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An age-structured emulator for the individual based energetics model

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The Scientific Committee has sought an age-structured emulation model that mimics the population level characteristics of individual based energetics models (IBEM) to be used in CLA simulation trials without entailing the long runtimes of the IBEM. This paper presents details of such an emulator that used demographic parameters calculated from the outputs of simulations using the IBEM. This work fulfils the requirements partly funded by a small grant from the IWC. The overall conclusion is that the amount of computation required to calculate the parameters for the emulator from the IBEM is comparable with the amount of computation that would arise from directly including the IBEM in the CLA simulations and hence there is no appreciable gain in efficiency from using the emulation model.

Over several years the Scientific Committee (SC) 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 on the full range of demographic parameters and the consequential effects on the likely properties of the yield curves of exploited whale populations.

Although it has been shown as feasible to use the IBEM directly in revised management procedure (RMP) simulations (de la Mare, 2014) the SC has expressed an interest in having a model that will emulate the properties of the IBEM, but with a much faster execution speed. Progress on a stage-based model towards this end was presented in de la Mare (2017). The stage-based model used demographic parameters derived from the IBEM to model classes of animals, calves, juveniles and matures, but the SC expressed a preference for an age-structured model. This paper presents such a model using age-specific density-dependent demographic parameters from the IBEM setup for a population with the characteristics of minke whales.

The catch limit algorithm (CLA) does not explicitly separate the sexes, and even though the IBEM models both sexes, the emulator is a combined sex model. For setting up an age-based emulator a range of demographic parameters are required as a function of depletion (*N*/*K,* where *N* is current abundance and *K* is current carrying capacity). Because the population model must allow for both variability and systematic variations in carrying capacity, density dependent demographic parameters for populations above *K* are also required. The demographic parameters required by the age-based emulator are age-dependent natural mortality, age-dependent maturity, and birth-rate. Parameters for density dependent growth are also calculated, but these are for illustrative purposes and have no effect on the age-based population dynamics. The details of the age-based model are given in the appendix 1. Appendix 2 is an annotated example of a parameter file used by the emulator.

The emulator uses a set of demographic parameters calculated from a series of runs of the IBEM with specified harvest rates for the mature population (as assumed in the CLA simulations). For populations below *K* the demographic parameters are calculated from runs of the IBEM where the population is depleted to different levels using various constant rates of exploitation until it has attained a stable equilibrium, albeit with a stochastic distribution about a mean abundance. Populations above *K* cannot have a stable abundance, except with negative exploitation rates, i.e. whales are returned to the population. Since this cannot occur in nature it would distort the model population in ways that cannot occur naturally, and so this cannot used for calculating demographic parameters for populations above *K*. Instead, the parameters are calculated from the age-dependent mortality and maturity rates that occur after a step reduction in *K* in the IBEM population, pooled over a span of 10 years while the population is declining but still distant from settling towards the reduced *K*. Some parameters will be subject to a time delay, such as those relating to sexual maturity, because earlier values will still be apparent in the age-length structure of the population, but this is a natural reflection of a declining population. Because natural mortality responds quickly to the change, for the transient response the mortality parameters are calculated using the natural deaths at each age (not the age structure under equilibrium assumptions) and so the values reflect the transient response without delay. This approach will not lead to very precise parameters because of the short time span and demographic stochasticity. Parameters from populations above *K* determine the rate at which such population decline towards *K*, but they do not affect the shape of the yield curve. Consequently, a lack of precision is probably not important for most RMP simulations since they have populations generally below *K*. A small scale-factor is included so that demographic parameters calculated above *K* are consistent with those calculated from the IBEM when in equilibrium at *K*.

The emulation model population age structure is determined by the number of births (N_0), calf mortality (M_0) and natural mortality for ages (a) given by:

$$M_a = -\ln\left(\left(\frac{N_{a+1} + C_a \exp\left(-M_a\left(1-t_C\right)\right)}{N_a}\right)\right) \tag{1}$$

where:

N_a is the number of animals in age class *a* at the beginning of the year,

C_a is the catch of animals from age class *a* at time of year t_C (in this case 150/365)

There is a pooled age class for animals aged a_s and above, which has a pooled mortality rate M_s. The natural mortality of animals in the pooled class is given by:

$$M_s = -\ln\left(1 - \frac{R_s - C_s \exp\left(M_{a_s}\left(1-t_C\right)\right)}{N_s}\right) \tag{2}$$

where:

R_s is the number of animals recruiting to the sink age class, i.e. the animals surviving natural mortality and catches one year from the pre-sink age class

N_s is the number of animals in the pooled age class (aged a_s and above),

C_s is the catch taken from the pooled class, and

Catches at age are determined either by uniform selectivity for the 1+ population or by the maturity logistic function for the mature population, given by:

$$p_a = \frac{1}{1+e^{k(a-a_{50})}} \tag{3}$$

The number of births is given by:

$$N_{0,t} = \rho P_t \sum_{a>0} N_{a,t} p_{a,t} \tag{4}$$

where ρ is the sex ratio correction, which also includes an adjustment required for the population to be stable at *K*.

The age-dependent mortality rates are calculated directly from the numbers at age generated by the IBEM pooled over 1000 years after reaching an equilibrium for a range of specified harvest rates or from the transient responses in cases where *N*>*K*; depletion (*N* and *K* refer to the 1+ population). Consequently, natural mortality rates depend on the degree of depletion (*N/K*). The parameters for the maturity function (which also depend on depletion) are determined in a similar way except that the fitting is by maximum likelihood assuming a binomial distribution for the proportion mature at each age. The values of the parameters at any given level of depletion are found using interpolating cubic splines for each parameter.

Two sets of runs of the IBEM are used to determine the demographic parameters for use in the emulator. The first set has an $MSYR_{1+}$ approximately equal to 0.032 (model 1), the second with $MSYR_{1+}$ approximately equal to 0.01 (model 3). These are a subset of models reported in detail in de la Mare (2017). The two models were run with four different levels of variability in summer food supply (which is close to linearly related to variability in carrying capacity). The coefficients of variation (CVs) of the food supply variability in the IBEM were set at 0., 0.3, 0.6 and 0.9. However, the variability in total population size is less than the variability in food supply (or *K*) because of the time lag in changes in abundance following changes in *K*. These results from the IBEM are summarised in table 1. The CVs for population abundance in for the emulator are set to be equal to the CVs for the IBEM abundance by setting the CV of the carrying capacity in the emulator. These CVs for *K* in the emulator are similar to the CVs for food supply in the IBEM.

The emulator model includes the possibility for adjusting the shape and height of the yield curve by transforming the value of *N/K* as follows:

$$\frac{N'}{K} = \frac{\alpha + \left(\frac{N}{K}\right)^z}{1+\alpha} \tag{5}$$

where *N'*/*K* is the adjusted value to be used with the interpolation functions when calculating the values of demographic parameters. The transformation does not affect *K* because *N'*=*K* when *N*=*K*. The effect of α is to modify MSY and *z* to modify MSYL. Also $N' = N$ when $\alpha = 0$ and $z = 1$, i.e. the transformation has no effect. Although this transformation works effectively with functional forms of the yield curve, it is not always successful with the interpolated parameters used in the emulator.

Table 1 gives $MSYR_{mat}$ and $MSYL_{mat}$ derived directly from the IBEM output compared with adjusted values from the emulator. The corresponding yield curves are shown in figs 1 to 8. The adjustments using equation (5) attempt to make the emulator yield curves correspond to $MSYR_{mat}$ rates given by the IBEM when $MSYR_{1+}$ is rescaled to have the values 0.04 and 0.01 (the values used in CLA simulations).

The table and figures show that the demographic parameters calculated from the IBEM used in the emulator do not always reproduce the IBEM yield curves faithfully; they become more left-skewed at the higher levels of variability and do not always reach the required level for $MSYR_{mat}$.

The emulator model has been implemented C++ such that it can be compiled and run imbedded in the standard CLA simulation program (using the Netbeans IDE and the GCC compiler suite in MinGW, which allows mixed Fortran and C++ source code). The results from running the CLA simulations are given in Figs 9 to 31 for $MSYR_{1+}$ levels of approximately 0.01 had 0.04. The runs are for the three standard initial depletion scenarios, 0.99, 0.6 and 0.3 of K_{mat}. These results indicate that the emulation model has been successfully integrated into the CLA simulation program and that the results are consistent with other trial results from using the CLA.

An additional comparison requested by the EM Steering Group was to examine the difference between the IBEM and the emulator following a catastrophic decline in carrying capacity. For the IBEM food density was decreased by a factor of 10, which leads to a rapid decline to extinction. Earlier results from the emulator did not lead to a rapid decline because the density dependent demographic parameters did not include the possibility of a ten-fold decline in carrying capacity, and so an additional point at $0.1K$ was added to the interpolating functions. This adjustment leads to the comparative results shown in figs 32 and 33. The results for the emulator are calculated after reducing K to near zero (less than one whale). The IBEM declines to extinction for a 10-fold decline in food density, which is not the same as a decline in carrying capacity in the way food is modelled in the IBEM. In this version of the IBEM food model the amount of food is reduced by reducing the density of food in all food patches, but the number of food patches is unchanged. The population will not survive if the food density declines below the critical level required for successful feeding. In contrast the emulator population declines more slowly and would not become extinct if carrying capacity was set to $0.1K$ because, in the emulation model, the population will persist at any level of K greater than zero. This is because density dependence is a function if relative depletion. This is an implicit assumption that a reduction in food does not lead to a reduction in food density, but rather a reduction in the number of food patches. The differences between the two models partly reflect the different underlying assumptions about the relationship between food density and food quantity. The two models are at the extremes of the possible effects of food reduction, with there being a continuum of possibilities in the relationship between food density and the number of food patches. This issue should be further considered in refining our assumptions about modelling whale prey and the feeding ecology of whales.

An adjustment might be required for the CLA simulations. The standard CLA simulations specify a level of additional variance in abundance deriving from processes not included in the estimates of uncertainty in abundance estimates alone. The emulator (or the IBEM if that were used in the CLA simulations directly) add to the extra variance because they explicitly model variability in abundance and thus the simulated extra variance in the standard CLA program may need to be adjusted if the results are to be strictly comparable with the usual simulation outputs.

The source code and runtime versions of the programs will be available from the IWC Secretariat.

Concluding remarks

The efforts to develop an emulator for the IBEM have not been completely successful. In terms of faster computation, the effort has been a success; the CLA simulation program using the emulator executes 400 trials in about 4 minutes. Using the IBEM in the CLA simulator take about 10 days on the same computer to run 400 trials. In terms of reproducing the population dynamics from the IBEM the emulator is not always faithful, particularly at higher levels of variability in carrying capacity. This is despite considerable effort in developing several methods for calculating density dependent demographic parameters, none of which were as successful as the direct enumeration of natural mortality used in the final version presented here.

To obtain better emulation, more and longer runs of the IBEM would be required to generate less stochastic parameter values for the emulator. Given that the existing IBEM runs took three months on a cluster of 26 processors suggests that the amount of computation involved to improve the emulator would likely be greater than that required to use the IBEM directly in the CLA simulations. Although the amount of computation for direct use of the IBEM is considerable, the development of cloud-based computing provides for an efficient and cost-effective means for this type of simulation. Hundreds of processors can now be hired on cloud-based servers at relatively low cost. Despite considerable resources put to its development the emulator is only a partial success, and consequently, I conclude that it is not efficient to continue along this path.

Table 1. Characteristics of yield curves from the IBEM calculated for different levels of food availability on migration and the emulator tuned to have the same degree of variability in abundance at carrying capacity.

Model	Food variability	Unadjusted $MSYR_{1+}$	Adjusted IBEM Mature				Emulator			
			K_{mat}	$CV(K_{1+})$	Adjusted $MSYR_{mat}$	MSYL	K_{mat}	$CV(K_{1+})$	MSYR	MSYL
1.0	0.	0.033	21858	0.012	0.068	0.640	22097	0.012	0.067	0.645
1.3	0.3	0.032	20902	0.089	0.069	0.609	22171	0.089	0.069	0.581
1.6	0.6	0.032	18225	0.186	0.069	0.552	9935	0.187	0.049	0.494
1.9	0.9	0.025	14513	0.303	0.088	0.549	3669	0.303	0.029	0.494
3.0	0.0	0.010	14214	0.012	0.017	0.737	10829	0.012	0.024	0.766
3.3	0.3	0.011	13205	0.080	0.017	0.699	12405	0.080	0.019	0.624
3.6	0.6	0.012	10502	0.164	0.017	0.624	7668	0.163	0.018	0.563
3.9	0.9	0.011	7380	0.300	0.017	0.577	2318	0.305	0.018	0.522

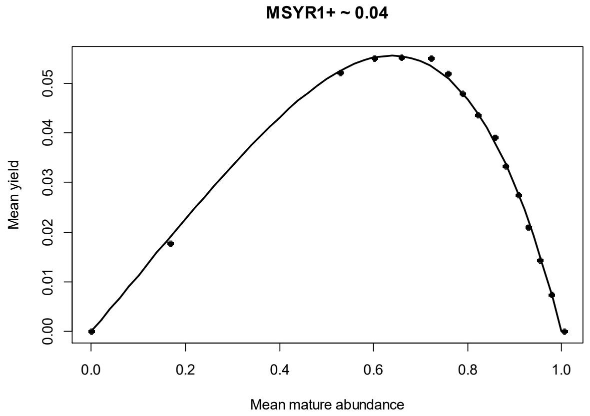


Fig 1a. Mature yield curve from IBEM for $MSYR_{1+} \approx 0.033$ with food supply CV = 0.0, $MSYR_{mat} = 0.056$, MSYL = 0.640.

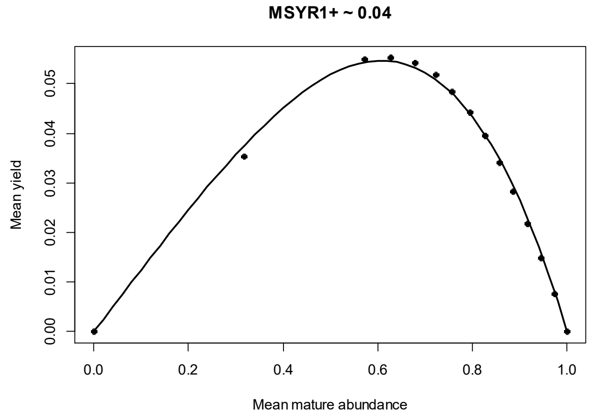


Fig 2a. Mature yield curve from IBEM for $MSYR_{1+} \approx 0.032$ with food supply CV = 0.3, $MSYR_{mat} = 0.055$, MSYL = 0.609.

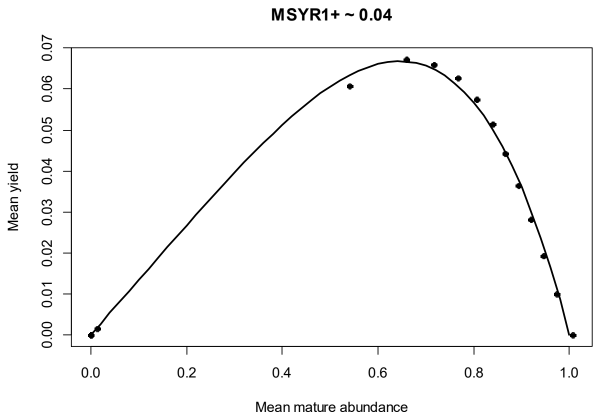


Fig 1b. Adjusted mature yield curve from emulator for $MSYR_{1+} \approx 0.04$ with CV(*K*) = 0.0, $MSYR_{mat} = 0.067$, MSYL = 0.645.

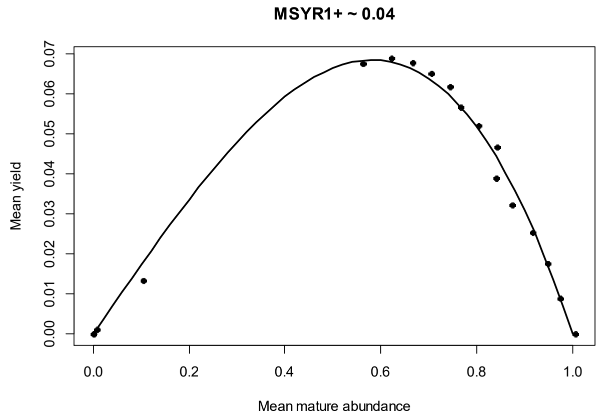


Fig 2b. Adjusted mature yield curve from emulator for $MSYR_{1+} \approx 0.04$ with CV(*K*) = 0.3, $MSYR_{mat} = 0.069$, MSYL = 0.581.

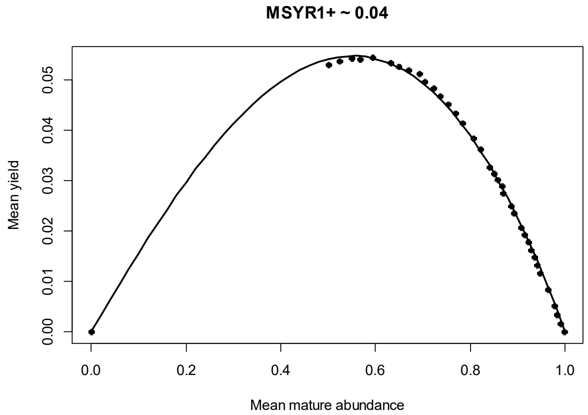


Fig 3a. Mature yield curve from IBEM for $MSYR_{1+}$ ≈ 0.032 with food supply CV = 0.6, $MSYR_{mat}$ = 0.055, MSYL = 0.552.

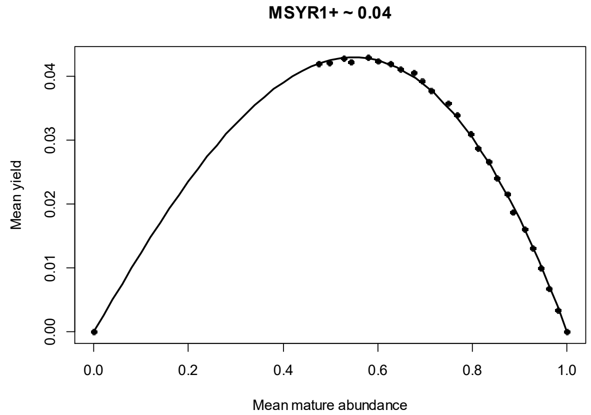


Fig 4a. Mature yield curve from IBEM for $MSYR_{1+}$ ≈ 0.025 with food supply CV = 0.9, $MSYR_{mat}$ = 0.043, MSYL = 0.549.

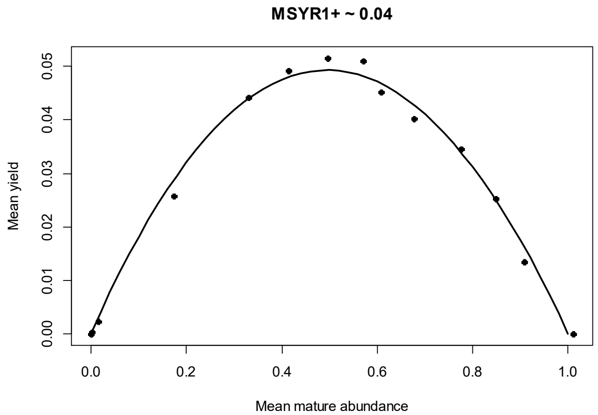


Fig 3b. Adjusted mature yield curve from emulator for MSYR1+ ≈ 0.04 with food supply CV = 0.6, $MSYR_{mat}$ = 0.049, MSYL = 0.494.

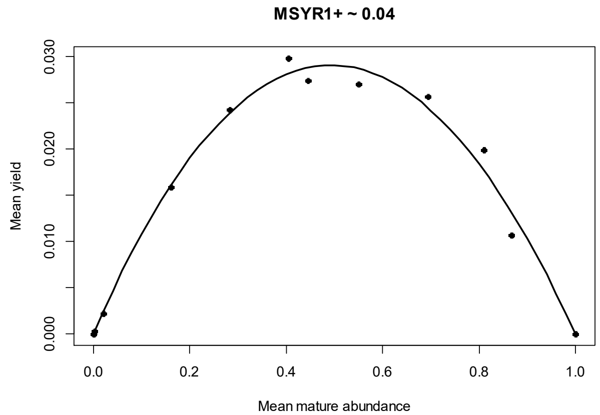


Fig 4b. Adjusted mature yield curve from emulator for $MSYR_{1+}$ ≈ 0.04 with food supply CV = 0.9, $MSYR_{mat}$ = 0.029, MSYL = 0.493.

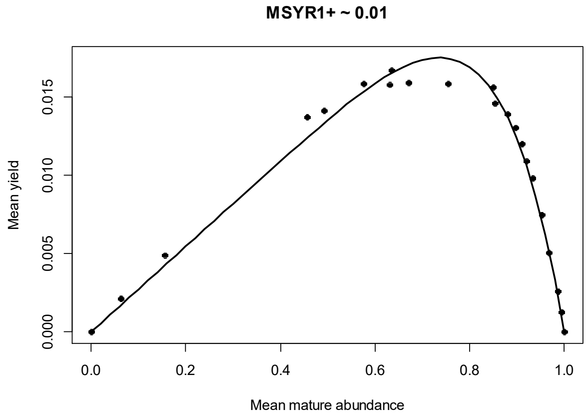


Fig 5a. Yield curve from IBEM for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.0, $MSYR_{mat}$ = 0.017, MSYL = 0.737.

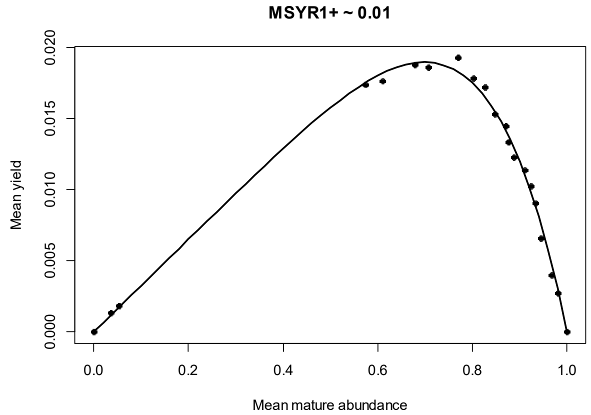


Fig 6a. Mature yield curve from IBEM for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.3, $MSYR_{mat}$ = 0.019, MSYL = 0.699.

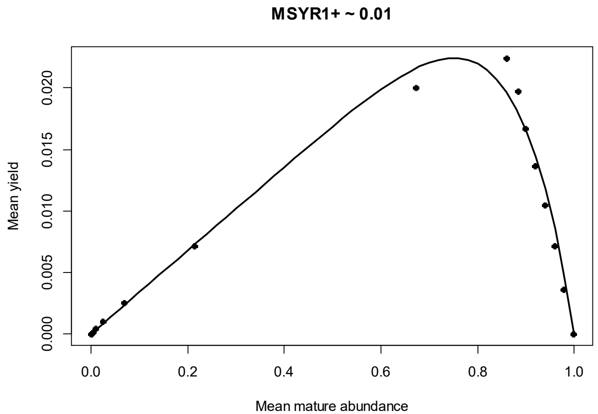


Fig 5b. Adjusted mature yield curve from emulator for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.0, $MSYR_{mat}$ = 0.024, MSYL = 0.766.

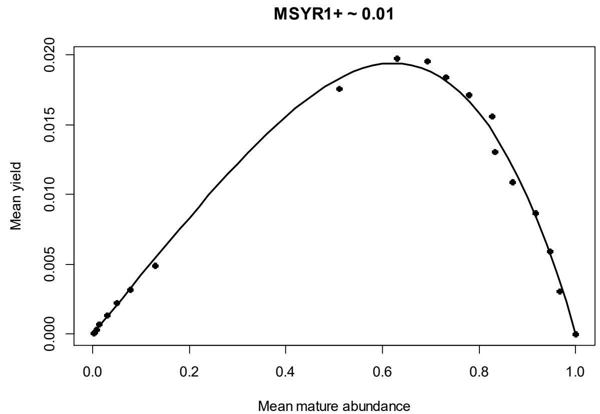


Fig 6b. Adjusted mature yield curve from emulator for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.3, $MSYR_{mat}$ = 0.019, MSYL = 0.624.

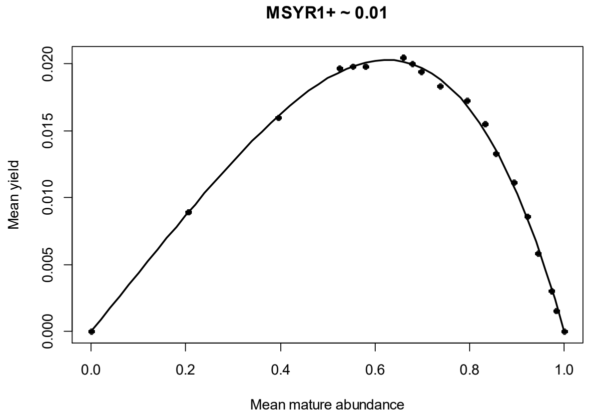


Fig 7a. Adjusted yield curve from IBEM for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.6, $MSYR_{mat}$ = 0.020, MSYL = 0.623.

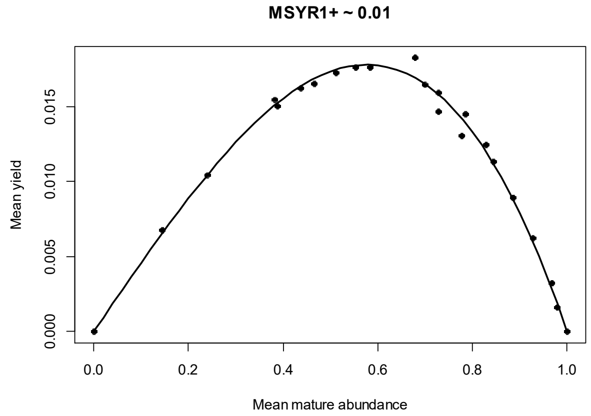


Fig 8a. Mature yield curve from IBEM for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.9, $MSYR_{mat}$ = 0.018, MSYL = 0.577.

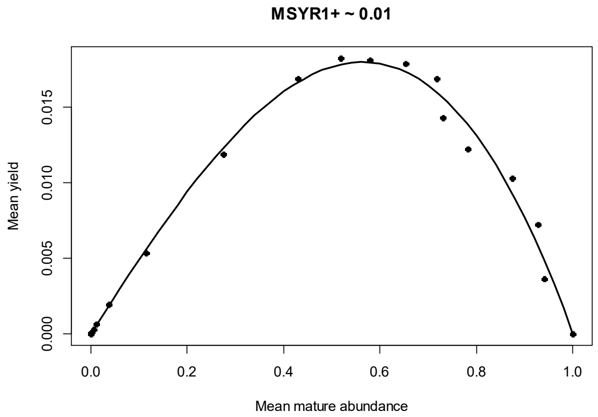


Fig 7b. Yield curve from emulator for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.6, $MSYR_{mat}$ = 0.018, MSYL = 0.564.

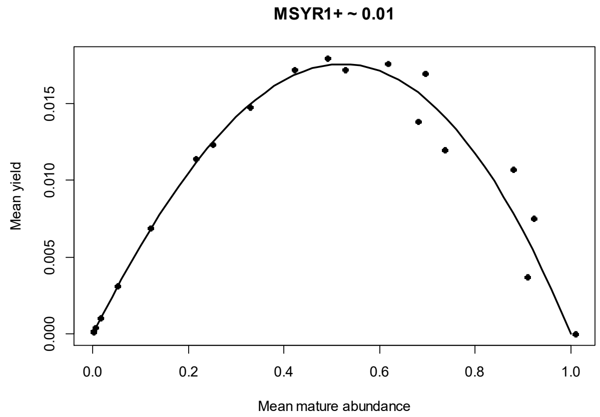


Fig 8b. Adjusted mature yield curve from emulator for $MSYR_{1+} \approx 0.01$ with food supply CV = 0.9, $MSYR_{mat}$ = 0.018, MSYL = 0.522.

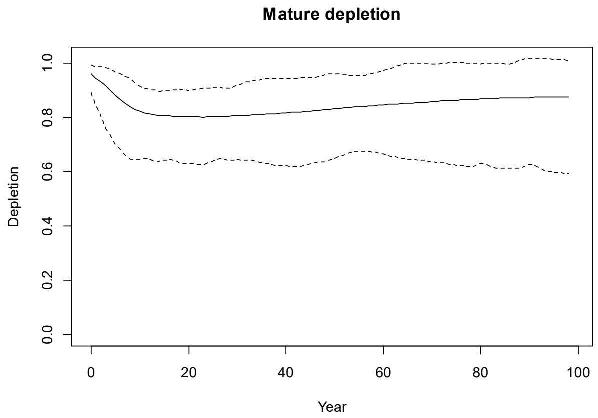


Fig 9a. Depletion of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.99, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

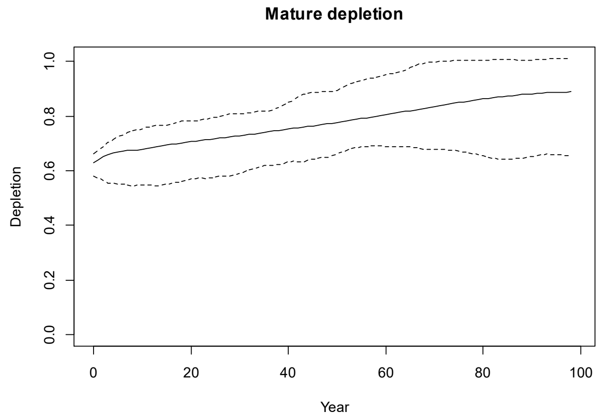


Fig 10a. Depletion of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.6, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

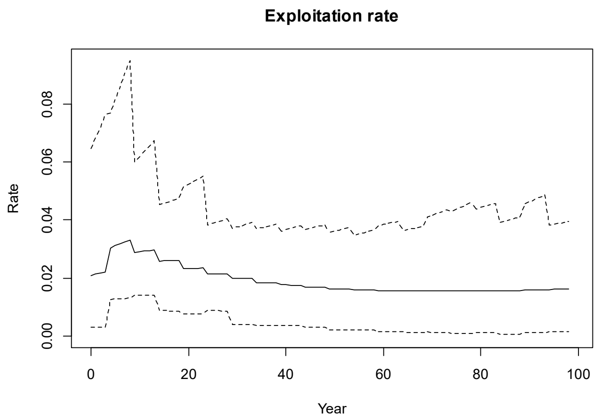


Fig 9b. Exploitation rate of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.99, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

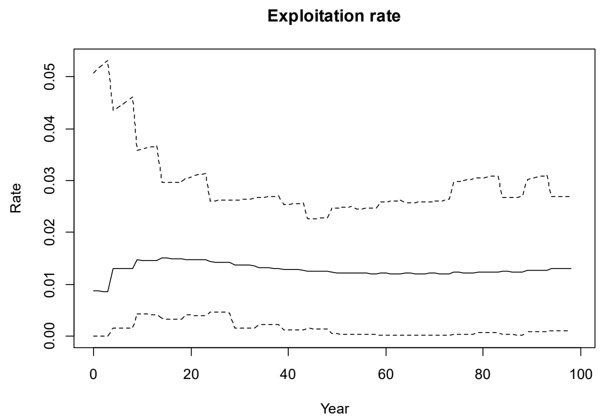


Fig 10b. Exploitation rate of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.6, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

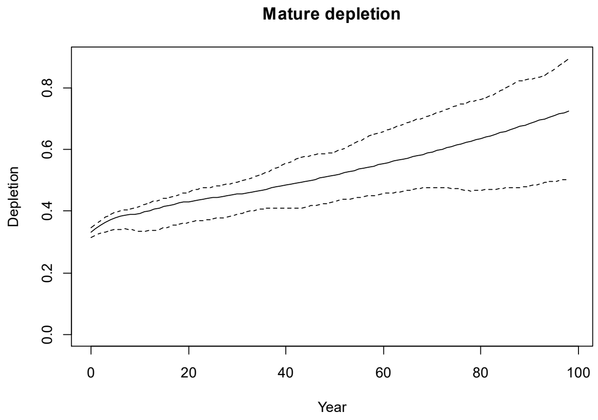


Fig 11a. Depletion of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.3, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

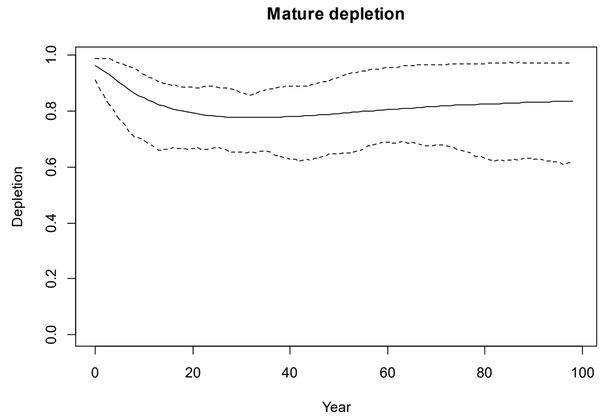


Fig 12a. Depletion of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.99, variability in carrying capacity = 0.270. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

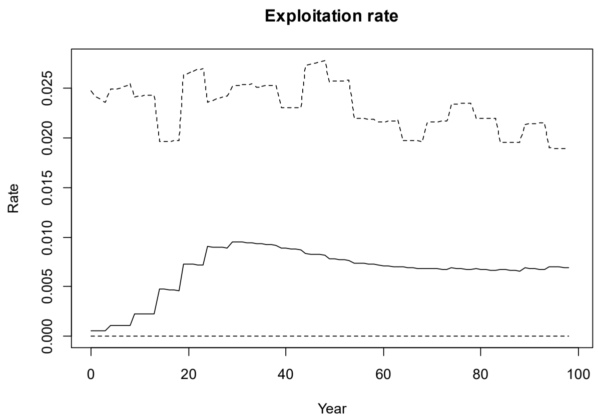


Fig 11b. Exploitation rate of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.3, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

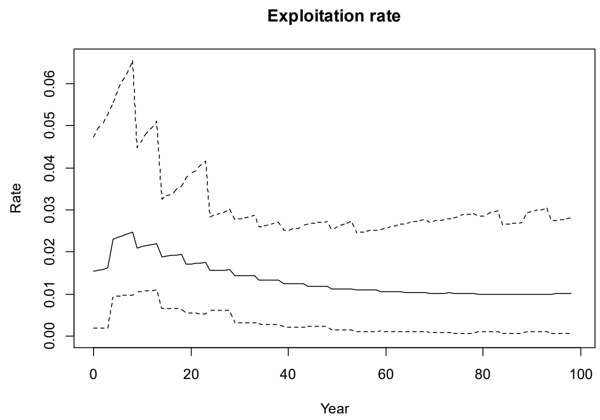


Fig 12b. Exploitation rate of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.99, variability in carrying capacity = 0.270. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

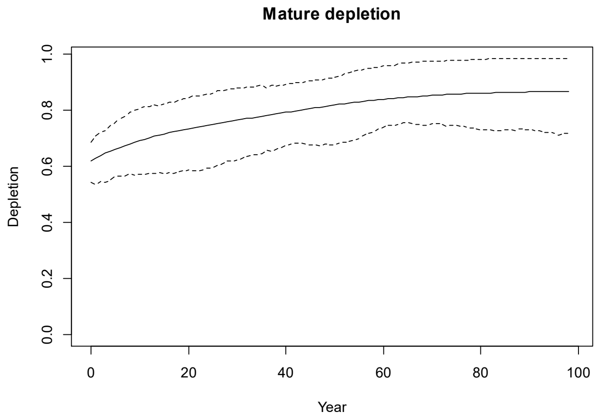


Fig 13a. Depletion of mature population for MSYR1+ ~1%, initial depletion = 0.6, variability in carrying capacity = 0.270. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

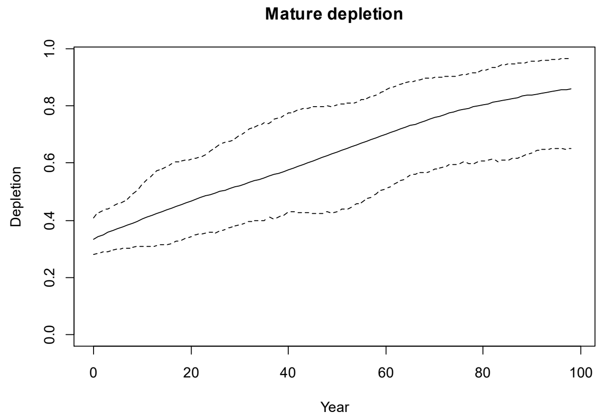


Fig 14a. Depletion of mature population for MSYR1+ ~1%, initial depletion = 0.3, variability in carrying capacity = 0.270. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

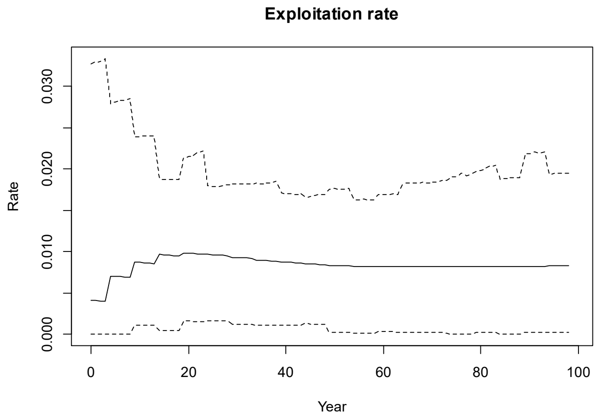


Fig 13b. Exploitation rate of mature population for MSYR1+ ~1%, initial depletion = 0.6, variability in carrying capacity = 0.270. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

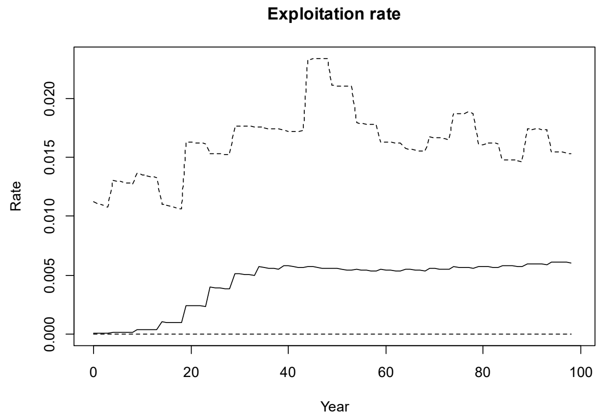


Fig 14b. Exploitation rate of mature population for MSYR1+ ~1%, initial depletion = 0.3, variability in carrying capacity = 0.270. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

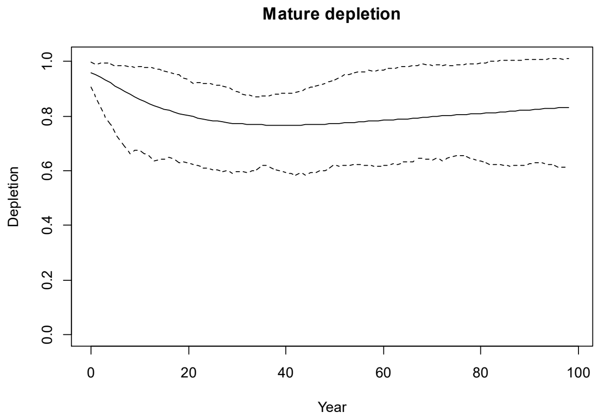


Fig 15a. Depletion of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.99, variability in carrying capacity = 0.565. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

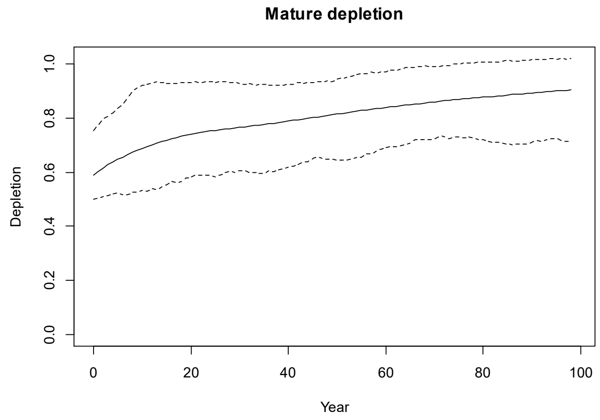


Fig 16a. Depletion of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.6, variability in carrying capacity = 0.565. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

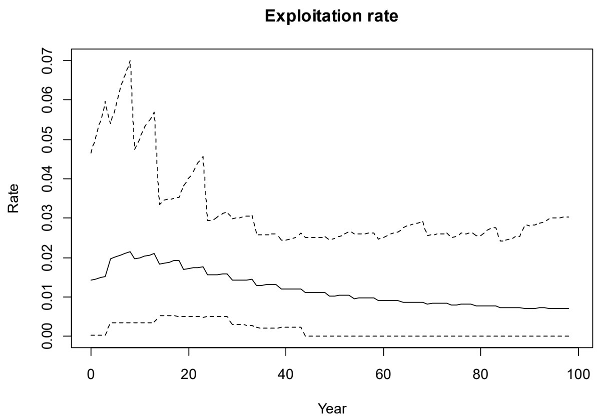


Fig 15b. Exploitation rate of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.99, variability in carrying capacity = 0.565. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

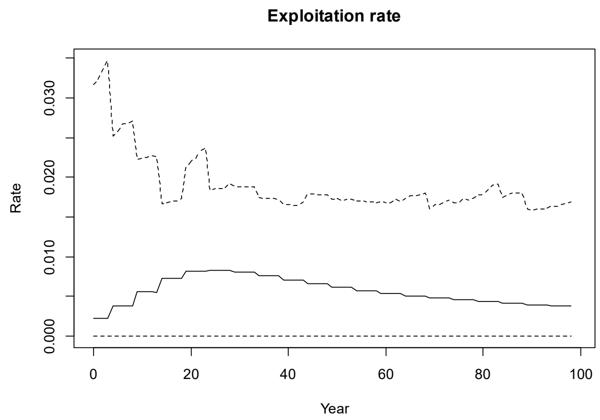


Fig 16b. Exploitation rate of mature population for $MSYR_{1+}$ ~1%, initial depletion = 0.6, variability in carrying capacity = 0.565. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

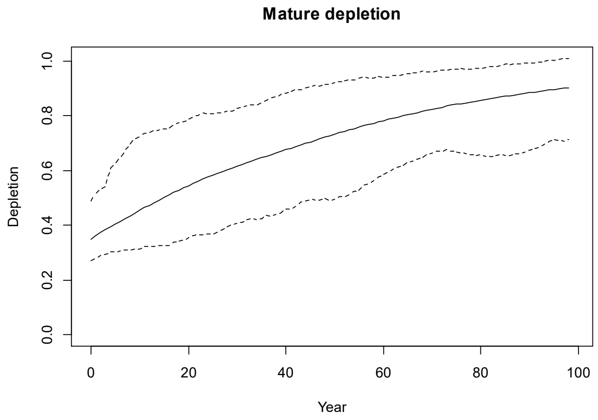


Fig 17a. Depletion of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.3, variability in carrying capacity = 0.565. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

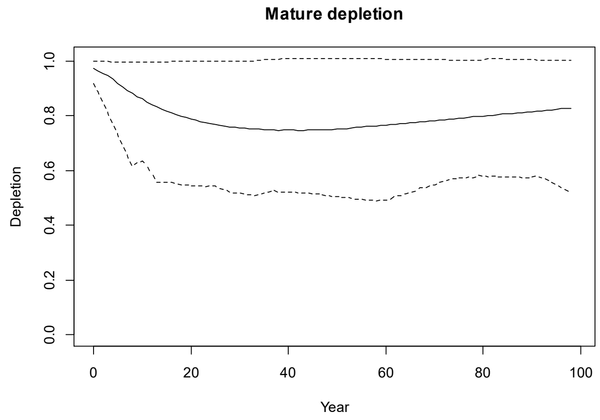


Fig 18a. Depletion of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.99, variability in carrying capacity = 0.867. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

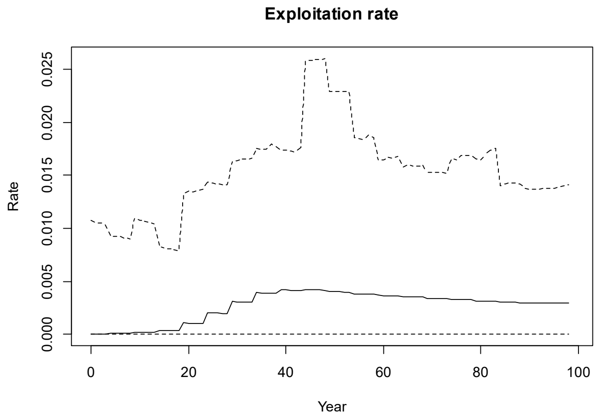


Fig 17b. Exploitation rate of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.3, variability in carrying capacity = 0.565. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

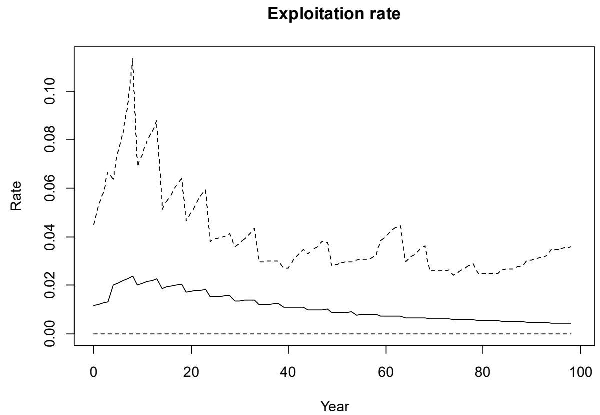


Fig 18b. Exploitation rate of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.99, variability in carrying capacity = 0.867. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

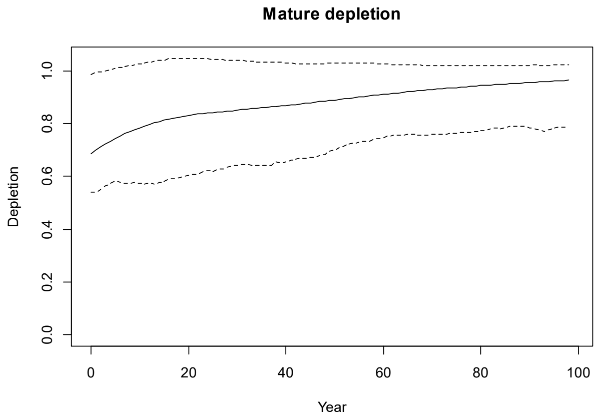


Fig 19a. Depletion of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.6, variability in carrying capacity = 0.867. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

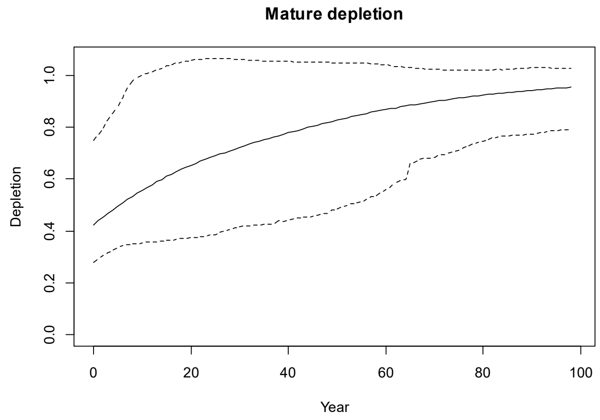


Fig 20a. Depletion of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.3, variability in carrying capacity = 0.867. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

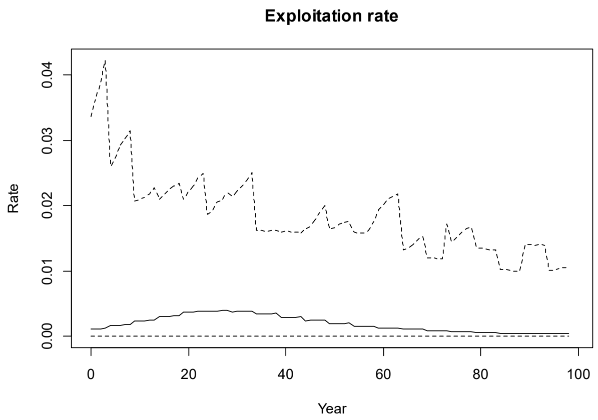


Fig 19b. Exploitation rate of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.6, variability in carrying capacity = 0.867. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

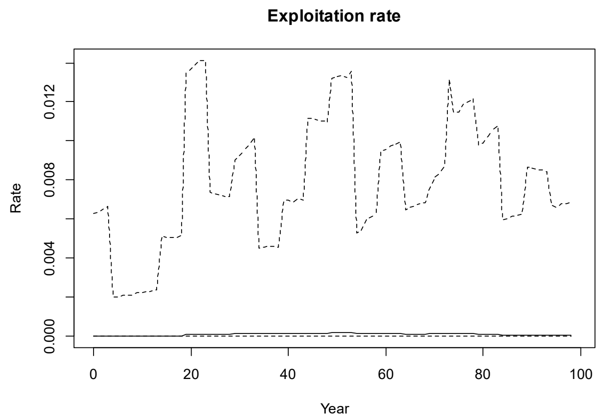


Fig 20b. Exploitation rate of mature population for MSYR$_{1+}$ ~1%, initial depletion = 0.6, variability in carrying capacity = 0.867. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

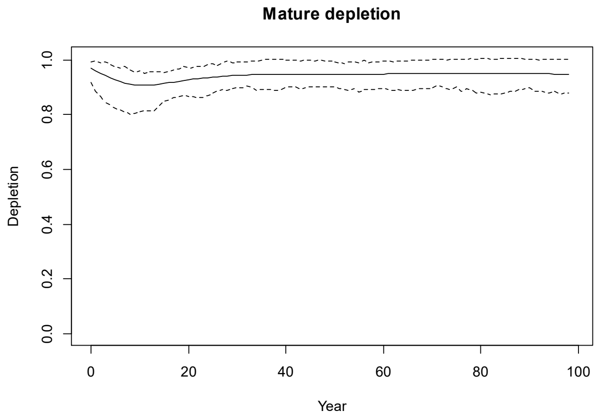


Fig 20a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

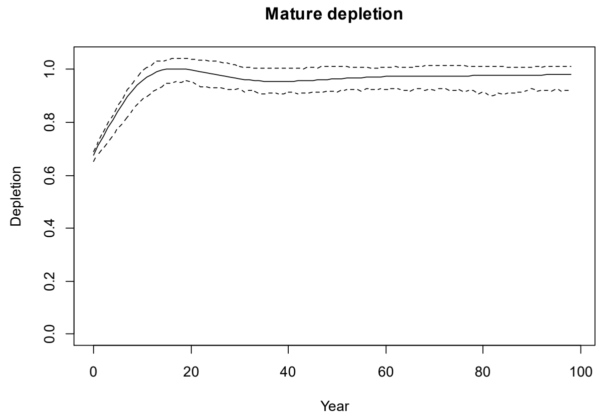


Fig 21a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

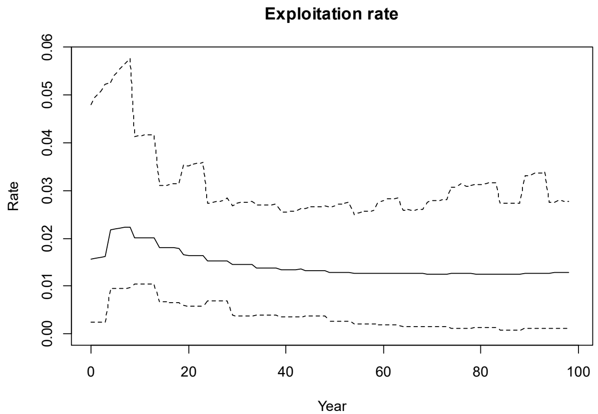


Fig 20b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

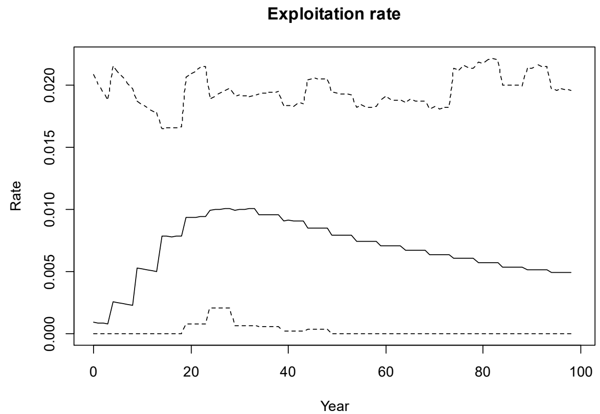


Fig 21b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

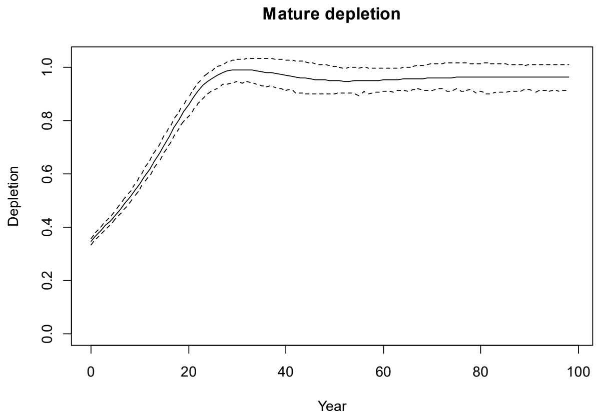


Fig 22a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

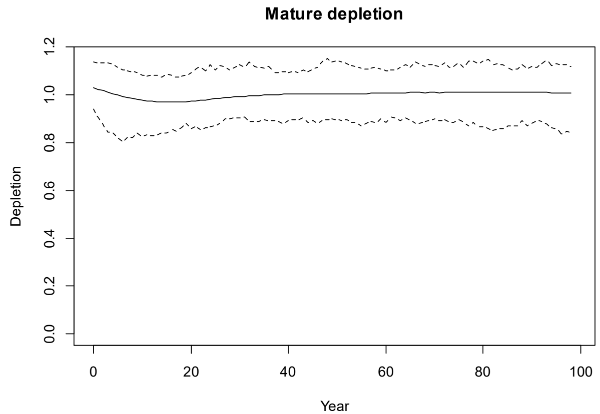


Fig 23a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, variability in carrying capacity = 0.208. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

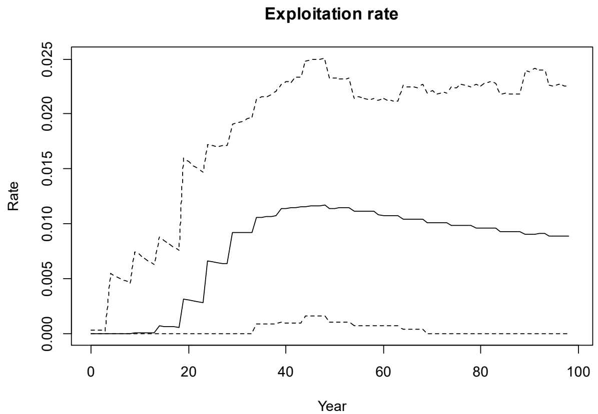


Fig 22b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, minimum variability in carrying capacity. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

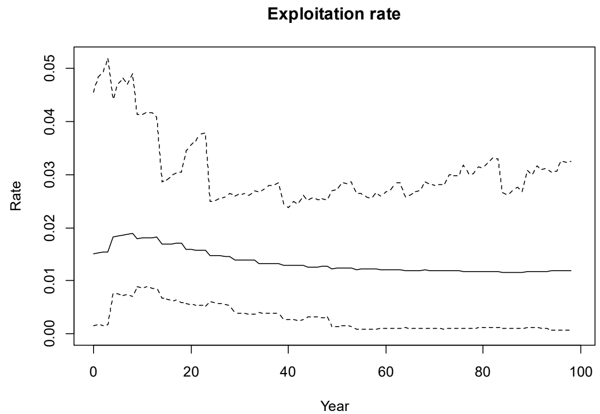


Fig 23b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, variability in carrying capacity = 0.208. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

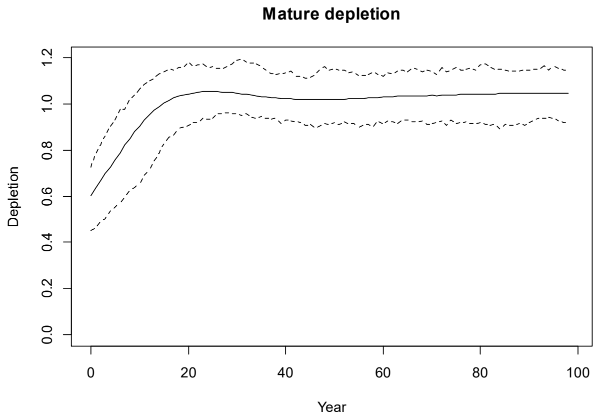


Fig 24a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, variability in carrying capacity = 0.208. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

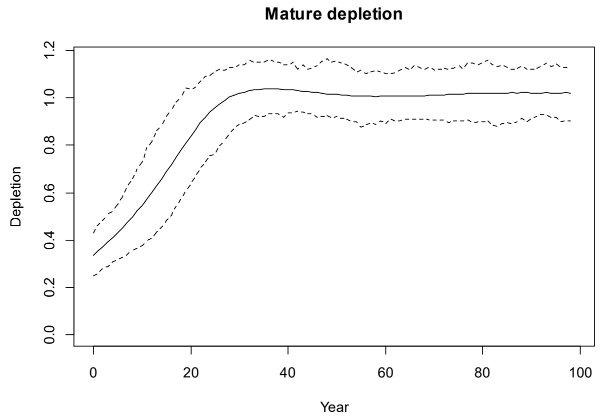


Fig 25a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, variability in carrying capacity = 0.208. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

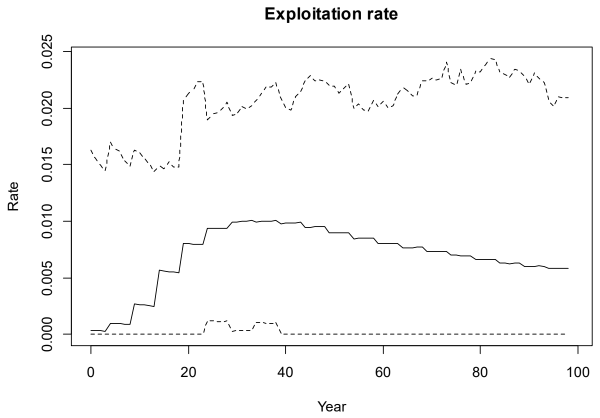


Fig 24b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, variability in carrying capacity = 0.208. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

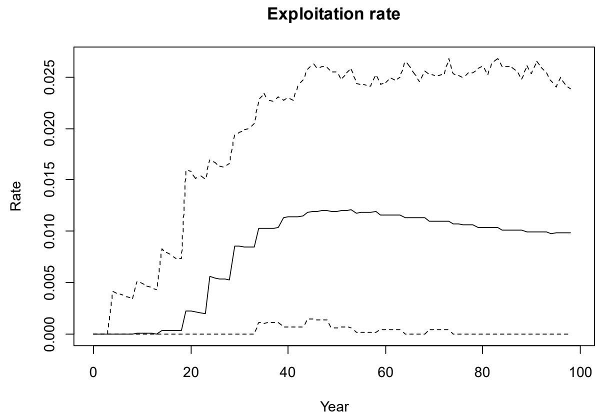


Fig 25b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, variability in carrying capacity = 0.208. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

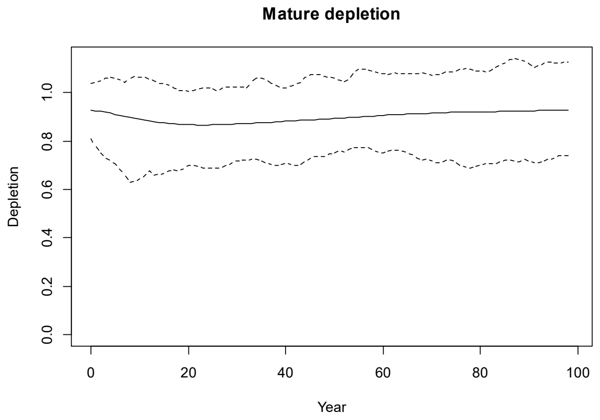


Fig 26a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, variability in carrying capacity = 0.542. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

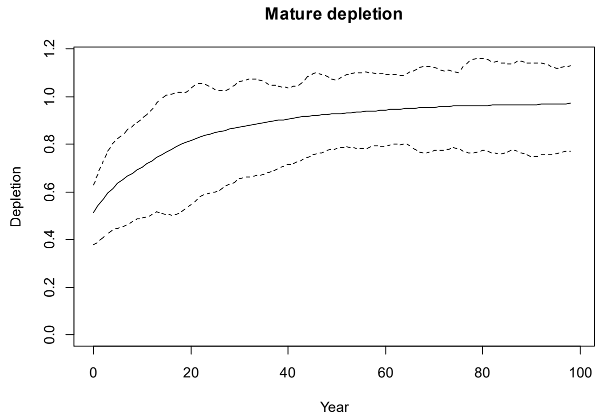


Fig 27a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, variability in carrying capacity = 0.542. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

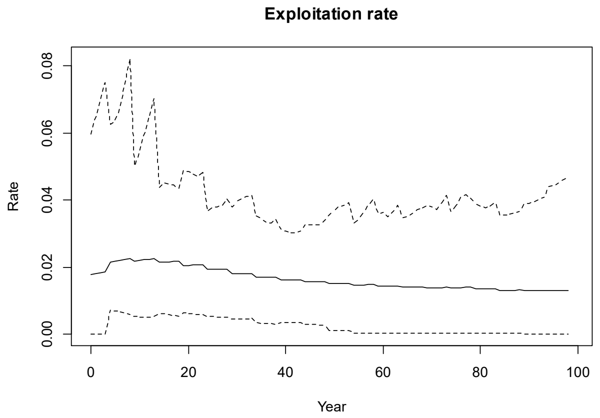
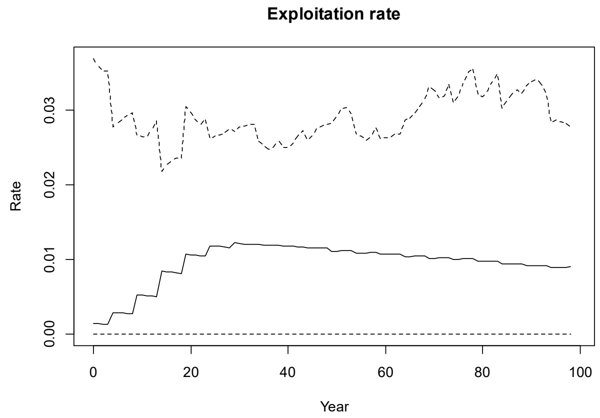


Fig 26b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, variability in carrying capacity = 0.542. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.



27b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, variability in carrying capacity = 0.542. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

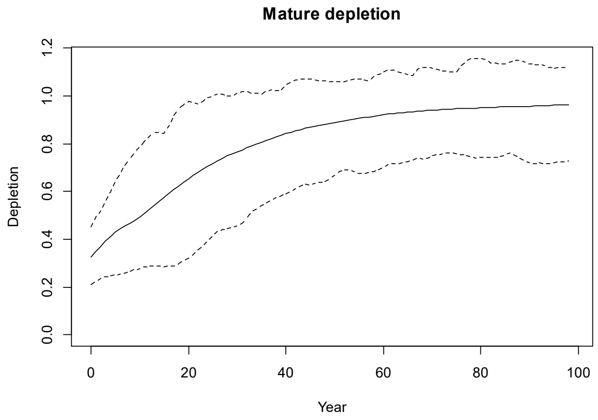


Fig 28a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, variability in carrying capacity = 0.542. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

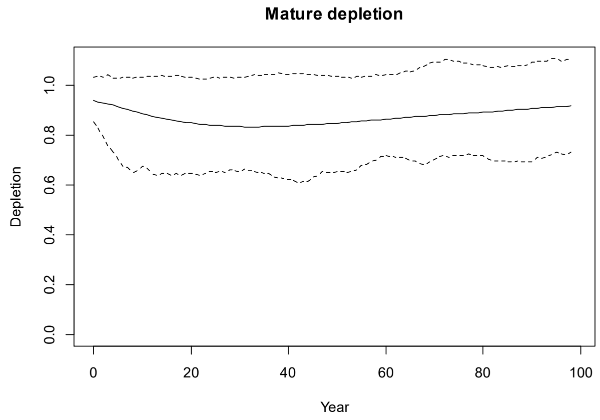


Fig 29a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, variability in carrying capacity = 0.870. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

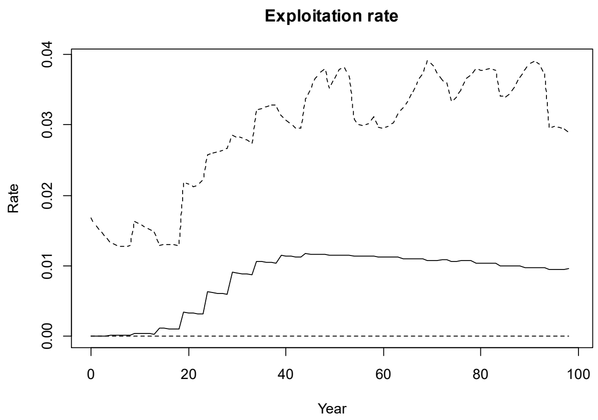


Fig 28b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, variability in carrying capacity = 0.542. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

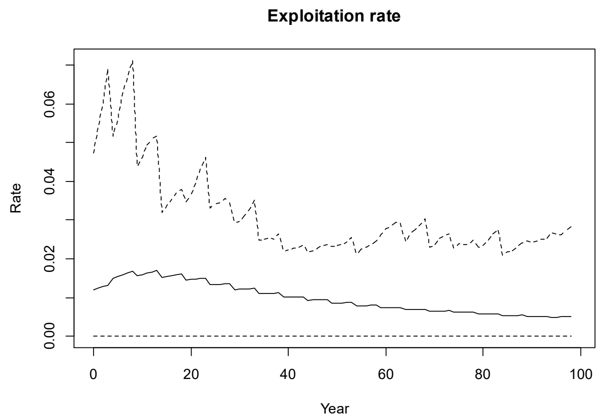


Fig 29b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.99, variability in carrying capacity = 0.870. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

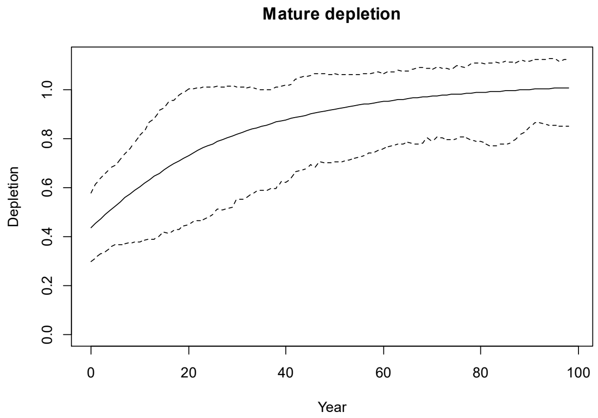


Fig 30a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, variability in carrying capacity = 0.870. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

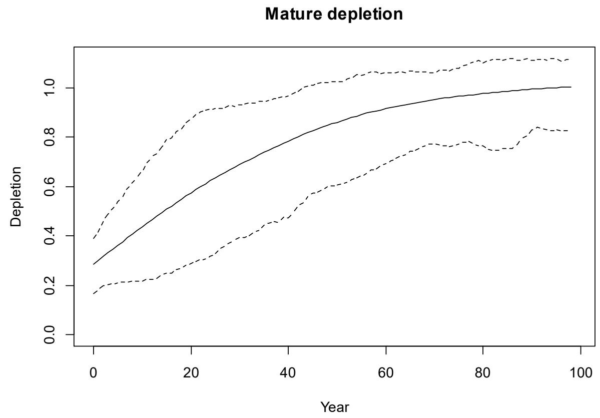


Fig 31a. Depletion of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, variability in carrying capacity = 0.870. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

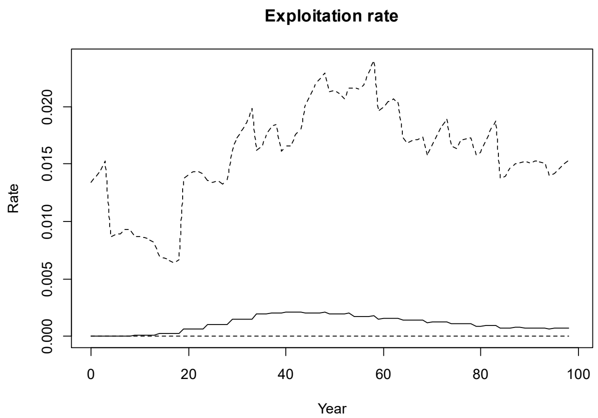


Fig 30b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.6, variability in carrying capacity = 0.870. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

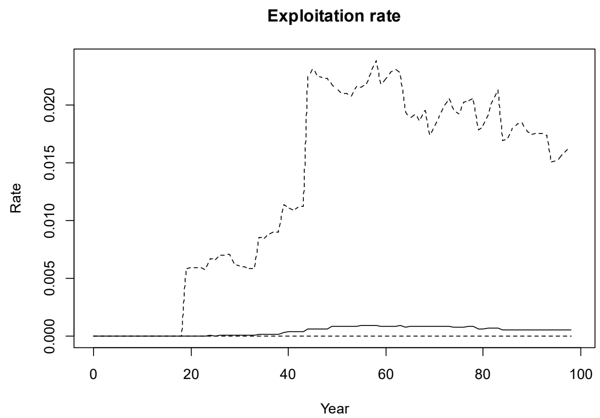


Fig 31b. Exploitation rate of mature population for $MSYR_{1+}$ ~4%, initial depletion = 0.3, variability in carrying capacity = 0.870. Solid line is mean trajectory of 400 trials, the dashed lines are the extreme values in each year.

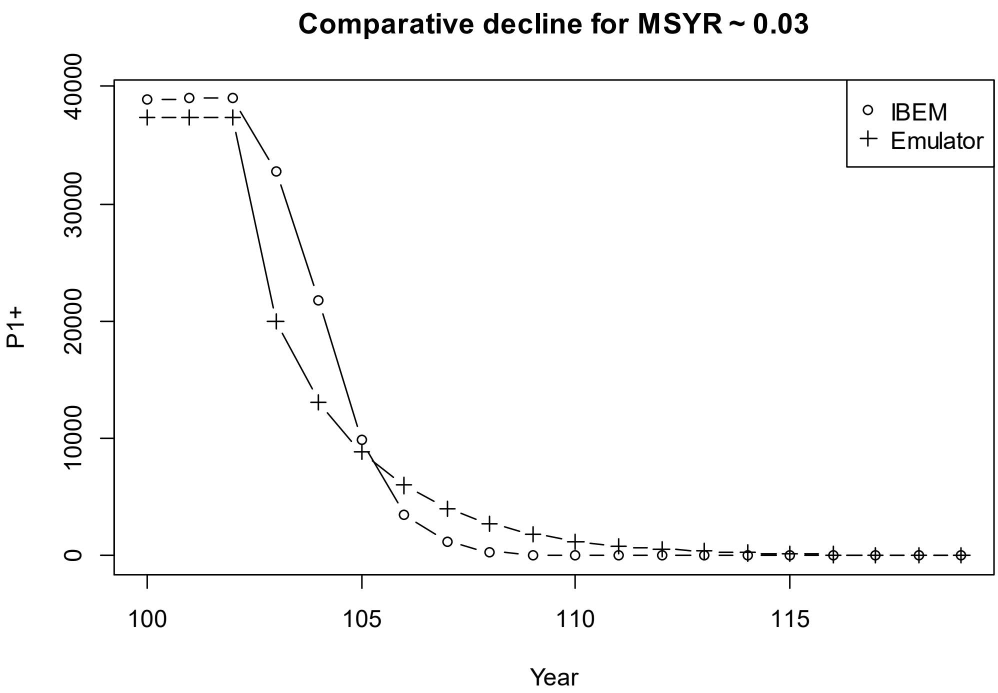


Fig. 32. Comparison of the decline in 1+ population from the IBEM with the emulator after a collapse in carrying capacity with MSYR ≈ 0.03.

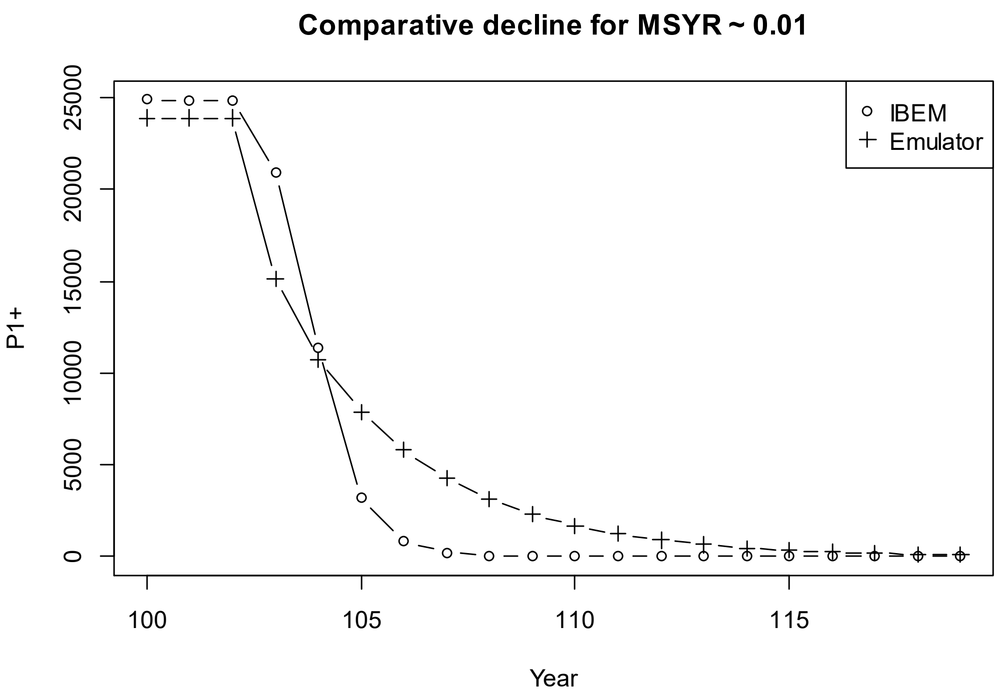


Fig. 33. Comparison of the decline in 1+ population from the IBEM with the emulator after a collapse in carrying capacity with MSYR ≈ 0.01.

APPENDIX 1: POPULATION DYNAMICS MODEL

Age-Structured Dynamics
The dynamics model an age-structured model derived from a class library written in C++. A list of the parameters used in the model is given in Table E.1. The basic dynamic equations are given by:

$$N_{a+1,t+1} = \left(N_{a,t} - C_{a,t}\right) S_{a,t} \qquad \left| 0 \le a < \left(a_{\max} - 1\right)\right. \tag{1}$$

with:

$N_{a,t}$ number in age class *a* in year *t*,

$C_{a,t}$ catch in number from age class *a* in year *t*,

$S_{a,t}$ proportion of animals that survive after natural mortality from age *a* to *a*+1 in year t

$$S_{a,t} = \mathrm{e}^{-M_{a,t}} \tag{2}$$

with:

$M_{a,t}$ natural mortality rate at age *a* in year *t*.

Natural mortality is age dependent and denoted as depending on time because it can be specified as being density dependent. The emulation model population age structure is determined by the number of births (N_0), calf mortality (M_0) and natural mortality for ages (a) given by:

$$M_a = -\ln\left(\left(\frac{N_{a+1} + C_a \exp\left(-M_a\left(1 - t_C\right)\right)}{N_a}\right)\right) \tag{3}$$

where:

N_a is the number of animals in age class *a* at the beginning of the year,

C_a is the catch of animals from age class *a* at time of year t_C

There is a pooled age class for animals aged a_s and above, which has a pooled mortality rate M_s. The natural mortality of animals in the pooled class is given by:

$$M_s = -\ln\left(1 - \frac{R_s - C_s \exp\left(M_{a_s}\left(1 - t_C\right)\right)}{N_s}\right) \tag{4}$$

where:

R_s is the number of animals recruiting to the sink age class, i.e. the animals surviving natural mortality and catches one year from the pre-sink age class

N_s is the number of animals in the pooled age class (aged a_s and above),

C_s is the catch taken from the pooled class, and

t_C is the proportion of the year that has elapsed when catches are taken.

Catches at age are determined either by uniform selectivity for the 1+ population or by the maturity logistic function for the mature population, given by:

$$p_a = \frac{1}{1+e^{k(a-a_{50})}} \tag{5}$$

The number of births is given by:

$$N_{0,t} = \rho P_t \sum_{a>0} N_{a,t} p_{a,t} \tag{6}$$

There is a pooled age class (plus class) at $a = a_s$. For this class:

$$N_{a_{\max},t+1} = \left(N_{a_{\max},t} - C_{a_{\max},t}\right) S_{a_{\max},t} + \left(N_{a_{\max}-1,t} - C_{a_{\max}-1,t}\right) S_{a_{\max}-1,t} \tag{7}$$

Catch-at-age in year *t* is calculated using:

$$C_{a,t} = H_t s_a N_{a,t} \tag{8}$$

with:

s_a age-specific selectivity, i.e. the proportion of age class a vulnerable to capture.

H_t is the proportional harvest rate in year *t*, specifically:

$$H_t = \frac{C_t}{\sum_{a=0}^{a_{\max}} N_{a,t} s_a} \tag{9}$$

with:

C_t total catch in number over all ages in year *t*

The model is coded so that time can be advanced in arbitrary increments, including zero. Catches can be removed at any time step and at as many time steps as required. Different catch series can be removed from the population at the same time step, or at different times if required. In the current application the time step used is one year.

The age-specific selectivity can be specified arbitrarily. In this current application selectivity is defined by the maturity function, which is a logistic given by:

$$s_a = \frac{1}{1+e^{-g\left(a-a_{s50}\right)}} \tag{10}$$

with:

$a_{s_{50}}$ age at which 50% of a cohort is sexually mature, and

g a constant which determines the rate at which maturity changes with age.

(11)

Appendix 2. Demographic parameter control file for the emulator model. The text in ***italics*** are annotations, which are not included in the runtime versions of the files.

```
Maximum age class                      40
Carrying capacity (1+ number)          50000.
Fecundity adjustment (incl. sex ratio) 0.513646
MSYR adjustment                        0.5
MSYL adjustment                        2.39
von Bertalanffy K (yr^-1)              0.298
Asymptotic length (mm)                 9.37
von Bertalanffy intercept              -1.383
Mass at length scale factor            26000.
Mass at length exponent                2.675
Carrying capacity CV                   0.
Carrying capacity autocorrelation coefficients (1st coeff is always
1.)
1. 0.3  0.2  -0.1

Demographic profiles as function of K
Fixed age for mortality function       60
The demographic parameters below are used in a set of cubic
interpolation splines with Depletion as the independent variable
Depletion
0 0.1729831 0.5418923 0.6154918 0.672045 0.7362637 0.7707317
0.8015545 0.8323238 0.8668722 0.8865184 0.9102653 0.9283302
0.9522112 0.97435 1.0 1.113696 1.321174 1.763897 2.591691 2.848539
3.241249 3.986974 4.842938 6.712838;
Age dependent mortality for ages 0 to 40+
      .
      .
      .
Birth rate
0.78579 0.78579 0.79097 0.79518 0.79834 0.80198 0.80506 0.80821
0.8114 0.81437 0.81716 0.81999 0.82262 0.82512 0.82726 0.82971
0.8350398 0.8421561 0.852157 0.858435 0.8596127 0.8591137 0.8595628
0.8601317 0.8622576;
Maturity rate parameter
1.56828 1.56828 1.57112 1.57229 1.57403 1.5761 1.57768 1.57954
1.58138 1.58362 1.58562 1.58763 1.58989 1.59782 1.59779 1.59721
1.605693 1.615464 1.625995 1.632879 1.633458 1.633958 1.636415
1.636465 1.635646;
Age at 50% maturity
4.57515 4.57515 4.61747 4.63481 4.66065 4.69132 4.71463 4.74206
4.76909 4.80201 4.8313 4.86059 4.89345 5.00817 5.00768 4.99934
5.120229 5.25793 5.404515 5.49938 5.507228 5.5141 5.547683 5.54843
5.537196;
Asymptotic mean length (not used)
9.5756 9.5756 9.5762 9.5768 9.5786 9.5781 9.5794 9.5796 9.5803 9.582
9.5821 9.5837 9.5838 9.5847 9.5861 9.5867 9.587 9.5859 9.5851 9.5851
9.5855 9.5853 9.5863 9.5861 9.5847;
Von Bertalanffy growth coefficient (not used)
0.3958 0.3958 0.385 0.3778 0.3717 0.3649 0.3598 0.3546 0.3498 0.3444
0.34 0.3353 0.3306 0.3257 0.3215 0.3173 0.3028681 0.2877297
0.2689582 0.2530124 0.2559392 0.2513977 0.2451405 0.2418101
0.2361584;
```

Von Bertalannfy intercept (not used)
-1.017 -1.017 -1.043 -1.0611 -1.0775 -1.0966 -1.1108 -1.1261 -1.1407 -1.1576 -1.1721 -1.1877 -1.2039 -1.2213 -1.236 -1.2517 -1.307218 -1.369215 -1.455333 -1.530686 -1.505469 -1.530586 -1.565273 -1.588696 -1.617801;