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Further developments of the individual based energetics model and progress on the development of an emulation model

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Abstract

Some improvements in the parameterisation of the individual based energetics model (IBEM) are described and illustrated. Some examples are given of the density dependent relationships for a range of demographic parameters and how these are affected by variability in food supply. The results show that the variability and correlation between demographic parameters is linked to variable food supply. A stage-based model is developed to use these parameter characteristics to emulate the results given by the full IBEM. Some illustrations show that some features of the IBEM are emulated by the stage-based model but some differences in dynamics are also evident. Possible future developments of the models are discussed.

Over several years the Scientific Committee has been presented with results from an individual based energetics model (IBEM) designed to examine the relationship between the energetics of individual whales and the demographic properties of populations of whales (de la Mare, 2013, 2014; de la Mare and Miller, 2015, 2016). A particular focus of these models has been examining the nature of density dependence and the consequential effects on the likely properties of the yield curves of exploited whale populations.

This paper presents some refinements to the IBEM to improve the properties of density dependence in growth and refinements to the modelling of pregnancy rates. The details of these changes are given in the updated model description in Annex 1. The pregnancy model has been simplified to enable more direct parameterisation of the relationship between an animal's birth-mass and subsequent fertility. The growth model has been changed to allow for specified allocation of energy to growth or storage, and to ensure that catch-up growth is limited when energy intake is low.

An animal's growth is controlled by a 'programmed' growth curve unique to each individual, acquired at birth with sex specific values for k and L_∞. The values for these parameters are partially inherited from the mother (as a weighted average of the mother's parameters and the population mean values – but re-scaled appropriately for males). The programmed growth curve describes the upper limit of the length of the animal on each birthday and is given by a conventional von Bertalanffy equation. Animals will grow on a realised growth curve that lies below the programmed curve when food availability is low. Moreover, growth is only possible when food has been ingested. The properties of the growth model are illustrated in figs 1 and 2 which show the resultant density dependence in the population means of parameters of the von Bertalannfy model from one example of the model based on humpback whales. In this case animals in a depleted stock grow faster, reach a somewhat larger size, and as a consequence of faster growth, reach sexual maturity at a younger age.

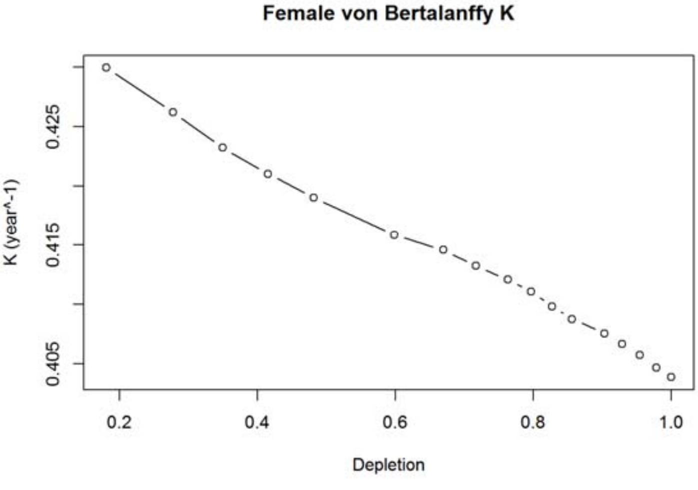

Fig 1. Density dependence in the von Bertalanffy growth rate term emerging from the improved IBEM growth model.

The second development reported here is the conversion of the output of runs of the IBEM used to build yield curves (see for example de la Mare and Miller, 2015) into functional relationships to describe density dependence in key demographic parameters. These relationships are then incorporated into a stage-based model designed to reproduce the main features of the IBEM, but with much faster execution time. Such a model has been requested by the Scientific Committee and could allow for exploration of what features of the IBEM lead to the differences in the relationship between MSYR1+ and MSYR mature from IBEM and BALEEN II reported in de la Mare and Miller (2015, 2016).

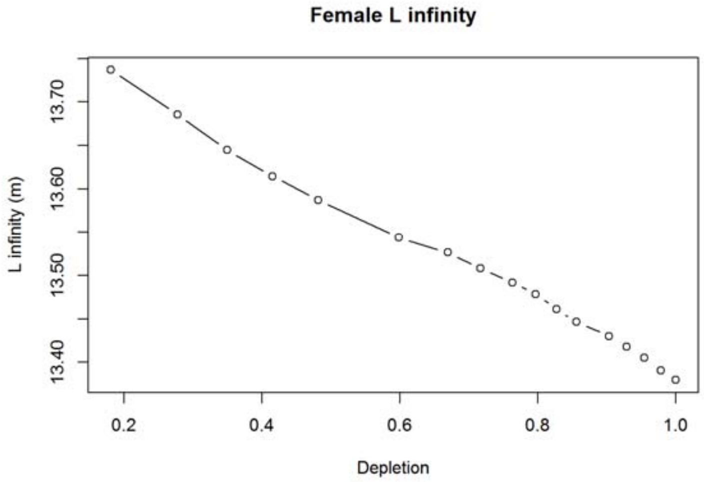

Fig 2. Density dependence in the von Bertalanffy L_∞ term emerging from the improved IBEM growth model.

Two examples are given below based on the humpback parameterisation of the IBEM to illustrate the density dependence in other demographic parameters. The two examples differ in the degree of variability in the amount of food available. The first example has no inter-annual variability in food supply, while the second example has food variability with a coefficient of variation (CV) of 0.3. The parameters shown are those required for the stage-based model described in the second section of this paper. Only the curves for females are shown, the curves for males are very similar.

Figs 3, 4 and 5 show the density dependence in survival rates of calves, juveniles and matures as well as pregnancy and maturation rates. As would be expected, juvenile and mature survival rates increase for depleted populations, as do the pregnancy and maturation rates. The sex ratio is not density dependent. There are two curves shown for calf survival; the upper curve shows the survival of calves whose mothers were not caught during the whaling season, while the lower curve shows the survival of all calves including those who died when their mothers were caught while suckling. Consequently the survival of calves falls in proportion to the catch-rates of mature females.

This will have the effect that the rate of increase of a depleted population without exploitation will be greater than the rate of exploitation that would maintain the population at the same equilibrium level. This is different from the BALEEN II model that assumes in effect that the survival of calves is independent of the survival of their mothers. This may be one of the reasons why the IBEM models lead to different ratios for the $\mathrm{MSYR}_{\mathrm{mat}}$ to MSYR_{1+} than those from BALEEN II. This process will also have some effect on the analyses of the range of MSYR determined from the rates of increase of depleted population. This effect warrants further investigation.

The figures also show that the demographic parameters are subject to inter-annual variability (shown as error bars ± 1 standard deviation). The extent of the variability is low in this model that lacks inter-annual variability in food supply. The distributions of the parameters across years are shown in figs 6, 7 and 8. In this low variability model the variation in the demographic parameters is reasonably symmetric and could be modelled as normally distributed. Table 1 gives the correlations between these parameters, showing that there is some relatively weak correlations between them. These should nevertheless be accounted for using a multi-normal model.

Figs 9, 10 and 11 show the density dependent parameters for the variable food case. The same general patterns for the mean values of the parameters is obtained, but the inter-annual variability in the parameters is much greater. Figs 12, 13 and 14 show that, in contrast to the constant food case, the distributions of the demographic parameters are considerably more skewed and would require transformations to make them more consistent with easily generated random numbers such as the multinormal distribution. Table 2 shows in the variable case there are much stronger correlations between the parameters and it is essential that these be preserved in any models generating random sets of the parameters.

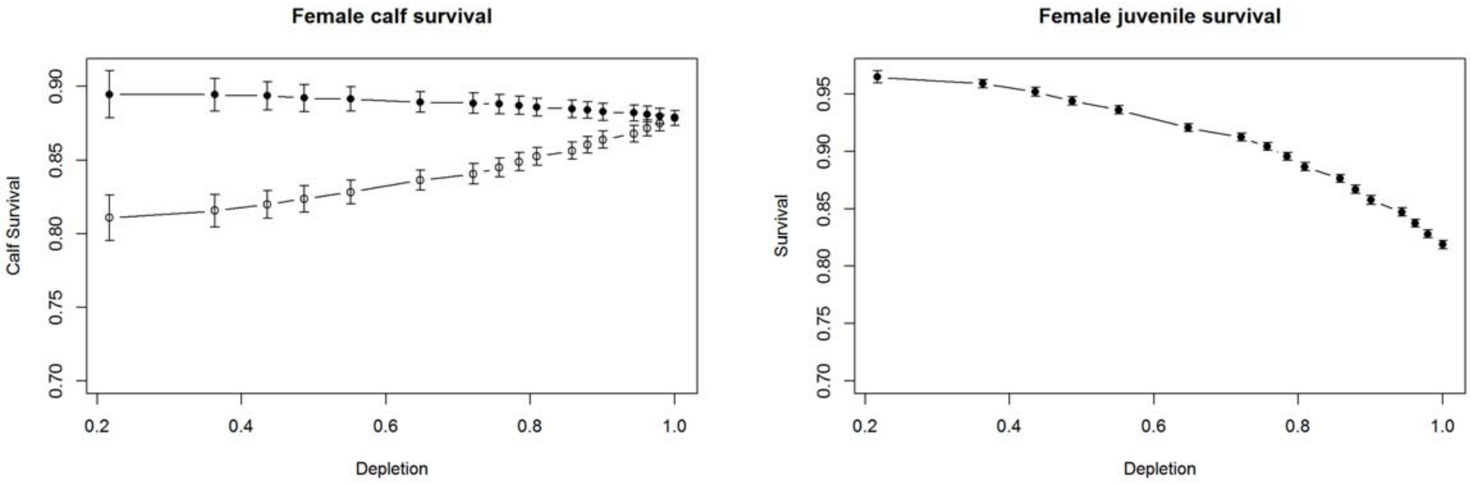

Fig 3. Density dependent relationships for female calf survival (without catches ●, with o) and juvenile survival rate for the constant food humpback IBEM.

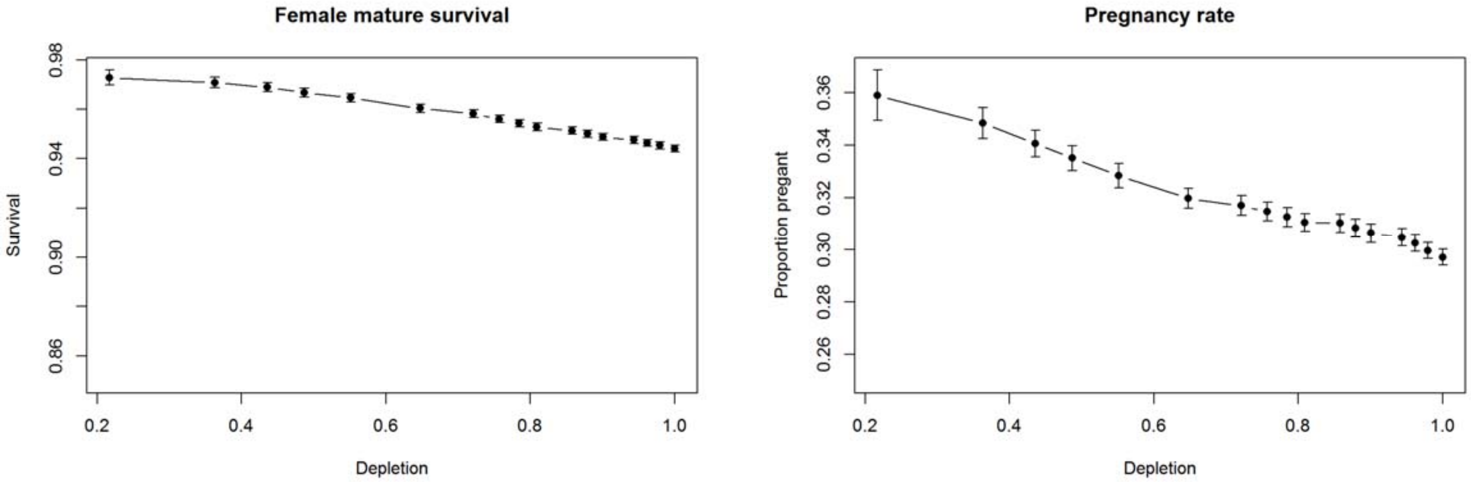

Fig 4 Density dependent relationships for female mature survival and pregnancy rates for the constant food humpback IBEM.

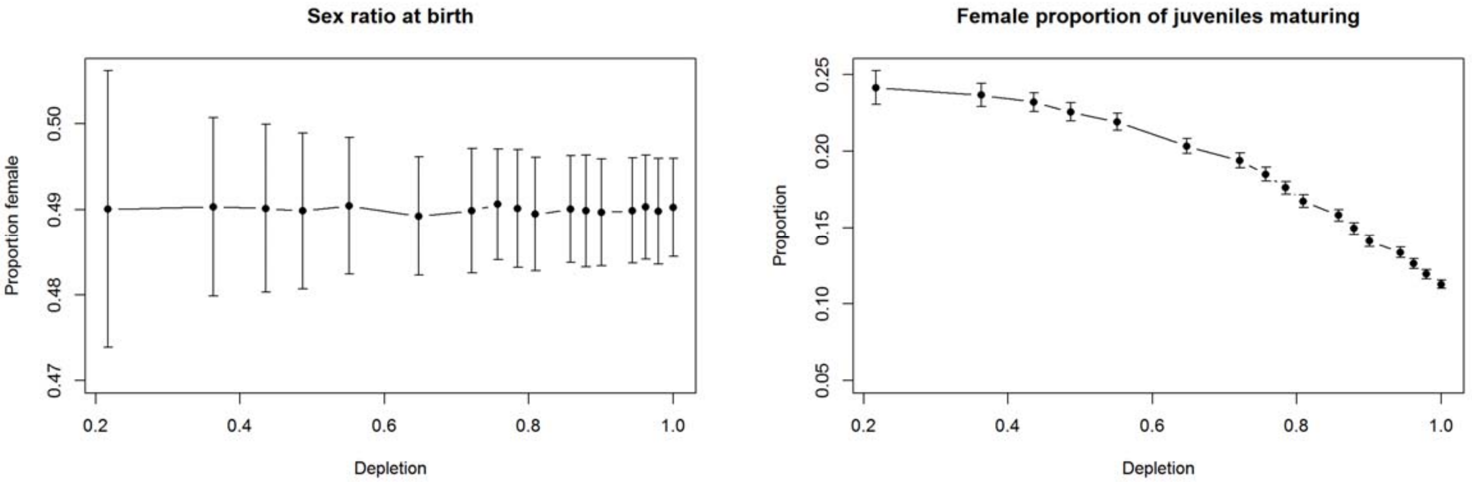

Fig 5 Density dependent relationships for sex ratio and the proportion of females maturing each year for the constant food humpback IBEM.

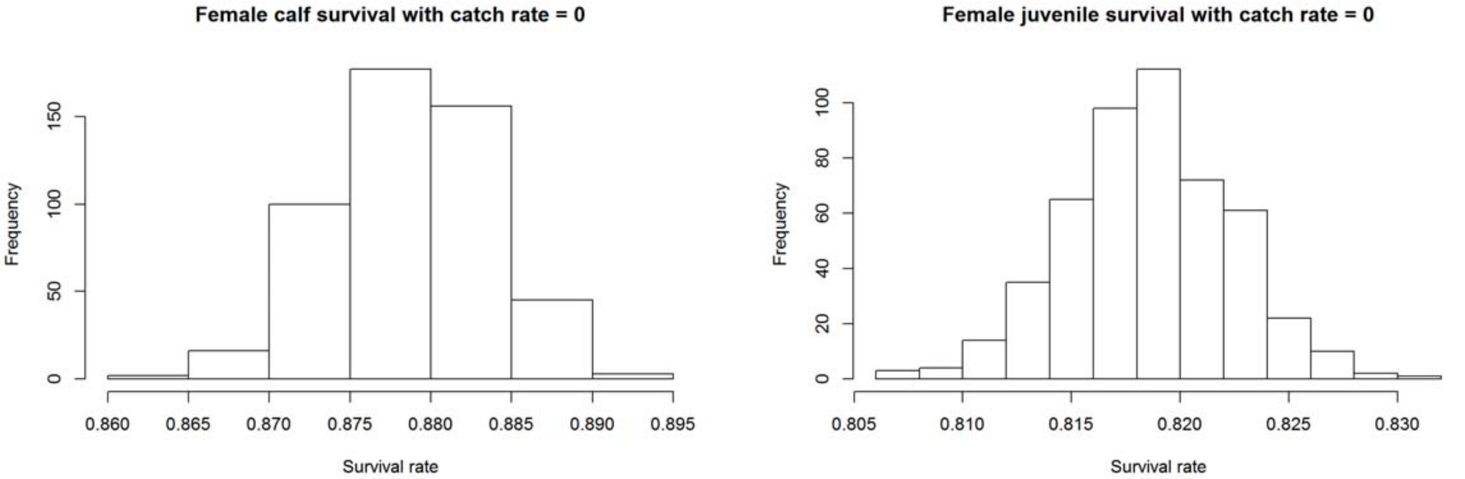

Fig 6 Distributions of yearly values of the female calf and juvenile survival rates for the constant food humpback IBEM.

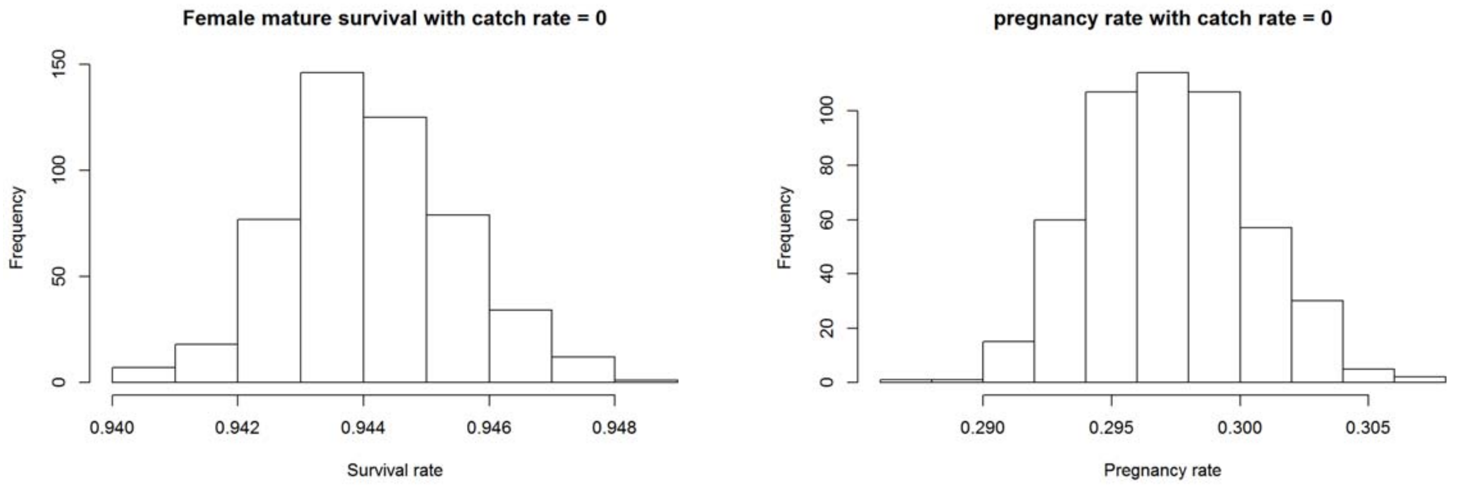

Fig 7. Distributions of yearly values of the female mature survival and pregnancy rates for the constant food humpback IBEM.

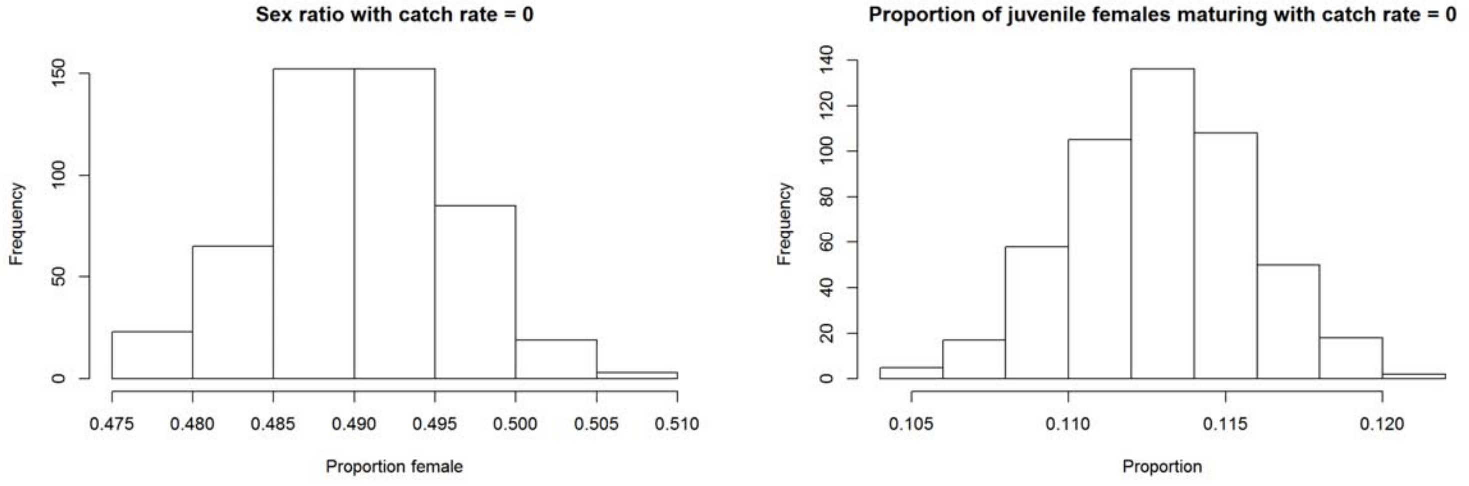

Fig 8. Distributions of yearly values of the sex ratio and the proportions of females maturing each year for the constant food humpback IBEM.

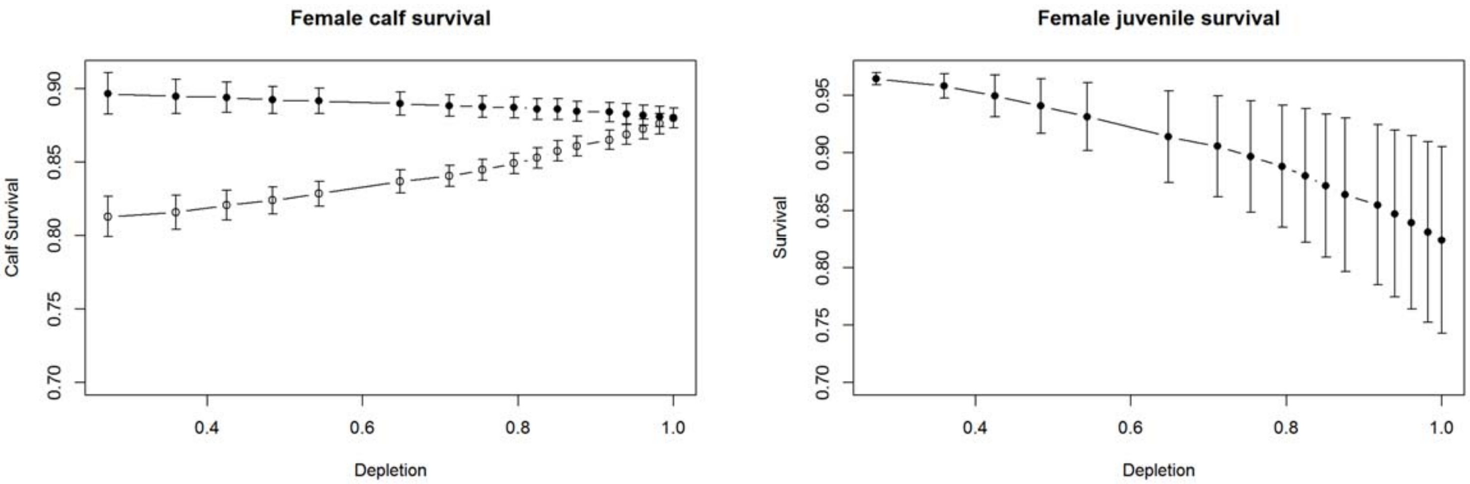

Fig 9 Density dependent relationships for female calf survival (without catches ●, with o) and juvenile survival rate for the variable food humpback IBEM.

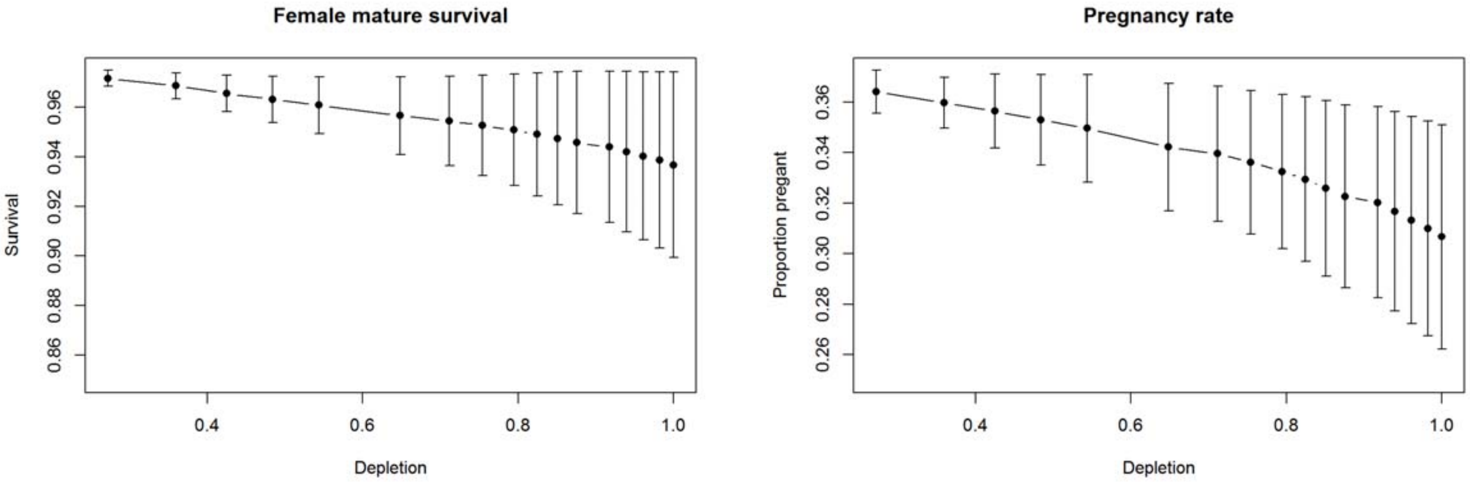

Fig 10 Density dependent relationships for female mature survival and pregnancy rates for the variable food humpback IBEM.

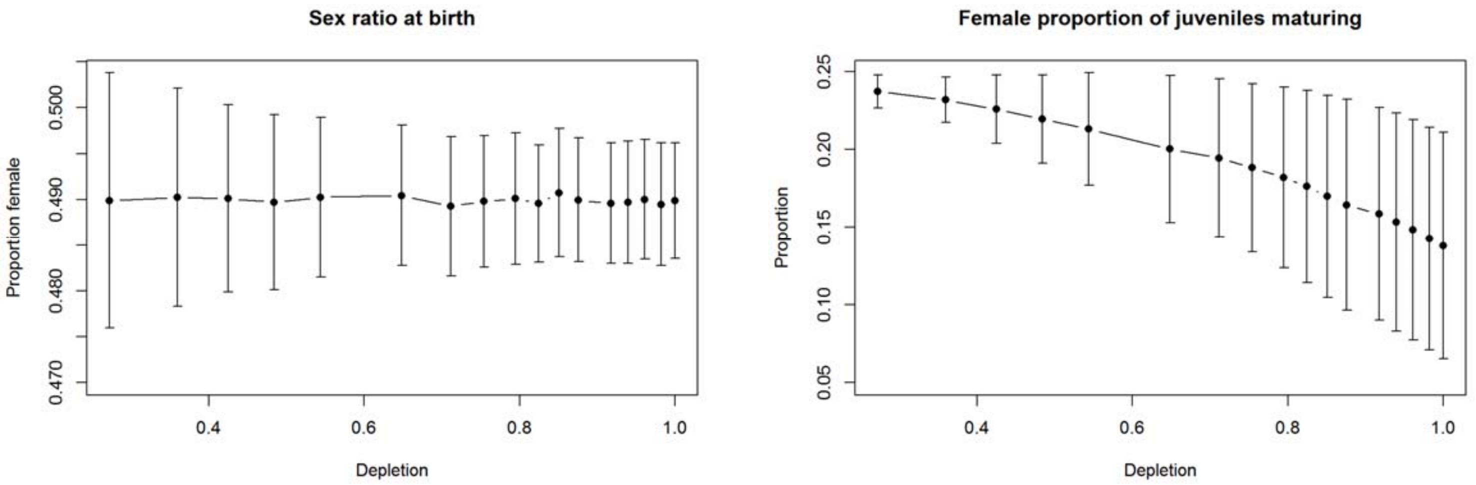

Fig 11 Density dependent relationships for sex ratio and the proportion of females maturing each year for the variable food humpback IBEM.

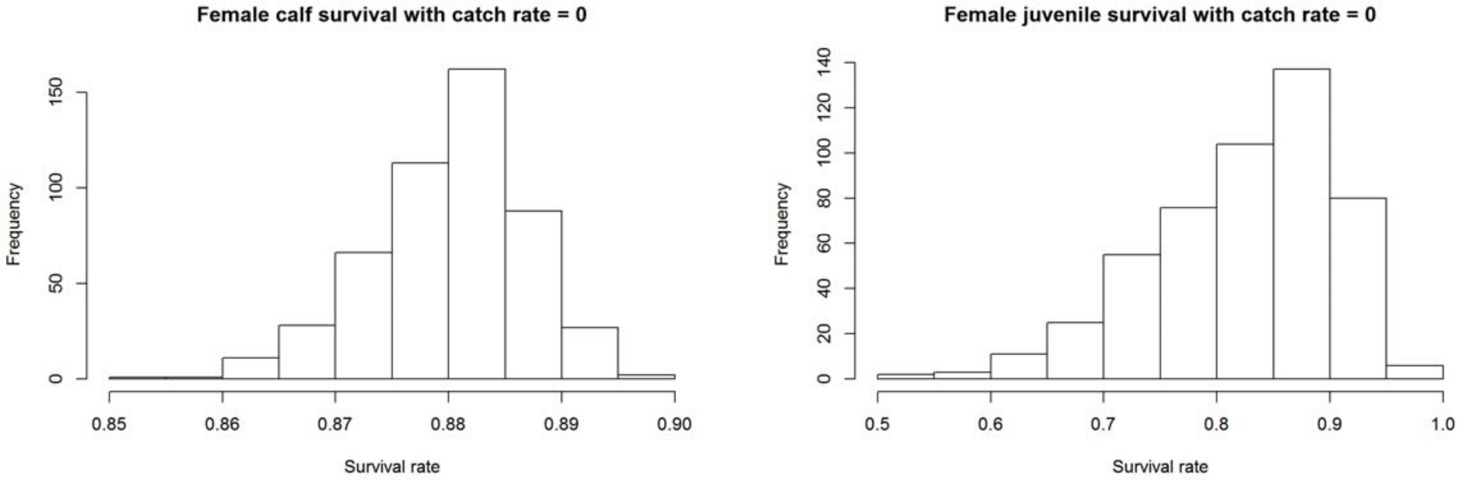

Fig 12 Distributions of yearly values of the female calf and juvenile survival rates for the variable food humpback IBEM.

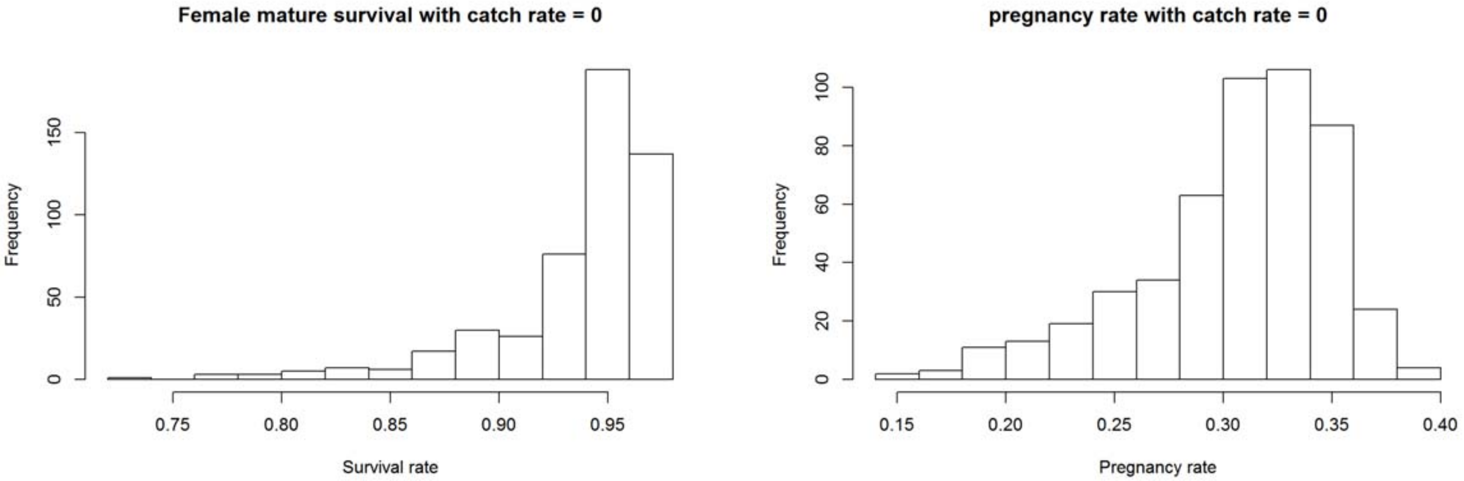

Fig 13 Distributions of yearly values of the female mature survival and pregnancy rates for the variable food humpback IBEM.

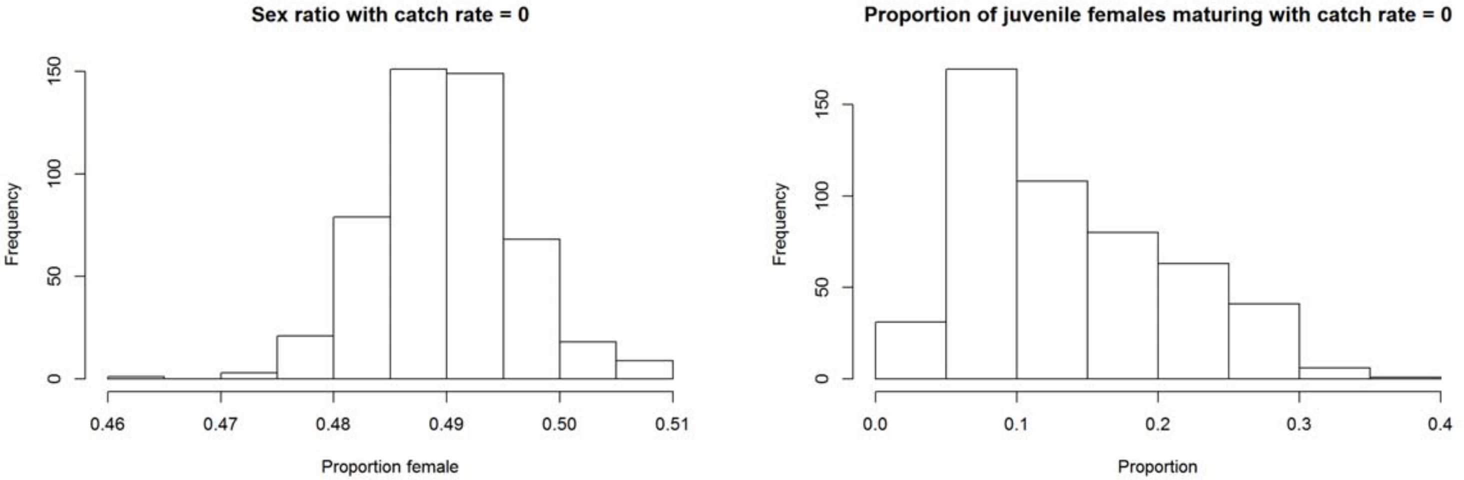

Fig 14 Distributions of yearly values of the sex ratio and the proportions of females maturing each year for the constant food humpback IBEM.

Table 1 correlation between the density dependent parameters for the constant food IBEM. (Sf1: female calf survival, Sf2: female juvenile survival, Sf3: female mature survival, Sm1: male calf survival, Sm2: male juvenile survival, Sm3 male mature survival, Preg: pregnancy rate, gf: female maturation rate, gm: male maturation rate).

Parameter	Sf1	Sf2	Sf3	Sm1	Sm2	Sm3	Preg	Sex ratio	gf	gm
Sf1	1									
Sf2	0.0429	1								
Sf3	0.0993	0.2039	1							
Sm1	-0.0663	-0.0410	0.1821	1						
Sm2	0.0010	0.1052	0.1161	0.0685	1					
Sm3	0.0154	-0.0687	0.0201	0.0433	0.0965	1				
Preg	0.0068	0.1767	0.0391	0.0451	0.1345	-0.0374	1			
Sex ratio	0.0483	0.1701	0.0316	-0.0639	-0.0909	0.0111	0.0140	1		
gf	-0.0574	0.1384	-0.0914	-0.0471	0.0439	-0.0887	-0.1079	-0.0980	1	
gm	-0.0503	0.0594	-0.0567	-0.0602	0.1523	-0.1200	-0.0886	0.1688	0.1643	1

Table 2 correlation between the density dependent parameters for the variable food IBEM

Parameter	Sf1	Sf2	Sf3	Sm1	Sm2	Sm3	Preg	Sex ratio	gf	gm
Sf1	1									
Sf2	0.4393	1								
Sf3	0.4506	0.7844	1							
Sm1	0.3061	0.4550	0.4342	1						
Sm2	0.4376	0.9943	0.7755	0.4598	1					
Sm3	0.3894	0.5832	0.8260	0.3985	0.5951	1				
Preg	0.0772	0.1434	-0.0659	0.0228	0.1432	-0.2727	1			
Sex ratio	0.0753	0.0064	0.0837	0.0323	-0.0055	0.0922	-0.0245	1		
gf	0.3048	0.6969	0.5021	0.3149	0.6874	0.4444	-0.2285	-0.0661	1	
gm	0.3192	0.7393	0.5256	0.3304	0.7349	0.4633	-0.1828	-0.0516	0.9889	1

Stage-based model

The basic model is a two sex stage based model dividing each sex into calves, juveniles and matures. The core of the model is a set of difference equations that update the model each year.

$$\begin{aligned}
N_{F,1,t+1} &= N_{F,3,t}\left(1-H_{3,t}\right)\mathrm{S}_{M,3}(D)\,\mathrm{P}(D)\rho \\
N_{M,1,t+1} &= N_{F,3,t}\left(1-H_{3,t}\right)\mathrm{S}_{M,3}(D)\,\mathrm{P}(D)\left(1-\rho\right) \\
N_{F,2,t+1} &= N_{F,1,t}\left(\mathrm{S}_{F,1}(D)-\beta H_{3,t}\right)+N_{F,2,t}\left(1-H_{2,t}\right)\left(\mathrm{S}_{F,2}(D)-\mathrm{g}_F(D)\right) \\
N_{M,2,t+1} &= N_{M,1,t}\left(\mathrm{S}_{M,1}(D)-\beta H_{3,t}\right)+N_{M,2,t}\left(1-H_{2,t}\right)\left(\mathrm{S}_{M,2}(D)-\mathrm{g}_M(D)\right) \\
N_{F,3,t+1} &= N_{F,2,t}\left(1-H_{2,t}\right)\mathrm{g}_F(D)+N_{F,3,t}\left(1-H_{3,t}\right)\mathrm{S}_{F,3}(D) \\
N_{M,3,t+1} &= N_{M,2,t}\left(1-H_{2,t}\right)\mathrm{g}_M(D)+N_{M,3,t}\left(1-H_{3,t}\right)\mathrm{S}_{M,3}(D)
\end{aligned} \tag{1.1}$$

where:

$N_{\bullet,b,t}$ is the number of animals in stage *b* for sex ● in year *t; b* take the values 1, 2 or 3 for calves, juveniles and matures respectively.

$H_{\bullet,b,t}$ is the proportion caught from stage *b* in year *t*.

β is the overlap between the whaling season and period of suckling – between 0 and 1

$\mathrm{P}(D)$ is a function returning the pregnancy rate for a specified depletion *D*.

ρ is the proportion of female calves (assumed density independent)

$\mathrm{S}_{\bullet,b}(D)$ is a function returning the survival rate of animals in stage *b* for sex ● for a specified depletion *D*.

$\mathrm{g}_{\bullet}(D)$ is a function returning for sex ● the proportion of juveniles that become mature as a function of *D*.

An equilibrium relative stage structure at *K* (*D*=1) is given by:

$$\begin{aligned}
N_{F,1} &= \rho \\
N_{M,1} &= 1-\rho \\
N_{F,2} &= \frac{\rho}{1-\mathrm{S}_{F,2}(1)}\left(\mathrm{S}_{F,1}(1)-\frac{1-\mathrm{S}_{F,3}}{\rho\,\mathrm{P}(1)}\right) \\
N_{M,2} &= \frac{\left(1-\rho\right)\mathrm{S}_{M,1}(1)}{1-\mathrm{S}_{M,2}(1)+\mathrm{g}_M(1)} \\
N_{F,3} &= \frac{1}{\mathrm{P}(1)} \\
N_{M,3} &= \frac{N_{M,2}\,\mathrm{g}_M(1)}{1-\mathrm{S}_{M,3}(1)}
\end{aligned} \tag{1.2}$$

The solution for $\mathrm{g}_F(1)$ is a balance equation given by:

$$g_F(1) = \frac{N_{F,3}\left(1 - S_{F,3}(1)\right)}{N_{F,2}} \tag{1.3}$$

This value is implicit in the equations (1.2) above and hence the female equilibrium state can be set from the pregnancy rate, sex ratio and mortality parameters alone. However the male equilibrium state needs the value of either $g_M(1)$ or $N_{M,3}$ to be fixed externally. For illustrative purposes the value of $g_M(1)$ can be set to the same value as $g_F(1)$.

Model setup using IBEM results

To set this model up as an emulator for the individual based energetics models (IBEM) requires that each of the density dependent functions be defined from outputs of the IBEM. The model stage-based model is implemented in R (R Core Development Team, 2016). The IBEM model outputs consist of summary statistics by year, and for the purposes of calculating the parameters of the stage-based model the following tables of age dependent statistics are compiled for each year of a simulation run:

- Total numbers of males and females at age $n_{\bullet,a,t}$
- Total numbers of mature males and females at age $n_{\bullet,a,m,t}$
- Total numbers of natural deaths of males and females at age $d_{\bullet,a,t}$
- Catch at age – both sexes combined

From these tables the values for all the stage-based model parameters can be tabulated for a range of depletions. Using these values, interpolating functions can be used to define the functions relating the stage-based model parameters to depletion. The numbers of calves ($N_{\bullet,1,t}$) for each sex and year from the IBEM are the zero age columns of the total number at age tables. The total numbers of mature animals are given by:

$$N_{\bullet,3,t} = \sum_{a=1}^{a_{\max}} n_{\bullet,a,m,t} \tag{1.4}$$

The numbers of juveniles are:

$$N_{\bullet,2,t} = \sum_{a=1}^{a_{\max}} \left(n_{\bullet,a,t} - n_{\bullet,a,m,t}\right) \tag{1.5}$$

The survival rates are the proportions of animals surviving for one year in each stage. For the calves there are only 'natural deaths', although in the case of humpback whales catching a mother also leads to the death of any suckling calf. The survival rate of calves is given by:

$$S_{\bullet,1,t} = \frac{d_{\bullet,a=0,t}}{n_{\bullet,a=0,t}} \tag{1.6}$$

The other survival function require the catch-at-age by sex, which, unfortunately were not included in the statistics output by the IBEM program, and so these are reconstructed by calculating the total deaths (including catches) and subtracting from those the natural deaths at age (which are included in the output of the IBEM). Total deaths at age are derived from the differences in the numbers of each cohort at successive ages, that is:

$$d_{\bullet,T,a,t} = n_{\bullet,a+1,t+1} - n_{\bullet,a,t} \tag{1.7}$$

Where the *T* subscript indicates that these are the total deaths due to natural causes and catches. Consequently, the catch-at-age for each sex is given by:

$$c_{\bullet,a,t} = d_{\bullet,T,a,t} - d_{\bullet,a,t} \tag{1.8}$$

Calculating the survival rates for juveniles and matures requires partitioning the deaths and catches-at-age into juveniles and matures. This is done proportionally using the ratio of juveniles to matures at each age. However, catches of juveniles are all zero in the case where exploitation only occurs in the mature population. The stage-based model assumes that catches are taken over a short period at the beginning of each time step and hence natural mortality occurs after catches. Hence the survival rate for the juveniles is given by:

$$S_{\bullet,2,t} = 1 - \frac{\sum_{a=1}^{a_{\max}} \left(\left(1. - \frac{n_{\bullet,m,a,t}}{n_{\bullet,a,t}} \right) d_{\bullet,a,t} \right)}{\sum_{a=1}^{a_{\max}} \left(n_{\bullet,j,a,t} - c_{\bullet,j,a,t} \right)} \tag{1.9}$$

Where the *j* subscript refers to juveniles. For matures the survival rate is given by:

$$S_{\bullet,3,t} = 1 - \frac{\sum_{a=1}^{a_{\max}} \left(\left(\frac{n_{\bullet,m,a,t}}{n_{\bullet,a,t}} \right) d_{\bullet,a,t} \right)}{\sum_{a=1}^{a_{\max}} \left(n_{\bullet,m,a,t} - c_{\bullet,m,a,t} \right)} \tag{1.10}$$

Pregnancy rate and sex ratio are calculated in the obvious way. The proportion transitioning from juvenile to mature is calculated by calculating the numbers of recruits to the numbers mature at each age. This requires calculating the numbers of animals surviving into each age class that attained maturity earlier. The difference between this number and the number of matures in each age class is the number of recruits from the juvenile stage. Thus the number of animals previously recruited in a given age class is given by:

$$n_{\bullet,p,a+1,t+1} = n_{\bullet,m,a,t} - d_{\bullet,m,a,t} - c_{\bullet,m,a,t} \tag{1.11}$$

Where *p* denotes previously mature and:

$d_{\bullet,m,a,t}$ is the number of mature natural deaths of matures of age *a* in year *t* and

$c_{\bullet,a,m,t}$ is the catch of matures of age a in year t,

The proportion of juveniles that mature is given by:

$$g_{\bullet t} = \frac{\sum_{a=1}^{a_{\max}} \left(n_{\bullet,m,a,t} - n_{\bullet,p,a,t} \right)}{\sum_{a=1}^{a_{\max}} n_{\bullet,j,a,t}} \tag{1.12}$$

In the test model presented here the functions returning the demographic parameters for a given level of depletion are natural cubic splines fitted to the mean values of the various parameters shown in figs 3,4 and 5 and 9,10 and 11. However, as shown above the demographic parameters are stochastic and correlated. To emulate these effects a multinormal random vector generated from the variance-covariance matrix is added to the values derived from the cubic splines of the parameters. Since the variance-covariance (Σ) matrix itself is dependent on depletion the terms in the Σ matrix are generated from smoothed splines fitted through each term for the various levels of depletion. A smoothed spline is used because the terms in the Σ matrix are somewhat variable – particularly for the covariances. The multinormal random numbers are generated using a singular value decomposition transformation (Mardia, Kent and Bibby, 1979) The random generator ensures that interpolated Σ matrices are made to be positive definite by setting any negative or zero eigen values (should they occur) of the singular value decomposition to a small positive value.

Fig 15 shows population trajectories from the stage-based model derived from the fixed and variable food IBEMs with zero catches for 500 years followed by 500 years with a constant harvest rate. In this illustration, the variable food annual randomised parameter values are generated from a multinormal generator, which may not be the best choice in this particular case[1]. Fig 16 provides similar realisations from the IBEM model. Superficially the outputs of the stage-based model is similar to the IBEM, however further diagnostic tests will be needed. One obvious difference in the fixed food case is the much slower rate of decline in abundance using the IBEM after exploitation begins in the 500th year.

Concluding remarks

Although the first steps of developing an emulator for the IBEM are promising, further development requires considerable work. This would include developing suitable random parameter generators that allow for transforming variables to more easily modelled distributions in the case of variable food models and also including the possibility of serial correlation in the parameter values and the shapes of the parameter distributions being dependent on depletion. Further work on model diagnostics would also be required, and the testing of the models for other species. To this end, runs of the IBEM for minke whales have already been developed. However, some of these and some earlier humpback runs will need to be repeated to include the recent improvements made to the IBEM. Although these results will not be substantially different, it is always preferable to use the better version of the model. If the IBEM is to be re-run the set of outputs can be increased to include the catches-at-age by stage and sex. Completely updating the library of results will involve some months of computation.

It is not obvious at this stage why the IBEM produces slower declines under exploitation, and whether this also means a different recovery after depletion. Adjusting the emulator to mimic these properties will require further development. Another issue is to examine the question raised earlier about whether the recovery rate of a depleted stock for the IBEM is proportionately greater than the rate of exploitation at equilibrium. The answer will partly depend on the degree of overlap between the whaling season and the period when calves are dependent on their mothers.

However, it would be prudent now to decide whether further development of the stage-based model warrants the amount of work required. For this to be so, the Scientific Committee needs to consider the types of questions to be asked of the model and whether those questions might not be equally well answered by addressing them using the IBEM. The run time of the IBEM is not so excessive as to prohibit its use in RMP simulation trials. A version of the RMP MANTEST program has already been adapted to include the IBEM (de la Mare, 2014). Running the simulations for the standard tunings would be the next logical step.

References

de la Mare, W. K. 2013. Implications of energy budgets in determining the characteristics of whale yield curves. Paper presented to the Fourth MSYR Workshop, La Jolla, March 2013.

de la Mare, W. K. 2014. Incorporating an individual based energetics model into the RMP trials software. SC/65b/RMP03

de la Mare, W. K. and Miller, E. 2015 Progress report on modelling the relationship between $\mathrm{MSYR}_{\mathrm{mat}}$ and MSYR_{1+} based on energetics modelling. SC/66a/EM/2.

de la Mare, W. K. and Miller, E. 2016. Further examination of the relationship between MSYR_{1+} and $\mathrm{MSYR}_{\mathrm{mature}}$ based on individual based energetics modelling. SC/66b/RMP/04.

Mardia, K.V., Kent, J.T., Bibby, J.M., 1979. Multivariate Analysis. Academic Press, London, 521pp.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

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[1] Also the variance-covariance matrices are slightly wrong because they are based on calf survival rates with catches

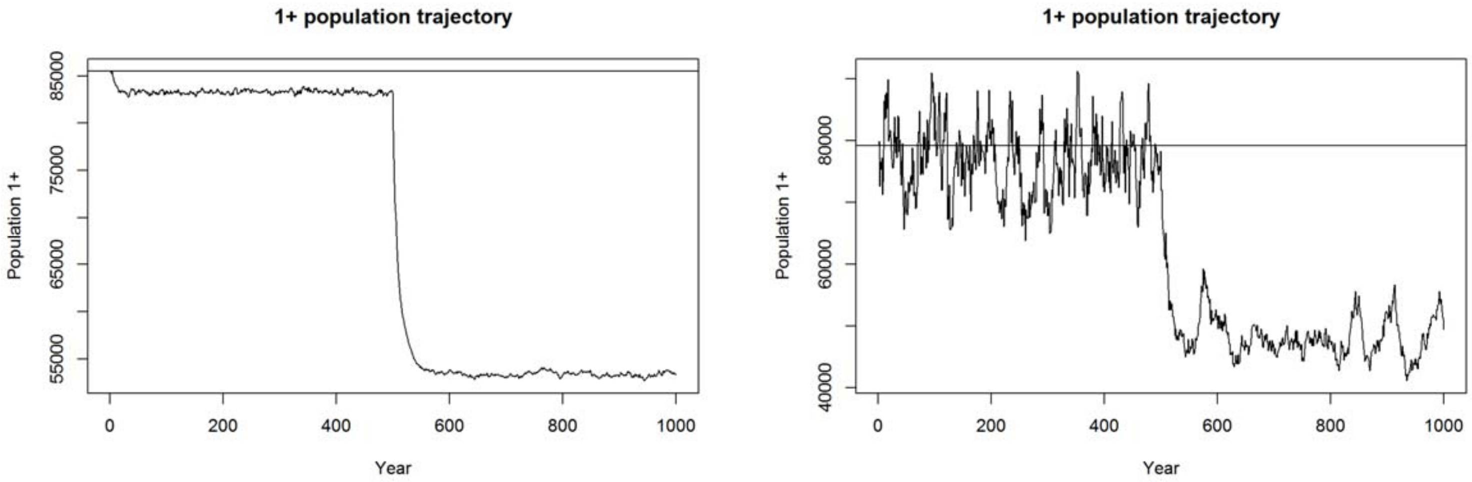

Fig 15 Example population trajectories from the stage-based model parameterised from the constant and variable food IBEMs

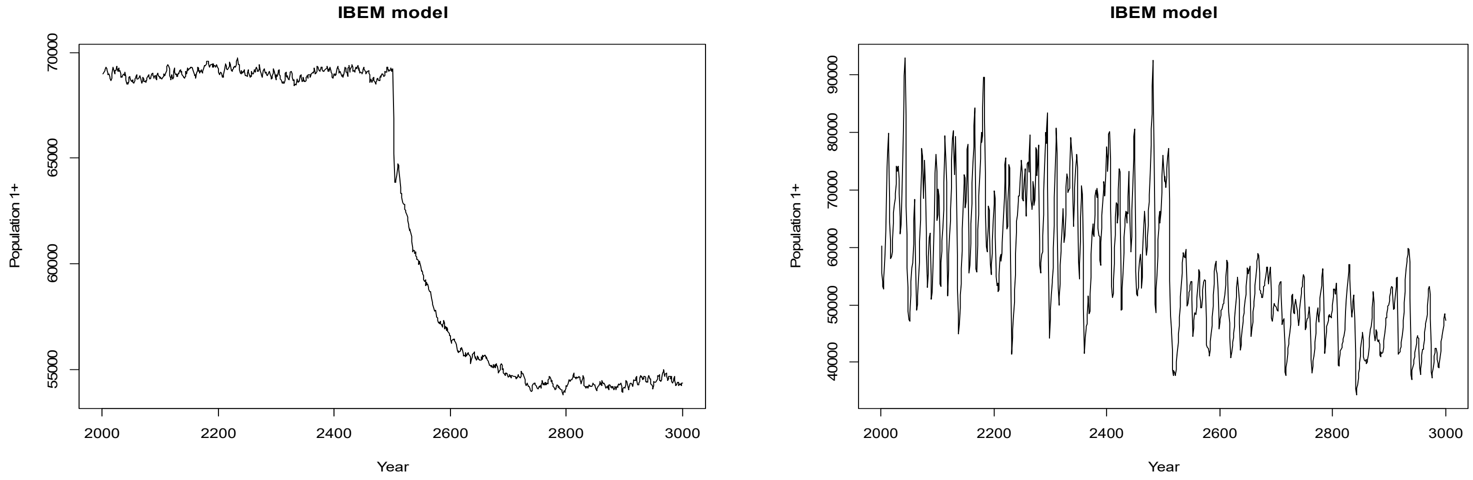

Fig 16 Example population trajectories from the constant and variable food IBEMs

APPENDIX

Population dynamics models for marine mammals are typically deterministic age-structured cohort models with specified forms of stock recruitment relationship. A typical example is the Baleen II model (de la Mare and Cooke, 1994) used in the International Whaling Commission (IWC). In such models density dependence is often determined entirely by the stock-recruitment relationship and effects such as density dependence in growth and natural mortality are not modelled. These deterministic aggregated models treat populations simply in terms of the numbers at each age and so ignore the differences between the individuals. The usual cohort models do not explicitly model the prey field or the animal's foraging strategy, but instead rely on simplifying assumptions about carrying capacity and usually no explicit structure for the distribution and abundance of prey and the extent to which these factors are subject to random variability. In particular the usual age-structured models do not readily allow for an environment to shape a population so that it consists of those animals possessing particular characteristics and behaviours that are more successful in that environment. Witting (2001) demonstrated that the dynamics of a population recovering from depletion can depend on structural details of the population life history other than simple abundance (density).

The class of model described here explores of the population effects of the interactions of individuals with their environment with individually-based energetic models. The model developed here allows for population density dependence to be shaped by epigenetic effects and heritable traits that improve the fit of the population to a given prey environment. It will be shown that such mechanisms are important for those marine mammals that are "capital breeders", such as the typical mysticete, that inhabit stochastic environments.

The model uses individual animal models with a detailed energy budget to determine reproductive success and mortality in an environment where food has a patchy spatial distribution. All the major processes of the 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. Details of the model are given in Appendix 1.

The animal state variables are

Age	a	years
day of year	n_d	1 = animal's nominal birthday
Length	L	m
Sex (0 = female, 1 = male)	S	
Sexual Maturity	S'	
Lean mass	w_l	tonnes
Fat mass	w_f	tonnes
Mass at birth	w_B	tonnes
Latitude	λ	decimal degrees
Longitude	φ	decimal degrees
Speed	v	$m.s^{-1}$
Direction	θ	decimal degrees
Pregnant (1 = pregnant)	P	
Maximum foetal growth rate	τ	$m.day^{-1}$
Foetal length	L_F	m
Mother identity	Q	
Calf identity	O	
Suckling (1 = suckling)	s	
Age at last parturition	a_B	years

Feeding history (food at places visited) (year, day, latitude, longitude, food density)	$H_{t,1...j}$
Migration state (function of day of year)	
Breeding	$\Gamma(t, ...) = 0$
Migrating to food	$\Gamma(t, ...) = 1$
Feeding	$\Gamma(t, ...) = 2$
Migrating to breeding	$\Gamma(t, ...) = 3$

Frequently used derived state variable

The ratio of fat to lean mass	$c = w_f \div w_l$

Demographic parameters with individual values

Individual parameter values are heritable as the weighted average of the individual and population values of the parameters (with some random variation)

von Bertalanffy growth parameters, where $\bullet$ represents either male or female: $L_{\infty\bullet}$, $k_{\bullet}$, $t_{0\bullet}$

Mass length	A	$tonnes.m^{-1/B}$
Mass length	B	
Calving Interval	t_c	years
Foetal growth rate	g_f	$m.day^{-1}$
Length at birth	L_0	m
Length sexual maturity	L_m	m

Fixed demographic parameters

Population nominal von Bertalanffy growth parameters,

where $\bullet$ represents either male or female: $\overline{L}_{\infty\bullet}$, $\overline{k}_{\bullet}$, $\overline{t}_{0\bullet}$

Heritability of growth characteristics	H_g	
Heritability of inter-calving interval	H_c	
Female minimum mortality at age a	$M_{f,a;} = f(a,\beta_{f,1} ... \beta_{f,5})$	$year^{-1}$
Male minimum mortality at age a	$M_{m,a} = f(a,\beta_{m,1} ... \beta_{m,5})$	$year^{-1}$

Additional mortality hazard parameters (additional mortality is a function of body condition)		
Maximum value	M	$year^{-1}$
Body condition at $M50$	c_{M50}	
Rate parameter	g_M	

Female proportional length sexual maturity	ψ_f

Male proportional length at sexual maturity	ψ_m	
Maximum age at sexual maturity	a_{max}	years
Sex ratio at birth	ρ	
Minimum viable calf length	L_{min}	m
Energetics parameters		
Energy content of fat	E_f	J.kg^{-1}
Energy content of non-fat tissues	E_n	J.kg^{-1}
Energy content of milk	E_m	J.kg^{-1}
Energy content of prey	E_p	J.kg^{-1}
Maximum body condition	c_{max}	
Minimum body condition to conceive	c_{min}	
Daily feeding rate per unit body mass	κ	kg.tonne^{-1}
Assimilation efficiency	q	
Milk assimilation efficiency	q_m	
Growth efficiency	γ	
Proportion of lean mass (in m-L relation)	R	
Body condition at birth	v	
Fat ratio at birth	Φ	
Male breeding FMR/BMR	ξ	
Drag coefficient	C_D	
Density of seawater	$\rho_{seawater}$	kg.m^{-3}
Nominal number of days in feeding period	n_e	
Proportion of year spent growing	$\Omega = n_e \div 365$	
Feeding parameters for females (a function of prey abundance)		
Prey abundance range	$f_{f\,range}$	
Prey abundance at food intake inflection	f_{f50}	tonnes
Rate parameter	h_f	tonnes^{-1}
Feeding parameters for males (a function of prey abundance)		
Prey abundance at 50% food intake	f_{m50}	tonnes
Rate parameter	h_m	tonnes^{-1}
Growth as a function of body condition		
Maximum proportion of energy for growth	$g_{\max}$	
Body condition at 50% point	c_{L50}	
Rate parameter	ε	
Foetal growth as a function of body condition		
body condition at 50% point	$c_{\tau 50}$	
Rate parameter	η	
Milk production as a function of body condition		
Body condition at 50% production	l_{50}	
Rate parameter	d	
Milk production as a function of calf size		
Minimum production	l_{min}	kg day^{-1}
Increase per unit calf mass	u	kg.(day.tonne)$^{-1}$
Common demographic parameters		
Calving interval determining parameters		
Expected calving interval at carrying capacity	I_K	years
Maximum nominal calving interval	$I_{\max}$	years
Minimum nominal calving interval	$I_{\min}$	years
Std. dev. of calving interval distribution	σ_c	years
Offset parameter	g_c	
Birth mass under good food conditions	w_G	tonnes
Birth mass at carrying capacity	w_K	tonnes

Timing parameters (day of year)

Birthday	t_0
Conception	t_c
Weaning	t_w
Arrive on breeding grounds	$t_{b\ldots}$
Migration towards feeding grounds	$t_{1\ldots}$
Arrive on feeding grounds	$t_{2\ldots}$
Migration towards breeding grounds	$t_{3\ldots}$

The dots indicate timings that depend on sex and reproductive state

Prey dynamics

Prey carrying capacity at time t	$K_{p,t}$
Prey biomass at time t	$B_{p,t}$
Prey daily survival probability	S_p
Prey maximum daily recruitment	r_p

Relations

Length and growth

An animal's growth is controlled by a 'programmed' growth curve unique to each individual, acquired at birth with sex specific values for k and L_∞, which are partially inherited from the mother (as a weighted average of the mother's parameters and the population mean values – but re-scaled appropriately for males). This growth curve describes the upper limit of the length of the animal on each birthday and is given by a conventional von Bertalanffy equation (shown as the dotted line in Fig A1):

$$L = L_{\infty\bullet}\left(1-\exp\left(-k_{\bullet}\left(a+\frac{n_d}{365}-t_{0\bullet}\right)\right)\right) \qquad \text{A - (13)}$$

Animals will grow on a realised growth curve that lies below the programmed curve when food availability is low. Moreover, growth is only possible when food has been ingested. Given that feeding is concentrated into a feeding season after migration, the growth curve is transformed into a piece-wise curve as shown by the solid line in Fig A1. This curve is made from segments derived from:

$$L = L_{\infty\bullet}\left(1-\exp\left(-\frac{k_{\bullet}}{\Omega}\left(\Omega a+\frac{n_d}{365}-t'_{0\bullet}\right)\right)\right) \qquad \text{A - (14)}$$

where

$$\Omega = \frac{n_e}{365} \qquad \text{A - (15)}$$

and

$$t'_{0\bullet} = \frac{\log\left(1-\dfrac{L_0}{L_{\infty\bullet}}\right)\Omega}{k_{\bullet}} + \frac{t_2}{365} \qquad \text{A - (16)}$$

However, during the first year of life the growth period includes suckling from birth and so the first step on the growth curve has different parameters. There are two cases: 1; there is some independent feeding when weaning occurs before the end of the feeding-season, and 2; suckling can continue past the end of the feeding season. For case 1, the following expressions redefines Ω in equation A – (2):

$$\Omega = \frac{t_3}{365} \qquad \text{A - (17)}$$

In case 2

$$\Omega = \frac{t_w}{365} \qquad \text{A - (18)}$$

In both cases $t'_{0\bullet}$ is redefined as

$$t'_{0\bullet} = \frac{\log\left(1 - \frac{L_0}{L_{\infty\bullet}}\right)\Omega}{k_\bullet} \qquad \text{A - (19)}$$

where Ω takes the value appropriate for the case.

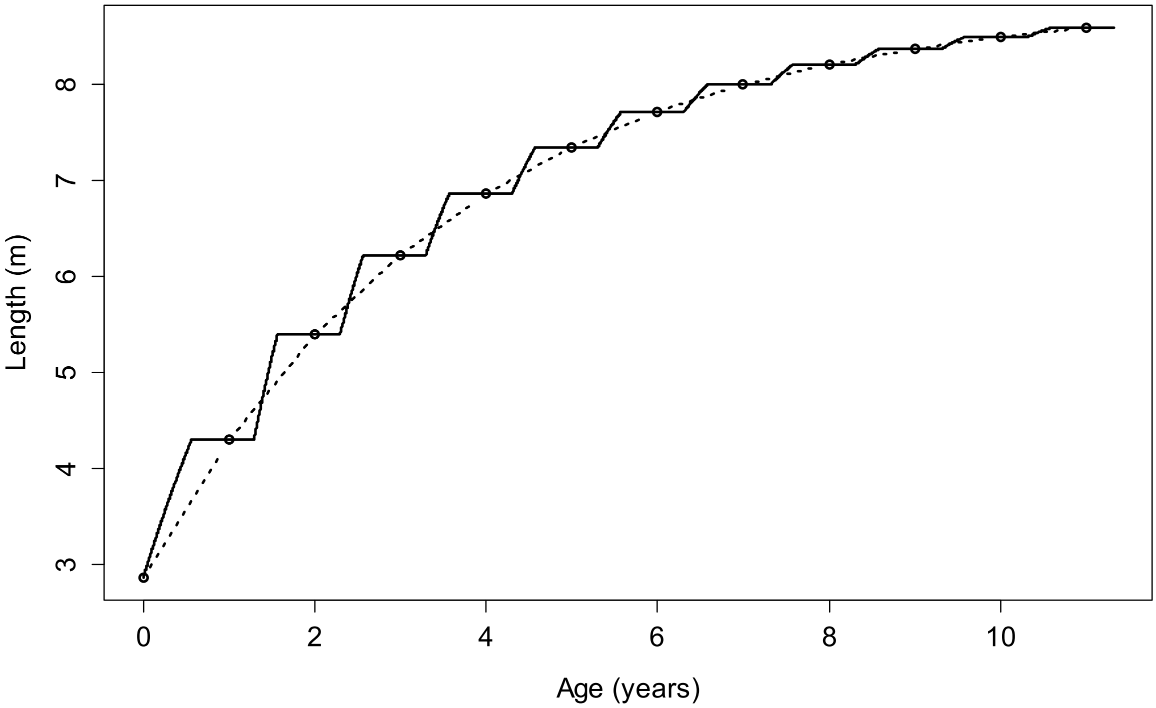

Fig. 1 Incremental programmed growth curve (solid line). Growth occurs during the annual feeding season but nominally stops between feeding seasons. The dotted line is the annualised growth curve referred to age at each birthday (shown as a point).

The programmed growth curve represents the sizes animals reach when they can feed to satiation. Otherwise, under worsening food conditions animals will grow more slowly. 'Catch up' growth can occur when energetically feasible but this is through an incremental approach so that an animal cannot exceed the size at age on its individual programmed growth curve. Nominal growth increments are dependent on body condition, so that more energy is diverted to fat storage when body condition is poor. There is also a limit on the amount of energy that can be used for growth and the maximum size of the growth increment is determined by the energy available. If the maximum allowed increment exceeds the nominal growth increment then the nominated growth occurs, otherwise only the maximum energetically allowable growth occurs. The following section clarifies the details.

To allow for food dependence, growth is modelled incrementally, the first step being to find the maximum growth increment needed to progress from current length to the length on the programmed growth curve; this is given by;

$$\Delta L_{prog} = L_\infty\left(1 - \exp\left(-\frac{k_\bullet}{\Omega}\left(\Omega a + \frac{n_d + 0.5n}{365} - t'_{0\bullet}\right)\right)\right) - L \qquad \text{A - (20)}$$

where n is the number of days elapsed, and L is state variable of the actual length of the animal prior to the current time step. This growth increment is reduced by a proportion that depends on current body condition to become the nominal growth increment and added to L to give the next nominal length:

$$L' = L + \frac{\Delta L_{prog}}{1 + \exp\left(-\varepsilon\left(c - c_{L50}\right)\right)} \qquad \text{A - (21)}$$

However, L' may not be reachable given the amount of food recently ingested. Calculating the maximum increase in length given the amount of food ingested is derived from the increase in lean mass available from the feeding energy intake (e_f). This potential increase in lean mass is given by:

$$\Delta w_{\max} = \frac{g_{\max} e_f \gamma}{E_N} \qquad \text{A - (22)}$$

Using the mass-length relationship this gives the maximum achievable length as:

$$L_{\max} = \left(\frac{\Delta w_{\max}}{RA} + L^B \right)^{\frac{1}{B}} \qquad \text{A - (23)}$$

This is approximate because it assumes that the ratio of lean mass to total mass is at the standard value (R) (as is the case for all the calculations that use the mass-length relationship). The realised new length is given by:

$$L = \inf\left(L', L_{\max}\right) \qquad \text{A - (24)}$$

These mechanisms ensure that an animal partitions energy into maintaining sufficient body condition while growing, and in particular, does not allow fat stores to be drawn down to provide energy for growth. Survival and reaching maturity depend on a trade-off between somatic growth and fat-storage.

Growth heritability

Each animal has a unique set of growth parameters, partly inherited from their mother and weakly dependent on its length at birth if undersized (although in the current version the term dependent on birth-length is not used, i.e. $\beta' = 1$). For females the individual's asymptotic length is:

$$L'_{\infty f} = \beta'\left(\left(1-H\right)\bar{L}_{\infty f} + HL_{\infty f,Q} + \text{Norm}\left(0, \sigma_{L_\infty}\right)\right) \qquad \text{A - (25)}$$

where H (with a value in the range [0:1]) is the heritability, which leads to the individual characteristic being a weighted mean of the mother's and population's values. For males:

$$L'_{\infty m} = L'_{\infty f} - \bar{L}_{\infty f} + \bar{L}_{\infty m} \qquad \text{A - (26)}$$

For females the rate parameter is:

$$k'_f = \beta'\left(\left(1-H\right)\bar{k}_f + Hk_{f,Q} + \text{Norm}\left(0, \sigma_k\right)\right) \qquad \text{A - (27)}$$

and for males:

$$k'_m = k'_f - \bar{k}_f + \bar{k}_m \qquad \text{A - (28)}$$

where β' is the effect of mass at birth given by:

$$\beta' = \inf\left(1 + \frac{0.1\left(w'_B - w^*_B\right)}{w^*_B}, 1.1\right)$$

where Norm(μ, σ) is a random number from an normal distribution with the specified mean μ and standard deviation σ and w^*_b is the population average birth mass under good conditions. $L_{\infty\bullet}$ and $k_\bullet$ are perfectly positively correlated. The value of $t_{0\bullet}$ is set so that an animal's length given by its individual growth curve on its day of birth is equal to the length of the foetus as delivered by its mother.

The energy used for growth is derived from the increase in mass (it is assumed that growth in length is reflected only in lean mass)

$$\Delta w_l = RA\left(L_{t+n}{}^B - L_t{}^B\right) \qquad \text{A - (29)}$$

Hence energy used in growth is

$$e_g = \Delta w_l \frac{E_n}{\gamma} \qquad \text{A - (30)}$$

Foetal growth

Growth rate of a foetus in a female is an individual characteristic partially inherited from its mother as a weighted average of the individual and population values in a similar way to the other growth terms above (equation A – (15)). The value is capped so that there is a maximum size for calves at birth.

The growth of an individual foetus in length is linear with time, but actual growth is dependent on the body condition of the mother.

$$L_{F,t+n} = L_{F,t} + \frac{n}{365}\left(\frac{\tau}{1+\exp\left(-\eta\left(c-c_{\tau 50}\right)\right)}\right) \qquad \text{A - (31)}$$

The maternal energy invested in growth is derived from the increase in foetal mass given by:

$$\Delta w_F = A\left(L_{F,t+n}{}^{B} - L_{F,t}{}^{B}\right) \qquad \text{A - (32)}$$

Energy used in foetal growth is:

$$e_F = \Delta w_F \frac{\left(1-\Phi\right)E_n + \Phi E_f}{\gamma} \qquad \text{A - (33)}$$

The partitioning of foetal growth to fat tissue (Φ) is assumed to be 30%.

Natural mortality

Natural mortality is dependent both on age and on body condition and can be different for males and females. The age dependent mortality is given by a Siler type of function:

$$M_{\bullet,a} = \beta_{\bullet,1}\exp\left(-\beta_{\bullet,2}a\right) + \beta_{\bullet,3} + \exp\left(\beta_{\bullet,4}\left(a-\beta_{\bullet,5}\right)\right) \qquad \text{A - (34)}$$

The hazard of death is given by:

$$z = M_{\bullet,a} + \frac{M}{1+\exp\left(-g_M\left(c-c_{M50}\right)\right)} \qquad \text{A - (35)}$$

The rate parameter g_M is negative and so the hazard of death increases with declining body condition. Death is a Bernoulli trial with the probability of death in an n day period given by:

$$\mathrm{p}\left(\mathrm{death}\right) = 1-\exp\left(\frac{-zn}{365}\right) \qquad \text{A - (36)}$$

Death by starvation is an additional form of mortality, and this is assumed to occur when the lean body mass has declined to less than 30% of the body mass given by the mass-length relationship. In the case of suckling calves, the death of the mother also results in the death of the calf. There is also a minimum viable size at birth for calves, below which they are considered to die at birth.

Pregnancy rate

There are three controls on pregnancy rate:

- An individual and partly heritable inter-calving interval which is fixed at birth depending on the animal's birth-mass as well as the mother's.
- A probability of becoming pregnant that increases with the number of years elapsed since the animal last gave birth.
- A minimum level of body condition – below which pregnancy will not occur.

Animals become sexually mature when of sufficient size and body condition:

$$L >= \psi_{\bullet} L_{\infty\bullet} \cap c >= c_{\min} \qquad \text{A - (37)}$$

The inter-calving interval is a phenotypical character that is expressed at birth depending on an animal's birth-mass, modulated by inheritance from its mother. The calving interval is an expected value in as much as it is not an integer but a continuous number used in the calculation of the probability that an animal will become pregnant given the time elapsed since it last gave birth. This number is determined from the weighted average of a calf's mass at birth and the mother's mass at birth. Thus, animals of low birth mass have longer inter-calving intervals than animals with high birth mass. Animals with low birth mass from mothers that also had low birth mass will have even longer inter-calving intervals. Both sexes are assigned a calving interval to allow for adding paternal inheritance in further development of the model. The weighted average is given by:

$$\overline{w} = H_c w_Q + \left(1-H_c\right)w \qquad \text{A - (38)}$$

Where w_{Ω} is the mother's mass birth at birth and *w* is that of the calf. The inter-calving interval is given by:

$$I_c = \frac{\left(I_{\max} - I_{\min}\right)}{1 + \exp\left(\vartheta\left(\overline{w} - w_G\right)\right)} + I_{\min} + \mathrm{Norm}\left(0, \sigma_I\right) \tag{A - (39)}$$

where $\mathrm{Norm}\left(\mu, \sigma\right)$ is a random deviate from a normal distribution with mean μ and standard deviation σ, which allows for some variability, for example derived from paternal or even older intergenerational inheritance. It is required that $\vartheta > 0$ and it is derived from reference inter-calving intervals and birth-masses:

$$\vartheta = \frac{\log\left(\frac{I_{\max} - I_{\min}}{I_K - I_{\min}} - 1\right)}{w_K - w_G} \tag{A - (40)}$$

Females that attain maturity become pregnant in the next breeding season. Becoming pregnant at age a for a female with a given inter-calving interval is a Bernoulli random variable;

$$P|a, I_c = \mathrm{B}\left(p_{I_c, a-a_B}\right) \tag{A - (41)}$$

$$p_{I_c, a-a_B} = \mathrm{N}\left(a - a_B + g_c\sigma_c, I_c, \sigma_c\right) \tag{A - (42)}$$

where $\mathrm{N}\left(x; \mu, \sigma\right)$ is a cumulative normal distribution with mean μ and standard deviation *σ*.

Feeding

The amount of food eaten per day by an animal is proportional to its body mass and depends on the amount of food available in its location on the feeding grounds and can be different for each sex, thus allowing for a crude form of “contest competition” between sexes. Otherwise, intra-specific competition is the form of “scramble competition”. In terms of energy the intake is over a period of n days given by:

$$e_f = \frac{nE_p\left(w_f + w_l\right)\kappa}{q}\left(f_{\bullet\min} + \frac{f_{\bullet range}}{1 + \exp\left(-h_{\bullet}\left(f - f_{\bullet 50}\right)\right)}\right) \tag{A - (43)}$$

For suckling calves the amount of energy acquired is directly proportional to the amount of milk produced by the mother, so that:

$$e_f = lq_mE_m \tag{A - (44)}$$

Lactation

The amount of milk produced by a mother depends on her body condition and on the mass of the calf.

$$l = n\left(\frac{l_{\min} + u\left(w_l + w_f\right)}{1 + \exp\left(-d\left(c - l_{50}\right)\right)}\right) \tag{A - (45)}$$

where w_l and w_f refer to the calf and *c* is the body condition of the mother. The energy expended by the mother is:

$$e_l = lE_m \tag{A - (46)}$$

Basal metabolic rate (Watts)

$$W_B = 0.034\left(1000\left(w_l + w_f\right)\right)^{0.75} \tag{A - (47)}$$

Power required for locomotion (Watts)

The power of locomotion depends the animal’s surface area and drag coefficient. The animal’s surface area is given by:

$$A_s = 0.08\left(1000\left(w_l + w_f\right)\right)^{0.65} \tag{A - (48)}$$

The force resisting locomotion is

$$F_r = 0.5 \times \rho_{seawater}C_DA_sv^2 \tag{A - (49)}$$

and hence power:

$$W_m = \frac{F_rv}{q_m} \tag{A - (50)}$$

Energy expended basal plus activity (FMR)

$$e_a = 86400 \times n\left(W_B + W_m\right) \qquad \text{A - (51)}$$

Male energy expenditure in the breeding season

It is assumed that mature males use additional energy in the breeding season while competing for females, with the cost of competition increasing as the proportion of males rises above 50%. This term helps to keep the sex ratio balanced near 50%. The energy expended is a multiplicative adjustment to the usual energy of activity.

$$e_B = e_a\left(\alpha_{\min} + \frac{\alpha_{range}}{1+\exp\left(-\zeta\left(\alpha-\alpha_{50}\right)\right)} - 1\right) \qquad \text{A - (52)}$$

where α is the current sex ratio of the mature population as males per female.

Net energy

An animal's net energy budget is:

$$e_{net} = e_f - e_a - e_B - e_g - e_F - e_l \qquad \text{A - (53)}$$

If the net energy budget is negative, growth does not occur and the energy shortfall is made up by drawing on fat. If fat is depleted, any further shortfall is made up by catabolising lean mass. If lean mass loss falls below a threshold (30% of the mass given by the mass-length relationship) the animal dies from starvation.

When the energy budget is positive, food energy is converted first to replacing any lean mass previously catabolised and partitioned into growth and fat storage after the lean mass has been restored. Any surplus not required for growth is converted to fat.

Annual cycle and migration

The animals have a typical baleen whale migratory cycle from breeding to feeding grounds. The beginning of the annual cycle is the nominal birthday of animals (day 1). Animals in the various reproductive classes have their own dates for migration to and from the feeding grounds. Table y shows the dates for the transitions between breeding and feeding times for the various classes of animals.

THE POPULATION

The population is the collection of living animals stored in a doubly linked list. Animals are added at the end of the list at birth and removed at death. The state of each animal is updated for a specified number of days working through the list in order. By adding calves at the end of the list, the state of their mothers have already been updated before the calf is updated, thus allowing for the energetics of lactation to be based on the mother's current state.

THE ENVIRONMENT

The animals move around an environment described by a grid in the form of a "ragged" array. The size of the grid cells are large on the breeding grounds and migration latitudes, which are devoid of prey. In the feeding grounds the grid cells are much smaller so as to better capture the interactions between whales and prey.

The prey dynamics in each grid cell has a simple logistic model.

$$B_{p,t+n} = \left(B_{p,t} - \sum_{whales} qe_f\right)S_p{}^n + B_{p,t}\left(1-S_p{}^n\right)\left(1+r_p\left(1-\frac{B_{p,t}}{K_{p,t}}\right)\right) \qquad \text{A - (54)}$$

The carrying capacity for prey in each grid cell and the prey biomass are both set from the same mixture of bivariate normal distributions at the beginning of each season. There is no prey diffusion or advection between cells. A diagram of a grid showing the carrying capacity is shown in Fig x. Within each season the carrying capacities ($K_{p,t}$) are adjusted multiplicatively by a sine function to give a seasonal signature to production.

FORAGING STRATEGY

Each whale remembers where it fed at each date during the last feeding season and the abundance of prey at each location. On setting off at the start of the next feeding season each animal heads towards the best location experienced last season (but with some random variation in speed and direction). Once on the feeding grounds foraging occurs according to the following strategy.

- if the available food in the current cell (location) allows at least 95% of maximum food intake the animal does not relocate (food intake has a stochastic term so that different animals will experience different food intakes in the same location, so that not all animals necessarily relocate in the same time step).
- Otherwise, the animal relocates:

- if there is a local gradient of increasing prey abundance the animal follows the gradient and so moves to the adjacent cell with the greatest prey abundance
- if there is no favourable gradient but the animal remembers a different location visited at around the same date last year with an adequate food supply, then the animal heads in that direction
- otherwise, the animal sets off on a random bearing either east or west, in the range 70° to 110° or 250° – 290° respectively, at a speed of around 2 m.s-1. Animals are reflected at the outer grid boundaries, and hence there is no emigration.
- if during the days spent relocating the animal enters a grid cell with prey abundance that allows it to feed at around one half of the maximum food intake it feeds there until the next time step. This means that an animal while relocating does not pass up the opportunity to follow a food gradient

Calves accompany their mothers during the feeding season, and so their first set of memories of good feeding grounds is set during this season. Thus yearlings visit the feeding grounds used by their mothers.
Animals do not feed whenever their body condition exceeds c_{max}.

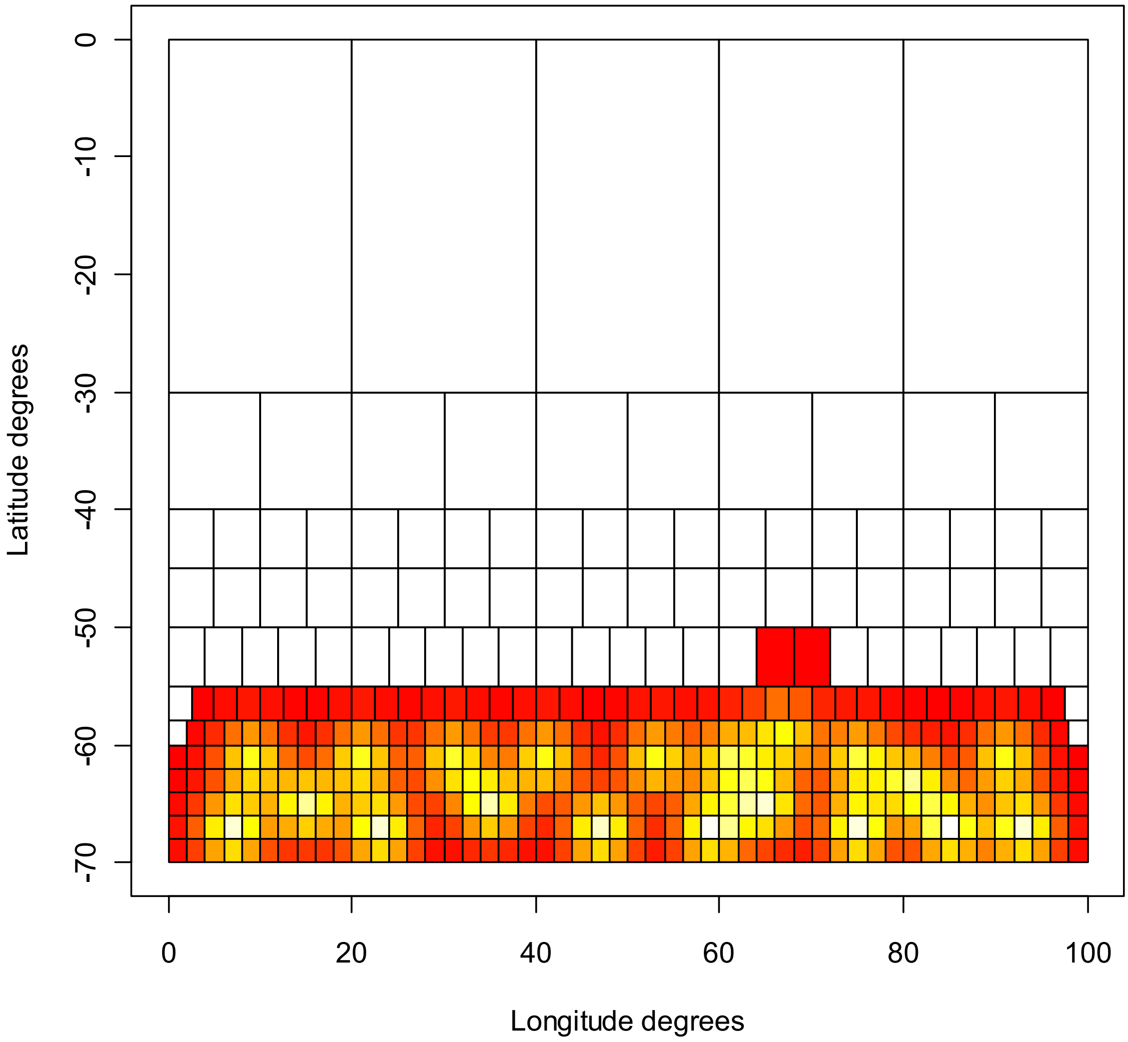

Fig 1. Grid plot of prey carrying capacity. The colours indicate where prey is not abundant as red and is more abundant yellow to white regions. The white cells outside the red region are devoid of prey.

Table y. Whale year to calendar dates

Date	Day	Date	Day	Date	Day	Date	Day
15/7	1	1/11	108	1/3	228	1/7	351
1/8	16	1/12	138	1/4	258	14/7	365
1/9	47	1/1	169	1/5	289	15/7	1
1/10	77	1/2	200	1/6	320		

Migration dates

Event	Class			
	Males	Pregnant	With calf	Resting
Leave Breeding Ground	46	46	76	46
Arrive Feeding Ground	106	106	131	106
Leave Feeding Ground	211	226	256	211
Arrive Breeding Ground	301	341	341	301

Life history values for models

Parameter	**Value**
Female maximum asymptotic length ($L_{\infty f}$)	13.08 m
Male maximum asymptotic length ($L_{\infty m}$)	12.28 m
Female growth coefficient (k_f)	0.382
Male growth coefficient (k_m)	0.382
Minimum natural mortality(M)	0.02