Final Report on the Assessment of the Southern Hemisphere Humpback Whale Breeding Stock B

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1. INTRODUCTORY ITEMS

1.1 Opening remarks

Robbins welcomed the participants to the meeting. The list of participants is provided in Appendix A. The meeting took place in Tromsø, Norway, immediately proceeding SC/63.

1.2 Election of Chair

Robbins and Zerbini were elected Chairs.

1.3 Appointment of Rapporteur

Jackson and Robbins undertook the duties of rapporteur.

1.4 Adoption of the Agenda

The adopted agenda is given in Appendix B.

1.5 Review of documents

The following documents were available for the meeting: SC/63/SH17, SH20, SH21 and SH26.

2. ASSESSMENT OF THE SOUTHERN HEMISPHERE HUMPBACK WHALE BREEDING STOCK B

The IWC Scientific Committee (SC) currently recognises seven humpback whale breeding stocks (BS) in the Southern Hemisphere (labelled A to G - IWC, 1998). BSB corresponds to whales inhabiting the western coast of the African continent, from Guinea to western South Africa (Fig. 1). Differences in the catch histories (Best and Allison, 2010) and population genetics (Rosenbaum et al., 2009) of whales off Gabon and west South Africa (WSA) suggest substructure within BSB. These differences have been formally recognised by referring to whales off Gabon as B1 and to whales from the west coast of South Africa as B2. However, while it is clear that the waters off Gabon represent a winter breeding ground for B1, the near-shore region sampled in WSA 3,000km to the south in spring and summer (Barendse et al., 2010) seems to represent a local feeding ground and/or migratory corridor for a relatively small number (<500) of whales (Barendse, 2011): the location of the breeding ground for whales from B2 is therefore unknown. The boundary between the two sub-stocks is unknown, but has been suggested to lie in the vicinity of Walvis Ridge, at the point where it meets the African coast (Rosenbaum and Mate, submitted) or the Angola/ Benguela Front (IWC, 2011b); SH/63/SH17).

The most current in-depth assessments of BSA (western South Atlantic), BSD (eastern Indian Ocean) and BSG (eastern South Pacific) were completed in 2006 (IWC, 2007) and the assessment of BSC (western Indian Ocean) was completed in 2009 (IWC, 2010). Since then, the completion of the assessment of BSB has been considered a priority by the Scientific Committee (IWC, 2010, p.234). At the IWC's 62^{nd} annual meeting in Agadir, the Scientific Committee reviewed new information on modern whaling catches, population structure and abundance of BSB (IWC, 2011b). Stock structure hypotheses were developed (Tables 2 and 3, IWC, 2011b) and these included:

(1) Single stock and multi-stock models (Models I [variants a, b, c, d and e], II [variants a and b], III and IV, illustrated in Appendix C).

(2) Various scenarios on how whales move within low latitude areas and to the Antarctic.

Models in (1) above were ranked for analysis, with Models Ia, IIa and III being given greater priority. The Scientific Committee also agreed on input data and sensitivity analysis (Appendix C, Table 1) during the development of assessment models and noted that considerable progress was made in reviewing information for BSB. An intersessional email group was created to complete tasks identified during SC/62 (IWC, 2011b, p.219) in order to facilitate the completion of the assessment of BSB during a meeting preceding the Scientific Committee's 63rd Annual Meeting in Norway. The intersessional email group discussions focused on preliminary assessment models and on a refinement of the input data, leading to the development of the model outputs presented in SC/63/SH26.

2.1 Evaluation of assessment models developed intersessionally

Paper SC/63/SH26 provided assessment results for models and sensitivity analysis agreed during SC/62. As for previous Southern Hemisphere humpback whale assessments (IWC, 2007; 2010), these models were age and sex-aggregated and were developed in a Bayesian framework. Preliminary estimates of current (2010) abundance relative to the preexploitation population (*K*, assumed to correspond to year 1900) ranged from 0.508 (90% probability interval [PI]= 0.261, 0.833) to 0.750 (90% PI=0.308, 1.000) for B1 and 0.045 (90% PI=0.026, 0.075) to 0.124 (90% PI=0.037, 0.850) for B2.

Discussion of input data and model assumptions in this paper is summarised below. Final assessment models are developed in Item 2.3. These models can be divided into reference cases and sensitivities. The reference case is the set of parameter values agreed to be most appropriate for conducting the population assessment of BSB. Sensitivities are the alternative scenarios that are used to assess the effect of different parameter inputs and model structures on the assessment outcome. Whenever applicable, discussion under this section specifies whether certain types of data or model assumptions can be used in reference cases or sensitivity analyses.

2.1.1 Lower Boundary on Minimum Bottleneck Population (N_{min})

The authors of SC/63/SH26 observed that prior incoherence resulting from the implementation of a lower boundary (minimum bottleneck size) on N_{min} had been found to be a constraint to the estimates of the population growth rate for many models explored intersessionally. In these exploratory models, N_{min} was implemented as 4x the number of haplotypes for each sub-stock (129 for Gabon and 71 for WSA) as originally specified by the Scientific Committee for the assessment of Southern Hemisphere humpback whales (IWC, 2007). For the assessments presented in SC/63/SH26, the N_{min} boundary was implemented in two ways. Case A imposed a constraint on Gabon and WSA minimum abundance (using the N_{min} values implemented in the exploratory models described above) and was applied to assessments considered to be of higher priority (Models Ia, IIa and III in Appendix C). This implementation resulted in

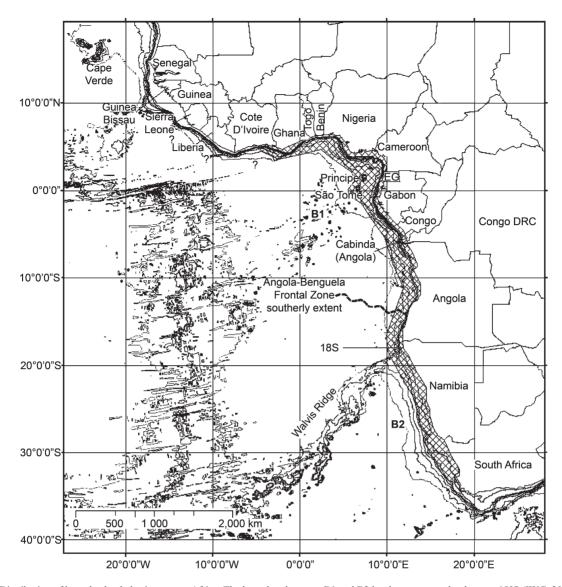


Fig.1. Distribution of humpback whales in western Africa. The boundary between B1 and B2 has been proposed to be near 18°S (IWC, 2011b).

estimation of growth rates (parameter r) that were considered too low. An alternative implementation of the N_{min} boundary (Case B) was applied to the overall stock in all assessment models, assuming there were 136 unique haplotypes in Gabon and WSA combined. It was noted that this alternative resulted in posterior distributions that were not as heavily influenced by the N_{min} constraint.

Further discussion of the N_{min} constraint during the meeting focused on three topics: (1) whether N_{min} represented an estimate or a lower bound of the minimum population size at bottleneck; (2) what was the appropriate number of haplotypes to use in light of movements of animals between Gabon and WSA; and (3) what was the appropriate multiplier to account for other (immature animals of both sexes) animals alive at the time of the bottleneck. It was clarified that N_{\min} can represent either an estimate of the number of individuals alive, or the absolute minimum number of individuals alive, at the bottleneck (a lower boundary). For the purpose of the current assessment, it was agreed that the latter was required. It was further noted that the haplotypes used for the N_{min} boundary should be those that are exclusive (private) to each region as an attempt to exclude those that might represent migrants between sub-stocks (Appendix 2, IWC, 2011a). It was clarified that private haplotypes are only necessary if N_{min} constraints for Gabon and WSA are to

be implemented separately. In the context of the Southern Hemisphere as a whole there are no haplotypes that are unique to BSB, but there is relatively low gene flow between BSB and other breeding stocks as compared to gene flow within BSB (Rosenbaum et al., 2009). In regards to (3) above, SC/63/SH26 had proposed, based on intersessional email discussions, an N_{min} value corresponding to the number of haplotypes +1. In discussion, this was considered too conservative as it assumes there was only one male alive that the time of bottleneck. A suggested alternative was to assign N_{\min} to a value corresponding to 2x the number of haplotypes, but that was also considered a low value because it assumes that only mature animals (in an even sex ratio) existed during the bottleneck. In conclusion, it was agreed that $N_{\rm min}$ specifications should be applied according to Case A, using the private number of haplotypes in each area (17 for Gabon and 6 for WSA [as specified in Appendix 2, Annex H, IWC, 2011]) and that this number should be multiplied by 4 for consistency with previous assessments of other Southern Hemisphere humpback whale stocks (IWC 2007, 2010). It was also agreed that the specification of the value of N_{min} is relevant for the assessment of whale stocks in general and that further discussion on the development of: (i) this boundary; and (ii) an estimator of N_{min} , should be conducted by the Scientific Committee.

2.1.2 Error rates for correction of abundance estimation using capture-recapture data

The use of microsatellite data for computing abundance estimates requires a correction for the percentage of duplicates that are missed due to sequencing or human error and the way these corrections were implemented in the models presented in SC/63/SH26 were discussed. It was **agreed** that the (1-q) component in Equation 3 in SC/63/ SH26 to correct for error rates should be implemented as (1 $q)^2$, to account for error at both the sighting and resighting stages. In discussion, it was further clarified that only false negatives are an issue for genotype-based capture-recapture estimates as the likelihood of false positives is negligible. There was also discussion of how the error rate correction in the assessment models compared to the misidentification correction in Program MARK. The approach implemented in the assessment models (using the Poisson distribution) an approximation of the multinomial likelihood is implementation in MARK and would have the desired effect as long as the probability of resighting was low. This was considered likely for the purpose of the BSB assessment.

2.1.3 Interchange value

Parameter p_{1} was defined in some of the models presented in SC/63/SH26 as the relative probability of detecting whales from B2 versus whales from B1 off Gabon and is included in all variants of Model I. The default value $(p_{2}=0.5)$ was arbitrarily chosen. It was noted that available capture-recapture data could potentially be used to estimate interchange, which could inform this parameter. However, interchange across regions is not implemented in the model and incorporating it would require substantial recoding to change the model structure. A more straightforward option would be to vary the value of p_1 using transition probabilities estimated by existing multi-strata models. However, it could not be ascertained how estimates from multi-strata models should be related to the probability of sighting B2 whales off Gabon. A concern was also raised that current levels of interchange between WSA and Gabon may not be representative of those in the past, prior to and during whaling. However, it was noted that while p_1 is fixed, p_2 (the proportion of B2 animals migrating to the Antarctic) changes through time in light of differential exploitation of the two populations. It was suggested that the effect of varying p_{2} , was likely to be low given that the WSA population is estimated to be small relative to the Gabon population. This was confirmed by comparing the results of Models IIa, Id and IV, which were structurally identical except for the value of p, for whales of B2 in Gabon. In conclusion, it was agreed that p, had minimal impact on the model outcome and did not need to be explored as a further sensitivity.

2.1.4 Parameter 'X'

In discussion of models in SC/63/SH26, it was observed that the estimated pre-exploitation abundance of whales in Gabon was greater than 1. It was clarified that for this single stock model, the stock pre-exploitation abundance corresponded to the sum of K in Gabon and K in WSA. One of these components is allowed to exceed its initial K as long as this value is less than the estimate of K for the two areas combined. This occurs because this model allowed for the proportion of whales migrating offshore and inshore to vary and therefore density dependent mechanisms can compensate for the decline in one population by increasing the size of the other (e.g. in Model III if B1E declines because of exploitation along the coast, B1W increases because density dependence is acting on both components of this stock). It was noted that other models exhibited this behaviour but their results had not been reported in SC/63/SH26.

The proportion of the pre-exploitation abundance of substock B1 migrating inshore and offshore is determined by parameter X in models containing two migratory components for whales in Gabon (Models Ic, Id, Ie, IIa, IIb, III, IV and V in SC/63/SH26). This parameter is estimated in Model III and fixed in all other models in which it is implemented because some models are fairly complex and there is currently no information to estimate X. In SC/63/SH26, X was set at 0.7 (i.e. 70% of the stock migrates offshore), but other values were not explored. It was agreed that alternate values of X, of 0.5 and 0.9, would be used in sensitivity analyses further described in Section 2.3. The lower value (0.5) was selected based on the value of X estimated directly in Model III (SC/63/SH26).

2.1.5 Catch data

In discussion of the catch series used in the model, it was **agreed** that in the absence of more informative data, the most appropriate scenarios for the allocation in the Antarctic were already implemented in the models (Allocation Hypothesis 1, IWC, 2010, fig. 2). Sensitivities of these models to alternate catch scenarios were then discussed.

With regard to catches north of 40° S, it was suggested that a catch scenario where all Angola catches are allocated to B1 ought to be explored. Some noted that this implies that B2 animals are breeding south of a front, in oceanographic conditions that are not consistent with previously reported humpback whale breeding habitats (Rasmussen *et al.*, 2007) and where observed sex ratios are not typical of a breeding ground (SC/63/SH17). In response it was noted that this catch scenario is possible if B2 exists north of B1, with B2 animals travelling offshore from WSA to their breeding grounds (see Item 2.2, below). In order to fully explore the catch allocations north of 40°S, four sensitivities were **agreed** where 100, 75, 25 and 0% of the catches taken in Angola was allocated to Gabon relative to WSA.

With regard to catches south of 40°S, it was noted that data are now available which can be used to specify the ratio of B1 and B2 whales in the Antarctic catch data, which was set at a default value of 0.5 in SC/63/SH26. A mixed stock analysis of mtDNA and microsatellites was undertaken intersessionally (Appendix D), but there was inadequate time to incorporate this new information into the reference cases during the meeting.

It was noted in discussion that the struck-and-lost rate that had been used in SC/63/SH26 (0.15) was in fact a maximum estimated value and no actual cases had been documented (Best, 2010). It was therefore **agreed** that the reference cases for the assessment would be taken as zero, but the value 0.15 would also be included as a sensitivity to bound the range of impact on the assessment model outputs. It was noted that there was little information to estimate this parameter and, in view of time constraints, the matter was not discussed further.

2.1.6 Capture-recapture data

Capture-recapture data collection in Gabon were obtained from four sites (Port Gentil, Iguela, Gamba and Mayumba) over 2000-06 but only two of these (Iguela and Mayumba) had regular survey effort (Collins *et al.*, 2010). There were concerns about the lack of temporal consistency in sampling among the additional sites, which could result in bias when there is also temporal heterogeneity in individual sighting probabilities as has previously been observed in other populations, e.g. Breeding Stock C3, (Cerchio *et al.*, 2009). However there was also discussion regarding the limited spatial extent of sampling if only two of the four sites were included in the assessment model. Some felt that the capture-recapture data should be used from all four of the available sampling sites within BSB to improve the spatial coverage of the stock. It was **agreed** that the two sites with more consistent sampling (Iguela and Mayumba) would be used in the base case, with four sites used as a sensitivity to bound the range of the impact on the assessment model outputs.

The group discussed whether right dorsal fins (with error corrections implemented as described for microsatellites) should be used for WSA (instead of tail flukes) as a sensitivity to the reference case. Some members preferred to use the dorsal fin data due to suspected individual heterogeneity of fluking behaviour at WSA (SC/63/SH20) and to include the error correction 11.4% calculated for these data. However others felt that this should not be implemented without substantial additional discussion of how the error rate was generated, and how it should be used. Since the error rate pertains to resighted animals only, systematic error in the dataset (including the possibility of false positives) has not yet been accounted for. It was also noted that the error rate is very high, which creates substantial uncertainty and potentially inaccuracy in the results. The group agreed to use flukes as a sensitivity scenario for the present assessment.

2.1.7 Interchange with BSC

It was discussed that the assessment of BSB is being undertaken without consideration of adjacent stocks, despite the fact that BSB is known to exhibit exchange with BSC. That has been demonstrated by movements of individuals between the two stocks and between BSC and the BSB nucleus feeding area as well as estimated gene flow (Pomilla and Rosenbaum, 2005; Rosenbaum *et al.*, 2009). It was noted that this should be explored in more detail in the future.

2.2 Evaluation of new proposed models

In addition to the stock structure models agreed at SC/62, two other models were considered during the meeting. Model V (Appendix C) was presented in SC/63/SH26 and proposed that the breeding ground for B2 whales occurs off Angola, and that there are inshore (B2E) and offshore (B2W) components migrating to either WSA or the Antarctic. In this model, whales in Gabon migrate to the Antarctic but not through WSA. Therefore, catches off Angola were allocated to B2. Best explained the rationale for adding Model V to the assessment. WSA data were collected in summer, in the vicinity of two small bays that formed part of the historical whaling ground from Saldanha Bay (ca 33°S). For logistical reasons sampling was confined to a few kilometers from the coast. Plots of available catch positions however showed that whalers from Saldanha also took humpback whales between 50 and 100 miles offshore, while Soviet fleets caught humpbacks 100s of kilometers offshore in spring en route to the Antarctic. While some of these offshore migrators may have been whales from B1, catch rates in Namibia and Angola from 1912-16 were very much higher than at Saldanha, suggesting that the migratory streams of whales converged on the coast to the north of WSA, as stated by contemporary observers at Saldanha Bay. These whales would be well to the south of Gabon and therefore could include a substantial proportion of B2 animals, depending on where the boundary between the two populations lies. Best also noted that there had been no matches yet between whales photographed in

Namibian and WSA waters (SC/63/SH21). WSA appears to be an aggregation of a small number of individuals that habitually use the Cape coast as a supplementary feeding ground on their way south. While some B2 individuals could migrate south using inshore and offshore routes, resighting data at WSA suggest a high rate of return to that feeding site. Thus, it was his view that other B2 individuals might pass routinely offshore. For these reasons, Best questioned the use of the WSA estimate as a proxy for B2 abundance in multi-stock assessment models, without any flexibility in the assumption of the fraction of the B2 stock that it might represent. Support for the development of Model V was also presented in SC/63/SH17.

In discussion, it was noted that the SC had agreed upon a procedure during SC/62 to select a suite of models for consideration in the assessment of BSB (IWC, 2011a). This process involved discussing the evidence for each model and excluding those that were inconsistent with the data. As Model V was proposed intersessionally, it did not receive the same level of prior review and agreement as the other models in SC/63/SH26. Some commented further that if Model V had been proposed at SC/62, it would have been excluded on the grounds that it did not allow for a connection between WSA and Gabon. As such, the model is not consistent with observed photographic and genetic matches between those two areas. They also noted that a key aspect of Model V (the unknown B2 breeding ground) was already captured in Model IIa, a model that also incorporates known exchange between WSA and Gabon. The observed exchange between these areas was not, in their view, inconsistent with the hypothesis of two sub-stocks. The passage of B2 animals through Gabon would be congruent with the capturerecapture data. Animals en route to another destination would have a shorter residency time in Gabon. This would translate to a lower sighting probability and explain both the existence of resightings and the estimated low rates of interchange. They noted that there is precedence for similar sub-stock dynamics in other areas of the world, such as the migration of Central American whales through Mexico in the North Pacific. They also raised the concern that Model V hypothesises a breeding ground and a migratory passage (B2W, Appendix C) that are both hypothetical and unsampled. It allows three components of BSB to feed in the Antarctic (B1, B2E, B2W) and there are currently no data with which to make an informed estimate of the proportion of B2W to B2E. Therefore, a portion of the population is speculative and the outcome of the assessment would rely on assumptions for which there are no reliable data inputs. Finally, it was their view that the allocation of 100% Angola catches to B2 was not supported by the data. Even in the scenario that this region were a primary breeding destination for B2, some portion of the animals caught would be B1 migrants.

It was discussed that the Antarctic mixed stock analysis presented in Appendix D might allow for an estimation of the relative proportions of B2E and B2W in Model V. However, there was insufficient time to explore this fully for the current assessment.

The meeting **agreed** that the relative plausibility of Model V could not be evaluated without additional information.

A single stock model (named Model 0, Appendix C) was introduced in discussion. This model was previously considered by the Scientific Committee (IWC, 2009) but was not adopted because it did not account for existing substructure within BSB. However, it was **agreed** that this model was useful to examine the effect of removing

population structure (including B1E and B1W components) on the assessment model outputs. This model structure was also expected to reduce difficulties in model fitting due to data limitations and/or complexity. In Model 0, all whales in BSB were hypothesised to breed off Gabon and only the abundance for this location is used in the assessment models.

2.3 Specification of final assessment models and sensitivities

After reviewing SC/63/SH26, the specifications of input data and stock structure models to finalise the assessment of BSB was discussed. It was noted that results were similar across most models presented in that document (Table 1 in SC/63/SH26). Considering the discussions on items 2.1 and 2.2 above it was agreed that the final models should include at least one single stock and one multi-stock model. Model 0 was selected as the single stock model for the purpose of the assessment. With regard to multi-stock models, it was noted that Model Id differed from IIa only because the former assumes that all whales from B2 travel past Gabon. Some preferred Model Id, noting that it is consistent with the hypothesised migration patterns and latitudinal substructure of humpback whales such as those observed in Mexico/ Central America in the North Pacific (Calambokidis et al., 2001) and western South America (Acevedo et al., 2007). In general, it was believed that Model IIa was nevertheless the best available multi-stock model because it had the most flexibility in terms of a mixture of animals at Gabon, while allowing for the possibility that B2 individuals migrate elsewhere. Therefore, it was agreed that Model IIa should be used as the reference case for multi-stock models.

Once reference case models were selected, a set of input data (Table 1) and sensitivity analyses to the choice of data and to alternate model scenarios were specified (Table 2). Additional sensitivity analyses were also proposed to assess changes in the assessment outputs for different stock structure hypotheses. It was agreed that the following model scenarios would be explored in these sensitivities: Id, III, V and Ia. It was also agreed that the following diagnostic tests would be performed: (1) examine fit of the model to capturerecapture data; (2) examine consistency with N_{min} constraints for B1+B2; (3) examine consistency with abundance estimates for 2005 estimated using Program MARK; and (4) compare the fit of models with and without the $(1-q)^2$ error correction.

2.4 Results of final assessment models

Results of assessment models were examined and it was agreed that the outputs from the reference cases (Table 3, Figs 2 and 3) and sensitivity C for model 0 and sensitivities B4, C, D1, D2 and E for Model IIa (Appendix E) would be used in making inference in regards to the status of BSB. The choice of sensitivity scenarios was based on the plausibility of the models as well as the deviation of parameter estimates relative to the reference case so that uncertainty in parameter estimates was considered to the greatest extent possible. An examination of diagnostics indicated that model fits were appropriate (Appendix E).

For comparison of model predicted outputs, an abundance estimate of 6,764 (95% CI: 4,398-10,404) in 2005 was generated for Gabon using Program MARK (Figs 2 and 3). This estimate was based on a closed population

	Table 1							
Final refer	Final reference cases for BSB.							
	Reference Model 0	Reference Model IIa						
Model assumptions								
p_I : Proportion of B2 migrating to the Antarctic	N/A	0.5						
X: Proportion of pristine B1 population that migrate West	N/A	X=0.7						
Struck-and-lost rate (applied to pre-1914 catches)	0	0						
Capture-recapture data								
Gabon	Microsatellite, males only, two sites (Iguela and Mayumba)	Microsatellite, males only, two sites (Iguela and Mayumba)						
WSA	NA	Microsatellite data all sexes						
N _{min} constraints								
Gabon # haplotypes	136 for B total	17						
WSA # haplotypes		6						
N _{min} value	4*# haplotypes	4*# haplotypes						
N _{min} implementation	Case B*	Case A						
Catch allocation								
Catches north of 40°S: Angola catches	50% Gabon and 50% WSA	50% Gabon and 50% WSA						
Catches south of 40°S	Allocated in proportion to relative abundances							

Table 1

*Since there are not Gabon and WSA components, a combined N_{min} constraint has to be used.

Sensitivity	Model applied to	Reference case assumption changed
А	Model 0 and IIa	Gabon microsatellite capture-recapture data: males only, four sites (Port Gentil, Iguela, Gamba and Mayumba)
B1	Model IIa	Angola catch allocation: 0% Gabon, 100% WSA
B2	Model IIa	Angola catch allocation: 100% Gabon, 0% WSA
B3	Model IIa	Angola catch allocation: 25% Gabon, 75% WSA
B4	Model IIa	Angola catch allocation: 75% Gabon, 25% WSA
С	Model 0 and IIa	WSA capture-recapture data: flukes replace microsatellites
D1	Model IIa	Parameter X=0.5
D2	Model IIa	Parameter X=0.9
Е	Model 0 and IIa	Struck-and-lost rate (pre-1914 catches) = 15%

Table 2

		Model 0	Model IIa				
		В		B1		B2	
"B	0.045	[0.006,0.081]	0.053	[0.010,0.097]	0.043	[0.005,0.078]	
K^{B}	24072	[19,686, 40,980]	18,732	[13,595, 36,551]	4,293	[224,6,627]	
V _{min}	1921	[603, 7,822]	1,532	[367, 6,604]	69	[25,172]	
V2005	9484	[7,581, 11,849]	9,310	[7,540, 11,730]	324	[117,471]	
V_{2010}/K	0.467	[0.229,0.711]	0.607	[0.252,0.893]	0.106	[0.033,0.980]	
V_{2040}/K	0.93	[0.272,0.999]	0.982	[0.346,1.000]	0.4	[0.039,1.000]	

Table 3 Assessment results for Model 0 and Model IIa. Reference case assumptions have been applied. Posterior median values are given along with their 90% probability intervals.

model, which used male only genotype capture-recapture data from 2004-2006 with an error rate correction of α = 0.9285. All other assumptions for computing abundance in a capture-recapture framework were the same as those in the assessment model (Collins *et al.*, 2010).

In discussion of the assessment results, it was **agreed** that neither of the proposed reference case models (Models 0 and IIa) adequately captured the complexity of the BSB population structure. However, it was **agreed** that these models were useful for making inferences about the current status of BSB.

Modeling BSB as a single stock (Model 0) yielded a 2005 abundance estimate of 9484 whales [90% PI=7,465, 12,221] and an intrinsic growth rate of 0.045 [90% PI=0.006, 0.081]. The 2010 abundance relative to the pre-exploitation level (N_{2010}/K) was 0.467 [90% PI=0.229, 0.711].

Model 0 is a simple, aggregated model that does incorporate all the existing data from this stock and does not account for the level of population sub-structure within BSB that had been recognised by the Scientific Committee. Results of this model are broadly indicative of the trend of the stock as a whole, but its generality might obscure important aspects of population trend for sub-stocks. Genetic information indicates more than one stock and if one of these had been more strongly depleted than others than a single stock model would not show it. Some considered Model 0 to be the best available model precisely because it avoided making assumptions about substructure for which related data are currently inadequate for the population models. Others believed the more complex models to be valid, but recognised that the data available and/or models in use might not adequately account for complexity on population structure.

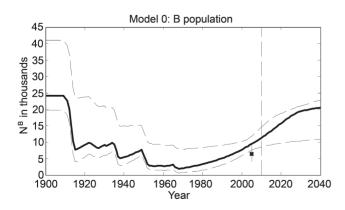


Fig. 2. Median trajectory and 90% probability interval for Model 0 reference case. The trajectories to the right of the vertical dashed line are projections into the future under the assumption of zero catch. The MARK generated capture-recapture abundance estimate (depicted by the symbol 'x') and 95% confidence interval (vertical line) for Gabon is presented for comparison.

The multi-stock scenario (Model IIa) generated comparable estimates for the total population, with the major sub-stock (B1) having an abundance in 2005 of 9,310 [95% PI=7,540, 11,730], an increase rate of 0.053 [95% PI=0.010, 0.097] and a depletion level (N_{2010}/K) of 0.607 [95% PI=0.252, 0.893]. Estimates for B2 indicated a smaller population [N_{2005} =324, 117, 471] with a rate of increase of 0.043 [95% PI=0.005, 0.078] that may be substantially farther from recovery (*r*=0.043 [95% PI=0.004, 0.078] and N_{2010}/K =0.106 [95% PI=0.032, 0.999]).

²⁰¹⁰ In reviewing the sensitivity scenarios, it was noted that the posterior median of N_{2010}/K for Model 0 ranged from 0.376 to 0.467 and for Model IIa ranged from 0.571 to 0.672 for B1 and from 0.073 to 0.179 for B2. However, the 90% probability intervals were wide (Appendix E) and substantial overlap was observed across all scenarios for each substock. It was noted that one of the greatest differences in the estimation of current status relative to the reference case was

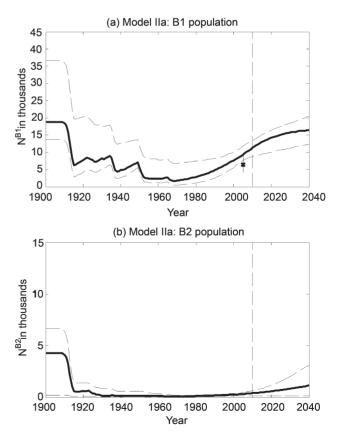


Fig. 3. Median trajectory and 90% probability interval for Model IIa reference case (B1 stock: top panel [A], B2 stock, bottom panel [B]). The trajectories to the right of the vertical dashed line are projections into the future under the assumption of zero catch. The MARK generated capture-recapture abundance estimate (depicted by the symbol 'x') and 95% confidence interval (vertical line) for Gabon is presented for comparison in the top panel.

the scenario where the struck-and-lost rate was increased to 15%. This resulted in a reduction of N_{2010}/K from 0.607 to 0.505, showing that correction to the catch series can have a large effect on the estimation of this parameter, as observed for other stocks, e.g. BSA and BSG (IWC, 2007). In light of this, it was **agreed** that the uncertainties in the catch series should be carefully considered in future assessments.

It was pointed out that any inferences regarding the status of B2 rest on the assumption that the WSA data are representative of the entire B2 stock. Some of the necessary inputs for this model (such as a reliable abundance estimate for the entirety of B2), are either not available or will require further investigation. The current capture-recapture estimate available for B2 was derived from sampling in St Helena and Saldanha Bays off WSA, ca 3,000km south of Gabon. This region is recognised as a feeding area/migratory corridor and not a breeding ground. Hence considerable doubt was raised over how representative the WSA sample was of B2 as a whole, especially if there was a substantial offshore migratory component. The ability to determine the geographical extent of sub-stocks is seriously limited by the distribution of the sampling effort. This meant that the allocation of some appreciable catches (such as off Angola) to one or other sub-stock in a multi-stock model was largely arbitrary and it could have substantial impacts on the respective assessments. These undisputed limitations in the data available for describing the multi-stock structure and population dynamics led to concerns regarding the applicability of some Model IIa parameter estimates.

Some nevertheless considered Model IIa to be more biologically realistic and reliable than Model 0 because it takes into consideration the evidence for population substructure that is known to exist. It also allows for potentially different degrees of recovery that would be possible in such a situation and would be important to investigate for management purposes.

In reviewing the Model IIa results, it was noted that the proportion of sub-stocks in the Antarctic (Appendix D) was consistent with microsatellite-based mixed stock analyses, assuming that the estimated Antarctic allocation proportions are similarly distributed within the 'unknown' (unassigned) proportion. It was also noted that while the results do not seem consistent with mtDNA-based mixed stock proportions (Appendix D), microsatellite data have greater resolution than mtDNA haplotype data, and therefore positive results were potentially more informative regarding the proportion of whales from B1 and B2 sampled in the Antarctic. It was **agreed** that the results of Model IIa were consistent with some aspects of the genetic mixed stock analysis, but further investigation was recommended in order to provide more representative inputs for capture-recapture and genetic data.

In discussion of the results of the final models, it was noted that all of them predicted low to moderate rates of increase for BSB relative to some other Southern Hemisphere populations. It was noted that the assessment had been hampered by the absence of any independent estimate of trend. The population dynamics models used an uninformative prior (uniform from 0 to 0.106) on the intrinsic growth rate (r). It was noted that the extent to which the model fitting process has updated this prior is minimal. This occurs because the capture-recapture data is not informative in regards to the population trend and hence the growth rate parameter. Consequently the posterior median estimate of r is very close to the mid-point of the prior of 0.053. This contrasts to the assessment of other humpback whale breeding stocks (e.g. A, D; IWC, 2007) for which there were observations that gave direct estimates of trend in abundance. Inclusion of such data in assessments leads to substantial updating of uninformative priors for r, with posterior medians higher than was the case here.

2.5 Conclusions

The meeting **concluded** that BSB has probably recovered to about half of its pre-exploitation level, noting that the probability interval about this estimate is wide. The assemblage that feeds off WSA has increased over time, although the current data do not allow precise quantification of the rate of increase. While the multi-stock model suggested that B2 was appreciably more depleted than B1, it is not possible to determine whether this is real or reflects the fact that the data do not fully represent B2 due to incomplete sampling coverage for this stock.

The meeting **agreed** that the current assessment of BSB was now complete, given the available data. Future assessments will require additional information on population abundance, trends and structure and suggestions for this work is given under Item 2.6.

2.6 Recommendations

It was **agreed** that recommendations made by the Scientific Committee during a Workshop to advance the Comprehensive Assessment of Southern Hemisphere humpback whales in Hobart, Tasmania (IWC, 2011b) were still applicable to BSB. In particular, it was **recommended** that the following items would improve future assessments of this stock.

- A more extensive and range-wide sampling of humpback whales for genetics and photo-identification coordinated amongst regions (i.e. SPLASH, YONAH type studies).
- Long-term study of targeted populations for estimates of trend.
- Strategic implementation of satellite tagging effort to assess movements throughout the region and patterns of connectivity.
- Surveys and sampling (genetic and photographic identification) of understudied areas where humpback whale concentrations are known or suspected, specifically Angola, Namibia, São Tomé and Príncipe, and Bight of Benin to characterise the importance of these potential areas.
- Passive acoustic monitoring to characterise the distribution of humpback whales in less well-studied parts of their range.
- Extension of coastal surveys and sampling into offshore areas (e.g. further offshore of the continental shelf)
- Further genetic sampling in the Antarctic to improve allocation of catches, dependent upon further understanding of the stock structure from low-latitude breeding grounds.
- A more comprehensive evaluation of the models and approaches to stock assessments (e.g. multi-stock assessments) that is:
 - informed by new data collected above;
 - considers a wider range of possibilities to ensure compatibility of models with data;
 - takes account of information on whales seen in more than one region.

3. ADOPTION OF THE REPORT

The report was adopted on 2 June 2011 at 01:30am. The Chairs acknowledged the efforts of all participants, both intersessionally as well as during the meeting, to bring the assessment of breeding stock B to a conclusion. The participants thanked the Chairs and the rapporteurs for their hard work.

REPORT OF THE ASSESSMENT OF THE SH HUMPBACK WHALE BREEDING STOCK B

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Annex A

List of Participants

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Annex B

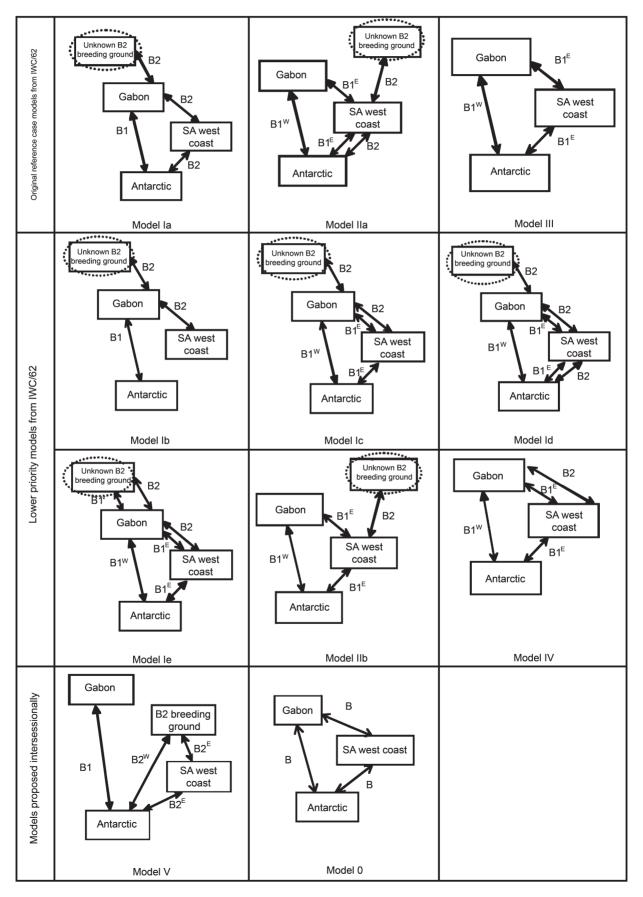
Agenda

1. Introductory items

- 1.1 Opening remarks
- 1.2 Election of Chair
- 1.3 Appointment of rapporteur
- 1.4 Adoption of the agenda
- 1.5 Review of documents
- 2. Assessment of the Southern Hemisphere Breeding Stock B
 - 2.1 Evaluation of assessment results from models developed in SC/62
- 2.2 Evaluation of proposed models developed intersessionally
- 2.3 Specification of final assessment runs and sensitivities
- 2.4 Results of final assessment models
- 2.5 Conclusions
- 2.6 Recommendations
- 3. Adoption of the Report

Annex C

Description of the Stock Structure Models used in the Assessment of BSB



Data category	Population	Reference case	Variants
Capture-recapture	Gabon	Microsatellites (males-only)	- Flukes
			- Microsatellites (both sexes)
Capture-recapture	WSA	Microsatellites (only if genotyping errors can be incorporated	 Right dorsal fin
		into assessment models; otherwise flukes)	- Flukes
N _{min}	Gabon	68 haplotypes (see Appendix 2)	None
N _{min}	WSA	24 haplotypes (see Appendix 2)	None
Catch allocation (north of 40°S)	Gabon	Congo and 50% Angola	- Congo and Angola
, , , , , , , , , , , , , , , , , , ,			- Congo only
Catch allocation (north of 40°S)	WSA	50% Angola, Namibia and WSA	- Namibia and WSA
, , , , , , , , , , , , , , , , , , ,		•	- Angola, Namibia and WSA
Catch allocation (south of 40°S)	Gabon	Allocation Hypothesis 1	None
Catch allocation (south of 40°S)	WSA	Allocation Hypothesis 1	None
Migration to unknown breeding ground	Gabon	25% (i.e. Model Ie)	None
Migration to Antarctic	WSA	50% (i.e. Model Id)	- 100%
č			- 0% (does not migrate)
Struck-and-lost rate	Both	0.15 (see Best, 2010)	- 0

Table 1 Input data agreed at SC/62 for use in assessment modelling, specified by reference case and variants (IWC, 2011).

Model description

Reference case models (Table 2 of Annex H)

MODEL IA

Assumes two independent breeding sub-stocks (B1 and B2) which mix on Antarctic feeding grounds. Whales from breeding sub-stock B1 feed in the Antarctic and migrate to Gabon for breeding. Whales from breeding sub-stock B2 feed off WSA, and migrate along the West African coast through Gabon to a separate unidentified breeding ground. Additionally, some portion of B2 animals migrate to the Antarctic feeding grounds.

MODEL IIA

Assumes two breeding sub-stocks B1 and B2. B1 has two migratory components B1W and B1E. Whales from B1W migrate from the Antarctic feeding grounds directly to Gabon while whales from B1E migrate through the waters off WSA before continuing onto the Gabon breeding grounds. Whales from sub-stock B2 feed primarily off WSA and do not migrate past Gabon but instead to a separate unidentified breeding area. In addition, some portion of animals from sub-stock B2 migrates to Antarctic feeding grounds.

MODEL III

Assumes a single breeding stock, B1, with two migratory components B1W and B1E. B1W migrates directly to Gabon from Antarctic feeding grounds, while B1E migrates through waters off WSA before continuing to the Gabon breeding grounds. In this assessment the proportion of animals using each migratory route does not change with time (other than as a result of the differential impact of catches).

Lower priority models (Table 3 of Annex H)

MODEL IB

Is a variant of Model Ia in which there are two independent breeding sub-stocks that do not mix on the Antarctic feeding grounds. B1 feeds in the Antarctic and migrates to Gabon for breeding. B2 feeds off WSA and migrates along the West African coast through Gabon to a separate unidentified breeding area.

MODEL IC

Is a variant of Model Ia in which breeding sub-stock B1 has two migratory components, B1^w and B1^E. B1^w migrates directly to Gabon from the Antarctic feeding grounds. B1^E migrates through the waters off WSA before reaching the Gabon breeding grounds.

MODEL ID

Is a variant of Model Ic in which some proportion of substock B2 also migrates to Antarctic feeding grounds.

MODEL IE

Is a variant of Model Ic in which some proportion of substock B1 migrates through Gabon to a separate unidentified breeding area.

MODEL IIB

Is a variant of Model IIa which assumes two breeding stocks, B1 and B2. B1 is assumed to have two components, B1^w and B1^E. B1^w migrates directly to Gabon from Antarctic feeding grounds while B1^E migrates through waters off WSA before continuing to the Gabon breeding grounds. B2 feeds off WSA, and does not migrate through the Gabon breeding ground but instead to a separate unidentified breeding area.

MODEL IV

Assumes two feeding sub-stocks, B1 and B2. B1 is assumed to have two migratory components, B1^w and B1^E. B1^E passes through WSA waters before going to Gabon, while B1^w migrates directly to Gabon breeding grounds from Antarctica. B2 feeds off WSA and migrates to Gabon breeding grounds.

Additional models

MODEL V

Allocates the Angolan catches (otherwise allocated 50% to Gabon and 50% to WSA for the reference case) to the catches off WSA. The model has stock B2 breeding off Angola, and splits this into two sub-stocks ($B2^{W}$ and $B2^{E}$) where only the latter visits the area off WSA to which capture-recapture data relate. Some proportion of the $B2^{E}$ population migrates to the Antarctic.

MODEL 0

Assumes a single breeding stock B. This model differs from Model III in that no distinction is made between Gabon and WSA, and only the Gabon capture-recapture data and abundance estimate are incorporated in the assessment. No split is made between the Gabon and WSA catches.

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Annex D

Genetic evaluation of the connectivity between BSB and BSC and their Antarctic feeding grounds

J. Loo, C. Pomilla, I. Carvalho, M. Leslie, T. Collins, S. Cerchio, M. Méndez, B. Best, M. Engel, P, Ersts, K. Findlay, S. Bonatto, P, Kotze, M. Meyer, J. Barendse, M. Thorton, Y. Razafindrakoto, S. Ngouessono, M. Vely, J. Kiszka and H. Rosenbaum.

Connectivity between Breeding Stocks B and C and Antarctic feeding grounds was evaluated using mitochondrial DNA (mtDNA) and microsatellite analyses under different catch allocation models. In addition, mixed-stock analyses are performed to investigate breeding stocks contribution to feeding grounds.

METHODS

Samples representing 3,330 individuals were collected from the Southeastern Atlantic (BSB) and Southwestern Indian Oceans (BSC): including Gabon and Angola (n=1,506), West South Africa (n=251), Mozambique and East South Africa (n=207), the Comoros Archipelago (n=80) and Madagascar (n=1,286). Most sample collection took place during the austral winter from July to September. All Antarctic samples were provided the IWC (189 individuals, Table 1). These range between 30°W and 70°E and were collected by IDCR/ SOWER cruises on an opportunistic basis during sighting surveys in Antarctic and sub-Antarctic waters. Collections took place mostly during the core feeding season between January and February.

A 550bp fragment of the mtDNA control region was amplified and sequenced according to methods described previously (Rosenbaum et al., 2009). A set of 10 microsatellite loci, which have proven to be polymorphic in humpback whales, were also amplified: 199/200, 417/418, 464/465 (Schlötterer et al., 1991); EV1Pm, EV37Mn, EV94Mn, EV96Mn (Valsecchi and Amos, 1996); and GATA028, GATA053, GATA417 (Palsbøll et al., 1997) using standard methods. Microsatellite alleles were identified by their sizes in base pairs using GENOTYPER v2.1 and GENEMAPPER v4.1 (Applied Biosystems, Inc). GENALEX v5.1 (Peakall and Smouse, 2006) was used to detect duplicate samples within each population and to calculate the average probability of two different individuals sharing the same multilocus genotype by chance. To reduce the rate of genotyping errors, specific guidelines were used during laboratory and scoring procedures.

- (1) Given the elevated number of samples, automation was introduced whenever possible during PCR setup and manipulation of genomic DNA or PCR products.
- (2) Negative controls were run at the PCR step to control for exogenous contamination.

Two previously typed samples were added to each amplification and subsequent analyses as a reference, and the presence of null alleles was monitored comparing the genotypes of known mother-offspring pairs. Scoring was automated in GENOTYPER 2.1 and GENEMAPPER 4.1, and allele sizing was successively checked by hand. Finally, samples that yielded ambiguous allele peaks were repeated. Genotypic error was estimated as described in Cerchio *et al.* (2009).

Mixed stock analyses of 10 microsatellite loci and mtDNA were conducted using the Statistical Program for Analysing Mixtures (SPAM 3.7b), which uses a maximum-likelihood approach that compares mixed areas directly with 'source' (or baseline) areas. Three main scenarios were evaluated, including two (Scenarios 1 and 3) suggested by the IWC Scientific Committee (IWC, 2011).

- Scenario 1: Gabon (B1) and West South Africa (B2) were assumed to represent two discrete breeding substocks mixing in a common feeding area in the Antarctic. B1 and B2 were assumed to be source stocks and their contributions to B nucleus feeding area (mixed stock) were estimated.
- Scenario 2: similar to the first, except that BSC regions are added as source stocks.
- Scenario 3: B nucleus feeding area and B2 are assumed to represent two discrete feeding grounds (source stocks), sharing a common breeding ground, Gabon (mixed stock).

For each scenario, two separate feeding ground configurations were used: (a) only the B nucleus area $(10^{\circ}W-10^{\circ}E)$; and (b) the B nucleus area combined with the B/C area as defined in Hypothesis 1 ($10^{\circ}E-30^{\circ}E$).

RESULTS AND CONCLUSIONS

Under all scenarios and feeding ground configurations, preliminary results based on microsatellite data indicate that B1 is the largest contributor to the B Nucleus feeding area (10°W-10°E), whereas there is little contribution from B2 (<6% in all cases). MtDNA results also show B1 as the largest contributor to the B Nucleus feeding area. However, the contribution from other source stocks becomes larger.

In the scenario of multiple breeding stocks mixing on a common feeding ground, preliminary microsatellite results strongly link B1 with the B Nucleus feeding area, with little contribution from B2. However, results based on mtDNA show a larger contribution not only from B2 but also from BSC1 and BSC3. Under Scenario 3, microsatellite data indicated that B1 is almost entirely composed of individuals from the Antarctic B Nucleus feeding area, whereas mtDNA data allocated a considerable part of B1 to B2.

The difference between the microsatellite and mtDNA datasets are likely attributed to the resolution and informativeness of the respective markers for assignment. Haplotypes are a single marker, and therefore represent a more coarse assessment for mixed stock analyses. Conversely, the 10 microsatellite genotypes per individual offer a far greater degree of variability with which to represent population variation in a mixed stock analysis. Often (though not always), different genetically distinct groups (populations or sub-stocks) share common haplotypes at different frequencies. Microsatellites often

Nucleus (nuc)/ margin (mar)	Hypoth	nesis X	Hypotl	nesis 1	Hypothesis 2	
		<i>n</i> =189	_	<i>n</i> =176		<i>n</i> =177
3	30°W-20°E	159	10°W-10°E	110	10°W-10°E	110
B/C	N/A	N/A	10°E-30°E	36	10°E-40°E	44
С	30°E-60°E	30	30°E-60°E	30	40°E-70°E	23

Table 2

 Table 1

 Distribution of humpback whales on the feeding grounds under Allocation Hypotheses 1 and 2

	Microsate	llite	MtDNA			
Scenario	Source stocks	Mixed stock	Source stocks	Mixed stock		
Scenario 1a*	B1 and B2	10°W-10°E (B)	B1 and B2	10°W-10°E (B)		
	B1	54.62% (0.0388)	B1	69.77% (0.1305)		
	B2	0.01% (0.0000)	B2	27.50% (0.1305)		
	Unknown	45.37%	Unknown	2.73%		
Scenario 1b	B1 and B2	10°W-30°E (B+BC)	B1 and B2	10°W-30°E (B+BC)		
	B1	58.70% (0.0379)	B1	69.12% (0.1056)		
	B2	0.45% (0.0003)	B2	27.45% (0.1056)		
	Unknown	40.85%	Unknown	3.42%		
Scenario 2a	B1, B2, C1-C3	10°W-10°E (B)	B1, B2, C1-C3	10°W-10°E (B)		
	B1	74.75% (0.0646)	B1	46.99% (0.4699)		
	B2	1.36% (0.0012)	B2	14.95% (0.1243)		
	C1	0.00% (0.0000)	C1	15.61% (0.1277)		
	C2	4.37% (0.0038)	C2	0% (0.0000)		
	C3	0.07% (0.0001)	C3	20.63% (0.1151)		
	Unknown	19.44%	Unknown	1.82%		
Scenario 2b	B1, B2, C1-C3	10°W-30°E (B+BC)	B1, B2, C1-C3	10°W-30°E (B+BC)		
	B1	72.66% (0.0556)	B1	33.80% (0.1043)		
	B2	5.24% (0.0040)	B2	9.63% (0.0963)		
	C1	0.00% (0.0000)	C1	25.52% (0.1256)		
	C2	2.92% (0.0022)	C2	0% (0.0000)		
	C3	0.07% (0.0017)	C3	28.99% (0.1104)		
	Unknown	16.90%	Unknown	2.05%		
Scenario 3a*	B Nuc, B2	B1	B Nuc, B2	B1		
	10°W-10°E (B)	80.8% (0.0187)	10°W-10°E (B)	72.25% (0.0488)		
	B2	0.01 % (0.0000)	B2	20.85% (0.0048)		
	Unknown	19.19%	Unknown	6.89%		
Scenario 3b	(B Nuc+BC Mar), B2	B1	(B Nuc+BC Mar), B2	B1		
	10°W-30°E (B+BC)	92.29% (0.0228)	10°W-30°E (B+BC)	58.42% (0.0053)		
	B2	0.01 % (0.0000)	B2	31.02% (0.0534)		
	Unknown	7.70%	Unknown	10.56%		

have more genetic variability, particularly across multiple loci. As a consequence of greater variation, population patterns of microsatellite variability can be complex, and thus MSA procedures may have a more difficult time confidently assigning some individuals, which results in a higher percentage of unknowns in the mixture. This may be a consequence of the complexity of the marker, or may indicate a missing reference population in the sample. MtDNA haplotypes represent maternal lineages and are most effective for discerning patterns of matrilineal structure and geographic fidelity; conversely nuclear microsatellites are bi-parentally inherited and thus represent behaviour and genetic mixtures of both sexes. With all these considerations, we believe that the microsatellite markers may in fact provide the more accurate assessment of mixture compositions.

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Annex E

Results of Sensitivity Analysis and Diagnostic Plots for BSB Assessment Models

Reference cases and sensitivity analyses illustrated in this Annex are specified under Item 2.3 of the report.

Table 1

Results for Reference case and Sensitivity C applied to Model 0. The reference case uses male-only microsatellite data all sites in Gabon as input in the capture-recapture model component. Sensitivity C implements photo-identification fluke data instead of microsatellite data. Sensitivity E implements a struck-and-lost rate of 0.15. Posterior median values are given along with their 90% probability intervals. Note that for Model 0 and its sensitivities only capture-recapture data from Gabon have been used, and none from WSA.

Model 0	Aodel 0 Reference case		Sensitivity C		Sensitivity E		
r	0.045	[0.006, 0.081]	0.051	[0.009, 0.072]	0.047	[0.012, 0.080]	
Κ	24,072	[19,686, 40,980]	22,906	[20,385, 36,697]	25,482	[22,101, 36,142]	
N _{min}	1,921	[603, 7,822]	1,158	[571, 5,161]	1,629	[600, 5,457]	
N_{2005}	9,484	[7,581, 11,849]	7,125	[5,735, 8,881]	9,549	[7,465, 12,221]	
N ₂₀₁₀ /K	0.467	[0.229, 0.711]	0.376	[0.194, 0.544]	0.447	[0.262, 0.657]	
N_{2040}/K	0.93	[0.272, 0.999]	0.916	[0.253, 0.994]	0.933	[0.414, 0.998]	

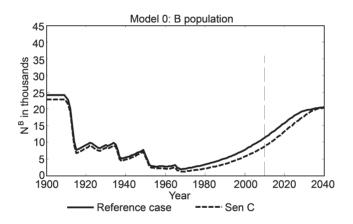


Fig. 1. Median population trajectories estimated by the reference case and Sensitivity C for Model 0. Projections after 2010 assume zero catches.

Table 2

Assessment model outputs for Model IIa sensitivity analysis. Ref: reference case. Sensitivity (Sen) B.4 allocates 75% of the Angolan catches to whales
from Gabon and 25% to whales from WSA. Sensitivity C uses fluke data rather than microsatellite data for Gabon and WSA. Sensitivities D1 and D2
implement a value of, respectively, 0.5 and 0.9 for parameter X (proportion of pristine abundance of substock B1 migrating offshore, B1W). Sen E:
Struck-and-lost rate of 0.15. Posterior median are given along with the 90% probability intervals.

		B1		B2		B1W		B1E
r								
Ref	0.053	[0.010, 0.097]	0.043	[0.005, 0.078]		r ^{B1}		r ^{B1}
Sen B4	0.066	[0.021, 0.103]	0.042	[0.003, 0.085]		r ^{B1}		r^{B1}
Sen C	0.071	[0.015, 0.102]	0.036	[0.003, 0.071]		r ^{B1}		r^{B1}
Sen D1	0.075	[0.042, 0.104]	0.046	[0.005, 0.082]		r ^{B1}		r ^{B1}
Sen D2	0.042	[0.005, 0.093]	0.037	[0.005, 0.074]		r ^{B1}		r^{B1}
Sen E	0.045	[0.007, 0.092]	0.037	[0.004, 0.078]		r^{BI}		r ^{B1}
Κ								
Ref	18,732	[13,595, 36,551]	4,293	[224, 6,627]	13,113	[9,516, 25,586]	5,620	[4,078, 10,965]
Sen B4	18,951	[15,682, 31,000]	2,279	[49, 3,902]	13,266	[10,977, 21,700]	5,685	[4,704, 9,300]
Sen C	16,110	[13,182, 31,894]	4,988	[1,125, 7,076]	11,277	[9,228, 22,326]	4,833	[3,955, 9,568]
Sen D1	18,159	[15,329, 24,508]	2,226	[63, 3,976]	9,080	[7,665, 12,254]	9,080	[7,665, 12,254]
Sen D2	18,414	[12,320, 35,765]	6,782	[5,132, 8,588]	16,573	[11,088, 32,188]	1,841	[1,232, 3,576]
Sen E	21,723	[15,205, 41,935]	4,835	[223, 7,832]	15,206	[10,644, 29,354]	6,517	[4,562, 12,580]
N _{min}								
Ref	1,532	[367, 6,604]	69	[25, 172]	1,532	[366, 6,404]	1	[0, 151]
Sen B4	998	[280, 4,396]	65	[16, 139]	987	[277, 4,268]	3	[0, 143]
Sen C	605	[202, 4,051]	75	[27, 199]	605	[199, 4,001]	1	[0, 31]
Sen D1	730	[279, 2,089]	49	[11, 95]	719	[277, 2,042]	5	[0,75]
Sen D2	2,230	[471, 7,947]	88	[27, 262]	2,225	[471, 7,947]	0	[0, 8]
Sen E	1,944	[422, 7,517]	85	[25, 219]	1,929	[416, 7,379]	2	[0, 165]
N ₂₀₁₀ /K								
Ref	0.607	[0.252, 0.893]	0.106	[0.033, 0.980]	0.866	[0.355, 1.270]	0.002	[0.000, 0.036]
Sen B4	0.630	[0.323, 0.856]	0.179	[0.038, 1.000]	0.894	[0.451, 1.211]	0.008	[0.000, 0.052]
Sen C	0.571	[0.234, 0.771]	0.073	[0.023, 0.314]	0.812	[0.331, 1.100]	0.002	[0.000, 0.040]
Sen D1	0.672	[0.428, 0.865]	0.167	[0.021, 0.999]	1.328	[0.833, 1.724]	0.010	[0.000, 0.044]
Sen D2	0.588	[0.272, 0.929]	0.063	[0.034, 0.113]	0.653	[0.302, 1.028]	0.000	[0.000, 0.024]
Sen E	0.505	[0.225, 0.813]	0.089	[0.032, 0.999]	0.719	[0.317, 1.152]	0.002	[0.000, 0.030]

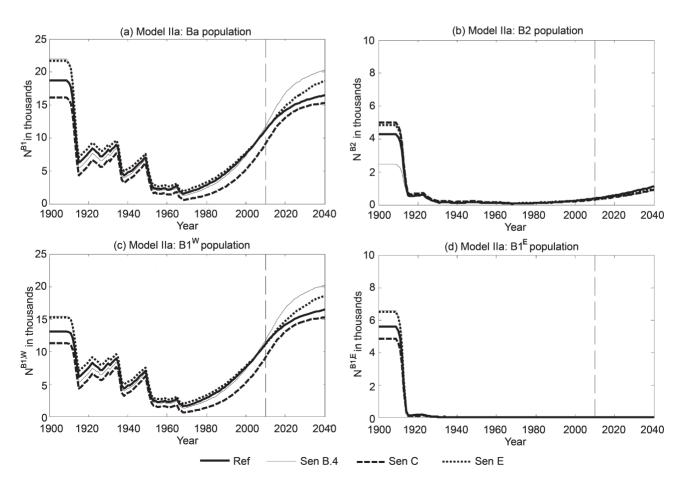


Fig. 2. Model IIa and sensitivities. Sen B.4, C and E.

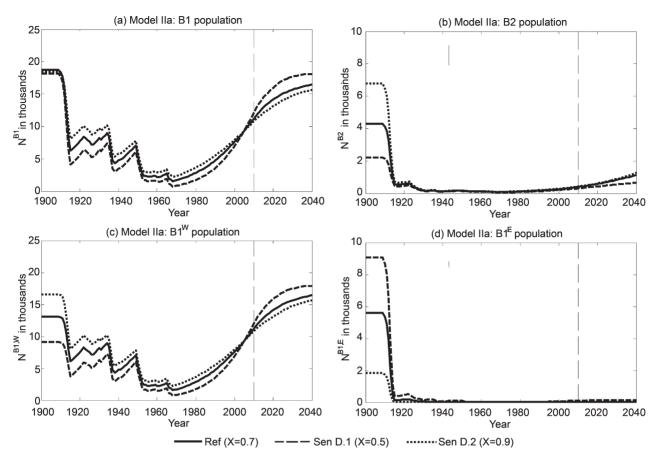


Fig. 3. Model IIa and sensitivities. Sen D.1 and D.2.

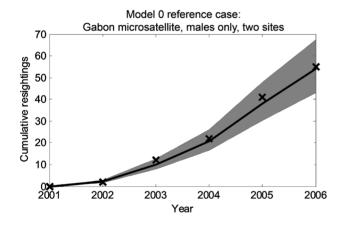


Fig. 4. Model IIa fits to the Gabon capture-recapture microsatellite data for the Model 0 reference case. The observed cumulative resightings are represented by the 'x's and the model predicted values correspond to the solid line. The 90% probability envelope is given by the shaded region.

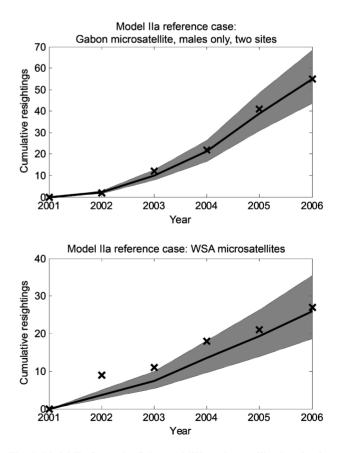


Fig. 5. Model IIa fits to the Gabon and WSA microsatellite data for the reference case. The observed cumulative resightings are given by the 'x's and the model predicted values are given by the solid line. The 90% probability envelope is given by the shaded region.