A note on the modelling of 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* and *Evaluation Trials* are based in the face of environmental variability in fecundity (birth rate) and survival. 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.

KEYWORDS: MANAGEMENT PROCEDURES; MSYR; SIMULATION; MODELLING; BIRTH RATE; COMMON MINKE WHALE

INTRODUCTION

Management advice for whale populations is provided by the Scientific Committee of the International Whaling Commission (IWC SC) on the basis of management procedures. These are pre-specified rules that specify the data on which scientific management recommendations are to be based and how those data are to be analysed to provide recommended levels of removals. Management procedures have been developed to calculate catch limits for commercial whaling of baleen whales on their feeding grounds and to calculate strike limits for aboriginal subsistence whaling. Catch limits for commercial whaling are calculated using the Revised Management Procedure (RMP) (IWC, 1994; 1999) whereas strike limits for aboriginal subsistence whaling are calculated using case-specific *Strike Limit Algorithms* (*SLAs*). To date, *SLAs* have been developed for the Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales, *Balaena mysticetus* (IWC, 2003a) and for the Eastern North Pacific (ENP) stock of gray whales, *Eschrichtius robustus* (IWC, 2005a).

The ability of candidate management procedures to achieve the management goals is determined using Monte Carlo simulation methods, often referred to as the Management Strategy Evaluation (MSE) approach. For example, the variants of the RMP for specific whale stocks have been selected so that they achieve the highest long-term yield whilst simultaneously achieving pre-agreed standards related to conservation (IWC, 2005b). In contrast, *SLAs* are selected to satisfy the 'need' of aboriginal communities subject to achieving conservation objectives (Punt and Donovan, 2007). Evaluation of anticipated conservation performance and resource use of candidate *SLAs* and RMP variants is based on simulation evaluation using *Implementation Simulation Trials* (RMP variants) and *Evaluation Trials* (*SLAs*) that attempt to capture the primary sources of uncertainty for the stocks concerned (Punt and Donovan, 2007).

A very wide range of uncertainties have been considered by the IWC SC when selecting RMP variants and *SLAs*. For example, trials have explored the impact of bias in survey estimates, levels of stock productivity, changes over time in demographic parameters and stock structuring, amongst very many others. However, all of the RMP *Implementation Simulation Trials* have been based on deterministic population dynamics models, while only a few of the *Evaluation Trials* used during the development of the *SLA* for the B-C-B bowhead whales (IWC, 2003b) included trials that took account of both environmental and demographic stochasticity. This relative lack of consideration of stochasticity in the population dynamics is perhaps surprising given that the extent of variation in recruitment has been found to impact the performance of management procedures for many fish and invertebrate species, as well as the ability to estimate current population size and productivity (Butterworth and Punt, 1999; Punt, 2006). Moreover, Cooke (2007) suggested that not only did the precision of population model-based estimates of the Maximum Sustainable Yield (MSY) rate for whale stocks deteriorate in the face of environmental stochasticity, but also that environmental variation led to biased estimates of MSY rate.

The values for the parameters that determine the MSY rate and MSY level, MSYL (A, the resilience parameter, and z, the degree of compensation), in the operating models in which there was stochastic variation 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 therefore outlines how the values for A and z can be calculated when there is stochasticity in the population dynamics. The method is general and can be applied to any stochastic population dynamics model. For the purposes of this paper, the method is applied to an extension of the population dynamics model on which *Implementation Simulation Trials* and *Evaluation Trials* have been based which allows for environmental stochasticity in both fecundity (birth rate) and survival. Differences in the values for A and z between the stochastic and deterministic variants of the model are illustrated for a minke whale-like biology.

METHODS

Population dynamics model

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

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

where

$N_{y,a}$	is the number of animals of age a at the start of year y,
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[2], and
x	is the maximum age (taken to be a plus-group).

Following IWC (2003b), the number of births during year y, B_y, is assumed to be stochastic and related to the expected fecundity, b^*_y, under the assumption that the logit of the birth rate is normally distributed[3],[4]:

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

and

$$b^*_y = f_0(1 + A(1 - (N_y^m / K^m)^z)) \quad (3)$$

where

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

$$N_y^m = \sum_a M_a N_{y,a} \quad (4)$$

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 a birth-rate parameter, selected so that the expected value of B_y, is $b^*_y N_y^m$, i.e.:

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

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 also assumed to be stochastic (and perfectly correlated among ages[5]). The logit of survival rate is assumed to be normally distributed so annual survival is generated using the equation:

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

where

ϕ	is a survival rate parameter, selected so that the expected value of $S_{y,a}$ is $\tilde{S}$, i.e.:

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

$\tilde{S}$	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.:

$$C_y = E_y \sum_a V_a N_{y,a} \quad (8)$$

The catches for a given exploitation rate (i.e. $E_y = E$) are stochastic because the population dynamics (and hence the numbers-at-age) are stochastic.

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 (1000) years many times (1000) under an exploitation rate equal to MSYR (i.e. E_y in Equation 1 is set equal to MSYR). The number of years and replicates were selected so that the distribution of population size (and catch) as a function of exploitation rate reached steady-state. 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 common minke whales

Table 1 lists the values for 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 parameterised for Bryde's (*Balaenoptera edeni*) and common minke whales (*B. acutorostrata*) (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, parameterised 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 common minke whales, animals of age two and younger are assumed to be immature (and not available for capture). A range of values for the parameters which determine the extent of environmental

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

[2] Exploitation rate is assumed to be constant over time for the analyses of this paper.

[3] This is equivalent to adding environmental stochasticity to calf survival.

[4] The assumption that the logit of birth-rate is stochastic is made to ensure that the birth-rate falls between 0 and 1. Equation 2 can be modified straightforwardly to allow for gestation periods that are longer than a year.

[5] Assuming perfect correlation of the factors impacting survival will maximise the impact of environmental stochasticity on the dynamics of the population and hence make any simulation trials based on this model 'more difficult'.

variation in fecundity and survival are considered. Note that Equations 2 and 6 ensure that fecundity and survival are never less than zero or greater than one even when σ_ε and σ_η are large. The catch used when finding MSY is set to the average over the last 500 years of the projection period.

Table 1

The parameters of the population dynamics model.

Parameter	Value(s)
MSYR$_{\text{mat}}$	0.01, 0.04
MSYL$_{\text{mat}}$	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).

RESULTS AND DISCUSSION

The primary outcome from the analysis is the steady-state relationship (equivalent to the equilibrium relationship for deterministic dynamics) between catch and exploitation rate and catch and population size (Figs 1 and 2). The upper left panels of Figs 1 and 2 compare the deterministic and stochastic (σ_ε = σ_η = 0.2) evaluations of *A* and *z* for MSYR$_{\text{mat}}$=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 Figs 1 and 2 show the distributions for the number of 'mature' animals (i.e. animals that have reached the age at 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 (Fig. 3).

There is considerable variability in individual trajectories of population size, with the extent of variation higher for MSYR$_{\text{mat}}$=0.01 than for MSYR$_{\text{mat}}$=0.04 (Fig. 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$_{\text{mat}}$=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 while Figs 4 and 5 show the relationships between the catch in year 1000 and exploitation rate for the

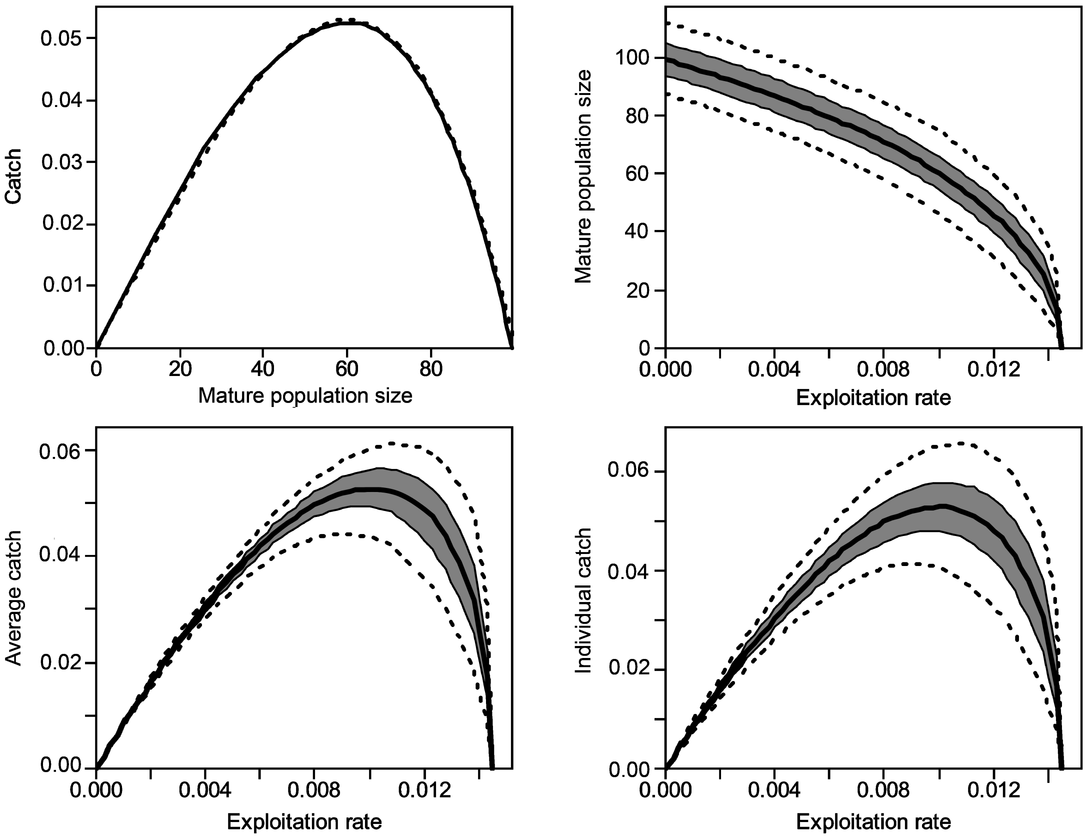

Fig. 1. Relationship between the number of mature animals (expressed as a percentage of the pre-exploitation level) and catch (in units of fractions of carrying capacity) based on deterministic analyses (solid line) and the mean of stochastic realisations (dotted line) (upper left panel), that between the depletion of the mature female component of the population (upper right panel) and exploitation rate (where exploitation rate is the proportion of the selected animals which are removed on an annual basis), 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$_{\text{mat}}$ =0.01, MSYL$_{\text{mat}}$ = 0.6, σ_ε = 0.2 and σ_η = 0.2. In the distribution plots, the solid line indicates the median, the shaded region the interquartile range, and the dotted lines the 90% intervals.

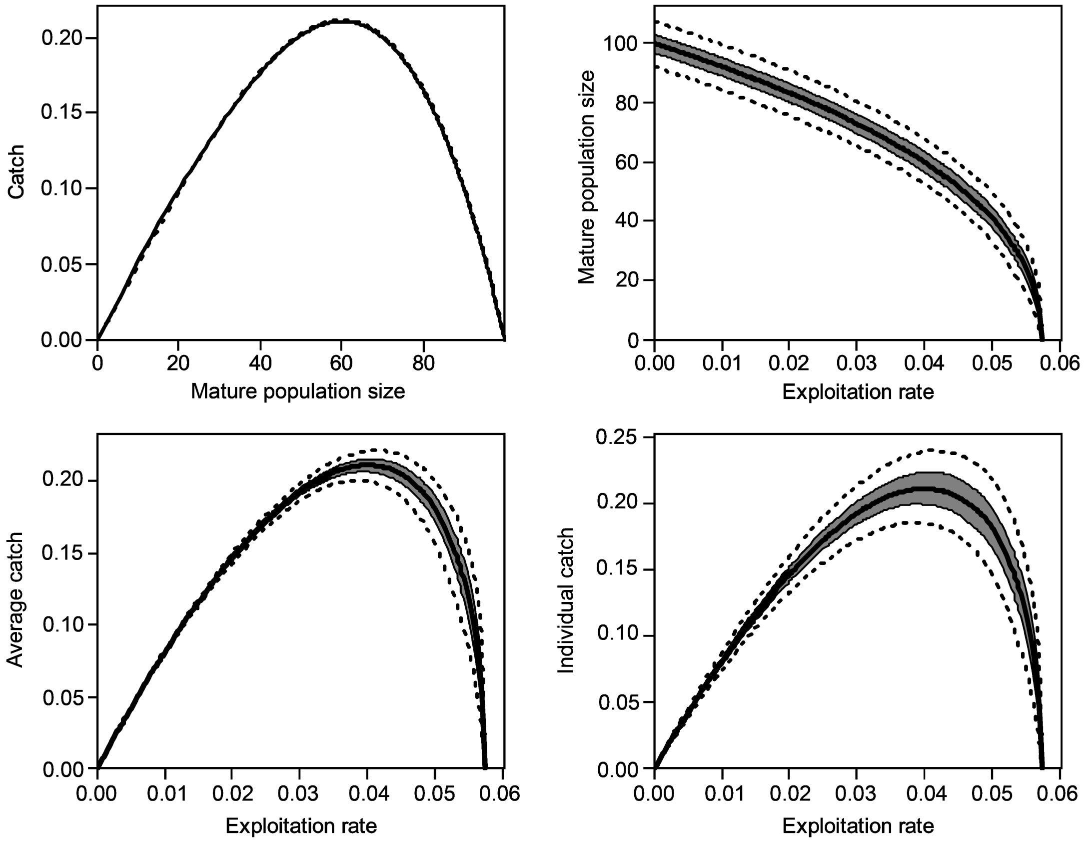

Fig. 2. As for Fig. 1, except that the analyses are based on $\mathrm{MSYR}_{\mathrm{mat}} = 0.04$.

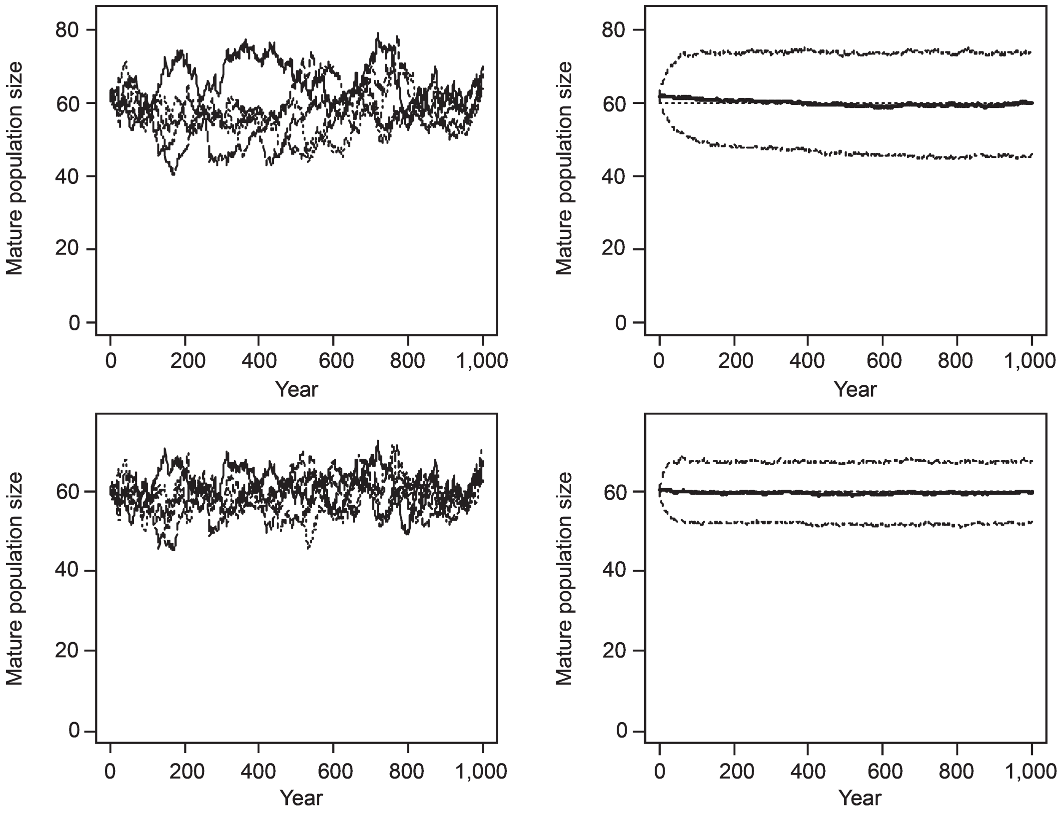

Fig. 3. Time-trajectories for the number of mature females (expressed as a percentage of the pre-exploitation number of mature females). The left panels show the results of five individual replicates and the right panels show the median and 90%iles for these time-trajectories. The results in this figure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

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	$\mathrm{MSYR}_{\mathrm{mat}} = 0.01$	$\mathrm{MSYR}_{\mathrm{mat}} = 0.04$
$\sigma_\varepsilon = 0; \sigma_\eta = 0$	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

combinations 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 Fig. 6 for examples of individual time-trajectories of population size for this case).

The results in Figs 4-5 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 (contrast the widths of the distributions of catch for cases a and b and those for cases d and e). 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 (given the assumption that deviations in survival are perfectly correlated among ages). 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 needs to be confirmed in specific cases.

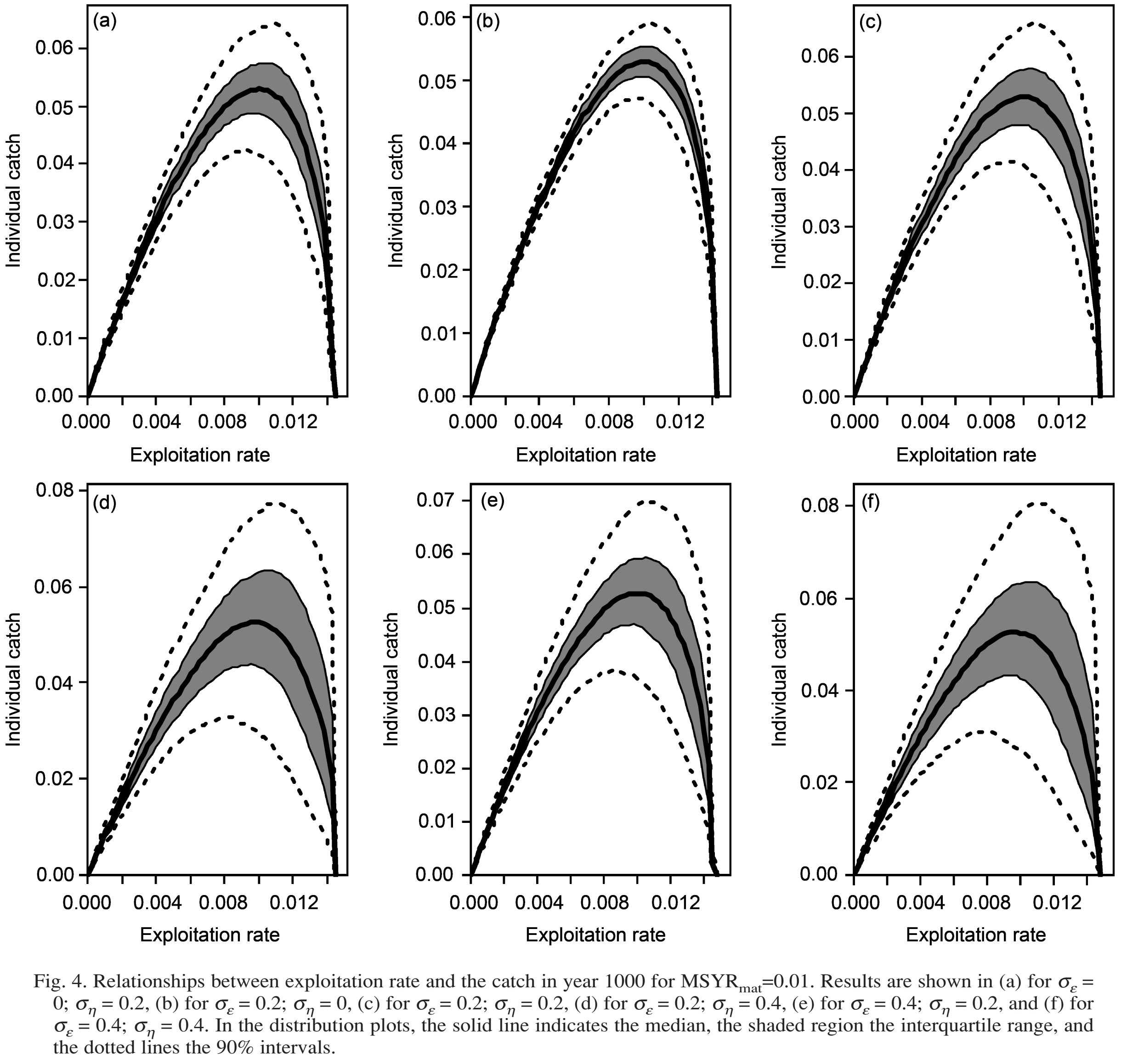

Fig. 4. Relationships between exploitation rate and the catch in year 1000 for $\mathrm{MSYR}_{\mathrm{mat}}$=0.01. Results are shown in (a) for σ_ε = 0; σ_η = 0.2, (b) for σ_ε = 0.2; σ_η = 0, (c) for σ_ε = 0.2; σ_η = 0.2, (d) for σ_ε = 0.2; σ_η = 0.4, (e) for σ_ε = 0.4; σ_η = 0.2, and (f) for σ_ε = 0.4; σ_η = 0.4. In the distribution plots, the solid line indicates the median, the shaded region the interquartile range, and the dotted lines the 90% intervals.

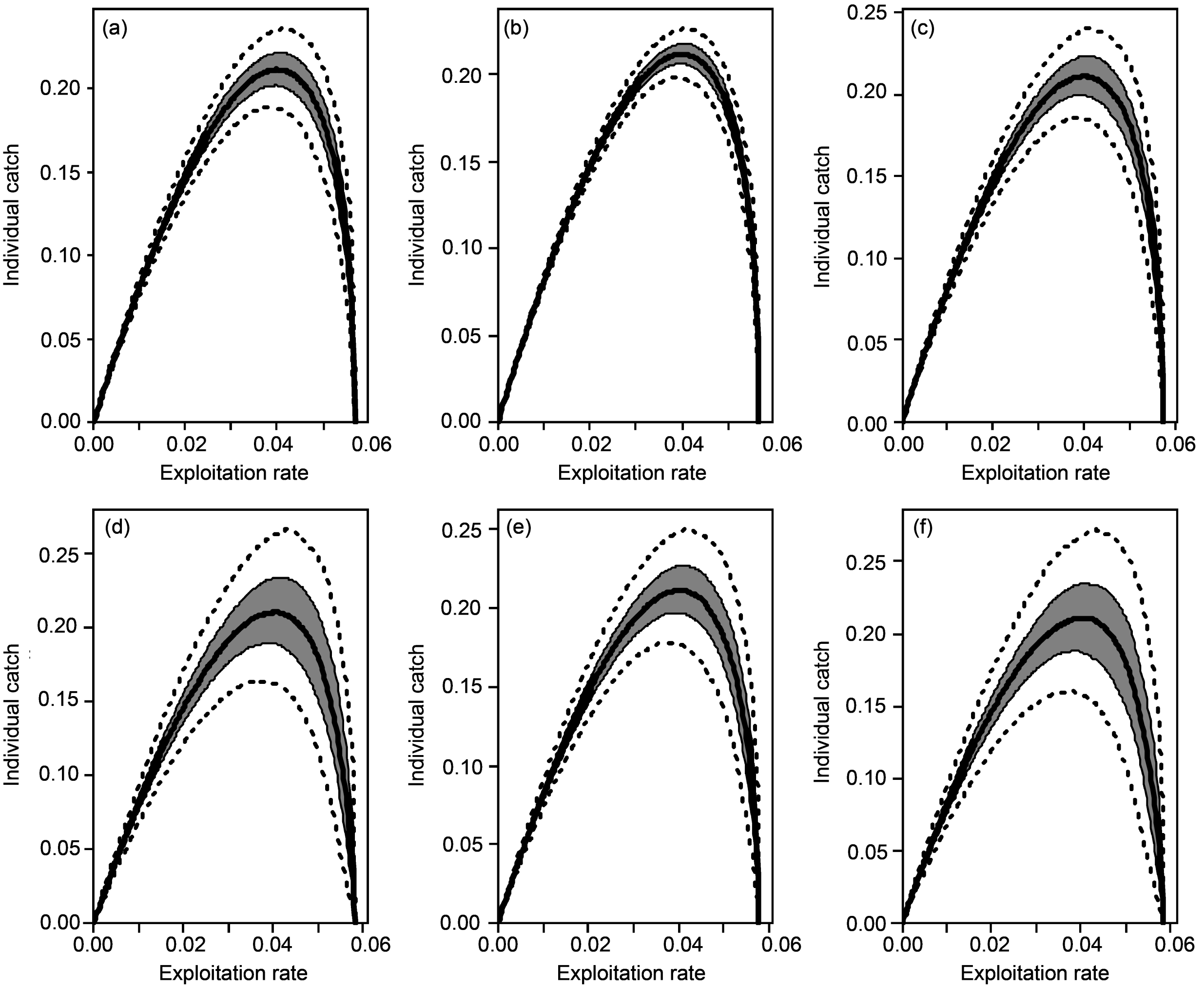

Fig. 5. As for Fig. 4, except that the results pertain to $\mathrm{MSYR_{mat}} = 0.04$.

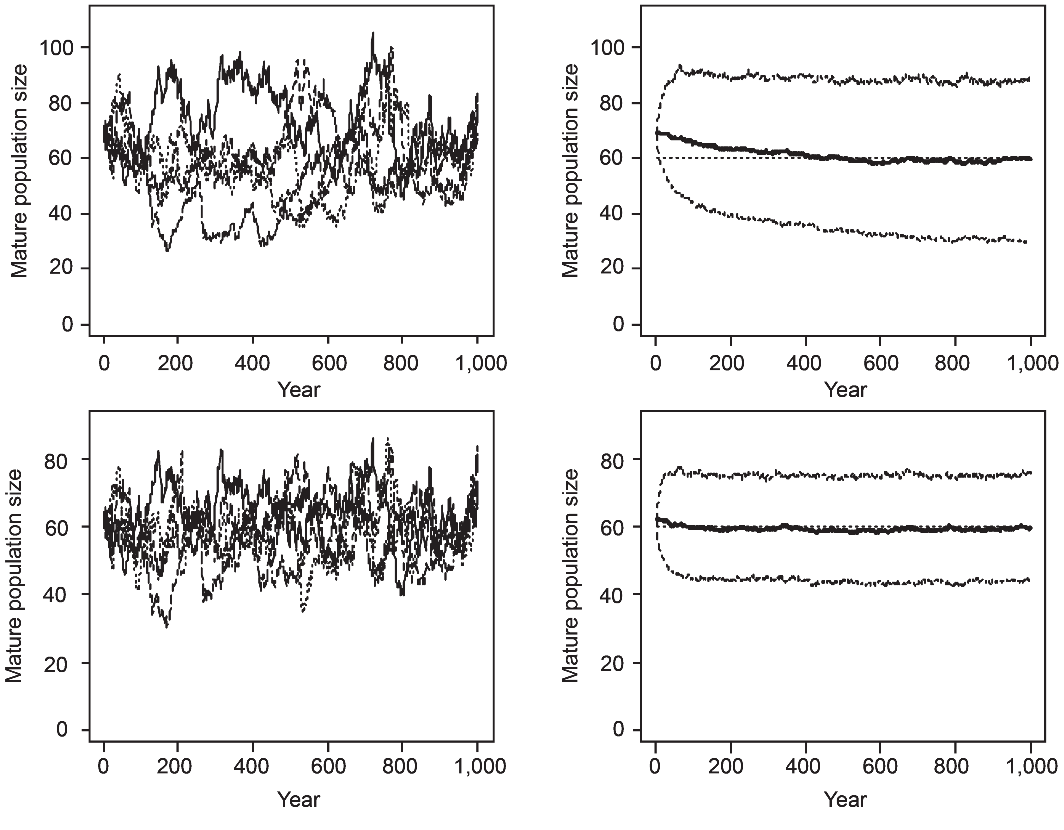

Fig. 6. As for Fig. 3, except that the results pertain to the case $\sigma_\varepsilon = 0.4$; $\sigma_\eta = 0.4$.

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. Fig. 7 shows how the standard deviation of fecundity changes as a function of mean fecundity and the value assumed for σ_ε.

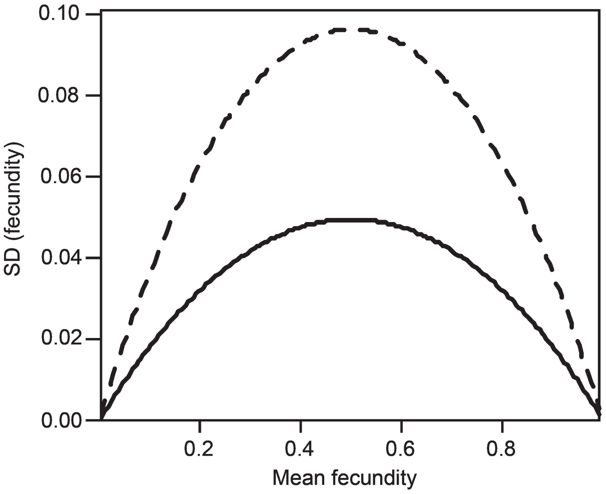

Fig. 7. Relationship between the mean and standard deviation of fecundity for two choices for σ_ε (0.2 – solid line; 0.4 – dashed line).

The approach taken in this paper has been to select values for *A* and *z* using a 'fixed exploitation rate' strategy, i.e. by selecting the values for these parameters so that the expected catch is maximised when a constant proportion of the selected animals is removed each year. This is not the only way to translate the notion of MSY from a deterministic concept into one that accounts for stochastic dynamics; a variety of definitions for stochastic MSY have been defined for fisheries management purposes in New Zealand, for instance (e.g. Francis and Mace, 2005). For example, MSY can be defined using a constant catch strategy. Adoption of this definition for MSY would mean that *A* and *z* would be selected so that the ratio of the constant catch at MSYL is MSYR. A fixed exploitation rate strategy was adopted for this paper because the management strategies used by the IWC are closer to fixed exploitation rate strategies than to constant catch strategies.

The example in this paper focused on environmental rather than demographic stochasticity because demographic stochasticity only has a noteworthy impact on the population dynamics at levels of abundance at which harvests under IWC management procedures would not be permitted anyway. However, for other cases, demographic stochasticity can be important. The method outlined here could be extended to deal with cases in which the population size is small, but it would necessitate the development of an individual-based model as well as accounting for the possibility of extinction even when the exploitation rate equals that corresponding to MSY.

Finally, the analyses of this paper ignore temporal auto-correlation in survival and fecundity caused by environmental variation. This can be incorporated straightforwardly into Equations 2 and 7 (see, for example, IWC, 2003b), 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. Similarly, the deviations in fecundity could be correlated with those in survival to reflect the hypothesis that poor environmental conditions are reflected simultaneously in both survival and fecundity (or *vice versa*). For example, preliminary modelling work (J. Brandon, UW, pers. comm.) based on the time-series of calf counts (Perryman *et al*., 2002) and strandings data for the ENP gray whales suggests that there is a correlation (albeit not linear) between the inter-annual deviations about mean fecundity and survival. Finally, allowance could be made for occasional major reductions in abundance, as has also been postulated for the ENP gray whales.

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