BAYESIAN ASSESSMENTS OF THE SOUTHERN HEMISPHERE HUMPBACK WHALE BREEDING STOCK B USING THREE DIFFERENT MODELS FOR STOCK-STRUCTURE

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ABSTRACT

Three different models are considered for Southern Hemisphere humpback breeding stock B: Model 1, a single fully-mixed stock; Model 2, reproductively independent stocks B1 off Gabon and B2 of the southern African coastline; and Model 3 with two stocks as in Model 2 but with B1 consisting of two sub-stocks, one of which migrates to Gabon along the southern African coastline. The models are fitted to mark-recapture data (both photo-ID and genetic) available for the Gabon and South African regions. The purpose of the paper is one of illustrating the stock-structure models and associated methods of analysis, anticipating that further discussion and selection of specific model input assumptions will take place during the Scientific Committee meeting.

KEYWORDS: HUMPBACK WHALES, BAYESIAN ASSESSMENT

INTRODUCTION

This document reports Bayesian stock assessment results for breeding stock B and investigates the implications of a two breeding stock structure:

B1: North of 18˚S (Angola, Congo, Gabon)

B2: South of 18˚S (Namibia, western coast of South Africa)

Only limited information on abundance and trend is available for breeding stock B, comprising tag-recapture data for B1 from the coastal waters of Gabon (see Collins *et al*., 2008) and new tag-recapture data from the west coast of South Africa now available for the region B2 (Barendse *et al*., 2010). Historic catches from the breeding grounds are given by region and can therefore be split into B1 and B2 catches. The historic catches from the feeding grounds (south of 40^{o}S) are for both stocks combined.

This assessment aims to investigate different possible migratory and interactive behaviours of the stocks. Three different scenarios are proposed here and tested in the form of models 1-3, which are briefly described in the methods section, with greater detail given in the Appendix.

Only a few illustrative implementations of these models are reported, anticipating that alternative input assumptions will be developed and investigated during the Scientific Committee meeting.

DATA

Historic Catch data

There are two sources of historic catch data that relate to breeding stocks B1 and B2.

i) Catches north of 40^{o}S

B1	those from “Congo”, “Congo/Ang”, and “Angola” from Allison’s database (Allison pers. commn)
B2	those from “Namib” and “SWCap” from Allison’s database.

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Records of a series of Russian catches are also available by 10 degree longitude and latitude bands. Catches for 20^oW-10^oE have been allocated to breeding stock B with catches taken above 18^oS allocated to B1 and those below 18^oS to B2.

ii) Catches south of 40^oS
This series refers to 100% of the catches recorded for the core area 10^oW-10^oE, 50% of the catches from the breeding stock A/B margin area of 20^oW-10^oW and 50% of the catches from the breeding stock B/C margin area of 10^oE-30^oE. These catches thus include both B1 and B2 whales. Table 1 reports these three historic catch series.

Absolute abundance data
An absolute abundance estimate for B1 is available from the MARK program, applied to the photo-ID capture-recapture data from Iguela only (lower estimate of 6342 in 2003, CV=0.18) and the genetic data from Iguela only (upper estimate of 7196 in 2003, CV=0.15). This estimate is not used as part of the likelihood (the actual capture-recapture data are used directly in the fitting process) but is used for a reality check, as well as in the initial step of model fitting procedure (backwards method) where given a random value of r^{B1} and a corresponding value of K^{B1} are needed – and this is done by fitting exactly to a recent population abundance estimate. Recent capture-recapture data for B2 have been used to obtain a ball-park estimate for B2 for this procedure.

Capture-recapture data
Data for B1

The capture-recapture data used here are as reported in Collins *et al.* (2008). Photographs and biopsies were collected from the coastal waters of Gabon during the austral winter (July-October) in each year between 2001 and 2006. Data analysed were from two sites (Iguela and Mayumba). This assessment uses the results for both areas combined, and both the photo-ID and genetic information. The data are reported in Tables 2a and 2b.

Data for B2
Recent work on capture-recapture data has produced the results given in Tables 2c and 2d. These arise from an electronic image database compiled for humpback whales photographed off the west coast of South Africa (Barendse *et al*. 2010). In this assessment, data from matches using right dorsal fin features for identification, and microsatellite matches have been used, as these are considered the most reliable (Barendse, *pers. commn.*)

METHODS

The three different models used in this assessment are briefly outlined here. Model 1 assumes only one breeding stock (i.e. B1 and B2 are combined as one homogeneous population). The population splits as it departs from high latitude feeding grounds in or near the Antarctic, and follows two migratory routes to the breeding area off Gabon.

Model 2 assumes two independent breeding stocks which mix for feeding in or near the Antarctic. Breeding stock B1 then migrates up to its breeding area in Gabon, whereas breeding stock B2 migrates up the west coast of southern Africa to its breeding grounds.

Model 3 assumes two breeding stocks, B1 and B2, as for Model 2. B1 is however assumed to be comprised of two sub-stocks, one of which ($B1^E$) passes through southern Africa coastal waters before going to Gabon, while the other ($B1^W$) migrates directly to the Gabon breeding region.

Further details of these models are given in the Appendix.

For catch allocation purposes for regions where more than one stock/sub-stock of whales is present, complete mixing is assumed with catches each year allocated amongst the stocks in proportion to their relative abundances.

Bayesian estimation framework

Priors

Prior distributions are defined for the following parameters:

i) $r^i \sim U[0, 0.106]$

ii) $\ln \tilde{N}^{i,obs}_{t\arg et} \sim U[\ln N^{i,obs}_{t\arg et} - 4CV, \ln N^{i,obs}_{t\arg et} + 4CV]$

For Model 1, there is only one population, and therefore $i = B$. For Models 2 and 3, two stocks are assumed and i can reflect either B1 or B2.

The uninformative r prior is bounded by zero (negative rates of growth are biologically implausible) and 0.106 (this corresponds to the maximum growth rate for the species agreed by the IWC Scientific Committee (IWC, 2007)). The prior distribution from which target abundance estimate $\tilde{N}^{i,obs}_{t\arg et}$ is drawn at random is uniform on a natural logarithmic scale. The lower and upper bounds are set by the CV multiplied by four. For these N targets, the Collins *et al.*(2008) estimate for 2003 of 7196 (CV=0.18) is used for B1, and the B2 capture-recapture data are used to provide a ball-park estimate for B2 (estimate for 2004 of 400, CV=0.2).

Using the randomly drawn vector of values of $\tilde{N}^{i,obs}_{t\arg et}$ and r^i, a downhill simplex method of minimization is used to calculate K^i such that the model estimate of $N^i_{t\arg et}$ is identical to the randomly drawn value $\tilde{N}^{i,obs}_{t\arg et}$.

For each simulation, using the r^i and calculated K^i values, the capture-recapture data are used to assign a likelihood to that particular combination. The components of the negative log likelihood are calculated as follows:

Captures: $n^i_y = p^i_y N^i_y$ i = B1, B2 (1)

Recaptures: $m^i_{y,y'}$ refers to humpbacks captured in region i in year y and recaptured in that same region in year y',

where the expected numbers in terms of the model are:

$$\hat{m}^i_{y,y'} = p^i_y p^i_{y'} N^i_y e^{-M(y'-y)} \tag{2}$$

where: n^i_y is the number of animals captured in breeding region i in year y,

$m^i_{y,y'}$ is the observed number of animals captured in i in year y that were recaptured in i in year y',

$\hat{m}^i_{y,y'}$ is the model-predicted number of animals in i captured in year y that were recaptured in i in year y',

M is the natural mortality rate (set here to equal 0.03), and

p^i_y is the probability that an animal is captured in i year y.

The contributions of the various data to the negative of the log-likelihood function are then given by:

$$-\ln L = \sum_i \sum_j \sum_{y=y_o}^{y_f-1} \sum_{y'=y+1}^{y_f} [-m^{i,j}_{y,y'} \ln \hat{m}^{i,j}_{y,y'} + \hat{m}^{i,j}_{y,y'}] \tag{3}$$

The negative log likelihood is then converted into a likelihood value (L). The integration of the prior distributions of the parameters and the likelihood function then essentially follows the Sampling-Importance-Resampling (SIR) algorithm presented by Rubin (1988) as described in Zerbini (2004). For a vector of parameter values θ_i, the likelihood of the data associated with this vector of parameters

(L) as described above is calculated and stored as $\tilde{L}$. This process is repeated until an initial sample of n_1 θ_i s is generated.

This sample is then resampled with replacement n_2 times with probability equal to weight w_j, where:

$$w_j = \frac{\tilde{L}(\theta_j / data)}{\sum_{j=1}^{n1} \tilde{L}(\theta_j / data)} \tag{4}$$

The resample is thus a random sample of size n_2 from the joint posterior distribution of the parameters (Rubin 1988).

Nmin constraints
Rosenbaum *et al.* (2006) provides the minimum number of haplotypes for B1 and B2 as 92 and 55 respectively. These have however not been implemented in the assessment at this stage and will be incorporated in future.

RESULTS

The results of the Bayesian assessments for the three models are given in Tables 3-5. Figures 1, 3 and 5 show the population trajectories for each model. Figures 2 and 4 show a plot of the model-predicted cumulative resightings compared to the observed values. Finally Figure 6 shows the median population trajectories for Model 3 for three different values of *X*, the parameter which characterizes the relative sizes of the two B1 sub-stocks in this model.

DISCUSSION

As the results obtained are intended only to illustrate the methodology, comments in relation to estimated current stock status and parameter values would not be immediately appropriate.

As would be expected, probability intervals about stock trajectories are wide except over the period for which the tag-recapture data are available (see Figures 1, 3 and 5).

Cumulative recapture numbers are generally consistent with model predictions (see Figures 2 and 4a and b). Note that the probability intervals shown reflect uncertainties in expected numbers as a result of estimation imprecision, and do not include the further variability associated with sampling variance.

For Model 3, breeding stock B2 becomes very small as an increasingly larger proportion of the B1 stock is assumed to migrate along the southern African coast rather than move directly to Gabon from their feeding grounds (i.e. as *X* is decreased) – see Tables 4 and 5 and Figure 6.

ACKNOWLEDGEMENTS

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Table 1: Historic catch series for stocks B1 and B2 (Allison, pers. commn).

Season	B1 Breeding grounds	B2 Breeding grounds	B1+B2 Feeding grounds
1900	0	0	0
1901	0	0	0
1902	0	0	0
1903	0	0	0
1904	0	0	0
1905	0	0	0
1906	0	0	0
1907	0	0	0
1908	0	0	0
1909	269	307	0
1910	718	244	0
1911	2264	339	0
1912	3917	775	0
1913	5311	651	0
1914	2615	258	0
1915	164	5	0
1916	66	4	0
1917	0	10	0
1918	0	10	0
1919	0	17	0
1920	0	40	0
1921	0	0	0
1922	613	13	0
1923	687	212	0
1924	566	96	0
1925	773	69	0
1926	327	115	0
1927	3	44	0
1928	37	31	0
1929	0	50	14.5
1930	578	36	105.5
1931	0	0	2.5
1932	0	0	21.5
1933	0	0	70.5
1934	723	0	163.5
1935	1238	0	958.5
1936	842	27	1401
1937	299	28	404.5
1938	0	0	0
1939	0	0	2
1940	0	0	186.5
1941	0	0	0
1942	0	0	0
1943	0	0	0
1944	0	0	0
1945	0	0	0
1946	0	0	0.5
1947	0	5	0.5
1948	0	14	81.05
1949	1356	15	511.9
1950	1404	7	249.9
1951	1105	9	475.25
1952	265	15	281.75
1953	0	9	111.25
1954	0	0	312.6
1955	0	0	113
1956	0	0	63.1
1957	0	3	71.85
1958	0	2	111.5
1959	161	7	121.85
1960	0	4	128.7
1961	0	7	30.5
1962	0	15	21.5
1963	0	9	2
1964	0	1	0
1965	0	1	929
1966	0	9	215.5
1967	0	3	379.5
1968	0	0	0
1969	0	0	0
1970	0	0	0
1971	0	0	0
1972	0	0	1
1973	0	0	0
1974	0	0	0
1975	0	0	0
1976-2009	0	0	0

Table 2a: Photographic capture-recapture data from all sites for breeding stock B1 from Collins *et al.* (2008)

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

n	2000	2001	2002	2003	2004	2005	2006
	24	111	233	161	138	216	199

m	2000	2001	2002	2003	2004	2005	2006
2000	X	0	1	0	0	0	0
2001		X	5	6	5	2	1
2002			X	12	2	2	4
2003				X	7	2	1
2004					X	2	2
2005						X	6
2006							X

Table 2b: Genetic capture-recapture data from all sites for B1 – from Collins *et al.* (2008)

n	2000	2001	2002	2003	2004	2005	2006
	82	155	257	270	188	296	207

m	2000	2001	2002	2003	2004	2005	2006
2000	X	1	1	4	2	3	0
2001		X	6	8	6	3	2
2002			X	6	6	6	4
2003				X	8	7	1
2004					X	3	3
2005						X	11
2006							X

Table 2c: Photographic (Right dorsal fins) capture-recapture data for B2 (Barendse *et al.* 2010)

n	2002	2003	2004	2005	2006	2007
	39	58	14	20	25	27

m	2002	2003	2004	2005	2006	2007
2002	X	7	1	2	0	1
2003		X	0	4	2	2
2004			X	0	0	0
2005				X	1	0
2006					X	0
2007						X

Table 2d: Genetic (microsatellites) capture-recapture data for B2 (Barendse *et al.* 2010)

n	2002	2003	2004	2005	2006	2007
	34	41	20	27	22	22

m	2002	2003	2004	2005	2006	2007
2002	X	9	1	1	1	1
2003		X	1	5	0	1
2004			X	1	1	1
2005				X	1	2
2006					X	1
2007						X

Note: In line with the methods of analysis used, these Tables are structured such that if a whale is recaptured twice, say, the second recapture is linked only to the first recapture treated as a new capture.

Table 3: **Model 1:** Assessment results for a simple breeding stock; posterior medians and 90% probability intervals are shown.

Model 1	**BS B**
***r* prior**	**U[0, 0.106]**
Historic catch	**Feeding grounds split 50% in fringe areas between neighbouring stocks**
Abundance and trend information	**Mark-recapture for Gabon, photo and genetic for all regions**
r	0.063 [0.014; 0.086]
K	21424 [19301; 34151]
N_{min}	911 [435; 4913]
N_{2006}	10576 [8377; 12393]
N_{min}/K	0.042 [0.022; 0.145]
N_{2006}/K	0.494 [0253; 0.632]
N_{2040}/K	0.984 [0.375; 0.999]

Table 4: **Model 2:** This approach assumes two independent breeding stocks B1 and B2. Both *r*'s have the same uniform prior and B1 is fit to the Gabon tag-recapture data (photo-ID and genetic for all sites), while B2 is fit to the west South Africa data (right dorsal fin and microsatellite). In other respects specifications are as for Model 1 (Table 3).

	BS B1	**BS B2**
r	0.0615 [0.0155; 0.0862]	0.0809 [0.0161; 0.1048]
K	18798 [16636; 30154]	2628 [2472; 4607]
N_{min}	950 [423; 4672]	28 [10; 296]
N_{2010}	10426 [8318; 12110]	677 [498; 1897]
N_{min}/K	0.051 [0.025; 0.155]	0.011 [0.004; 0.0621]
N_{2010}/K	0.56 [0.28; 0.72]	0.26 [0.11; 0.35]
N_{2040}/K	0.99 [0.43; 1.00]	0.98 [0.18; 1.000]

Table 5: **Model 3:** This approach assumes two independent breeding stocks. Breeding stock B1 has and eastern and a western substock. r^{B1} and r^{B2} have the same uniform prior, and the substocks of B1 have the same r as B1 (r^{B1}). B1 (=$B1^W$+$B1^E$) is fit to the Gabon tag-recapture data (photo-ID and genetic for all sites), while B2+$B1^E$ is fit to the west South Africa data (right dorsal fin and microsatellite). Other specifications are as for Model 1. Given the carrying capacity for B1, the carrying capacities for its substocks are given by:

$$K^{BS1,W} = XK^{BS1} \text{ and } K^{BS1,E} = (1-X)K^{BS1}$$

a) X=0.8

	BS B1	**BS B2**	**$B1^W$**	**$B1^E$**
r	0.073 [0.020,0.088]	0.054 [0.005; 0.102]	r^{B1}	r^{B1}
K	19254 [17767,30410]	1070 [203, 3354]	15403 [14213,24328]	3850 [3553, 6082]
N_{min}	658 [417,3869]	56 [12,120]	644 [406,3726]	8 [0.05, 147]
N_{2010}	10960 [8679,12572]	463[49,701]	10759 [8386,12456]	112 [1,556]
N_{min}/K	0.035 [0.023,0.126]	0.0378 [0.014,0.436]	0.042 [0.028,0.153]	0.002 [0.000,0.024]
N_{2010}/K	0.565 [0.295,0.697]	0.501 [0.0224,0.995]	0.697 [0.354,0.861]	0.027 [0.000,0.154]
N_{2040}/K	0.995 [0.524,0.999]	0.978 [0.025,1.000]	1.217 [0.631,1.248]	0.048 [0.000,0.244]

b) X=0.6

	BS B1	**BS B2**	**$B1^W$**	**$B1^E$**
r	0.081 [0.073,0.088]	0.063[0.033,0.101	r^{B1}	r^{B1}
K	19475 [18884,20249]	190 [67,476]	11685 [11330,12150]	7790 [7553, 8100]
N_{min}	488 [404,626]	10 [10,15]	462 [384,585]	26 [16,41]
N_{2010}	11354 [10077,12840]	91 [40,149]	10777 [9419,12299]	587 [440,802]
N_{min}/K	0.025 [0.022,0.031]	0.056 [0.022,0.154]	0.039 [0.034,0.048]	0.003 [0.002,0.005]
N_{2010}/K	0.582 [0.504,0.674]	0.644 [0.090,0.999]	0.924 [0.784,1.074]	0.075 [0.057,0.102]
N_{2040}/K	0.998 [0.994,0.999]	0.993 [0.233,1.000]	1.576 [1.539,1.603]	0.129 [0.093,0.179]

Note that with X=1 Model 3 is identical to Model 2, hence the results are not duplicated here.

Figure 1: **Model 1** population trajectory for single breeding stock B. The posterior medians and 90% probability interval envelopes are shown. Results shown for years to the right of the vertical dashed line are projections under zero future catch.

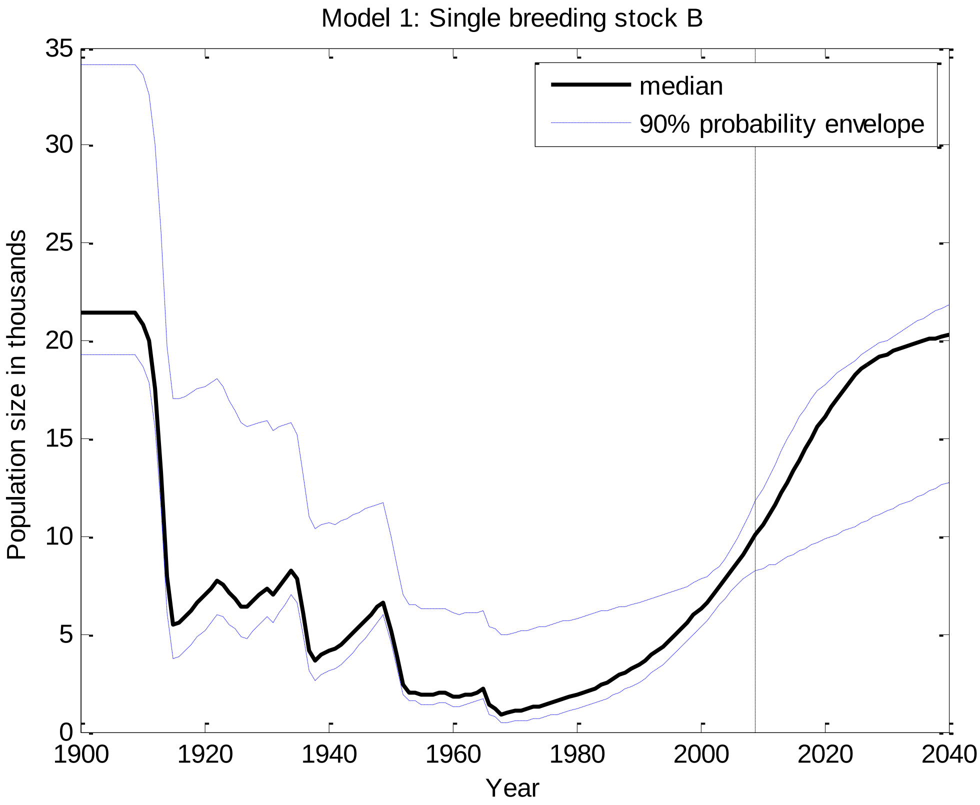


Figure 2: **Model 1** plot of model-predicted cumulative resightings (posterior medians and 90% probability interval envelopes) compared to the numbers observed for both photo-ID and genetic data.

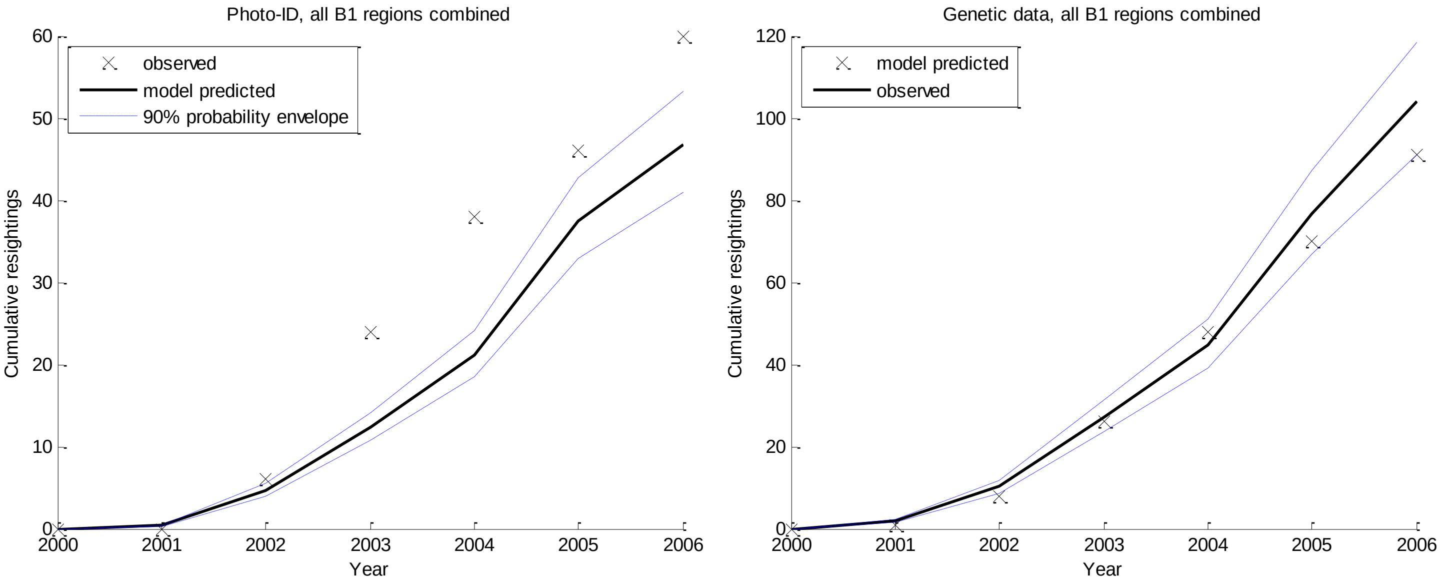
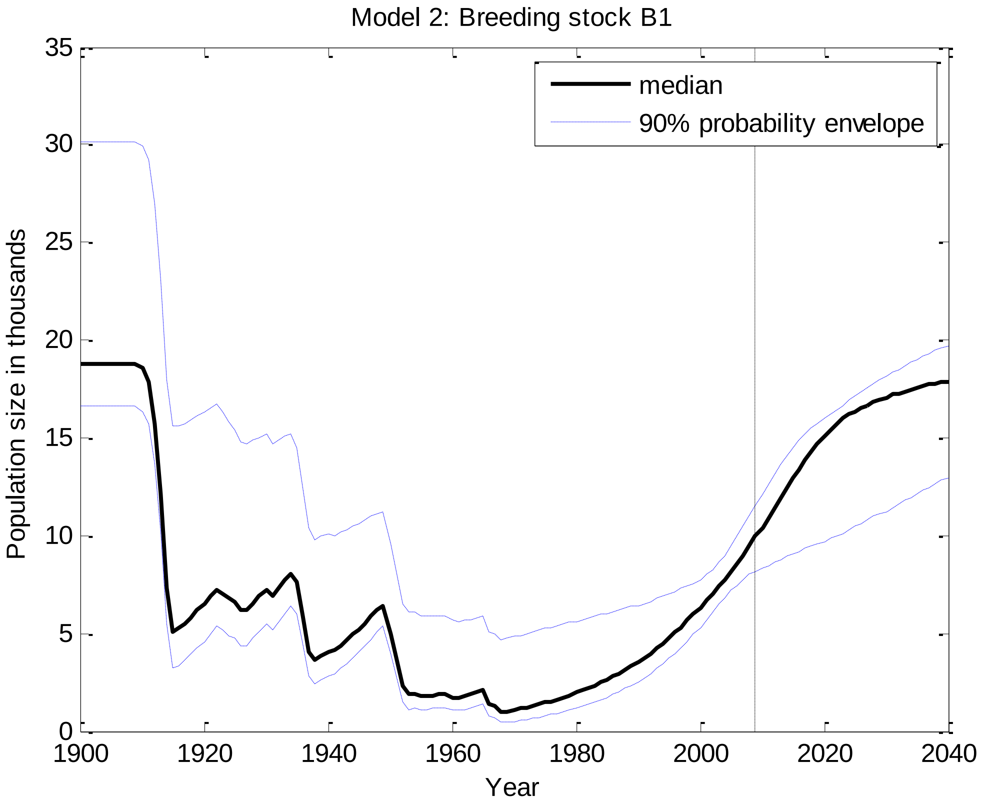


Figure 3: **Model 2** population trajectory for breeding stocks B1 and B2. The posterior medians and 90% probability interval envelopes are shown. Results shown for years to the right of the vertical dashed line are projections under zero future catch. Note the different vertical scales.



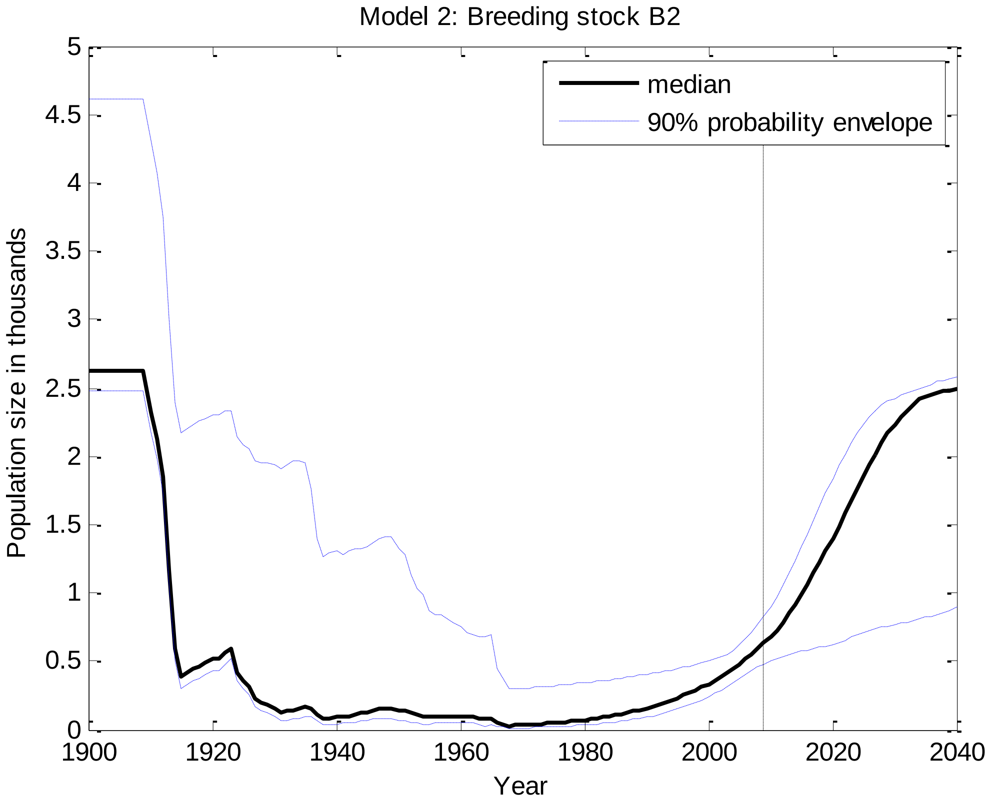
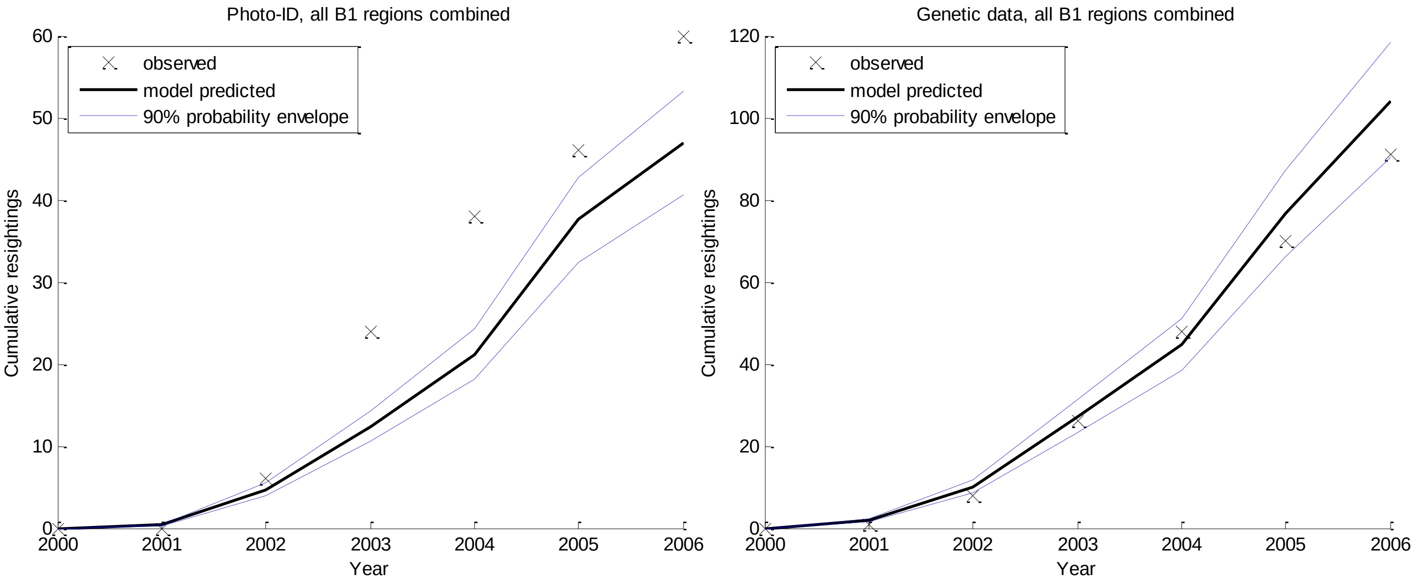


Figure 4: **Model 2** plot of model-predicted cumulative resightings (posterior medians and 90% probability interval envelopes) compared to the numbers observed for both photo-ID and genetic data.

a) B1



b) B2

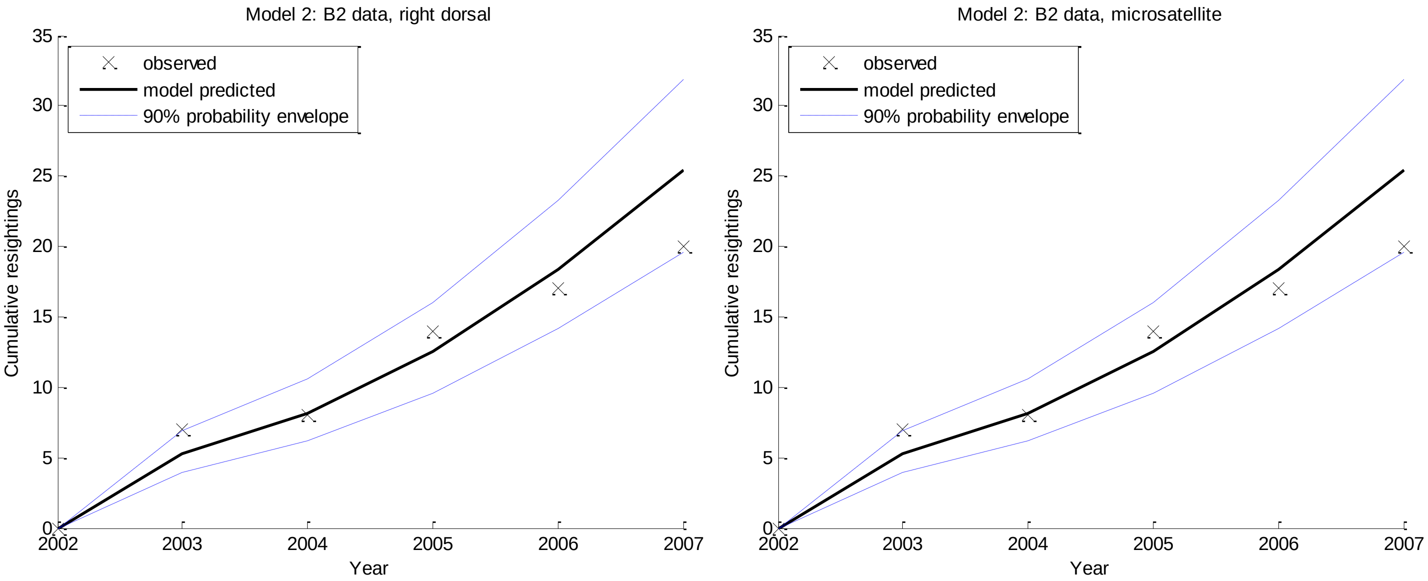


Figure 5: **Model 3** population trajectories for stocks B1 and B2, and for B1 sub-stocks B1^{W} and B1^{E}, for X = 0.8. The posterior medians and 90% probability interval envelopes are shown. Results shown for years to the right of the vertical dashed line are projections under zero future catch. Note the different vertical scales

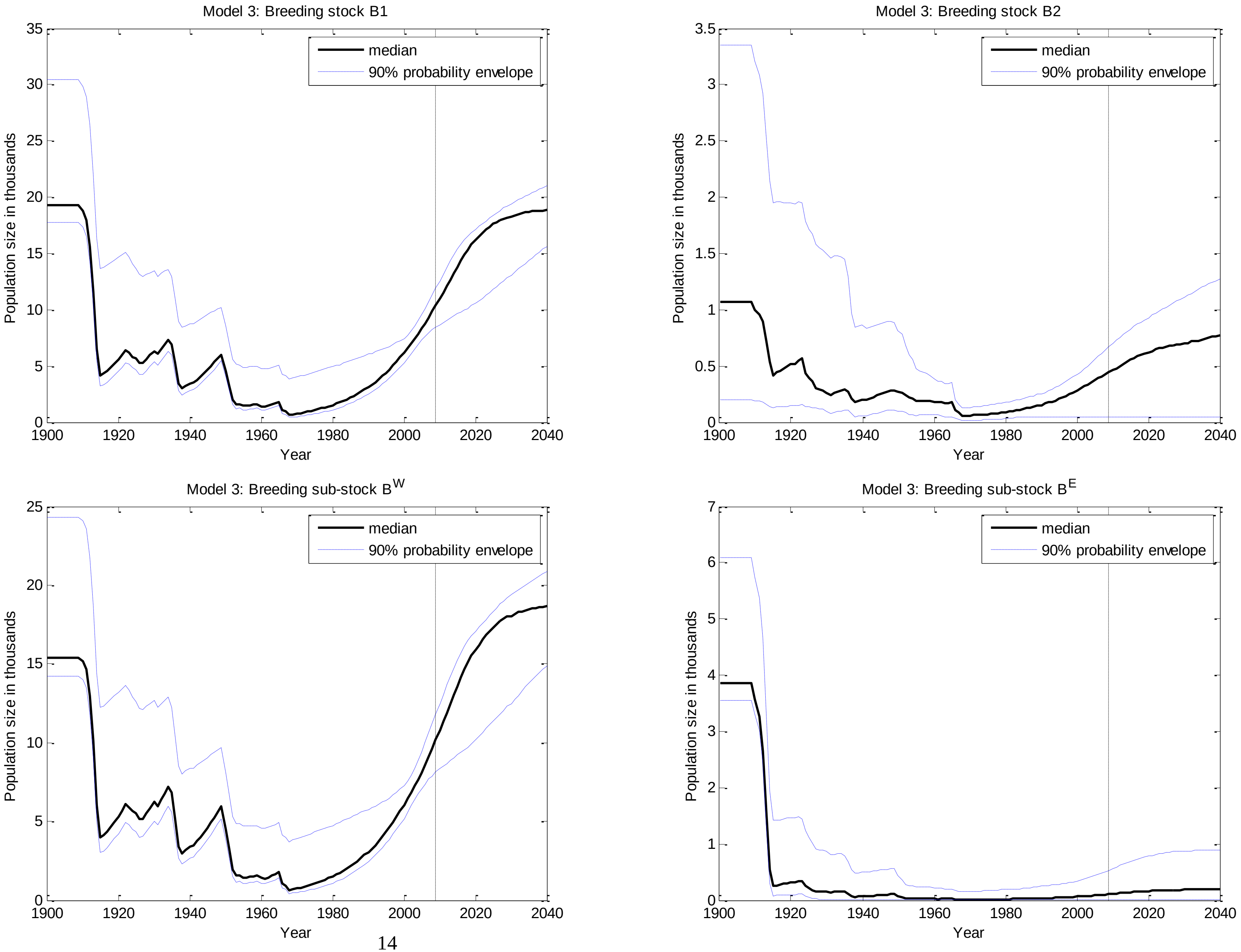
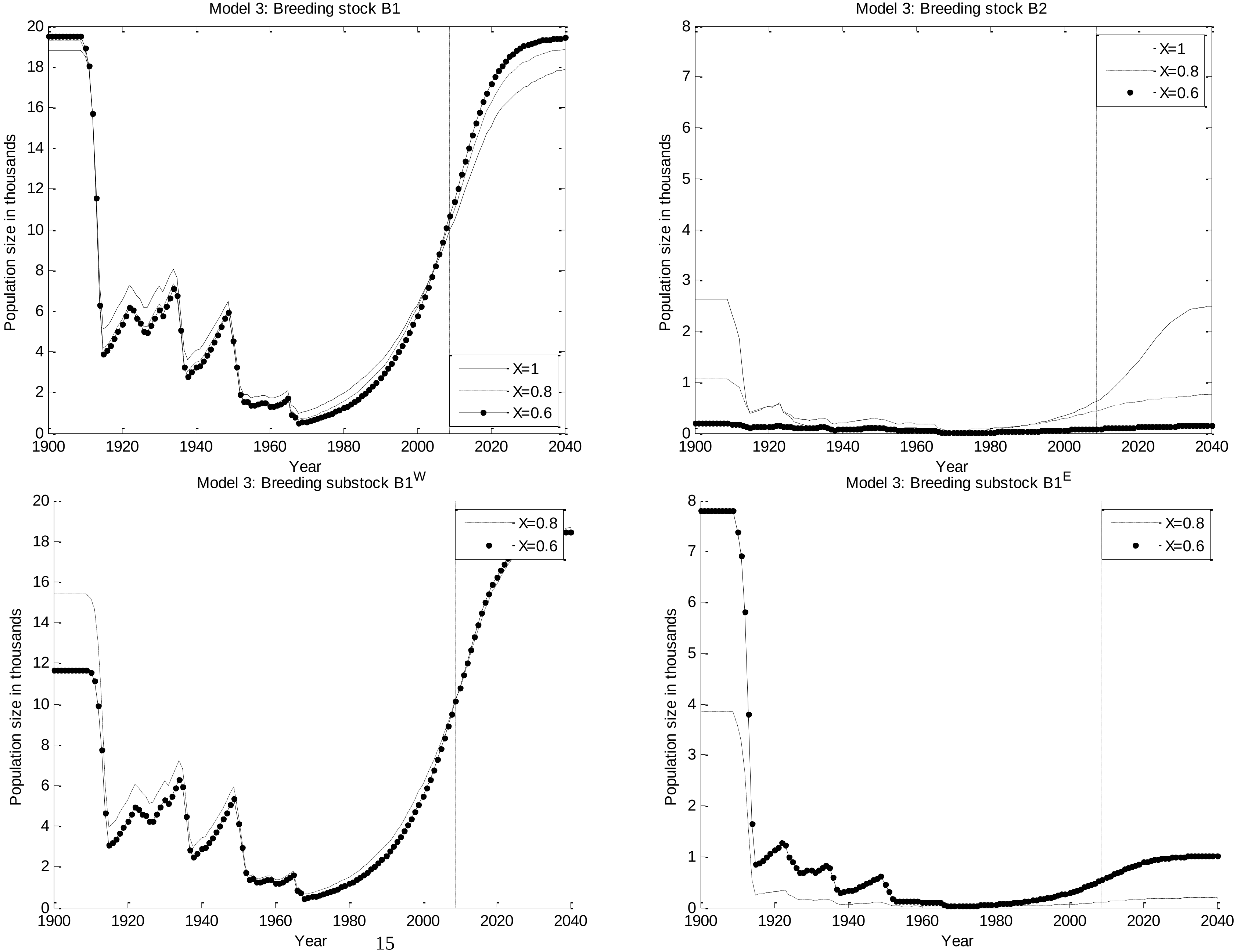


Figure 6: **Model 3** – comparing the posterior median trajectories for *X*=1, *X*=0.8 and *X*=0.6. Note that Model 3 with *X*=1 is identical to Model 2.



APPENDIX

Model 1 assumes only one breeding stock (i.e. B1 and B2 are combined as one homogeneous population). The population splits as it departs from high latitude feeding grounds, and follows two migratory routes to the breeding area off Gabon.

Model 2 assumes two independent breeding stocks which mix for feeding in the Antarctic. Breeding stock B1 then migrates up to its breeding area in Gabon, whereas breeding stock B2 migrates up the west coast of southern Africa to its breeding grounds.

Model 3 assumes two breeding stocks, B1 and B2, as for model 2. B1 is however assumed to be comprised of two sub-stocks, one of which ($B1^E$) passes through southern African coastal waters before going to Gabon, while the other ($B1^W$) migrates directly to the Gabon breeding region.

<u>Model 1</u>: Single breeding stock

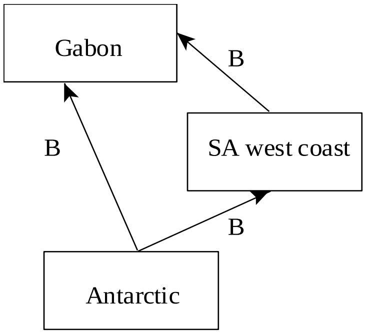


Figure App.1: Schematic representation of model 1

Breeding stock population dynamics

$$N_{y+1}^B = N_y^B + r^B N_y^B \left(1-(\frac{N_y^B}{K^B})^\mu\right) - C_y^B \tag{1}$$

where

N_y^B is the number of whales in the breeding population at the start of year *y*,

r^B is the intrinsic growth rate (the maximum per capita the population can achieve when its size is very low) ,

K^B is the carrying capacity,

μ is the “degree of compensation” parameter; this is set at 2.39, which fixes the MSY level to MSYL = 0.6*K*, as conventionally assumed by the IWC Scientific Committee, and

C_y^B is the total catch (in terms of animals) in year *y*.

The catches are given by

$$C_y^B = C_y^G + C_y^S + C_y^A \tag{2}$$

where

C_y^G is the catch taken in breeding area 1 (Gabon) in year *y*,

C_y^S is the catch taken in area 2 (southern Africa) in year *y*, and

C_y^A is the high latitude southern feeding grounds catch taken in year *y*.

Abundance and trend information

The model is fit to the B1 capture-recapture data.

<u>Model 2</u>: Two breeding stocks

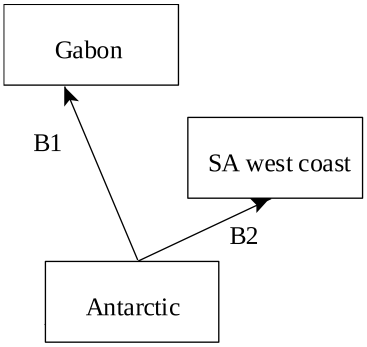


Figure App.2: Schematic representation of model 2

Breeding stock population dynamics

$$N_{y+1}^{B2} = N_y^{B2} + r^{B2} N_y^{B2}\left(1 - \left(\frac{N_y^{B2}}{K^{B2}}\right)^{\mu}\right) - C_y^{B2} \qquad (3)$$

$$N_{y+1}^{B1} = N_y^{B1} + r^{B1} N_y^{B1}\left(1 - \left(\frac{N_y^{B1}}{K^{B1}}\right)^{\mu}\right) - C_y^{B1} \qquad (4)$$

where

N_y^{B1} is the number of whales in the breeding population B1 at the start of year *y*,

N_y^{B2} is the number of whales in the breeding population B2 at the start of year *y*,

r^{B1} is the intrinsic growth rate for B1 (the maximum per capita the population can achieve, when its size is very low),

r^{B2} is the intrinsic growth rate for B2,

K^{B1} is the carrying capacity for population B1,

K^{B2} is the carrying capacity for population B2,

μ is the "degree of compensation" parameter; this is set at 2.39, which fixes the MSY level to MSYL = 0.6*K*, as conventionally assumed by the IWC Scientific Committee,

C_y^{B1} is the total B1 catch (in terms of animals) in year *y*, and

C_y^{B2} is the total B2 catch (in terms of animals) in year *y*.

The catches are given by:

$$C_y^{B1} = C_y^G + p_y C_y^A$$

$$C_y^{B2} = C_y^S + (1 - p_y) C_y^A \qquad (5)$$

where

$p_y = \dfrac{N_y^{B1}}{N_y^{B1} + N_y^{B2}}$ and C_y^G, C_y^S and C_y^A are as described above, i.e. the catches from each stock are proportional to their relative abundances (full mixing).

Abundance and trend information

The model is fit N_y^{B1} to all the B1 capture-recapture data and N_y^{B2} to the B2 capture-recapture data.

<u>Model 3</u>: Two breeding stocks; eastern sub-stock of B1 transits south west African coastal region

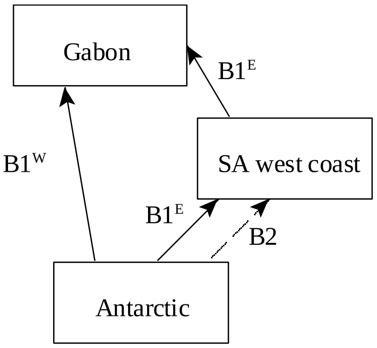


Figure App.3: Schematic representation of model 3

Breeding stock population dynamics

$$N_{y+1}^{B1,W} = N_y^{B1,W} + r^{B1} N_y^{B1,W}\left(1 - \left(\frac{N_y^{B1,W} + N_y^{B1,E}}{K^{B1}}\right)^{\mu}\right) - C_y^{B1,W} \qquad (6)$$

$$N_{y+1}^{B1,E} = N_y^{B1,E} + r^{B1} N_y^{B1,E}\left(1 - \left(\frac{N_y^{B1,W} + N_y^{B1,E}}{K^{B1}}\right)^{\mu}\right) - C_y^{B1,E} \qquad (7)$$

$$N_{y+1}^{B2} = N_y^{B2} + r^{B2} N_y^{B2} \left(1 - \left(\frac{N_y^{B2}}{K^{B2}}\right)^{\mu} \right) - C_y^{B2} \tag{8}$$

where

$N_y^{B1,W}$ is the number of whales in the western substock of B1 at the start of year *y*,

$N_y^{B1,E}$ is the number of whales in the eastern substock of B1 at the start of year *y*,

$C_y^{B1,W}$ is the total number of western B1 animals caught in year *y*,

$C_y^{B1,E}$ is the total number of eastern B1 animals caught in year *y*,

N_y^{B2}, r^{B1}, r^{B2}, K^{B1}, K^{B2}, μ, C_y^{B1} and C_y^{B2} are as described above.

The catches are given by:

$$C_y^{B1,W} = \frac{N_y^{B1,W}}{N_y^{B1,W} + N_y^{B1,E}} C_y^G + \frac{N_y^{B1,W}}{N_y^{B1,W} + N_y^{B1,E} + N_y^{B2}} C_y^A$$

$$C_y^{B1,E} = \frac{N_y^{B1,E}}{N_y^{B1,W} + N_y^{B1,E}} C_y^G + \frac{N_y^{B1,E}}{N_y^{B1,E} + N_y^{B2}} C_y^S + \frac{N_y^{B1,E}}{N_y^{B1,W} + N_y^{B1,E} + N_y^{B2}} C_y^A$$

$$C_y^{B2} = \frac{N_y^{B2}}{N_y^{B1,E} + N_y^{B2}} C_y^S + \frac{N_y^{B2}}{N_y^{B1,W} + N_y^{B1,E} + N_y^{B2}} C_y^A \tag{9}$$

The model has four parameters: *K* and *r* for each breeding stock B1 and B2. Given K^{B1}, the pre-exploitation abundances for the western and eastern sub-stocks are given by $K^{B1,W} = XK^{B1}$ and $K^{B1,E} = (1-X)K^{B1}$, where *X* is a further parameter fixed on input and the model is run for various values of *X*.