Accounting for female reproductive cycles in a superpopulation capture–recapture framework

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Abstract. Superpopulation capture–recapture models are useful for estimating the abundance of long-lived, migratory species because they are able to account for the fluid nature of annual residency at migratory destinations. Here we extend the superpopulation POPAN model to explicitly account for heterogeneity in capture probability linked to reproductive cycles (POPAN-t). This extension has potential application to a range of species that have temporally variable life stages (e.g., non-annual breeders such as albatrosses and baleen whales) and results in a significant reduction in bias over the standard POPAN model. We demonstrate the utility of this model in simultaneously estimating abundance and annual population growth rate (λ) in the New Zealand (NZ) southern right whale (Eubalaena australis) from 1995 to 2009. DNA profiles were constructed for the individual identification of more than 700 whales, sampled during two sets of winter expeditions in 1995–1998 and 2006–2009. Due to differences in recapture rates between sexes, only sex-specific models were considered. The POPAN-t models, which explicitly account for a decrease in capture probability in non-calving years, fit the female data set significantly better than do standard superpopulation models (ΔAIC > 25). The best POPAN-t model (AIC) gave a superpopulation estimate of 1162 females for 1995–2009 (95% CL 921, 1467) and an estimated annual increase of 5% (95% CL –2%, 13%). The best model (AIC) gave a superpopulation estimate of 1007 males (95% CL 794, 1276) and an estimated annual increase of 7% (95% CL 5%, 9%) for 1995–2009. Combined, the total superpopulation estimate for 1995–2009 was 2169 whales (95% CL 1836, 2563). Simulations suggest that failure to account for the effect of reproductive status on the capture probability would result in a substantial positive bias (+19%) in female abundance estimates.

Key words: abundance; Auckland Islands; calving interval; capture–recapture models; Eubalaena australis; heterogeneity; New Zealand; POPAN model; southern right whale; superpopulation.

INTRODUCTION

Estimating abundance and trends in demographic parameters is important for the management of populations, particularly in the context of endangered or threatened species (Norris 2004). Estimation can be problematic for highly mobile and migratory animals, as individuals often occupy habitats asynchronously. Evidence suggests that capture–recapture methods that account for the temporal variability of annual residency are robust approaches for estimating abundance (Williams et al. 2011). Hence, one of the most commonly used models to estimate abundance at migratory destinations is the superpopulation POPAN model (Arnason and Schwarz 1996, 1999), a derivative of the Jolly-Seber model (Jolly 1965, Seber 1965). The superpopulation parameter (N0), estimated by POPAN, is defined as the total number of individuals that ever enter the sampled population between the first and last survey occasions, in addition to individuals present at the start of the first survey. During each survey occasion, a proportion of N0 enters the survey area and is available for capture. This proportion is estimated by a parameter referred to as probability of entry. Superpopulation models have been used to estimate abundance and demographic trends in a range of species, including whale sharks Rhincodon typus (Meekan et al. 2006) and
North Pacific right whales *Eubalaena japonica* (Wade et al. 2011). Estimates of abundance are important for species such as cetaceans, because it is primarily the level of recovery compared with the pre-exploitation abundance that will determine future hunting pressure (Baker and Clapham 2004).

A complexity not yet addressed by available super-population models is variation in capture probability linked to breeding patterns. Factors such as environmental conditions, food availability, age, experience, previous breeding events, and population density can affect the breeding intervals of individuals (Lunn et al. 1994, Leaper et al. 2006). In many species with non-annual breeding cycles, females are more available for capture on breeding or nursery grounds in breeding years than in nonbreeding years. Heterogeneity in capture probability is typically thought of as an intrinsic characteristic of an individual that will create a bias in abundance estimates if unaccounted for (Seber 1982). In contrast, breeding status is not a permanent characteristic but one that can vary cyclically, and the bias induced by this type of heterogeneity has not been characterized previously in a superpopulation framework.

Here we present a novel version of the superpopulation POPAN model that explicitly accounts for the variation in capture probability of females due to reproductive status. We use the model to estimate abundance for the New Zealand (NZ) southern right whale *Eubalaena australis* (Baker et al. 2010; see Plate 1). The population is considered nationally endangered due to a combination of range restriction, low abundance, and low estimated rate of increase (Baker et al. 2010). Southern right whales migrate between high-latitude, pelagic feeding grounds in the austral summer and sheltered, coastal calving grounds in the austral winter (IWC 1986). As most of the pelagic feeding areas are not well characterized, the majority of our knowledge of the species comes from data collected on the coastal calving grounds where the whales predictably congregate each winter. Long-term (20–40 year) photo-identification studies have been conducted on coastal calving grounds in Australia, Argentina, and South Africa (Cooke et al. 2003, Burnell 2008, Brandão et al. 2010). Reproductive females in these studies demonstrate heterogeneity in capture probability linked to their reproductive cycle (Burnell 2001, Rowntree et al. 2001, Best et al. 2005). Females calve at intervals of 2–5 years, with an average of 3 years (Burnell 2001, Cooke et al. 2003, Brandão et al. 2010). In non-calving years, females have a decreased probability of capture, possibly due to a shorter residency period or visiting alternative wintering grounds (Payne 1986, Rowntree et al. 2001).

For these long-term, data-rich studies, the problem of breeding-induced heterogeneity in capture probability has been addressed using multi-state models that characterize females as calving, resting, or receptive (e.g., Brandão et al. 2010). Demographic parameters are estimated by these models using detailed histories of individual sightings and reproductive status (Cooke et al. 2003). This method requires abundant, high-quality data from long-term annual sightings records: for example, Brandão et al. (2010) had 1968 sightings of 954 individual cows with calves collected during annual aerial surveys from 1971 to 2006, from which they were able to estimate age at first parturition, survival, and population rate of increase.

The NZ population of southern right whales congregates during the austral winter in the subantarctic Auckland Islands in the vicinity of Port Ross (Fig. 1; see Patenaude et al. 1998, Patenaude 2002, Baker et al. 2010). Difficult conditions and the expense of working in the subantarctic during the austral winter mean that detailed long-term data sets are not available. Instead, two sets of winter expeditions have been conducted in the Auckland Islands: the first from 1995 to 1998 and the second from 2006 to 2009 (Patenaude and Baker 2001, Patenaude 2002, Carroll 2011). Rather than photo-ID, these surveys concentrated on the collection of skin biopsy samples for individual identification through DNA profile construction, including sex, mitochondrial (mtDNA) control region haplotype, and multilocus microsatellite genotype. These surveys, conducted a decade apart, provide an opportunity to examine trends in demographic parameters in the NZ population. However, in the absence of continuous annual sightings records, new methods are needed to deal with heterogeneity in female capture probability.

Analysis of mitochondrial DNA haplotype data suggests that the NZ population is genetically distinct from neighboring populations in Australia (Patenaude et al. 2007, Carroll et al. 2011a). Matching of DNA profile and photo-ID data suggests that the right whales found around the main islands of NZ are an extension of the primary concentration in the subantarctic, although this might not have been the case historically (Carroll et al. 2011a). Furthermore, evidence such as consistent use and high density of whales suggests that estimates of demographic parameters derived from data collected in the Port Ross area are representative of the overall NZ population (Patenaude et al. 1998, Childerhouse et al. 2010, Carroll et al. 2011a, b, Rayment et al. 2012). Previously, using the 1995–1998 field surveys, capture–recapture analyses yielded superpopulation estimates of ∼900 whales for the NZ population over this period, using photo-identification data (908 whales; 95% CL 755, 1123) and DNA profiles (910 whales; 95% CL 641, 1354) (Carroll et al. 2011b). This estimate is less than 5% of the estimated pre-whaling abundance (Jackson et al. 2009).

Here, using individuals identified with DNA profiles, we develop an extension of the POPAN model (POPAN-τ) to account for heterogeneity in female capture probability, and apply it to the extended survey period from 1995 to 2009. The parameters of interest are abundance, apparent survival (Φ), and annual rate of
increase ($\lambda$) for the NZ population of southern right whales. We also conduct simulations to test the robustness of the POPAN-$t$ model to misclassification of female reproductive status. Misclassification of reproductive status can arise if fieldwork can only be conducted for part of the breeding season, because some females could calve after the observation period.

**METHODS**

**Sample collection**

Fieldwork was conducted from small vessels (4.6–5.2 m) in and near Port Ross, Auckland Islands (50°32′ S, 166°15′ E), during the austral winters of 1995–1998 and 2006–2009, following methods described by Patenaude and Baker (2001). The length of the field seasons was between 12 and 35 days (Table 1). Skin biopsy samples were collected using small, stainless steel biopsy darts deployed from a crossbow in 1995–1998 (Lambertsen 1987) or a modified veterinary capture rifle in 2006–2009 (Krutzen et al. 2002). Skin samples were preserved in 70% ethanol on location and transferred to the University of Auckland for storage at −20°C.

In the field, sampled whales were classified into two age groups based on their body length: adult or calf. The latter was defined as a whale whose portion of body visible at the surface was less than half of the length of an accompanying adult (Carroll et al. 2011b). Adults in close association with a calf were noted in the field as cows and presumed to be their mothers.

**Laboratory methods**

Total genomic DNA was extracted from skin biopsy samples using standard proteinase K digestion and phenol/chloroform methods (Sambrook et al. 1989), as modified for small samples by Baker et al. (1994). The sex of the sampled whale was identified by amplification of the male-specific SRY gene, multiplexed with an amplification of the ZFY/ZRX region as positive control (Aasen and Medrano 1990, Gilson et al. 1998). Sequencing of the mitochondrial control region (500 bp) was conducted as described by Carroll et al. (2011a). Briefly, the primers dlp1.5 (Baker et al. 1998) and tphe (Carroll et al. 2011a), both modified with a 5′-M13 primer extension to facilitate subsequent sequencing reactions, were used to amplify ~950 bp of the mtDNA control region. PCR products were purified for sequencing with ExoSAP-IT (USB, Cleveland, Ohio, USA) and sequenced using BigDye Dye Terminator Chemistry (Applied Biosystems, Foster City, California, USA) on an ABI 3730 or ABI 3130 (Applied Biosystems). Sequences were aligned and edited in Sequencher v4.2 (Gene Codes Corporation, Ann Arbor, Michigan, USA) or Geneious (Drummond et al. 2006), and haplotypes were identified from a 500 bp consensus region using haplotype codes established by Carroll et al. (2011a).
TABLE 1. Number of samples collected and unique genotypes (assumed to represent individual whales) from southern right whales at the New Zealand subantarctic Auckland Islands during winter field surveys 1995–1998 and 2006–2009.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total samples, n</th>
<th>Quality control, n QC</th>
<th>Unique genotypes, n U</th>
<th>Males</th>
<th>Females</th>
<th>Dependent calves</th>
<th>Unknown sex</th>
<th>Field effort (d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1995</td>
<td>70</td>
<td>68</td>
<td>61</td>
<td>29</td>
<td>28</td>
<td>4</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td>1996</td>
<td>51</td>
<td>48</td>
<td>43</td>
<td>21</td>
<td>20</td>
<td>2</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>1997</td>
<td>75</td>
<td>59</td>
<td>52</td>
<td>31</td>
<td>19</td>
<td>2</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td>1998</td>
<td>158</td>
<td>128</td>
<td>105</td>
<td>51</td>
<td>46</td>
<td>4</td>
<td>4</td>
<td>35</td>
</tr>
<tr>
<td>1995–1998 total</td>
<td>354</td>
<td>303</td>
<td>261</td>
<td>113</td>
<td>106</td>
<td>12</td>
<td>4</td>
<td>88</td>
</tr>
<tr>
<td>2006</td>
<td>142</td>
<td>131</td>
<td>111</td>
<td>53</td>
<td>50</td>
<td>8</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>2007</td>
<td>234</td>
<td>218</td>
<td>167</td>
<td>60</td>
<td>86</td>
<td>21</td>
<td>0</td>
<td>17</td>
</tr>
<tr>
<td>2008</td>
<td>204</td>
<td>197</td>
<td>158</td>
<td>48</td>
<td>92</td>
<td>17</td>
<td>1</td>
<td>15</td>
</tr>
<tr>
<td>2009</td>
<td>254</td>
<td>240</td>
<td>191</td>
<td>76</td>
<td>103</td>
<td>9</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>2006–2009 total</td>
<td>834</td>
<td>766</td>
<td>627</td>
<td>208</td>
<td>308</td>
<td>55</td>
<td>4</td>
<td>48</td>
</tr>
<tr>
<td>Overall total</td>
<td>1188</td>
<td>1089</td>
<td>888</td>
<td>314</td>
<td>388</td>
<td>67</td>
<td>8</td>
<td>136</td>
</tr>
</tbody>
</table>

Notes: The number of samples after quality control is n QC; n U is the number of unique genotypes by year; for “unknown” samples, sex could not be genetically determined. The number of males and females sampled is totalled by year, by survey period, and overall. For male and female columns only, recaptures within survey periods (1995–1998 and 2006–2009) were reconciled, so these numbers represent unique individuals. Dependent calves are included in the table but are not used in the model in the year of birth. Field effort is given in days.

Thirteen microsatellite loci (EV1, EV37, and EV14 [Valsecchi and Amos 1996]; GATA28 and GATA98 [Palsboll et al. 1997]; RW18, RW31, RW410, and RW48 [Waldick et al. 1999]; GT23 [Bérubé et al. 2000]; TR3G2 and TR3F4 [Frasier et al. 2006]) were amplified in individual 10-μL PCR reactions as previously described by Carroll et al. (2011a). Each 96-well tray included a set of seven standard samples as an internal control to ensure consistent allele sizing and a negative control to detect contamination. Amplicons from 4–6 loci were co-loaded for capillary electrophoresis with an ABI 3730 or an ABI 3130. Alleles were sized with Genemapper v 4.0 (Applied Biosystems) and all automated calling was confirmed by visual inspection (Bonin et al. 2004).

Identification of matching genotypes, i.e., recaptures, was conducted as described in Carroll et al. (2011a). Briefly, matching genotypes were identified using CERVUS v3.0 (Kalinowski et al. 2007). As a precaution against false exclusion due to allelic dropout and other genotyping errors (Waits and Leberg 2000, Waits et al. 2001), the initial comparison allowed for mismatches at up to three loci. The genotype error rate was calculated per allele using the number of mismatching loci found in replicate samples (Pompanon et al. 2005).

A capture was defined as the identification of an individual within one year, and an individual was recaptured if it was sampled in a subsequent year. Captures and recaptures were categorized into males and females based on genetic sex identification results. Using data collected in the field, dependent calves were identified, and females were further categorized into cows with calves (denoted breeders) and cows without calves (denoted nonbreeders) in each year of capture. We did not use dependent calves in the superpopulation analyses because they have a lower survival rate than other age classes (Brandão et al. 2010).

Evaluating assumptions of capture–recapture models

To test for evidence of behavioral response to capture and transiency, we used the program U-CARE (Choquet et al. 2009). The 2006–2009 and 1995–2009 time periods for male, female, and combined data sets were tested separately to examine overall and sex-specific patterns. The 1995–1998 data were previously tested by Carroll et al. (2011b). The strict Bonferroni correction was used to account for multiple tests on the same data due to the nested nature of the data (Rice 1989).

We tested for significant differences in recapture frequencies due to sex (male vs. female), and female reproductive status (observed breeder vs. nonbreeder). Reproductive females are expected to be more available for capture in the year of calving, and typically have a calving interval of 2–5 years. We hypothesized that this could create a difference in the pattern of recapture between males and females. Specifically, we used a χ² test to see if there was a difference in the proportion of males and females that were captured in consecutive years, for the survey period 2006–2009.

Estimating POPAN superpopulation abundance (N S) and population rate of increase (λ)

We constructed a version of the standard superpopulation POPAN model in program R (R Development Core Team 2011) to estimate male superpopulation size (N S). The assumptions of the POPAN Jolly-Seber model are general to most capture–recapture models: for a review see Pollock et al. (1990). For t capture occasions, the POPAN model provides up to t estimates of capture probability (p); t − 1 estimates of apparent survival (Φ); t − 1 estimates of the proportion...
of the superpopulation making their first entry into the study site at each occasion \( (p_{ent}) \); and superpopulation size \( (N_S) \). Superpopulation models constrain \( p_{ent} \) values to sum to 1, by definition, so there are \( t \) values of \( p_{ent} \) in total. We investigated two parameterizations of the POPAN model: the standard version, available through MARK (White and Burnham 1999), and one we term \( \lambda \)-POPAN. In the standard POPAN parameterization, \( p_{ent}(2) \ldots p_{ent}(t) \) are estimated as free parameters. In the \( \lambda \)-POPAN parameterization, the \( p_{ent} \) parameters are constrained to follow a growth curve controlled by a single parameter, \( \lambda \), where \( \lambda \) is the annual growth rate, taken as constant throughout the time period, such that

\[
\frac{\text{EN}(t+1)}{\text{EN}(t)} = \lambda
\]

where \( \text{EN}(t) \) is the expected number of animals in the population at time \( t \), including new entrants at time \( t \) and survivors from previous years. If there are sampling periods missing from the data set, such as 1999 to 2005 in the right whale data set, the \( p_{ent} \) calculation is adjusted such that the value for 2006 accommodates the survival and recruitment of the missing intervening years (See the Appendix and R code in Supplement 2 for additional information). The \( \lambda \)-POPAN model has the advantage of directly estimating the parameter \( \lambda \); the standard POPAN model does not.

To estimate male and female abundance, we explored models with constant (i.e., time-invariant) survival denoted \( \Phi(.); \) either time-variable entry proportions \( p_{ent}(t) \) or a single constant annual growth rate \( \lambda; \) and time-variable probability of capture \( p(t) \). Given the variation in field season lengths (Table 1), models that held \( p \) constant in all years except for 1998 were explored. Furthermore, due to a combination of a shorter field season and a lower level of experience in the crew, we explored models that held \( p \) constant in all years except 2006. We also explored models that held \( p_{ent} \) constant in all years after the first year 1995, with the exception of 2006 to allow for the 8-year interval between survey periods, and denoted these by \( p_{ent}(06). \)

In cases where not all model parameters were estimable or boundary estimates were obtained, some parameters were constrained. The first two \( p \) were constrained to be equal in the \( p(t) \) models (i.e., \( p_1 = p_2 \)). Survival could be fixed at 0.99, denoted \( \Phi(0.99) \), a value found for females in long-term studies of conspecific populations (Brandão et al. 2010). The Akaike Information Criterion (AIC; Akaike 1973) was used to assess support for each model (Burnham and Anderson 2002). All models described were run in program R. Where possible, the equivalent models were run in program MARK (White and Burnham 1999) to validate our custom model results.

Due to strong evidence of lifelong site fidelity among females, it is likely that the survival parameter \( \Phi \) reflects true survival only. Therefore we can estimate the number of females alive in each survey year as derived quantities from the fitted model. We construct annual estimates using a parametric bootstrap from the fitted model. Values of \( N_S \) and \( \lambda \) are drawn from a bivariate normal distribution with mean and variance matrix given by their fitted values under the selected model. For each value of \( N_S \) and \( \lambda \), we simulate a superpopulation with size \( N_S \), and with \( p_{ent} \) probabilities specified by \( \lambda \), and subject each animal to annual mortality governed by \( \Phi \). We then find the number of animals alive in each year of the superpopulation. We repeat this 1000 times and use the mean and (2.5%, 97.5%) quantiles of the 1000 results as our estimate and 95% confidence interval for the number alive in each year.

**Accounting for the female reproductive cycle in a superpopulation framework**

As well as the standard POPAN and \( \lambda \)-POPAN models described previously, we developed an extended model, which we term POPAN-\( \tau \), to account for the female reproductive cycle. This model includes additional parameters \( \tau_1 \) and \( \tau_2 \) to simulate the reduction in capture probability in non-calving years. We refer to the reduction in capture probability in the year prior to calving as the “precall” effect and model it by adding the parameter \( \tau_1 \) to the model. If the whale is sampled as a breeder at time \( t \), \( \tau_1 \) is applied as a multiplier on the capture probability of that whale in the single year prior to calving, \( t-1 \). The capture probability for this whale at time \( t-1 \) is therefore \( \tau_1 \cdot (\cdot) \). This treatment is similar to the \( M_b \) model for behavioral response to capture (Chao et al. 2000); however, \( \tau_1 \) only applies to the capture probability in the year prior to capture as a breeder, rather than to all years subsequent to capture as in model \( M_b \). Similarly, we describe the reduction in capture probability in the year after calving as the “postcall” effect, incorporating the parameter \( \tau_2 \) into the model. If the whale is sampled as a breeder at time \( t \), \( \tau_2 \) applies as a multiplier on the capture probability of that whale in the single year after calving, \( t+1 \). If a female was captured without a calf, it was classified as a nonbreeder, and the capture probabilities were not modified in the surrounding years. For estimating female abundance, the standard POPAN and \( \lambda \)-POPAN models were run with and without parameters \( \tau_1 \) and \( \tau_2 \), either estimated separately \( (\tau_1, \tau_2) \) or jointly \( (\tau_1 = \tau_2 = \tau) \).

**Estimating combined male and female abundance**

We estimated the combined male and female superpopulation size by adding the sex-specific estimates. The standard lognormal confidence interval for total \( N_S \) is constructed by taking the variance of the combined estimate to be the sum of the two component variances, commensurate with independent estimates. It is reasonable to assume independence in the distributions of male and female estimates about their true values, because these distributions are governed by the randomness in capture histories. We have no evidence that male and
female individuals form permanent social groups that would lead to correlation in capture histories across the two data sets.

**Testing the robustness of POPAN-τ to misclassification of reproductive status**

The reproductive status of all females sampled cannot be known with certainty, as some may calve after the survey period ends or could have lost calves prior to being observed. Females not seen with calves were assumed to be nonbreeders. Therefore this model was based on the observed reproductive status of females sampled as breeders during the field surveys, which is an approximation of the true status. We ran simulations in R to investigate how robust the estimates of λ and NS are to the misclassification of reproductive status. We constructed a right whale population that comprised 50% adult females and 50% juvenile females in 1995 (Taylor et al. 2007). The juvenile females were randomly assigned an age of 1 to 8 years with a probability of 1/8 each. The adult females were assumed to have last calved 1, 2, or 3 years ago with a probability of 1/3 each. The calving interval distribution for adult females was approximated from studies on conspecific calving grounds, such that females had a probability of 0.02 of calving at an interval of 2 years, 0.83 of 3 years, 0.08 of 4 years, and 0.07 of 5 years (Cooke et al. 2001, Brandão et al. 2010). We also applied these intervals to a whale from 6 years of age so that first parturition was most commonly at age 9, as reported in the Australian and Argentinean right whale populations (Cooke et al. 2003, Burnell 2008). The NS, λ, and Φ values were taken to be those from the best (AIC) superpopulation model for the female data set.

This simulated population was then subject to a simulated capture-recapture study, where the capture probabilities and τ were those from the top-ranked superpopulation model for the female data set. We simulated imperfect classification of reproductive status by specifying the probability that a breeding animal that is seen in year t is correctly classified as a breeder in year t. This probability was variously set at 40%, 60%, 80%, and 100% for different simulation sets. We then fitted the POPAN-τ model to the sightings data with imperfect classification. The whole process from generating the population to fitting the model was repeated 500 times at each level of classification accuracy, and the mean and distribution of estimates of λ and NS were examined and compared to the values used to generate the simulations (see Supplement 2 for R code).

**RESULTS**

**Genotyping and individual identification**

During the 1995–1998 field surveys, 354 skin biopsy samples were collected, as described by Carroll et al. (2011b). During the 2006–2009 field surveys, 834 samples were collected (Table 1). From a total of 1188 samples collected over both sets of surveys, 1089 (92%) were successfully amplified at between 9 and 13 loci (average 12.3 loci) and were retained for further analysis (Table 1).

Pairwise comparisons showed that replicate samples matched at an average of 11 loci, and all pairs of replicate samples were supported by mtDNA control region haplotypes and genetically identified sex. The least variable 11 loci provided a probability of identity, or the chance that two individuals will have the same genotype by chance, of $7.8 \times 10^{-14}$ (Paetkau and Strobeck 1994) and a probability of identity for siblings, or the probability that two closely related individuals will have the same genotype by chance, of $1.7 \times 10^{-5}$ (Evett and Weir 1998). Given these low probabilities, we considered that the suite of microsatellite loci could be used to confidently differentiate between even closely related individuals in a population estimated to number 900 whales in 1998 (Carroll et al. 2011b). Based on replicate samples, there were 103 single-allele errors in 16770 successfully amplified alleles, giving a per allele error rate of 0.61% (Pompanon et al. 2005).

During the 1995–1998 field survey period, 223 non-calf whales were captured: 113 males, 106 females, and 4 whales of unknown sex, as previously described in Carroll et al. (2011b). During the 2006–2009 field survey period, 520 non-calf whales were captured, including 208 males, 308 females, and 4 whales of unknown sex. Overall, 710 non-calf whales were sampled, including 314 males, 388 females, and 8 whales of unknown sex during the 8 years of surveys. Of the 710 whales, 610 (85.9%) were captured in one year, 90 were captured in two years (12.7%), 9 were captured in three years (1.2%), and 1 was captured in four years (0.11%). The numbers of unique genotypes sampled per year and survey period are summarized in Table 1; between-year recaptures are summarized in Table 2 by sex (see Supplement 1 for capture history files).

**Tests of model assumptions**

The Stanley and Burnham (1999) Tests 3.SR and 2.CT implemented in U-CARE did not find significant evidence of transiency or behavioral response to capture (trap happy/shy), for any data set or time period (Appendix: Table A1).

For the time period 2006–2009, there was no evidence that the proportion of whales recaptured differed between males (26/208) and females (23/308) ($\chi^2 = 3.10$, df = 1, $P = 0.08$). In addition, there was no evidence that the recapture rate differed due to female reproductive state, i.e., between females never seen with a calf (nonbreeders, 14/158) and those seen in at least one year with a calf (breeders, 9/150) ($\chi^2 = 0.54$, df = 1, $P = 0.46$). Both of these results are consistent with the findings from the 1995–1998 data set by Carroll et al. (2011b).

However, there was evidence for a difference in the pattern of recaptures between males and females: males (15/208) were more likely to be captured in consecutive years compared with females (8/308; $\chi^2 = 5.17$, df = 1, $P$
Furthermore, the number of females recaptured between the two survey periods (n = 26/388) was significantly greater than the number of males recaptured (n = 7/314) between the 1995–1998 and 2006–2009 periods ($\chi^2 = 6.78, df = 1, P = 0.009$). These results indicate heterogeneity in recapture due to sex, both within the 2006–2009 survey period and between the 1995–1998 and 2006–2009 survey periods. Due to the need to estimate sex-specific parameters such as capture probability and apparent survival, only separate super-population models for males and females are considered in the rest of the study. This means that the capture histories of whales of unknown sex (n = 8), in addition to dependent calves (n = 67), were excluded from analysis.

**Female $N_S$ and $\lambda$ estimates for 1995–2009**

The best (AIC) model for the female data set was $\Phi(0.99), p(98), \lambda, \tau$, providing an estimate of $N_S = 1162$ females (95% CL 921, 1467) for 1995–2009 (see Table 3 and Appendix Table A2 for results and Supplement 1 for capture history files). Modeling $\tau_1$ and $\tau_2$ separately did not improve model fit compared with modeling the parameters jointly; therefore, we only report models with a single estimate of $\tau$ (Table 3). The addition of the parameter $\tau$ significantly improved the fit of the models, with the best-fitting standard or $\lambda$-POPAN model without $\tau$ having $\Delta$AIC > 25 compared with the best-fitting POPAN-$\tau$ model (Table 3). There was a correlation between AIC and $N_S$, with poor-fitting models (AIC > 10) producing higher estimates of abundance (Fig. 2).

The best estimate of $\lambda$ was 1.05, suggesting a population increase of 5% per year; however, the 95% confidence interval was wide (0.98–1.13) and contained the value 1, so a positive rate of increase could not be confirmed with 95% confidence. Worse-fitting models ($\Delta$AIC > 2) produced higher estimates of $\lambda$, suggesting annual increases of up to 12% (Appendix: Table A2), but this is above the estimated maximum rate of increase for the southern right whale (Best et al. 2001). Female survival ($U$) was estimated to be high ($\geq 0.97$; Table 3) and hit the boundary of 1.00 in many models. Fixing $U$ at 0.99 marginally improved model fit but did not have a substantive effect on estimates of $N_S$ and $\lambda$ (Table 3), as found previously (Carroll et al. 2011, Wade et al. 2011).

The standard POPAN model implemented in program MARK (White and Burnham 1999) and the R-based version converged to the same solution for the same model (see Appendix Tables A2 and A3 for model results and Supplement 1 for MARK project files). The estimated number of females alive in 2009 was 1074 (95% CL 812, 1339), which was close to the $N_S$ estimate of 1162 females (95% CL 921, 1467) for 1995–2009. The estimated numbers alive in 1995, 1998, 2006, and 2009 were, respectively, 533 (95% CL 219, 1012), 610 (95% CL 305, 1022), 910 (95% CL 692, 1130), and 1074 (95% CL 812, 1339).

**Male $N_S$ and $\lambda$ estimates for 1995–2009**

The best estimate for male abundance was $N_S = 1007$ (95% CL 794, 1276) from the $\Phi(\lambda), p(98)$ model (Table 3). All models explored had comparable estimates of $N_S$ (995–1066) and similar 95% CL. The models also
Table 3. Parameter settings and estimates (with 95% CL in parentheses) of non-calf female and male New Zealand southern right whale superpopulation abundance ($N_s$), apparent survival ($\Phi$), and population growth rate ($\lambda$) from a modified version of the superpopulation model, POPAN-$\tau$, implemented in program R.

<table>
<thead>
<tr>
<th>Model parameters</th>
<th>Estimates (95% CL)</th>
</tr>
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<tbody>
<tr>
<td>$\Phi$</td>
<td>$p$</td>
</tr>
<tr>
<td>A) Females</td>
<td></td>
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<tr>
<td>0.99</td>
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<td>0.99</td>
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<td>B) Males</td>
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<td>0.98</td>
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<td>0.96</td>
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Notes: Model parameters are shown on the left: $\Phi$, survival; $p$, capture probability; $\rho_{ent}$, entry proportion; $\lambda$, annual growth rate; $\tau$, capture probability multiplier accounting for a calving event. Cells are blank where parameters are not estimated by the particular model (e.g., standard parameterizations of POPAN do not estimate $\lambda$, $\rho_{ent}$, and $\lambda$). For each model, the number of parameters ($n_p$) and the increase in AIC from the best fitting model ($\Delta AIC$) are reported. The estimate is based on individuals identified from DNA profiles, using data from the 1995–1998 and 2006–2009 survey periods. The five best-fitting models are reported, and also for the female data set the best-fitting standard or $\lambda$-POPAN model without $\tau$. A “0” indicates that the parameter is constant over time; a dot (.) indicates that the parameter varies with capture occasion; a dot (.) indicates that the parameter was allowed to vary in the 2006 capture occasion but was held constant over other capture occasions; similarly, “98” indicates that the parameter was allowed to vary in the 1998 capture occasion but was held constant over other capture occasions; “fixed” indicates that survival was fixed at 0.99 and as such has no CLs.

The simulations were based on the best-fitting POPAN-$\tau$ model for the female data set, $\Phi(0.99), p(t), \lambda, \tau$ (Table 3), and the probability of a sampled breeder being correctly classified as a breeder ranged from 40% to 100%. Results when breeding classification is 80% correct are shown in Fig. 3A. The differences between the true values of $N_s$ and $\lambda$, namely the values used to set up the simulations and their mean estimates derived from the simulations, are minor, with <5% bias for $N_s$ and <1% bias for $\lambda$. The CI coverage percentage, or the percentage of the time the CI contains the true value, is equal to the nominal 95% (Fig. 3). Results for other levels of breeding classification accuracy are shown in the Appendix: Fig. A1. High CI coverage and accurate estimates of $N_s$ and $\lambda$ indicate that the POPAN-$\tau$ model produced similar estimates of $\lambda$, with the best model producing $\lambda = 1.07$ (95% CL 1.05, 1.09). Male estimates of $\Phi$ were lower than the female estimates at 0.82–0.83 (95% CL 0.75–0.90) (Table 3). The standard POPAN model implemented in program MARK (White and Burnham 1999) and the R-based version converged to the same solution for the same model (see Appendix Tables A2 and A4 for model results and Supplement 1 for MARK project files).

Combined $N_s$ for 1995–2009

The combined estimate of male and female total $N_s$ was 2169 (95% CL 1836, 2563).

Robustness of POPAN-$\tau$ to misclassification of breeders

The simulations were based on the best-fitting POPAN-$\tau$ model for the female data set, $\Phi(0.99), p(t), \lambda, \tau$ (Table 3), and the probability of a sampled breeder being correctly classified as a breeder ranged from 40% to 100%. Results when breeding classification is 80% correct are shown in Fig. 3A. The differences between the true values of $N_s$ and $\lambda$, namely the values used to set up the simulations and their mean estimates derived from the simulations, are minor, with <5% bias for $N_s$ and <1% bias for $\lambda$. The CI coverage percentage, or the percentage of the time the CI contains the true value, is equal to the nominal 95% (Fig. 3). Results for other levels of breeding classification accuracy are shown in the Appendix: Fig. A1. High CI coverage and accurate estimates of $N_s$ and $\lambda$ indicate that the POPAN-$\tau$ model.

Fig. 2. Superpopulation estimate ($N_s$) for the female component of the New Zealand southern right whale population plotted against $\Delta AIC$ for POPAN-$\tau$ models and standard or $\lambda$-POPAN models without $\tau$. POPAN-$\tau$ models incorporate the parameter $\tau$, which models the decrease in capture probability of females at the wintering ground in non-calving years. The estimate is based on southern right whales sampled at the Auckland Islands during winter field surveys from 1995–1998 and 2006–2009 and identified using DNA profiles comprising genetically identified sex, mitochondrial DNA haplotype, and multi-locus microsatellite genotype (up to 13 loci).
is able to estimate $N_S$ and $\lambda$ robustly, although with increasing positive bias in $N_S$ as the probability of correctly assigning the reproductive status of a breeder decreases to 40%.

Results of the simulations conducted with the $\lambda$-POPAN model without $\tau$ are shown in Fig. 3B. The difference between the mean estimate of $N_S$ and the true $N_S$ is +19%, implying that the model without $\tau$ has a +19% bias under the simulation scenario. Even when only 40% of sampled breeders are correctly classified, the bias in $N_S$ (+12%) is substantially less than that of the $\lambda$-POPAN model without $\tau$ (+19%). In contrast, estimates and CI coverage of $\lambda$ appear to be extremely robust in models with and without $\tau$. However, confidence intervals for $\lambda$ are wide for all models, as found in the empirical data for females with these parameter values.

**DISCUSSION**

We have shown that our novel superpopulation POPAN-$\tau$ model, which explicitly accounts for the variation in capture probability of females linked to their reproductive cycle, performs substantially better than the conventional POPAN model. It is an improvement both in terms of improved fit for our data ($\Delta$AIC $> 25$) and in terms of bias following our simulation results. The POPAN-$\tau$ model provided a 1995–2009 estimate of female abundance for the NZ southern right whale population of 1162 (95% CL 921, 1467), compared with 1520 (95% CL 1185, 1951) for the best-ranked superpopulation model without $\tau$ (Table 3). The POPAN model’s 1995–2009 estimate of male abundance was 1007 (95% CL 794, 1276). The addition of the parameter $\tau$ largely eliminated the difference in abundance estimates between males and females, suggesting parity between the sexes in the NZ population. This is consistent with the observed equal sex ratio of calves (Carroll et al. 2011b).

In the case of the NZ southern right whale, females appear to have a lower capture probability in non-calving years, possibly linked to shorter residency time on the wintering ground when without a calf (Payne 1986, Rowntree et al. 2001, Best et al. 2003). If this is not
accounted for, the overall capture probability of all females is decreased and the standard POPAN model produces a positively biased estimate of the female superpopulation size. In fact, the bias in the POPAN model without \( \tau \) was larger than that of the POPAN-\( \tau \) model even if a substantial amount of misclassification of breeding females occurred (up to 60% misclassified). Hence, we consider that the POPAN-\( \tau \) model represents a significant improvement for modeling superpopulation abundance in species that show variation in capture probability linked to reproductive cycle.

**Recovery of the NZ population**

The annual rate of change was estimated most precisely with the male data set, and showed a significant positive trend of 7% (95% CL 5%, 9%) for the NZ population. This estimate is captured within the wider 95% CL of (−2%, 13%) gained from the female estimate of \( \lambda \). The complexity of the female model (requiring 10 parameters compared with 5 parameters in the male estimate) reduced the precision of the estimate of \( \lambda \); a longer time series is required to obtain a precise estimate of \( \lambda \) based on data from females alone. The point estimates of rates of increase for the NZ population are slightly lower than those in southwest Australia (8.1%, 95% CL 4.5%, 10%; Bannister 2008); and very similar, although less precise than those in South Africa (6.9%, 95% CL 6.4%, 7.4%; Brandão et al. 2010) and Peninsula Valdes (6.8%, SE 0.5%; Cooke et al. 2001).

The female point estimate of apparent survival or \( \Phi \) often hit the boundary at 1.00, whereas the male estimate of \( \Phi \) was consistently estimated at 0.82–0.84. Survival has previously been estimated to be 0.99 in females based on multi-state models fitted to sightings data (Cooke et al. 2003, Brandão et al. 2010), and there are no published estimates of \( \Phi \) for male southern right whales. The POPAN-\( \tau \) estimate of \( \Phi \), or apparent survival, is a composite of true survival and fidelity, and the difference between males and females is intriguing. There is no evidence that males have a higher mortality rate than female right whales. For example, deaths due to anthropogenic activities do not show a sex bias and there is little evidence for male–male aggression leading to injury or mortality in right whales (Kraus and Hatch 2001, Kemper 2008).

If males show weaker migratory fidelity to calving grounds compared with females, it would explain the difference in apparent survival between the sexes. Plasticity in philopatric behavior is known to occur in a low level in southern right whales, but sex-biased dispersal has not been detected (Best et al. 1993, Pirzl et al. 2009, Carroll et al. 2011a). On the Peninsula Valdes calving ground, males are regularly sighted, although the resighting rate decreases with maturity (Rowntree et al. 2001). However, as we do not have information on individual ages, we can only conjecture that our results for the NZ male population could be explained by a similar age-related decline in site fidelity.

Available genetic and demographic evidence, based on paternity analyses and comparisons of mtDNA haplotype frequencies across wintering areas in NZ and Australia, are consistent with the hypothesis that the NZ population represents a relatively discrete, reproductively autonomous unit. As such, the superpopulation size represents the number of whales that used the wintering ground over the course of the survey period, 1995–2009, and should represent this relatively discrete population. The estimate of number of females alive in 2009 (1074, 95% CL 812, 1339) is similar to the estimate of \( N_s \), suggesting that for females \( N_s \) is a useful and meaningful parameter. Superpopulation size does not take into account mortality: for females, this appears to be minor, even over a 15-year period.

**Utility of POPAN-\( \tau \)**

The POPAN-\( \tau \) model could be applied in circumstances where species have irregular breeding intervals for reasons such as variation in food resources linked to environmental conditions (Forcada et al. 2008). This is because it does not require direct information on the breeding interval, but rather an observation of the breeding event. Another advantage of the POPAN-\( \tau \) model is its efficiency even when capture probabilities are low. Standard multi-state and individual-based models for estimating survival and abundance require rich data sets to be effective (Lebreton et al. 1992). Here we have demonstrated the success of the method using a data set with a resighting rate of \( \sim 10\% \), low compared with many capture-recapture studies, but typical for cetacean species, e.g., 5.8% resighting rate in North Atlantic humpback whales (Smith et al. 1999); 3.4% resighting rate in humpback whales off Madagascar (Cerchio et al. 2009); 21% resighting rate in Oceania humpback whales (Constantine et al. 2012). We believe that this method allows the effective use of data that might otherwise be considered sparse. The POPAN-\( \tau \) model uses observed breeding status as an approximation of true breeding status, so we recommend that its performance is first verified by simulation if it is to be applied in situations with very different parameters from those presented here.

The POPAN-\( \tau \) model has the potential for use in other species that have differences in behavior linked to reproduction, including other baleen whales, seals, and oceanic birds (Dawbin 1966, Tickell 1968, Gregor et al. 2000). For example, humpback whales migrate between tropical and subtropical winter breeding grounds and high-latitude summer feeding grounds (Dawbin 1966). The timing of migration varies between demographic classes, based on the analysis of whaling station catch data from across the Southern Hemisphere (Dawbin 1966). Females with calves have a longer residency time in the wintering grounds than receptive or newly pregnant females, who spend approximately two months longer in the feeding grounds (Dawbin 1966). This means that on the wintering ground, newly pregnant
females have a lower capture probability than females with calves, and there is often a male sex bias (Smith et al. 1999). Because humpback whales have a modal reproductive cycle of two or three years (although it can vary between one and five years), the migratory timing of individual whales, and therefore availability for capture on wintering grounds, appears to vary across years depending on reproductive status (Baker et al. 1987, Craig et al. 2003). There is also evidence that sei whale Balaenoptera borealis migration is structured by age, sex, and reproductive status in a way similar to that of humpback whales (Gregor et al. 2000, Best and Lockyer 2002).

The apparent sex bias in capture records has posed a problem when estimating abundance in humpback whales. For example, Constantine et al. (2012) doubled the male-specific value to estimate humpback whale abundance on their breeding grounds in Oceania to account for the difference in capture probability between the sexes. Another study on humpback whales in the North Pacific found that the known male sex bias in breeding areas did not bias abundance estimates if both sexes are proportionately sampled in the feeding areas (Barlow et al. 2011). The POPAN-τ model would be suitable for estimating abundance of humpback whales on their wintering grounds because it would be able to account for the heterogeneity in female capture probability linked to the reproductive cycle. This situation can produce a substantial positive bias in the standard POPAN model (Fig. 2) and should be considered when using the model to estimate abundance or rate of recovery in endangered or vulnerable populations. Overestimating recovery can have implications for the protection measures afforded to populations, and in the case of baleen whales, potential implications for exploitation should the moratorium on commercial whaling be lifted (IWC 1999).

**Conclusion**

POPAN-τ represents a significant improvement in the modeling of superpopulation abundance for a species that shows variation in capture probability linked to the reproductive cycle. Based on the results of this study, we suggest that failing to account for variation in capture probability linked to reproductive status can create bias in abundance estimates, although we did not see bias in estimates of λ. Overestimating the abundance of endangered or threatened species has important management implications, because abundance and evidence of recovery are measures used to decide listings such as IUCN red list status. POPAN-τ is an example of the tailoring of a superpopulation model to the reproductive cycle.
cycle of a specific species, but the model and general concept are applicable in a wider context.

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**SUPPLEMENTAL MATERIAL**

**Appendix**

Equation for calculating \(p_{\text{out}}\) parameters given \(\lambda\) and \(\Phi\) (*Ecological Archives* A023-086-A1).

**Supplement 1**

Capture history files and program MARK files (*Ecological Archives* A023-086-S1).

**Supplement 2**

R code for POPAN (\(\lambda\)-POPAN and POPAN-\(t\)) models and simulations (*Ecological Archives* A023-086-S2).