

Report of the Third Intersessional Workshop on the Review of MSYR for Baleen Whales

The Workshop was held at the School of Aquatic and Fishery Sciences, University of Washington, Seattle (20-24 April 2010). The participants were Brandon, Butterworth (Convenor), Cooke (participating remotely), Donovan, Gabriele, Kitakado, Koski, Kraus, Punt, Ramp, Robbins, Straley and Wade.

1. INTRODUCTORY ITEMS

1.1 Opening remarks

Butterworth welcomed the participants and advised that Cooke and Øien were unable to attend because their flights were cancelled as a result of the Icelandic volcanic eruption. He drew attention to the Workplan for completion of the MSYR review (IWC, 2010a; 2010c), explaining the relationship of this review to the RMP, and the manner in which the issues considered during the Workshop would contribute to the review.

A critical aspect of the RMP review was reconsideration of the plausible range used for maximum sustainable yield rate (MSYR) in population models used for testing the *Catch Limit Algorithm (CLA)* of the RMP, which was currently 1% to 7% when expressed in terms of the mature component of the population. Information on observed population growth rates at low population sizes was being used to inform the review, but it had been pointed out that in circumstances where variability and/or temporal autocorrelation in the effects of environmental variability on population growth rates was high, use of these observed population growth rates could lead to mis-inference about the lower end of the range of plausible values for MSYR. The particular objective of discussions at the Workshop was to inform on whether the observed levels of variation in baleen whale reproduction and annual survival rate parameters were sufficiently large that biases of the nature identified from population models incorporating environmentally-induced variability might be of concern.

He thanked Cooke for his efforts to prepare potential data sets. He also thanked the data providers for making their information available.

1.2 Election of Chair

Donovan was elected as Chair.

1.3 Appointment of rapporteurs

Butterworth and Robbins acted as rapporteurs.

1.4 Adoption of Agenda

The adopted agenda is given as Annex A.

1.5 Review of documents

New documents available to the meeting were SC/A10/MSYR1-3 (see Annex B).

2. ESTIMATION OF VARIABILITY FROM DATASETS FOR BALEEN WHALE SPECIES

2.1 General overview of time series data

Time series data from several species and populations were reviewed and assessed in preparation for the workshop, following on from previous work by the Committee and earlier workshops on this topic (IWC, 2009; 2010a). Based on this review, the following data types were identified as being the most common and potentially informative: calf counts, calving rates, calving intervals, abundance estimates and stranding data. A summary of the data received by the workshop is provided in Table 1 and relevant population details are summarised below.

2.1.1 North Atlantic Right whales

Kraus summarised photo-identification studies of North Atlantic right whales from the western North Atlantic, 1980 to the present. The data provided to the workshop included calving rate and calving interval through 2009. A total of 581 animals have been catalogued since 1935 and an estimated 406 were alive in 2009. Survey effort was variable in the early 1980s but has been more consistent since 1986. Calving data were derived from a combination of breeding and feeding ground surveys, but results suggest that nearly 100% of all calving events are captured within 3 months. Issues with sighting heterogeneity meant that the population size has been calculated annually as the minimum number of whales known to be alive rather than through mark-recapture analyses. With respect to survivorship/mortality, although some carcasses are recovered, many are thought to go unobserved. Consequently, North Atlantic right whale abundance and stranding data were not considered useful time series for the purposes of the present workshop.

Table 1

Summary of potential data sets considered

Area	Method	Total span (yrs)	Yrs missed/gaps ¹	Potential data (and variance) types ²	Data provider
Blue					
Gulf of California	Photo-ID	25	1/1	Calf count, Calving propn	Sears/Ramp
Bowhead					
Bering-Chukchi-Beaufort Seas	Photo-ID	20	12/2	Calving propn (SE)	Koski
Fin					
Gulf of St. Lawrence	Photo-ID	19	0/0	Calf count	Sears/Ramp
Gray					
Eastern North Pacific	Shore counts-southbound	40	17/7	Abundance-1+ (CV)	Laake, Perryman and Brownell Jr
Eastern North Pacific	Shore counts-northbound	16	0/0	Calf count (SE)	As above
Eastern North Pacific	Reports	32	0/0	Strandings	As above
Humpback					
Gulf of Maine	Photo-ID	27	0/0	Calf count, Calving interval ³ (SE), Calving propn	Robbins
Gulf of St. Lawrence	Photo-ID	28	0/0	Calf count, Calving interval ³ (SE), Calving propn	Sears/Ramp
Southeast Alaska	Photo-ID	32	0/0	Calf count, Calving interval ³ (SE), Calving propn	Gabriele/Straley
West Coast US	Photo-ID	18	0/0	Abundance-total (CV)	Calambokidis
North Atlantic Right					
western North Atlantic	Photo-ID	30	0/0	Calf count, Calving interval ³ (SE), Calving propn	Kraus
Southern Right					
southeastern Atlantic	Photo-ID	28	0/0	Calf count, Calving interval ⁴ (SE), Calving propn	Best
southwestern Atlantic	Photo-ID	38	0/0	Calf count, Calving interval ⁴ (SE), Calving propn	Cooke
southwestern Atlantic	Reports	39	0/0	Strandings	Cooke

¹The total number of years with no research effort versus the number of resulting gaps in the sequential data series

² For methods of estimation for modelling purposes see Item 2.2. Some estimates were limited to a subset of the study span, depending on the analysis.

³Calving interval data available from complete or incomplete female sighting histories

⁴Calving interval data available from incomplete female sighting histories

2.1.2 South Atlantic right whales

South Atlantic right whales were photo-identified annually during aerial surveys around Península Valdés in Argentina since 1971 (Cooke *et al.*, 2003). Data from cow/calf pairs provide the most reliable inference for this breeding population and so the data submitted to the workshop consisted primarily of calf counts, calving rates, calving intervals through 2008, although stranding data were also included. Prior modelling of reproduction suggested that the greatest inter-annual variation in reproduction occurred among females transitioning from “ready to conceive” to “resting” (Cooke *et al.*, 2003).

South Atlantic right whales were photo-identified during annual helicopter surveys of the southern coast of South Africa (Cape Town to Plettenberg Bay) since 1979 (Best, 2004; Best *et al.*, 2005; Best *et al.*, 2001). Photo-identification concentrated on cow-calf pairs along the same stretch of coastline at same time of year (mid-October). Earlier fixed-wing surveys had identified this stretch of coast as containing over 90% of cow-calf pairs on the South African coastline in spring, and the timing of the surveys was set to coincide with the end of the calving season but before the main exodus of whales from the coast. Matching (originally done by only by eye) is now undertaken in conjunction with the Hiby-Lovell automated procedure (Hiby and Lovell, 2001). The catalogue (up to and including 2006) contained 954 adult females from which 1,959 calving intervals were recorded.

SC/A10/MSYR3 analysed the resightings data for female right whales with calves from aerial surveys conducted off South Africa from 1979 to 2006 for evidence of a change in calving interval over this period. Statistically significant indications were found of a small decrease in the mean calving interval from 3.2 to 3.1 years somewhere between about 1985 and 1990.

2.1.3 Bowhead whales

Koski described the dataset provided for the Bering-Chukchi-Beaufort (BCB) stock of bowhead whales. Several sources of information are available for estimates of year-to-year variation in calf production; these include either aerial or ice-based surveys, or both, during most years from 1978 to 2010 and aerial photographic surveys during spring, summer and early fall of most years from 1981 to 2009. However, most of these data sets are biased due to segregation during migration or in the summering areas, and the biases cannot be properly accounted for. Therefore, the submitted data were restricted to eight years of photographic data collected near Barrow in spring from 1985 to 2004 (Koski *et al.*, 2008). The proportion of calves in the population was estimated and the data were fully corrected for all known biases, which include age-related timing of migration and the changes in the proportion of whales passing through the survey area throughout the spring migration period. Population estimates with confidence intervals are available for 12 years of ice-based surveys from 1978 to 2001 (George *et al.*, 2004; Zeh and Punt, 2005); an additional estimate, including confidence intervals, is available for 2004 from 2003-2004 photographic surveys (Koski *et al.*, 2004). Long-term rates

of increase are available from the 12-year series of population estimates from ice-based surveys (Zeh and Punt, 2005). No reliable data are currently available for strandings or year-to-year mortality rates. On-going analyses show promise for quantifying first year mortality but results will not be available for another year or so.

2.1.4 Humpback whales

2.1.4.1 NORTH ATLANTIC

North Atlantic humpback whales were photo identified during ship-based surveys in the Gulf of St. Lawrence since 1980 with an increase in spatial and temporal effort in the first years of the study. The Gulf is one of several summer feeding aggregation of the North Atlantic humpback whale population. Data provided to the workshop were calving rates and calving intervals of individually identified mature females through 2009. Almost all females were sexed using skin sample biopsies before they started to reproduce, resulting in a rather high age at apparent first birth (12+ years). Mark-recapture estimates of sex-specific annual survival were available for adult whales, but not for calves/juveniles due to a low re-sighting rate (Ramp *et al.*, 2010). Abundance and stranding time series were not available.

Robbins described vessel-based photo-identification studies of North Atlantic humpback whales in the Gulf of Maine annually since the late 1970s. Sampling effort increased in both intensity and geographic coverage during the first decade and there continues to be considerable heterogeneity in individual sighting probabilities. Mark-recapture statistical analyses to date suggest annual variation in calf survival and calving probabilities, but not adult survival (Robbins, 2007; Rosenbaum *et al.*, 2002; Weinrich and Corbelli, 2009). There has been a significant increase in the age at first calving in the Gulf of Maine (Robbins, 2007), as well as significant differences in parameter values compared to other humpback whale populations (e.g. Gabriele *et al.*, 2007). Calf count, calving rate and calving interval data were provided to the workshop for the period 1979-2005. Neither available abundance estimates nor carcass counts were considered reliable time series for this population.

2.1.4.2 NORTH PACIFIC

Humpback whale photo-identification vessel-based surveys have been conducted annually in Southeast Alaska (SEAK) since the 1970s. This North Pacific feeding aggregation ranges from northern Vancouver Island to Yakutat, Alaska. The data submitted to the workshop came from the northern part of SEAK, and primarily from two research groups. They consisted of annual calf counts, 184 birth intervals and calving rate data for 361 females through 2008. SEAK humpback whales are also studied on their Hawaiian breeding ground, but individuals were not consistently encountered and so those data were not included. Effort in some areas has been inconsistent across years and there is a potential for variability calving rates relative to feeding behaviour. There are also several population estimates (with CVs) based upon subsets of these data, the most recent one is bounded by the years 1994-2000 (Straley *et al.*, 2009). Stranding data were not available.

Data were also available from a population of North Pacific humpback whales that migrate between the US West Coast (California/Oregon/Washington) in summer and Mexico/Central America in winter. Mark-recapture estimates of abundance were available for near-shore California from photo-identification studies, 1991-2008 (Calambokidis, 2009).

2.1.5 Fin whales

Ship-based photo-identification data from North Atlantic fin whales from the Gulf of St. Lawrence were available from 1980 on. The data provided to the workshop included calf counts, calving rates and calving intervals through 2008. However, few calves have been observed in this population, especially prior to 2005. The Gulf of St. Lawrence is a summer feeding ground and females might have weaned their calves by their arrival. Due to a temporal shift in their distribution, more calving data was available since 2005. Due to the small time span of data with calving data, it was decided not to use the data set but was regarded as useful for future assessments. Neither abundance nor stranding data were available.

The North Atlantic Fin Whale Catalogue (Allied Whale, College of the Atlantic) is another potential source of time series data for this species that might be explored in the future.

2.1.6 Blue whales

Ramp described photo-identification data available for North Pacific blue whales from the Gulf of California since 1983. Sampling was performed in a nursery area where calves are thought to be 1-3 months in age. This work was undertaken during 4-6 weeks per year and annual sample sizes tended to be highly variable. The data provided to the workshop consisted of calving rates and intervals. The sample likely represents only a proportion of the reproductive active females of the Californian population. Population estimates are also available for this population using mark-recapture photo ID and line transect surveys (Calambokidis, 2009; Calambokidis and Barlow, 2004). In recent years, the two survey methods yielded contradicting results. Analysis based on photo-ID studies showed an increase of less than 3% (Calambokidis, 2009).

2.1.7 Gray whales

Three time series of data were supplied for the eastern North Pacific stock of gray whales. These included: (i) abundance estimates; (ii) calf production estimates; and (iii) stranding counts. There are 23 annual abundance estimates (of the 1+ component) during 1967-2006, with associated covariances (Laake *et al.*, 2009). The abundance estimates are derived from the land-based survey of the southbound migration along the coast of central California. Calf production estimates are available annually during 1994-2009, from a land-based survey of the northbound migration along central

California (e.g. Perryman *et al.*, 2002). Finally, the strandings data are annual gross counts during 1975-2006, from the states of California, Oregon and Washington, where stranding network effort has been consistent through time (Brownell *et al.*, 2007).

Table 2

Basis of “calving proportion indices” used in workshop analysis

Area	Description of “calving proportion index”
Blue	
Gulf of California	Number of calves produced by mature females (a subset of total calf count) / number of mature females
Bowhead	
Bering-Chukchi-Beaufort	Proportion of calves in the population, corrected for sampling biases
Gray	
Eastern North Pacific	Calf index / mature females
Humpback	
Gulf of Maine	Number of calves produced by mature females (a subset of total calf count) / number of mature females
Gulf of St. Lawrence	Number of calves produced by mature females (a subset of total calf count) / number of mature females
Southeast Alaska	Number of calves produced by mature females (a subset of total calf count) / number of mature females. The first few years of the series were excluded from analysis due consistently low numbers of mature females.
North Atlantic Right	
western North Atlantic	Number of calves produced by mature females (a subset of total calf count) / number of mature females
Southern Right	
southeastern Atlantic	Expected number of calves / estimated number of mature females (based on an exponential trend fitted to calf data)
southwestern Atlantic	Number of calves / estimated number of mature females (based on an exponential trend fitted to calf data)

Table 3

Parameters for use as input to the population models described under Item 2.3. Observed values in bold and inferred values in regular type.

Stock	Mean survivorship	Age at attainment of maturity	r_0
BCB bowhead	0.99	22	0.04
<i>Survival</i> : estimated using mark-recapture for 13 years 1981 to 1998 (Zeh <i>et al.</i> , 2002) and valid for marked whales only (primarily mature animals). <i>Maturity</i> : a ‘blended’ estimate from (1) estimates of growth of individuals to age at sexual maturity from six years of photography data collected from 1982 to 1990 (Koski <i>et al.</i> , 1992; 1993), (2) baleen growth rates in small whales extrapolated to age at sexual maturity (Schell <i>et al.</i> , 1989) and (3) aspartic acid age estimates (George <i>et al.</i> , 1999). <i>Increase</i> : estimated from 12 years census data from 1978 to 2001 (Zeh and Punt, 2005) and incorporating harvest mortality (0.006).			
Eastern gray	0.98	7	0.06
<i>Survival</i> : The median non-calf survival rate estimated from most recent assessment (Punt and Wade, 2010). <i>Maturity</i> : The median of the posterior for this parameter from the most recent assessment (Punt and Wade, 2010). <i>Increase</i> : Information on changes in abundance is available from most recent assessment (Punt and Wade, 2010).			
Gulf of California blue	0.975	10+	0.07
<i>Survival</i> : 0.975 – adult survival (non-calf) from photo-id data (1979-2002) (Ramp <i>et al.</i> , 2006). <i>Maturity</i> : 10+ years. N=2 females, 12 and 13 returned with their own calves to the Sea of Cortez (MICS unpublished data). Whaling data and earplug counts suggest earliest is age 10 (Laurie, 1937; Lockyer, 1984; Ruud <i>et al.</i> , 1950; Yochem and Leatherwood, 1985). <i>Increase</i> : under 3% (Calambokidis, 2009) [around 7-8%, modelled values for Antarctic blue whales – Branch <i>et al.</i> (2007; 2003)]			
Gulf of Maine humpback	0.955	7	0.065
<i>Survival</i> : 0.955 (an approximation based on available estimates). Survival has been estimated to range from 0.925 (2000-2005) (Robbins, 2007) to 0.964 (1979-1995) (Rosenbaum <i>et al.</i> , 2002), but most estimates are in the 0.95-0.96 range. <i>Maturity</i> : 7 years (range 5-13 years 1979-2000) (Robbins, 2007). This is based on individual females observed annually until their first calf. <i>Increase</i> : 0.065 Barlow and Clapham (1997) (more recent data suggest a lower present rate 0-4% (Clapham <i>et al.</i> , 2003).			
Gulf of St Lawrence humpback	0.982	12+	0.065
<i>Survival</i> : Both sexes pooled (adult – males 0.971 and females 0.992) from photo-id data (years) – (Ramp <i>et al.</i> , 2010) <i>Maturity</i> : from photo-id data (years) 12+ years. (Ramp, 2008). <i>Increase</i> : 0.065 based on Barlow and Clapham (1997) for adjacent areas.			
Southeast Alaskan humpback whale	0.97+	12	0.06
<i>Survival</i> : Mizroch <i>et al.</i> (2004)’s judgement of best of several estimates using data from southeastern Alaska and Hawaii 1979-1996 was 0.957 (0.943-0.967). Here chose to use the high end of the 95% confidence interval, 0.967, because it seems more consistent with available data on observed population increases. <i>Maturity</i> : Age at Sexual Maturity: 11 Gabriele <i>et al.</i> (2007) used re-sighting histories of 10 individually identified female humpback whales of known age from southeastern Alaska to estimate ASM. The females were observed with their first observed calf at a mean of 11.8 years (range: 8-16 years; one whale was 8 yrs, most were 10-12 yrs old). Since publication, 7 additional known age females had their first calf at ages, although one female had her first calf at age 6. Using all of all the current data on females of known age resulted in a mean age at first calving of 11.0 years. (n=16, range = 6-16). <i>Increase</i> : Average of available relevant estimates - Calambokidis <i>et al.</i> (2008) 5.5-6.0% for the main breeding area, Hawaii, using three methods to compare mark recapture population estimates from SPLASH (2004-2006) with estimates from 1991-1993 and Mobley <i>et al.</i> (2001) aerial surveys in 1994-2000 for Hawaii, 7%			
Western North Atlantic right whale	0.96	9	0.01
<i>Survival</i> : Fujiwara and Caswell (2001); Kraus and Pace (2007) – photo-id and mark-recapture data 1980-2005, different analytical approaches <i>Maturity</i> : Kraus <i>et al.</i> (2007) - Individual analysis mean of all calving events to known age females for the period 1980-2005 <i>Increase</i> : Kraus and Pace (2007) – population viability analyses based on 1980-2005 photo-id data - re-sampling the estimated survival rates from the time varying models of survival rates and the observed calf numbers for the period.			
Southeastern Atlantic southern right whale	0.99	7.7	0.073
<i>Survival, Maturity and Increase</i> : all from Best <i>et al.</i> (2005) from photo-id data of females and calves (years) and computer models			
Southwestern Atlantic southern right whale	0.98	9.1	0.068
<i>Survival, Maturity and Increase</i> : all from Cooke <i>et al.</i> (2003) from photo-id data of females and calves (years) and computer models			

2.2 Summary of data to be used in further analyses

Cooke had prepared initial tabulations of the data provided to him on reproduction and survival rates. These data were checked and modified where necessary by participants at the workshop. A subset of the available data ('calving proportion indices' and 'calving interval estimates') were selected for further analysis; few data were available to inform on survival rate variation. The calving proportion indices were developed by dividing calf counts by numbers of mature females, where both numerator and divisor might reflect only a relative measure. For example, calf counts might constitute only a proportion of the number of calves born that year, while the number of mature females might be indexed by an exponential trend line fitted to a time series of some measure of population abundance. In the case of gray whales, the number of mature females was taken from output of the most recent stock assessment for this population (Punt and Wade, 2010). The basis of the "calf proportion index" for each population shown in Table 2.

Calving intervals were calculated for individually identified females, as the number of years elapsed since the prior calf. Analysis was restricted to intervals in which the female was seen in all intervening years; such data were available from four populations (see Table 1). Intervals ending in the same year were averaged to yield a single estimate for that year. The first six years of any series were excluded to avoid bias through underrepresentation of longer intervals.

Computations carried out under Item 2.3 below required values for demographic parameters of the populations modelled. The values used for this purpose and their sources are listed in Table 3.

2.3 Analysis

As an initial approach, the Workshop first applied the methodology set out in Annex C to estimate the coefficient of variation (CV) and temporal autocorrelation for the time series of calving proportion index and calving interval data discussed above. This methodology ignores observation error, so that the resultant estimates of CV listed in Table 4 are positively biased. The Workshop noted that the variability in annual calving proportion was always greater than that for calving interval. This probably arises from the negative correlation in calving proportion from one year to the next which arises because (apart from minke whales) baleen whales reproducing in one year do not generally also calve the following year.

Annex D sets out methodology which relates variability in calving proportion to variability in the annual growth rate of a population by means of a population dynamics model. The values in Table 3 cannot be input directly into this model, because account has to be taken of the fact that there is an upper bound of 1 on the proportion of mature females that can calve in any one year, and further those females that have calved in one year cannot calve again in the next one or two years (depending on the species – minke whales are not under consideration here). The Annex D model builds in these constraints, and is tuned by adjusting the input CV and temporal autocorrelation estimates in Table 4 upwards until the corresponding model outputs for these quantities match those in Table 4, i.e. until the variability simulated by the model matches that observed in the field. The model then outputs the CV and temporal autocorrelation to be expected in the growth of the population from year to year (see example results in Tables 2 and 3 of Annex D).

Two further steps are needed before such results can be used to draw inferences about the plausible ranges for the CV and temporal autocorrelation parameters describing the effects environmental variability on population dynamics in model of Cooke (2007). First the model of Annex C needs to be improved in the manner detailed towards the end of that Annex. The first stage of this process involves adjusting that model to allow estimates of observation error for each calving proportion index or calving interval to be taken into account so as to reduce the positive bias that arises from the existing model ignoring that effect. In the second stage, an approach that is technically more correct will be developed to formally integrate out what are random effects in the original model, and to use case-specific error models for each series rather than assume normal distributions throughout.

The second step is needed because the CV and temporal autocorrelation parameters input to the environmental variability model (Cooke, 2007) do not correspond exactly to the CV and temporal autocorrelation in the growth of the population from year to year output by the population model of Annex D. An appropriate selection, focusing on the higher value options for CV and temporal autocorrelation, from the standard set of scenarios for the environmental variability model (Table 2 in IWC, 2010a) needs to be run to output corresponding statistics for the growth of the population from year to year, so that these can in turn be compared with such outputs from the population model of Annex D.

Most of the data available to the Workshop related to the reproduction process (calving). Environmentally induced variability in population abundance can arise also from variation in the annual survival rate, and the model of Annex D can also take this into account. However only two data series (from strandings) related to variations in survival rate were available to the Workshop, which noted that these seemed to indicate brief periods of heightened natural mortality for which the AR1 models used to represent variability in reproduction would probably not constitute the best form of statistical representation. The Workshop **agreed** that it was necessary that the impact of such survival rate variations also be considered as a component of this investigation, but that decisions on the specific form of representations of this effect to be included in further runs of the model of Annex D should be deferred to the 2010 Annual Meeting.

Table 4

Estimated parameters for the effects of environmental variability on reproductive success are shown for nine stocks of mysticetes, for which time series of calving data were available to the workshop. The number of years with observations is given under “n”. “Gaps” denotes how many times there were missing years (regardless of the number of missing years) between any two observations in a time series. The CV is equal to σ/μ , where σ is the standard deviation of the residual errors about the expected calving value μ . The standard deviations for each case are assumed to be correlated through time, given the corresponding coefficients under ρ . The standard errors of the three estimated parameters (ρ , μ and σ) are shown to the right of each, under “SE”. The details of the modelling methods used to estimate these parameters are given in Annex C.

Stock	Calving Data Type	n	gaps	CV	ρ	SE	μ	SE	σ	SE
Bowhead										
BCB	Proportion	8	2	0.581	0.075	0.521	0.060	0.013	0.035	0.009
Gray										
Eastern	Proportion	16	0	0.484	0.362	0.234	0.100	0.018	0.048	0.009
Blue										
Gulf of California	Proportion	18	4	0.915	-0.544	0.184	0.171	0.027	0.157	0.026
Humpback										
Gulf of Maine	Interval	22	0	0.161	0.197	0.210	2.457	0.104	0.395	0.060
Gulf of Maine	Proportion	27	0	0.454	-0.749	0.203	0.320	0.016	0.145	0.020
Gulf St. Lawrence	Interval	15	5	0.236	0.283	0.321	2.981	0.230	0.703	0.131
Gulf St. Lawrence	Proportion	25	1	0.859	-0.494	0.219	0.250	0.029	0.214	0.030
SE Alaska	Interval	23	0	0.179	0.410	0.192	2.674	0.164	0.479	0.071
SE Alaska	Proportion	25	0	0.224	0.121	0.202	0.219	0.011	0.049	0.007
NA right										
western	Proportion	29	0	0.416	0.160	0.189	0.179	0.016	0.074	0.010
western	Interval	25	0	0.150	0.609	0.155	4.124	0.300	0.617	0.087
Southern right										
SE Atlantic	Proportion	25	0	0.085	-0.336	0.188	0.990	0.013	0.084	0.012
SW Atlantic	Proportion	38	0	0.321	-0.151	0.160	1.248	0.057	0.401	0.046

3. OTHER SOURCES OF INFORMATION

This section relates to progress made on other issues listed in the Work Plan for Completion of the MSYR Review (IWC, 2010c).

3.1 Other taxa

The workplan had suggested that a review of information on variability of population size and vital rates from other taxa, especially large mammals, would be useful, drawing attention to the literature cited in Inchausti and Halley (2001). Those authors had made use of the GPDD (Global Population Dynamics Database – <http://www.cpb.bio.ic.ac.uk>), which is said to be one of the largest collections of animal and plant population data in the world.

SC/A10/MSYR1 provided an initial summary of the contents of that database, and provided an extraction of those series that seemed most representative of larger mammals. However those constraints, coupled with a reliability factor of 3 or above in the range 1-5 assigned in the database, and a length of at least 11 years, resulted in the selection of only 35 data sets from the over 5000 contained in the database. Only 8 of these 35 series are longer than 20 years.

Following inspection of the series so identified, the Workshop considered that they were very unlikely to contain information that would assist in the present Review. Workshop participants were aware of some other data series not included in the GPDD that might be more information in the context of the objectives of this Review. However these series were not generally readily available, so that obtaining them and possible other further series not in the GPDD could prove a substantial task. The Workshop **agreed** that further discussion on this issue should be deferred to the 2010 Annual Meeting, when the Scientific Committee should be better placed to determine the need or otherwise for pursuing such an investigation further.

3.2 Genetic data

In the absence of participants with expertise in genetics at the Workshop, further consideration of this aspect was deferred to the 2010 Annual Meeting.

3.3 Variability – length of series relationship

Of the three items for attention on this issue – estimates of variance tending to increase with length of series – that are set out in the workplan, the compilation of data from other taxa had not proved helpful (see Item 3.1 above), whereas the inclusion of data series length as a factor in the meta-analysis of population growth rates had been accomplished (see Item 4 below).

Because of pressure of time to complete other computations needed urgently by the Commission, Allison had yet to complete the simulation study based on the environmental variability population model (Cooke, 2007) to determine the predicted relationship between the length of series and estimated level of variability for the standard scenarios (Table 2 in IWC, 2010a). The Workshop **requested** that Allison attempt to complete this work to enable consideration of the results during the 2010 Annual Meeting.

4. REVISED META-ANALYSIS OF POPULATION GROWTH RATES

SS/A10/MSYR2 outlines an approach would could be used to construct a probability distribution for the rate of increase for an 'unknown' stock in the limit of zero population size, r_0 , using data on observed rates of increase and their standard errors. This approach extends an approach presented to the 2009 Annual Meeting by being based on a beta distribution prior for the ratio of r_0 to the maximum demographically feasible rate of increase, r_{\max} , and by accounting for environmental impacts on the population growth rate as well as uncertainty in the estimate of the realized growth rate. Estimation is based on Bayesian methods. Analyses based on simulation are conducted to evaluate the performance of this approach in data-rich and data-poor cases when estimates of r_0 are based on time-series of 20 years. As expected, performance is best when sample sizes are large and observation error is low.

The Workshop thanked Punt for this work. It suggested that further simulation runs be conducted with variance and temporal autocorrelation parameter values more typical of the higher ends of the ranges considered for the environmental variability model (Cooke, 2007), and observation error variance typical of those for the rates of increase in Table 2 of IWC (2010b). It further **recommended** that the approach be recoded to be able to consider data sets of different lengths rather than all of the same length as at present. The Workshop **agreed** that the recoded approach would represent an improvement on that used last year to construct a probability distribution for the rate of increase for an 'unknown' stock in the limit of zero population size, r_0 , and hence should be used for this purpose at the 2010 Annual Meeting.

5. WORKPLAN

The following schedule of further work was **agreed**, and would desirably be completed before or during the 2010 Annual Meeting. (1) Further development of the methodology of Annex C to estimate series CVs and temporal autocorrelation to:

- (a) take account of observation error (Brandon); and
- (b) integrate out the random effects and make case-specific choices for error distributions (Brandon and Kitakado).

(2) Application of the model of Annex D to all the data sets listed in Table 3 to estimate the resultant CV and temporal autocorrelation predicted for the growth of the population from year to year (Punt).

(3) Implementation of the environmental variability population model (Cooke, 2007) to provide CVs and temporal autocorrelation estimates for the growth of the population from year to year for the higher value options for CV and temporal autocorrelation in the standard set of scenarios for that model (Table 2 in IWC, 2010a) (Punt assisted by Allison).

(4) Implementation of the environmental variability population model (Cooke, 2007) to determine the predicted relationship between the length of series and estimated level of variability in the population rate of increase for the standard scenarios (Table 2 in IWC, 2010a) (Allison).

(5) Reruns of the simulation testing of the meta-analysis approach of SC/A10/MSYR2 for the scenarios specified in Section 4 above, and extending the approach to be able to input data series of different lengths (Punt).

(6) Analysis of calving rate, calving interval and survival rate data using a Bayesian mixed effects model (Cooke).

In addition, the following issues were referred to the 2010 Annual Meeting for further consideration there:

- (a) Implementation of the model of Annex D including an appropriate representation of variation in annual survival rates based on information on strandings.
- (b) Application of a refined version of the approach in SC/A10/MSYR2 to provide an updated probability distribution for the rate of increase for an 'unknown' stock in the limit of zero population size, r_0 , using data on observed rates of increase and their standard errors.
- (c) Consideration of whether further efforts should be expended to search for population-variability-related data series for other large mammalian taxa.
- (d) Consideration of whether genetic data might be able to place bounds on the plausible range of values for variation and temporal autocorrelation parameters in the environmental variability population model (Cooke, 2007).

6. ADOPTION OF REPORT

The Chair thanked the rapporteurs, participants (both present and contributing from afar) for their contributions and Punt for the meeting arrangements. Although progress might not have been as great as had been anticipated, partly due to the ‘volcanic disruption’, the Workshop had been fruitful and good humoured. The participants thanked the Chair for handling the meeting with informality and tolerance!

6. ADOPTION OF REPORT

The report was adopted by email. The Chair expressed special thanks to Jooke Robb

REFERENCES

- Barlow, J. and Clapham, P.J. 1997. A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecology* 78(2): 535-46.
- Best, P.B. 2004. Trends in the southern right whale population wintering in South African waters, 1971-2003. Paper SC/56/SH5 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 9pp. [Paper available from the Office of this Journal].
- Best, P.B., Brandao, A. and Butterworth, D.S. 2005. Updated estimates of demographic parameters for southern right whales off South Africa. Paper SC/57/BRG2 presented to the IWC Scientific Committee, June 2005, Ulsan, Korea. 17pp. [Paper available from the Office of this Journal].
- Best, P.B., Brandão, A. and Butterworth, D.S. 2001. Demographic parameters of southern right whales off South Africa. *J. Cetacean Res. Manage. (special issue)* 2: 161-69.
- Branch, T.A. 2007. Abundance of Antarctic blue whales south of 60°S from three complete circumpolar sets of surveys. *J. Cetacean Res. Manage* 9(3): 253-62.
- Branch, T.A., Matsuoka, K. and Miyashita, T. 2003. Antarctic blue whales are recovering. Paper SC/55/SH6 presented to the IWC Scientific Committee, May 2003, Berlin. 21pp.
- Brownell, R.L., Makeyev, C.A.F. and Rowles, T.K. 2007. Stranding trends for eastern gray whales, *Eschrichtius robustus*: 1975-2006. Paper SC/59/BRG40 presented to the IWC Scientific Committee, May 2007, Anchorage, Alaska (unpublished). 11pp. [Paper available from the Office of this Journal].
- Calambokidis, J. 2009. Abundance estimates of humpback and blue whales off the US West Coast based on mark-recapture of photo-identified individuals through 2008. Report to the NMFS Scientific Review Group.
- Calambokidis, J. and Barlow, J. 2004. Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. *Mar. Mammal Sci.* 20(1): 63-85.
- Clapham, P., Barlow, J., Bessinger, M., Cole, T., Mattila, R., Pace, R., Palka, D., Robbins, J. and Seton, R. 2003. Abundance and demographic parameters of humpback whales from the Gulf of Maine, and stock definition relative to the Scotian shelf. *J. Cetacean Res. Manage.* 5(1): 13-22.
- Cooke, J., Rowntree, V. and Payne, R. 2003. Analysis of inter-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identification of calving females observed off Peninsula Valdes, Argentina, during 1971-2000. Paper SC/55/O23 presented to the IWC Scientific Committee, May 2003, Berlin (unpublished). 16pp. [Paper available from the Office of this Journal].
- Cooke, J.G. 2007. The influence of environmental variability on baleen whale sustainable yield curves. Paper SC/N07/MSYR1 presented to the MSYR Workshop, Seattle, USA, 16-19 November 2007 (unpublished). 19pp. [Paper available from the Office of this Journal].
- Fujiwara, M. and Caswell, H. 2001. Demography of the endangered north Atlantic right whale. *Nature* 414(November 2001): 537-41.
- Gabriele, C.M., Straley, J.M. and Neilson, J.L. 2007. Age at first calving of female humpback whales in southeastern Alaska. *Mar. Mammal Sci.* 23(1): 226-39.
- George, J.C., Bada, J., Zeh, J., Scott, L., Brown, S.E., O'Hara, T. and Suydam, R. 1999. Age and growth estimates of bowhead whales (*Balena mysticetus*) via aspartic acid racemization. *Can. J. Zool.* 77: 571-80.
- George, J.C., Zeh, J., Suydam, R. and Clark, C. 2004. Abundance and population trend (1978-2001) of western arctic bowhead whales surveyed near Barrow, Alaska. *Mar. Mammal Sci.* 20(4): 755-73.
- Hiby, L. and Lovell, P. 2001. A note on an automated system for matching the callosity patterns on aerial photographs of southern right whales. *J. Cetacean Res. Manage. (special issue)* 2: 291-95.
- Inchausti, P. and Halley, J. 2001. Investigating long-term ecological variability using the Global Population Dynamics Database. *Science* 293: 655-57.
- International Whaling Commission. 2009. Report of the MSYR Workshop, 16-19 November 2007, National Marine Mammal Laboratory, Alaska Fisheries Science Center, Seattle, WA, USA. *J. Cetacean Res. Manage. (Suppl.)* 11:467-80.
- International Whaling Commission. 2010a. Report of the Intersessional Workshop on MSYR for Baleen Whales, 6-8 February 2009, Seattle. *J. Cetacean Res. Manage. (Suppl.)* 11(2):493-508.

- International Whaling Commission. 2010b. Report of the Scientific Committee. Annex D. Report of the Sub-committee on the Revised Management Procedure (RMP). *J. Cetacean Res. Manage (Suppl.)* 11(2):114-34.
- International Whaling Commission. 2010c. Report of the Scientific Committee. Annex P. Work Plan for Completion of the MSYR Review. *J. Cetacean Res. Manage (Suppl.)* 11(2):399-400.
- Koski, W.R., Davis, R.A., Miller, G.W. and Withrow, D.E. 1992. Growth rates of bowhead whales as determined from low-level aerial photogrammetry. *Rep. int. Whal. Commn* 42: 491-99.
- Koski, W.R., Davis, R.A., Miller, G.W. and Withrow, D.E. 1993. Reproduction. pp.239-74. In: Burns, J.J., Montague, J.J. and Cowles, C.J. (eds). *The Bowhead Whale*. Special Publication No.2. The Society for Marine Mammalogy, Lawrence, Kansas. 787pp.
- Koski, W.R., George, J.C., Suydam, R., Rugh, D.J. and Brandon, J. 2004. Aerial photography of bowhead whales at Barrow, Alaska, during the 2003 and 2004 spring migrations. Paper SC/56/BRG26 presented to the IWC Scientific Committee, July 2004, Sorrento, Italy (unpublished). 9pp. [Paper available from the Office of this Journal].
- Kraus, S.D., Pace, R.M., III. and Frasier, T.R. 2007. High investment, low return: The strange case of reproduction in *Eubalaena glacialis*. pp.172-99. In: Kraus, S.D. and Rolland, R.M. (eds). *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Harvard University Press, Cambridge, MA.
- Laake, J., Punt, A., Hobbs, R., Ferguson, M., Rugh, D. and Breiwick, J. 2009. Re-analysis of gray whale southbound migration surveys 1967-2006. *NOAA Tech. Mem. NMFS-AFSC* 203. 55pp.
- Laurie, A.H. 1937. The age of female blue whales and the effect of whaling on the stock. *Discovery Rep.* 15(2): 223-84.
- Lockyer, C. 1984. Review of baleen whale (Mysticeti) reproduction and implications for management. *Rep. int. Whal. Commn (special issue)* 6: 27-50.
- Mizroch, S.A., Herman, L.M., Straley, J.M., Glockner-Ferrari, D.A., Jurasz, C., Darling, J., Cerchio, S., Gabriele, C.M., Salden, D.R. and von Ziegesar, O. 2004. Estimating the adult survival rate of central north Pacific humpback whales (*Megaptera novaeangliae*). *J. Mammal.* 85(5): 963-72.
- Mobley, J.M., Spitz, S., Grotenfeld, R., Forestell, P., Frankel, A.S. and Bauer, G.B. 2001. Abundance of humpback whales in Hawaiian waters: results of 1993-2000 aerial surveys. Report to the Hawaiian Islands Humpback Whale National Marine Sanctuary. 16pp.
- Perryman, W.L., Donahue, M.A., Perkins, P.C. and Reilly, S.B. 2002. Gray whale calf production 1994-2000: Are observed fluctuations related to changes in seasonal ice cover? *Mar. Mammal Sci.* 18(1): 121-44.
- Punt, A.E. and Wade, P.R. 2010. Population status of the eastern North Pacific stock of gray whales in 2009. US Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-207. 43pp.
- Ramp, C. 2008. Population dynamics and social organisation of humpback whales (*Megaptera novaeangliae*) in the Gulf of St. Lawrence - a long-term study. Phd thesis, University of Bremen, Bremen, Germany. <http://nbn-resolving.de/urn:nbn:de:gbv:46-diss000111355>.
- Ramp, C., Bérubé, M., Hagen, W. and Sears, R. 2006. Survival of adult blue whales *Balaenoptera musculus* in the Gulf of St. Lawrence, Canada. *Mar. Ecol. Prog. Ser.* 319: 287-95.
- Ramp, C., Berube, M., Palsboll, P., Hagen, W. and Sears, R. 2010. Sex-specific survival in the humpback whale (*Megaptera novaeangliae*) in the Gulf of St. Lawrence, Canada. *Mar. Ecol. Prog. Ser.* 400: 267-76.
- Robbins, J. 2007. Structure and dynamics of the Gulf of Maine humpback whale population, University of St Andrews, St Andrews, Scotland. [Available at: <http://hdl.handle.net/10023/328>].
- Rosenbaum, H.C., Weinrich, M.T., Stoleson, S.A., Gibbs, J.P., Baker, C.S. and DeSalle, R. 2002. The effect of differential reproductive success on population genetic structure: Correlations of life history with matriline in humpback whales of the Gulf of Maine. *J. Hered.* 93(6): 389-99.
- Ruud, J.T., Jonsgard, A. and Ottestad, P. 1950. Age-studies on blue whales. *Hvalrådets Skrifter* 33: 5-63.
- Schell, D.M., Saupe, S.M. and Haubenstock, N. 1989. Natural isotope abundances in bowhead whale (*Balaena mysticetus*) baleen: markers of ageing and habitat usage. *Ecol. Stud.* 68: 260-69.
- Straley, J.M., Quinn, T.J. and Gabriele, C.M. 2009. Assessment of mark-recapture models to estimate the abundance of a humpback whale feeding aggregation in Southeast Alaska. *J. Biogeography* 36: 427-38.
- Weinrich, M. and Corbelli, C. 2009. Does whale watching in Southern New England impact humpback whale (*Megaptera novaeangliae*) calf production or calf survival? *Biol. Conserv.* 142: 2931-40.
- Yochem, P.K. and Leatherwood, S. 1985. Blue whale - *Balaenoptera musculus* (Linnaeus, 1758). pp.193-240. In: Ridgway, S.H. and Harrison, R. (eds). *The Sirenians and Baleen Whales*. Academic Press, London and Orlando. xviii+362pp.
- Zeh, J., Poole, D., Miller, G., Koski, W., Baraff, L. and Rugh, D. 2002. Survival of bowhead whales, *Balaena mysticetus*, estimated from 1981-98 photo-identification data. *Biometrics* 58: 832-40.
- Zeh, J.E. and Punt, A.E. 2005. Updated 1978-2001 abundance estimates and their correlations for the Bering-Chukchi-Beaufort Seas stock of bowhead whales. *J. Cetacean Res. Manage.* 7(2): 169-75.

Annex A

Agenda

1. INTRODUCTORY ITEMS

- 1.1 Opening remarks
- 1.2 Election of Chair
- 1.3 Appointment of rapporteurs
- 1.4 Adoption of agenda
- 1.5 Review of documents

2. ESTIMATION OF VARIABILITY FROM DATASETS FOR BALEEN WHALE SPECIES

- 2.1 General overview of time series data
 - 2.1.1 North Atlantic right whale
 - 2.1.2 South Atlantic right whales
 - 2.1.3 Bowhead whales
 - 2.1.4 Humpback whales
 - 2.1.4.1 North Atlantic
 - 2.1.4.2 North Pacific
 - 2.1.5 Fin whales
 - 2.1.6 Blue whales
 - 2.1.7 Gray whales
- 2.2 Summary of data to be used in further analyses
- 2.3 Analysis

3. OTHER SOURCES OF INFORMATION

4. REVISED META-ANALYSIS OF POPULATION GROWTH RATES

5. WORKPLAN

6. ADOPTION OF REPORT

Annex B

List of Documents

SC/A10/MSYR1. Lurman, L. GPP: Initial summary.

SC/A10/MSYR2. Punt, A.E. A revised Bayesian meta-analysis for estimating a posterior distribution for the rate of increase for an “Unknown” stock

SC/A10/MSYR3. Brandão, A., Best, P.B. and Butterworth, D.S. A note on possible change in the mean calving for Southern Right whales off South Africa.

Annex C

Preliminary estimates of calving variability for nine stocks of mysticetes

JOHN R. BRANDON AND TOSHIHIDE KITAKADO

Given a time series of observations (i.e., calving proportions or intervals) it is assumed that the i^{th} observation is related to the expected value, such that:

$$x_i = \mu + \varepsilon_i \quad (1)$$

where:

- x_i is the i^{th} value of interest (e.g., calving proportions in year i);
- μ is the expectation of the value of interest;
- ε_i is the deviation of the i^{th} value from the expectation, where:

$$\varepsilon_i \sim N(0, \sigma^2), \text{ and } \sigma^2 \text{ is the variance of the deviations.}$$

Further, it is assumed that the deviations were correlated through time, such that:

$$\varepsilon_{i+1} = \rho \varepsilon_i + \eta_i \quad (2)$$

where:

- ρ is the correlation coefficient, and:

$$\eta_i \sim N(0, (1 - \rho^2) \sigma^2) \text{ i.i.d.}$$

The likelihood of observing a time series of data incorporated the possibility that the time series in question may have missing years of observations. That is: let t be the span of years over which observations are available, such that $i = 1, \dots, t$. Each time series of observations are available for n out of those t years, such that $j = 1, \dots, n$. In order to allow for $n \leq t$, the negative log-likelihood of observing a given time series is:

$$-\ln(LL) = \ln(\sigma_1) + \frac{(x_1 - \mu)^2}{2\sigma_1^2} + \sum_{j=2}^n \left[\ln(\sigma_j) + \frac{1}{2\sigma_j^2} (\varepsilon_j - \rho^{r_j} \varepsilon_{j-1})^2 \right] \quad (3)$$

where:

$$\sigma_1^2 = \sigma^2 / (1 - \rho^2);$$

- r_j is the number of years between successive observations (i.e., if observations between the $j-1$ and j^{th} time-step are in successive years, then $r_j = 1$; if there is one missing year between observations $r_j = 2$, etc...), and;

σ_j^2 is the variance of the deviations taking into account the possibility of missing years, which leads to:

$$\sigma_j^2 = \sum_{s=1}^{r_j} \sigma^2 \rho^{2(s-1)}$$

Three parameters were estimated: μ , σ and ρ . The estimates and their standard errors were calculated by using the *mle* function in the statistical software *R* (v. 2.9.1). In addition to the estimated parameters, the CV of the deviations (i.e., $CV = \sigma / \mu$) was also derived for comparison. The CVs are approximately equal to the standard deviations in log-space, which is a typical parameterization of environmental variability in population dynamics models (here an initial log-transformation could not be used because of zeros in some series). Results are given in Table 4 of the main report.

These preliminary estimates are based on empirical observations and provide a basis on which to consider the extent of the effect of environmental variability in reproductive success of mysticetes. However, there are certain limitations in this modeling approach which need to be addressed before any conclusions are drawn from these examples. Notably, there has been no attempt to account for observation (sampling) error in the time series. Hence, the estimated extent of environmental variability may be biased high because it is assumed here that the calving values are known exactly. In order to take observation error into account, it will be necessary to model error variance for each data point as the sum of the unknown process variance and the observation error. Where the latter are not available, some distributional assumption will need to be made. For example, the sampling error for calf count data can be modelled using a Poisson distribution.

Once observation error has been taken into account, alternative methods will be needed in order to account for the remaining deviations due to environmental variability. For example, the deviations may be treated as nuisance parameters and integrated out of the likelihood when fitting the model. It seems likely that this integration will be performed using numerical (in contrast to analytical) approaches for some, if not all of the data sets. For those situations, the random effects module for AD Model Builder may be used to implement these suggested improvements, which should provide a more accurate representation of the extent of environmental variability in these case studies.

Annex D

Population model projections under different levels of process error

ANDRÉ E. PUNT

The following population dynamics model forms the basis for the forecasts under different levels of variability in calving rate (and in principle survival):

$$N_{y,a} = \begin{cases} f_y (N_y^m - N_{y-1,0} S_{y-1}) & \text{if } a = 0 \\ N_{y-1,a-1} S_{y-1} & \text{if } 1 \leq a < x \\ (N_{y-1,x} + N_{y-1,x-1}) S_{y-1} & \text{if } a = x \end{cases} \quad (1)$$

where $N_{y,a}$ is the number of animals of age a at the start of year y ,

N_y^m is the number of “mature” females at the start of year y :

$$N_y^m = 0.5 \sum_{a=a_m}^x N_{y,a}$$

f_y is the calving rate (number of calves per mature female which did not calf the previous year – this number of mature females is given by N_y^m) during year y :

$$f_y = f e^{\varepsilon_y^f - \sigma_f^2/2} \quad \varepsilon_y^f = \rho^f \varepsilon_{y-1}^f + \sqrt{1 - (\rho^f)^2} \eta_y^f \quad \eta_y^f \sim N(0; \sigma_f^2)^1 \quad (2)$$

f is the expected calving rate (in the absence of density-dependence),

ρ^f is the extent of auto-correlation in calving rate,

σ_f is the extent of variation in calving rate,

S_y is the survival rate during year y ($S_y = e^{-M_y}$):

$$M_y = \bar{M} + \varepsilon_y^M \quad \varepsilon_y^M = \rho^M \varepsilon_{y-1}^M + \sqrt{1 - (\rho^M)^2} \eta_y^M \quad \eta_y^M \sim N(0; \sigma_M^2) \quad (3)$$

ρ^M is the extent of auto-correlation in natural mortality, and

σ_M is the extent of variation in natural mortality (set equal to 0 for the analyses of this document).

Table 1 lists the values for the parameters of this model. Table 1 does not list a value for f . The value for this parameter (0.3644) is selected so that the deterministic rate of increase is equal to the pre-specified value for r_{\max} . The population is projected ahead for 2,000 years, and the annual rate of increase, $\tilde{r}_y = \ln(N_y^m / N_{y-1}^m)$ is computed. Table 2 lists the

¹ Subject to the constraint that calving rate cannot exceed 1 (if a generated value for the calving rate exceeds 1, the value for η_y^f is generated again and this process repeated until the calving rate is less than 1).

values for four output statistics (mean, standard deviation, CV and lag-1 autocorrelation over years 200-2000) for \tilde{r}_y and the “raw” calving rate $N_{y,0} / N_y^{m2}$. Results are shown in Table 2 for five runs of the model based on different sequences of random numbers. The CV and lag-1 autocorrelations in Table 2 are appreciably lower than the input values for σ_f and ρ^f in Table 1. Application of the model in which $\sigma_f=0.6$ and $\rho^f=0.9$ leads to much closer agreement between the outputs of the model and the values for the CV and lag-1 autocorrelation coefficient for the calving rate in Table 1 (Table 3). Fig. 1 shows the annual values for \tilde{r}_y and the “raw” calving rate (called ‘calving proportion’ elsewhere in this report) corresponding to the parameters in Table 3.

Table 1

Values for the parameters of the population dynamic model.

\bar{M}	X	a_m	r_{\max}	σ_M	σ_f	ρ^M	ρ^f
$-\ln 0.9$	20	5	0.05	0	0.44	0	0.7

Table 2

Summary statistics for the application of the model based on the parameter values in Table 1. Auto is the temporal autocorrelation.

ROI				Calving rate			
Mean	SD	CV	Auto	Mean	SD	CV	Auto
0.0445	0.0278	0.6239	0.2276	0.2536	0.0915	0.3608	0.3457
0.0468	0.0283	0.6058	0.2393	0.263	0.0947	0.3600	0.3625
0.0471	0.0290	0.6145	0.2636	0.2653	0.0993	0.3743	0.3855
0.0469	0.0287	0.6119	0.2771	0.2643	0.0976	0.3691	0.4087
0.0461	0.0286	0.6212	0.2598	0.2613	0.0978	0.3742	0.3943

Table 3

Summary statistics for the application of the model based on the parameter values in Table 1, except that $\sigma_f=0.6$ and $\rho^f=0.9$.

ROI				Calving rate			
Mean	SD	CV	Auto	Mean	SD	CV	Auto
0.0371	0.0280	0.7552	0.6247	0.2282	0.1006	0.4409	0.7291
0.042	0.0283	0.675	0.5913	0.2474	0.1031	0.4166	0.7031
0.0424	0.0293	0.6922	0.6160	0.25	0.1082	0.4328	0.7220
0.0421	0.0301	0.7150	0.6287	0.2493	0.1109	0.4447	0.7299
0.0401	0.0299	0.7463	0.6374	0.2412	0.1100	0.4562	0.7366

² The raw calving rate was chosen for consistency with the approach used when analysing the data for the actual populations.

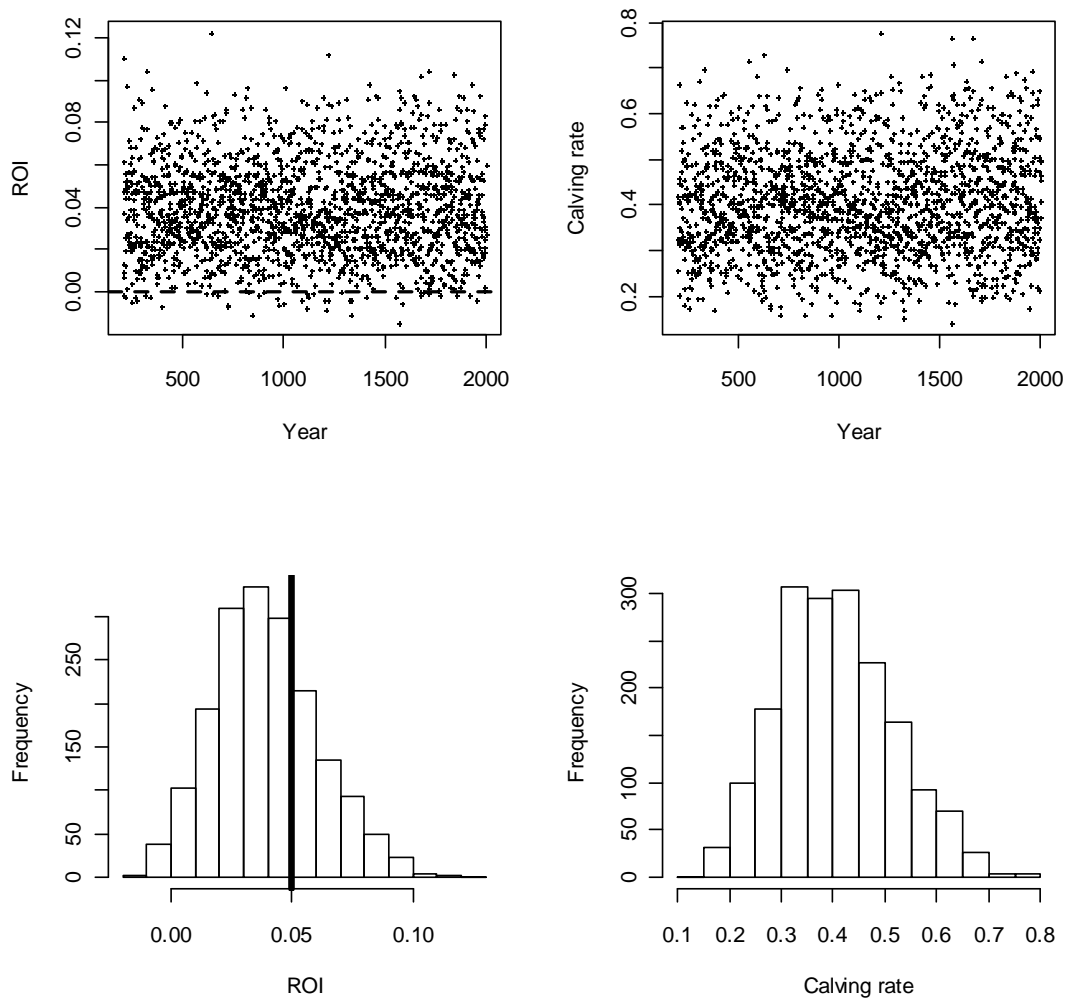


Fig. 1. Time-series of the annual rate of increase and the annual “raw” calving rate based on $\sigma_f=0.6$ and $\rho^f=0.9$.