were less well supported than the fully directional models; this was significant for the 3-stratum model but not the 4-stratum model, possibly as the latter data were more sparse (Table 4). Fully directional models were also significantly better fitting to both datasets than a model where one movement rate is imposed over all neighbouring strata (Table 4). For 3- and 4- stratum datasets the best supported models gave one interchange rate into New Caledonia from neighbouring strata (East Australia and Tonga) and a second movement rate out of New Caledonia into neighbouring strata. For the 4-stratum dataset a single interchange rate into Tonga from EA, New Caledonia and French Polynesia, and out of Tonga to all strata was also strongly supported (Figure 2). A 2-rate movement model was therefore found to be the best fit to both datasets, with movements between strata where no movements have been observed fixed to zero.

Annual movement probabilities from New Caledonia to East Australia and Tonga were estimated at 6.9% (95% CI 3-7-12.4%) in the 4-stratum model and 7.0% (95% CI 3.7-13.1%) in the 3-stratum model. Movement into New Caledonia from East Australia and Tonga was much lower, at 0.5% (95% CI 0.1-2%) in the 4-stratum model and 0.5% (95% CI 0.7-3.8%) in the 3-stratum model (Table 6). These models were strongly supported over those where bidirectional exchange was equal. It is worth noting that the 95% CI values of these estimates are not overlapping for the former estimate and slightly overlapping for the latter, indicating in the former case a possibly significant difference in the two movement rates.

## DISCUSSION

Movements are so sparse between breeding grounds that we view the estimated movement parameters in these models with extreme caution; however from this first effort to model interchange in the South Pacific region we learn the following things:

(1) The data provide no support for a hypothesis of higher movement rates among Oceania breeding grounds compared to between them and East Australia. All strongly supported models gave a roughly 10x higher rate of interchange from New Caledonia to East Australia than from Tonga to New Caledonia.

(2) The data do not strongly suggest any gross expansion of individuals from East Australia to the breeding grounds to the east, since so few movements ‘from’ East Australia to New Caledonia have been documented. In contrast, the rate of ‘movement’ from New Caledonia to East Australia may be 10x higher. This may be suggestive of East Australian humpbacks using New Caledonian waters on migration and may be explored in more detail by considering the time and capture location of the samples that underlie these movements. The greatly reduced transience signal in New Caledonian males when East Australia is included as a stratum also indicates that this may be a possibility. Valsecchi *et al*. (2010) proposed that the humpback breeding ground off East Australia may be fed by geographically discrete, sex-segregated migratory streams possibly travelling past New Zealand and Norfolk Island as well as along the Australian coastline. Our data suggest more extensive connections between New Caledonia and East Australia than previously thought, which may be consistent with this hypothesis. While only one of the five documented movements between these strata was by a female, females had lower capture probabilities than males in both regions. Sex specific differences in movement rates were not favoured over sex-aggregated movement models (Tables 3 and 4) but this is likely due more to data sparseness than lack of signal, since total inter-stratum movements were of only 10 males and 3 females.

(3) Capture probabilities were higher for males than for females in East Australia and New Caledonia. In Tonga and French Polynesia there is no support for differences in capture probabilities between the sexes. The biological rationale for this is unclear as Tonga and New Caledonia have similar sample sizes in terms of individual genotypes, although the no data are available from 2004 for the former.

*Management implications*

A number of metrics suggest demographic independence between the breeding grounds of the Southwestern Pacific; differences in trend, genetic differentiation and low rates of inter-ground movement relative to intra-ground movement. However the clustering of Oceania into E2/E3/F as a distinct unit from East Australia (E1) is not supported by the current analysis. Instead the data support East Australia as being similarly distinct from New Caledonia (E2) as it is from Tonga (E3) to the east. These data suggest that grouping E1 and E2/E3/F into two units for assessment may not be an appropriate approach as levels of demographic independence are similar between East Australia, New Caledonia and Tonga, i.e. East Australia may not be more isolated from Oceania than animals within Oceania are from one another. It is hard to comment regarding the autonomy of French Polynesia as captures are particularly sparse from that region and only two movements (to/from Tonga) are included in the present analysis.

## REFERENCES

Anderson MJ (2010) *Genetic connectivity to and within eastern Australian humpback whales*, Southern Cross University. PhD thesis.

Anderson MJ, Steel D, Baverstock P, Olavarría C, Baker CS (2003) Final report on the standardization of genetic analysis protocols used in humpback whale research (ed. Department of the Environment and Heritage A).

Arnason AN (1972) Parameter estimates for mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* **13**, 99-113.

Arnason AN (1973) The estimation of population size, migration rates and survival in stratified populations. *Researches on Population Ecology* **15**, 1-8.

Barlow J, Clapham PJ (1997) A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecology* **78**, 535-546.

Chittleborough RG (1965) Dynamics of two populations of the humpback whale, Megaptera Novaeangliae (Borowski). *Australian Journal of Marine and freshwater research* **16**, 33-128.

Constantine R, Allen J, Beeman P*, et al.* (2011) Comprehensive photo-identification matching of Antarctic Area V humpback whales. In: *Paper SC/63/SH16 presented to the IWC Scientific Committee, June 2011 (unpublished). 11pp. [Available from the office of this Journal]*.

Constantine R, Jackson JA, Steel D*, et al.* (In Press) Abundance of humpback whales in Oceania using photo-identification and microsatellite genotyping. *Marine Ecology Progress Series*.

Dawbin WH (1956) The migration of humpback whales as they pass the New Zealand Coast. *Transactions of the Royal Society of New Zealand* **84**, 147-196.

Dawbin WH (1964) Movements of humpback whales marked in the southwest Pacific Ocean 1952 to 1962. *Norsk Hvalfangsttid* **53**, 68-78.

Franklin T, Franklin W, Brooks L*, et al.* (2011) Seasonal changes in pod characteristics of eastern Australian humpback whales (*Megaptera novaeangliae*), Hervey Bay 1992-2005. *Marine Mammal Science* **27**, E134-152.

Franklin W, Franklin T, Brooks L*, et al.* (In press-a) Antarctic waters (Area V) near the Balleny Islands are a summer feeding area for some Eastern Australia (E (i) breeding group) humpback whales (*Megaptera novaeangliae*). *Journal of Cetacean Research and Management*.

Franklin W, Franklin T, Gibbs N*, et al.* (In press-b) Photo-identification confirms that humpback whales (*Megaptera novaeangliae*) from eastern Australia migrate past New Zealand but indicates low levels of interchange with breeding grounds of Oceania. *Journal of Cetacean Research and Management*.

Gales N, Double MC, Robinson S*, et al.* (2009) Satellite tracking of southbound East Australian humpback whales (*Megaptera novaeangliae*): challenging the feast or famine model for migrating whales. In: *Paper SC/61/SH17 presented to the IWC Scientific Committee, May 2009 (unpublished). 12pp. [Available from the office of this Journal]*.

Garrigue C, Baker CS, Constantine R*, et al.* (2007) Interchange of humpback whales in Oceania (South Pacific) 1999 to 2004 (revised SC/A06/HW55, March 2007). In: *Paper SC/59/SH14 presented to the IWC Scientific Committee, May 2007 (unpublished). 10pp. [Available from the office of this Journal]*.

Garrigue C, Franklin T, Russell K*, et al.* (2011) First assessment of interchange of humpback whales between Oceania and the east coast of Australia. *Journal of Cetacean Research and Management* **Special Issue 3**.

Garrigue C, Zerbini AN, Geyer Y*, et al.* (2010) Movements of satellite-monitored humpback whales from New Caledonia. *Journal of Mammalogy* **91**, 109-115.

Hauser N, Zerbini AN, Geyer Y, Heide-Jørgensen M-P, Clapham P (2010) Movements of satellite-monitored humpback whales, *Megaptera novaeangliae*, from the Cook Islands. *Marine Mammal Science* **26**, 679-685.

Jackson JA, Zerbini A, Clapham PJ*, et al.* (2009) Update to SC/60/SH14: Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. In: *Paper SC/F09/SH8 submitted to the IWC Intersessional Workshop on Southern Hemisphere Humpback Whale Modelling Assessment Methodology. 12pp. [Available from the office of this Journal]*.

Noad M, Dunlop RA, Paton D, Kniest H (2011) Abundance estimates of the east Australian humpback whale population: 2010 survey and update. In: *Paper SC/63/SH22 presented to the IWC Scientific Committee, May 2011 (unpublished). 12pp. [Available from the office of this Journal]*.

Noad MJ, Dunlop RA, Paton D, Cato DH (2008) An update of the east Australian humpback whale population (E1) rate of increase. In: *Paper SC/60/SH31 presented to the IWC Scientific Committee, May 2008 (unpublished). 13pp. [Available from the office of this Journal]*.

Olavarría C, Anderson M, Paton D*, et al.* (2006) Eastern Australia humpback whale genetic diversity and their relationship with Breeding Stocks D, E, F and G. In: *Paper SC/58/SH25 presented to the IWC Scientific Committee, May 2006 (unpublished). 6pp. [Available from the office of this Journal]*.

Olavarría C, Baker CS, Garrigue C*, et al.* (2007) Population Structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series* **330**, 257-268.

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* **6**, 288-295.

Robbins J, Dalla Rosa L, Allen JM*, et al.* (2011) Return movement of a humpback whale between the Antarctic Peninsula and American Samoa: a seasonal migration record. *Endangered Species Research* **13**, 117-121.

Schwarz CJ, Schweigert JF, Arnason AN (1993) Estimating migration rates using tag recovery data. *Biometrics* **49**, 177-193.

Steel D, Garrigue C, Poole M*, et al.* (2008) Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas based on genotype matching. In:

*Paper SC/60/SH13 presented to the IWC Scientific Committee, May 2008 (unpublished). 9pp. [Available from the office of this Journal].*

Valsecchi E, Corkeron PJ, Galli P, Sherwin W, Bertorelle G (2010) Genetic Evidence for Sex-Specific Migratory Behaviour in the Western South Pacific Humpback Whales. *Marine Ecology Progress Series* **398**, 275-286.

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, S120-139.

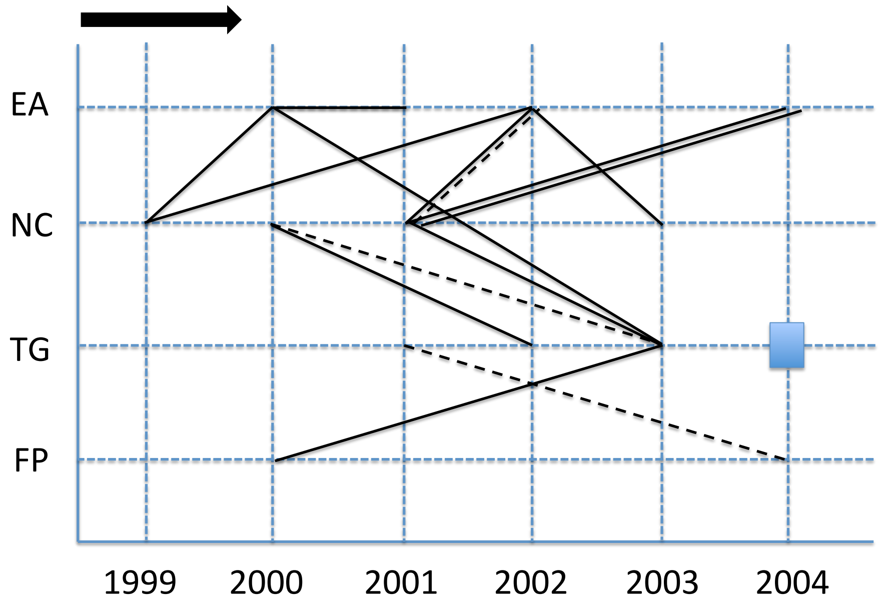

**Figure 1.** Individual capture histories showing movements from 1999 to 2004 between strata in the South Pacific. Black and dashed lines represent males and female movements respectively. No capture data are available from Tonga in 2004. EA= East Australia, NC=New Caledonia, TG=Tonga, FP=French Polynesia.

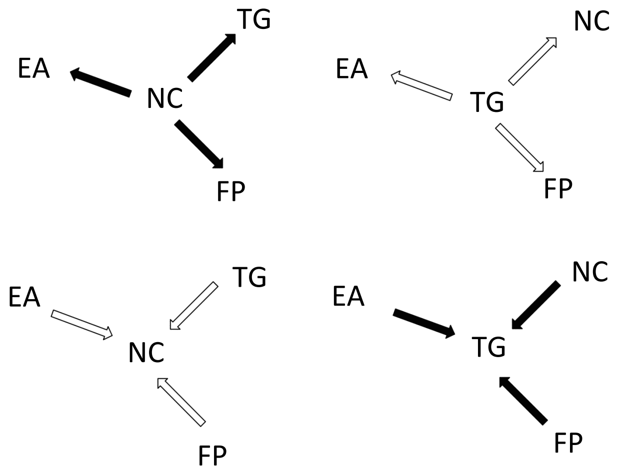

**Figure 2.** Best fitting interchange model for EA-NC-TG-FP. Black arrow denotes Ψ=6.9% (95% CI 3.7-12.4%). White arrow denotes Ψ=0.5%, (95% CI 0.1-2.0%).

**Table 1.** Total captures in each region through time

| | Unique IDs | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 |
|---|---|---|---|---|---|---|---|
| East Australia | | | | | | | |
| Males | 397 | 2 | 38 | 96 | 128 | 84 | 80 |
| Females | 310 | 2 | 34 | 91 | 94 | 70 | 46 |
| New Caledonia | | | | | | | |
| Males | 153 | 15 | 30 | 56 | 15 | 43 | 22 |
| Females | 107 | 14 | 13 | 33 | 16 | 26 | 22 |
| Tonga | | | | | | | |
| Males | 217 | 11 | 34 | 56 | 53 | 76 | 0 |
| Females | 114 | 9 | 25 | 21 | 23 | 48 | 0 |
| French Polynesia | | | | | | | |
| Males | 62 | 1 | 8 | 8 | 16 | 12 | 19 |
| Females | 46 | 2 | 4 | 9 | 7 | 11 | 16 |

**Table 2.** Within- and between-region genotypic recaptures of males and females respectively from 1999 to 2004

| | East Australia | New Caledonia | Tonga | French Polynesia |
|---|---|---|---|---|
| East Australia | 31,23 | 6,1 | 1,0 | 0,0 |
| New Caledonia | | 20,15 | 2,1 | 0,0 |
| Tonga | | | 13, 11 | 1,1 |
| French Polynesia | | | | 2,3 |

**Table 3.** Most strongly supported multistrata models for EA-NC-TG-FP dataset (model likelihood range 0.001-1). Model descriptions show probabilities of Capture (p), survival (Φ) and movement (Ψ) by time (t), sex(s), or sex and time invariant (.).

| CJS Multistate models (p Φ Ψ) | AICc | Delta AICc | AICc weight | Model likelihood | # P | Deviance |
|---|---|---|---|---|---|---|
| Φ(.) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG=EA->TG=FP->TG) Ψ(EA->NC=TG->NC=TG->FP=TG->EA) Ψ (EA<->FP = NC<->FP = 0) | 1216.26 | 0 | 0.443 | 1.000 | 17 | 193.88 |
| Φ(.) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG=EA->TG=FP->TG) Ψ(EA->NC=TG->NC=TG->FP) Ψ(TG->EA) Ψ (EA<->FP = NC<-> FP = 0) | 1219.60 | 3.33 | 0.084 | 0.190 | 18 | 193.10 |
| Φ(.) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG = EA->TG =FP->TG) Ψ(EA->NC=TG->NC=TG->FP) Ψ(TG->EA) Ψ (EA<->FP= 0) | 1223.72 | 7.45 | 0.011 | 0.024 | 19 | 193.10 |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG =FP->TG) Ψ(EA->NC=TG->NC=TG->FP) Ψ(TG->EA) Ψ (EA->TG) Ψ (EA<->FP= NC<-> FP = 0) | 1224.22 | 7.96 | 0.008 | 0.019 | 22 | 189.47 |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG=EA >TG=FP->TG) Ψ(EA->NC=TG->NC=TG->FP) Ψ(TG->EA) Ψ (EA<->F = 0) | 1225.75 | 9.49 | 0.004 | 0.009 | 21 | 193.08 |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG) Ψ(EA->NC=TG->NC) Ψ(TG->EA) Ψ(EA->TG) Ψ(TG->FP) Ψ(FP->TG) Ψ (EA<->FP = NC<->FP=0) | 1226.66 | 10.4 | 0.002 | 0.006 | 24 | 187.77 |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(TG->FP=TG->NC) Ψ(NC->TG=FP->TG) Ψ(EA->NC) Ψ(EA->TG) Ψ(NC->EA) Ψ(TG->EA) Ψ (EA<->FP = NC<->FP=0) | 1227.78 | 11.52 | 0.001 | 0.003 | 24 | 188.89 |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG) Ψ(EA->NC) Ψ (TG->NC) Ψ(TG->EA) Ψ(EA->TG) Ψ(TG->FP) Ψ(FP->TG) Ψ (EA<->FP = NC<->FP=0) | 1228.11 | 11.85 | 0.001 | 0.003 | 25 | 187.15 |
| Φ(.) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA=NC->TG=EA->NC=TG->NC=TG->EA=EA->TG=TG->FP=FP->TG) Ψ (EA<->FP = NC<->FP=0) | 1229.35 | 13.08 | 0.001 | 0.001 | 15 | 209.01 |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(.) pFP(.) Ψ(NC->EA) Ψ (NC->TG) Ψ(EA->NC) Ψ (TG->NC) Ψ(TG->EA) Ψ(EA->TG) Ψ(TG->FP) Ψ(FP->TG) Ψ | 1229.80 | 13.54 | 0.001 | 0.001 | 26 | 186.76 |

| CJS Multistate models (p Φ Ψ) | AICc | Delta AICc | AICc weight | Model likelihood | # P | Deviance |
|---|---|---|---|---|---|---|
| (EA<->FP = NC<->FP=0) | | | | | | |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(t+s) pFP(.) Ψ(NC->EA) Ψ (NC->TG) Ψ(EA->NC) Ψ (TG->NC) Ψ(TG->EA) Ψ(EA->TG) Ψ(TG->FP) Ψ(FP->TG) Ψ (EA<->FP = NC<->FP=0) | 1231.51 | 15.25 | 0.000 | 0.001 | 30 | 180.11 |
| Φ(s) pEA(t+s) p(NC(t+s) pTG(s) pFP(s) Ψ(NC->EA) Ψ (NC->TG) Ψ(EA->NC) Ψ (TG->NC) Ψ(TG->EA) Ψ(EA->TG) Ψ(TG->FP) Ψ(FP->TG) Ψ (EA<->FP = NC<->FP=0) | 1231.90 | 15.64 | 0.000 | 0.000 | 28 | 184.68 |

**Table 4.** Most strongly supported multistrata models for EA-NC-TG dataset (model likelihood range 0.001-1). Model descriptions show probabilities of Capture (p), survival (Φ) and movement (Ψ) by time (t), sex(s), or sex and time invariant (.).

| CJS Multistate models (p Φ Ψ) | AICc | Delta AICc | AICc weight | Model likelihood | # P | Deviance |
|---|---|---|---|---|---|---|
| Φ(.) pEA(t+s) pNC(t+s) pTG(.) Ψ(EA->NC)(.)=(TG->NC)(.) Ψ(EA->TG)(.) = (NC->EA)(.) = (NC->TG)(.) Ψ(TG->EA)(.)= (TG->NC)(.)=0 | 1095.60 | 0 | 0.330 | 1.000 | 15 | 146.00 |
| Φ(.) pEA(t+s) pNC(t+s) pTG(.) Ψ(EA->NC)(.)=(TG->NC)(.), Ψ(EA->TG)(.) Ψ(NC->EA)(.) = (NC->TG)(.), Ψ(TG->EA)(.)=0 | 1095.80 | 0.2 | 0.299 | 0.907 | 16 | 144.15 |
| Φ(.) pEA(t+s) pNC(t+s)pTG(s) Ψ(EA->NC)(.)=(TG->NC)(.), Ψ(EA->TG)(.) Ψ (NC->EA)(.) = (NC->TG)(.), Ψ (TG->EA)(.)=0 | 1097.72 | 2.12 | 0.114 | 0.347 | 17 | 144.01 |
| Φ(s) pEA(t+s) pNC(t+s)pTG(.) Ψ(EA->NC)(.) Ψ(EA->TG)(.) = (NC->EA)(.) = (NC->TG)(.) Ψ (TG->EA)(.)= (TG->NC)(.)=0 | 1099.71 | 4.11 | 0.042 | 0.128 | 17 | 146.00 |
| Φ(s) pEA(t+s) pNC(t+s)pTG(.) Ψ(EA->NC)(.)=(TG->NC)(.), Ψ(EA->TG)(.) Ψ (NC->EA)(.) = Ψ(NC->TG)(.), Ψ(TG->EA)(.)=0 | 1099.91 | 4.31 | 0.038 | 0.116 | 18 | 144.14 |
| Φ(s) pEA(t+s) pNC(t+s)pTG(.) Ψ(EA->NC)(.)=(TG->NC)(.), Ψ(EA->TG)(.) = Ψ(NC->EA)(.) = Ψ(NC->TG)(.), Ψ(TG->EA)(.)=0 | 1100.70 | 5.09 | 0.026 | 0.078 | 17 | 146.99 |
| Φ(s) pEA(t+s) pNC(t+s)pTG(.) Ψ(EA->NC)(.)=(TG->NC)(.), Ψ(EA->TG)(.) = (NC->EA)(.) = Ψ(NC->TG)(.)= (TG->EA)(.)=0 | 1100.70 | 5.09 | 0.026 | 0.078 | 17 | 146.99 |
| Φ(s) pEA(t+s) pNC(t+s) pTG(s) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ(NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->EA)(.)=(TG->NC)(.)=0 | 1100.80 | 5.2 | 0.025 | 0.074 | 19 | 142.97 |
| Φ(s) pEA(t+s) pNC(t+s) pTG(s) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ (NC->EA)(.) = (NC->TG)(.) Ψ (TG->EA)(.)=0 Ψ(TG->NC)(.) | 1100.92 | 5.32 | 0.023 | 0.070 | 19 | 143.09 |
| Φ(s) pEA(t+s) pNC(t+s) pTG(.) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ(NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->EA)(.) Ψ (TG->NC)(.)= (TG->EA)(.)=0 | 1100.93 | 5.33 | 0.023 | 0.070 | 19 | 143.10 |
| Φ(.) pEA(t+s) pNC(t+s) pTG(.) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ(NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->NC)(.) Ψ (TG->EA)(.)=0 | 1100.94 | 5.34 | 0.023 | 0.069 | 19 | 143.11 |
| Φ(.) pEA(t+s) pNC(s) pTG(.) Ψ(EA->NC)(.)=(TG->NC)(.), Ψ(EA->TG)(.) Ψ (NC->EA)(.) = (NC->TG)(.), Ψ(TG->EA)(.)=(TG->NC)(.)=0 | 1101.58 | 5.98 | 0.017 | 0.050 | 12 | 158.12 |
| Φ(s) pEA(t+s) pNC(t+s) pTG(.) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ(NC->EA)(.) Ψ(NC->TG)(.) Ψ(TG->NC)(.) Ψ(TG->EA)(.)=0 | 1102.99 | 7.39 | 0.008 | 0.025 | 20 | 143.10 |
| Φ(s) pEA(t+s) pNC(t+s) pTG(.) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ(NC->EA)(.) Ψ(NC->TG)(.) Ψ(TG->EA)(.) Ψ(TG->NC)(.)} | 1105.07 | 9.47 | 0.003 | 0.009 | 21 | 143.11 |

| CJS Multistate models (p Φ Ψ) | AICc | Delta AICc | AICc weight | Model likelihood | # P | Deviance |
|---|---|---|---|---|---|---|
| Φ(s) pEA(t+s) pNC(t+s) pTG(.) Ψ (EA->NC)(.) Ψ (EA->TG)(.) Ψ (NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->NC)(.) Ψ (TG->EA)(.) | 1105.07 | 9.47 | 0.003 | 0.009 | 21 | 143.11 |
| Φ(s) pEA(t+s) pNC(t+s) pTG(s) Ψ (EA->NC)(.) Ψ (EA->TG)(.) Ψ (NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->EA)(.) Ψ (TG->NC)(.) | 1107.01 | 11.41 | 0.001 | 0.003 | 22 | 142.97 |
| Φ(s) pEA(t+s) pNC(s) pTG(.) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ (NC->EA)(.) Ψ (NC->TG)(.) Ψ (TG->EA)(.) Ψ (TG->NC)(.) | 1110.57 | 14.97 | 0.000 | 0.001 | 17 | 156.86 |
| Φ(.) pEA(t+s) pNC(t+s) pTG(t+s) Ψ(EA->NC)(s) Ψ(EA->TG)(s) Ψ(NC->EA)(s) Ψ (NC->TG)(s) Ψ (TG->EA)(s) Ψ (TG->NC)(s) | 1112.95 | 17.35 | 0.000 | 0.000 | 28 | 136.40 |
| Φ(s) pEA(t+s) pNC(t+s) pTG(t+s) Ψ(EA->NC)(s) Ψ(EA->TG)(s) Ψ(NC->EA)(s) Ψ(NC->TG)(s) Ψ(TG->EA)(s) Ψ(TG->NC)(s) | 1113.23 | 17.63 | 0.000 | 0.000 | 29 | 134.58 |
| Φ(s) pEA(s) pNC(t+s) pTG(.) Ψ(EA->NC)(.) Ψ(EA->TG)(.) Ψ(NC->EA)(.) Ψ(NC->TG)(.) Ψ(TG->EA)(.) Ψ(TG->NC)(.)} | 1113.48 | 17.88 | 0.000 | 0.000 | 17 | 159.77 |

**Table 5.** Likelihood ratio testing of multistate models. Significant $\chi^2$ values are given in bold.

| Model comparison | EA-NC-TG $\chi^2$ | EA-NC-TG-FP $\chi^2$ |
|---|---|---|
| Φ (sex) vs Φ (.) | 0.01 | 0.03 |
| Best Ψ versus fully directional | 1.049 | |
| Best Ψ versus all neighbouring Ψ equal | **101.40** | **15.13** |
| Bidirectional versus fully directional model | **95.12** | 6.96 |
| TG (.) vs TG sex | 0.13 | 2.04 |
| FP (.) vs FP sex | | 1.38 |
| EA(t+sex) vs EA(sex) | **79.6** | |
| NC(t+sex) vs NC(sex) | **14.0** | |

**Table 6.** Multistrata parameter estimates from the best fitting models of the 4 and 3-stratum datasets.

| | 4-strata | | | | 3-strata | | | |
|---|---|---|---|---|---|---|---|---|
| Parameters | Estimate | Standard error | Lower 95% | Upper 95% | Estimate | Standard error | Lower 95% | Upper 95% |
| Φ (males) | 1 | 0 | - | - | 1 | 0.012 | 0 | 1 |
| Φ (females) | 1 | 0 | - | - | 1 | 0.003 | 0 | 1 |
| p(2000) EA males | 0.1601 | 0.1513 | 0.0206 | 0.6338 | 0.1617 | 0.1528 | 0.0207 | 0.6373 |
| p(2001) EA males | 0.1084 | 0.0382 | 0.0531 | 0.2087 | 0.1092 | 0.0385 | 0.0535 | 0.2102 |
| p(2002) EA males | 0.0872 | 0.0206 | 0.0543 | 0.1369 | 0.0879 | 0.0208 | 0.0548 | 0.1382 |
| p(2003) EA males | 0.0410 | 0.0108 | 0.0244 | 0.0681 | 0.0415 | 0.0109 | 0.0247 | 0.0689 |
| p(2004) EA males | 0.0311 | 0.0082 | 0.0185 | 0.0518 | 0.0308 | 0.0081 | 0.0183 | 0.0514 |
| p(2000) EA females | 0.1492 | 0.1438 | 0.0187 | 0.6175 | 0.1505 | 0.1450 | 0.0188 | 0.6207 |
| p(2001) EA females | 0.1006 | 0.0365 | 0.0483 | 0.1977 | 0.1012 | 0.0367 | 0.0486 | 0.1989 |
| p(2002) EA females | 0.0808 | 0.0201 | 0.0491 | 0.1300 | 0.0814 | 0.0203 | 0.0495 | 0.1310 |
| p(2003) EA females | 0.0379 | 0.0106 | 0.0217 | 0.0651 | 0.0382 | 0.0107 | 0.0219 | 0.0658 |
| p(2004) EA females | 0.0287 | 0.0081 | 0.0165 | 0.0495 | 0.0284 | 0.0080 | 0.0163 | 0.0490 |
| p(2000) NC males | 0.1335 | 0.0744 | 0.0419 | 0.3520 | 0.1349 | 0.0752 | 0.0423 | 0.3553 |
| p(2001) NC males | 0.1710 | 0.0562 | 0.0867 | 0.3097 | 0.1734 | 0.0571 | 0.0877 | 0.3140 |
| p(2002) NC males | 0.0458 | 0.0210 | 0.0184 | 0.1094 | 0.0464 | 0.0213 | 0.0186 | 0.1110 |
| p(2003) NC males | 0.1603 | 0.0420 | 0.0939 | 0.2601 | 0.1634 | 0.0432 | 0.0951 | 0.2663 |
| p(2004) NC males | 0.0610 | 0.0206 | 0.0311 | 0.1162 | 0.0655 | 0.0227 | 0.0328 | 0.1267 |
| p(2000) NC females | 0.1100 | 0.0635 | 0.0335 | 0.3059 | 0.1111 | 0.0642 | 0.0338 | 0.3087 |
| p(2001) NC females | 0.1420 | 0.0527 | 0.0662 | 0.2785 | 0.1439 | 0.0535 | 0.0670 | 0.2824 |
| p(2002) NC females | 0.0371 | 0.0183 | 0.0139 | 0.0953 | 0.0375 | 0.0186 | 0.0140 | 0.0966 |
| p(2003) NC females | 0.1327 | 0.0401 | 0.0717 | 0.2326 | 0.1353 | 0.0413 | 0.0727 | 0.2381 |
| p(2004) NC females | 0.0495 | 0.0187 | 0.0234 | 0.1019 | 0.0532 | 0.0205 | 0.0247 | 0.1108 |
| p(.) TG | 0.0499 | 0.0096 | 0.0341 | 0.0725 | 0.0434 | 0.0095 | 0.0281 | 0.0663 |
| p(.) FP | 0.0358 | 0.0145 | 0.0160 | 0.0781 | NA | NA | NA | NA |
| Ψ(EA->NC) | 0.0049 | 0.0035 | 0.0012 | 0.0198 | 0.0052 | 0.0053 | 0.0071 | 0.0377 |
| Ψ(EA->TG) | 0.0686 | 0.0214 | 0.0368 | 0.1243 | 0.0704 | 0.0229 | 0.0368 | 0.1308 |
| Ψ(EA->FP) | 0.0000 | 0.0000 | 0.0000 | 0.0000 | NA | NA | NA | NA |
| Ψ(NC->EA) | 0.0686 | 0.0214 | 0.0368 | 0.1243 | 0.0704 | 0.0229 | 0.0368 | 0.1308 |

| | 4-strata | | | | 3-strata | | | |
|---|---|---|---|---|---|---|---|---|
| Parameters | Estimate | Standard error | Lower 95% | Upper 95% | Estimate | Standard error | Lower 95% | Upper 95% |
| Ψ (NC->TG) | 0.0686 | 0.0214 | 0.0368 | 0.1243 | 0.0704 | 0.0229 | 0.0368 | 0.1308 |
| Ψ(NC<->FP) | 0 | 0 | 0 | 0 | NA | NA | NA | NA |
| Ψ(TG->EA) | 0.0049 | 0.0035 | 0.0012 | 0.0198 | 0 | 0 | 0 | 0 |
| Ψ(TG->NC) | 0.0049 | 0.0035 | 0.0012 | 0.0198 | 0 | 0 | 0 | 0 |
| Ψ(TG->FP) | 0.0049 | 0.0035 | 0.0012 | 0.0198 | NA | NA | NA | NA |
| Ψ(FP->EA) | 0 | 0 | 0 | 0 | NA | NA | NA | NA |
| Ψ(FP->NC) | 0 | 0 | 0 | 0 | NA | NA | NA | NA |
| Ψ(FP->TG) | 0.0686 | 0.0214 | 0.0368 | 0.1243 | NA | NA | NA | NA |

APPENDIX

**Table 1** Goodness of fit multistate tests. No values were significant except where indicated.

| Tests | | 1999-2004 |
|---|---|---|
| WBWA | Males | 0 |
| | Females | 0 |
| 3GSR | Males | 10.305 |
| (NC) | Males 2001 | 4.735 ($p<0.05$) |
| | Females | 6.84 |
| 3G.Sm | Males | 0 |
| | Females | 0.559 |
| M.ITEC $\chi_2$ | Males | 2.829 |
| | Females | 1.322 |
| g2 | Males | 3.344 |
| | Females | 1.702 |
| M.LTEC | Males | 0.876 |
| | Females | 1.001 |
| | Males | 1.106 |
| | Females | 1.048 |
| GLOBAL 3G | Males | 10.305 |
| | Females | 7.4 |
| GLOBAL M | Males | 3.705 |
| | Females | 2.323 |
| GLOBAL JMV | Males | 14.01 |
| | Females | 9.723 |