CAPTURE-RECAPTURE ANALYSES OF HUMPBACK POPULATION SIZES AND INCREASE RATES: BREEDING STOCKS C1-C3

S.J. Johnston and D.S. Butterworth

Marine Resources Assessment and Management Group (MARAM) Department of Mathematics and Applied Mathematics University of Cape Town Rondebosch 7701 South Africa

Abstract

Both maximum likelihood and Bayesian methodologies are developed to analyse the photo-ID and genotypic capture-recapture data available for the C1 and C3 breeding sub-stocks of humpback whales in the western Indian Ocean. A simple exponential growth population model is assumed, and estimates of annual growth rate and abundances determined. Maximum likelihood estimates of *r* are generally imprecise and often the point estimates are demographically infeasible. The most reliable results are probably those from the Bayesian analyses with a prior for r of U[0; 0.106]. The data update this prior somewhat more for C3 than for C1, with a median posterior estimate of 8.0% for the former. Posterior median estimates of abundance for each sub-stock when analysed in isolation are both a little more than 6500. An interchange model is developed to take account of photo-ID information on exchanges between the C1 and C3 regions (only one such exchange has been recorded thus far). The results show little difference between the combined abundances estimated for the two sub-stocks with such interchange, compared to the sum of results for the two analysed in isolation; the posterior median annual probability of an animal from either sub-stock visiting the other's region in any one year is a little more than 5%, with an upper 5%-ile of some 19%. It should be understood that the results presented are intended to be illustrative, not definitive, having the purpose of facilitating further runs and refinements of the models during Scientific Committee discussions.

Introduction

This paper fits exponential growth models to both the photo-ID and genotypic capture-recapture available for the C1 and C3 breeding sub-stocks of humpbacks in the western Indian Ocean. Both maximum likelihood and Bayesian estimation approaches are developed. The approaches are first applied treating the sub-stocks as completely separate, and then an interchange model is developed to analyse them jointly allowing for the possibility of animals from one sub-stock travelling in some years to the region in which the other sub-stock aggregates.

The analyses presented are not intended to be definitive but rather illustrative. Their purpose is to introduce the methodology and to provide a basis upon which to formulate alternative model runs and develop model refinements during discussions in the IWC Scientific Committee.

Data

The capture-recapture data used here are reported in Cerchio *et al*. (2008a and b). These consist of both photo-ID and genotypic mark-recapture data from Antongil Bay (C3) (Cerchio *et al.* 2008a), as well as photo-ID mark-recapture data for C1 (Cerchio *et al.* 2008b). The data span the period 2000-2006 and are reproduced in Appendix 1.

Methods

Maximum Likelihood

The following simple exponential population growth model is considered in conjunction with the capture-recapture data (where "capture" can refer to either photographic or genetic identification):

$$
N_{y+1} = N_y + rN_y \tag{1}
$$

$$
n_{y} = p_{y} N_{y} \tag{2}
$$

$$
\hat{m}_{y',y} = p_{y'} p_y N_y e^{-M(y'-y)} \tag{3}
$$

where: n_v

n = number of animals captured in year *y*

- $m_{v',v'}$ = number of animals captured in year *y* that were recaptured in year *y*'
- $\hat{m}_{y'y'}$ $=$ model predicted number of animals captured in year ν that were recaptured in year v'

 $r =$ the population growth rate $M =$ natural mortality rate p_{y} $=$ probability animal is seen in year γ *N^y* = population size in year *y.*

For each potential recapture cell (ignoring some year recaptures), the likelihood contribution assuming a Poisson distribution is given by:

$$
L = \frac{(\hat{m}_{y',y})^{m_{y',y}}}{m_{y',y}!} e^{-\hat{m}_{y',y}}
$$
 (4)

Hence the overall *–lnL* to be minimised is:

$$
-lnL = \sum_{y=y_0}^{y_j-1} \sum_{y=y_1}^{y_j} \left[-m_{y',y} \ln \hat{m}_{y',y} + \hat{m}_{y',y} \right] + const
$$
 (5)

where:

 y_0 = the first year of captures

 y_f = the last year of captures

and the minimisation is over the estimable parameters r and N_{y_0} . Note that the approach makes allowance for the reduction over time in the numbers of animals potentially recaptured as a result of natural mortality.

Bayesian

Results are produced for two priors on r – either $r \sim U[-1, 1]$ i.e. essentially an uninformative prior, or *r* ~ U[0; 0.106] to take into account Scientific Committee deliberations on demographically plausible bounds for this parameter. The prior for *N*(2003) is U[200; 80 000], i.e. again essentially uninformative. If an independent abundance estimate from a sightings survey is available, the following term is added to –*lnL*:

$$
\left(\ln N_{y}^{obs} - \ln \hat{N}_{y}\right)^{2} / 2CV^{2}
$$
\n⁽⁶⁾

where: N_y^{obs}

 is the observed abundance estimate for year *y*, and *CV* is the coefficient of variation associate with this estimate.

General

A "Reference Case" analysis is one which uses all the data available for a certain data type and sets $M = 0.03$ yr⁻¹. Hessian-based CVs are provided for the maximum likelihood estimable parameters, but to minimise covariance impacts, these are reported rather for N_{2003} than for year y_0 (N_{y_0}). For the Bayesian results, medians plus 95% PIs are reported for *r* and for the N_y and p_y values.

Findlay *et al.* (in press) estimated the population abundance for C1 to be 5965 (CV=0.17) in 2003 from a sighting survey. This information is used in one of the Bayesian analyses following.

Sensitivity tests

The following sensitivity tests are carried out for the maximum likelihood analyses**:**

Sensitivity 1: Remove year 2002 from the analysis for C3 due to small sample size. Sensitivity 2: Fix $r = 0$ yr⁻¹. Sensitivity 3: Fix $r = 0.106$ yr⁻¹. Sensitivity 4: $M = 0.02$ yr⁻¹. Sensitivity 5: $M = 0.04$ yr⁻¹.

Bayesian C1-C3 assessment model allowing for interchange

This model fits to all the photo-ID and genotypic capture-recapture data reported in Cerchio *et al*. (2008a) for C1 and C3, together with the C1-C3 photo-ID interchange data reported in Cerchio *et al.* (2008b). Further it fits to the absolute abundance estimate for C1 provided by Findlay *et al.* (in press).

The interchange model considered is shown schematically below. There are two breeding substocks C1 and C3 of sizes N^1 and N^3 respectively each growing exponentially. However each year there is a probability $q¹$ that an animal from sub-stock C1 travels to the C3 region, and similarly a probability q^3 that one from sub-stock C3 travels to the C1 region. Note that the model assumes that an animal "visits" only one of these two regions in any one year. The numbers in regions C1 and C3 each year are then given by \tilde{N}^1 and \tilde{N}^3 respectively, and these are the variables to which observations apply (both capture-recapture and survey data).

(8)

The following equations then apply:

Breeding populations: *ⁱ*

y i i $N_{y+1}^i = N_y^i + r^i N_y^i$ (7) where *i* refers to breeding sub-stock C1 or C3

Observed populations: $\tilde{N}_y^i = (1 - q^i) N_y^i + q^k N_y^k$

Captures: $n_y^i = p_y^i \tilde{N}_y^i$

 $Recaptures:$

J $\overline{\mathcal{L}}$ J $\overline{\mathcal{L}}$ J $\overline{\mathcal{L}}$ 1 3 *k* $i = 1,3$ (9) refers to humpbacks captured in region *i* in year *y* and

∤ \int =

1 *or*

 $\left\{ \right\}$ \mathcal{I}

∤ \int

i

recaptured in region *j* in year y', while the expected numbers in terms of the interchange model are:

 $\left\{ \right\}$ 1

∤ \int

3

 $\left\{ \right\}$ \mathcal{L}

$$
\hat{m}_{y',y}^{j,i} = p_y^i [(1-q^i)N_y^i e^{-M(y^i-y)} q^i + q^j N_y^j e^{-M(y^i-y)} (1-q^j)] p_y^j
$$
(10a)

$$
\hat{m}_{y',y}^{i,i} = p_y^i [(1-q^i)N_y^i e^{-M(y^i-y)} (1-q^i) + q^j N_y^j e^{-M(y^i-y)} q^j] p_y^i
$$

where:

$$
\begin{Bmatrix} i \\ j \end{Bmatrix} = \begin{Bmatrix} 1 \\ 3 \end{Bmatrix} or \begin{Bmatrix} 3 \\ 1 \end{Bmatrix}; \begin{Bmatrix} i \\ j \end{Bmatrix} = \begin{Bmatrix} 1 \\ 1 \end{Bmatrix} or \begin{Bmatrix} 3 \\ 3 \end{Bmatrix}
$$

(10b)

,

and the contributions to the negative log likelihood from the photo-ID capture-recapture data and Findlay *et al.*'s (in press) abundance estimate for 2003 are:

$$
-\ln L = \sum_{i} \sum_{j} \sum_{y=y, \ y=y+1}^{y_{i}-1} [-m_{y',y}^{j,i} \ln \hat{m}_{y',y}^{j,i} + \hat{m}_{y',y}^{j,i} + \frac{[\ln \tilde{N}_{2003}^{1} - \ln(5965)]^{2}}{2(0.17)^{2}} \tag{11}
$$

For application of the Bayesian estimation approach *r* is first taken to be the same for the two breeding sub-stocks, i.e. $r^1 = r^3 = r$, and then to differ, with an associated U[0; 0.106] priors in each case. The priors for each of $N^1(2003)$ and $N^3(2003)$ are U[200; 80000] as before. For q^1 and $q³$ the priors are each set to U[0.001; 0.6]. The reason for the lower bound is to avoid possible

difficulties with logarithms of zero occurring in computations. The upper bound is set to avoid an ambiguity in the model corresponding to an alternative equivalent solution of:

$$
q1 \to 1 - q3 \qquad N1 \to N3
$$

$$
q3 \to 1 - q1 \qquad N3 \to N1
$$
.

which arises because of its symmetrical nature.

Results

C3 – no interchange

Tables 1a and b report the results for BS C3 for the photographic and genotypic data respectively, and Table 1c reports results for BS C3 where both data types have been used together in the assessment. These results are for the maximum likelihood method. Table 1d reports results for BS C3 using Bayesian estimation; medians and 95% PIs are reported.

Figure 1a shows population trends estimated by the maximum likelihood approach for both the photo-ID and the genotypic data (RC, Sen 2 and 3). Figure 1b compares the RC trends with the reported abundance estimates in Cerchio *et al.* (2008a). Figures 1d-h show the population trends as estimated by the Bayesian approach – medians and 95% PIs are shown.

Note that the Cerchio *et al.* (2008a) preferred estimates using Chapman's modified Petersen estimator (see Appendix 1 for more details) are:

Photo-ID data: 7715 (CV=0.24) for 2003-2006 period, and 6737 (CV=0.31) for 2004-2006 period, with

 $r = 0.063$.

Genotypic data: 10123 (CV=0.24) for 2003-2006 period, and 8348 (CV=0.32) for 2004-2006 period, with

 $r = 0.136$.

Data relating to the 2002 capture year were eliminated from the Cerchio *et al*. (2008a) analyses due to poor capture size that year.

Note that Cerchio *et al.* (2008a) comment that the point estimate of $r = 0.136$ from the genotypic data is demographically implausible.

C1 – no interchange

Table 2a reports the maximum likelihood results for BS C1 (using the photo-ID data). Table 1b reports the results from Bayesian estimation for BS C1. Results are also reported in Table 2b for the case where both the photo-ID data as well as the Findlay *et al.* (in press) abundance estimate of 5965 (CV=0.17) in 2003 is used.

Figure 2a shows the maximum likelihood population abundance trends (RC, Sen 2 and 3). The Findlay *et al.* (in press) abundance estimate is also shown on the plot for comparison. Figures 2b and c show the Bayesian estimated population abundance trends for the two *r* prior assumptions. Figure 2c shows the Bayesian estimated population trend for the case where the Findlay (in press) population abundance estimate is fitted to in conjunction with the photo-ID mark-recapture data.

C1-C3 with interchange

The results for application of the Bayesian estimation approach to the interchange model are given in Tables 3a and b. Results in Table 3a are for the assumption that *r* is constant between the two substocks, i.e. $r^1 = r^3 = r$, whilst results in Table 3b allow for both r^1 and r^2 to be estimated separately. Figures 4a and b show the population trends estimated for each sub-stock separately and also for their combined numbers for the both the $r' = r^3 = r$ model, and for the model where the *r* parameters are estimated separately. Figures 5 and 6 shows the associated posterior distributions for the *r* (or r^1 and r^3), q^1 and q^3 parameters.

Discussion

For most of the applications of the maximum likelihood estimation approach reported (Tables 1a-c and 2a), estimates of annual growth rate *r* are imprecise, and point estimates often demographically infeasible. Bayesian results, particularly those restricting *r* to the demographically realistic range of U[0; 0.106] probably offer the greatest reliability.

For the C3 sub-stock, genotypic and photo-ID data separately offer similar results for population abundances, both in terms of absolute values and of precision (Table 1d). When the data are analysed in combination, the uniform *r* prior is updated to the same degree to yield a posterior median growth rate estimate of 8.0% (Fig. 3a), while the median estimate for abundance in 2003 is 6600 with 95% PI [5600; 8100].

For the C1 sub-stock with less capture-recapture data (no genotypic data) but the advantage of a survey estimate of abundance, results are slightly less precise with the *r* prior less updated than for C3 (Fig. 3b) (posterior median 6.6%), and median 2003 abundance at 6700 with 95% PI [5300; 8700] (Table 2b). Note that capture probabilities are less for C1, with the largest median value in 2005 at 1.8%, compared to C3 for which these are near 2% for most years and sometimes approach 3% (Tables 1d and 2b).

When interchange is admitted, interestingly the posterior median estimates for *r* are lower than for either sub-stock analysed in isolation, though this should be seen in the context of the poor precision of those estimates anyway. Aside from differences caused by different posteriors for *r*, estimates of abundance differ little from those for the sub-stocks analysed in isolation; for the abundance in mid-series (2003), the analyses with interchange estimate posterior median abundances for the two sub-stocks together which are only about 2% greater than the 13400 obtained by summing those values for the two analysed separately. The posterior median probabilities for an animal belonging to one sub-stock "visiting" the other's region in any one year is a little more than 5% for both sub-stocks, with an upper 5%-ile of some 19%.

Clearly variations in data input and refinements of the models presented are possible. In particular, it should be noted that the "visitor-like" interchange model presented and analysed involves but one of a number of different exchange mechanisms that could be postulated.

Acknowledgements

The authors thank the providers of the original photo-ID and genotype material and the analysts thereof for the provision of the capture-recapture data upon which these analyses are based. The National Research Foundation, South Africa, is thanked for financial support.

References

- Cerchio, S, Ersts, P., Pomilla, C., Loo, J., Razafindrakoto, Y., Leslie, M., Andrianrivelo, N., Minton, G., Dushane, J., Murray, A., Collins, T. and Rosenbaum, H. (2008a) Revised estimation of abundance for breeding stock C3 of humpback whales, assessed through photographic and genotypic mark-recapture data from Antongil Bay, Madagascar, 2000-2006. IWC document SC/60/SH32.
- Cerchio, S., Findlay, K., Ersts, P., Minton, G., Bennet, D., Meyer, M.A., Razafindrakoto, Y., Kotze, P.G.H., Oosthuizen, H., Leslie, M., Andrianarivelo, N. and Rosenbaum, H. 2008b. Initial assessment of exchange between breeding stocks C1 and C3 of humpback whales in the western Indian Ocean using photographic mark-recapture data, 2000-2006. IWC document SC/60/SH33.
- Findlay, K., Meyer, M, Elwen, S., Kotze, D., Johnson, R., Truter, P., Uamusse, C., Sitoe, S., Wilke, C., Kerwath, S., Swanson, S., Stavarees, L. and J. van der Westhuizen. (in press). Distribution and abundance of humpback whales, *Megaptera novaeangliae*, off the coast of Mozambique, 2004. J. Cetacean Res. Manage. (Special Issue)

Table 1a: **C3** results based on **photo-ID** data. Values in brackets are the Hessian based CVs. Values fixed on input are shown as bold. Non-comparable –*ln*L values are sown in square brackets.

Table 1b: **C3** results – based on **genotypic** data. Values in brackets are the Hessian based CVs. Values fixed on input are shown as bold. Non-comparable –*ln*L values are sown in square brackets.

Table 1c: C3 results – based on **both** photo-ID and genotypic data.

8

Table 1d: C3 Bayesian posterior estimates. Median and 95% PIs are reported. [For the "both data sources" scenarios, the "pho" refers to photo-ID data, and the "gen" refers to the genotypic data.]

Table 2a: C1 results – based on photo-ID data. Values in brackets are the Hessian based CVs. Values fixed on input are shown as bold.

Table 2b: C1 Bayesian posterior estimates. Median and 95% PIs are reported.

	RC photo-ID	RC photo-ID	RC photo-ID and Findlay
			et al. (in press) estimate
r prior	$r \sim U[-1; 1]$	$r \sim U[0; 0.106]$	$r \sim U[0; 0.106]$
R	0.310 [-0.254; 0.876]	0.054 [0.006; 0.101]	0.066 [0.010; 0.102]
N(2000)	3653 [623; 68490]	10273 [5342; 23177]	5633 [4229; 7624]
N(2001)	4815 [1123; 52342]	10831 [5720; 24121]	5976 [4574; 7888]
N(2002)	6367 [1990; 40652]	11402 [6088; 25115]	6338 [4932; 8222]
N(2003)	8369 [3382; 32308]	12011 [6475; 26414]	6728 [5288; 8658]
N(2004)	11004 [5446; 28454]	12639 [6810; 27691]	7139 [5605; 9183]
N(2005)	14021 [7587; 30485]	13343 [7204; 29052]	7584 [5901; 9854]
N(2006)	18032 [7877; 45736]	14119 [7556; 30584]	8052 [6173; 10635]
p(2000)	0.000 [0.000; 0.001]	0.000 [0.000; 0.001]	0.001 [0.000; 0.001]
p(2001)	0.002 [0.001; 0.004]	0.002 [0.001; 0.004]	0.004 [0.003; 0.005]
p(2002)	0.004 [0.002; 0.008]	0.004 [0.002; 0.008]	0.008 [0.006; 0.010]
p(2003)	0.010 [0.004; 0.018]	0.010 [0.004; 0.018]	0.017 [0.013; 0.022]
p(2004)	0.002 [0.001; 0.003]	0.002 [0.001; 0.003]	0.003 [0.002; 0.004]
p(2005)	0.010 [0.005; 0.019]	0.010 [0.005; 0.019]	0.018 [0.014; 0.023]
p(2006)	0.008 [0.004; 0.015]	0.008 [0.004; 0.015]	0.014 [0.011; 0.018]

SC/60/SH37*rev*

Table 3a: Bayesian posterior estimates for the C1-C3 interchange model. Median and 95% PIs are reported. Genotypic "gen" (C3) as well as photo-ID ("pho") (C1 and C3) capture-recapture data are included in the analysis (along with the Findlay *et al.* (in press) C1 abundance estimate). The *r* prior is U[0; 0.106] and each *q* prior U[0.001; 0.6]. It is assumed $r' = r^2 = r$.

SC/60/SH37*rev*

Table 3b: Bayesian posterior estimates for the C1-C3 interchange model. Median and 95% PIs are reported. Genotypic "gen" (C3) as well as photo-ID ("pho") (C1 and C3) capture-recapture data are included in the analysis (along with the Findlay *et al.* (in press) C1 abundance estimate). Both the *r* priors are U[0; 0.106] and each *q* prior U[0.001; 0.6]. Here $r¹$ and $r²$ are estimated.

Figure 1a: BS C3 population abundance estimates from the capture-recapture analysis. The sensitivities to different *M* are not shown because they are virtually indistinguishable from the Reference Case (RC).

Figure 1b: BS C3 population abundance estimates from the RC capture-recapture analysis compared with abundance estimates from Cerchio *et al.* (2008a). These estimates are for the 2003- 2006 (1) and 2004-2006 (2) periods.

Figure 1d: Bayesian C3 estimates using the photo-ID data with a prior for *r* of U[-1; 1] (i.e. uninformative).

Figure 1e: Bayesian C3 estimates using the genotypic data with a prior for *r* of U[-1; 1] (i.e. uninformative).

Figure 1f: Bayesian C3 estimates using the photo-ID data with a prior for *r* of U[0; 0.106].

Figure 1h: Bayesian C3 – both photo-ID + genotypic data - prior on $r \sim [0; 0.106]$.

Figure 2a: BS C1 population abundance estimates from the capture-recapture analysis using the photo-ID data, compared with a sighting survey abundance estimate from Findlay (in press). The sensitivities to different *M* are not shown because they a virtually indistinguishable from the Reference Case (RC).

Figure 2b: Bayesian C1 estimates using the photo-ID data with a prior for *r* of U[-1; 1] (i.e. uninformative).

Figure 2c: Bayesian C1 estimates using the photo-ID data with a prior on *r* of U[0; 0.106].

Figure 2d: Bayesian C1 estimates using both the photo-ID data + the Findlay *et al.* (in press) estimate with a prior on *r* of U[0; 0.106].

Figure 3a: Histogram of the *r* posterior distribution for the C3 Bayesian analysis that includes both data sources and has an *r* prior of U[0; 0.106]. The bars indicate the proportion of the distribution between the value shown and that immediately less; results shown as for 0.11 are between 0.10 and 0.106.

Figure 3b: Histogram of the *r* posterior distribution for the C1 Bayesian analysis that includes both the photo-ID data and the Findlay estimate, and has an *r* prior of U[0; 0.106].

Figure 4a: Bayesian estimates of the interchange model which uses all the capture-recapture (photo-ID as well as genotypic) data as well as the Findlay *et al.* (in press) abundance estimate for C1. The prior for *r* is U[0; 0.106] with $r^1 = r^3 = r$.

Figure 4b: Bayesian estimates of the interchange model which uses all the capture-recapture (photo-ID as well as genotypic) data as well as the Findlay *et al.* (in press) abundance estimate for C1. The prior for both r^1 and r^3 is U[0; 0.106] with r^1 and r^3 estimated separately.

Figure 5a: Histogram of the *r* posterior distribution for the C1+3 Bayesian interchange analysis that includes all capture-recapture data (photo-ID and genotypic) as well as the Findlay *et al.* (in press) abundance estimate for C1, and has a prior for *r* of U[0; 0.106] with $r^1 = r^3 = r$. The bars indicate the proportion of the distribution between the value shown and that immediately less; results for *r* shown as for 0.11 are between 0.10 and 0.106.

Figure 5b: Histogram of the $q¹$ (probability that a C1 breeding sub-stock animal goes to C3 in any one year) posterior distribution for the C1+3 Bayesian interchange analysis for the $r^1 = r^3 = r$ model.

Figure 5c: Histogram of the q^3 (probability that a C3 breeding sub-stock animal goes to C1 in any one year) posterior distribution for the C1+3 Bayesian interchange analysis for the $r^1 = r^3 = r$ model.

Figure 6a: Histogram of the *r* posterior distribution for the C1+3 Bayesian interchange analysis that includes all capture-recapture data (photo-ID and genotypic) as well as the Findlay *et al.* (in press) abundance estimate for C1, and has a prior for both r^1 and r^3 of U[0; 0.106] with r^1 and $r³$ estimated separately . The bars indicate the proportion of the distribution between the value shown and that immediately less; results for *r* shown as for 0.11 are between 0.10 and 0.106.

Figure 6b: Histogram of the $q¹$ (probability that a C1 breeding sub-stock animal goes to C3 in any one year) posterior distribution for the C1+3 Bayesian interchange analysis for the r^T and $r³$ estimated separately model.

Figure 6c: Histogram of the q^3 (probability that a C3 breeding sub-stock animal goes to C1 in any one year) posterior distribution for the C1+3 Bayesian interchange analysis for the r^T and *r*³ estimated separately model.

Appendix 1: Data from Cerchio *et al***. (2008a and b) used in these analyses**

Table A1.1: Photographic capture-recapture data from BS C1 – from SC/60/SH33 (Cerchio *et al.* **2008b)**

 $[n =$ number of different individuals sighted each year, $m =$ total recaptures between pairs of years]

Table A1.2 Photographic capture-recapture data from C3 – from SC/60/SH33 (Cerchio *et al.* **2008a)**

 $[n =$ number of different individuals sighted each year, $m =$ total recaptures between pairs of years]

Table A1.3: Genotypic "capture-recapture" data from C3 – from SC/60/SH33 (Cerchio *et al.* **2008a)**

 $[n =$ number of different individuals sighted each year, $m =$ total recaptures between pairs of years]

Abundance estimates used from Cerchio *et al.* **(2008a):**

For C3: from Antongil Bay (NE Madagascar). Recommendations are a lower bound estimate of 6737 (CV=0.31) for a mid-year of 2005, and an upper bound estimate of 7715 (CV=0.24) for a mid-year of 2005 (These estimates are from the Chapman's Modified Petersen estimator applied to the **photo-ID** mark-recapture dataset).

For C3: from Antongil Bay (NE Madagascar). A lower bound estimate of 8348 (CV=0.32) for a mid-year of 2005, and an upper bound estimate of 10123 (CV=0.24) for a mid-year of 2005. (These estimates are from a Chapman's Modified Petersen estimator applied to the **genotypic** mark-recapture dataset). Note that Cerchio *et al.* (2008a) warn of an improbably ROI from the genetic data.

Table A1.4 Photographic capture-recapture data between C1 and C3 – from SC/60/SH33 (Cerchio *et al.* **2008a)**

 $[n =$ number of different individuals sighted each year, $m =$ total recaptures between pairs of years; the entries above the diagonal in the matrix reflect animals first seen in C3 and later re-sighted in C1, whereas entries below the diagonal reflect the reverse, animals first seen in C1 and later resighted in C3.

