

**The Fourth intersessional workshop on the review of maximum sustainable yield rates (MSYR) in baleen whales**

## Contents

1	Introductory items .....	2
1.1	Welcoming remarks .....	2
1.2	Election of Chair .....	2
1.3	Appointment of rapporteurs .....	2
1.4	Adoption of Agenda .....	2
1.5	Review of documents.....	2
2	Progress since Annual Meeting in relation to the Workplan.....	2
2.1	Overview of present methods.....	2
2.2	Refinement of population model used to estimate variability parameters.....	3
2.3	Coding of methods that generate variability in survival rate.....	3
3	Estimates of $r$ and associated variability (reproductive component) .....	3
3.1	Update of estimates .....	3
4	Methods specifying variability in survival.....	5
5	The $r_0/r_{\max}$ distribution .....	6
5.1	Estimates of the $r_0/r_{\max}$ distribution.....	6
5.2	Approaches to relate the $r_0/r_{\max}$ distribution to an appropriate MSYR range.....	10
6	Recommendations for the Scientific Committee .....	10
7	Workplan until Scientific Committee meeting.....	11
8	Adoption of report .....	11

## FOURTH MSYR WORKSHOP

The Workshop took place at the Southwest Fisheries Science Center, La Jolla, USA, from 26-28 March 2013. The list of participants is given as Annex A.

### 1 INTRODUCTORY ITEMS

#### 1.1 Welcoming remarks

Butterworth (Convenor) welcomed participants to the Workshop. Since 2007, the Committee has been discussing maximum sustainable yield rate (MSYR) in the context of a general reconsideration of the plausible range to be used in population models used for testing the *Catch Limit Algorithm (CLA)* of the RMP (IWC, 2008; 2009a; 2009b; 2010a; 2010b; 2010c; 2011a; 2011b; 2012). The current range is 1% to 7%, in terms of the mature component of the population. At the 2012 Annual Meeting, the Committee had expressed concern that once again the process had not been completed and it carefully examined whether it was worth continuing the process. Given progress made at that meeting and the workplan developed, the Committee had agreed that one more year be allocated for the MSYR Review, but that if it could not be completed at the 2013 meeting, the current range of MSYR rates would be retained (IWC, 2013b; 2013c).

Butterworth thanked the hosts, the National Marine Fisheries Service for making their facilities available, and especially Weller for assisting in the meeting organisation. Weller explained the logistical arrangements for the Workshop.

#### 1.2 Election of Chair

Donovan was elected Chair.

#### 1.3 Appointment of rapporteurs

Butterworth and Punt served as rapporteurs with the assistance of the Chair.

#### 1.4 Adoption of Agenda

The adopted Agenda is given as Annex B.

#### 1.5 Review of documents

A list of the documents prepared for the Workshop is given as Annex C.

### 2 PROGRESS SINCE ANNUAL MEETING IN RELATION TO THE WORKPLAN

Not as much progress had been made prior to the Workshop as had been anticipated in the workplan agreed at the 2012 Annual Meeting (IWC, 2013b). However, sufficient progress had been made to hold the Workshop.

#### 2.1 Overview of present methods

The approach agreed at the 2012 Annual Meeting (IWC, 2013b) involves developing a posterior distribution for the quantity  $r_0/r_{\max}$ , i.e. the ratio of the increase rate in the limit of zero population size to the maximum rate of increase of a whale stock which is demographically possible. The value for  $r_{\max}$  for each stock is computed from values for adult survival rate, calf survival rate, fecundity rate (female calves per mature female) and the age-at-first-parturition. The subsequent analysis is based on the application of a Bayesian hierarchical model in which  $r_0/r_{\max}$  is assumed to be interchangeable among stocks and beta-distributed. The parameters of the beta distribution are assumed to be U[0,10]. The data agreed at that time for inclusion in the likelihood function were the estimates of rates of increase for 15 stocks, while the variances of the model estimates of the rates of increase combined sampling error and 'process error'. 'Process error' is the variation in the true value for  $r_0/r_{\max}$  caused by environmental variation. The estimates of the extent of process error depend on the number of years for which data are available to estimate  $r_0$ , the true value for  $r_0/r_{\max}$  (lower for values of  $r_0/r_{\max}$  close to 1 in terms of the model used for the effects of environmental variability (Cooke, 2007a)), and the extent of environmentally-induced variation (and its autocorrelation) in the rate of increase.

Punt (2012) describes the model used to determine the extent of process error in  $r_0/r_{\max}$ . The key inputs to this model are  $r_0/r_{\max}$  and the variation and temporal autocorrelation in the annual rate of increase. The values for these parameters for each stock are derived from a population dynamics model which is parameterized in terms of adult survival rate, calf survival rate, fecundity rate, and the age-at-first-parturition, as well as the variation and temporal autocorrelation in the fecundity.

In discussion, it was noted that assuming U[0,10] hyperpriors on the two hyperparameters ( $\alpha$ ,  $\beta$ ) of the beta distribution for the rate of increase is not non-informative regarding  $r_0/r_{\max}$ , i.e. the posterior for  $r_0/r_{\max}$  when there

are no data is not flat across the range 0-1. Kitakado determined that a prior on the logarithms of  $\alpha$  and  $\beta$  from 0 to 3.3 implied an approximately uniform prior on  $r_0/r_{\max}$ , and the Workshop consequently **agreed** to replace the U[0,10] hyperpriors on  $\alpha$  and  $\beta$  by U[0,3.3] hyperpriors on  $\ln\alpha$  and  $\ln\beta$ .

## 2.2 Refinement of population model used to estimate variability parameters

Punt reported that the population dynamics model used to calculate the extent of variation and temporal autocorrelation in the annual rate of increase had been modified to impose the constraint that females which had calves which survived their first year cannot give birth in successive years (common and Antarctic minke whales usually give birth every year but are not included in the meta-analysis). In discussion, it was noted that females of some species (e.g. humpback and fin whales) do occasionally give birth in successive years while the inter-calving intervals for other species (e.g. right whales) can be a mixture of two, three and more years.

## 2.3 Coding of methods that generate variability in survival rate

Punt reported that an option had been added to the software developed to implement the meta-analysis that allows for variation in natural mortality rather than fecundity. This involves selecting the central value for natural mortality and the variance parameter for log-normal variation in natural mortality so that the expected rate of increase and its variation match pre-specified values. The Workshop noted that ideally account should be taken of correlation between natural mortality and fecundity; this is discussed further under Item 4.

Table 1

Estimates of rates of increase used as  $r_0$  and the associated time periods over which they were estimated based upon the review provided in IWC (2010a) apart from for southern right whales which was based upon IWC (2013a). The main reference is given for each population but a fuller discussion of depletion and reliability can be found in the two reports. L=low; M=medium; H=high.

	Population level	Reliability of data	$r_0$ (%) (95% CI)	SE	Time period	Year-span	Refs
<b>Blue whale</b>							
Central N Atlantic	L	H	9.0 (2.0, 17.0)	3.83	1987-2001	15	(Pike <i>et al.</i> , 2007)
S Hemisphere	L	H	8.2 (1.6, 14.8)	3.37	1978/9-2003/4	26	(Branch, 2007)
EN Pacific	L	H	3.2	1.4	1991-2005	16	(Calambokidis <i>et al.</i> , 2007)
<b>Fin whale</b>							
N Norway	L	H	5 (-13, 26)	9.95	1988-98	11	(Vikingsson <i>et al.</i> , 2007)
EN Pacific	L	H	4.8 (-1.6, 11.1)	3.24	1987-2003	15	(Zerbini <i>et al.</i> , 2006)
<b>Humpback whale</b>							
W Australia	L	H	10.1 (0.9, 19.3)	4.69	1982-94	13	(Bannister and Hedley, 2001)
E Australia	L	H	10.9 (10.5, 11.4)	0.23	1984-2007	24	(Noad <i>et al.</i> , 2008)
EN Pacific	L	H	6.4	0.9	1992-2003	12	(Calambokidis and Barlow, 2004)
Hawaii	L	H	10 (3-16)	3.32	1993-2000	18	(Mizroch <i>et al.</i> , 2004)
<b>Bowhead whale</b>							
B-C-B	M	H	3.9 (2.2, 5.5)	0.84	1978-2001	24	(Zeh and Punt, 2005)
<b>Southern right whale</b>							
SE Atlantic (S Africa)	L	H	6.8 (6.4, 7.2)	0.2	1979-2010	32	(Brandão <i>et al.</i> , 2011)
SW Atlantic (Argentina)	L	H	6.0 (5.5, 6.6)	0.28	1971-2010	40	(Cooke <i>et al.</i> , 2001)
SE Indian (Australia)	L	H	6.6 (3.8, 9.3)	1.40	1993-2010	18	(Bannister, 2011)

## 3 ESTIMATES OF $r$ AND ASSOCIATED VARIABILITY (REPRODUCTIVE COMPONENT)

### 3.1 Update of estimates

The Workshop briefly reviewed the previous work and agreements on appropriate data sources to use, in particular estimates of rates of increase to use as  $r_0$  equivalents in the meta-analysis, and values for calving rates used in the calculation of  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$  (the standard deviation and temporal autocorrelation in fecundity) using the agreed method (Brandon and Kitakado, 2011; Cooke, 2011b)<sup>1</sup>.

With respect to the former, the Workshop **agreed** that in order to satisfy the condition that the observed rates of increase could be used to approximate  $r_0$ , it would limit the stocks included in the meta-analysis to those that had been depleted to 'low' levels (less than about 30% of initial, based on discussions in IWC (2010a)), apart from the Bering-Chukchi-Beaufort Seas stock of bowhead whales which was classified as 'medium' although it may

<sup>1</sup> The  $\sim$  notation here is used to signify that these estimates are derived from the actual data. Without the  $\sim$ , these symbols signify equivalent values used in the environmental variation population dynamics model of Cooke (2007) – see Adjunct A of Appendix 2 of IWC (2013c).

FOURTH MSYR WORKSHOP

have been ‘low’ at the start of the series. Given concerns about the relationship between feeding aggregations and the remainder of the stock, the Workshop also **agreed** to exclude western North Pacific gray whales and Gulf of Maine humpback whales from the meta-analysis. The final list of stocks included in the meta-analysis is given in Table 1.

As part of its discussions and decisions, the Workshop took into account SC/M13/MSYR1, which investigated the potential for biases in the estimates of the annual variation in the average birth rates of baleen whale populations based on the report of the 2010 workshop (IWC, 2010a). In particular, it examined the appropriateness of the geographical and temporal scales of the data collections, as well as indications for other sources of additional variation and categorised the data quality.

Originally, the values for the demographic parameters were based on estimates for individual stocks (IWC, 2011a). However, given the paucity of direct data, especially for some of the stocks for which  $r_0$  values were available, and the fact that the values are not that well-determined such that differences in point estimates amongst different stocks within the same species are probably not meaningful, the Committee agreed its 2012 meeting (IWC, 2013c) to combine some estimates within certain species groups to set all equal to a rounded figure. At the Workshop, this process was taken to its natural conclusion by agreeing single estimates for each species (Table 2). These rounded values were based on the estimates listed in IWC (2012), except that values for different stocks for southern right whales were taken from updated values provided in IWC (2013a).

Table 3 lists the percentiles of the posterior distributions of  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$  based on the meta-analysis of annual calving rates (IWC, 2012) while Table 4 summarises the input values for the reference case.

Table 2

Values of demographic parameters used to calculate  $r_{max}$  on a per-species basis.  $S$  is the annual adult survival rate, assumed to apply from age 1 and above;  $S_1$  is the survival rate for the first year of life which is assumed to equal  $S^2$ ,  $a_{fp}$  is the age at first parturition,  $f$  is the highest fecundity considered possible, and  $r_{max}$  is the corresponding exponential growth rate in steady unexploited conditions.

	$S$	$S_1$	$a_{fp}$	$f$	$r_{max}$
Blue whale	0.98	0.96	5	0.5	0.114
Fin whale	0.98	0.96	5	0.5	0.114
Humpback whale	0.97	0.941	5	0.5	0.103
Bowhead whale	0.99	0.98	22	0.33	0.043
Southern right whale	0.99	0.98	8	0.33	0.076

Table 3

Percentiles of the posterior distributions of  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$  based on the meta-analysis of annual calving rates (IWC, 2012). The values in bold-underline typeface are used in the reference case meta-analysis of rate of increase.

Species	Stock	Percentiles										
		1	2.5	5	10	25	50	75	80	95	97.5	99
<b>Sigma</b>												
Blue	EN Pacific	0.020	0.037	0.056	0.093	0.188	<b><u>0.380</u></b>	0.607	0.857	1.028	1.183	1.386
Bowhead	BCB	0.578	0.618	0.663	0.721	0.835	<b><u>0.995</u></b>	1.189	1.413	1.555	1.668	1.778
Fin	Gulf of St Lawrence	0.034	0.069	0.125	0.235	0.455	<b><u>0.765</u></b>	1.088	1.363	1.532	1.662	1.800
Gray	Eastern	0.013	0.027	0.044	0.079	0.174	0.378	0.727	1.199	1.440	1.626	1.786
Humpback	Gulf of Maine	0.044	0.072	0.094	0.117	0.161	0.209	0.264	0.330	0.379	0.423	0.515
Humpback	Gulf of St Lawrence	0.020	0.037	0.060	0.092	0.175	0.294	0.427	0.566	0.668	0.748	0.869
Humpback	SE Alaska	0.006	0.012	0.019	0.034	0.075	<b><u>0.135</u></b>	0.214	0.309	0.398	0.489	0.636
Right	SE Atlantic	0.002	0.004	0.006	0.011	0.023	<b><u>0.042</u></b>	0.068	0.100	0.136	0.205	0.395
Right	SW Atlantic	0.213	0.226	0.237	0.251	0.277	<b><u>0.308</u></b>	0.344	0.383	0.408	0.435	0.469
Right	N. Atlantic	0.143	0.179	0.208	0.241	0.298	0.366	0.444	0.532	0.599	0.667	0.761
<i>Generic</i>		<i>0.010</i>	<i>0.027</i>	<i>0.045</i>	<i>0.077</i>	<i>0.179</i>	<i>0.371</i>	<i>0.710</i>	<i>1.100</i>	<i>1.340</i>	<i>1.561</i>	<i>1.737</i>
<b>Rho</b>												
Blue	EN Pacific	-0.941	-0.902	-0.860	-0.790	-0.575	<b><u>-0.181</u></b>	0.291	0.646	0.818	0.906	0.961
Bowhead	BCB	-0.672	-0.566	-0.472	-0.373	-0.167	<b><u>0.065</u></b>	0.309	0.509	0.602	0.672	0.748
Fin	Gulf of St Lawrence	-0.737	-0.569	-0.351	-0.117	0.281	<b><u>0.636</u></b>	0.800	0.882	0.914	0.936	0.956
Gray	Eastern	-0.934	-0.862	-0.772	-0.627	-0.312	0.093	0.458	0.714	0.838	0.925	0.971
Humpback	Gulf of Maine	-0.952	-0.924	-0.888	-0.825	-0.677	-0.412	-0.054	0.225	0.389	0.516	0.634
Humpback	Gulf of St Lawrence	-0.940	-0.887	-0.799	-0.674	-0.414	-0.002	0.440	0.727	0.838	0.910	0.959
Humpback	SE Alaska	-0.943	-0.861	-0.702	-0.473	-0.119	<b><u>0.320</u></b>	0.729	0.904	0.948	0.972	0.986
Right	SE Atlantic	-0.895	-0.783	-0.642	-0.481	-0.169	<b><u>0.169</u></b>	0.575	0.898	0.966	0.990	0.998
Right	SW Atlantic	-0.546	-0.478	-0.417	-0.339	-0.220	<b><u>-0.074</u></b>	0.074	0.222	0.315	0.396	0.514
Right	N. Atlantic	-0.746	-0.526	-0.380	-0.237	-0.027	0.195	0.409	0.593	0.683	0.758	0.839
<i>Generic</i>		<i>-0.953</i>	<i>-0.895</i>	<i>-0.807</i>	<i>-0.656</i>	<i>-0.307</i>	<i>0.076</i>	<i>0.421</i>	<i>0.696</i>	<i>0.816</i>	<i>0.881</i>	<i>0.945</i>

FOURTH MSYR WORKSHOP

Table 4

Summary of the values for the reference case to be used in the meta-analysis. The values in bold-underline typeface are taken from estimates that pertain to the stock in question; other values are assigned from stocks of the same species listed in Table 3.

	$r_0$ (%) (SE)	Year-span	$r_{max}$	$\tilde{\sigma}_f$	$\tilde{\rho}_f$
<b>Blue whale</b>					
Central N Atlantic	9.0 (3.83)	15	0.114	0.380	-0.181
S Hemisphere	8.2 (3.37)	26	0.114	0.380	-0.181
EN Pacific	3.2 (1.4)	16	0.114	<b><u>0.380</u></b>	<b><u>-0.181</u></b>
<b>Fin whale</b>					
N Norway	5 (9.95)	11	0.114	0.765	0.636
EN Pacific	4.8 (3.24)	15	0.114	0.765	0.636
<b>Humpback whale</b>					
W Australia	10.1 (4.69)	13	0.103	0.135	0.320
E Australia	10.9 (0.23)	24	0.103	0.135	0.320
EN Pacific	6.4 (0.9)	12	0.103	<b><u>0.135</u></b>	<b><u>0.320</u></b>
Hawaii	10 (3.32)	18	0.103	0.135	0.320
<b>Bowhead whale</b>					
B-C-B	3.9 (0.84)	24	0.043	<b><u>0.995</u></b>	<b><u>0.065</u></b>
<b>Southern right whale</b>					
SE Atlantic (S African)	6.8 (0.2)	32	0.076	<b><u>0.042</u></b>	<b><u>0.169</u></b>
SW Atlantic (Argentinian)	6.0 (0.28)	40	0.076	<b><u>0.308</u></b>	<b><u>-0.074</u></b>
SE Indian (Australian)	6.6 (1.40)	18	0.076	<b><u>0.042</u></b>	<b><u>0.169</u></b>

4 METHODS SPECIFYING VARIABILITY IN SURVIVAL

Cooke (2011a) addressed correlation between variability in reproductive rates and in survival rates. If the correlation is positive, these two sources of variability will compound each other with regard to the variability in net recruitment rate. The model developed by Cooke (2011a) assumes that each individual ‘chooses’ how much of the available energy to allocate to reproduction, so as to maximise the sum of survival and reproduction. The available energy varies with environmental conditions. When the available energy is low, the optimal choice is not to reproduce at all.

Explorations of the model by the author over a range of parameters that are plausible for whales showed that the correlation between survival and reproduction is positive at higher energy levels, but can, in the absence of individual variability, become negative at lower levels, because the survival rate of parents is higher when the energy is not quite enough for reproduction than when it is just enough for reproduction. However, when individual variability is introduced, the population average correlation between reproduction and survival becomes positive for all the parameter combinations considered. This is because, in the presence of individual variation, the population proportion of individuals that reproduce varies smoothly with the average available energy, even though the relationship is non-smooth for each individual. The author considered that a substantial level of individual variation in whales is likely, because, in the few cases which have been studied, there are considerable individual differences in the choice of prey or feeding ground.

The Workshop **agreed** that positive correlation between survival rate and reproduction was the most likely case, but **agreed** to include the cases of negative, zero and positive correlation in the meta-analysis as sensitivity checks, consistent with the view of the Scientific Committee (IWC, 2013c).

The Workshop noted that the analysis requires not only the correlation between survival and reproduction to be specified but also the absolute level of variability in survival (or mortality). Cooke **agreed** to further explore the plausible parameter space for the model in (Cooke, 2011a), with a view to determining the plausible range of variability in survival, and to present the findings to the 2013 Scientific Committee meeting. If this is not successful, the conclusions will continue to be based on sensitivity tests which assume that mortality and reproduction contribute in equal measure to the variation in the net recruitment rate.

SC/M13/MSYR2 described an individual based model for a whale population based on standard energetic relationships. The model uses a detailed energy budget to simulate whale reproductive success and mortality in an environment where food has a patchy spatial distribution. The major processes of an animal’s seasonal activities are modelled, including migration, breeding and feeding. Animals have to search for food, and look for new food patches when local food abundance falls due to the effects of local intra-specific competition and stochastic variability.

SC/MM13/MSYR2 gave examples from the model of relationships between the values of the annual births, which were subject to variation due to stochastic prey availability (as characterised here by  $\tilde{\sigma}_f$ ), and additional deaths. Additional deaths are those due to shortages of prey, and hence that are not taken into account in the minimum

mortality arising from the lower bound on natural mortality. The model led to similar predictions to those in Cooke (2013) that there is a positive correlation between survival rate and birth-rate in stochastic variability in prey abundance. The paper also demonstrated how the model could be used to develop an emulator of the model outputs that would produce additional deaths as a function of stochastic births at a much lower computational overhead, such that they could be used in existing programs. Setting up the emulator would require tuning the energetics model so that it reproduced the values for  $r_{\max}$ ,  $r_0$  and  $\tilde{\sigma}_f$  given in Tables 1 and 2.

In discussion, another approach was suggested in which the model is used directly to generate the values of  $\sigma_r$  at fixed values of  $r_0/r_{\max}$  after conditioning on the estimated variability in birth rate. The Workshop **encouraged** de la Mare to provide further analysis on both these approaches to the 2013 Annual Meeting, so that they could be used in examining the effects on the meta-analysis arising from combined variability in births and deaths.

Given the absence of data to allow direct estimation of the extent of variability in survival, unlike the situation for variability in reproductive success, the Workshop **agreed** that analyses including variability in the former as well as the latter should be seen as providing robustness tests for the results of analyses taking account of the latter alone.

Following wide ranging discussion regarding the quantification of the extent of variability in survival and its correlation to variability in reproductive success, a set of sensitivity runs which explore the implications variation in natural mortality was **agreed**, the results of which are reported and discussed in the following section.

## 5 THE $r_0/r_{\max}$ DISTRIBUTION

### 5.1 Estimates of the $r_0/r_{\max}$ distribution

The reference case analysis is based on the rate of increase data for the stocks in Table 4. It involves defining the extent of variation in the rate of increase using the environmental model parameterized in terms of the posterior medians for the extent and autocorrelation of variation in fecundity ( $\tilde{\sigma}_f$ ,  $\tilde{\rho}_f$ ) (see Item 3). Note that this reference case only considers variation in fecundity; variation in survival rate is considered only in sensitivity tests. Fig. 1 shows the posterior distribution for the ratio  $r_0/r_{\max}$  for an unknown stock, expressed as a probability density function and as a cumulative probability distribution, as well as the posterior distributions for  $r_0/\hat{r}_0$ , the ratio of the rate of increase relative the observed rate of increase, for each stock.

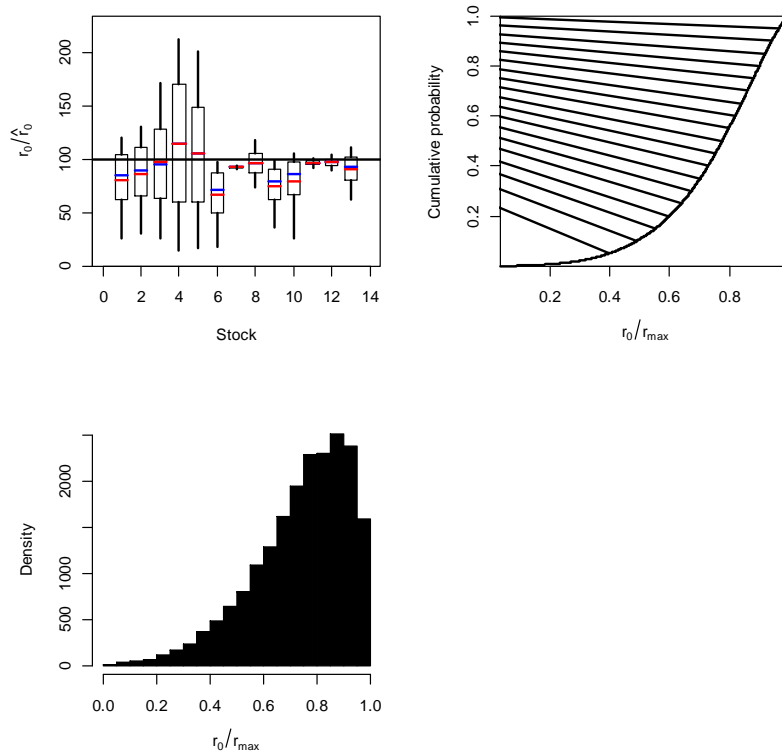


Fig. 1. Posterior distributions for the ratio of  $r_0$  to the observed rate of increase (upper left panel), the cumulative posterior distribution for  $r_0/r_{\max}$  (upper right panel), and the posterior distribution for  $r_0/r_{\max}$ .

Fig. 2 contrasts the sampling distributions for the rate of increase for the 13 stocks, with the posterior distributions for  $r_0$ , illustrating the effect of imposing a prior on  $r_0/r_{\max}$  which has support from 0 to 1. The posterior distributions for stocks for which the sampling distribution for the rate of increase includes values below 0 or above  $r_{\max}$  must differ from the sampling distributions. The posteriors for  $r_0$  for stocks for which environmental variation is estimated to be high are flat because there is little information on  $r_0/r_{\max}$  given high observation and process noise.

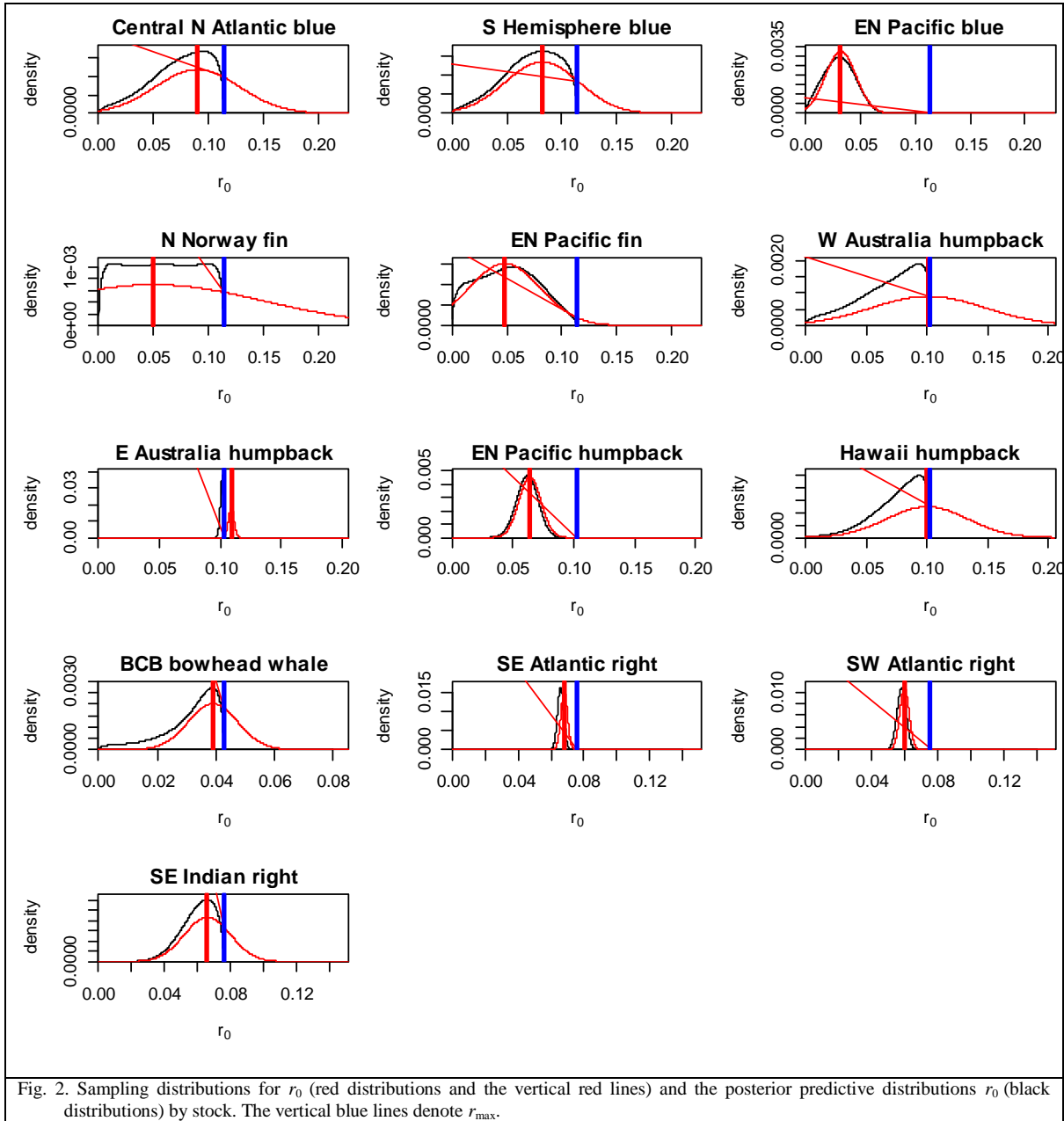


Table 5 lists the lower 5<sup>th</sup> and 10<sup>th</sup> percentiles for  $r_0/r_{\max}$ , along with estimates of  $MSYR_{1+}$  for stocks with the lowest and highest  $r_{\max}$  values in Table 4 (right and blue/fin whales respectively), under the assumptions that (a)  $MSYR_{1+} = r_0/2$  and (b)  $MSYR_{1+} = r_0/1.619$ . The reasons for these choices are explained in the following section.

The sensitivity of the outputs from the meta-analysis to varying the value for  $r_{\max}$  was explored by increasing and decreasing the maximum fecundity rates by 20%. The posterior distribution of for  $r_0/r_{\max}$  is shifted to the left when the  $r_{\max}$  values are increased, and to the right when the  $r_{\max}$  values are decreased. The posterior distributions for  $r_0/\hat{r}_0$  are centered closer to 1 when the values for  $r_{\max}$  are increased because increasing  $r_{\max}$  reduces the impact of the prior assumption that  $r_0 \leq r_{\max}$  (Fig. 3; Table 5b).

Table 5a lists the sensitivity of outputs from the meta-analysis to varying the specifications of the analysis.

- Application of the environment model. The options considered were: (a) ignore the effects of the environment (“No environmental effects” in table 5a), (b) assume that  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$  for all stocks are equal to the medians of the posterior distributions for these parameters for an unknown stock from the meta-analysis conducted by Brandon *et al.* (2012) (“common median  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$ ” in Table 5a), (c) assume that  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$  for each stock are equal to the upper 75%iles of the posterior distributions for these parameters for an unknown stock from the meta-analysis conducted by Brandon *et al.* (2012) (“75%  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$ ” in Table 5a), and (d) assume that  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$  for each stock are equal to the upper 95%iles of the posterior distributions for these parameters for an unknown stock from the meta-analysis conducted by (Brandon *et al.*, 2012) (“95%  $\tilde{\sigma}_f$  and  $\tilde{\rho}_f$ ” in Table 5a).
- Data sets included in the meta-analysis. The options considered were: (a) ignore the data for bowhead whales (“No bowhead whale data” in Table 5a), (b) ignore the data for fin whales (“No fin whale data” in Table 5a), and (c) use only the data for right whales (“Right whale data only”).
- Allowing for variation in natural mortality as well as fecundity. The extent of variation in natural mortality,  $\sigma_M$ , for each stock is selected so that the variance in the rate of increase when there is stochastic natural mortality only matches that when there is stochastic fecundity only (see item 2.3). Three sensitivity tests explore cases in which there is variation in both natural mortality and fecundity: (a) variation in natural mortality and fecundity are independent (“Independent M and F” in Table 5a), (b) variation in natural mortality and fecundity are perfectly positively correlated (“Positive correlation M and F” in Table 5a), and (c) variation in natural mortality and fecundity are perfectly negatively correlated (“Negative correlation M and F” in Table 5a).

Table 5(b) shows the sensitivity of outputs to higher and lower specifications for the value of  $r_{max}$ , effected by modifying the values assumed for the highest fecundity which are given in Table 2.

The results of the meta-analysis were generally insensitive to changing the assumptions upon which it is based, with a few exceptions (Fig. 3). In particular, increasing the extent of variation and autocorrelation of fecundity leads to a posterior distribution for  $r_0/r_{max}$  which emphasises higher values for  $r_0/r_{max}$ . This is because higher environmental variation leads to higher overall variation (process and observation) for stocks with lower  $r_0/r_{max}$ . Consequently, the relative weight given to stocks for which the rate of increase is close to  $r_0$  (especially the right whale stocks) becomes greater. The rates of increase for the right whale stocks are generally close to  $r_{max}$  (see the results for “Right whale data only” in Fig. 3).

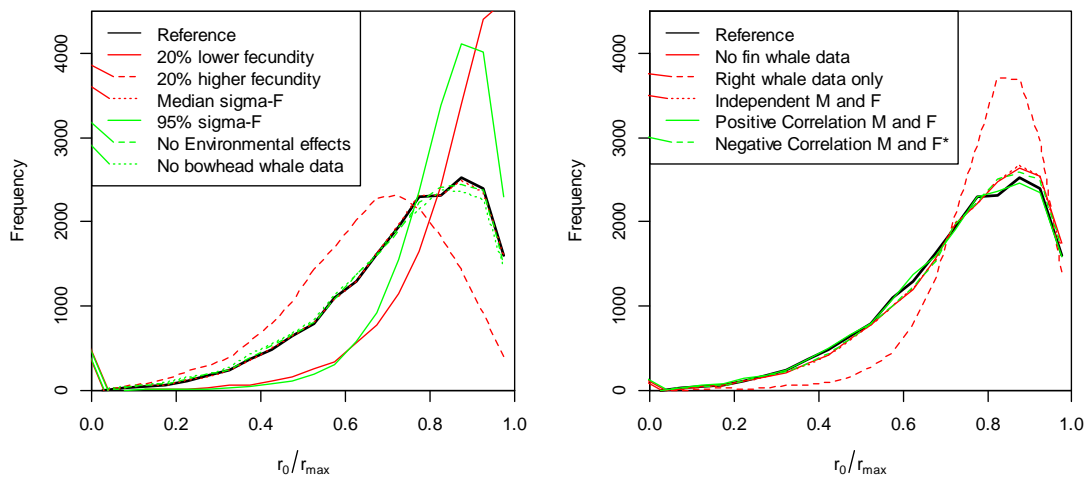


Fig. 3. Posterior distributions for  $r_0/r_{max}$  for the reference case analysis and the sensitivity tests.



FOURTH MSYR WORKSHOP

Table 5

Outputs from the Bayesian meta-analysis. Results are shown for the lower 5<sup>th</sup> and 10<sup>th</sup> percentiles of the posterior for  $r_0/r_{max}$ . For each percentile, results are shown are: (a)  $r_0/r_{max}$ ,  $r_0/r_{max}/2$ ,  $r_0/r_{max}/1.619$ , and (b) the product of  $r_{max}$  and  $r_0/r_{max}/2$ ,  $r_0/r_{max}/1.619$  for two choices for  $r_{max}$ . See main text for the definitions of the sensitivity tests.

	Lower 5 <sup>th</sup> percentile							Lower 10 <sup>th</sup> percentage						
	$r_0/r_{max} * r_{max} / \text{Divisor}$							$r_0/r_{max} * r_{max} / \text{Divisor}$						
	$r_0/r_{max}$	$r_0/r_{max} / \text{Divisor}$	$r_{max}=0.0426$		$r_{max}=0.114$		$r_0/r_{max}$	$r_0/r_{max} / \text{Divisor}$	$r_{max}=0.0426$		$r_{max}=0.114$			
	1	2	1.619	2	1.619	2	1.619	1	2	1.619	2	1.619	2	1.619
Reference	0.396	0.198	0.245	0.008	0.01	0.022	0.028	0.490	0.245	0.303	0.01	0.013	0.028	0.034
Case														
<b>(a) Sensitivity tests to assumptions</b>														
No environmental effects	0.386	0.193	0.239	0.008	0.010	0.022	0.027	0.481	0.241	0.297	0.010	0.013	0.027	0.034
Common median $\tilde{\sigma}_f$ and $\tilde{\rho}_f$	0.395	0.198	0.244	0.008	0.010	0.022	0.028	0.488	0.244	0.302	0.010	0.013	0.028	0.034
75% $\tilde{\sigma}_f$ and $\tilde{\rho}_f$	0.431	0.216	0.266	0.009	0.011	0.024	0.03	0.524	0.262	0.323	0.011	0.014	0.03	0.037
95% $\tilde{\sigma}_f$ and $\tilde{\rho}_f$	0.621	0.311	0.384	0.013	0.016	0.035	0.044	0.688	0.344	0.425	0.015	0.018	0.039	0.048
No bowhead whale data	0.370	0.185	0.228	0.008	0.010	0.021	0.026	0.464	0.232	0.287	0.010	0.012	0.026	0.033
No fin whale data	0.412	0.206	0.255	0.009	0.011	0.023	0.029	0.506	0.253	0.313	0.011	0.013	0.029	0.036
Right whale data only	0.579	0.29	0.358	0.012	0.015	0.033	0.041	0.651	0.325	0.402	0.014	0.017	0.037	0.046
Independent $M$ and $F$	0.414	0.207	0.256	0.009	0.011	0.024	0.029	0.508	0.254	0.314	0.011	0.013	0.029	0.036
Positive correlation $M$ and $F$	0.391	0.195	0.241	0.008	0.010	0.022	0.027	0.485	0.242	0.299	0.010	0.013	0.028	0.034
Negative correlation $M$ and $F^*$	0.406	0.203	0.251	0.009	0.011	0.023	0.028	0.500	0.250	0.309	0.011	0.013	0.028	0.035
<b>(b) Sensitivity to specifications for <math>r_{max}</math></b>														
20% higher fecundity	0.595	0.297	0.367	0.013	0.016	0.034	0.042	0.679	0.339	0.419	0.014	0.018	0.039	0.048
20% lower fecundity	0.335	0.167	0.207	0.007	0.009	0.019	0.023	0.42	0.21	0.259	0.009	0.011	0.024	0.029

\* Ignoring the data for fin and bowhead whales because the populations do not persist given the assumed levels of variation of natural mortality and fecundity.

## 5.2 Approaches to relate the $r_0/r_{\max}$ distribution to an appropriate MSYR range

The last discussion of this matter took place during the 2009 intersessional workshop on MSYR for baleen whales (IWC, 2010a), at which two views emerged. One view, based on Butterworth and Best (1990), argued that estimates for  $MSYR_{1+}$  could be inferred from estimates of  $r_0$  given the bound  $MSYR_{1+} \geq r_0/2$ . This view arises from the assumptions that the relationship between the per capita growth rate and population size is smooth and convex. The alternative view is that  $MSYR_{1+}$  can be lower than this bound, and is based on arguments of ‘supercompensation’ (Holt, 1985) whereby high growth rates at low population size drop rapidly thereafter, queries concerning the analyses that led to the conclusion of convex per capita growth rate relationships, and the effects of stochasticity. That workshop had concluded that while both views remained, the fact that regularly monitored right and humpback whale populations had shown no evidence for a reduction in high growth rates over the past two decades implied that the ‘supercompensation’ argument was not as plausible as it had been earlier.

In the light of those discussions, a proposal made in the past Workshop to assume  $MSYR_{1+} = r_0/2$  was again put forward. An alternative proposal advanced during the Workshop was to assume  $MSYR_{1+} = r_0/1.619$  as follows from the age-aggregated Pella-Tomlinson population model with  $MSYL = 0.6K$ , which is used frequently in the Scientific Committee.

However, the basis for these inferences was questioned on the grounds that they failed to take account of more recent work (Cooke, 2007a; de la Mare, 2011) on the impacts on the shape of yield curves resulting from environmental stochasticity and predator-prey effects.

The Working Group **agreed**, as an interim approach, to list results based on both assumptions above for the relationship between  $MSYR_{1+}$  and  $r_0$ . This matter will be revisited at the 2013 Scientific Committee meeting in the light of work to be undertaken by Cooke in the interim using the environmental stochasticity model of (Cooke, 2007b) to inform on the likely relationship between these two variables.

To provide an indication of the implications of these assumptions for the range of plausible  $MSYR_{1+}$  values for the unknown stock, Table 5 gives results for  $MSYR_{1+}$  for both assumptions coupled to the highest and lowest values for  $r_{\max}$  in Table 4.

The interpretation of the resultant sets of values in Table 5 is taken forward in the section following.

## 6 RECOMMENDATIONS FOR THE SCIENTIFIC COMMITTEE

The Workshop **agreed** that while it had made considerable progress, it was not in a position to develop recommendations for the Scientific Committee on the appropriate range of MSYR rates. In the time available, the Workshop summarised the issues that must be explored more fully during the 2013 Scientific Committee meeting. In summary, these related to three major areas:

- (1) the limitations of the modelling approach itself;
- (2) the limitations within the approach (e.g. paucity of data); and
- (3) the interpretation of the results in the context of the RMP.

Inclusion of the summary issues below does not imply that all members of the Workshop necessarily agreed with each.

- (a) *The validity of the assumption that the distribution of  $r_0/r_{\max}$  is independent of  $r_{\max}$ .* In species such as right whales, where there is high maternal investment and the maximum breeding rate is quite low, the realized  $r$  may often approach  $r_{\max}$ , as has been observed in the two Southern Hemisphere populations included in the analysis. Common minke whales, by contrast, might be an example of a species with an annual breeding cycle, but lower maternal investment (early weaning) such that the potential  $r_{\max}$  is quite high, but the realized  $r$  may come close to  $r_{\max}$  only rarely, if at all, if the consequence of early weaning was higher calf mortality or a consequence of annual breeding was lower female survival. The Workshop noted that there are no data available to be able to evaluate this suggestion directly.
- (b) *The validity of extrapolating to species with a higher  $r_{\max}$  than those included in the meta-analysis and how this should be done.* It was suggested that a meta-analysis similar to that performed for  $r_0/r_{\max}$  be performed for  $r_0$ , i.e. corresponding to the assumption that it is  $r_0$  rather than  $r_0/r_{\max}$  which has a universal distribution. While such an assumption is clearly problematic in certain respects, the purpose would be to use the lower tail of this distribution to bound the extent to which the extrapolation concern might impact the interpretation of the results in Table 5. This analysis would ignore environmental variability, given that this had had little impact on the results for the base case for the  $r_0/r_{\max}$  distribution (Table 5a). The Workshop **agreed** that a beta distribution ranging from 0 to 20% be used for this analysis, with the

## FOURTH MSYR WORKSHOP

priors on the beta distribution parameters being chosen to yield a roughly uniform prior for  $r_0$ . Punt agreed undertake this analysis.

- (c) *The effect of the  $r_{max}$  constraint, uncertainty in  $r_0$  and the variability in fecundity.* There was some discussion of the fact that the assumed  $r_{max}$  constraint of the model, in combination with the uncertainty in the  $r_0$  estimates and the amount of variability in fecundity caused the median of the posterior for  $r_0$  to be smaller than actual observed value for  $r_0$  for 11 of the 13 stocks in the reference case (Fig. 1). The sampling distribution for  $r_0$  may exceed  $r_{max}$  owing to either observation error, an incomplete model (including  $r_{max}$  values which are too low), or a combination of these factors. In this situation, and as indicated for the majority of the stocks analysed, the posterior for  $r_0$  will have the bulk of its mass below the observed value for  $r_0$ , generating  $r_0$  estimates that are smaller than the estimates from the data.
- (d) *Sample size limitations.* The Workshop also noted the limitations of any meta-analysis which relies on a small number of populations from a limited number of species (and the absence of some key species such as common and Antarctic minke whales). In particular, the analysis here can be said to over-represent populations recovering in regions where most other large whales populations are also depleted and where there are limited, if any, effects from forage fisheries. These conditions are not representative for a substantial number of other populations. Even for the populations included in the analysis, multi-species and changes in fisheries effects mean that current observed ratios of  $r_0/r_{max}$  may not relate to future MSY rates when the populations have recovered in the same or similar ways as assumed in section 5.2.
- (e) *Use within the RMP.* In terms of possible uses within the RMP, one suggestion was given for using the appropriate result for  $MSYR_{1+}/r_{max}$  from Table 5 (given the selection of an  $r_0 - MSYR_{1+}$  relationship and the percentile of the distribution of  $r_0/r_{max}$  on which to base a lower bound on the range of MSYR to be considered for the RMP). When *ISTs* for the species and stocks under consideration for an RMP *Implementation (Review)* were developed, a plausible range of  $r_{max}$  should be developed for the species and region concerned from the demographic parameter and other pertinent information available. This range would then multiply the appropriate value for  $MSYR_{1+}/r_{max}$  from Table 5 to provide a basis to choose the lowest plausible value for  $MSYR_{1+}$  for use in those *ISTs*.
- (f) *Reference component of the population.* The Workshop noted that the tuning of the RMP is expressed in terms of the MSYR for the mature component of the population. It recalled the Scientific Committee's previous finding that the relationship between  $MSYR_{1+}$  and  $MSYR_{mat}$  could for practical purposes be expressed as a simple scaling factor of approximately 1:0.67 (IWC, 2004, p.6). However, that finding was based on a deterministic model, and the relationship would not necessarily be as simple in the presence of high levels of variability in the net recruitment rate. The Workshop **recommended** that the relationship between  $MSYR_{1+}$  and  $MSYR_{mat}$  be re-examined in the context of variability for the sets of parameter values given in Table 3. Cooke **agreed** to undertake this analysis.

## 7 WORKPLAN UNTIL SCIENTIFIC COMMITTEE MEETING

The Workshop noted four areas of work that, if able to be completed, would assist discussions at the 2013 Annual Meeting.

- (1) Cooke **agreed** to explore further the plausible parameter space for the model in Cooke (2011a), with a view to determining the plausible range of variability in survival.
- (2) de la Mare **agreed** to investigate use of his individual based model (SC/M13/MSYR2) to examine the relationship between variability in reproduction and survivorship further.
- (3) Cooke **agreed** to examine the relationship between  $MSYR_{1+}$  and  $MSYR_{mat}$  in the context of variability in net recruitment.
- (4) Punt **agreed** to conduct a meta-analysis of  $r_0$  values.

The Workshop **agreed** that for the results of these analyses to be properly considered at the 2013 Annual Meeting, they should be circulated by **15 May 2013**. Cooke, de la Mare and Punt each agreed to do so or notify the Workshop participants if they were unable to complete the work.

The Workshop also **agreed** that it would be valuable if short papers were developed addressing the issues raised under Item 6.

## 8 ADOPTION OF REPORT

The Chair thanked the participants for their co-operative attitude and contributions to the Workshop. In particular, he thanked Punt and Butterworth for their work on the report and Punt for undertaking the computing work. The

## FOURTH MSYR WORKSHOP

report was adopted by email on 26 April 2013. The participants thanked the Chair for his usual good humoured and efficient handling of the meeting.

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## **Annex A List of Participants**

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**Norway**  
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**Invited Participants**  
D.S Butterworth  
J.G. Cooke  
A.E. Punt

**Secretariat**  
G.P. Donovan

## **Annex B Agenda**

- 1 Introductory items
  - 1.1 Welcoming remarks
  - 1.2 Election of Chair
  - 1.3 Appointment of rapporteurs
  - 1.4 Adoption of Agenda
  - 1.5 Review of documents
- 2 Progress since Annual Meeting in relation to the Workplan
  - 2.1 Overview of present methods
  - 2.2 Refinement of population model used to estimate variability parameters
  - 2.3 Coding of methods that generate variability in survival rate
- 3 Estimates of  $r$  and associated variability (reproductive component)
  - 3.1 Update of estimates
- 4 Methods specifying variability in survival
- 5 The  $r_0/r_{max}$  distribution
  - 5.1 Estimates of the  $r_0/r_{max}$  distribution
  - 5.2 Approaches to relate the  $r_0/r_{max}$  distribution to an appropriate MSYR range
- 6 Recommendations for the Scientific Committee
- 7 Workplan until Scientific Committee meeting
- 8 Adoption of report

## **Annex C**

### **List of Documents**

SC/F13/MSYR1- Witting, L. and Brandon, J. Potentials for positive biases in estimates of the annual variation in average birth rate of baleen whale populations

SC/F13/MSYR2 – de la Mare, W.K. Implications of energy budgets in determining the characteristics of whale yield curves (Draft)