A Note Regarding How to Model MSY-related parameters when Population Dynamics are Stochastic

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ABSTRACT

A method is outlined for calculating the values for the parameters which determine MSYR and MSYL in the types of population dynamics models on which *Implementation Simulation Trials* are based in the face of environmental variability. The method is illustrated using a minke whale-like biology in which MSYR is defined in terms of harvesting of the mature female component of the population. Results are shown for various levels of environmental variation in survival and fecundity.

INTRODUCTION

Cooke (2007) showed that not only did the precision of population model-based estimates of MSY rate deteriorate in the face of environmental variability, but also that environmental variation led to biased estimates of MSY rate. All of the *Implementation Simulation Trials* developed to evaluate the conservation and utilization performance of variants of the *Revised Management Procedure*, RMP, have been based on deterministic population dynamics models, while some of the *Evaluation Trials* used during the development of the *Strike Limit Algorithm* for the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales (IWC, 2003) included trials in which account was taken of both environmental and demographic stochasticity. However, the values for the parameters that determine MSY rate and MSYL (A, the resilience parameter, and z, the degree of compensation) in these latter trials were based on the same approach as is used to calculate the values for these parameters when there is no environmental or demographic stochasticity.

This note outlines one way in which the population dynamics model on which *Implementation Simulation Trials* are based could be extended to allow for environmental stochasticity and how the values for A and z can be set for this extended model. Differences between stochastic and deterministic variants of the model are illustrated for a minke whale-like biology. This paper focuses on environmental rather than demographic stochasticity because demographic stochasticity only has a noteworthy impact on population dynamics at levels of abundance at which harvests under the RMP would not be permitted anyway.

METHODS

Population dynamics model

The dynamics of the population are governed by the equation[1]:

[1] The dependence of numbers-at-age on sex has been omitted for ease of presentation.

$$N_{y+1,a} = \begin{cases} B_{y+1} & \text{if } a = 0 \\ N_{y,a-1} S_{y,a-1} (1 - V_{a-1} E_y) & \text{if } 1 \le a \le x-1 \\ N_{y,x-1} S_{y,x-1} (1 - V_{x-1} E_y) + N_{y,x} S_{y,x} (1 - V_x E_y) & \text{if } a = x \end{cases} \tag{1}$$

where $N_{y,a}$ is the number of animals of age *a* at the start of year *y*,
B_y is the number of births at the start of year *y*,
V_a is the selectivity of the fishery on animals of age *a*,
$S_{y,a}$ is the survival rate of animals of age *a* during year *y*,
E_y is the exploitation rate during year *y*, and
x is the maximum age (taken to be a plus-group).

The number of births during year *y*, B_y, is assumed to be stochastic and related to the expected fecundity, b_y^*, according to the equation:

$$B_y = N_y^m \frac{1}{1 + e^{\mu_y + \varepsilon_y}} \qquad \varepsilon_y \sim N(0; \sigma_\varepsilon^2) \tag{2}$$

and

$$b_y^* = f_0 (1 + A(1 - (N_y^m / K^m)^z)) \tag{3}$$

where N_y^m is the number of animals that have reached the age-at-first-parturition by the start of year *y*:

$$N_y^m = \sum_a M_a \, N_{y,a} \tag{4}$$

M_a is the proportion of females of age *a* that could have given birth,
K^m is the number of animals that have reached the age-at-first-parturition in the unfished state,
μ_y is selected so that the expected value of B_y is $b_y^* N_y^m$, i.e.:

$$b_y^* = \int_{-\infty}^{\infty} (1 + e^{\mu_y + \varepsilon})^{-1} \tfrac{1}{\sqrt{2\pi}\sigma_\varepsilon} e^{-\frac{\varepsilon^2}{2\sigma_\varepsilon^2}} \, d\varepsilon \tag{5}$$

σ_ε determines the extent of stochasticity in fecundity, and
f_0 is the (expected) fecundity rate at pre-exploitation equilibrium.

The survival rate during year *y* for animals of age *a*, $S_{y,a}$, is assumed to be stochastic and perfectly correlated among ages. It is generated using the equation:

$$S_{y,a} = (1+e^{\lambda+\eta_y})^{-1} \qquad\qquad \eta_y \sim N(0;\sigma_\eta^2) \tag{6}$$

where λ is selected so that the expected value of $S_{y,a}$ is $\tilde{S}$, i.e.:

$$\tilde{S} = \int_{-\infty}^{\infty} (1+e^{\lambda+\eta})^{-1} \frac{1}{\sqrt{2\pi}\sigma_\eta} e^{-\frac{\eta^2}{2\sigma_\eta^2}} \, d\eta \tag{7}$$

$\tilde{S}$ is the (pre-specified) expected survival rate, and
σ_η determines the extent of stochasticity in survival.

The catch during year *y*, C_y, is calculated assuming that the fishery occurs before natural mortality, i.e.:

$$C_y = E_y \sum_a V_a N_{y,a} \tag{8}$$

Solving for *A* and *z*
The values for *A* and *z* are selected so that if the exploitation rate is set to MSYR, the derivative of the mean yield function with respect to exploitation rate is zero and so that the mean population size, when expressed relative to the corresponding pre-exploitation equilibrium size, equals MSYL. The mean yield and population size are computed by projecting the population ahead for many years many times under an exploitation rate equal to MSYR (i.e. E_y in Equation 1 is set equal to MSYR). The age-structure at the start of the projection period is set equal to that corresponding to the deterministic equilibrium under MSYR (note: this age-structure depends on both *A* and *z*).

Application to minke whales
Table 1 lists the values of the pre-specified parameters of the population dynamics model for the example application. MSYR is defined in terms of harvesting of the mature component of the population (i.e. MSYR_{mat}) for consistency with how *Implementation Simulation Trials* have been parameterized for Brydes and minke whales (IWC, 2004, 2007), and MSYL is also defined in terms of this population component. Selectivity is set equal to having reached first parturition and both selectivity and maturity are assumed to be logistic functions of age, parameterized in terms of the ages at 50%- and 95%-maturity (Table 1). Consistent with the *Implementation Simulation Trials* for the North Atlantic and western North Pacific minke whales, animals of age 2 and younger are always assumed to be immature (and not available for capture). A range of values for the parameters which determine the extent of environmental variation in fecundity and survival are considered. Note that even in the cases in which σ_ε and σ_η are large, Equations 2 and 6 ensure that fecundity and survival are never less than 0 or greater than 1. These equations could be modified to impose alternative bounds (such as that births occur no more frequently than once every second year).

All of the stochastic analyses are based on *N*=1000 simulations and the evaluation of Equation 8 is based on 1000-year projections in which the catch used when finding MSY is set to the average over the final 500 years of the projection period.

RESULTS AND DISCUSSION

The upper left panels of Figures 1 and 2 compare the deterministic and stochastic ($\sigma_\varepsilon = \sigma_\eta = 0.2$) evaluations of *A* and *z* for $MSYR_{mat}$=0.01 and 0.04 respectively. As expected, the mean yield curve based on stochastic dynamics is similar to the deterministic relationship, even though the estimates of *A* and *z* differ slightly between the deterministic and stochastic cases (Table 2). The remaining panels of Figures 1 and 2 show the distributions of the number of animals that have reached first parturition relative to the pre-exploitation number of such animals as a function of exploitation rate, and the distributions of the average catch (over years 500-1000 of the projection period) and catch in year 1000 as a function of exploitation rate. As expected, the distribution for the catch in year 1000 is broader than that of the average catch. However, the extent to which this is the case is lower than might be expected because population sizes (and hence catches) are strongly temporally auto-correlated (Figure 3).

There is considerable variability in individual trajectories of population size, with the extent of variation higher for $MSYR_{mat}$=0.01 than for $MSYR_{mat}$=0.04 (Figure 3), and this is reflected in the distributions of catch and population size as a function of exploitation rate. There are some transient effects in the first 200 years of the projection period (particularly for $MSYR_{mat}$=0.01), which presumably reflects the impact of all of the analyses starting from the same age-structure, and in the absence of stochasticity.

Table 2 lists the values for *A* and *z* for each combination of σ_ε and σ_η whiles Figures 4 and 5 show the relationships between the catch in year 1000 and exploitation rate for the combination of σ_ε and σ_η in Table 2. *A* and *z* are not impacted noticeably by the values specified for σ_ε and σ_η (Table 2), except when σ_η is set to 0.4 (see Figure 6 for examples of individual time-trajectories of population size for this case).

The results in Figures 4-6 highlight that environmental variation in survival has a larger impact on the population dynamics than environmental variation in fecundity for the same amount of environmental variation. This is not unexpected because environmental variation in fecundity only impacts a single age-class whereas environmental variation in survival impacts all age-classes simultaneously. It is perhaps noteworthy therefore that the “stochastic” *Evaluation Trials* for the B-C-B bowhead whales were based only on environmental variation in fecundity (although some *Robustness Trials* examined the impact of catastrophic events – a form of environmental variation in survival).

Although the values for *A* and *z* differ from the deterministic values (Table 2), the effect is small, which suggests that setting the values for *A* and *z* based on deterministic analyses should not lead to results of evaluations of management procedures which differ markedly from those using values for *A* and *z* based on the method of this paper. However, this should be confirmed for some specific cases.

The choices for σ_ε and σ_η considered in this paper are arbitrary, there being no way at present to quantify the extent of inter-annual variation in fecundity or survival for minke whales. Figure 7 shows how the standard deviation of fecundity changes as a function of mean fecundity and the value assumed for σ_ε.

Finally, the analyses of this paper ignore temporal auto-correlation in survival and fecundity caused by environmental variation. This can be incorporated straightforwardly, although it is likely that it will be necessary for there to be much longer projection periods when there is (high) auto-correlation in fecundity and survival if reliable values for *A* and *z* are needed.

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Table 1. The parameters of the population dynamics model

Parameter	**Value(s)**
$MSYR_{mat}$	0.01, 0.04
$MSYL_{mat}$	0.6
$V_{50\%}$, $V_{95\%}$	7yr; 10.53yr*
$M_{50\%}$, $M_{95\%}$	7yr; 10.53yr
$\tilde{S}$	0.07 yr^{-1}
σ_ε	0, 0.2, 0.4
σ_η	0. 0.2, 0.4

* Set equal to the parameters of the maturity ogive (IWC, 1992)

Table 2. Values for the resilience and degree of compensation parameters for various choices for the extent of environmental variation in fecundity and survival.

Scenario	$MSYR_{mat}$ = 0.01	$MSYR_{mat}$ = 0.04
$\sigma_\varepsilon = 0; \sigma_\eta = 0$	0.1938, 2.393	0.7714, 2.402
$\sigma_\varepsilon = 0; \sigma_\eta = 0.2$	0.1949, 2.491	0.7744, 2.415
$\sigma_\varepsilon = 0.2; \sigma_\eta = 0$	0.1939, 2.434	0.7719, 2.413
$\sigma_\varepsilon = 0.2; \sigma_\eta = 0.2$	0.1966, 2.481	0.7801, 2.381
$\sigma_\varepsilon = 0.2; \sigma_\eta = 0.4$	0.1978, 3.007	0.7895, 2.437
$\sigma_\varepsilon = 0.4; \sigma_\eta = 0.2$	0.1982, 2.550	0.7841, 2.385
$\sigma_\varepsilon = 0.4; \sigma_\eta = 0.4$	0.1993, 3.127	0.7933, 2.443

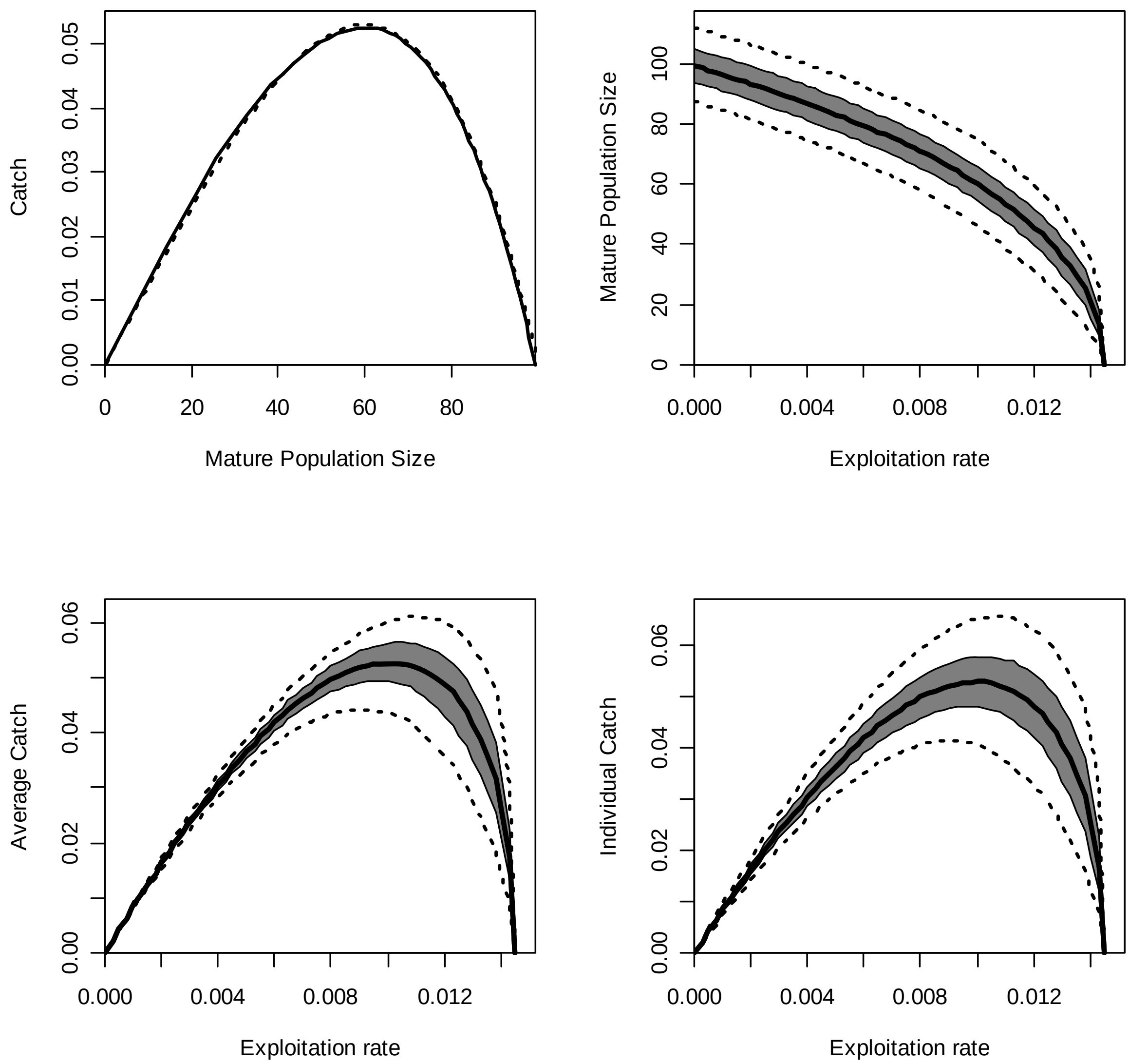

Figure 1. Relationship between the number of mature animals (expressed relative to the corresponding pre-exploitation level) based on deterministic (solid line) analyses and the mean of stochastic realizations (dotted line) (upper left panel), that between the depletion of the mature female component of the population (upper right panel) and exploitation rate, and that between average catch and exploitation rate (lower panels). Results are shown in the lower left panel for the average catch over the last 500 years of a 1000-year projection period and in the lower right panel for the catch in the 1000th year. The analyses on which this figure are based assume that $MSYR_{mat}$ =0.01, $MSYL_{mat}$ = 0.6, $\sigma_\varepsilon = 0.2$ and $\sigma_\eta = 0.2$. In the distribution plots, the solid line indicates the median, the shaded regions the interquartile range, and the dotted lines the 90% intervals.

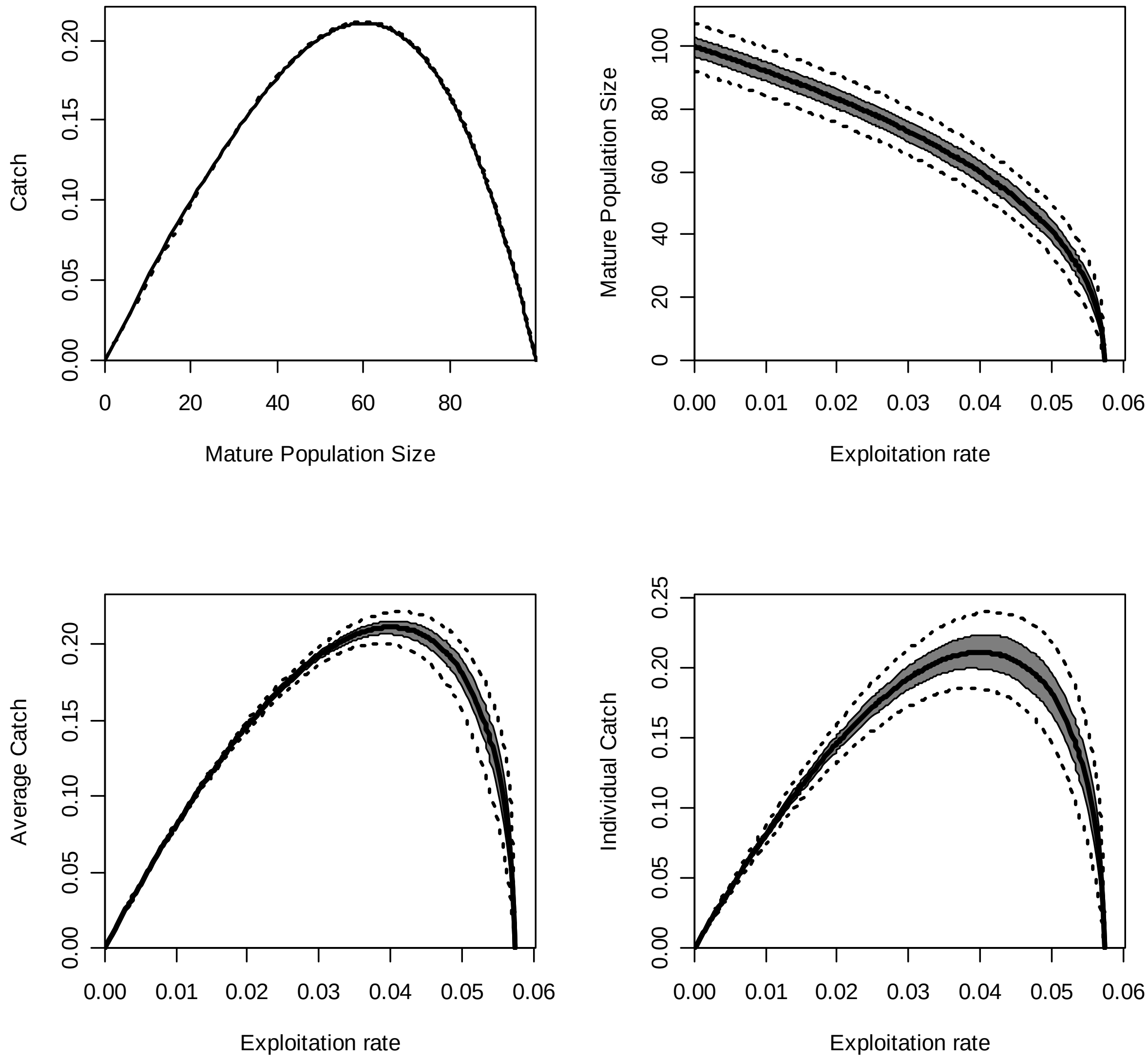

Figure 2. As for Figure 1, except that the analyses are based on $MSYR_{mat} = 0.04$.

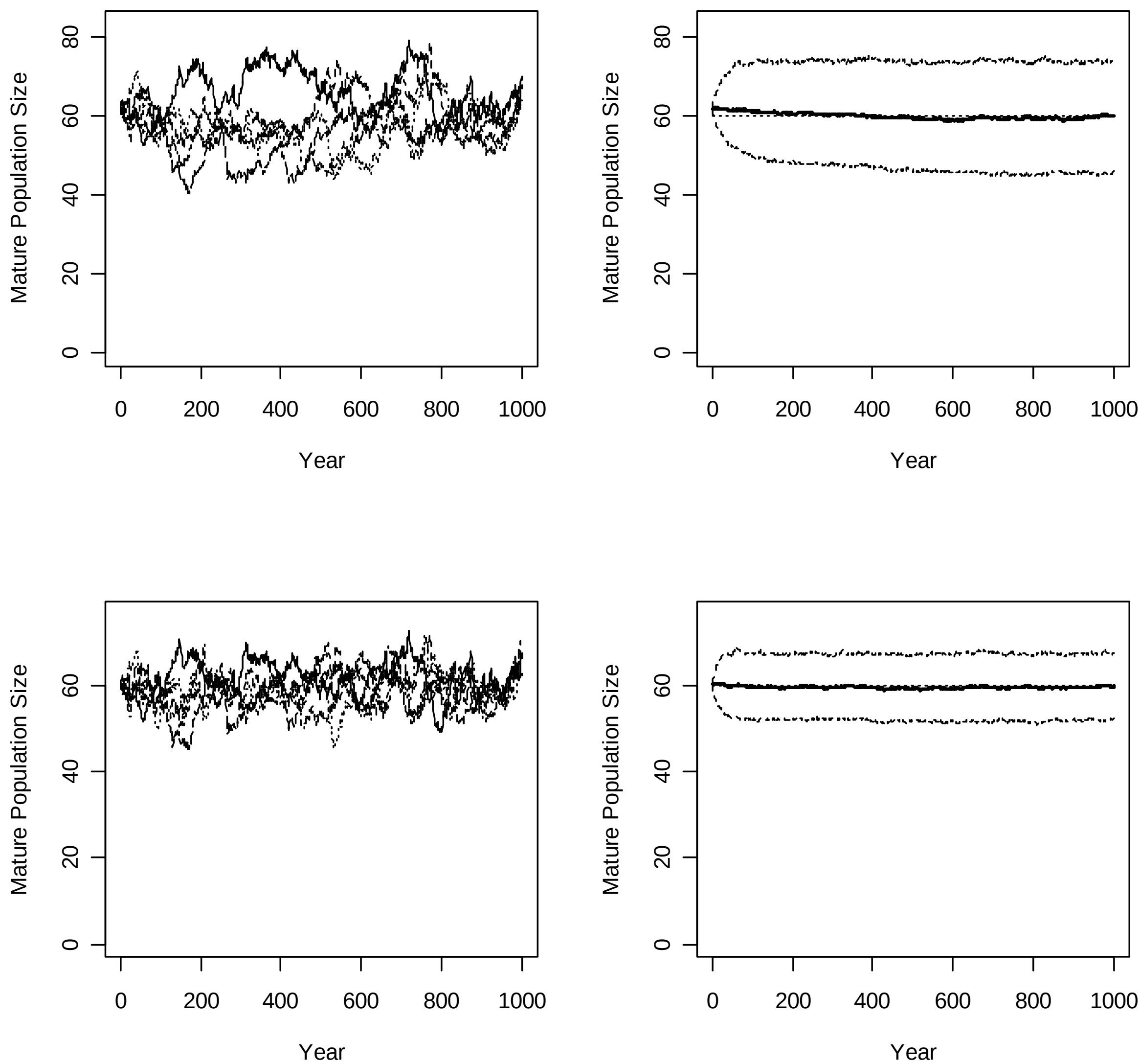

Figure 3. Time-trajectories for the number of mature females (expressed as a percentage of the pre-exploitation number of mature females). The left panels show the results of five replicates and the right panels show the median and 90%iles for these time-trajectories. The results in this figure pertain to $MSYL_{mat}$ = 0.6, $\sigma_{\varepsilon} = 0.2$ and $\sigma_{\eta} = 0.2$, with the upper panels based on $MSYL_{mat}$ = 0.01 and the lower panels on $MSYL_{mat}$ = 0.04.

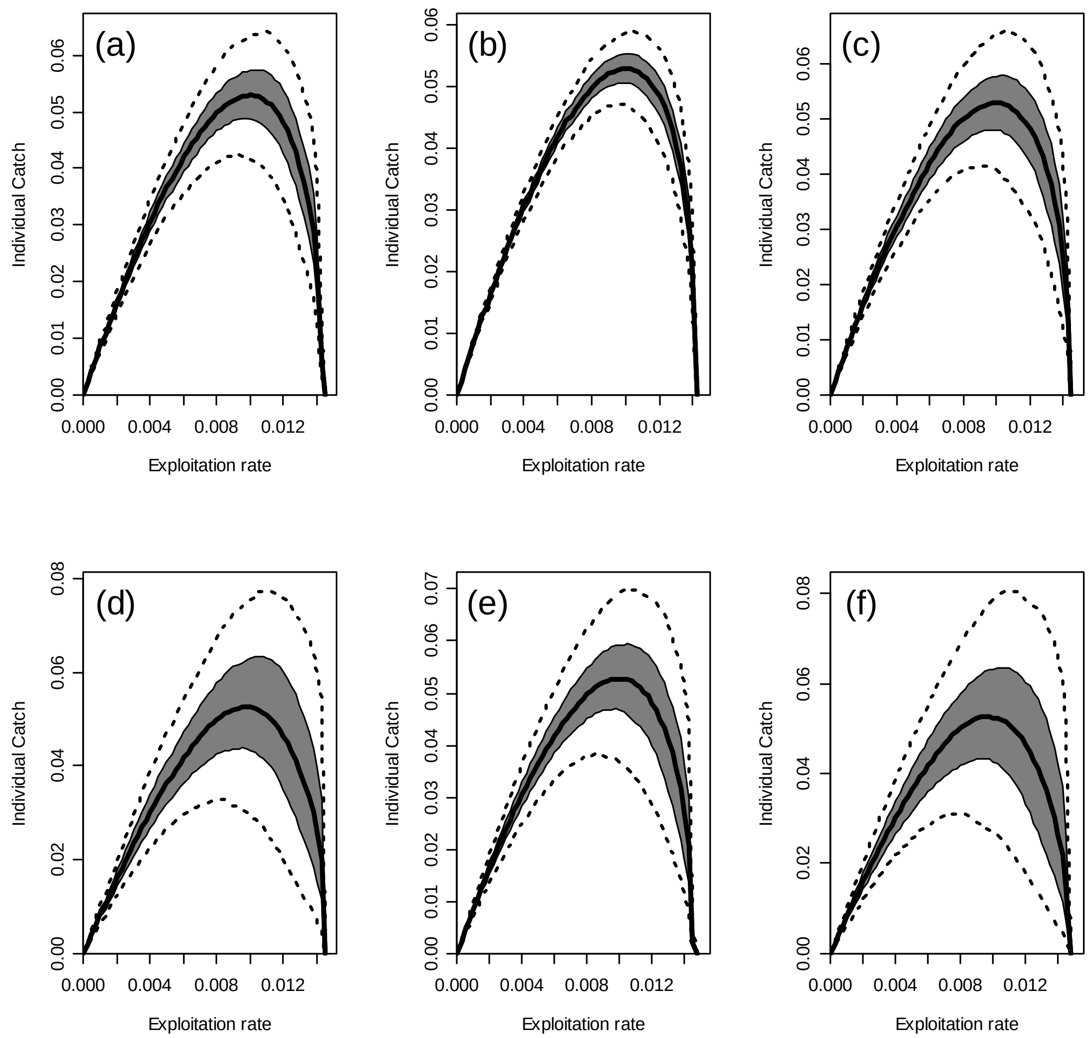

Figure 4. Relationships between exploitation rate and the catch in year 1000 for $MSYR_{mat}$=0.01. Results are shown in (a) for $\sigma_{\varepsilon}=0;\sigma_{\eta}=0.2$, (b) for $\sigma_{\varepsilon}=0.2;\sigma_{\eta}=0$, (c) for $\sigma_{\varepsilon}=0.2;\sigma_{\eta}=0.2$, (d) for $\sigma_{\varepsilon}=0.2;\sigma_{\eta}=0.4$, (e) for $\sigma_{\varepsilon}=0.4;\sigma_{\eta}=0.2$, and (f) for $\sigma_{\varepsilon}=0.4;\sigma_{\eta}=0.4$. In the distribution plots, the solid line indicates the median, the shaded regions the interquartile range, and the dotted lines the 90% intervals.

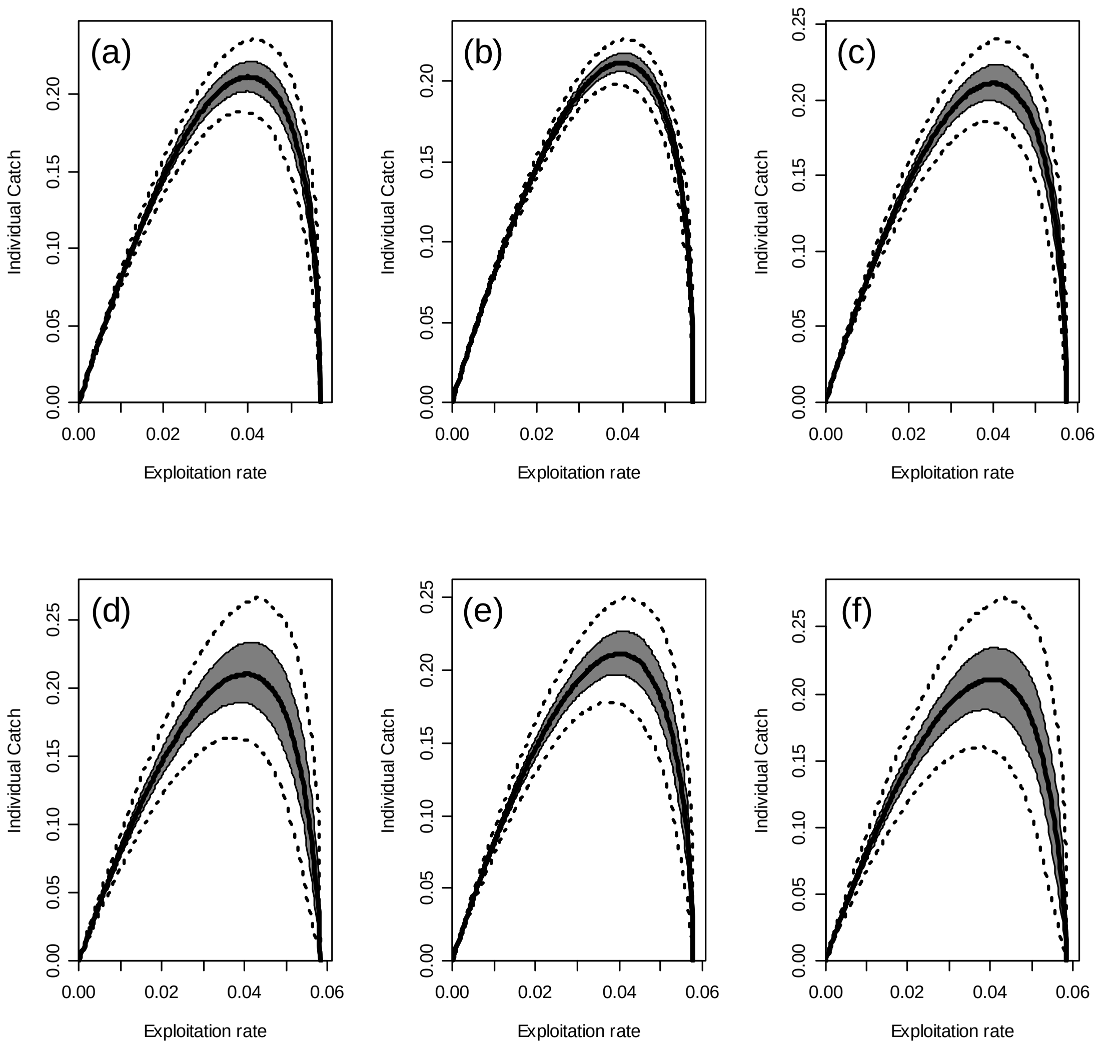

Figure 5. As for Figure 4, except that the results pertain to $MSYR_{mat}$ = 0.04.

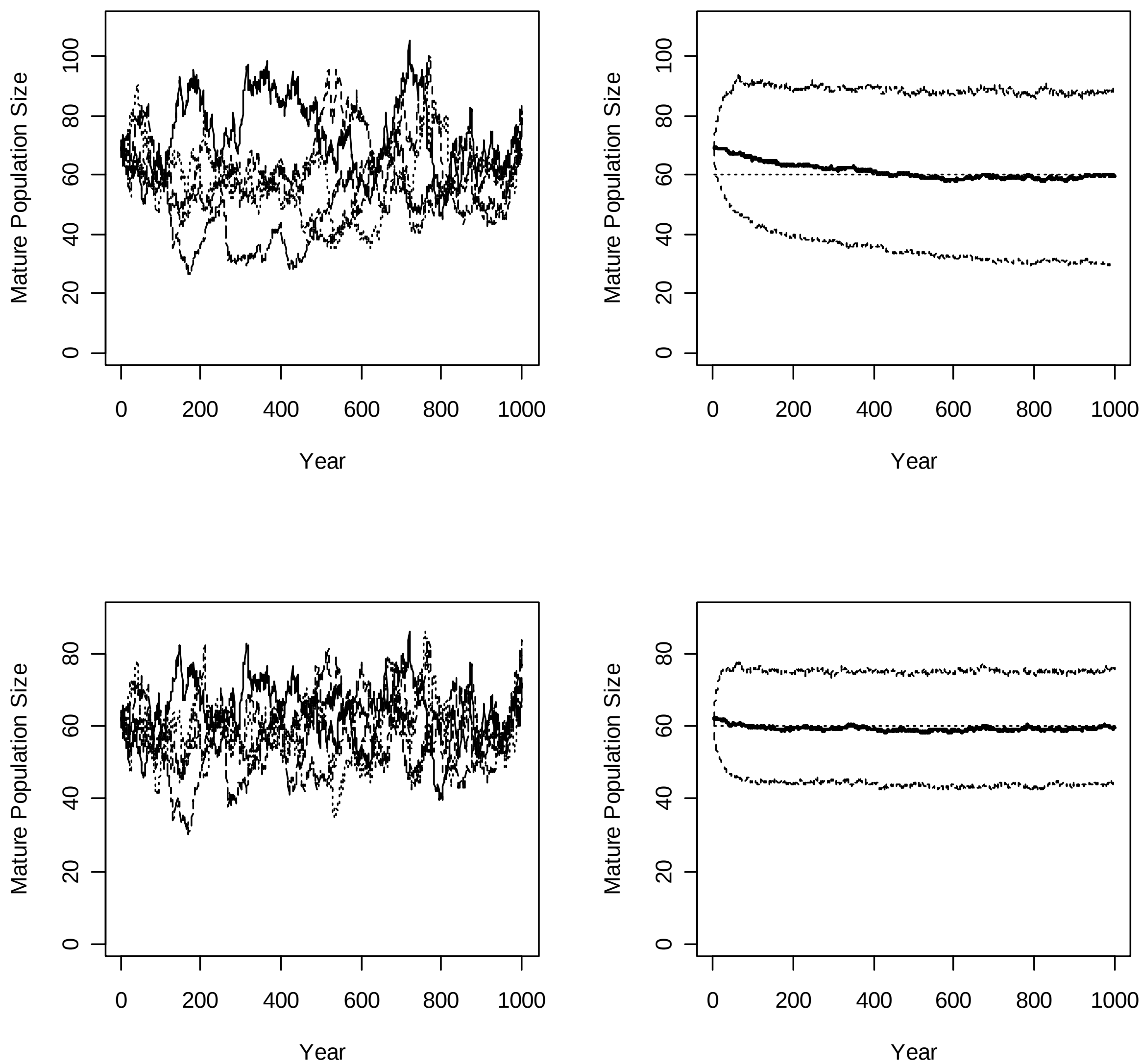

Figure 6. As for Figure 3, except that the results pertain to the case $\sigma_{\varepsilon} = 0.4; \sigma_{\eta} = 0.4$.

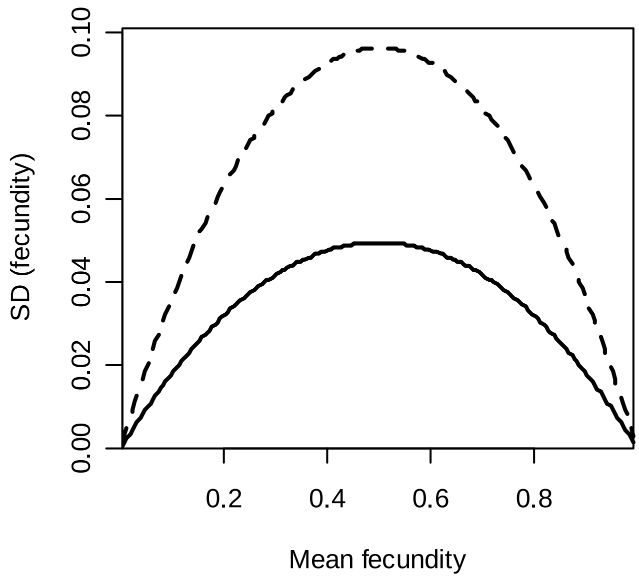

Figure 7. Relationship between the mean and standard deviation of fecundity for two choices for σ_ε (0.2 – solid line; 0.4 – dashed line).